COMBINING ALASKA FORAGE FISH DATA FROM RESEARCH SURVEYS AND PREDATOR DIETS TO ASSESS FORAGE FISH RESPONSE TO CLIMATIC REGIME SHIFTS

by
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Abstract

Forage fish play a crucial role in the marine ecosystems of Alaska through the transfer of energy from lower trophic levels to marine predators. Understanding and quantifying Alaskan forage fish responses to rapid climatic shifts is needed to inform adaptive management strategies under a warmer and more variable future in Alaska. However, data on the occurrence and abundance of forage fish in Alaska are limited due to the diversity of life history strategies and patchy distribution that make their capture in fisheries-independent surveys difficult. In this thesis, I address current gaps in the data available on forage fish through the publication of an Alaska Forage Fish Database (AFFD) comprised of data from trawls, beach seines, and the diets of predator consuming forage fish, collected by a variety of contributing agencies and organizations. This data compilation effort resulted in a database containing forage fish abundance data from 461,449 sampling events spanning the years 1953 – 2023. Using the compiled dataset, I then assess large-scale spatial and temporal patterns in the occurrence of Pacific capelin (*Mallotus catervarius*), Pacific herring (*Clupea pallasii*), and sand lance (*Ammodytes* spp.) in the Bering Sea and Gulf of Alaska. Interannual trends in the encounter probability for each species, based on models fit to data from fisheries surveys, groundfish diets, and seabird diets, exhibit coherence in large-scale changes among observation types in the Gulf of Alaska (1972 - 2023) and Bering Sea (1980 – 2023). I compare the distribution of species' encounter probability across decadal climate stanzas and demonstrate the differences in distribution of species during the 2014 – 2019 heatwaves compared to prior stanzas, as well as reoccurring distribution patterns in response to similar climatic characteristics among stanzas. Findings from this thesis facilitate an expanded understanding of forage fish population dynamics and spatial distribution in response to rapid climatic shifts.

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Chapter 1: General Introduction

Forage species are nutrient rich small pelagic fish, juvenile fish, and invertebrates (henceforth referred to as forage fish) that transfer energy from lower trophic levels to marine predators, including seabirds, marine mammals, and commercial and culturally important fish (Cury, 2000). Globally, forage fish support some of the world's largest fisheries and are key to meeting human consumption and food production needs (e.g., fishmeal and fish oil), making them a critical component of global food security (Alder et al., 2008; Essington et al., 2015; Pikitch et al., 2014). As an energy-rich food source for marine predators and component of subsistence harvest, forage fish play a crucial role in the socioeconomic and cultural livelihood of Alaskans (Rivers et al. 2013, Thornton, 2015). While herring are the only forage fish commercially harvested in Alaska (Szuwalski et al., 2023), changes in forage fish populations can have substantial bottom-up effects, influencing the abundance of commercially important predators, such as Pacific cod (*Gadus macrocephalus*) and Pacific salmon (*Oncorhynchus* spp.), as well as seabirds and marine mammals (Anderson et al., 1997; Piatt & Anderson, 1996; Yang et al., 2019). Given their pivotal role in the marine trophic system, a comprehensive understanding of forage fish populations and the factors influencing their dynamics is essential for ensuring sustainable management practices.

The productivity of forage fish can be influenced by biotic (predation, changes in food availability), abiotic (sea surface temperature, sea surface pressure) and anthropogenic (overfishing, oil spills) factors. Climatic regime shifts, defined as significant and persistent shifts in multiple climate indices, can be driven in the North Pacific by anthropogenic influences (such as overfishing or oil spills) (Peterson et al., 2003; Thornton et al., 2010) and large-scale climatic patterns, including the Pacific Decadal Oscillation (PDO), El Nino Southern Oscillation (ENSO), and North Pacific Gyre Oscillation (NPGO) (Beaugrand et al., 2015; Overland et al., 2008; Yasunaka & Hanawa, 2002). In the wake of the 1976/1977 community reorganization in the North Pacific that followed a major regime shift in the marine climate, research has sought to identify the impacts and persistence of rapid forage fish community changes. The crash of smaller pelagic species in the late 1970's included a decline >50% in pandalid shrimp and capelin, in tandem with an increase in groundfish (Gadidae) and decline of piscivorous sea birds (murres, etc.) and marine mammals (Anderson & Piatt, 1999; Piatt & Anderson, 1996). This event coincided with a shift into a positive PDO phase and an intensified Aleutian Low (pressure) that caused sea surface temperature to warm, and increased water column stratification as upwelling decreased (Anderson & Piatt, 1999; Hare & Mantua, 2000). However, the correlation between ecosystem dynamics and multi-decadal oscillatory patterns (e.g., PDO and NPGO) has progressively weakened since the late 1980s, diminishing the efficacy of these oscillatory indices in predicting physical-ecological interactions (Litzow et al., 2020). In more recent years, the onset of the 2014-2016 heatwave and warmer years in 2018-2019 caused an abrupt, semi-persistent reorganization across trophic communities in the Gulf of Alaska and Bering Sea (Arimitsu et al., 2021; Suryan et al., 2021). Other regime shifts with variable intensities have been documented since 1976/1977, including the 1988/1989 intensification of the Arctic vortex and variable sea surface temperature interannually (Aydin et al., 2006; Litzow, 2006), the 1998/1999 shift with minimal sea-ice extent and marine heatwave from 2001-2005 (Overland et al., 2012), and a 2006/2007 shift to cooler SST and greater sea-ice extent (Stabeno et al., 2017).

Changes in fish population productivity in response to climatic regime shifts can vary among species due to differences in species resilience to certain climate effects and the intensity of climatic shifts. Identifying the vulnerability of different forage fish species to both directional climate change and abrupt regime shifts is critical for informing management needs and improving ecosystem-based management practices. A better understanding of forage fish distribution and occurrence is needed to identify Environmental Resource Areas, which are areas important for social, biological, and economic resources, in order to inform management strategies, reduce anthropogenic impacts, and conserve habitats necessary for vulnerable forage species.

Improved understanding of the underlying influences of biotic and abiotic factors on forage fish can help inform management priorities. However, forage fish are data limited, in part due to fluctuations in forage fish productivity on seasonal, interannual, and decadal scales and their patchy distribution across space (McClatchie et al., 2017; Soutar & Isaacs, 1969). The species tendency to move in dense, shifting schools, complicates efforts to estimate population size, leading to limited and sometimes unreliable data on their population dynamics (Fréon et al., 2005). Variation in catchability and selectivity by trawl gear often employed for fisheries-independent surveys further exacerbates the problem, requiring the use of specialized equipment to capture representative samples (De Robertis et al., 2017). Commercial harvest of forage fish (with the exception of herring) is prohibited under the “FMP Forage group” in the federal marine waters surrounding Alaska and the Forage Fish Management Plan (Section 5 AAC 39.212) within Alaska state waters. This results in limited funding for research surveys specifically targeting forage fish within the marine waters surrounding Alaska (Witherell et al., 2000). Fisheries independent surveys with broad spatial coverage and a greater diversity of target species may incidentally catch forage fish but given that they are not designed to target forage fish, the realized catch rate is often low.

Population and habitat assessments are typically conducted by utilizing quantitative statistical models in conjunction with data from an individual fisheries independent survey. However, a single fishery-independent survey may be insufficient to meet the data needs for understanding the ecosystem processes that influence the species populations. In Alaska, forage fish lack a fisheries independent survey with broad coverage in the Bering Sea and Gulf of Alaska that directly targets these species and has operated over a suitably long time period to permit valid inference about long-term changes in response to variation in climate regimes. Under these circumstances, the integration of multiple sources of information to derive integrated indices of occurrence presents an avenue to address the data limitations present for Alaskan forage fish. Previous research has demonstrated the integration of catch rate data from multiple surveys with gear types and sample designs, using statistical models as a means of improving estimated indices of abundance and species distribution shifts (Grüss et al., 2018; Grüss & Thorson, 2019; Ono et al., 2018). As an alternative to fisheries surveys, the diets of generalist, opportunistic predators can provide an index of abundance for forage fish (Fahrig et al., 1993; Hatch & Sanger, 1992; Link, 2004) and inform population trends, distributional shifts (Grüss et al., 2023; Ng et al., 2021; Piatt et al., 2018) and response to climate variability (Arimitsu et al., 2021; Barnes et al., 2020; Gunther et al., 2023).

In my second chapter, I address data needs by combining available forage fish abundance, occurrence, and biomass data into an Alaska Forage Fish Database (AFFD) (Turner et al., 2024). Organizations that provided data include the US Fish and Wildlife Service (US FWS), US Geological Survey (USGS), National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center (AFSC), and Alaska Department of Fish and Game (ADF&G). Through the contributions of a multitude of agencies and individuals, the database spans the years 1953-2023, covering all large marine ecosystems in Alaska. The AFFD is comprised of data from sources including pelagic trawls, shrimp small-mesh trawls, incidental catch via groundfish bottom trawls, and predator diets. Core species included in the database are: smelts (Family: Osmeridae) including Pacific capelin (*Mallotus catevarius*), and eulachon (*Thaleichthys pacificus*), Pacific herring (*Clupea pallasii*), Pacific and Arctic sand lance (*Ammodytes personatus* and *A. hexapterus*, respectively), lanternfishes (Family: Myctophidae), juvenile walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. macrocephalus*), krill (Order: Euphausiacea), and squid (superorder: Decapodiformes). The purpose behind the compilation of an Alaska-wide forage fish database was to provide a foundation for future research quantifying forage fish distribution shifts, population dynamics trends, responses to climate variation, and to inform future surveys.

In my third chapter, I utilize the data compiled and standardized within the AFFD described in my second chapter to assess forage fish occurrence and distribution in the Gulf of Alaska and Bering Sea and quantify responses to changes among climate regimes. Analysis focused on three species: Pacific capelin, Pacific herring, and sand lance (*Ammodytes* spp.), chosen for their importance to the marine trophic structure of Alaska. These three forage fish species serve as case studies for comparing the influence of data source (e.g., fisheries surveys vs. predator diets) on estimated trends across space and time, and to quantify the response of species with well-established behaviors, habitat preference, and life histories, to climate regime shifts within the Bering Sea and Gulf of Alaska regions. To quantify interannual variation in the encounter probability of these forage fish species among regions, I fit spatiotemporal models to data from fisheries independent surveys (i.e. pelagic and benthic trawls, beach seines), groundfish and seabird predator diets (i.e. generalist predators that are commonly sampled in surveys) and integrated data (combined survey and predator diets). I then compare the resulting smoothed annual indices of encounter probability, fitted separately to fisheries-independent surveys, groundfish diets, and seabird diets, to assess coherence in the temporal trends estimated. I justify the use of integrated models by demonstrating similarities in annual trends derived from predator diets and fisheries surveys, and I compare these results with previous literature. The analysis is conducted using a binomial generalized linear mixed-effects model (GLMM) with a smoothed year effect to estimate trends over time and a fixed effect for data source to account for differences in sampling methods, implemented via the sdmTMB package (Anderson et al., 2022).

As a secondary objective, I compare the overall magnitude and distribution of species' encounter probability across decadal climate stanzas, partitioned by regime shifts identified in prior studies. To predict species distributions among climate stanzas, I apply a binomial GLMM with fixed effects for data source and decadal climate stanza. I also explore the inclusion of spatially varying catchability to account for spatial heterogeneity due to variable gear performance dependent on habitat and changes in fish distribution outside sampling ranges. Results from the Bering Sea, a region sampled interannually with gridded survey designs, are compared to those from the Gulf of Alaska, where surveys exhibit limited spatial and temporal overlap.

With the expanded spatial and temporal data availability from the AFFD compilation effort, I provide region-wide assessments for distributional and temporal patterns of key forage fish in the eastern Bering Sea and Gulf of Alaska. The large-scale analysis provided in this thesis aids in our understanding of forage fish responses to regime shifts in the North Pacific. My research highlights the value of an integrated approach, considering both fisheries surveys and predator diets, to improve the assessment of forage fish population dynamics and distribution.

1.1 References

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., & Pauly, D. (2008). Forage Fish: From Ecosystems to Markets. *Annual Review of Environment and Resources*, *33*(Volume 33, 2008), 153–166. https://doi.org/10.1146/annurev.environ.33.020807.143204

Anderson, P. J., Blackburn, J. E., & Johnson, B. A. (1997). Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. In *Forage fishes in marine ecosystems.* (pp. 531–543). University of Alaska Faribanks.

Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, *189*, 117–123. https://doi.org/10.3354/meps189117

Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. K. (2022). sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields. *bioRxiv*. https://doi.org/10.1101/2022.03.24.485545

Arimitsu, M. L., Piatt, J. F., Hatch, S., Suryan, R. M., Batten, S., Bishop, M. A., Campbell, R. W., Coletti, H., Cushing, D., Gorman, K., Hopcroft, R. R., Kuletz, K. J., Marsteller, C., McKinstry, C., McGowan, D., Moran, J., Pegau, S., Schaefer, A., Schoen, S., … von Biela, V. R. (2021). Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology*, *27*(9), 1859–1878. https://doi.org/10.1111/gcb.15556

Aydin, K., Boldt, J., Gaichas, S., & Ianelli, J. (2006). In: Boldt J (ed) Ecosystem considerations for 2007. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, 24–89.

Barnes, C. L., Beaudreau, A. H., Dorn, M. W., Holsman, K. K., & Mueter, F. J. (2020). Development of a predation index to assess trophic stability in the Gulf of Alaska. *Ecological Applications*, *30*(7), e02141. https://doi.org/10.1002/eap.2141

Beaugrand, G., Conversi, A., Chiba, S., Edwards, M., Fonda-Umani, S., Greene, C., Mantua, N., Otto, S. A., Reid, P. C., Stachura, M. M., Stemmann, L., & Sugisaki, H. (2015). Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130272. https://doi.org/10.1098/rstb.2013.0272

Cury, P. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. https://doi.org/10.1006/jmsc.2000.0712

De Robertis, A., Taylor, K., Williams, K., & Wilson, C. D. (2017). Species and size selectivity of two midwater trawls used in an acoustic survey of the Alaska Arctic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *135*, 40–50. https://doi.org/10.1016/j.dsr2.2015.11.014

Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., Siple, M. C., & Stawitz, C. C. (2015). Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences*, *112*(21), 6648–6652. https://doi.org/10.1073/pnas.1422020112

Fahrig, L., Lilly, G. R., & Miller, D. S. (1993). Predator Stomachs as Sampling Tools for Prey Distribution: Atlantic Cod (Gadus morhua) and Capelin (Mallotus villosus). *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(7), 1541–1547. https://doi.org/10.1139/f93-175

Fréon, P., Cury, P., Shannon, L., & Roy, C. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulleton Of Marine Science*, *76*(2).

Grüss, A., Drexler, M. D., Ainsworth, C. H., Babcock, E. A., Tarnecki, J. H., & Love, M. S. (2018). Producing Distribution Maps for a Spatially-Explicit Ecosystem Model Using Large Monitoring and Environmental Databases and a Combination of Interpolation and Extrapolation. *Frontiers in Marine Science*, *5*, 16. https://doi.org/10.3389/fmars.2018.00016

Grüss, A., & Thorson, J. T. (2019). Developing spatio-temporal models using multiple data types for evaluating population trends and habitat usage. *ICES Journal of Marine Science*, *76*(6), 1748–1761. https://doi.org/10.1093/icesjms/fsz075

Grüss, A., Thorson, J. T., Anderson, O. F., O'Driscoll, R. L., Heller-Shipley, M., & Goodman, S. (2023). Spatially varying catchability for integrating research survey data with other data sources: Case studies involving observer samples, industry-cooperative surveys, and predators as samplers. *Canadian Journal of Fisheries and Aquatic Sciences*, cjfas-2023-0051. https://doi.org/10.1139/cjfas-2023-0051

Gunther, K., Baker, M., & Aydin, K. (2023). Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea. *Marine Ecology Progress Series*, *SPF2*. https://doi.org/10.3354/meps14389

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, *47*(2), 103–145. https://doi.org/10.1016/S0079-6611(00)00033-1

Hatch, S., & Sanger, G. (1992). Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. *Marine Ecology Progress Series*, *80*, 1–14. https://doi.org/10.3354/meps080001

Link, J. (2004). Using fish stomachs as samplers of the benthos: Integrating long-term and broad scales. *Marine Ecology Progress Series*, *269*, 265–275. https://doi.org/10.3354/meps269265

Litzow, M. A. (2006). Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/1977? *ICES Journal of Marine Science*, *63*(8), 1386–1396. https://doi.org/10.1016/j.icesjms.2006.06.003

Litzow, M. A., Hunsicker, M. E., Bond, N. A., Burke, B. J., Cunningham, C. J., Gosselin, J. L., Norton, E. L., Ward, E. J., & Zador, S. G. (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. Proceedings of the National Academy of Sciences, 117(14), 7665–7671. https://doi.org/10.1073/pnas.1921266117

McClatchie, S., Hendy, I. L., Thompson, A. R., & Watson, W. (2017). Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophysical Research Letters*, *44*(4), 1877–1885. https://doi.org/10.1002/2016GL071751

Ng, E. L., Deroba, J. J., Essington, T. E., Grüss, A., Smith, B. E., & Thorson, J. T. (2021). Predator stomach contents can provide accurate indices of prey biomass. *ICES Journal of Marine Science*, *78*(3), 1146–1159. https://doi.org/10.1093/icesjms/fsab026

Ono, K., Ianelli, J. N., McGilliard, C. R., & Punt, A. E. (2018). Integrating data from multiple surveys and accounting for spatio-temporal correlation to index the abundance of juvenile Pacific halibut in Alaska. *ICES Journal of Marine Science*, *75*(2), 572–584. https://doi.org/10.1093/icesjms/fsx174

Overland, J. E., Wang, M., Wood, K. R., Percival, D. B., & Bond, N. A. (2012). Recent Bering Sea warm and cold events in a 95-year context. *Deep Sea Research Part II: Topical Studies in Oceanography*, *65–70*, 6–13. https://doi.org/10.1016/j.dsr2.2012.02.013

Peterson, C. H., Rice, S. D., Short, J. W., Esler, D., Bodkin, J. L., Ballachey, B. E., & Irons, D. B. (2003). Long-term ecosystem response to the Exxon Valdez oil spill. *Science (New York, N.Y.)*, *302*(5653), 2082–2086. https://doi.org/10.1126/science.1084282

Piatt, J. F., & Anderson, P. J. (1996). Response of Common Murres to the Exxon Valdez Oil Spill and Long-Terme Changes in the Gulf of Alaska Marine Ecosystem. *American Fisheries Society Symposium*, *18*, 720–737.

Piatt, J. F., Arimitsu, M. L., Sydeman, W. J., Thompson, S. A., Renner, H., Zador, S., Douglas, D., Hatch, S., Kettle, A., & Williams, J. (2018). Biogeography of pelagic food webs in the North Pacific. *Fisheries Oceanography*, *27*(4), 366–380. https://doi.org/10.1111/fog.12258

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Heppell, S. S., Houde, E. D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R. S., Geers, T. M., Gownaris, N., & Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, *15*(1), 43–64. https://doi.org/10.1111/faf.12004

Soutar, A., & Isaacs, J. D. (1969). History of fish populations inferred from fish scales in anaerobic sediments off California. *California Marine Research Committee*, *13*, 63–70.

Stabeno, P. J., Duffy-Anderson, J. T., Eisner, L. B., Farley, E. V., Heintz, R. A., & Mordy, C. W. (2017). Return of warm conditions in the southeastern Bering Sea: Physics to fluorescence. *PLOS ONE*, *12*(9), e0185464. https://doi.org/10.1371/journal.pone.0185464

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, *11*(1), 6235. https://doi.org/10.1038/s41598-021-83818-5

Szuwalski, C., Yasumiishi, E., Andrews, A., Dimond, A., Murphy, J., Farley, E., & Siddon, E. (2023). 2023 Bering Sea and Aleutian Islands forage report. North Pacific Fishery Management Council.

Turner, L. C., Arimitsu, M., Piatt, J. F., Eckert, G. L., & Cunningham, C. J. (2024). *Alaska Forage Fish Database (AFFD)*. U.S. Geological Survey. https://doi.org/10.5066/P9WZQJ8N

Witherell, D., Pautzke, C., & Fluharty, D. (2000). An ecosystem-based approach for Alaska groundfish fisheries. *ICES Journal of Marine Science*, *57*(3), 771–777. https://doi.org/10.1006/jmsc.2000.0719

Yang, Q., Cokelet, E. D., Stabeno, P. J., Li, L., Hollowed, A. B., Palsson, W. A., Bond, N. A., & Barbeaux, S. J. (2019). How “The Blob” affected groundfish distributions in the Gulf of Alaska. *Fisheries Oceanography*, *28*(4), 434–453. https://doi.org/10.1111/fog.12422

Yasunaka, S., & Hanawa, K. (2002). Regime Shifts Found in the Northern Hemisphere SST Field. *Journal of the Meteorological Society of Japan. Ser. II*, *80*(1), 119–135. https://doi.org/10.2151/jmsj.80.119

Chapter 2: Expanding data availability of Alaska forage fish

2.1 Abstract

Forage fish are energy rich species that play a crucial role in the diets of seabirds, marine mammals, and commercially important fish species in Alaska. However, data limitations present a challenge for quantifying the spatial and temporal dynamics of forage fish. To address the data needs of forage fish, we have published the Alaska Forage Fish Database (AFFD) as part of a USGS Alaska Science Center data release (Turner et al., 2024). Through the collaborative effort of several agencies, we have aggregated 10 data sources (57 different projects) including forage fish occurrence and catch rate information from independent fisheries surveys and the diets of seabirds and groundfish as indicators of forage fish. The AFFD is the largest assemblage of forage fish data in Alaska, with 478,012 forage fish samples from 461,449 sampling events at 105,420 unique sites, covering the years 1953-2023. Species of focus include smelts (Family: Osmeridae), including Pacific capelin (*Mallotus catevarius*), eulachon (*Thaleichthys pacificus*), Pacific herring (*Clupea pallasii*), Pacific and Arctic sand lance (*Ammodytes personatus* and *A. hexapterus*, respectively); lanternfishes (Family: Myctophidae); juvenile walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. macrocephalus*); krill (Order: Euphausiacea); and squid (superorder: Decapodiformes) (WoRMS Editorial Board, 2024). Here, we describe the spatial and temporal scope of forage fish observations throughout Alaska presently available from the AFFD. The compiled data within the Alaska Forage Fish Database provides the foundations for exploring the tropic role of forage fish in complex predator-prey interactions, informing trends in forage fish abundance and occurrence across time and space, and realized responses to climate change.

2.2 Introduction

The Alaska marine ecosystem is sustained through complex trophic interactions with forage fish. Forage fish are energetically rich, schooling species that transfer energy from lower trophic levels (zooplankton) to seabirds, marine mammals, and predatory fish (Cury, 2000). The socio-cultural, ecological, and commercial importance of forage fish extends across Alaska, making them of crucial value to the livelihood of many Alaskan communities (Konar et al., 2019). Predator-prey interactions and forage fish population dynamics can also serve as indicators of the health of the Alaska marine-food web and inform ecosystem-based fisheries management strategies (Pikitch et al., 2014; Rose, 2005; Surma et al., 2018).

Despite their importance, major data gaps limit our understanding of forage fish populations in the waters surrounding Alaska. Forage fish exhibit sporadic recruitment dynamics and highly variable distribution, making effective sampling to produce meaningful indices of change across space and time difficult (Fréon et al., 2005; Sydeman et al., 2022). With the exception of herring, forage fish are generally not targeted by fisheries and have limited research funding in Alaska (Witherell et al., 2000). Scientific surveys that are conducted are typically short term, spatially restricted, and employ a variety of different sampling methods, making long-term assessment of forage communities challenging. Incidental catch data from research surveys are often used to estimate the abundance and distribution of forage fish on a long-term scale for the purpose of managing fisheries within Alaska's large marine ecosystems (Szuwalski et al., 2023). However, there are recognized biases in quantifying forage fish occurrence and abundance using surveys that do not target pelagic fish (Cordue, 2007; Cunningham et al., 2018; Ormseth, 2014), given constraints due to habitat accessibility (Baker et al., 2019) and the use of sampling gear not designed to capture forage fish (De Robertis et al., 2023).

Assessments of forage fish abundance and distribution have typically relied on surveys conducted using a single fisheries independent survey. An alternative approach to address the constraints inherent in fisheries survey methods for indexing forage fish is the use of predator diets to estimate relative abundance and distribution. Predator species, including groundfish and seabirds, can sample pelagic fish species that may not be well indexed by trawls or other survey gears that are often limited by gear selectivity and catchability. Diet data from seabirds and groundfish can fill in the gaps in space and time where forage fish are not reliably sampled by fisheries surveys (Serrano et al., 2003), as well as in habitats where trawls cannot effectively sample due to a rocky habitat or hazardous conditions (Zimmermann, 2003). For seabirds, surface feeders (black-legged kittiwakes, *Rissa tridactyla*) and divers (e.g., horned puffin, *Fratercula corniculata,* tufted puffin, *Fratercula cirrhata*, and rhinocerous auklet, *Cerorhinca monocerata*) have been used to assess walleye pollock year-class strength (S. Hatch & Sanger, 1992; Sydeman et al., 2022), measure trophic synchrony (Arimitsu et al., 2021), and estimate the impacts of habitat features (Piatt et al., 2018; Schoen et al., 2018) and environmental influences on local abundance, distribution, and community composition (Thayer et al., 2008). Similarly, groundfish stomach contents have been used to estimate trends in forage fish abundance and distribution (Aydin et al., 2006; Grüss et al., 2023; Link, 2004; Ng et al., 2021) and the impacts of climate variation (Gunther et al., 2023). Given forage species' pivotal role in sustaining marine ecosystems and fisheries, we have assembled an Alaska-wide database of forage fish abundance and occurrence. The Alaska Forage Fish Database (AFFD) includes data from trawls (surface, midwater, and bottom trawls), nearshore sampling techniques (i.e. beach seines, purse seines, jigs, gill nets, cast nets), ichthyoplankton surveys, "incidental catch" and predator diets. The compilation of available data from many contributing organizations and individuals may be useful in assessing population status, informing current management decisions, and understanding the processes influencing the dynamics of forage fish populations across Alaska. Given the growing body of research on the integration of fisheries survey data with predator diets to understand population and spatial dynamics, the AFFD provides a useful source of standardized data from multiple observation methods over a large spatial scale. Comprehensive abundance and occurrence data at this scale, derived from a wide array of direct and indirect sampling methods, provide a foundation for exploration of temporal trends and climate impacts on forage fish communities, and spatial processes including habitat associations. Research that synthesizes multiple methods is needed to identify and prioritize Environmental Resource Areas (ERAs), which are habitats and use areas critical to social, biological, and economic resources. Research that synthesizes multiple methods is needed to inform oil spill risk assessments, reduce anthropogenic impacts and conserve habitats necessary for vulnerable forage species. Further, the AFFD may be useful in highlighting the regions and forage fish species for which data are limited, as a means for identifying future research and data collection needs.

Here, we describe the compilation of available datasets indexing forage fish across Alaska from multiple sources and collection methods and describe the present data availability across space and time. Using the AFFD, we summarize forage fish distribution in Alaska and identify data gaps. We then highlight the potential uses of the AFFD with respect to integrated statistical approaches and describe the caveats of different sampling methods in terms of selectivity, and spatial and temporal coverage.

2.3 Methods

2.3.1 Study areas

The database covers Alaska's six large marine ecosystems: Gulf of Alaska, Aleutian Islands, eastern Bering Sea, northern Bering Sea, Beaufort Sea, and Chukchi Sea. Data include nearshore and offshore sampling locations across variable temporal and spatial scales.

2.3.2 Species

The AFFD includes the following forage species: Osmeridae (Pacific capelin (*Mallotus catevarius*), eulachon (*Thaleichthys pacificus*), and other smelts), Pacific herring (*Clupea pallasii*), Ammodytidae (Pacific sand lance (*Ammodytes personatus*) and Arctic sand lance (*A. hexapterus*), Lanternfishes (Family: Myctophidae), juvenile Gadidae (walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. macrocephalus*)), Euphausiacea (krill, including Thysanopoda, Euphausia, Thysanoessa, Stylocheiron), and Squid (superorder: Decapodiformes). (See Supplement for detailed list). While squid and euphausiacea are not teleost fishes, we included them here because they constitute important forage species for marine predators in some or all of Alaska's large marine ecosystems.

2.3.3 Database structure

The AFFD is a compilation of data collected by multiple agencies, sampled using a diversity of gear surveys (small and large-mesh trawls, beach seines, purse seines, jigging, and gill, dip, fyke, and cast nets), and incorporating forage fish abundance and occurrence in groundfish diets (i.e. stomach contents) and seabird diets (i.e. regurgitation, stomach contents, or bill loads for adult bird or chicks).

Six tables (csv files) are included in the database. Information regarding the agencies that have contributed to this project (i.e. contact information, project description, and individual dataset availability) can be found in the data contributor table (data_contributor_information.csv). The event table (event_table.csv) details the location, time, gear, effort, and catch size of each sampling station. The event table includes data from both fisheries surveys and predator diets. For fisheries surveys, there is a corresponding gear table (gear_table.csv) which describes the different types of sampling gear used and net dimensions. For predators, a taxonomic table (pred_taxon_table.csv) includes the taxonomy of groundfish and seabird predators in the event table. The species catch table (catch_table.csv) contains the prey species common and scientific name, weight (g) (total catch weight or individual weight of species), and count (# of individuals in the sample), along with individual morphological characteristics including length (mm), length type (standard, fork, total, or mantle length), life history stage, and sex. Corresponding to the catch table is a taxon table (taxon_table.csv) with taxonomic details of all invertebrates and fish to species or lowest taxonomic rank identified.

For each sampling event, the sample date and time, location and methods were recorded. Descriptions vary depending on the data source, with details of each survey's unique collection methods and design described. To indicate whether data could be used for abundance estimation, the independent fisheries survey sample designs are differentiated as being within a stratified random sampling design, a gridded or systematic design, or collected during trawls associated with hydroacoustic surveys that target specific species. To standardize the database, collection methods were generalized into broader categories with additional information for fisheries surveys available in the gear table. For observations of forage fish species within predator diets, the predator species name, length (cm), weight (g), and sex are recorded, along with the total content weight and number of prey items within the diet sample.

2.3.4 Quality control

For data quality control, we reviewed data accuracy and flagged samples that were determined to be "unsatisfactory" by the source contributors. To combine datasets, all fields, formats, and units were standardized into a unified format. Additional information on the contributor methods for quality assurance and quality control, along with links to the individual data and metadata, can be found in the source reference table (data_contributor_information.csv).

Scientific names of species were synchronized with the Integrated Taxonomic Information System (ITIS) for consistency amongst datasets. In cases where the ITIS Taxonomic Code was not up to date with current nomenclature, the taxonomy was relabeled to match the current classification of the species. This includes recent changes to the scientific name of Pacific sand lance from the former classification as *Ammodytes hexapterus* to the current *A. personatus* (Orr et al., 2015), Pacific capelin from the former Mallotus villosus to M. catervarius (Mecklenburg & Steinke, 2015) and walleye pollock from former Theragra chalcogramma to Gadus chalcogrammus (Byrkjedal et al., 2008; Carr & Dawn Marshall, 2008). Potential input errors, such as substantial outliers in length and weight data, were identified and removed from the database. In the case of juvenile walleye pollock (*G. chalcogrammus*) and Pacific cod (*G. macrocephalus*), samples were filtered for larval and juvenile age classes when life history data was available. Cases where life history was not identified remain in the database. This choice was to allow for users to choose their weight and length limits of juveniles. Samples that recorded only bulk weights on walleye pollock and Pacific cod (i.e. the sum of total catch weight and count) were not removed.

2.3.5 Datasets

The AFFD includes data from four main sample categories: 1) surface, midwater, and bottom trawls, 2) nearshore sampling via purse seines, beach seines, gill nets, cast nets, and jigs, 3) seabird diets, and 4) groundfish stomach contents (Fig. 2.1). Below are brief descriptions of the datasets included in the AFFD. Please refer to the data contributor table for additional information on and access to individual datasets.

2.3.5.1 Surface trawls

The Bering Arctic Subarctic Integrated Survey (BASIS) (originally named Bering-Aleutian Salmon International Survey) is an ongoing research effort to sample the epipelagic zone in the southern and northern Bering Sea, and in more recent years, the Arctic and Gulf of Alaska (https://www.fisheries.noaa.gov/alaska/population-assessments/bering-arctic-and-subarctic-integrated-survey). These surveys began in 2002 through the North Pacific Anadromous Fish Commission and continue through the National Marine Fisheries Service (NMFS) Alaska Fisheries Science Center (AFSC). The Ecosystem Research Survey has been conducted in 4 regions: southern (originally southern and northern) Bering Sea (BASIS) from 2002 – 2012, 2014 – 2016, 2018, 2022; Chukchi Sea (Arctic Integrated Ecosystem Research Program and Arctic Ecosystem Integrated Survey in 2007, 2012, 2013, and 2018 – 2019; eastern Gulf of Alaska (GOA Integrated Ecosystem Research Program) from 2010 to 2017; western GOA from 2012-2013; and northern Bering Sea (NBS Survey) from 2002 – 2007 , 2009 – 2019, and 2021 – 2022. BASIS has conducted surface trawls and mid-water acoustic surveys from 2002 to present (data through 2022 are included in the AFFD). The pelagic trawls lasted 30 minutes and were sampled across 2.8 – 4.6 km (Farley et al., 2005; Farley & Moss, 2009). Acoustic-midwater trawls were deployed to identify acoustic backscatter and estimate the abundance and distribution of dominant pelagic species (Blake, 2014). Additionally, oblique bongo tows (10m from bottom or 300m) were collected to assess zooplankton abundance and community structure (Siddon, 2022). A full description of methods can be found in Farley & Moss (2009).

2.3.5.2 Groundfish bottom trawl survey

The Resource Assessment and Conservation Engineering Division (RACE) Groundfish Assessment Program (GAP) of the Alaska Fisheries Science Center (AFSC) conducts bottom trawl surveys in the Bering Sea (eastern Bering Sea shelf, eastern Bering Sea slope, northern Bering Sea), Gulf of Alaska, and Aleutian Islands. Methods and trawl types for the eastern and northern Bering Sea continental shelf (Markowitz et al., 2023), Aleutian Islands (von Szalay et al., 2023), Gulf of Alaska (von Szalay & Raring, 2018), and Bering Sea upper continental slope (Hoff, 2016) varied among surveys. The eastern (sampled annually 1982 – 2023; no survey 2020) and northern (sampled 1982, 1985, 1988, 1991, 2010, 2017-2022; no survey 2020) Bering Sea continental shelves are sampled along a 20x20 nautical mile grid (except 30x30 nautical miles in the northern Bering Sea in 2018), whereas the Aleutian Islands (sampled biennially 2002 - 2022 with no survey in 2008 and 2020), Gulf of Alaska (sampled triennially 1984, 1987, 1990, 1993, 1996, and biennially 1999 - 2023), and Bering Sea upper continental slope (sampled 2002, 2004, 2008, 2010, 2012, 2016) are surveyed using a stratified random sample design (https://www.fisheries.noaa.gov/alaska/science-data/groundfish-assessment-program-bottom-trawl-surveys). Differences in methods applied across regions can be found in the data contributor information file, and gear type is specified in the gear table.

2.3.5.3 Nearshore Fish Atlas

The Nearshore Fish Atlas (NFA) is an online database developed by the NOAA Fisheries Alaska Regional Office and Alaska Fisheries Science Center's Auke Bay Laboratories. It is comprised of studies from a multitude of agencies and organizations in Alaska, with data collection beginning in 1976 (Alaska Fisheries Science Center, 2022). The AFFD includes data up to 2021, but the NFA continues to release updated versions. Methods include beach seine, jig, purse seine, trawl (surface, midwater and bottom), crab pot, dip net, fyke net, gill net, and minnow trap. Samples were collected across the entirety of the Alaska shoreline (Gulf of Alaska, Bering Sea, Aleutian Islands, Chukchi Sea, and Beaufort Sea).

2.3.5.4 Inshore trawl surveys

The US Geological Survey (USGS) Seabird Forage Fish Ecology Program (SFFEP) conducts trawls paired with hydroacoustic samples in Cook Inlet, Prince Williams Sound, Glacier Bay and other fjords to assess the status of seabird and forage fish in inshore regions of the Gulf of Alaska. Data from Prince William Sound was collected from 2012 – 2022 using modified herring trawl, purse seine, beach seine, gillnet, cast net, dip net, and jig (Arimitsu et al., 2023). Cook Inlet forage fish catch and size data was collected during hydroacoustic trawl surveys to estimate biomass and quality of forage fish from 1995 – 1999 and 2016 – 2021 (Arimitsu et al., 2024; Speckman et al., 2005). Glacier Bay sampling included sampling of fish communities from 1999 – 2004 for prey availability using a modified herring trawl (Arimitsu et al., 2008). Trawl samples were also collected from GOA fjords using a random survey design in Glacier Bay (2004, as noted above), Prince William Sound (2010), Icy Bay (2011), and Yakutat Bay (2011) (Arimitsu et al., 2016).

2.3.5.5 Southeast Alaska Steller Sea Lion Prey Project

The Southeast Alaska Steller Sea Lion Prey Project was conducted to assess the seasonal availability of pelagic prey for Steller sea lions (*Eumetopias jubatus*). Sampling via midwater trawls and gill nets took place between 2001 and 2005 in Berners Bay, Frederick Sound, and Lynn Canal (Csepp et al., 2011; Sigler et al., 2009; Sigler et al., 2004; Sigler & Csepp, 2007). Acoustic data was collected on target prey species and verified using opportunistic midwater trawls and gillnets to collect length, weight, and species classification data in areas of high acoustic backscatter. Acoustic data are not included in the AFFD, but the classification data from midwater trawls and gillnets were included as part of the database. Acoustic surveys were used to index eulachon abundance in Berners Bay (Sigler et al., 2004), herring and pollock abundance in Favorite Channel, lower Lynn canal (Sigler & Csepp, 2007), and pelagic fish species biomass in Stephens passage and Frederick sound (Csepp et al., 2011). While these surveys were designed to target specific forage fish species (i.e. herring and pollock), the weight and count of all other species caught in the midwater trawls were recorded.

2.3.5.6 Late-summer, small-mesh trawl survey

Since 1993, the Ecosystems and Fisheries-Oceanography Coordinated Investigations (EcoFOCI) program of the National Marine Fisheries Service (NMFS) has conducted the late-summer, small-mesh trawl survey. This survey is part of an ongoing study to monitor the distribution and abundance of age-0 walleye pollock. The AFFD includes data from this survey through 2019. In 2001, a 48-site sampling grid was constructed between the Shelikof sea valley and Shumagin Islands; untrawlable or hazardous sites were re-allocated to locations representing major bathymetric regions (Wilson, 2009). Sites were sampled biennially in 2000, 2001, and 2003. In 2005, the survey area expanded to include sampling sites in the central GOA at a shelf along the southeast side of Kodiak Island (McGowan et al., 2019). In addition to the western-central sampling sites, a small subset of sampling events occurred near the Pribilof Islands, Bering Sea between 1994 – 1997 (Schabetsberger, 2000). Midwater trawls were conducted using a shrimp or Stauffer (aka anchovy trawl) midwater trawl (Brodeur & Wilson, 1996; Echeverria et al., 1990).

2.3.5.7 Small-mesh shrimp bottom trawl survey

The small-mesh shrimp trawl is a long-term survey conducted by NMFS and the Alaska Department of Fish and Game (ADF&G). Collection was initiated by the Bureau of Commercial Fisheries in 1953 (Ronholt, 1963), and expanded into an annual systematic survey design in 1970 (Anderson & Gaffney, 1977). Sampling is primarily conducted in the Western Gulf of Alaska. The primary sampling regions include Prince William Sound, Lower Cook Inlet, Kodiak, Kenai, Shelikof Straight, and the Shumagin Islands (Anderson et al., 1995). Data collected between 1953 and 1962 recorded only primary commercial species catch (Anderson et al., 1995). Surveys gradually expanded the types and form of information recorded, and by 1970 surveys took full records of catch, weight, count of the catch to the lowest possible taxonomic level (Anderson et al., 1995). Small-mesh sampling gears were designed to target shrimp via a high-opening shrimp trawl towed 0.4 – 5 meters above the sea floor (Anderson et al., 1995; Wathne, 1977). Details on the gear are recorded in the gear table and described in depth in Wathne (1977). While NMFS collection ended in 2004, the project has continued over a smaller spatial scale by ADF&G within Pavlof Bay (Jackson, 2007; Knutson, 2018).

2.3.5.8 Seabird diets

The U.S. Fish and Wildlife Service Alaska Maritime National Wildlife Refuge (FWS AMNWR) has collected diet data from seabirds since 1975 across 82 colonies in Alaska (Drummond, 2016). Data collection is ongoing, but the AFFD contains diets from 1975 to 2021.

The AFFD includes the mass of the entire sample, the count of prey items, and mass/length/sex/life history of individual prey items. Several diet sampling methods have been employed historically, including lethal bird collections and non-lethal sample methods (regurgitation, burrow screens, etc). A detailed description of the methodology is available in Hatch & Sanger (1992) and Barrett et al. (2007).

Middleton Island seabird diets are collected as part of the Gulf Watch Alaska forage fish monitoring program by the Institute for Seabird Research and Conservation. This dataset spans from 1978 to the present, with sampling occurring between April and August. Diet samples of surface-feeding black-legged kittiwakes (*Rissa tridactyla*) are collected from regurgitations (Hatch, 2013) and diets of diving rhinoceros auklets (*Cerorhinca monocerata*) provisioning their chicks are collected from bill loads (Hatch and Sanger, 1992). Similar to the data collection methods of the FWS AMNWR, the dataset includes details such as total weight, prey type and weight, and the count of individual prey items. Data are available for download at https://doi.org/10.5066/P93I0P67 (Hatch et al., 2023). Additional details on sampling methods can be found in Hatch (2013), Hatch et al. (2023), Schoen et al. (2018), and Thayer et al. (2008).

2.3.5.9 Groundfish diets

During the AFSC-GAP groundfish bottom trawl surveys, the Resource Ecology and Ecosystem Modeling (REEM) program collected and analyzed the stomach contents of groundfish predators. The AFFD includes stomach content data from the years 1981 – 2019, but the project is ongoing and subject to continued updates. Trawl protocols are previously described in the groundfish bottom trawl survey section above. Individual fish were chosen from the AFSC bottom trawl catch based off of species-specific length categories (Livingston et al., 2017). Stomach contents were primarily from four core species: walleye pollock, Pacific cod, Pacific halibut, and arrowtooth flounder (Livingston et al., 2017). From these stomachs, the contents were weighed, and prey were counted and weighed by species, with individual prey length and life history stage recorded. The full protocol is described in Livingston et al. (2017).

2.4 Results

2.4.1 Spatial and temporal overview

In total, the AFFD has 476,626 forage fish samples from 105,420 unique sites, making it the most comprehensive data repository on Alaskan forage fish to date. With the combined datasets, the AFFD includes sampling events from all marine regions in Alaska (Fig. 2.2). Samples primarily cover the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands. Temporally, the AFFD covers 70 years of data in Alaska, ranging from 1953 to 2023. However, data prior to 1970 (collected by the ADF&G/NOAA small-mesh bottom trawl survey) are less reliable, as sampling was primarily focused on commercially important fish species. Following 1970, the ADF&G/NOAA survey standardized the collection methods, thus making the data more dependable for estimation of occurrence and distribution.

The seasonal timing of sample collection varied depending on region and sampling method (Supplementary Fig. S2.1). A majority of sampling occurred during the summer months May through September (95.5%). Collection of groundfish stomach contents during the AFSC-GAP bottom trawl survey took place between May and September, but primarily during June and July (87.8%). Seabird diet sampling occurred earlier in the year (March to September), with most samples collected between June and August (93.5%). For fisheries surveys, sampling events occurred at all times of the year, although primarily between June and September (87.5%).

2.4.1.1 Bering Sea

In terms of regional spatial coverage and sampling design, the eastern Bering Sea (EBS) is sampled predominantly via surface trawls, large-mesh bottom trawls, and groundfish stomach contents on an annual basis with gridded survey designs (Fig. 2.2, 2.3, Supplementary Table S2.2), and has been consistently sampled since 1980. By comparison, the northern Bering Sea (NBS) has been sampled less frequently over a shorter span of time, with consistent sampling only available via surface trawls beginning in 2001 (Fig. 2.3). While seabird colonies in the Bering Sea (Cape Pierce, St. Matthew, Hall, High, St. Paul, Otter, and St. George Island) have been sampled since 1975, they are spatially limited in comparison to trawl surveys and groundfish stomach contents (Fig. 2.2).

2.4.1.2 Gulf of Alaska

The Gulf of Alaska (GOA) surveys with large spatial coverage (i.e. the AFSC groundfish bottom trawl and groundfish stomach collection) were conducted on a triennial basis from 1984 to 1996, changing to a biennial frequency thereafter (1999 - 2023), following a stratified random sample design (Fig. 2.2, 2.3). However, the western-central GOA (WC GOA) has a wide temporal range with data collection beginning in 1953 (Fig. 2.3). Additionally, there are midwater trawl samples following a gridded design within the WC GOA (Fig. 2.2). In addition to trawl and groundfish stomach contents, frequent sampling of seabird colonies in the WC GOA aid in the availability of long-term data (Fig. 2.2, 2.3). While long-term data are available for the WC GOA, the eastern GOA (EGOA) is more limited to short-term surveys, with a lack of consistency in methods employed (Fig. 2.3). Since 1998, the EGOA has been sampled annually, but the lack of spatial overlap still presents challenges for estimations of abundance/distribution (Fig. 2.3). For example, midwater trawls in the EGOA do not overlap spatially or temporally with surface trawls. Beach seines are the most consistent annual sampling type within the EGOA inshore waters (e.g. straits and sounds) – specifically Lynn Canal (Fig. 2.2, 2.3). However, the spatial coverage of beach seines sampling is limited. Only three seabird colonies have been sampled historically in the EGOA (St. Lazaria, Gannet, and Bluff Island). Similar to the WC GOA, sampling with extensive spatial coverage on the EGOA shelf (i.e. outer coast) from the AFSC bottom trawl and groundfish stomach contents is triennial (1984-1996) and then biennial (1999 - 2023).

2.4.1.3 Aleutian Islands

Survey data from the Aleutian Islands primarily comes from seabird diets, the AFSC bottom trawl survey, and groundfish stomach contents (Fig 2.2, 2.3). There are very few beach seines, surface trawls, and midwater trawl events within this region. Seabird diet sampling has occurred at many locations across the Aleutian Islands, however, annual sampling occurs only at Aiktak (eastern Aleutians) and Buldir (western Aleutians).

2.4.1.4 Arctic

Sampling has been far less frequent in the Arctic than in other regions. In the Chukchi Sea, seabird diet samples were collected from 1975 – 1999 at Cape Thompson and Cape Lisburne, but there is no overlap between seabird sampling and the nearshore sampling in the 2000's. The Chukchi Sea lacks long-term fisheries surveys, with a few short-term studies using midwater trawls, surface trawls, and beach seines. There was substantial spatial coverage of the Chukchi Sea from surface trawls, but sampling only occurred in 2007, 2012, and 2013. Sampling in the Beaufort Sea began in 2004 and has consisted of multiple short-term nearshore sampling events via beach seines and small-mesh bottom trawls. Seasonally, the Chukchi Sea was sampled from June to September, and the Beaufort Sea from July to September.

2.4.2 Species distribution

Of the Osmeridae included in the database, Pacific capelin is the most frequently encountered and exhibits the broadest spatial distribution. Capelin are commonly found in the GOA, eastern and northern Bering Sea, and Arctic, with rare occurrences on the EBS Shelf and along the AI (Fig. 2.4, Supplementary Table S2.3). In comparison, Eulachon are encountered primarily in the GOA and EBS, with very few occurrences in the AI, and none recorded in the Arctic (Fig. 2.4, Supplementary Table S2.3). Smelt (such as surf, longfin, and rainbow smelt) are the most infrequently encountered osmeridae (Fig. 2.4). However, the classification of smelt as "unidentified Osmerids" in surveys may confound encounter frequency with that of capelin and eulachon, so caution should be taken in interpretation of encounter. Smelt have been observed across the Alaska coastline from the EGOA to the Beaufort Sea. Compared to eulachon and capelin, this species is scarcely encountered offshore.

Other small pelagic species include Pacific herring and *Ammodytes* spp. (sand lance). The differentiation of Pacific sand lance and Arctic sand lance in historical records is confounded by the reclassification of Pacific sand lance as *A. personatus* from the former *A. hexapterus*, and introduction of Arctic sand lance as *A. hexapterus* in 2015 (Orr et al., 2015). Pacific herring are encountered in high abundance across the entirety of the BS and GOA (Fig 2.4, Supplementary Table S2.3). Herring are encountered at higher latitudes in the Arctic, but there are limited encounters in the AI. *Ammodytes spp.* (sand lance) are frequently encountered in shallow waters across the BS and GOA (Fig 2.4, Supplementary Table S2.3). Sand lance are reliant on habitats with sandy substrate in shallow water depths (Winslade, 1974) with limited presence in the offshore waters. Sand lance are also observed in the AI and throughout the Arctic (Fig. 2.4), with recent increases in Arctic sand lance (*Ammodytes hexapterus*) abundance in higher latitudes (Baker et al., 2022).

Myctophidae (Lanternfish) exhibited a relatively low encounter rate and are found in the EBS shelf, AI, and parts of GOA (Fig. 2.4, Supplementary Table S2.3). They occur more frequently offshore along the EBS Shelf and western Aleutian Islands. Some instances of lanternfish occurrence in Gulf of Alaska have been recorded, with observations primarily occurring offshore and across Shelikof straight. Additionally, there are some encounters in the SE GOA within inshore environments such as Lynn Canal and Frederick Sound. A majority of the lanternfish encounters within a given sampling event are found in diet data (~92.7%).

Fisheries surveys contained within the AFFD infrequently sample mesopelagic depths that lanternfish occupy during daylight hours, which potentially limited lanternfish observations at a given location.

Euphausiidae (krill) are the most frequently occurring taxonomic group of forage organisms at each site and are encountered in the GOA, Bering Sea, and AI (Fig. 2.4, Supplementary Table S2.3). However, like myctophids, nearly all encounters of euphausiidae in the AFFD are within predator diets (99.8%). There were no recorded encounters in offshore trawls within the Chukchi and Beaufort seas. This may be due to the very low capture rate of euphausiidae in the surface trawl gears, as many euphausiidae undergo diel vertical migration and occupy deeper ocean depths during daylight hours. Euphausiidae were present in beach seines along the Arctic coast. Squid species have been frequently encountered in the GOA and AI, and are primarily found offshore along the EBS Shelf and north to the Chukchi Sea. While walleye pollock and Pacific cod are frequently encountered (Supplementary Table S2.3), several surveys do not differentiate amongst life history stages due to formatting incompatible with the structure of the AFFD (i.e. the NOAA bottom trawl survey and small-mesh bottom trawl data exists but were not incorporated in the AFFD), which artificially inflates the number of juvenile gadids present in AFFD observations.

2.5 Discussion

With the combination of datasets, the AFFD represents the first step towards a spatially and temporally comprehensive database of forage fish abundance and occurrence in the waters surrounding Alaska. Not only does the AFFD allow us to identify the data presently available, but it also helps to highlight data gaps and research needs for these trophically-important species.

2.5.1 Variability in data

The AFFD represents a patchwork of observations in space and time, with a diversity of gears employed in offshore or nearshore habitats, and sampling occurring at a diversity of depths. The intent of each data collection effort varied in accordance with the objectives of the projects. The AFFD incorporates observations from resource surveys for larger groundfish (i.e. the AFSC-GAP bottom trawl survey) assessments of juvenile walleye pollock (EcoFOCI midwater trawl), juvenile salmon (AFSC BASIS/IERP surface trawl), and shrimp (ADF&G/NOAA small-mesh bottom trawl), nearshore habitat sampling to improve understanding of community dynamics (Nearshore Fish Atlas), diet collections to inform predator-prey dynamics and trophic structure (REEM groundfish stomach contents, seabird diets) and sampling designed to ground truth acoustic surveys of forage fish or assess prey condition and availability (USGS and SEAK sea lion midwater trawls). Because of this, the spatial coverage and temporal extent varies substantially among observation types.

Directed ecosystem surveys that employ gear specifically designed to capture forage fish are generally rare (Arimitsu et al., 2008), which poses an issue for describing long-term variability in forage fish abundance (Siple et al., 2019). The spatial limitations of directed forage fish surveys also make large scale changes in biomass and distribution more difficult to detect (Siple et al., 2019). Targeted sampling with trawls using acoustic detection can target specific forage fish, but can be biased by vessel avoidance (Løland et al., 2007) and other factors. Incidental catch of forage fish species in fisheries resource surveys, such as the AFSC-GAP groundfish bottom trawl survey, have the advantage of both long timeseries and a broad spatial scale (Szuwalski et al., 2023). However, the gear often used to target larger commercially-valuable species is not designed to retain small species and pelagic fish (Cook & Bundy, 2012) and survey locations often do not align with key forage fish habitats (Lankowicz et al., 2020).

The incorporation of seabird diets and the groundfish stomach contents collected during the AFSC-GAP bottom trawl may provide an alternative means of sampling in areas where trawl performance is hindered by ocean floor topography (Baker et al., 2019), and sampling size classes of fish otherwise difficult to capture in trawls (Thompson et al., 2019). When implementing diet data as a means of indexing abundance or occurrence, it is important to consider the ontogenetic behavior, dietary preferences, and abundance of alternative prey species in the context of the predator species (Gunther et al., 2023; Murdoch, 1969; Ng et al., 2021). However, research suggests that predator diets can detect similar decadal trends and indicate community shifts from a broad marine ecosystem perspective (Gunther et al., 2023; S. A. Hatch, 2013; S. Hatch & Sanger, 1992; Ng et al., 2021; Piatt et al., 2018; Sydeman et al., 2022), which leverages its applicability for assessment of population trends and distributional shifts. The AFFD's broad coverage of available data on forage fish in Alaska can help determine the best uses of each dataset and explore the potential of using datasets in conjunction with one another to understand coherence among them, and to fill spatial and temporal gaps in coverage.

2.5.2 Caveats and considerations

In highlighting what data are available as part of the AFFD it is equally important to highlight what is not included. Specifically, we emphasize a need for qualitative data (Zador et al. 2017) and indigenous and local knowledge (TK and LK, respectively) to fully understand Alaska's forage fish communities and their dynamics. Western science operates within a limited time span in Alaska, and there remains a deficit in observations from nearshore habitats. Recent studies on the long-term history of herring have connected ethnographic and ethnohistorical data with archaeological methods to better understand the patterns of herring populations over the course of thousands of years. Moss et al. (2016) used this combination of methods to estimate abundance and distribution of herring. Interviews, indigenous practices for processing fish, archaeological records, and DNA analysis were all used to gain insight on population diversity and abundance changes over time. As an example in the Canadian arctic, Tallman and Marcoux (2019) studied the arctic food web with Inuit Qaujimajatuqangit (IQ), the system of Inuit knowledge which has also tracked the northward expansion of Pacific Sand Lance into the Arctic (Falardeau 2017).

There also remain other survey methods for indexing forage fish abundance and occurrence which are not included in the AFFD, such as acoustic data, aerial spawning surveys, and fishery-dependent catch rate observations (Donnelly et al., 2024; Ferriss et al., 2022; Grüss et al., 2023). Acoustic data are frequently used to estimate key forage fish abundance and may be more directly applicable in indexing a given species of interest, making these observations a useful resource that can address the selectivity and catchability issues inherent in indexing forage fish based on other survey methods. Use of this data can be especially useful in the Gulf of Alaska, where acoustic data are available from the EcoFOCI spring/late-summer surveys (https://www.ecofoci.noaa.gov/), MACE summer acoustic trawl surveys (https://www.fisheries.noaa.gov/contact/midwater-assessment-and-conservation-engineering-program), and the NSF's Northern Gulf of Alaska's Long Term Ecological Research surveys (https://lternet.edu/site/northern-gulf-alaska/), and in the Chukchi Sea, where data is available from the Arctic EIS acoustic survey (2012 – 2013) (https://www.uaf.edu/cfos/research/projects/arctic-ecosystem-integrat/). The herring aerial surveys conducted by ADF&G are currently used to inform fishery and bycatch management by providing information on the spatial distribution and biomass of herring in nearshore environments (Hebert, 2020).

Users of the AFFD should exercise caution when identifying which sources among the compiled observations best fits their research objectives. When analyzing data contained within the AFFD, users should contact researchers with understanding of the data collection process, sample design and purpose, to ensure proper interpretation.

2.5.3 Future work

The formation of the AFFD is motivated by the need to identify knowledge gaps to guide future research priorities and improve ecosystem-based approaches for management strategies. Using data from the multiple observation types contained within the AFFD can potentially overcome spatial and temporal gaps in sampling effort and potential biases associated with individual surveys or sampling procedures. With the availability of data from 10 data sets comprising 57 different projects detailed in the AFFD, we hope that this repository will facilitate a greater understanding of forage fish dynamics, trophic processes in marine ecosystems, and the responses to a changing climate.

2.6 References

Alaska Fisheries Science Center. (2022). *AFSC/ABL: Nearshore Fish Atlas of Alaska.* https://www.fisheries.noaa.gov/inport/item/17274

Anderson, P. J., Blackburn, J. E., Bechtol, W. R., & Piatt, J. F. (1995). Synthesis and Analysis Gulf of Alaska of Small-Mesh Trawl Data 1953 to 1998. *Exxon Valdez Oil Spill Restoration Project Report, Restoration Project (APEX) 96163L.*

Anderson, P. J., & Gaffney, F. G. (1977). Shrimp of the Gulf of Alaska. *Alask Seas Coasts*, *5*(3), 1–3.

Arimitsu, M. L., Piatt, J. F., Hatch, S., Suryan, R. M., Batten, S., Bishop, M. A., Campbell, R. W., Coletti, H., Cushing, D., Gorman, K., Hopcroft, R. R., Kuletz, K. J., Marsteller, C., McKinstry, C., McGowan, D., Moran, J., Pegau, S., Schaefer, A., Schoen, S., … von Biela, V. R. (2021). Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology*, *27*(9), 1859–1878. https://doi.org/10.1111/gcb.15556

Arimitsu, M. L., Piatt, J. F., Heflin, B. M., & Marsteller, C. E. (2023). *Gulf Watch Alaska—Pelagic Ecosystems Forage Fish Component—Data from Prince William Sound: Distribution, abundance, and morphology of fish, zooplankton, and predators and oceanographic Conditions* (Version 3.0) [Dataset]. U.S. Geological Survey data release. https://doi.org/10.5066/F74J0C9Z

Arimitsu, M. L., Piatt, J. F., Litzow, M. A., Abookire, A. A., Romano, M. D., & Robards, M. D. (2008). Distribution and spawning dynamics of capelin (Mallotus villosus) in Glacier Bay, Alaska: A cold water refugium. *Fisheries Oceanography*, *17*(2), 137–146. https://doi.org/10.1111/j.1365-2419.2008.00470.x

Arimitsu, M. L., Piatt, J. F., & Mueter, F. (2016). Influence of glacier runoff on ecosystem structure in Gulf of Alaska fjords. *Marine Ecology Progress Series*, *560*, 19–40. https://doi.org/10.3354/meps11888

Arimitsu, M. L., Schoen, S. K., Piatt, J. F., & Marsteller, C. E. (2024). *Assessing the Status and Trends of Seabirds and Forage Fish in Lower Cook Inlet, Alaska* (Version 3.0) [Dataset]. U.S. Geological Survey data release. https://doi.org/10.5066/P961LWWE

Aydin, K., Boldt, J., Gaichas, S., & Ianelli, J. (2006). In: Boldt J (ed) Ecosystem considerations for 2007. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, 24–89.

Baker, M. R., De Robertis, A., Levine, R. M., Cooper, D. W., & Farley, E. V. (2022). Spatial distribution of arctic sand lance in the Chukchi Sea related to the physical environment. *Deep Sea Research Part II: Topical Studies in Oceanography*, *206*, 105213. https://doi.org/10.1016/j.dsr2.2022.105213

Baker, M. R., Palsson, W., Zimmermann, M., & Rooper, C. N. (2019). Model of trawlable area using benthic terrain and oceanographic variables—Informing survey design and habitat maps in the Gulf of Alaska. *Fisheries Oceanography*, *28*(6), 629–657. https://doi.org/10.1111/fog.12442

Barrett, R. T., Camphuysen, K. (C. J.), Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe, S., Hüppop, O., Leopold, M. F., Montevecchi, W. A., & Veit, R. R. (2007). Diet studies of seabirds: A review and recommendations. *ICES Journal of Marine Science*, *64*(9), 1675–1691. https://doi.org/10.1093/icesjms/fsm152

Blake, W. (2014). *DY 14-08 Bering Arctic Subarctic Integrated Survey (BASIS) / Ecosystem Monitoring and Assessment (EMA) Fisheries-Oceanography Coordinated Investigations*. https://repository.library.noaa.gov/view/noaa/16521/

Brodeur, R. D., & Wilson, M. T. (1996). A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography*, *5*(s1), 148–166. https://doi.org/10.1111/j.1365-2419.1996.tb00089.x

Byrkjedal, I., Rees, D. J., Christiansen, J. S., & Fevolden, S.-E. (2008). The taxonomic status of Theragra finnmarchica Koefoed, 1956 (Teleostei: Gadidae): perspectives from morphological and molecular data. *Journal of Fish Biology*, *73*(5), 1183–1200. https://doi.org/10.1111/j.1095-8649.2008.01958.x

Carr, S. M., & Dawn Marshall, H. (2008). Phylogeographic analysis of complete mtDNA genomes from Walleye Pollock (Gadus chalcogrammus Pallas, 1811) shows an ancient origin of genetic biodiversity. *Mitochondrial DNA: The Journal of DNA Mapping, Sequencing & Analysis*, *19*(6), 490–496. https://doi.org/10.1080/19401730802570942

Cook, A., & Bundy, A. (2012). Spies of the ocean: Improving our understanding of biodiversity and ecosystem functioning using fish as sampling tools. *Marine Ecology Progress Series*, *454*, 1–18. https://doi.org/10.3354/meps09773

Cordue, P. L. (2007). A note on non-random error structure in trawl survey abundance indices. *ICES Journal of Marine Science*, *64*(7), 1333–1337. https://doi.org/10.1093/icesjms/fsm134

Csepp, D. J., Vollenweider, J. J., & Sigler, M. F. (2011). Seasonal abundance and distribution of pelagic and demersal fishes in southeastern Alaska. *Fisheries Research*, *108*(2–3), 307–320. https://doi.org/10.1016/j.fishres.2011.01.003

Cunningham, J., Elliott, K., Cottenie, K., Hatch, S., & Jacobs, S. (2018). Individual foraging location, but not dietary, specialization: Implications for rhinoceros auklets as samplers of forage fish. *Marine Ecology Progress Series*, *605*, 225–240. https://doi.org/10.3354/meps12761

Cury, P. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. https://doi.org/10.1006/jmsc.2000.0712

De Robertis, A., Levine, R., Williams, K., & Wilson, C. (2023). Modifying a pelagic trawl to better retain small Arctic fishes. *Deep Sea Research Part II: Topical Studies in Oceanography*, *207*, 105225. https://doi.org/10.1016/j.dsr2.2022.105225

Donnelly, D., Arimitsu, M., Pegau, S., & Piatt, J. (2024). Quantifying spatiotemporal variation of nearshore forage fish schools with aerial surveys in Prince William Sound, Alaska. *Marine and Coastal Fisheries*, *16*(2), e10283. https://doi.org/10.1002/mcf2.10283

Drummond, B. A. (2016). Summary figures of diet data from birds on the Alaska Maritime National Wildlife Refuge. *AMNWR 2016/06, U.S. Fish and Wildlife Service.*

Echeverria, T. W., Lenarz, W. H., & Reilly, C. A. (1990). Survey of the abundance and distribution of pelagic young-of-the-year Rockfishes, Sebastes, off central California. *NOAA Technical Memorandum NMFS, NOAA-TM-NMFS-SWFC*, *147*.

Farley, E. V., & Moss, J. H. (2009). Growth Rate Potential of Juvenile Chum Salmon on the Eastern Bering Sea Shelf: An Assessment of Salmon Carrying Capacity. *North Pacific Anadromous Fish Communication Bulletin*, *5*, 265–277.

Farley, E. V., Murphy, J. M., Wing, B. W., Moss, J. H., & Middleton, A. (2005). Distribution, Migration Pathways, and Size of Western Alaska Juvenile Salmon Along the Eastern Bering Sea Shelf. *North Pacific Anadromous Fish Communication Bulletin*, *11*(1), 15–26.

Ferriss, B., Thorson, J., McGowan, D., Vollenweider, J., Ormseth, O., Zaleski, M., Rogers, L., Zeppelin, T., & Siple, M. (2022, 19). *2022 AFSC Forage Species Congress*. Joint Groundfish Plan Team.

Fréon, P., Cury, P., Shannon, L., & Roy, C. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulletin Of Marine Science*, *76*(2).

Grüss, A., Pirtle, J. L., Thorson, J. T., Lindeberg, M. R., Neff, A. D., Lewis, S. G., & Essington, T. E. (2021). Modeling nearshore fish habitats using Alaska as a regional case study. *Fisheries Research*, *238*, 105905. https://doi.org/10.1016/j.fishres.2021.105905

Grüss, A., Thorson, J. T., Anderson, O. F., O'Driscoll, R. L., Heller-Shipley, M., & Goodman, S. (2023). Spatially varying catchability for integrating research survey data with other data sources: Case studies involving observer samples, industry-cooperative surveys, and predators as samplers. *Canadian Journal of Fisheries and Aquatic Sciences*, cjfas-2023-0051. https://doi.org/10.1139/cjfas-2023-0051

Gunther, K., Baker, M., & Aydin, K. (2023). Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea. *Marine Ecology Progress Series*, *SPF2*. https://doi.org/10.3354/meps14389

Hatch, S. A. (2013). Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Marine Ecology Progress Series*, *477*, 271–284. https://doi.org/10.3354/meps10161

Hatch, S. A., Arimitsu, M. L., Piatt, J. F., Shannon, W., & Marsteller, C. E. (2023). Seabird Diet Data Collected on Middleton Island, Gulf of Alaska. *U.S. Geological Survey Data Release.* https://doi.org/10.5066/P93I0P67

Hatch, S., & Sanger, G. (1992). Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. *Marine Ecology Progress Series*, *80*, 1–14. https://doi.org/10.3354/meps080001

Hebert, K. (2020). Southeast Alaska 2019 herring stock assessment surveys. *Alaska Department of Fish and Game*.

Hoff, G. R. (2016). *Results of the 2016 Eastern Bering Sea Upper Continental Slope Survey of Groundfish and Invertebrate Resources* [PDF]. https://doi.org/10.7289/V5/TM-AFSC-339

Jackson, D. R. (2007). Trawl survey of shrimp and forage fish in Alaska’s Westward Region, 2006. *Alaska Department of Fish and Game, Fishery Management Report No. 07-13.*

Knutson, M. (2018). Special project plan: 2018 large-mesh bottom trawl survey of crab and groundfish for Kodiak, Chignik, South Peninsula, and Eastern Aleutian districts. *Alaska Department of Fish and Game, Regional Information Report 4K18-07, Kodiak.*

Konar, M., Qiu, S., Tougher, B., Vause, J., Tlusty, M., Fitzsimmons, K., Barrows, R., & Cao, L. (2019). Illustrating the hidden economic, social and ecological values of global forage fish resources. *Resources, Conservation and Recycling*, *151*, 104456. https://doi.org/10.1016/j.resconrec.2019.104456

Lankowicz, K. M., Bi, H., Liang, D., & Fan, C. (2020). Sonar imaging surveys fill data gaps in forage fish populations in shallow estuarine tributaries. *Fisheries Research*, *226*, 105520. https://doi.org/10.1016/j.fishres.2020.105520

Link, J. (2004). Using fish stomachs as samplers of the benthos: Integrating long-term and broad scales. *Marine Ecology Progress Series*, *269*, 265–275. https://doi.org/10.3354/meps269265

Livingston, P. A., Aydin, K., Buckley, T. W., Lang, G. M., Yang, M.-S., & Miller, B. S. (2017). Quantifying food web interactions in the North Pacific – a data-based approach. *Environmental Biology of Fishes*, *100*(4), 443–470. https://doi.org/10.1007/s10641-017-0587-0

Løland, A., Aldrin, M., Ona, E., Hjellvik, V., & Holst, J. C. (2007). Estimating and decomposing total uncertainty for survey-based abundance estimates of Norwegian spring-spawning herring. *ICES Journal of Marine Science*, *64*(7), 1302–1312. https://doi.org/10.1093/icesjms/fsm116

Markowitz, E. H., Dawson, E. J., Anderson, C. B., Rohan, S. K., Charriere, N. E., Prohaska, B. K., & Stevenson, D. E. (2023). Results of the 2022 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. *U.S. Department of Commerce*, 213.

McGowan, D., Goldstein, E., Arimitsu, M., Deary, A., Ormseth, O., De Robertis, A., Horne, J., Rogers, L., Wilson, M., Coyle, K., Holderied, K., Piatt, J., Stockhausen, W., & Zador, S. (2020). Spatial and temporal dynamics of Pacific capelin Mallotus catervarius in the Gulf of Alaska: Implications for ecosystem-based fisheries management. *Marine Ecology Progress Series*, *637*, 117–140. https://doi.org/10.3354/meps13211

McGowan, D., Horne, J., & Rogers, L. (2019). Effects of temperature on the distribution and density of capelin in the Gulf of Alaska. *Marine Ecology Progress Series*, *620*, 119–138. https://doi.org/10.3354/meps12966

Mecklenburg, C. W., & Steinke, D. (2015). Ichthyofaunal Baselines in the Pacific Arctic Region and RUSALCA Study Area. *Oceanography*, *28*(3), 158–189. https://doi.org/10.5670/oceanog.2015.64

Murdoch, W. W. (1969). Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations. *Ecological Monographs*, *39*(4), 335–354. https://doi.org/10.2307/1942352

Ng, E. L., Deroba, J. J., Essington, T. E., Grüss, A., Smith, B. E., & Thorson, J. T. (2021). Predator stomach contents can provide accurate indices of prey biomass. *ICES Journal of Marine Science*, *78*(3), 1146–1159. https://doi.org/10.1093/icesjms/fsab026

Ormseth, O. A. (2014). Appendix 2. Forage species report for the Gulf of Alaska. In Plan Team for Groundfish Fisheries of the Gulf of Alaska (compiler), Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council, 1001–1039.

Orr, J., Wildes, S., Kai, Y., Raring, N., Nakabo, T., Katugin, O., & Guyon, J. (2015). Systematics of North Pacific sand lances of the genus Ammodytes based on molecular and morphological evidence, with the description of a new species from Japan. *Fishery Bulletin-National Oceanic and Atmospheric Administration*, *113*, 129–156. https://doi.org/10.7755/FB.113.2.3

Piatt, J. F., Arimitsu, M. L., Sydeman, W. J., Thompson, S. A., Renner, H., Zador, S., Douglas, D., Hatch, S., Kettle, A., & Williams, J. (2018). Biogeography of pelagic food webs in the North Pacific. *Fisheries Oceanography*, *27*(4), 366–380. https://doi.org/10.1111/fog.12258

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Heppell, S. S., Houde, E. D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R. S., Geers, T. M., Gownaris, N., & Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, *15*(1), 43–64. https://doi.org/10.1111/faf.12004

Ronholt, L. L. (1963). Distribution and Relative Abundance of commercially important Pandalid shrimps in the Northeastern Pacific Ocean. *United States Fish and Wildlife Service Special Scientific Report*, *449*.

Rose, G. A. (2005). Capelin (Mallotus villosus) distribution and climate: A sea “canary” for marine ecosystem change. *ICES Journal of Marine Science*, *62*(7), 1524–1530. https://doi.org/10.1016/j.icesjms.2005.05.008

Schabetsberger, R. (2000). Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (Theragra chalcogramma) at a frontal region near the Pribilof Islands, Bering Sea. *ICES Journal of Marine Science*, *57*(4), 1283–1295. https://doi.org/10.1006/jmsc.2000.0814

Schoen, S. K., Piatt, J. F., Arimitsu, M. L., Heflin, B. M., Madison, E. N., Drew, G. S., Renner, M., Rojek, N. A., Douglas, D. C., & DeGange, A. R. (2018). Avian predator buffers against variability in marine habitats with flexible foraging behavior. *Marine Biology*, *165*(3), 47. https://doi.org/10.1007/s00227-018-3304-4

Serrano, A., Velasco, F., Olaso, I., & Sánchez, F. (2003). Macrobenthic crustaceans in the diet of demersal fish in the Bay of Biscay in relation to abundance in the environment. *Sarsia North Atlantic Marine Science*, *88*, 36–48. https://doi.org/10.1080/00364820308469

Siddon, E. (2022). Ecosystem Status Report 2022: Eastern Bering Sea. Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council.

Sigler, M. F., & Csepp, D. J. (2007). Seasonal abundance of two important forage species in the North Pacific Ocean, Pacific herring and walleye pollock. *Fisheries Research*, *83*(2–3), 319–331. https://doi.org/10.1016/j.fishres.2006.10.007

Sigler, M. F., Womble, J. N., & Vollenweider, J. J. (2004). Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: A prespawning aggregation of eulachon (*Thaleichthys pacificus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(8), 1475–1484. https://doi.org/10.1139/f04-086

Sigler, M., Tollit, D., Vollenweider, J., Thedinga, J., Csepp, D., Womble, J., Wong, M., Rehberg, M., & Trites, A. (2009). Steller sea lion foraging response to seasonal changes in prey availability. *Marine Ecology Progress Series*, *388*, 243–261. https://doi.org/10.3354/meps08144

Siple, M. C., Essington, T. E., & E. Plagányi, É. (2019). Forage fish fisheries management requires a tailored approach to balance trade-offs. *Fish and Fisheries*, *20*(1), 110–124. https://doi.org/10.1111/faf.12326

Speckman, S. G., Piatt, J. F., Minte-Vera, C. V., & Parrish, J. K. (2005). Parallel structure among environmental gradients and three trophic levels in a subarctic estuary. *Progress in Oceanography*, *66*(1), 25–65. https://doi.org/10.1016/j.pocean.2005.04.001

Surma, S., Pitcher, T. J., Kumar, R., Varkey, D., Pakhomov, E. A., & Lam, M. E. (2018). Herring supports Northeast Pacific predators and fisheries: Insights from ecosystem modelling and management strategy evaluation. *PLOS ONE*, *13*(7), e0196307. https://doi.org/10.1371/journal.pone.0196307

Sydeman, W. J., Thompson, S. A., Piatt, J. F., Zador, S. G., & Dorn, M. W. (2022). Integrating seabird dietary and groundfish stock assessment data: Can puffins predict pollock spawning stock biomass in the North Pacific? *Fish and Fisheries*, *23*(1), 213–226. https://doi.org/10.1111/faf.12611

Szuwalski, C., Yasumiishi, E., Andrews, A., Dimond, A., Murphy, J., Farley, E., & Siddon, E. (2023). 2023 Bering Sea and Aleutian Islands forage report. North Pacific Fishery Management Council.

Thayer, J. A., Bertram, D. F., Hatch, S. A., Hipfner, M. J., Slater, L., Sydeman, W. J., & Watanuki, Y. (2008). Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: Synchrony and relationships with sea surface temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(8), 1610–1622. https://doi.org/10.1139/F08-076

Thompson, S. A., García-Reyes, M., Sydeman, W. J., Arimitsu, M. L., Hatch, S. A., & Piatt, J. F. (2019). Effects of ocean climate on the length and condition of forage fish in the Gulf of Alaska. *Fisheries Oceanography*, *28*(6), 658–671. https://doi.org/10.1111/fog.12443

Thornton, T. F., Butler, V., Funk, F., Moss, M., Hebert, J., & Elder, T. (2010). Herring Synthesis: Documenting and Modeling Herring Spawning Areas Within Socio-ecological Systems Over Time in the Southeastern Gulf of Alaska. North Pacific Research Board Project, Project #728.

Turner, L. C., Arimitsu, M., Piatt, J. F., Eckert, G. L., & Cunningham, C. J. (2024). *Alaska Forage Fish Database (AFFD)*. U.S. Geological Survey. https://doi.org/10.5066/P9WZQJ8N

von Szalay, P. G., & Raring, N. W. (2018). *Data Report: 2017 Gulf of Alaska bottom trawl survey.* [PDF]. https://doi.org/10.7289/V5/TM-AFSC-374

von Szalay, P. G., Raring, N. W., Siple, M. C., Dowlin, A. N., Riggle, B. C., & Laman, E. A. (2023). *Data Report: 2022 Aleutian Islands bottom trawl survey.* https://doi.org/10.25923/85CY-G225

Wathne, F. (1977). Performance of Trawls Used in Resource Assessment. *Marine Fisheries Review*, *39*(6).

Wilson, M. (2009). Ecology of small neritic fishes in the western Gulf of Alaska. I. Geographic distribution in relation to prey density and the physical environment. *Marine Ecology Progress Series*, *392*, 223–237. https://doi.org/10.3354/meps08160

Winslade, P. (1974). Behavioural studies on the lesser sandeel Ammodytes marinus (Raitt) II. The effect of light intensity on activity. *Journal of Fish Biology*, *6*(5), 577–586. https://doi.org/10.1111/j.1095-8649.1974.tb05101.x

Witherell, D., Pautzke, C., & Fluharty, D. (2000). An ecosystem-based approach for Alaska groundfish fisheries. *ICES Journal of Marine Science*, *57*(3), 771–777. https://doi.org/10.1006/jmsc.2000.0719

WoRMS Editorial Board (2024). World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2024-10-23. https://doi.org/10.14284/170

Zimmermann, M. (2003). Calculation of untrawlable areas within the boundaries of a bottom trawl survey. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(6), 657–669. https://doi.org/10.1139/f03-055

2.7 Figures

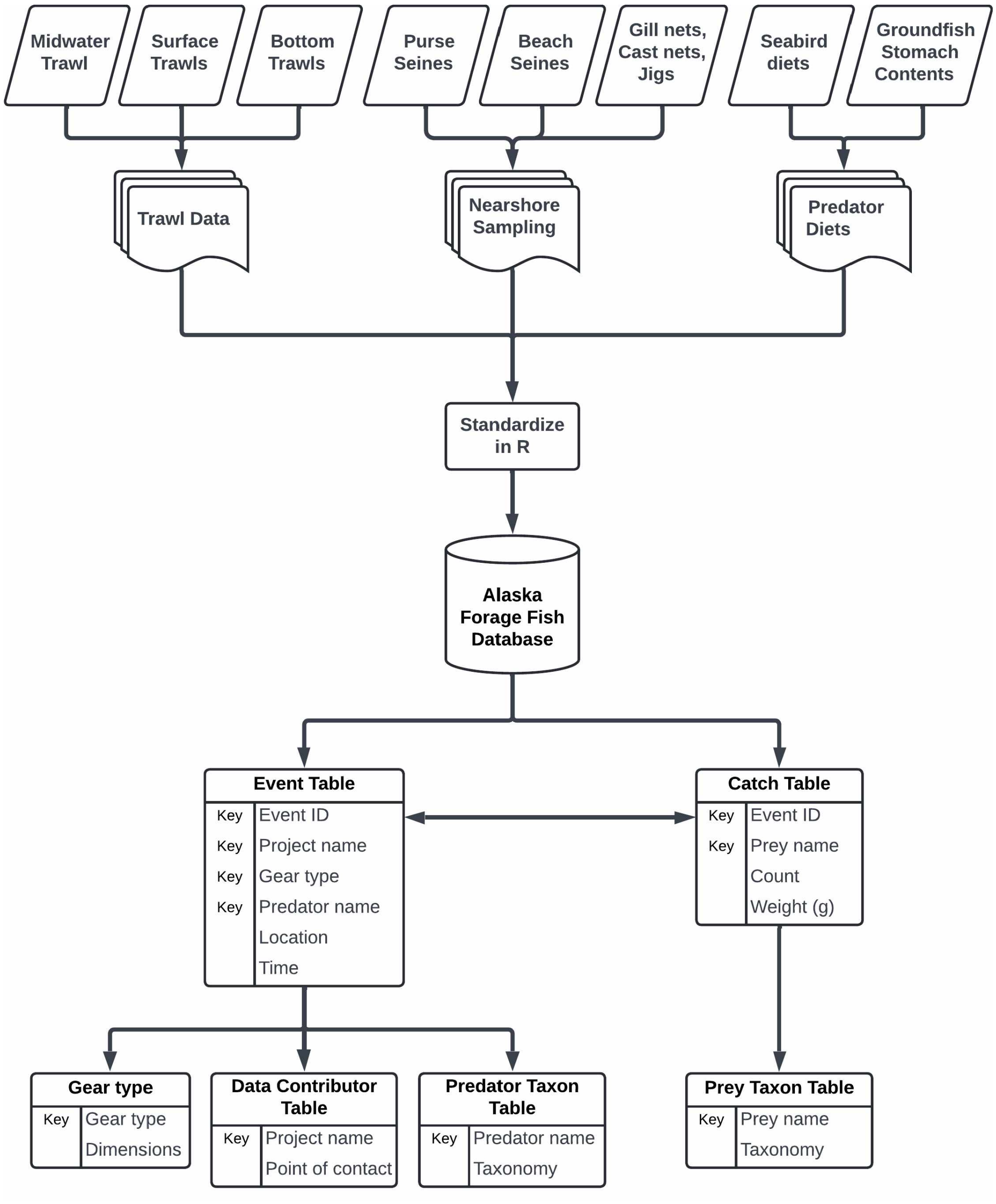

Figure 2.1: Schematic of the AFFD dataset inputs (rhombuses), dataset categories (stacked shapes), and hierarchical database (cylinder). The rectangle represents the processing steps to standardize and merge the database. Database tables (labeled boxes) contain keys (arrows) that link related tables and a generalization of fields within each table.

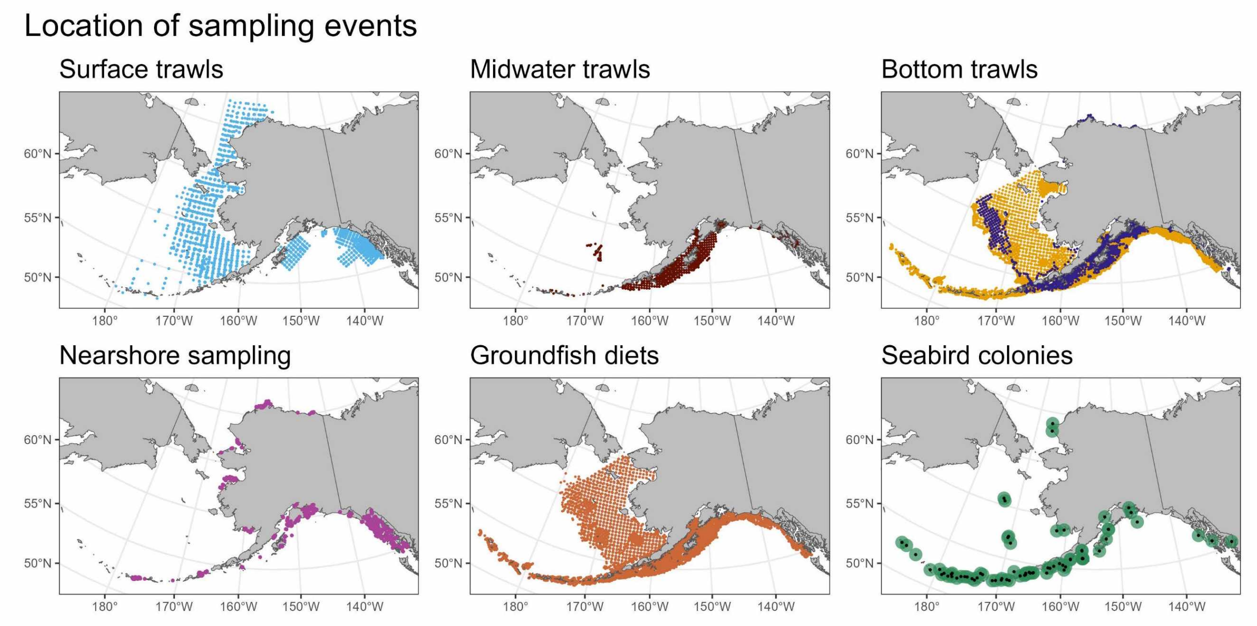

Figure 2.2: Spatial coverage of the six primary sampling methods: a) surface trawls (light blue), b) midwater trawls (dark red), c) bottom trawls (small-mesh in dark blue, large-mesh in yellow), d) nearshore sampling (purple), e) locations of groundfish stomach content collection (orange), and f) seabird colonies (green circle with black point). All individual sampling events are included as points, with the exception of seabird colony data which highlight colony locations.

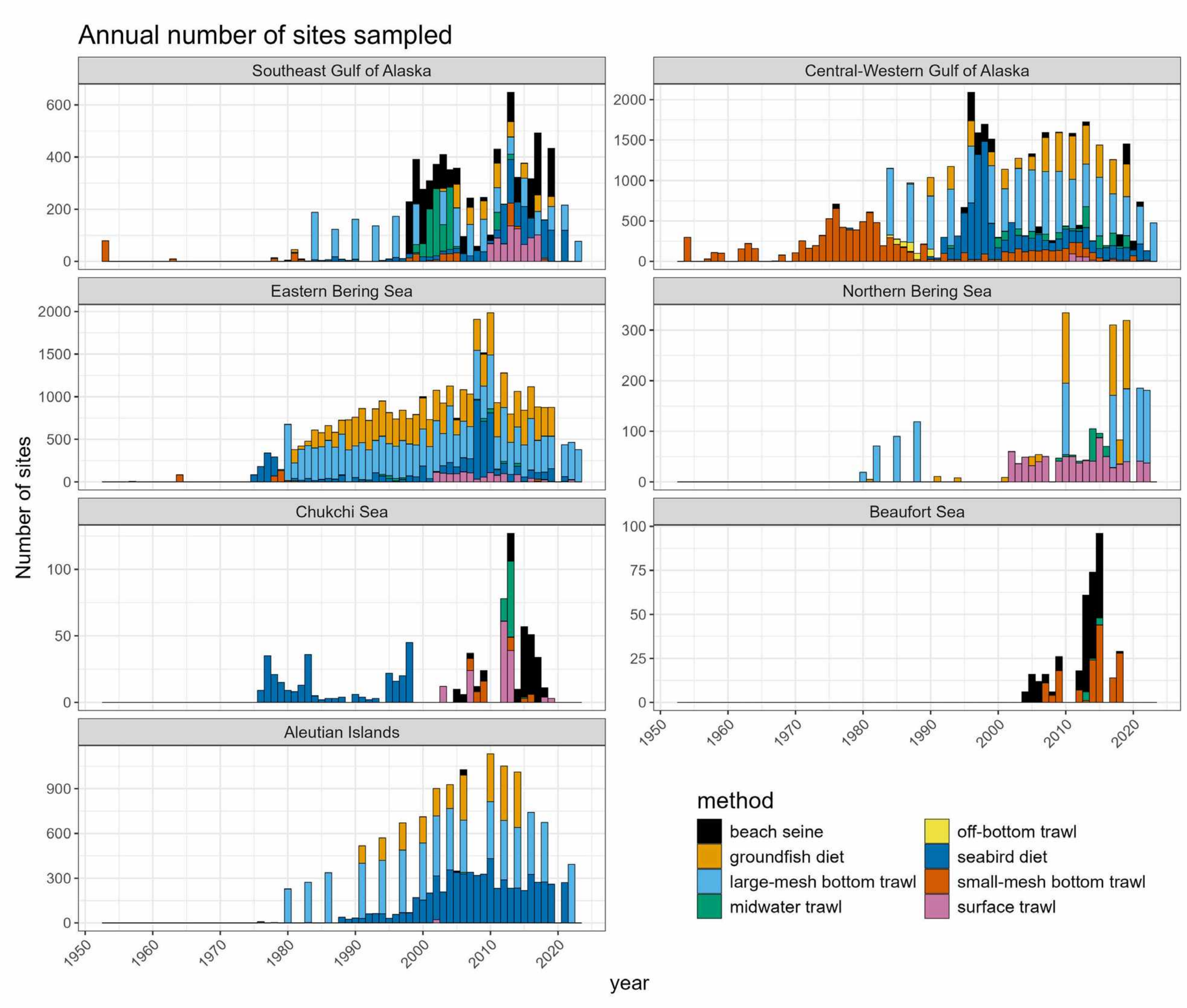

Figure 2.3: Sites sampled at each marine region from 1953-2023 via nets (beach seines and surface, midwater, off-bottom and bottom trawls), groundfish stomachs, and seabird diets. Note the scaling of y-axes differs among regions.

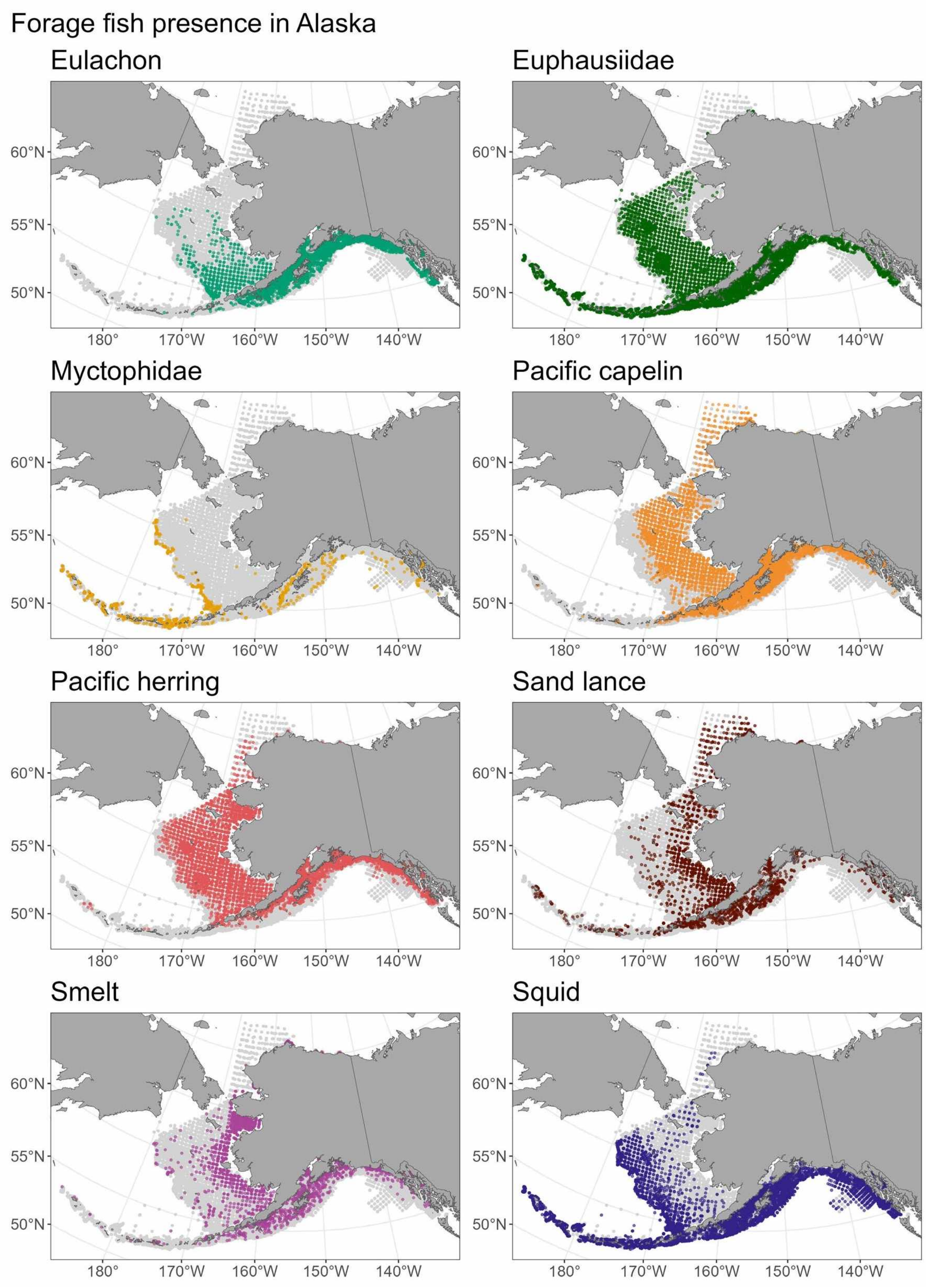

Figure 2.4: Map of locations where forage species were encountered (color). Grey points represent sites where sampling occurred, but the specific forage species was not encountered.

2.8 Supplementary Information

2.8.1 Supplementary Tables

Table S 2.1: Table of forage species names and length (mm) range in the AFFD.

Common Name	Scientific Name	Group Name	Min Length	Max Length
Pacific herring	Clupea pallasii	Pacific herring	5.6	310
Arctic sand lance	Ammodytes hexapterus	Sand lance	24	139
Pacific sand lance	Ammodytes personatus	Sand lance	1.09	250
Sand lance	Ammodytes spp.	Sand lance	3.35	204
Walleye pollock, juvenile	Gadus chalcogrammus	Walleye pollock	0.67	242
Pacific cod, juvenile	Gadus macrocephalus	Pacific cod	11	335
Pacific capelin	Mallotus catervarius	Pacific capelin	1.1	191
Eulachon	Thaleichthys pacificus	Eulachon	21	223
Smelt	Osmeridae	Smelt	17	180
Longfin smelt	Spirinchus thaleichthys	Smelt	21	215
Night smelt	Spirinchus starksi	Smelt	91	104
Pond smelt	Hypomesus olidus	Smelt	28	128
Rainbow smelt	Osmerus mordax	Smelt	11	280
Surf smelt	Hypomesus pretiosus	Smelt	34	237
Lanternfish	Myctophidae	Myctophidae	1	150
Bigeye lanternfish	Protomyctophum thompsoni	Myctophidae	60	60
Bigfin lanternfish	Symbolophorus californiensis	Myctophidae		
Broadfin lanternfish	Nannobrachium ritteri	Myctophidae		
Brokenline lanternfish	Lampanyctus jordani	Myctophidae		
California headlightfish	Diaphus theta	Myctophidae	56	65
Garnet lanternfish	Stenobrachius nannochir	Myctophidae		
Lanternfish	Diaphus spp.	Myctophidae		
Lanternfish	Lampanyctus spp.	Myctophidae		
Lanternfish	Stenobrachius spp.	Myctophidae		
Pinpoint lanternfish	Nannobrachium regale	Myctophidae		
Euphausiidae	Euphausia spp.	Euphausiidae		
Euphausiidae	Euphausiacea	Euphausiidae		
Euphausiidae	Euphausiidae	Euphausiidae	6	56.5
Euphausiidae	Bentheuphausiidae	Euphausiidae		
Euphausiidae	Nematoscelis spp.	Euphausiidae		
Euphausiidae	Stylocheiron maximum	Euphausiidae		
Euphausiidae	Thysanoessa inermis	Euphausiidae	15	39
Euphausiidae	Thysanoessa inspinata	Euphausiidae		
Euphausiidae	Thysanoessa longipes	Euphausiidae		

Table S 2.1 cont.

Euphausiidae	**Thysanoessa parva**	**Euphausiidae**		
Euphausiidae	Thysanoessa raschii	Euphausiidae	9	27
Euphausiidae	Thysanoessa spp.	Euphausiidae	12	41
Euphausiidae	Thysanoessa spinifera	Euphausiidae	34	35
Northern pacific krill	Euphausia pacifica	Euphausiidae		
Squid, octopus, cuttlefish, or nautilis	Cephalopoda	Squid		
Squid and octopus	Coleoidea	Squid		
Squid	Decapodiformes	Squid	1.3	40
Northern pacific bobtail squid	Rossia pacifica	Squid	15	55
Squid	Oegopsida	Squid	2	331.5
Whip-lash squid	Chiroteuthis spp.	Squid		
Swordtail squid	Chiroteuthis calyx	Squid		
Glass squid	Cranchiidae	Squid		
Northern cranch squid	Taonius borealis	Squid		
Peacock cranch squid	Taonius pavo	Squid		
Cockatoo squid	Galiteuthis phyllura	Squid		
Armhook squid	Gonatidae	Squid	0.2	235
Armhook squid	Berryteuthis spp.	Squid	38.7	43.4
Magister armhook squid	Berryteuthis magister	Squid	25	160
Minimal armhook squid	Berryteuthis anonychus	Squid	24.5	43.1
Armhook squid	Gonatus spp.	Squid	20.8	73.7
Berry armhook squid	Gonatus berryi	Squid		
Longfin squid	Gonatus kamtschaticus	Squid		
Shortarm gonate squid	Gonatus kamtschaticus	Squid	5.2	67.6
Madokai armhook squid	Gonatus madokai	Squid	13	65
Clawed armhook squid	Gonatus onyx	Squid		
Fiery armhook squid	Gonatus pyros	Squid		
Squid	Gonatopsis spp.	Squid		
Boreopacific armhook squid	Gonatopsis borealis	Squid	40	40
Makko gonate squid	Gonatopsis makko	Squid		
Hooked squid	Onychoteuthidae	Squid		
Robust clubhook squid	Onykia robusta	Squid		
Squid	Myopsida	Squid		
Pencil squid	Loliginidae	Squid		
Pencil squid	Loligo spp.	Squid		
California market squid	Doryteuthis opalescens	Squid	46	90

Table S 2.2: Number of samples taken at each region by method. The most frequently sampled groundfish and seabird predators are included.

Method	SE GOA	CW GOA	AI	EBS	NBS	CHUK	BEAU
Surface trawl	2259	747	66	3585	2538	429	
Midwater trawl	2883	4413	30	801	330	225	30
Small-mesh bottom trawl	1146	29586	6	1020	3	156	453
Large-mesh bottom trawl	6093	34962	17757	55050	3045		
Off-bottom trawl		1305		21			
Beach seine	6090	6111	156	186		606	639
Purse seine	309	483					
Jig	684	288				30	
Black-legged kittiwake	1038	26526	1524	8523		1854	
Common murre	708	19314	465	2808		978	
Tufted puffin	57	24876	18759	1728		6	
Horned puffin	15	6276	2451	555		9	
Rhinoceros auklet	4254	19884		3			
Walleye pollock	3576	32577	13275	238155	8328		
Pacific cod	2046	29121	12564	163218	4341		
Arrowtooth flounder	4179	49572	13536	52857	6		
Pacific halibut	2178	23583	4635	27321	342		

Table S 2.3: Frequency of occurrence (in descending order) from all survey methods in the south-eastern Gulf of Alaska (SE GOA), western-central Gulf of Alaska (CW GOA), Aleutian Islands (AI), eastern Bering Sea (EBS), northern Bering Sea (NBS), Chukchi Sea (CHUK), and Beaufort Sea (BEAU), and all regions combined. Walleye pollock and Pacific cod include unspecified life histories that are not indicative of the frequency of juvenile occurrences.

	Frequency of occurrence (%) in regions							
Species	**SE GOA**	**CW GOA**	**AI**	**EBS**	**NBS**	**CHUK**	**BEAU**	**Total**
Euphausiidae	11.75	13.69	15.97	24.34	7.13	2.96	0.74	19.4
Walleye pollock*	16.33	20.99	10.89	14.95	12.97	0.81	0.49	15.86
Pacific cod*	6.58	11.95	6.72	7.14	6.15	0.14	0	8.24
Pacific capelin	7.31	11.9	0.59	2.39	5.99	10.47	21.32	4.94
Sand lance	7.79	11.74	3.02	1.65	2.33	21.97	18.38	4.85
Squid	9.38	5.38	8.49	1.72	0.5	0.42	0	3.85
Pacific herring	10.39	4.92	0.43	2.35	12.18	9.17	1.23	3.31
Eulachon	5.88	5.97	0	0.67	0.07	0	0	2.13
Myctophidae	1.15	1.14	2.93	0.61	0	0	0	1.07
Smelt	2.32	1.77	0.05	0.33	6.81	4.37	17.16	0.93

2.8.2 Supplementary Figures

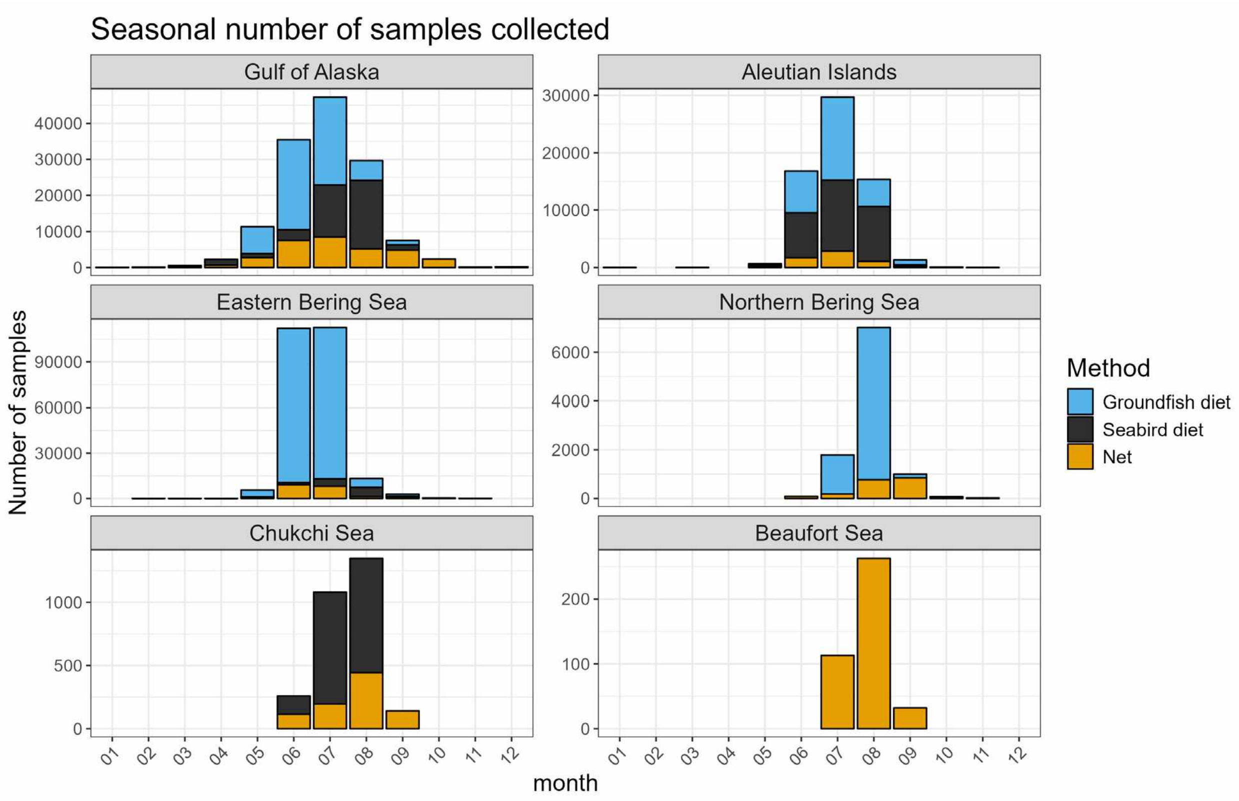

Figure S 2.1: Number of samples collected per month by region from nets (trawl or nearshore sampling method), groundfish stomachs, or seabird diets.

Chapter 3: Integrating multiple data sources for spatial and temporal dynamic assessments of forage fish in Alaska

3.1 Abstract

Forage fish are a critical part of the marine trophic ecosystem in Alaska that transfer energy from primary and secondary producers (phytoplankton and zooplankton) to upper trophic level marine predators. Using fisheries independent surveys (trawls and beach seines), groundfish stomach contents, and seabird diets, we assessed distributional shifts and changes in probability of encounter for Pacific capelin (*Mallotus catervarius*), Pacific herring (*Clupea pallasii*), and sand lance (*Ammodytes* spp.) in the Bering Sea and Gulf of Alaska. We estimated differences in species distribution among stanzas partitioned by climatic regime shifts (i.e. years of significant shifts in multiple climate indices) and assessed latitudinal and longitudinal shifts based on center-of-gravity (COG). Model performance and predictions were compared when fit to individual data sources (fisheries survey, groundfish diet, and seabird diet data) and a combined dataset, and among-stanza variation in the probability of encounter were estimated for each species within each region. Comparison of predictions from models fit to separate data sources indicate coherent trends in the interannual timing of record highs and lows of species' occurrence across models, which are supported by previous literature. The long-term data in the Gulf of Alaska (1972 - 2023) captures the scale of Pacific capelin decline in response to the 1977 regime shift. Analysis in the Bering Sea suggests a northern shift of sand lance in response to anomalously high temperatures (2014-2019), and a northern shift of Pacific herring during the cold period (2006-2013), with herring not returning to previously occupied habitats following the 2014-2016 marine heatwave. Pacific capelin in the eastern Bering Sea contracted into the inner domain (<50 m depth) but did not contract north as expected. In the Gulf of Alaska, sand lance primarily remained in similar habitats across climate stanzas, while herring shifted further south, and Pacific capelin contracted inshore in response to warmer climate stanzas. In this paper, we present novel findings on the Gulf of Alaska previously not possible due to data limitations. We demonstrate the potential for integration of seemingly disparate data to provide broader spatial coverage over a longer time span, and to improve estimates for data-limited forage species and inform our understanding of forage fish response to environmental shifts.

3.2 Introduction

Forage fish are an essential component of the trophic structure of marine ecosystems, acting to transfer energy from lower trophic levels to marine mammals, seabirds, and higher trophic level fish species (Cury, 2000). Generally, forage fish respond quickly to shifts in climate due to their short life spans and a strong coupling with the zooplankton community (Rose, 2005). Dramatic changes in the trophic structure and community composition of Alaska's marine ecosystems can occur as a result of climatic regime shifts, which are persistent deviations in multiple climate indices, and ecosystem regime shifts, which are changes in the dominant species and spatial displacement of other species (Francis et al., 1998; Overland et al., 2008; Yasunaka & Hanawa, 2002). Rapid shifts in bio-physical conditions, including ocean temperature, water column stability, and ice extent, affect forage fish growth (von Biela et al., 2019; Robards et al., 2002), spawn time (McGowan et al., 2021), abundance (Anderson & Piatt, 1999; Francis et al., 1998; Mueter & Norcross, 2011), distribution (Andrews et al., 2016; Hunt et al., 2002; Suca et al., 2021) and community composition (Thompson et al., 2019). Changes in community composition are linked to varying responses of forage fish to environmental factors, shifts in lower trophic level productivity (Rovellini et al., 2024), and predation (Mueter & Norcross, 2000). While trophic stability is often observed despite fluctuations in individual forage fish populations, the resilience of the forage fish community to environmental shifts may be lost under extreme and extended periods of anomalous environmental conditions, such as the 2014-2016 marine heatwave (Arimitsu et al., 2021; Suryan et al., 2021). Estimation of forage fish abundance and distribution are critical for assessing the vulnerability of these species to climate related changes and identifying critical habitats in which to focus conservation efforts.

Quantifying past forage fish responses to climatic regime shifts can provide insight into possible future change and forage fish populations and by extension the tropic structure and stability of marine ecosystems. Changes in forage fish population dynamics can be driven by multidecadal and interdecadal oscillations in atmospheric and oceanic circulation, as well as anthropogenic influences. Across the North Pacific, climatic regime shifts associated with climate change and trends from El Niño/Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and Pacific/North American (PNA) patterns have exhibited broad-reaching effects on marine community composition (Benson & Trites, 2002; Bond et al., 2003; Hare & Mantua, 2000; Yasunaka & Hanawa, 2002), including reorganization of marine communities in the Gulf of Alaska (Anderson & Piatt, 1999) and Bering Sea (Hunt et al., 2002), along with synchronous responses across forage communities in the California Current Large Marine Ecosystem (Thompson et al., 2019). As an example in the North Pacific, the rapid climatic regime shift in 1977/1978, associated with a positive phase in PDO, led to a reconfiguration of the trophic food-web that has persisted for decades in the Gulf of Alaska (Anderson & Piatt, 1999; Hare & Mantua, 2000). In the North Atlantic, changes in the Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), and a contraction of the subpolar gyre during the 1990's have coincided with northern shifts of pelagic clupeoid fish (e.g., anchovy, sardine, sardinella, sprat, herring) in the eastern north and central Atlantic (Alheit et al., 2012, 2014) and a community wide shift in the English Channel with a decline in the abundance of small-bodied fish and increased abundance of larger-bodied fish (Auber et al., 2015). While temperature is often the focus of these regime shifts, the compounding effects of abiotic (such as such as ocean acidification, deoxygenation, and currents) and biotic (bottom-up trophic effects and changes in predation) factors play a crucial role in community reorganization (Gruber et al., 2021; Hauri et al., 2024; Olsen et al., 2024).

As of the late 1980s, multidecadal oscillation (e.g. PDO and NPGO) indices have become less representative of previously correlated physical-ecological processes (Litzow et al., 2020). In 2014-2019, climatic characteristics of anomalously high sea surface temperature and sea level pressure, increased acidity, and weakened offshore upwelling led to novel shifts in the trophic community (Bond et al., 2015; Litzow et al., 2020). In response to the heatwave, the quality, composition, and seasonal transition of the zooplankton community shifted (McKinstry et al., 2022), which in turn decreased forage fish quality and quantity (von Biela et al., 2019), leading to mass mortality events in marine predators (Arimitsu et al., 2021; Suryan et al., 2021). As anomalous climate events deviate from prior understandings of oscillatory climate processes, it is critical to better understand the influence of biotic and abiotic factors on forage fish and develop adaptive management strategies.

Assessments of the status of forage fish and research exploring the impact of bio-physical variables on spatial distribution require observations of occurrence or abundance at representative spatial and temporal scales. Typically, data collected by fisheries independent surveys are used to derive indices of abundance for marine species and quantify species' distribution, but data from surveys specifically indexing forage fish abundance in Alaska are limited in both their spatial resolution and temporal scale. Forage fish occupy the pelagic zone and form aggregated schools, which leads to a patchy distribution otherwise difficult to target without the use of survey gear designed for their capture (Fréon et al., 2005; McGowan et al., 2019). Additionally, forage fish populations exhibit high interannual variation and undergo "boom and bust" population cycles, with periodic collapse and recovery (Arimitsu et al., 2021; McClatchie et al., 2017; Soutar & Isaacs, 1969). Apart from Pacific herring, forage fish are not commercially targeted in Alaska, which results in limited funding for forage fish specific surveys (Piatt et al., 2018; Witherell et al., 2000). As a result, studies focused on indexing forage fish directly are usually short in duration (i.e. several years) or represent small spatial scales relative to the distribution of the stock, therein limiting the use of fisheries independent surveys for informing estimates of Alaskan forage fish distribution and temporal trends (Arimitsu et al., 2008; Siple et al., 2019). However, incidental catch of forage fish in surveys targeting other species including groundfish can also provide indices of abundance and encounter rate across longer temporal scales, but deriving inference from these data may be complicated by survey methods not designed to specifically sample pelagic fish species or the habitats occupied by forage fish (Cordue, 2007; Cunningham et al., 2018; Ormseth, 2014).

Deriving inference on forage fish dynamics within a region is often limited by a single survey's ability to accurately index forage fish occurrence, abundance, and distribution. For pelagic schooling fish, such as Pacific capelin (*Mallotus catervarius*) or Pacific herring (*Clupea pallasii*), such studies using a single data source have been limited by spatial coverage, temporal duration (annually or seasonally) and fisheries survey gear selectivity (McGowan et al., 2020). In the case of sand lance (*Ammodytes* spp.), benthic trawls often struggle to target the shallow, nearshore habitats where they burrow beneath the substrate (Robards et al., 2000; Szuwalski et al., 2023). While a fisheries-independent survey may be designed to broadly target forage species, it may still introduce biases towards particular age classes or species. In the Alaska Arctic, De Robertis et al., (2017) compared the catch of a larger-mesh midwater trawl and a smaller-mesh midwater trawl, and found a higher proportion of larger size classes of capelin in the larger mid-water trawl as opposed to the higher proportion of sand lance in the smaller mid-water trawl. Variation in the catchability among different survey gear types and mesh-sizes may result in misleading assessment of forage fish age-classes and community composition.

Integrating observations from multiple fisheries surveys employing different sampling gears provides a possible means of quantifying finer-scale spatial variation over an expanded spatial area, and extending temporal coverage among years or across seasons (Grüss et al., 2018; Grüss & Thorson, 2019; Pinto et al., 2019; Thompson et al., 2023). By integrating multiple data sources including fisheries surveys using different gear types, or considering occurrence observations within diets of groundfish and seabird predators, it may be possible to derive more precise estimates of interannual trends in occurrence and distribution for data limited species such as forage fish (Grüss et al., 2023; Piatt et al., 2018; Sydeman et al., 2022). However, differing catchability resulting from variation in survey design and gear type must be accounted for within statistical intercalibration methods (Ono et al., 2018). One approach is to estimate an index of encounter probability across time or space using multiple data sources from fisheries independent surveys and predator diet samples, while accounting for differences in catchability among survey and observation methods. By specifically controlling for inherent differences in catchability of forage fish species among alternative sources of abundance or occurrence data, spatiotemporal models can expand coverage and increase precision (Grüss et al., 2018; Grüss & Thorson, 2019; Thompson et al., 2023). In Alaska, integrated models have previously been applied to evaluate the influence of environmental variables on forage fish distribution (Gunther et al., 2023; McGowan et al., 2020; Piatt et al., 2018) and assess trophic stability in response to climate shifts (Arimitsu et al., 2021) and predator abundance (Barnes et al., 2020).

To account for spatial heterogeneity of forage species, spatially varying catchability (SVC) can be incorporated into species distribution models (SDMs). Spatial variability can arise when the catchability or detectability of the sampling method are inconsistent over space and time (Barnett et al., 2019; Grüss et al., 2023), while spatial heterogeneity in abundance can arise from responses to environmental processes or human disturbances (Barnett et al., 2019; Ward et al., 2022). As an example, habitat heterogeneity leads to variability in bottom trawl performance, as steep and rocky ocean floors alter escapement in bottom trawls (Baker et al., 2019; Somerton et al., 1999; Thorson et al., 2013). The incorporation of SVC's into integrated SDMs can improve assessments of distribution shifts over broad spatial extents by accounting for gear performance and fish movement out of detectable ranges (Barnett et al., 2019). In this way, accounting for both average differences in catchability and spatial variation in catchability among different data sources including different survey gears, or between survey observations and predator diets is imperative to accurately quantifying population trends in space and time.

In the Bering Sea, large-scale assessments of forage fish responses to abrupt region-wide, biophysical changes have been aided through the consistent interannual sampling by pelagic trawls in the eastern and northern Bering Sea since 2002 (Farley et al., 2005; Farley & Moss, 2009). Over a similar time horizon information on the incidental catch of forage fish NOAA groundfish bottom trawl surveys (NOAA-BTS) (Lauth, 2011; Markowitz et al., 2023), and corresponding groundfish stomach collections (Livingston et al., 2017) are available in the eastern Bering Sea and northern Bering Sea. However, significant gaps in spatial and temporal coverage of fisheries surveys indexing forage fish specifically remain limited. Further, comparable long-term, interannual surveys are absent from the Gulf of Alaska (GOA); Broad-scale analysis requires the standardization of datasets with less spatial-temporal overlap than that of the Bering Sea in order to understand the complex change in forage fish population dynamics and distribution (McGowan et al., 2020) and corresponding impacts of climatic regime shifts (Anderson & Piatt, 1999; Hare & Mantua, 2000).

Here we explore the potential to integrate data from multiple observation methods (i.e., data sources) for indexing forage fish occurrence across space and time, including fisheries surveys using different gear types (e.g. pelagic trawls, benthic trawls, and beach seines), and the diets of seabird and groundfish predators. The Alaska Forage Fish Database (AFFD; Turner et al., 2024) consolidates fisheries independent survey and predator diet data from multiple agencies. With the expansion of available forage fish occurrence and distribution data through a variety of sampling methods, the AFFD provides a means to expand the scale of assessment on a broader spatio-temporal basis. Specifically, we leverage SDMs integrating data from multiple sources to estimate temporal trends in the encounter probability and distribution of three forage fish species in the Bering Sea and Gulf of Alaska: Pacific capelin (hereafter “capelin”), Pacific herring (hereafter “herring”) and sand lance (hereafter “sand lance”). These three species are chosen based on their diverse life histories, habitats, and varying sensitivities to climate conditions. Capelin and herring are both migratory species that primarily reside offshore, migrating to nearshore environments to spawn (Arimitsu et al., 2008; Pahlke, 1985). Capelin are semelparous, meaning that they typically die shortly after spawning around age 2-3, whereas herring are longer-lived (11+ years) and reach maturity around age-3. Sand lance are non-migratory species that reside in shallow, fine gravel and sandy habitats. Sand lance reach maturity at age-2 (living up to 6 years) and spawn intertidally once per year (Robards et al., 2000). In terms of environmental sensitivities, capelin occurrence and distribution are influenced by temperature and temperature indexed changes to zooplankton (McGowan et al., 2019; Rose, 2005), while sand lance are generally more resilient to temperature fluctuations (Robards et al., 2000; Sydeman et al., 2017).

The three primary objectives for this study were: (1) to assess the extent of coherence in interannual trends of forage fish encounter probability estimated by models fit to survey and predator diet data, (2) to identify whether the overall encounter probability of Alaskan forage species differed among decadal climate stanzas, (3) to evaluate distributional shifts among decadal climate stanzas, and (4) to compare climate responses among forage fish species and between the Bering Sea and Gulf of Alaska regions.

3.3 Methods

3.3.1 Data

The Alaska Forage Fish Database (AFFD) is an Alaska-wide assemblage of fisheries survey data and predator diets indexing forage fish abundance and encounter (Turner et al., 2024). The AFFD includes data from trawl surveys (surface, midwater, and bottom trawls), nearshore sampling techniques (i.e. beach seines, purse seines, jigs, gill nets, cast nets), ichthyoplankton surveys, "incidental catch" and predator diets (e.g. groundfish and seabirds). Due to the diversity of a variety of sample designs among surveys and predator diet observations, the spatial coverage and temporal extent of forage fish abundance and occurrence data varies substantially among observation types. Metadata within the AFFD provides descriptions of the projects, associated sampling methods, and links to the published datasets from which the data were derived. Chapter 2 contains extensive information on the AFFD and in-depth descriptions of each dataset. Prior to analysis, data from the AFFD were filtered as to remove observations of larval, age-0, and YOY forage fish. When individual length and/or weight of a fish was provided, we filtered for capelin with a length > 70mm and weight > 0.7g. Sand lance adults were classified as lengths > 90mm and weight (g) > 0.8. We also include data in cases where age or individual morphological features were not recorded. Unspecified samples from large-mesh bottom trawls are unlikely to contain larval stages due to the large-mesh size of the sampling gear. Together these data provide the basis for analyses of juvenile and adult forage fish across the entirety of the western-central Gulf of Alaska and the northern and eastern Bering Sea.

3.3.2 Case studies

We use case studies of the eastern Bering Sea and Gulf of Alaska to compare model performance in broad regions with differing data availability. The Bering Sea has been sampled annually since 1980 by bottom trawl surveys conducted using a systematic (i.e., gridded) survey design, and since 2002 by several surface trawl surveys that utilized a gridded design but with interannual variation in the extent of survey coverage. In comparison, the survey observations within the Gulf of Alaska represent a variety of sampling methods employed with variable spatial and temporal overlap. Unlike the Bering Sea, the Gulf of Alaska lacks annual bottom trawl and surface trawl surveys that sample the majority of the region. Large scale surveys within the Gulf of Alaska have occurred biennially (triennially prior to 1999), or were downscaled in the 2000's. In addition to sampling design, both regions have unique oceanographic and bathymetric properties.

3.3.2.1 Eastern Bering Sea

The eastern Bering Sea is bounded in the south by the Aleutian Islands, in the north by the Bering Strait, in the east by the Alaska coastline and in the west along Russian coast continental shelf. It is characterized by a weakly stratified inner domain (0 – 50m depth), strongly stratified middle domain (50 – 100m deep), outer domain (100 – 200m deep), and slope (>200 m deep) (Stabeno et al., 2001). The northern Bering Sea (NBS), partitioned above 60° N, is characterized by "continuous winter sea ice cover", strong currents flowing north through the Bering Strait, as well as the influx of nutrients from the Yukon and Kuskokwim Rivers (Favorite, 1977). In the southeastern Bering Sea (SEBS), the sea-ice coverage fluctuates interannually, leading to high variability in water temperature (Favorite, 1977). The Bering Sea experiences variability on seasonal, interannual, and decadal scales driven by the Southern Oscillation and Pacific Northern atmospheric pressure patterns (Niebauer 1988) and has experienced drastic climate-change related shifts in recent years. The region is also influenced by the Aleutian Low (a pressure system from migration of storms from Aleutian Island chain,) which intensifies cyclonic wind in the winter and supplies nutrients through winter wind-mixing (Favorite, 1977; Ueshima et al., 2006). Variability in ice extent (which influences bottom temperature), along with wind-forced mixing, strongly impact productivity in the Bering Sea (Gunther et al., 2023; Hunt Jr et al., 2002; Overland & Stabeno, 2004). The range of our data for the Bering Sea has latitudinal coverage from 54.173 – 65.547 N°, and longitudinal coverage from 157.96 - 179.62W°.

To estimate the probability of encounter for the three focal forage fish species within the northern and eastern Bering Sea regions, we incorporated observations from three datasets: (1) The Bering Arctic Subarctic Integrated Survey (BASIS) surface trawls, (2) the NOAA Alaska Fisheries Science Center (AFSC) Groundfish Assessment Program (GAP) bottom trawl surveys (NOAA-BTS), and (3) groundfish stomach content data from the Resource Ecology and Ecosystem Modeling (REEM) sampling and analysis program collected during the AFSC GAP bottom trawl survey. The three sources of information are available annually via a gridded survey design.

BASIS has been conducted in the Bering Sea since 2002, with 30 minute pelagic trawls (Farley et al., 2005; Farley & Moss, 2009). A full description of methods can be found in Farley & Moss (2009). For the NOAA-BTS, the eastern (sampled annually 1982 – 2023; no survey 2020) and northern (sampled 1982, 1985, 1988, 1991, 2010, 2017 – 2022; no survey 2020) Bering Sea continental shelves are sampled along a 20x20 nautical mile grid (Markowitz et al., 2023) with a trawl duration of 30 minutes. The REEM groundfish stomach contents were collected during the AFSC-GAP bottom trawl survey in the EBS (1981 – 2019) and NBS (2010, 2017 – 2019). During each trawl, the stomach contents of individual groundfish were sampled based on species-specific length stratified design (Livingston et al., 2017). Due to the low sample size of groundfish stomach contents from 1981 – 1984, data from 1985 onwards is used to inform our Bering Sea models. Stomach contents were primarily extracted and analyzed from four groundfish species: Walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Arrowtooth flounder (*Atheresthes stomas*).

3.3.2.2 Gulf of Alaska

The Gulf of Alaska (GOA) is a basin in the North Pacific Ocean with complex habitats and conditions found across its narrow shelf and steep continental slope (20 – 250 km in width) (Baker et al., 2019; Lindeberg et al., 2022; Stabeno et al., 2004). It is characterized by inshore bays and inlets along the coast, high current flow channels, and course rocky substrate in the nearshore environment. The region is influenced by the Alaska Coastal current (ACC), and cyclonic subarctic Alaska Gyre, which in turn influence shelf circulation and transport of organic matter (Favorite, 1977). In addition, oceanographic changes in response to climate change, or on decadal scales from Pacific Decadal Oscillations (PDO), Pacific North American Oscillation (PNAO) and El Nino Southern Oscillation (ENSO), can cause major shifts in the primary productivity of the region (Hare & Mantua, 2000; Stabeno et al., 2004). Our analysis covers the western and central Gulf of Alaska with a latitudinal range from 52.4060 to 60.998 N° and longitudinal range from 141.5135 to 169.99 W°.

In comparison to the Bering Sea, available data for the Gulf of Alaska have more limited spatial and temporal overlap. For the Gulf of Alaska models, we utilized fisheries survey data collected via midwater trawls, bottom trawls, beach seines, as well as predator diets from groundfish and seabirds.

Midwater trawl data came from two sources: (1) the EcoFOCI program late-summer, small-mesh trawl survey (2001 – 2019), which sampled the western GOA in the Shelikof sea valley and areas surrounding Kodiak, and (2) the USGS Seabird Forage Fish Ecology Program (SFFEP)'s midwater trawls in Cook Inlet (sampled from 1995 – 1999 and 2016 – 2021), Prince Williams Sound (sampled from 2012 – 2022), and Glacier Bay (sampled 1999 – 2004). Beach seine data for the GOA obtained from the Nearshore Fish Atlas (NFA), a database of nearshore fish surveys developed by the NOAA Fisheries Alaska Regional Office and Alaska Fisheries Science Center's Auke Bay Laboratories (Alaska Fisheries Science Center, 2022).

Small-mesh bottom trawl data comes from the NMFS and ADF&G small-mesh shrimp trawl, which began annual systematic survey design in 1970 (Anderson & Gaffney, 1977), and switched to a smaller spatial scale by ADF&G in 2004 within Pavlof Bay (Jackson, 2007; Knutson, 2018). Surveys are conducted with a high-opening shrimp trawl towed between 0.4 – 5 meters above the sea floor (Anderson et al., 1995; Wathne, 1977). Bottom trawl data are available via the NOAA-BTS in the GOA (sampled triennially 1984, 1987, 1990, 1993, 1996, and biennially 1999 – 2023), which is surveyed using a stratified random sampling design and a trawl duration of 30-minutes prior to 1996 and 15 minutes after 1996.

Diets from forage fish predators include groundfish stomach contents from the REEM program sampled in the GOA (1981, 1987, 1990, 1993, 1996, 1999, 2001 – 2019 (odd)) in conjunction with the BTS (Livingston et al., 2017). Data from 1990 onward were included in the GOA model. Seabird diets were provided by The U.S. Fish and Wildlife Service Alaska

Maritime National Wildlife Refuge (FWS AMNWR) and The Gulf Watch Alaska program. We used diet data from 32 colonies in the GOA, collected between 1979 and 2021, to describe patterns in forage fish occurrence. Updated seabird diet data from Middleton Island through Gulf Watch Alaska's long term monitoring program are also available as a USGS data release (Hatch et al. 2023).

3.3.3 Decadal climate stanzas

Decadal stanzas were defined based on known climatic regime shifts, or abrupt transitions between climate states (Yasunaka & Hanawa, 2002, Overland et al., 2008). Examining changes in spatial distribution across decadal-scale stanzas allowed us to quantify the influence of climate regime shifts on forage fish encounter probability and distribution across space, in both the NBS/EBS and GOA. Quantifying spatial variation in forage fish encounter probability among climate stanzas rather than among individual years also helped to account for spatial-temporal imbalance in survey observations, which was most prevalent in the Gulf of Alaska, where the NOAA-BTS was conducted every three years until 1999 and on a biennial basis thereafter. Five stanzas were defined in the Gulf of Alaska and Bering Sea: 1977 – 1988, 1989 – 1998, 1999 – 2005, 2006 – 2013, and 2014 – 2019. The 1976/1977 regime change originated from a shift an intensified Aleutian Low, warmer water temperatures, and increased water column stability that persisted through the 1980's (Anderson & Piatt, 1999; Aydin et al., 2006; Francis et al., 1998; Hare & Mantua, 2000). A weaker regime shift occurred in 1988/1989, with the onset of a more average Aleutian Low, and cooler, more variable water temperatures (Aydin et al., 2006; Litzow, 2006). Effects of this shift continued until the 1998/1999 North Pacific, and 2000 Arctic, regime shifts led into anomalously warm climate conditions from 2001 – 2005 (Overland et al., 2012), and a concomitant decline in sea level pressure (Bond et al., 2003) and minimal sea-ice extent (Stabeno et al., 2012), corresponding with fluctuations in the El Nino/Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) (Bond et al., 2003). A shift occurred between 2006/2007, as conditions switched to below-average water temperatures and increased sea-ice extent (Stabeno et al., 2017), followed by the 2014-2016 marine heatwave and re-intensified warming in 2018 – 2019 (Arimitsu et al., 2021; Suryan et al., 2021).

3.3.4 Estimation models

To estimate the temporal trends and spatiotemporal distribution of each forage fish, we implemented two forms of binomial generalized linear mixed effects models (GLMM) with the sdmTMB package (Anderson et al., 2022). The package sdmTMB employs Stochastic Partial Differential Equation (SPDE), which explicitly estimates parameters representing spatial covariance using Gaussian random fields with a Matern function to describe spatial correlation as a function of distance between observations and prediction locations. Continuous random fields are approximated using a triangulated mesh (Lindgren et al., 2011) calculated with the INLA R package (Rue et al., 2009) with a cutoff (i.e., distance at which two points are no longer considered dependent) of 15km. In the Gulf of Alaska, a mesh barrier is applied to account for variable coastlines and islands.

Two alternative estimation model structures were implemented. A temporal model was used to explore smoothed among-year trends in encounter probability for each species within each region and evaluate whether different data sources predicted similar trends in occurrence across time. The spatio-temporal climate stanza model used the previously defined climate stanzas to represent variation across time and quantified change in both absolute encounter probability and spatial distribution among discrete climate stanzas, which was treated as the time reference. Both classes of models were fit to data from individual sources (e.g. fisheries survey data, seabird or groundfish predator diets), as well as an aggregated dataset of all individual sources. Each of the two model types accounted for absolute differences in catchability among data sources with a categorical effect of data source, and a spatially varying catchability (SVC) effect.

Variation in encounter probability among years, climate stanzas, and across space was quantified by fitting models to: (1) fisheries survey data, (2) groundfish stomach contents, (3) seabird diets, and (4) and integrated model including all data sources. For the fisheries survey model, data sources were aggregated up to: midwater trawls (USGS & EcoFOCI trawls), surface trawls (NOAA AFSC BASIS), small-mesh bottom trawls (ADF&G/NOAA shrimp trawl), large-mesh bottom trawls (NOAA BTS), and beach seines (NFA surveys aggregated up to "beach seine") and these aggregated data sources representing similar gear configuration categories were used to estimate average and spatially-varying differences in catchability.

For groundfish diets, we treated Walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Arrowtooth flounder

(*Atheresthes stomas*) as separate data sources to account for differences in diet preference, habitat, and life history. Similarly, we separated seabirds into categories of surface feeders (black-legged kittiwakes, *Rissa tridactyla*) and divers (horned puffin, *Fratercula corniculata,* tufted puffin, *Fratercula cirrhata*, and rhinocerous auklet, *Cerorhinca monocerata*). Seabird diet data for forage fish spatio-temporal assessment is only applied in the Gulf of Alaska, wherein seabird colonies are frequently sampled interannually and provide spatial coverage across the east-west gradient (Piatt et al., 2018). For spatial analysis in the Gulf of Alaska, seabird colonies are treated as spatially referenced observations under the assumption that the spatial location of the colony represents the forage fish population in that specific location. In the case of groundfish diets, within each survey tow, each individual predator is treated as an independent sample. This does not account for differences in predator length and weight, which can influence presence of prey species (Ng et al., 2021; Thompson, 2015), but permits a general description of forage fish encounters within diets of the forage fish of a species present at a given point in space and time. Because the model treats each individual predator as a separate sample, there are several samples taken at a single tow site, which may lead to pseudo-replication. Initial analysis explored aggregating encounter/non-encounter to the sampling event (i.e. survey tow) level by predator species to account for replication. However, aggregating to the event level resulted in model convergence failure, so groundfish predator diet data were used on a disaggregated basis for all analyses. Future studies could investigate the effects of pseudo-replication of predators within survey sampling events on integrated model estimates. To compare the probability of encounter during each climate stanza, we used the R package "visreg" (Breheny & Burchett, 2017). The package visualizes the change in encounter by stanza when all other variables are held constant. We examined the effect of decadal stanzas on the overall encounter rate for each species and region combination, and on estimated spatial variation in estimated encounter rate. To assess the influence of data source, we also compared the encounter by decadal stanza for models fit separately to fisheries survey data and groundfish diet data in order to assess coherence amongst models. Center of gravity (COG), i.e. the center of the population's distribution, has been used to evaluate the shifts in latitude and longitude during different decadal stanzas (Thorson et al., 2016). COG was calculated using the R package sdmTMB (Anderson et al., 2022) with the function "get_cog" . The latitudinal and longitudinal COG ($\bar{X}_{lat}$

and $\bar{X}_{lon}$) were calculated during each climate stanza for models fit to the integrated data sources with the following equations:

$$\bar{X}_{lat} = \frac{\sum_{i=1}^{n} p_i * Latitude_i}{\sum_{i=1}^{n} p_i}$$

$$\bar{X}_{lon} = \frac{\sum_{i=1}^{n} p_i * Longitude_i}{\sum_{i=1}^{n} p_i} \tag{3.1}$$

Where p_i is the probability of encounter of the species during the climate stanza k in sample i, n is the number of samples, and $Latitude_i$ and $Longitude_i$ are the latitude and longitude of sample i. Estimates of COG are compared between climate stanzas and overlaid on the gridded map of probability of encounter estimates.

To estimate trends in probability of encounter over time, we implemented a binomial model of the following form:

$$g\big(p(s_i, t_i)\big) = \beta(m_i) + f(t_i) + \zeta_m(s_i)$$

$$\zeta \sim MVNormal\,(0, \Sigma_\zeta) \tag{3.2}$$

Where p is the encounter (1) or non-encounter (0) for spatial location s during the year t for sample i, with a logit link function $g()$. The model includes data source (e.g. fisheries survey and predator diets) as a fixed effect $\beta(m_i)$ for data source m, and $f(t_i)$ is a penalized smoothing function for year t implemented using thin-plate splines (Wood, 2017). A spatially varying catchability (ζ_m) effect is specified as a Gaussian Markov random field following a multivariate normal (MVN) distribution, with covariance function Σ_ζ.

We estimated spatial trends in probability of encounter across climate stanzas using a binomial model of the following form:

$$g\big(p(s_i, k_i)\big) = \beta(m_i) + \alpha(k_i) + \zeta_m(s_i) + \varepsilon_k(s_i)$$

$$\zeta \sim MVNormal\,(0, \Sigma_\zeta)$$

$$\varepsilon \sim MVNormal\,(0, \Sigma_\varepsilon) \tag{3.3}$$

Where p is the probability of encounter (1) or non-encounter (0) and $g()$ is the logit link function. Site s_i is the sample i collection location, and k_i is the decadal stanza in which the sample i was collected. Data source $\beta(m_i)$ and decadal stanza $\alpha(k_i)$ effects are estimated as categorical fixed effects. The spatio-temporal (ε_k) (treated as independent and identically distributed (IID)), and spatially varying catchability (ζ_m) effects are specified as Gaussian Markov random fields following a multivariate normal (MVN) distribution. Spatially-varying catchability effects can help control for differences in catch efficiency among data sources (i.e., sampling methods) across space, while spatio-temporal effects describe among-climate stanza differences in the spatial distribution of encounter probability.

3.3.5 Model performance

We compared the performance of candidate model structures of varying complexity (i.e., those including different combinations of the explanatory variables described above) using percent deviance explained, and out-of-sample metrics including area under the curve (AUC) and 8-fold cross validation (Supplementary Table S3.1). Cross validation was performed using the function "sdmTMB_cv" from the R package "sdmTMB" (Anderson et al., 2022), and AUC was calculated with the package pROC (Robin et al., 2011). For cross-validation, data was randomly partitioned into testing and training datasets across eight folds, and models were fit to each of the eight training datasets and used to back predict the respective eight testing datasets. The sum of log-likelihoods (SLL) from the resulting eight subset models were used to compare performance between different model structures. We estimated predictive accuracy by calculating AUC from the pooled predictions across all cross-validation folds. An AUC < 0.5 indicates that the model performs worse than random chance. Models with an SLL closer to zero and AUC closer to one were considered the best performing models out-of-sample.

Within sample performance was calculated by estimating the percent deviance explained (i.e. variation in data explained by full model in comparison to null model) to assess goodness of fit. The null model is fit with an intercept (~1), without spatial, spatio-temporal, catchability, and SVC effects, written in the form:

$$Null: g\big(p(s_i, t_i)\big) = \alpha \tag{3.4}$$

Where p is the probability of encounter (1) or non-encounter (0), $g()$ is the logit link function, site s_i is the sample i collection location, and t_i is the time reference for sample i which may reflect the climate stanza k_i in the context of spatio-temporal models, and α is the average encounter probability in logit space. Deviances of the full and null models were calculated as:

$$D_{model} = -2 * \log(L_{model}) \tag{3.4}$$

Where the likelihood of the model given the data (L_{model}) is proportional to the probability of observing the data given the model prediction. The equation for percent of deviance explained is as follows:

$$DE = 100 * (1 - \frac{D_{model}}{D_{null}}) \tag{3.4}$$

In which $\boldsymbol{D_{model}}$ and $\boldsymbol{D_{null}}$ are the deviance of the full and null model, respectively. Resulting estimates of deviance explained are compared between models to assess performance.

3.4 Results

3.4.1 Model performance

Comparison of the within and out-of-sample predictive performance indicates that the inclusion of the spatially-varying catchability (SVC) effect in both temporal and spatio-temporal models, and climate regime associated spatiotemporal variation in the case of the spatio-temporal model, improved model performance (Table 3.1, Supplementary Tables S3.1, S3.2). All models converged when fit to data, except for the Bering Sea capelin spatio-temporal model with the SVC effect fit to groundfish diet data in isolation, which resulted in a non-positive definite Hessian matrix (Table 3.1).

For temporal models, the full model including the SVC effect had higher deviance explained and sum log-likelihood than alternative models across all species and region combinations, but a lower AUC, with some exceptions (Supplementary Table S3.1). There was lower out-of-sample performance for full SVC models fit to diet data (Bering Sea capelin, Bering Sea and GOA herring) and fisheries survey data (Bering Sea herring), and a lower within-sample performance for Bering Sea herring models fit to groundfish diet data alone (Supplementary Table S3.1). In the Gulf of Alaska, temporal SVC models fit to seabird diet data had much lower AUC values for herring (decreased by 0.11) and sand lance (decreased by 0.08) (Supplementary Table S3.1). For all species in the Bering Sea, candidate models fit to fisheries survey data alone had poor out-of-sample performance, with AUC values less than 0.7, and three or more of the eight subset cross-validation models not converging (Supplementary Table S3.1).

In the context of the spatio-temporal models, the full SVC model exhibited superior performance when fit to all data sources. The model had higher sum log-likelihood and percent deviance explained, and minimal differences in AUC, in comparison to models without an SVC effect (Supplementary Table S3.2). The SVC models fit to integrated data had an AUC greater than ~0.8, indicating good discriminative ability by the model (Table 3.1). Models fit to separate data sources had variable performance. In the Bering Sea, spatio-temporal models fit separately to fisheries survey data alone had poor out-of-sample performance (AUC < 0.7). The full SVC model fit to fisheries survey data also had lower AUC than the non-SVC (average spatial field effect) model for herring (decreased by 0.056) and sand lance (decreased by 0.029) (Supplementary Table S3.2) in the Bering Sea. The low within-sample performance of Bering Sea herring models fit separately to fisheries survey and groundfish diet data (across all candidate models) indicates poor explanatory power (Supplementary Table S3.2). For herring, poor performance of models fit to groundfish diets may be attributed to the absence of herring in walleye pollock diets, which are the most frequently sampled groundfish predator species.

3.4.2 Temporal trends

In the Bering Sea and GOA, the encounter probability predicted by models fit to groundfish diets exhibited greater variability over shorter time periods in comparison to models fit to fisheries surveys and/or seabird diets (Fig. 3.1). Despite interannual variation, substantial coherence in decadal trends can be seen amongst the models fit to fisheries survey, seabird diet, and groundfish diet data in isolation (Fig. 3.1).

3.4.2.1 Capelin

Across both the Bering Sea and GOA regions and models fit to different data sources, estimates for capelin all indicate an increased encounter probability in 2007 – 2013 and rapid decline in 2014 – 2016. In the case of Bering Sea capelin, estimates from models fit to fisheries survey and groundfish diet data share an increasing encounter probability during the 2006 – 2013 cold period, followed by a sharp decline in encounter going into the 2014 – 2016 marine heatwave (Fig. 3.1). However, the stark declines in encounter probability estimated in 1989, 1998, and 2006 by models fit to groundfish diet data in isolation were either not present in predictions from models fit to the fisheries survey data, or occur on a relatively smaller amplitude (Fig. 3.1).

Similarly, the predicted encounter probability for capelin in the Gulf of Alaska follows a strong boom-bust trend among years when estimated using groundfish diet data alone, that is much less prevalent in estimates from both fisheries survey and seabird diet models. Predictions for GOA capelin from models fit to both groundfish and seabird diet data show coherence in the increasing probability of encounter in the colder period (2006 – 2013), and a large decline following the heatwave in 2014 – 2016 (Fig. 3.1). While estimates from models fit to fisheries survey data exhibit some of these trends to a lesser degree (increased occurrence during the colder period and a decrease post heatwave), the addition of long-term (1972 – 2022) data from the small-mesh bottom trawl survey conducted by NOAA and the Alaska Department of Fish and Game into the fisheries survey data indicates that the 1977 regime shift caused a large-scale decline in the capelin encounter probability, from which the capelin have yet to fully recover (Fig. 3.1).

3.4.2.2 Herring

Predictions for herring in the Bering Sea appear to exhibit oscillating trends representative of a boom-bust cycle, with a time lag in the estimated cycle between models fit to fisheries survey and groundfish diet data (Fig. 3.1). While the trend is offset, estimates from both data sources exhibit a decline in encounter probability during the cooler 2006 – 2013 period, followed by an initial increase during the heatwave (Fig. 3.1). More recently, predictions from models fit to groundfish diet data show a decline in encounter probability beginning in 2017, whereas predictions based on fisheries survey data show a continued increase in encounter rate continuing into 2022 (Fig. 3.1).

For herring in the Gulf of Alaska, models fit separately to groundfish and seabird diets exhibit greater coherence when compared to predictions from models fit to fisheries survey data alone (Fig. 3.1). Diet models estimate the probability of encounter increasing with the onset of the 1999 regime shift, followed by a decline in the cooler 2007 – 2013 period, and increase with the 2014-2016 heatwave (Fig. 3.1). Predictions from fisheries survey models follow an asynchronous trend to the diet models, with a higher probability of encounter in the mid 1990's and a decreasing probability following the 1999 regime shift (Fig. 3.1). All three trends predict lower encounter rates during the 2006/2007 cool-period and increasing encounter probability during the 2014 – 2016 heatwave (Fig. 3.1). Encounter probability continues to rise after the 2014 – 2016 heatwave for estimates fit to groundfish diets and fisheries surveys, whereas seabird diets show a decreasing probability of encounter starting in 2017.

3.4.2.3 Sand lance

The predicted trends in encounter probability for sand lance in the Bering Sea show similar dynamics when estimated by either groundfish diet or fisheries survey data (Fig. 3.1). Sand lance encounter exhibits a decline in the 1980's, followed by an increase following the 1989 regime shift which peaks in the mid 1990's, and another decline coinciding with the beginning of the 1999 regime shift. Whereas the model fit to the fisheries survey data shows an increase after the warmer period in the early 2000's, the estimated encounter probability from the groundfish diet model continues to decline during this period. High relative probability of encounter is estimated in 2009 and 2011 from models fit to fisheries survey and groundfish diet data, respectively. Afterwards, models fit to fisheries survey data estimates of sand lance have continued to decline since 2009, whereas groundfish diet model estimates begin to increase in 2016.

In the case of GOA sand lance, all three models fit to separate data sources estimate high encounter probability around 2000 – 2001 (Fig. 3.1). However, models fit separately to seabird and groundfish diet data estimate an increase in encounter rate of sand lance following the onset of the 2014 heatwave, as well as a slight decline in encounter probability during the mid-1990s. While estimates from the model fit to fisheries survey also predict a high relative probability of encounter around 2000, there is not the same variability in encounter rate estimated from the presence of sand lance in the diets of either predator. Probability of encounter in years post 2020 shows a decreasing encounter probability in fisheries survey model estimates.

3.4.3 Decadal stanzas

Estimates of decadal climate stanza effects on encounter probability are generally consistent between models fit to groundfish diet and fisheries survey data (Fig. 3.2). Overall, coherence in estimated responses across forage fish species to decadal climate stanzas was most common for the 2014 – 2019 warm stanza. Although the 1999 – 2005 and 2014 – 2019 stanzas both encapsulating periods with anomalously high temperatures, encounter probabilities of the species showed a different response between the two stanzas (Fig. 3.2). Both models fit to fisheries survey and groundfish diet data predicted that sand lance in the GOA and capelin in the Bering Sea had higher encounter probability in response to 1999 – 2005, but lower encounter probability in 2014 – 2019. Herring in the GOA exhibited opposite climate stanza responses, with below average encounter rate in 1999 – 2005, but higher encounter rate estimated for 2014 – 2019 (Fig. 3.2). Model estimates from fits to fisheries surveys indicated minimal response to heatwaves for capelin in the Gulf of Alaska, which is likely due to the below-average encounter probability in 1977 – 1988 during which groundfish diet data are not available (Fig. 3.2).

In the Bering Sea, capelin show coherent changes among climate stanzas across models fit to fisheries survey or groundfish diet data, with lower occurrence during the 1980 – 1988 and 2014 – 2019 stanza, average occurrence from 1989 – 1999, and higher occurrence in 1999 – 2005 and 2006 – 2013 (Fig. 3.2). In the GOA, capelin climate stanza responses estimated by groundfish diet and fisheries survey data depict similar responses with intermediate encounter probability in 1989 – 1998 and 1999 – 2005, and above average encounter probability in 2006 – 2013 (Fig. 3.2). During the 2014 – 2019 stanza in the GOA, encounter probability for capelin was below average when estimated from groundfish diet data, whereas estimates based on fisheries survey data remains slightly above average relative to the low encounter probability estimated for the 1977 – 1988 stanza (Fig. 3.2).

For herring in the Bering Sea, the large confidence intervals and poor model performance (Table 3.1) for estimated decadal stanzas effect from models fit only to survey data suggest limited evidence from these data alone for among-stanza variation in encounter probability (Fig. 3.2). Predictions from models fit to groundfish diet data alone generally indicate lower encounter probability during climate stanzas within the 1980 – 1988 and 1989 – 1998 period and higher encounter probability during stanzas within the 1999 – 2019 periods (Fig. 3.2). Climate stanza effects show coherence for herring in all but the 2006 – 2013 period, where predicted relative encounter from groundfish diets is higher than that estimated from fisheries survey data (Fig. 3.2). Herring in the Gulf of Alaska are predicted to have exhibited average encounter probability during 1989 – 1998 decadal stanza, slightly below average within the warmer decadal stanza (1999 – 2005), but above average encounter probability during and after 2014 heatwave (Fig. 3.2).

Sand lance in the Bering Sea were predicted to have slightly below average encounter probability during the warmer period (2014 – 2019) and average encounter probability in 1989 – 1998, but show some evidence for contradictory temporal patterns between models fit to groundfish diet and fisheries survey data (Fig. 3.2). The encounter probability estimated by models fit to groundfish diet data are above average in 1999 – 2005 and below average in the colder years of 2006 – 2013, compared to those estimated by fisheries survey data (Fig. 3.2). The opposite response occurs in model estimates from fisheries survey data, in which encounter probability was estimated to be below average in 1999 – 2005 and above average in 2006 – 2013. In the GOA, the estimates of sand lance encounter probability from the groundfish diet and fisheries survey data sources exhibit coherent responses to climate stanzas, with a lower probability of encounter from 1977 – 1988, a higher probability during the 1999 – 2005 climate stanza, and a below average encounter probability during the 2014 – 2019 heatwave (Fig. 3.2).

3.4.4 Spatial distribution

Comparison of the predicted spatial distribution of encounter probability across decadal stanzas showed mixed responses to regime shifts (Fig 3.3, 3.4, 3.5). In the NBS, there are no data available in any survey during the 1989 – 1998 stanza, and groundfish diet collection in the NBS is limited to the years 2010 and 2017 – 2019. Because of this, COG has high uncertainty in the 1989 – 1998 period and distribution shifts in the NBS are unreliable for this period of the analysis, as they represent the average spatial distribution of encounter probability across stanzas for which observations were available in this region. Additionally, a majority of the 1977 – 1988 data comes from the ADF&G/NOAA small-mesh shrimp trawl, which sampled the WGOA around Kodiak. Spatial coverage is limited in the CGOA of this period and may not accurately inform forage fish distributions to the east of Kodiak Island or within Cook Inlet.

3.4.4.1 Pacific capelin

Model estimates for the spatial extent of capelin occurrence in the Bering Sea show this species to be primarily distributed within the Inner Domain (<50m depth) and extending further into the middle domain (50 – 100 m depth) in the northern Bering Sea (Fig 3.4). Persistent hot spots in occurrence are estimated around Cape Newenham across time (Fig. 3.4, 3.6). During the 2006 – 2013 cold period, the area of high encounter probability for capelin shifts further offshore in the eastern Bering Sea, with a higher encounter probability east of St. Matthew Island (Fig. 3.4, 3.6). The capelin distribution subsequently appears to contract inshore in the southeastern Bering Sea during anomalously higher temperatures from 2014 – 2019, with the highest encounter probability north of Cape Newenham, whereas the distribution of higher relative encounter probability does not appear to contract in the northern Bering Sea (Fig. 3.4, 3.6). During the 1999 – 2005 warm period, capelin are estimated to exhibit higher encounter probability further inshore of the Kotzebue Sound (Fig. 3.4, 3.6). Despite these apparent shifts in occurrence, estimated COG is relatively similar among stanzas (Fig. 3.3).

Gulf of Alaska capelin models fit to all data sources estimate inshore movement during periods of anomalously high temperatures. In terms of distributional shifts, in high temperature periods (1977 – 1988 and 2014 – 2019) capelin are estimated to have exhibited a higher encounter probability within Cook Inlet and its confluence with the Gulf of Alaska, whereas during colder periods (1989 – 1998, 2006 – 2013) the capelin distribution is predicted to extend offshore of Kodiak Island (Fig. 3.5, 3.7). During the 2014 – 2019 warmer period, capelin appear to have contracted inshore from the southern side of Kodiak Island, with lower estimated encounter probability east of Kodiak. Changes in the capelin COG indicates a south-western shift during the warm periods of 1977 – 1988 and 2014 – 2019, but not during the 1999 – 2005 warm period (Fig. 3.3).

3.4.4.2 Pacific herring

In the Bering Sea, the estimated encounter probability for herring does not show substantial differences among climate stanzas but has shifted north from the shores surrounding the Alaska Peninsula and Bristol Bay over time (Fig. 3.4, 3.6). The population generally tends to aggregate north of Nunivak Island, as evident from the higher predicted encounter probability in this region. In 2014 – 2019, herring estimates of encounter probability increase between St. Lawrence and the Gulf of Anadyr. Spatial predictions (Fig. 3.3) and COG analysis (Fig. 3.3) show that there appears to have been a northward shift over time.

Herring in the Gulf of Alaska are aggregated in central GOA surrounding Prince William Sound, and along the shore of Kodiak, Shelikof Strait, and Cook Inlet. During the heatwave, higher herring encounter probability is predicted offshore to the east of Kodiak Island (Fig 3.5). During decadal stanzas with cooler temperatures, the COG for herring is further north-east in the GOA (Fig. 3.3).

3.4.4.3 Sand lance (Ammodytes spp.)

Sand lance in the Bering Sea did not show noticeable shifts in their primary habitats within the inner domain of the eastern Bering Sea, and populations surrounding St. Lawrence (Fig. 3.4, 3.6). Integration of the groundfish diets into the model fit increases the probability of sand lance encounter surrounding the Pribilof Islands and in the northeast corner closest to Cape Navarin (Fig. 3.4, 3.6, Supplementary Fig. S3.4). Based on COG analysis, sand lance occurrence shifted towards the south-east following the 1989 regime shift and returned to the earlier 1977 – 1988 latitude following the cold period of 2007 – 2013. Following the 2014 – 2016 heatwave, sand lance COG shifted further north. Corresponding with the northern shift in COG is a hotspot around the western side of St. Lawrence.

Sand lance in the Gulf of Alaska are primarily encountered in Cook Inlet around Kachemak Bay, to the east of the Kodiak Archipelago, and in the sandy substrate in shallow waters off the Alaska Peninsula (Fig. 3.5, 3.7). Despite differences in encounter probability in response to stanzas (Fig. 3.2), the distribution of encounter probability predicted for sand lance generally suggests this species was found in the same habitats across climate stanzas, with marginal shifts in COG between stanzas (Fig. 3.3).

3.5 Discussion

3.5.1 Trends amongst models

Coherence in large-scale changes was found among estimated trends in encounter of forage fish within seabird diet, groundfish diet, and fisheries survey samples, for all species in the GOA and BS (Fig 3.1, Fig 3.2). Coherence was most apparent in species-specific responses to the marine heatwave in 2014 – 2016 (Fig 3.2), which emphasizes the scale of the impact seen across forage fish species independent of whether indexed by predator diets or fisheries surveys. In general, estimated trends in encounter probability from models fit to seabird and groundfish diet data were more consistent with each other than with estimates from fisheries survey data. However, estimates from models fit to groundfish diet data had greater interannual variability in comparison to those fit to survey and seabird diet data. This may be partly due to the low frequency of forage fish species in groundfish diets, especially herring. Capelin, herring, and sand lance are rarely eaten by most of the groundfish species sampled (e.g., walleye pollock and Pacific cod). While sand lance and capelin are more common in arrowtooth flounder and Pacific halibut diets, herring are rarely consumed (<1% of diets contained herring). The interannual variability in groundfish diets may also be amplified by prey switching dependent on the availability of lower or higher quality prey, giving potential bias to estimated prey encounter probability (Murdoch, 1969). In addition to seabirds, predators such as salmon and marine mammals could be considered as alternative sources of diet data where available.

The high encounter probability of capelin during the cold period (2006 – 2013) followed by the sharp decline in encounters during the 2014 – 2019 anomalously hot period aligns with previous literature describing negative capelin responses to heatwaves in the GOA and Bering Sea (Arimitsu et al., 2021; Ormseth & Yasumiishi, 2021; Szuwalski, 2022; Szuwalski et al., 2023). In comparing temporal trends in the EBS to previous literature, we found that the fluctuations in capelin probability of encounter estimated from groundfish diets (highs in 1993, 2004, and 2012), and coherent trends in low encounter probability of capelin during the mid to late 1990's, match inference described in prior analyses derived from NOAA-BTS data (Ormseth & Yasumiishi, 2021; Szuwalski et al., 2023). In the Gulf of Alaska, the probability of encounter estimated using groundfish diet data aligns closest with Szuwalski (2022) estimates using NOAA-BTS data. Results from models fit to groundfish and seabird diets suggest a record high in capelin encounter probability in response to the below-average temperatures from 2007 – 2013, similar to patterns previously documented from surveys and seabird diets (McGowan et al. 2020, Arimitsu et al. 2021). However, the inclusion of trawl data pre-1977 expands estimations of probability of encounter spanning from 1972 – 2022 in the GOA and suggests that capelin populations have yet to recover from the 1976/1977 regime shift. The severe decline in capelin during the late 1970's has been associated with warmer temperatures and increased water column stability due to a 1976/1977 PDO shift and intensified Aleutian Low (Anderson & Piatt, 1999; Piatt & Anderson, 1996). The estimated trends in encounter probability pre-1976/1977 regime shift emphasize the importance of long-term data in understanding species occurrence relative to that of historic records.

Trends in herring encounter probability were asynchronous among fisheries survey and diet data, until the synchronous increase in encounter probability during the 2014 – 2016 heatwave in both regions. In the Bering Sea, the estimated prevalence in NOAA- BTS data show highs in 1999 that align with our groundfish diet encounter probability estimates, as well as higher prevalence in the end of the 2002 – 2005 heatwave and 2014 – 2016 heatwave (Ormseth & Yasumiishi, 2021; Szuwalski et al., 2023). Validation of herring trends in encounter rate are more limited in the Gulf of Alaska, as most previous research has mostly been conducted at smaller regional scales. The trends in encounter probability we estimated by fitting to diet data in isolation align with previous estimates of herring encounters in predator diets from Burch (2023), which show a peak in the year 1990, highs in 2005, and an increasing population following the heatwave. The decline in herring during the early to mid-1990's is potentially driven by the collapse of herring stock in 1993 following the *Exxon Valdez* oil spill and fishery overexploitation (McGowan et al., 2021; Quinn et al., 2001). Recent increases in herring encounter follow the 2016 high recruitment year in Prince William Sound (McGowan et al., 2021).

Several factors may explain the offset temporal trends in herring encounter probability estimated by fisheries independent survey and diet data. One possible source of discrepancy is the ontogeny of groundfish, as diet compositions and spatial distributions shift with maturity (Gunther et al., 2023). Walleye pollock, Pacific cod, and Pacific halibut migrate from inshore, deeper offshore waters as they mature, while arrowtooth flounder move from the shelf break to the EBS slope (Barbeaux & Hollowed, 2018; Gunther et al., 2023). The estimates described here do not account for differences in predator age-class and size, or diet preference, which may influence encounter probability trends. Groundfish may also be consuming different age-classes of herring than those captured by trawl, which may contribute to trend asynchrony.

Sand lance trends are more difficult to estimate from surveys with large-spatial coverage (i.e., NOAA-BTS), due to the large mesh-size of the net along with burrowing behavior in nearshore, sandy habitats which may make sand lance unavailable to many survey gear types. In the Bering Sea, there are similar trends among the encounter rates estimated from groundfish diet and fisheries survey data for sand lance. Model predictions indicate higher encounter rates in the mid-1990s and 2010, as well as a high in 1980. While previous analysis of NOAA-BTS data for sand lance show similar trends they are highly variable among years (Szuwalski et al., 2023), which isn’t captured by our models due to the smoother applied to the annual temporal trend. High interannual variability was not as prevalent in prior analyses of groundfish diet data (Aydin et al., 2006), which align more closely with our results indicating a high probability of encounter during the mid-1990’s. Sand lance encounters in the Gulf of Alaska reach record highs between 2000 – 2003 in all individual model estimates. Similar highs around the year 2000 are also described in other analyses of GOA sand lance encounter in the diets of groundfish (Burch, 2023) and rhinoceros auklet (Hatch et al., 2021), and puffins (Sydeman et al., 2017).

Of the three estimates to individual data sources, current assessments of forage fish prevalence and abundance based with NOAA-BTS data (Ormseth & Yasumiishi, 2021; Szuwalski, 2022; Szuwalski et al., 2023) are more consistent with our encounter probability estimates based on groundfish diet data as the sole source. The similarities found between our estimates of encounter probability in groundfish diets and that of estimates from the EBS bottom trawl survey are likely driven by the concurrent sampling of groundfish stomachs at bottom trawl tow sites. Inclusion of surface trawls from BASIS in the Bering Sea, and a variety of surveys (beach seines, midwater trawls, small-mesh bottom trawls) in the Gulf of Alaska with NOAA-BTS data may dampen the decadal signals we see between our trends predicted from groundfish diets and reports estimated with NOAA-BTS data.

3.5.2 Climate response

3.5.2.1 Pacific capelin: Bering Sea

In the EBS, capelin are primarily found within the inner domain (<50m depth), while in the NBS capelin have greater distribution across domains ranging from 0 to 100 m depth (Fig 3.4). High concentrations of capelin in shallower depths of the well-mixed nearshore region align with previous findings (Parker-Stetter et al., 2013). During the warm decadal stanzas (1999 – 2005, 2014 – 2019), capelin encounters in the EBS appear to be further inshore, suggesting a contraction in distribution in response to warmer temperatures. The inshore shift in 2014 – 2019 corresponds with a sharp decrease in probability of encounter (Fig. 3.2). Expansion of capelin in the EBS during the warm years contrasts with Hollowed et al. (2012), who analyzed NOAA-BTS data and found that in warm years capelin were found further out into the middle shelf than in cold years. The results of our analysis suggesting a contraction of the capelin distribution in the EBS during warmer climate regimes aligns more with findings from prior studies leveraging surface trawl (BASIS) survey data (Andrews et al., 2016; Parker-Stetter et al., 2013). Andrews et al. (2016) suggests that the offshore distribution of capelin in the SEBS corresponds to the southern expansion of the Bering Sea cold pool identified in Hollowed et al. (2012). Despite contractions in the EBS distribution, the COG for capelin in the Bering Sea shows little change latitudinally or longitudinally in relation to climate stanzas. Our results from the integrated model fit to multiple sources of encounter data contrast previous literature using the BASIS surface trawls, which identified a northward shift in response to above average temperatures (Andrews et al., 2016; Yasumiishi et al., 2020). Comparison of the distributions predicted from model fits to individual data sources suggest northward contractions based on survey data, while an opposing distribution shift is evident in the groundfish diet data (Supplementary Fig. S3.3). Discrepancies in distributions may be attributed to capelin shifting deeper into the water column in response to the anomalously high temperatures of 2014-2019 (Methven & Piatt, 1991). A change in capelin vertical distribution could lead to the surface trawl catching fewer capelin in the SEBS, while simultaneously making capelin more readily available as prey to groundfish (McGowan et al., 2019). Other studies found areas of high capelin occurrence primarily in the NBS during warm periods, with distributions further south during the 2006 – 2013 cool periods (Andrews et al., 2016; Ciannelli & Bailey, 2005; Yasumiishi et al., 2020). While our predictions estimated from groundfish diets alone indicate an absence of latitudinal shift in response to the 2014 – 2019 warm period, Gunther et al. (2023) found significant northward movement of capelin during this period when estimates were based on the same groundfish species diet data. Given the limited groundfish diet data availability in the NBS (2010, 2017, and 2019), our decadal predictions of distribution may inaccurately capture latitudinal shifts across the entire EBS.

3.5.2.2 Pacific capelin: Gulf of Alaska

In the Gulf of Alaska, capelin are predicted to aggregate around Kodiak Island, Cook Inlet and offshore of Prince William Sound and the Alaska peninsula, similar to previous assessments of core habitats (McGowan et al., 2020; Ormseth, 2014). During the cooler periods (1989 – 1998, 2006 – 2013), spatial predictions show distinct hot spots offshore of Kodiak Island (Fig. 3.5, 3.7). The increased occupation of capelin in the Kodiak shelf corresponds with a higher encounter probability of capelin during the 2006 – 2013 cool period (Fig. 3.2, 3.5). In their description of GOA forage fish distribution, Ormseth (2014) describe a similar distribution for this species offshore of Kodiak between 2001 – 2011 when estimated based on NOAA-BTS data. In 2014 – 2019, the capelin range contracted inshore while the encounter probability declined simultaneously (Fig 3.2, 3.5). The northeastern shift estimated in the COG during the 2006 – 2013 cool period (Fig. 3.3) is supported by similar findings from McGowan et al. (2019). Specifically, McGowan et al. (2019) found that capelin shifted northeast towards the Kodiak Archipelago in cold years, and suggested that warmer temperatures at higher latitudes in the CGOA shelf may have increased capelin presence along the CGOA shelf in cold years due to thermal preference or biotic factors. During the 2014 – 2019 marine heatwaves, the drastic decline in capelin encounter probability in the Kodiak Shelf, a crucial foraging habitat for marine predators, may have contributed to the subsequent mass mortality event in predators (McGowan et al., 2019). It is difficult to discern how the compounding effects of temperature tolerance, water column stratification, larval dispersion, predator avoidance and prey availability influence the habitat shifts of capelin in the WCGOA. In general, capelin concentrate in areas with increased vertical mixing that provide greater prey abundance (Arimitsu et al., 2008; McGowan et al., 2021). In addition to the warmer temperatures in the GOA continental shelf during the 2014 – 2019 period, the occurrence of weakened offshore upwelling from a weaker cyclonic circulation may have limited prey abundance and driven capelin populations further inshore (Hauri et al., 2024).

3.5.2.3 Pacific herring: Bering Sea

Overall, herring within the Bering Sea were predicted to be encountered across both middle and inner domains (Fig. 3.4, 3.6). Herring were found to have higher encounter probability in the areas surrounding Bristol Bay and around Nunivak Island but were generally broadly distributed in space. The predicted distribution of herring during the 1980 – 1988 climate stanza was found to be much more spatially heterogenous when compared with other climate stanzas. While the patchiness in data during the 1980 – 1988 stanza could be attributed to limited spatial coverage of the NBS in the NOAA-BTS and fewer groundfish diet samples, the concentrated distribution of herring between St. Matthews and Nunivak Island align with distributions of herring from Brodeur et al. (1999) in 1986 and 1987.

The distribution of herring in the Bering Sea does not indicate pronounced shifts in response to climate stanzas but does show a northern shift over time irrespective of warmer and cooler periods (Fig 3.3, Fig 3.4). Across time the predicted probability of encounter for herring shifted north of Bristol Bay and expanded further offshore in the NBS (Fig 3.4, 3.6). The COG of herring shifted northwest following the 2006 – 2013 cool period (Fig. 3.3), and distributions slightly further offshore in the 2014 – 2019 warm period (Fig 3.3, 3.4, 3.6). Previous research has found contradictory responses of herring distribution to the effects of sea surface temperature. In an analysis of herring distributional shifts from 2002 – 2018 Yasumiishi et al. (2020) found no evidence of range expansion or northward movement of herring across time or response to sea surface temperature. Gunther et al. (2023) found a significant longitudinal shift between warm and cool temperature stanzas in groundfish diets, a more dispersed distribution and higher presence in groundfish diets during warm years, and a more aggregated distribution within the inner and middle domain during cooler years. In comparison, our predictions suggest a patchier, concentrated distribution during the 1980 – 1988 climate stanza that disperses in 1999 – 2005. In the Bering Sea, Brodeur et al. (1999) found a westward shift in herring distribution between 1986 and 1987, in which a concentrated population of herring between St. Matthews and Nunivak island in 1986 (colder year) shifted west of St. Lawrence in 1987 (warmer year). Brodeur's work implies migration shifts on an interannual scale, which may not be captured through our decadal evaluation.

3.5.2.4 Pacific herring: Gulf of Alaska

In the Gulf of Alaska, herring are found predominantly in the CGOA in waters within and surrounding Prince William Sound (PWS), while smaller populations reside in Shelikof Strait and within Cook Inlet, particularly in Kamishak Bay (Fig. 3.5, 3.7). Similar distributions were found in Piatt et al. (2018), with a majority of herring around Seal Island (within PWS) and Middleton Island (offshore of PWS outflow) and a very small population at Suklik Island (south-west of Kodiak near the lower end of Shelikof Strait). The low presence of herring offshore of Kodiak Island aligns with results from McGowan et al. (2019), who did not observe herring in 2011 and 2013 in acoustic-trawl surveys within CGOA between the southeast of Kodiak Island and the mouth of Amatuli Trough. In our predictions of herring distributional shifts, there is a distinct south-western shift in response to warmer temperatures. Herring encounter rates increase (Fig. 3.1, Fig. 3.2) from 2014 – 2019, coinciding with an increased probability of encounter offshore, a greater presence in the Alaska Peninsula, and a concentrated hotspot offshore of PWS (Fig. 3.5, 3.7). While spawning in PWS initially declined in response to the heatwave (Arimitsu et al., 2021; McGowan et al., 2021), herring recruitment in PWS increased substantially in 2016. Observed distribution shifts may signal changes in offshore migration patterns, as herring migrate across the GOA shelf post-spawn in June and return to the spawning grounds in the fall (September-October) (Bishop & Eiler, 2018). While incorporating multiple data sources can improve our understanding of larger-scale changes in the distribution of herring, it may not encapsulate the small-scale complexities within herring metapopulations (Okamoto et al., 2020). Therefore, results should be interpreted with caution given the local complexities in herring dynamics.

3.5.2.5 Sand lance (Ammodytes spp.): Bering Sea

Sand lance occurred primarily within the shallower inner domain (<50 m in depth) across the coastal waters of the EBS, consistent with their expected habitat preference for shallow, sandy substrate (Ostrand et al., 2005; Reay, 1970; Robards et al., 2002). With the addition of groundfish diet data to inform the model, we estimated higher encounter probability offshore with shallow 50m isobaths around the St. Matthews and the Pribilof Island that were otherwise not observed in the predicted distribution from models fit to survey data in isolation (Supplementary Fig. S3.7).

The northern shift during the 2014 – 2019 period could potentially be linked to the warmer 2018 – 2019 years in the northern Bering-Chukchi Sea. Arctic sand lance exhibited a dramatic northern shift in response to warming temperatures in that region (Axler et al., 2023; Baker et al., 2022). Shifts in Pacific sand lance into Arctic waters have been observed recently in the Canadian Arctic Archipelago, with increasing densities between 2011 and 2016 observed by local Inuit harvesters and sampling via oblique tows and beam trawls (Falardeau et al., 2017).

3.5.2.6 Sand lance (Ammodytes spp.): Gulf of Alaska

Sand lance distributions show similarities to the presence estimates around the Alaska Peninsula reported by Piatt et al. (2018), which were based on tufted puffin diets, as well as a combined index from NOAA-BTS, groundfish diets, and beach seines. Sand lance probability of occurrence was found to be high in Kachemak Bay, along the Kodiak Archipelago, and in the waters off and surrounding Unimak Island and Semidi Bank (Robards et al., 2002). As a non-migratory species, the distribution of adult sand lance is confined to sandy habitats (Ostrand et al., 2005; Robards et al., 2002), which aligns with our findings of minimal distributional changes in response to climate stanzas. In the Gulf of Alaska, sand lance have been shown to change in response to water temperature and productivity shifts, and tend to prefer warmer temperatures than capelin and herring (Robards et al., 2000). However, Sydeman et al. (2017) found local differences in response to environmental shifts, complicating the interpretation of results. Sand lance recruitment in relation to temperature has been characterized as a "dome-shaped", where recruitment declines during periods with extreme lows or highs in temperature (Bertram et al., 2001; Sydeman et al., 2017). This provides an explanation for the higher encounter in the warm 1999 – 2005 stanza and low encounter in the warmer 2014 – 2019 stanza. The El Nino period of 1997/1998 may be responsible for the increase in adult sand lance around 2000 – 2002 (Abookire & Piatt, 2005; Litzow et al., 2000). Sand lance failed to recover from declines in the cold 2007 – 2013 period despite increased temperatures in 2014 – 2016, potentially due to anomalously high temperatures in the heatwave exceeding a temperature threshold (von Biela et al. 2019).

3.5.3 General conclusions

Based on our findings, predator diets capture major shifts in probability of encounter that help validate trends observed in estimates derived from fisheries survey data. Improvements in model performance by accounting for spatially-varying catchability in the Gulf of Alaska indicate the importance of accounting for spatial heterogeneity in the efficiency of different sampling methods in regions with limited data overlap in space and time, and fundamental differences in the ability of different species or gears to sample the target species across space. Our study presents an initial step in accounting for the heterogeneity of data in the Gulf of Alaska to define larger-scale spatial patterns. Given the interspecific schooling of forage fish and asynchronous trends, future studies could explore the implementation of a joint species distribution model to account for patterns in co-occurrence (Thorson, Ianelli, et al., 2016).

The high encounter probability of capelin pre-1977 emphasizes the importance of long-term perspectives on fish population recovery. In terms of long-term data, fisheries-independent surveys are relatively limited compared to the knowledge of forage fish from local and traditional knowledge (LTK), as well as archaeological, historical, and biological data. A synthesis of these data sources was applied in research from the Herring Synthesis Project (https://uas.alaska.edu/research/herringsynthesis/index.html), which suggests that herring stocks in Southeast Alaska are in a depleted state, as the population has yet to recover from the commercial fisheries overharvest that began in the late 1800s (Thornton et al., 2010). The project's results provide crucial information on anthropogenic and environmental changes affecting herring and identifies areas critical to herring spawning, highlighting the importance of combined cultural, historical, and spatial knowledge to inform sustainable management strategies.

The causes of discrepancy amongst our models fit to fisheries survey and diet data may be due to several factors. To improve model convergence, we did not account for differences in age-classes of predators, and treated predator samples from the same trawl as independent. Future research should consider the potential biases associated with these assumptions and explore the impacts of such assumptions on model predictions. There are additional caveats in the use of seabird colony diets for spatial analysis. Our analysis operates under the assumption that the spatial location of the colony represents the forage fish population in that specific location. The seabird colony is treated as a spatially referenced observation, but foraging behavior and locations of prey can drive seabirds to consume forage fish across regions that are tens to even hundreds of km from the colony. In comparison, fisheries survey and groundfish stomach collections are collected at a specific location. Despite the spatial limitations of seabird colonies, the estimated distribution of each species did not appear to cause persistent highs or lows in encounter probability localized around the colonies. The inclusion of spatially varying catchability may aid in accounting for heterogenous seabird foraging distances at different colonies. Additional research on the application of seabirds in spatial estimates across time would help to identify potential benefits for filling in temporal gaps, as well as associated biases in localized encounter probability estimates.

In terms of environmental influences, the driving mechanisms behind forage fish population dynamics in response to regime shifts warrant further research, as temperature can act as a proxy of compounding effects. Changes from regime shifts in water stratification, large scale ocean circulation, and salinity (amongst others) may all play a role in what causes rapid changes in occurrence or distribution of forage fish populations. Our research highlights the region-wide impacts of climatic regime shifts on key forage fish in Alaska and stresses the importance of continued research on the many biotic and abiotic factors influencing forage fish population dynamics.

3.6 References

Abookire, A., & Piatt, J. (2005). Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. *Marine Ecology Progress Series*, *287*, 229–240. https://doi.org/10.3354/meps287229

Alaska Fisheries Science Center. (2022). *AFSC/ABL: Nearshore Fish Atlas of Alaska*. https://www.fisheries.noaa.gov/inport/item/17274

Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M. T. G., Slotte, A., & Tsikliras, A. C. (2014). Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. *Journal of Marine Systems*, *131*, 21–35. https://doi.org/10.1016/j.jmarsys.2013.11.002

Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., O'Driscoll, K., Vorberg, R., & Wagner, C. (2012). Climate variability drives anchovies and sardines into the North and Baltic Seas. *Progress in Oceanography*, *96*(1), 128–139. https://doi.org/10.1016/j.pocean.2011.11.015

Anderson, P. J., Blackburn, J. E., Bechtol, W. R., & Piatt, J. F. (1995). Synthesis and Analysis Gulf of Alaska of Small-Mesh Trawl Data 1953 to 1998. *Exxon Valdez Oil Spill Restoration Project Report, Restoration Project (APEX) 96163L.*

Anderson, P. J., & Gaffney, F. G. (1977). Shrimp of the Gulf of Alaska. *Alask Seas Coasts*, *5*(3), 1–3. Alaska Sea Grant Coll. Prog., Univ. Alaska, Fairbanks.

Anderson, P. J., & Piatt, J. F. (1999). Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series*, *189*, 117–123. https://doi.org/10.3354/meps189117

Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. K. (2022). sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields. *bioRxiv*. https://doi.org/10.1101/2022.03.24.485545

Andrews, A. G., Strasburger, W. W., Farley, E. V., Murphy, J. M., & Coyle, K. O. (2016). Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *134*, 235–246. https://doi.org/10.1016/j.dsr2.2015.10.008

Arimitsu, M. L., Piatt, J. F., Hatch, S., Suryan, R. M., Batten, S., Bishop, M. A., Campbell, R. W., Coletti, H., Cushing, D., Gorman, K., Hopcroft, R. R., Kuletz, K. J., Marsteller, C., McKinstry, C., McGowan, D., Moran, J., Pegau, S., Schaefer, A., Schoen, S., … von Biela, V. R. (2021). Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology*, *27*(9), 1859–1878. https://doi.org/10.1111/gcb.15556

Arimitsu, M. L., Piatt, J. F., Litzow, M. A., Abookire, A. A., Romano, M. D., & Robards, M. D. (2008). Distribution and spawning dynamics of capelin (Mallotus villosus) in Glacier Bay, Alaska: A cold water refugium. *Fisheries Oceanography*, *17*(2), 137–146. https://doi.org/10.1111/j.1365-2419.2008.00470.x

Auber, A., Travers-Trolet, M., Villanueva, M. C., & Ernande, B. (2015). Regime Shift in an Exploited Fish Community Related to Natural Climate Oscillations. *PLOS ONE*, *10*(7), e0129883. https://doi.org/10.1371/journal.pone.0129883

Axler, K. E., Goldstein, E. D., Nielsen, J. M., Deary, A. L., & Duffy-Anderson, J. T. (2023). Shifts in the composition and distribution of Pacific Arctic larval fish assemblages in response to rapid ecosystem change. *Global Change Biology*, *29*(15), 4212–4233. https://doi.org/10.1111/gcb.16721

Aydin, K., Boldt, J., Gaichas, S., & Ianelli, J. (2006). In: Boldt J (ed) Ecosystem considerations for 2007. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, 24–89.

Baker, M. R., De Robertis, A., Levine, R. M., Cooper, D. W., & Farley, E. V. (2022). Spatial distribution of arctic sand lance in the Chukchi Sea related to the physical environment. *Deep Sea Research Part II: Topical Studies in Oceanography*, *206*, 105213. https://doi.org/10.1016/j.dsr2.2022.105213

Baker, M. R., Palsson, W., Zimmermann, M., & Rooper, C. N. (2019). Model of trawlable area using benthic terrain and oceanographic variables—Informing survey design and habitat maps in the Gulf of Alaska. *Fisheries Oceanography*, *28*(6), 629–657. https://doi.org/10.1111/fog.12442

Barbeaux, S. J., & Hollowed, A. B. (2018). Ontogeny matters: Climate variability and effects on fish distribution in the eastern Bering Sea. *Fisheries Oceanography*, 27(1), 1–15. https://doi.org/10.1111/fog.12229

Barnes, C. L., Beaudreau, A. H., Dorn, M. W., Holsman, K. K., & Mueter, F. J. (2020). Development of a predation index to assess trophic stability in the Gulf of Alaska. *Ecological Applications*, *30*(7), e02141. https://doi.org/10.1002/eap.2141

Barnett, L. A. K., Ward, E. J., Jannot, J. E., & Shelton, A. O. (2019). Dynamic spatial heterogeneity reveals interdependence of marine faunal density and fishery removals. *Ecological Indicators*, *107*, 105585. https://doi.org/10.1016/j.ecolind.2019.105585

Benson, A. J., & Trites, A. W. (2002). Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. *Fish and Fisheries*, *3*(2), 95–113. https://doi.org/10.1046/j.1467-2979.2002.00078.x

Bertram, D. F., Mackas, D. L., & McKinnell, S. M. (2001). The seasonal cycle revisited: Interannual variation and ecosystem consequences. *Progress in Oceanography*, *49*(1–4), 283–307. https://doi.org/10.1016/S0079-6611(01)00027-1

Bishop, M. A., & Eiler, J. H. (2018). Migration patterns of post-spawning Pacific herring in a subarctic sound. *Deep Sea Research Part II: Topical Studies in Oceanography*, *147*, 108–115. https://doi.org/10.1016/j.dsr2.2017.04.016

Bond, N. A., Overland, J. E., Spillane, M., & Stabeno, P. (2003). Recent shifts in the state of the North Pacific. *Geophysical Research Letters*, *30*(23). https://doi.org/10.1029/2003GL018597

Breheny, P., & Burchett, W. (2017). Breheny P and Burchett W (2017). Visualization of Regression Models Using visreg. *The R Journal*, *9*, 56–71.

Brodeur, R. D., Wilson, M. T., Walters, G. E., & Melnikov, I. V. (1999). *Forage Fishes in the Bering Sea: Distribution, Species Associations, and Biomass Trends.*

Burch, C. (2023). *Temperature Effects on Spatiotemporal Patterns of Forage Fish and Crustaceans in Gulf of Alaska Groundfish Diets* [Master's thesis, University of Washington]. https://www.proquest.com/docview/2864087631?fromopenview=true&pq-origsite=gscholar

Ciannelli, L., & Bailey, K. (2005). Landscape dynamics and resulting species interactions: The cod-capelin system in the southeastern Bering Sea. *Marine Ecology Progress Series*, *291*, 227–236. https://doi.org/10.3354/meps291227

Cordue, P. L. (2007). A note on non-random error structure in trawl survey abundance indices. *ICES Journal of Marine Science*, *64*(7), 1333–1337. https://doi.org/10.1093/icesjms/fsm134

Cunningham, J., Elliott, K., Cottenie, K., Hatch, S., & Jacobs, S. (2018). Individual foraging location, but not dietary, specialization: Implications for rhinoceros auklets as samplers of forage fish. *Marine Ecology Progress Series*, *605*, 225–240. https://doi.org/10.3354/meps12761

Cury, P. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. https://doi.org/10.1006/jmsc.2000.0712

De Robertis, A., Taylor, K., Williams, K., & Wilson, C. D. (2017). Species and size selectivity of two midwater trawls used in an acoustic survey of the Alaska Arctic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *135*, 40–50. https://doi.org/10.1016/j.dsr2.2015.11.014

Falardeau, M., Bouchard, C., Robert, D., & Fortier, L. (2017). First records of Pacific sand lance (Ammodytes hexapterus) in the Canadian Arctic Archipelago. *Polar Biology*, *40*(11), 2291–2296. https://doi.org/10.1007/s00300-017-2141-0

Farley, E. V., & Moss, J. H. (2009). Growth Rate Potential of Juvenile Chum Salmon on the Eastern Bering Sea Shelf: An Assessment of Salmon Carrying Capacity. *North Pacific Anadromous Fish Communication Bulletin*, *5*, 265–277.

Farley, E. V., Murphy, J. M., Wing, B. W., Moss, J. H., & Middleton, A. (2005). Distribution, Migration Pathways, and Size of Western Alaska Juvenile Salmon Along the Eastern Bering Sea Shelf. *North Pacific Anadromous Fish Communication Bulletin*, *11*(1), 15–26.

Favorite, F., Laevastu, T., & Straty, R. R. (1977). Oceanography of the Northeastern Pacific Ocean and Eastern Bering Sea, and relations to various living marine resources. Northwest and Alaska Fisheries Center Processed Report, *U.S. Department of Commerce.*

Francis, R. C., Hare, S. R., Hollowed, A. B., & Wooster, W. S. (1998). Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fisheries Oceanography*, *7*(1), 1–21. https://doi.org/10.1046/j.1365-2419.1998.00052.x

Fréon, P., Cury, P., Shannon, L., & Roy, C. (2005). Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulletin Of Marine Science*, *76*(2).

Gruber, N., Boyd, P. W., Frölicher, T. L., & Vogt, M. (2021). Biogeochemical extremes and compound events in the ocean. *Nature*, *600*(7889), 395–407. https://doi.org/10.1038/s41586-021-03981-7

Grüss, A., Drexler, M. D., Ainsworth, C. H., Babcock, E. A., Tarnecki, J. H., & Love, M. S. (2018). Producing Distribution Maps for a Spatially-Explicit Ecosystem Model Using Large Monitoring and Environmental Databases and a Combination of Interpolation and Extrapolation. *Frontiers in Marine Science*, *5*, 16. https://doi.org/10.3389/fmars.2018.00016

Grüss, A., & Thorson, J. T. (2019). Developing spatio-temporal models using multiple data types for evaluating population trends and habitat usage. *ICES Journal of Marine Science*, *76*(6), 1748–1761. https://doi.org/10.1093/icesjms/fsz075

Grüss, A., Thorson, J. T., Anderson, O. F., O'Driscoll, R. L., Heller-Shipley, M., & Goodman, S. (2023). Spatially varying catchability for integrating research survey data with other data sources: Case studies involving observer samples, industry-cooperative surveys, and predators as samplers. *Canadian Journal of Fisheries and Aquatic Sciences*, cjfas-2023-0051. https://doi.org/10.1139/cjfas-2023-0051

Gunther, K., Baker, M., & Aydin, K. (2023). Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea. *Marine Ecology Progress Series*, *SPF2*. https://doi.org/10.3354/meps14389

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography*, *47*(2), 103–145. https://doi.org/10.1016/S0079-6611(00)00033-1

Hatch, S. A., Arimitsu, M. L., & Piatt, J. F. (2021). Seabird-Derived Forage Fish Indicators from Middleton Island. *Cosystem Status Report 2021: Gulf of Alaska, Stock Assessment and Fishery Evaluation Report*, 94–98.

Hatch, S. A., Arimitsu, M. L., Piatt, J. F., Shannon, W., & Marsteller, C. E. (2023). Seabird Diet Data Collected on Middleton Island, Gulf of Alaska. *U.S. Geological Survey Data Release*. https://doi.org/10.5066/P93I0P67

Hauri, C., Pagès, R., Hedstrom, K., Doney, S. C., Dupont, S., Ferriss, B., & Stuecker, M. F. (2024). More Than Marine Heatwaves: A New Regime of Heat, Acidity, and Low Oxygen Compound Extreme Events in the Gulf of Alaska. *AGU Advances*, *5*(1), e2023AV001039. https://doi.org/10.1029/2023AV001039

Hollowed, A. B., Barbeaux, S. J., Cokelet, E. D., Farley, E., Kotwicki, S., Ressler, P. H., Spital, C., & Wilson, C. D. (2012). Effects of climate variations on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *65–70*, 230–250. https://doi.org/10.1016/j.dsr2.2012.02.008

Hunt Jr, G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M., & Bond, N. A. (2002). Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(26), 5821–5853. https://doi.org/10.1016/S0967-0645(02)00321-1

Jackson, D. R. (2007). Trawl survey of shrimp and forage fish in Alaska's Westward Region, 2006. *Alaska Department of Fish and Game, Fishery Management Report No. 07-13*.

Knutson, M. (2018). Special project plan: 2018 large-mesh bottom trawl survey of crab and groundfish for Kodiak, Chignik, South Peninsula, and Eastern Aleutian districts. *Alaska Department of Fish and Game, Regional Information Report 4K18-07, Kodiak.*

Lauth, R. R. (2011). Results of the 2010 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. *NOAA Tech Memo NMFS-AFSC, 227*. https://repository.library.noaa.gov/view/noaa/3852

Lindeberg, M. R., Baker, M., Dickson, D. M. S., Kimmel, D. G., Ormseth, O. A., Strom, S. L., & Suryan, R. M. (2022). Long-term monitoring and integrated research – Understanding ecosystem processes in the Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, *206*, 105208. https://doi.org/10.1016/j.dsr2.2022.105208

Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between Gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(4), 423–498. https://doi.org/10.1111/j.1467-9868.2011.00777.x

Litzow, M. A. (2006). Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/1977? *ICES Journal of Marine Science*, *63*(8), 1386–1396. https://doi.org/10.1016/j.icesjms.2006.06.003

Litzow, M. A., Piatt, J. F., Abookire, A. A., Prichard, A. K., & Robards, M. D. (2000). Monitoring temporal and spatial variability in sandeel (Ammodytes hexapterus) abundance with pigeon guillemot (Cepphus columba) diets. *ICES Journal of Marine Science*, *57*(4), 976–986. https://doi.org/10.1006/jmsc.2000.0583

Livingston, P. A., Aydin, K., Buckley, T. W., Lang, G. M., Yang, M.-S., & Miller, B. S. (2017). Quantifying food web interactions in the North Pacific – a data-based approach. *Environmental Biology of Fishes*, *100*(4), 443–470. https://doi.org/10.1007/s10641-017-0587-0

Markowitz, E. H., Dawson, E. J., Anderson, C. B., Rohan, S. K., Charriere, N. E., Prohaska, B. K., & Stevenson, D. E. (2023). Results of the 2022 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. *U.S. Department of Commerce*, 213.

McClatchie, S., Hendy, I. L., Thompson, A. R., & Watson, W. (2017). Collapse and recovery of forage fish populations prior to commercial exploitation. *Geophysical Research Letters*, *44*(4), 1877–1885. https://doi.org/10.1002/2016GL071751

McGowan, D., Goldstein, E., Arimitsu, M., Deary, A., Ormseth, O., De Robertis, A., Horne, J., Rogers, L., Wilson, M., Coyle, K., Holderied, K., Piatt, J., Stockhausen, W., & Zador, S. (2020). Spatial and temporal dynamics of Pacific capelin Mallotus catervarius in the Gulf of Alaska: Implications for ecosystem-based fisheries management. *Marine Ecology Progress Series*, *637*, 117–140. https://doi.org/10.3354/meps13211

McGowan, D. W., Branch, T. A., Haught, S., & Scheuerell, M. D. (2021). Multi-decadal shifts in the distribution and timing of Pacific herring (*Clupea pallasii*) spawning in Prince William Sound, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(11), 1611–1627. https://doi.org/10.1139/cjfas-2021-0047

McGowan, D. W., Horne, J. K., & Parker-Stetter, S. L. (2019). Variability in species composition and distribution of forage fish in the Gulf of Alaska. *Deep Sea Research Part II: Topical Studies in Oceanography*, *165*, 221–237. https://doi.org/10.1016/j.dsr2.2016.11.019

McGowan, D., Horne, J., & Rogers, L. (2019). Effects of temperature on the distribution and density of capelin in the Gulf of Alaska. *Marine Ecology Progress Series*, 620, 119–138. https://doi.org/10.3354/meps12966

Methven, D. A., & Piatt, J. F. (1991). Seasonal abundance and vertical distribution of capelin (Mallotus villosus) in relation to water temperature at a coastal site off eastern Newfoundland. *ICES Journal of Marine Science*, *48*(2), 187–193. https://doi.org/10.1093/icesjms/48.2.187

Mueter, F., & Norcross, B. (2000). Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1169–1180. https://doi.org/10.1139/cjfas-57-6-1169

Ng, E. L., Deroba, J. J., Essington, T. E., Grüss, A., Smith, B. E., & Thorson, J. T. (2021). Predator stomach contents can provide accurate indices of prey biomass. *ICES Journal of Marine Science*, *78*(3), 1146–1159. https://doi.org/10.1093/icesjms/fsab026

Okamoto, D. K., Hessing-Lewis, M., Samhouri, J. F., Shelton, A. O., Stier, A., Levin, P. S., & Salomon, A. K. (2020). Spatial variation in exploited metapopulations obscures risk of collapse. *Ecological Applications*, *30*(3), e02051. https://doi.org/10.1002/eap.2051

Olsen, T., Stige, L. C., Dupont, N., Durant, J. M., & Langangen, Ø. (2024). Repeated large declines in the Barents Sea capelin population are associated with different ecosystem conditions. *ICES Journal of Marine Science*, fsae101. https://doi.org/10.1093/icesjms/fsae101

Ono, K., Ianelli, J. N., McGilliard, C. R., & Punt, A. E. (2018). Integrating data from multiple surveys and accounting for spatio-temporal correlation to index the abundance of juvenile Pacific halibut in Alaska. *ICES Journal of Marine Science*, 75(2), 572–584. https://doi.org/10.1093/icesjms/fsx174

Ormseth, O. A. (2014). *Appendix 2. Forage species report for the Gulf of Alaska*. In Plan Team for Groundfish Fisheries of the Gulf of Alaska (compiler), Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council, 1001–1039.

Ormseth, O. A., & Yasumiishi, E. (2021). Status of forage species in the Bering Sea and Aleutian Islands region. In Plan Team for Groundfish Fisheries of the Gulf of Alaska (compiler), Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council.

Ostrand, W. D., Gotthardt, T. A., Howlin, S., & Robards, M. D. (2005). Habitat Selection Models for Pacific Sand Lance (Ammodytes Hexapterus) in Prince William Sound, Alaska. *Northwestern Naturalist*, *86*(3), 131–143. https://doi.org/10.1898/1051-1733(2005)086[0131:SMFPSL]2.0.CO;2

Overland, J. E., & Stabeno, P. J. (2004). Is the climate of the Bering Sea warming and affecting the ecosystem? *Eos, Transactions American Geophysical Union*, *85*(33), 309–312. https://doi.org/10.1029/2004EO330001

Overland, J. E., Wang, M., Wood, K. R., Percival, D. B., & Bond, N. A. (2012). Recent Bering Sea warm and cold events in a 95-year context. *Deep Sea Research Part II: Topical Studies in Oceanography*, *65–70*, 6–13. https://doi.org/10.1016/j.dsr2.2012.02.013

Parker-Stetter, S. L., Horne, J. K., Farley, E. V., Barbee, D. H., Andrews, A. G., Eisner, L. B., & Nomura, J. M. (2013). Summer distributions of forage fish in the eastern Bering Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *94*, 211–230. https://doi.org/10.1016/j.dsr2.2013.04.022

Piatt, J. F., Arimitsu, M. L., Sydeman, W. J., Thompson, S. A., Renner, H., Zador, S., Douglas, D., Hatch, S., Kettle, A., & Williams, J. (2018). Biogeography of pelagic food webs in the North Pacific. *Fisheries Oceanography*, *27*(4), 366–380. https://doi.org/10.1111/fog.12258

Pinto, C., Travers-Trolet, M., Macdonald, J. I., Rivot, E., & Vermard, Y. (2019). Combining multiple data sets to unravel the spatiotemporal dynamics of a data-limited fish stock. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(8), 1338–1349. https://doi.org/10.1139/cjfas-2018-0149

Quinn, T. J., Marty, G. D., Wilcock, J., & Willette, M. (2001). Disease and population assessment of Pacific herring in Prince William Sound, Alaska. In Herring: Expectations for a new millennium. *University of Alaska Sea Grant*, 363–379.

Reay, P. J. (1970). *Synopsis of biological data on north atlantic sand eels of the genus ammodytes A. tobianus, A. dubius, A. americanus and A. marinus.*

Robards, M. D., Rose, G. A., & Piatt, J. F. (2002). Growth and Abundance of Pacific Sand Lance, Ammodytes hexapterus, under differing Oceanographic Regimes. *Environmental Biology of Fishes*, *64*(4), 429–441. https://doi.org/10.1023/A:1016151224357

Robards, M. D., Willson, M. F., Armstrong, R. H., & Piatt, J. F. (2000). *Sand lance: A review of biology and predator relations and annotated bibliography.* PNW-RP-521. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-RP-521

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, *12*(1), Article 1. https://doi.org/10.1186/1471-2105-12-77

Rose, G. A. (2005). Capelin (Mallotus villosus) distribution and climate: A sea “canary” for marine ecosystem change. *ICES Journal of Marine Science*, *62*(7), 1524–1530. https://doi.org/10.1016/j.icesjms.2005.05.008

Rovellini, A., Punt, A. E., Bryan, M. D., Kaplan, I. C., Dorn, M. W., Aydin, K., Fulton, E. A., Alglave, B., Baker, M. R., Carroll, G., Ferriss, B. E., Haltuch, M. A., Hayes, A. L., Hermann, A. J., Hernvann, P.-Y., Holsman, K. K., Liu, O. R., McHuron, E., Morzaria-Luna, H. N., … Weise, M. T. (2024). Linking climate stressors to ecological processes in ecosystem models, with a case study from the Gulf of Alaska. *ICES Journal of Marine Science*, fsae002. https://doi.org/10.1093/icesjms/fsae002

Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *71*(2), 319–392. https://doi.org/10.1111/j.1467-9868.2008.00700.x

Siple, M. C., Essington, T. E., & E. Plagányi, É. (2019). Forage fish fisheries management requires a tailored approach to balance trade-offs. *Fish and Fisheries*, *20*(1), 110–124. https://doi.org/10.1111/faf.12326

Somerton, D., Ianelli, J., Walsh, S., Smith, S., Godø, O. R., & Ramm, D. (1999). Incorporating experimentally derived estimates of survey trawl efficiency into the stock assessment process: A discussion. *ICES Journal of Marine Science*, *56*(3), 299–302. https://doi.org/10.1006/jmsc.1999.0443

Soutar, A., & Isaacs, J. D. (1969). History of fish populations inferred from fish scales in anaerobic sediments off California. *Calif. Mar. Res. Comm*, *13*, 63–70.

Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W., & Overland, J. E. (2004). Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research*, *24*(7), 859–897. https://doi.org/10.1016/j.csr.2004.02.007

Stabeno, P. J., Bond, N. A., Kachel, N. B., Salo, S. A., & Schumacher, J. D. (2001). On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fisheries Oceanography*, *10*(1), 81–98. https://doi.org/10.1046/j.1365-2419.2001.00157.x

Stabeno, P. J., Duffy-Anderson, J. T., Eisner, L. B., Farley, E. V., Heintz, R. A., & Mordy, C. W. (2017). Return of warm conditions in the southeastern Bering Sea: Physics to fluorescence. *PLOS ONE*, *12*(9), e0185464. https://doi.org/10.1371/journal.pone.0185464

Stabeno, P. J., Kachel, N. B., Moore, S. E., Napp, J. M., Sigler, M., Yamaguchi, A., & Zerbini, A. N. (2012). Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. *Deep Sea Research Part II: Topical Studies in Oceanography*, *65–70*, 31–45. https://doi.org/10.1016/j.dsr2.2012.02.020

Suca, J. J., Deroba, J. J., Richardson, D. E., Ji, R., & Llopiz, J. K. (2021). Environmental drivers and trends in forage fish occupancy of the Northeast US shelf. *ICES Journal of Marine Science*, *78*(10), 3687–3708. https://doi.org/10.1093/icesjms/fsab214

Suryan, R. M., Arimitsu, M. L., Coletti, H. A., Hopcroft, R. R., Lindeberg, M. R., Barbeaux, S. J., Batten, S. D., Burt, W. J., Bishop, M. A., Bodkin, J. L., Brenner, R., Campbell, R. W., Cushing, D. A., Danielson, S. L., Dorn, M. W., Drummond, B., Esler, D., Gelatt, T., Hanselman, D. H., … Zador, S. G. (2021). Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports*, *11*(1), 6235. https://doi.org/10.1038/s41598-021-83818-5

Sydeman, W. J., Piatt, J. F., Thompson, S. A., García-Reyes, M., Hatch, S. A., Arimitsu, M. L., Slater, L., Williams, J. C., Rojek, N. A., Zador, S. G., & Renner, H. M. (2017). Puffins reveal contrasting relationships between forage fish and ocean climate in the North Pacific. *Fisheries Oceanography*, *26*(4), 379–395. https://doi.org/10.1111/fog.12204

Sydeman, W. J., Thompson, S. A., Piatt, J. F., Zador, S. G., & Dorn, M. W. (2022). Integrating seabird dietary and groundfish stock assessment data: Can puffins predict pollock spawning stock biomass in the North Pacific? *Fish and Fisheries*, *23*(1), 213–226. https://doi.org/10.1111/faf.12611

Szuwalski, C. (2022). 2022 Gulf of Alaska forage report. North Pacific Fishery Management Council.

Szuwalski, C., Yasumiishi, E., Andrews, A., Dimond, A., Murphy, J., Farley, E., & Siddon, E. (2023). 2023 Bering Sea and Aleutian Islands forage report. North Pacific Fishery Management Council.

Thompson, A. R., Harvey, C. J., Sydeman, W. J., Barceló, C., Bograd, S. J., Brodeur, R. D., Fiechter, J., Field, J. C., Garfield, N., Good, T. P., Hazen, E. L., Hunsicker, M. E., Jacobson, K., Jacox, M. G., Leising, A., Lindsay, J., Melin, S. R., Santora, J. A., Schroeder, I. D., … Williams, G. D. (2019). Indicators of pelagic forage community shifts in the California Current Large Marine Ecosystem, 1998–2016. *Ecological Indicators*, *105*, 215–228. https://doi.org/10.1016/j.ecolind.2019.05.057

Thompson, K. A. (2015). *The Factors Affecting the Diets of Groundfish in the Gulf of Alaska: Ecological and Modeling Considerations*. [Doctoral dissertation, Oregon State University].

Thompson, P. L., Anderson, S. C., Nephin, J., Robb, C. K., Proudfoot, B., Park, A. E., Haggarty, D. R., & Rubidge, E. M. (2023). Integrating trawl and longline surveys across British Columbia improves groundfish distribution predictions. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(1), 195–210. https://doi.org/10.1139/cjfas-2022-0108

Thorson, J. T., Clarke, M. E., Stewart, I. J., & Punt, A. E. (2013). The implications of spatially varying catchability on bottom trawl surveys of fish abundance: A proposed solution involving underwater vehicles. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(2), 294–306. https://doi.org/10.1139/cjfas-2012-0330

Thorson, J. T., Ianelli, J. N., Larsen, E. A., Ries, L., Scheuerell, M. D., Szuwalski, C., & Zipkin, E. F. (2016). Joint dynamic species distribution models: A tool for community ordination and spatio-temporal monitoring. *Global Ecology and Biogeography*, *25*(9), 1144–1158. https://doi.org/10.1111/geb.12464

Thorson, J. T., Pinsky, M. L., & Ward, E. J. (2016). Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. *Methods in Ecology and Evolution*, *7*(8), 990–1002. https://doi.org/10.1111/2041-210X.12567

Turner, L. C., Arimitsu, M., Piatt, J. F., Eckert, G. L., & Cunningham, C. J. (2024). *Alaska Forage Fish Database (AFFD)* U.S. Geological Survey. https://doi.org/10.5066/P9WZQJ8N

Ueshima, T., Yamamoto, M., Irino, T., Oba, T., Minagawa, M., Narita, H., & Murayama, M. (2006). Long term Aleutian Low dynamics and obliquity-controlled oceanic primary production in the mid-latitude western North Pacific (Core MD01-2421) during the last 145,000 years. *Global and Planetary Change*, *53*(1), 21–28. https://doi.org/10.1016/j.gloplacha.2006.01.017

von Biela, V. R., Arimitsu, M. L., Piatt, J. F., Heflin, B., Schoen, S. K., Trowbridge, J. L., & Clawson, C. M. (2019). Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. *Marine Ecology Progress Series*, *613*, 171–182. https://doi.org/10.3354/meps12891

Ward, E. J., Barnett, L. A. K., Anderson, S. C., Commander, C. J. C., & Essington, T. E. (2022). Incorporating non-stationary spatial variability into dynamic species distribution models. *ICES Journal of Marine Science*, *79*(9), 2422–2429. https://doi.org/10.1093/icesjms/fsac179

Wathne, F. (1977). Performance of Trawls Used in Resource Assessment. *Marine Fisheries Review*, *39*(6).

Witherell, D., Pautzke, C., & Fluharty, D. (2000). An ecosystem-based approach for Alaska groundfish fisheries. *ICES Journal of Marine Science*, *57*(3), 771–777. https://doi.org/10.1006/jmsc.2000.0719

Wood, S. N. (2017). Generalized Additive Models: An Introduction with R, Second Edition (2nd ed.). *Chapman and Hall/CRC*. https://doi.org/10.1201/9781315370279

Yasumiishi, E. M., Cieciel, K., Andrews, A. G., Murphy, J., & Dimond, J. A. (2020). Climate-related changes in the biomass and distribution of small pelagic fishes in the eastern Bering Sea during late summer, 2002–2018. *Deep Sea Research Part II: Topical Studies in Oceanography*, *181–182*, 104907. https://doi.org/10.1016/j.dsr2.2020.104907

Yasunaka, S., & Hanawa, K. (2002). Regime Shifts Found in the Northern Hemisphere SST Field. *Journal of the Meteorological Society of Japan. Ser. II*, *80*(1), 119–135. https://doi.org/10.2151/jmsj.80.119

3.7 Tables

Table 3.1: Summary of final model performance for spatial (eq. 2) and spatio-temporal models (eq. 3) with a spatially-varying catchability effect. Within-sample performance metrics include the percent deviance explained. Out-of-sample performance metrics for model comparisons include the average area under the curve (AUC) (the discriminative ability of the model) across 8 testing data sets, where an AUC closer to 1 has a better model performance. AUC that are less than 0.7 are in red. Positive-definite Hessian (P Hess) is the number of folds (8 folds total) that converged (i.e., Hessian was invertible). The asterisks (**) indicate that the full model did not converge.

Model	Region	Species	Data type	% Dev Exp	AUC	P Hess
Temporal	Bering Sea	Capelin	Fisheries survey	43.5	0.59	3/8
			Groundfish Diet	30.6	0.78	
			Integrated	**60.5**	**0.92**	
		Herring	Fisheries survey	23.9	0.65	
			Groundfish Diet	13.0	0.75	
			Integrated	**54.7**	**0.94**	
		Sand lance	Fisheries survey	36.5	0.66	
			Groundfish Diet	42.0	0.77	
			Integrated	**41.7**	**0.77**	
	GOA	Capelin	Fisheries survey	19.9	0.66	
			Groundfish Diet	26.8	0.71	
			Seabird Diet	21.8	0.71	
			Integrated	**27.6**	**0.77**	
		Herring	Fisheries survey	27.0	0.64	3/8
			Groundfish Diet	19.9	0.77	7/8
			Seabird Diet	18.2	0.65	
			Integrated	**32.5**	**0.83**	
		Sand lance	Fisheries survey	42.5	0.89	5/8
			Groundfish Diet	35.4	0.80	
			Seabird Diet	29.8	0.70	
			Integrated	**45.7**	**0.88**	
Spatio-temporal	Bering Sea	Capelin	Fisheries survey	43.9	0.59	
			Groundfish Diet	30.3	0.85	**
			Integrated	**60.8**	**0.91**	
		Herring	Fisheries survey	25.0	0.57	
			Groundfish Diet	11.8	0.74	
			Integrated	**54.7**	**0.93**	
		Sand lance	Fisheries survey	37.2	0.64	6/8
			Groundfish Diet	42.9	0.90	
			Integrated	**42.5**	**0.80**	
	GOA	Capelin	Fisheries survey	20.7	0.70	
			Groundfish Diet	31.7	0.87	

Table 3.1 cont.

		Integrated	**31.2**	**0.80**
	Herring	Fisheries survey	31.2	0.68
		Groundfish Diet	23.7	0.83
		Integrated	**36.3**	**0.84**
	Sand lance	Fisheries survey	42.4	0.86
		Groundfish Diet	38.7	0.91
		Integrated	**46.9**	**0.88**

3.8 Figures

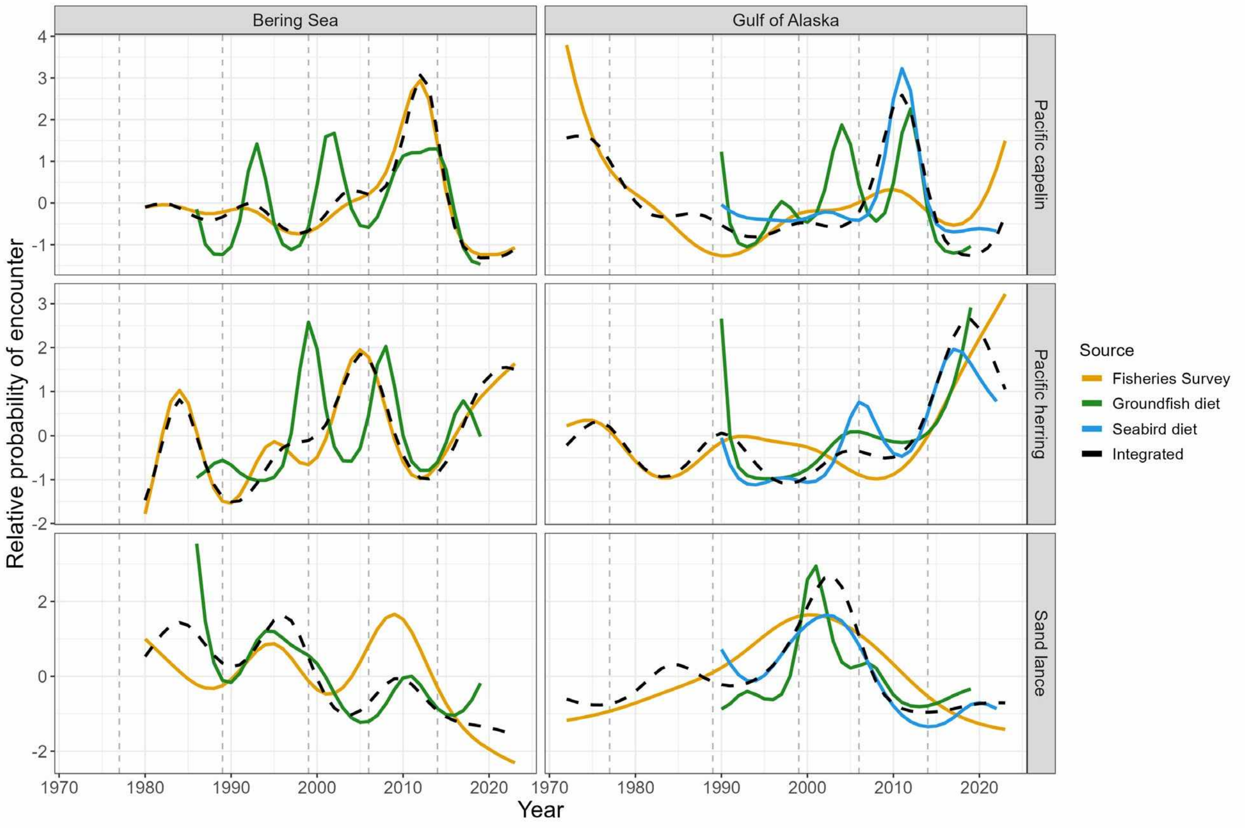

Figure 3.1: Interannual trends in estimated probability of encounter, standardized (mean = 0, SD = 1) for models fit to fisheries survey (gold) and groundfish diet (green), data in the Bering Sea (left panels) and fisheries survey, groundfish diet, and seabird diet (blue) data in the Gulf of Alaska (right panels). Aggregate trend from all data combined are overlayed in black (dashed). The confidence intervals are omitted for clarity when comparing model trends.

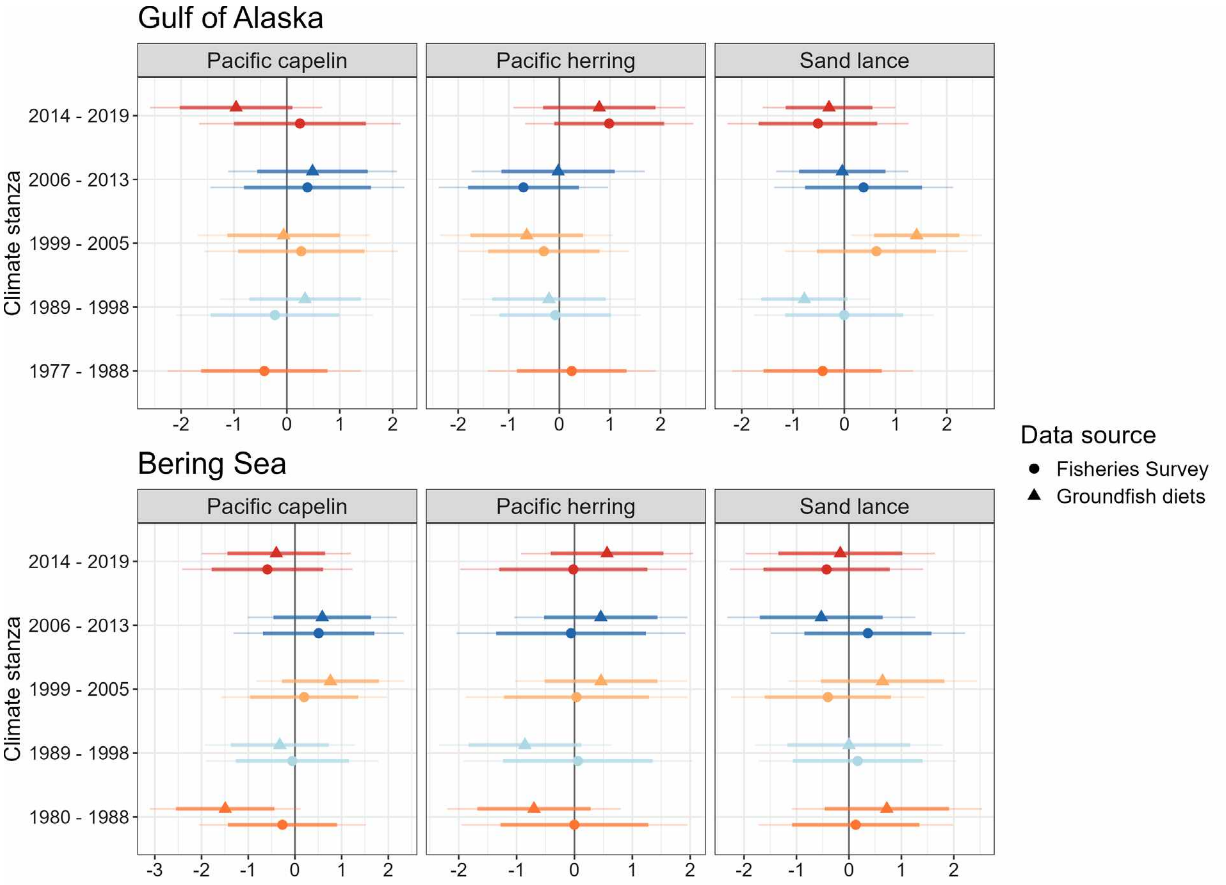

Figure 3.2: Estimates of probability of encounter that is standardized (mean = 0, SD = 1) in response to the effect of decadal stanzas. Points represent the mean of groundfish diets (triangles) and fisheries survey (circles) relative to the overall mean (vertical line on 0), with 80% confidence intervals shown as colored lines extending from points, and 95% confidence intervals as grey lines extending further. Colors correspond with general trends in temperature. Warmer colors indicate regime shifts into warmer temperatures, whereas cooler temperatures indicate shifts into cooler temperatures.

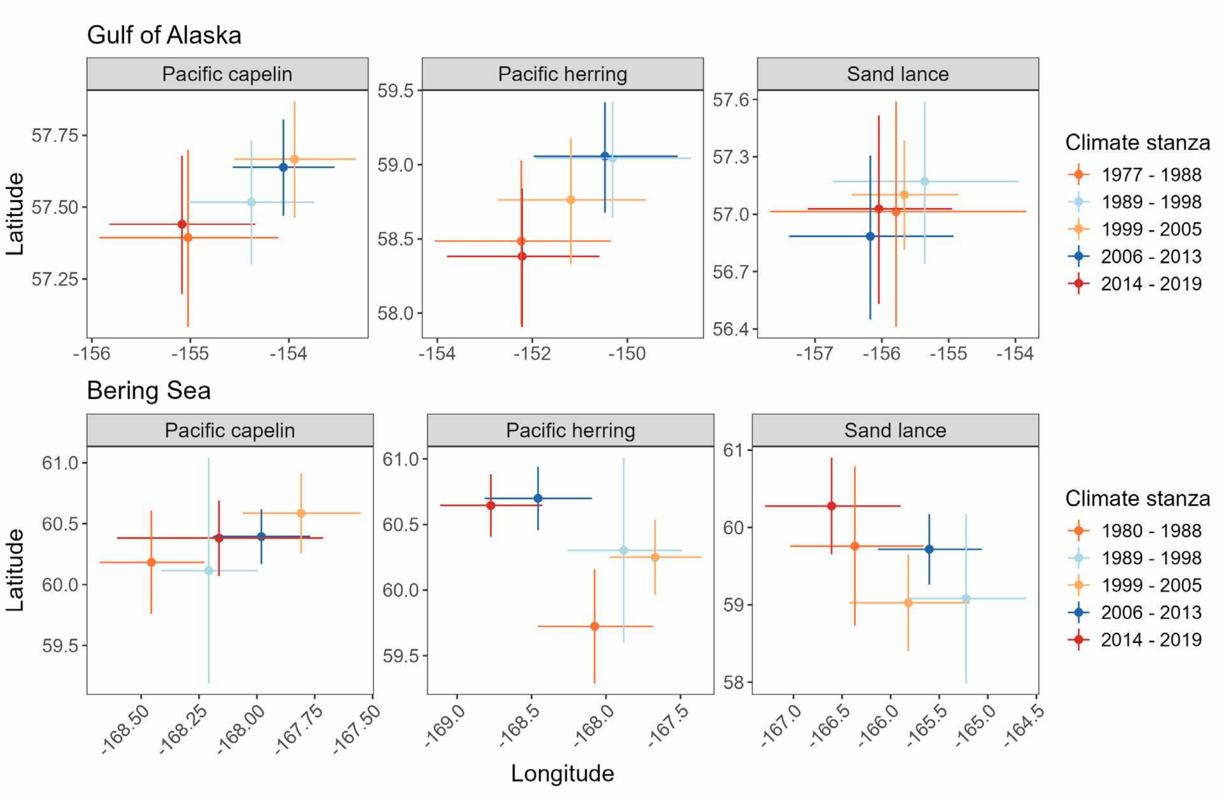

Figure 3.3: Decadal effects on center of gravity (COG) estimates for each species-region across the same latitudinal and longitudinal scale. Warmer colors represent climate stanzas associated with increased temperatures, and cooler colors represent stanzas associated with lower temperatures.

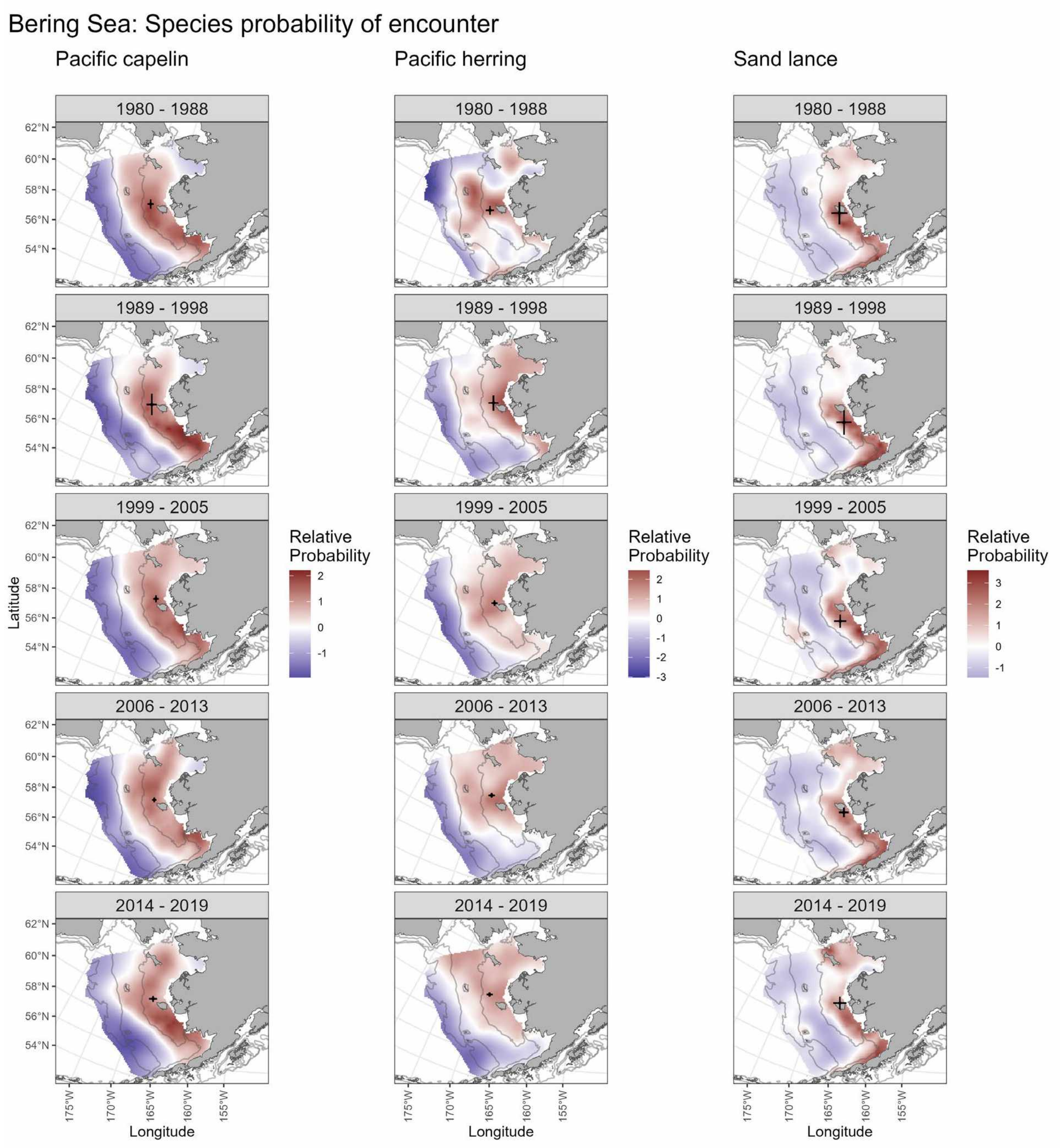

Figure 3.4: Distribution of capelin, herring, and sand lance in the Bering Sea from model estimates fit to integrated data source. The logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

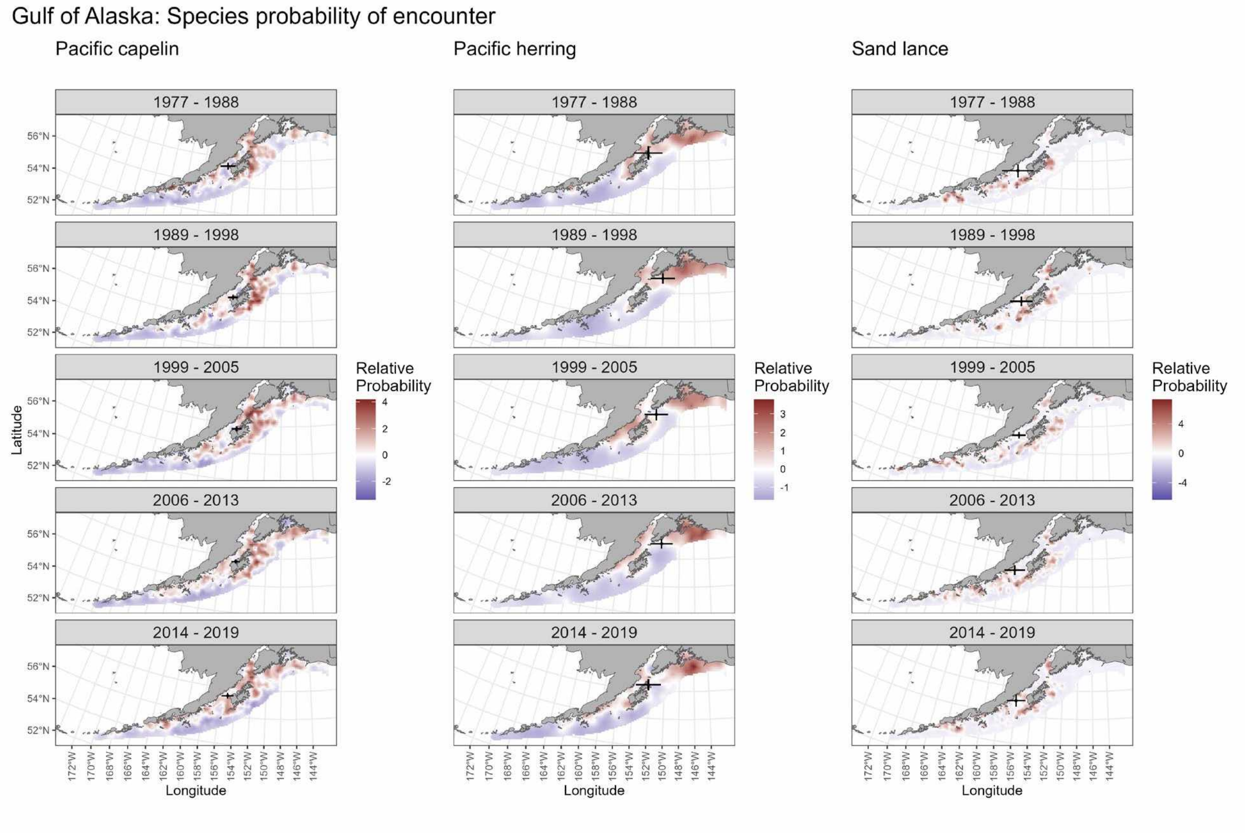

Figure 3.5: Distribution of capelin, herring, and sand lance in the Gulf of Alaska from model estimates fit to integrated data source. The logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

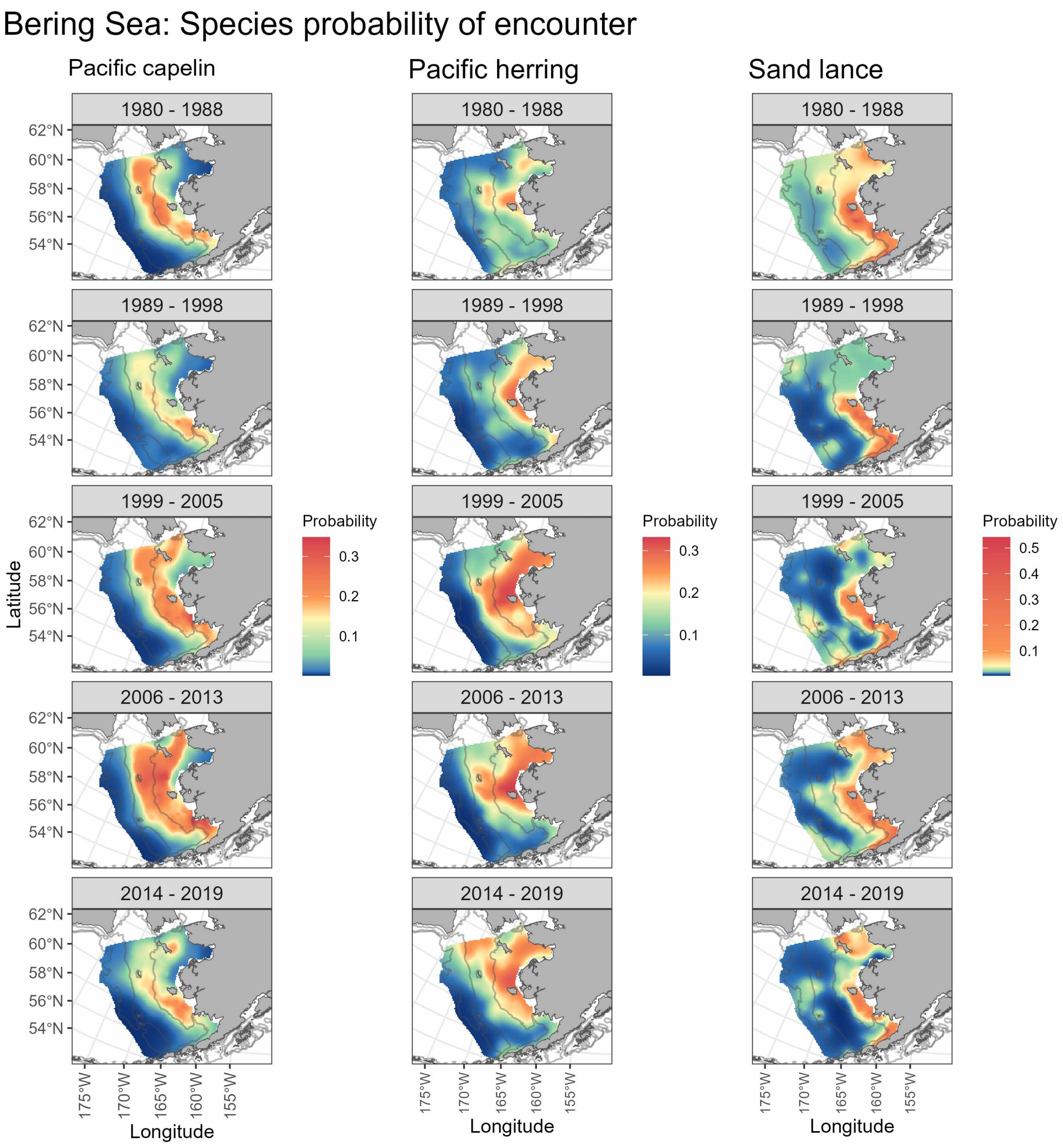

Figure 3.6: Distributional probability of encounter of capelin, herring, and sand lance in the Bering Sea fit to integrated data source. The scaled warmer to cooler color corresponds with higher to lower probabilities.

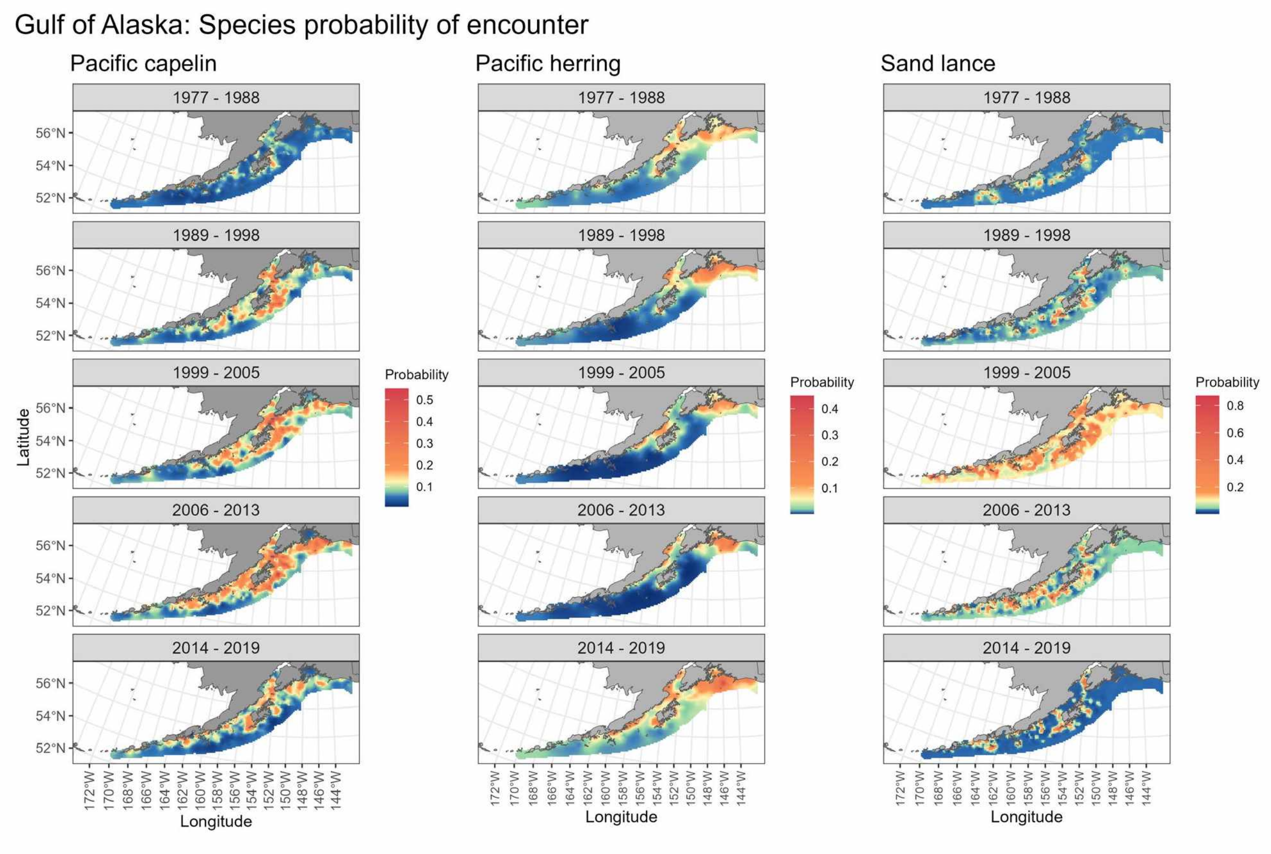

Figure 3.7: Distributional probability of encounter of capelin, herring, and sand lance in the Gulf of Alaska fit to integrated data source. The scaled warmer to cooler color corresponds with higher to lower probabilities.

3.9 Supplementary Information

3.9.1 Supplementary Tables

Table S 3.1: Summary of model selection for temporal models. The fixed effects and random effects columns represent the model structure. Random effects in the models include a spatial effect (ω), or spatially-varying catchability effect (ζ_m). Predictors include the fixed effects of data source and smoothed year effect (referred to as "year" in the table). Within-sample performance metrics include the percent deviance explained. Out-of-sample performance metrics for model comparison from cross-validation results are presented in the last three columns. The sum log likelihood (SLL) is the sum across all withheld (testing) data across eight cross-validation folds. A more positive SLL indicates a better model performance. The more positive SLL of the two models is bolded. Positive-definite Hessian ("P Hess") is the number of folds (eight folds total) that converged (i.e., Hessian was invertible). Cases where the Hessian was not invertible for the model fit to each fold are in red. Area under the curve (AUC) is the discriminative ability of the model as averaged across models fit to the cross-validation folds, where an AUC closer to 1 has a better model performance.

Model #	Data type	Fixed effects	Random effects	% Dev exp	SLL	AUC	P Hess (#/8)
Pacific capelin (Bering Sea)							
1	Integrated	year, source	ω	59.5	-15705.8	0.915	
2	Integrated	year, source	ζ_m	60.4	-15481.5	0.915	
1	Groundfish diet	year, source	ω	30.8	-4677.32	0.794	
2	Groundfish diet	year, source	ζ_m	30.6	-4657.34	0.781	
1	Fisheries survey	year, source	ω	42.1	-11083.6	0.583	5
2	Fisheries survey	year, source	ζ_m	43.5	-11060.9	0.589	3
Pacific herring (Bering Sea)							
1	Integrated	year, source	ω	54.3	-14898.1	0.939	
2	Integrated	year, source	ζ_m	54.7	-14886.7	0.938	
1	Groundfish diet	year, source	ω	12.1	-3393.91	0.759	
2	Groundfish diet	year, source	ζ_m	13	-3421.01	0.753	7
1	Fisheries survey	year, source	ω	23.5	-11449.9	0.670	5
2	Fisheries survey	year, source	ζ_m	23.9	-11469	0.653	3
Sand lance (Bering Sea)							
1	Integrated	year, source	ω	41.1	-12115.7	0.782	
2	Integrated	year, source	ζ_m	41.7	-11903.3	0.765	
1	Groundfish diet	year, source	ω	42.1	-9001.02	.776	
2	Groundfish diet	year, source	ζ_m	42	-8902.94	0.768	
1	Fisheries survey	year, source	ω	35	-3042.32	0.682	3
2	Fisheries survey	year, source	ζ_m	36.5	-3034.86	0.657	5
Pacific capelin (Gulf of Alaska)							
1	Integrated	year, source	ω	25.6	-24530.1	0.780	

Table S 3.1 cont.

2	Integrated	year, source	ζ_m	27.9	-23524	0.769	
1	Seabird diet	year, source	ω	21.7	-8837.37	0.706	
2	Seabird diet	year, source	ζ_m	28.3	-8792.86	0.705	
1	Groundfish diet	year, source	ω	26.5	-5559.95	0.713	
2	Groundfish diet	year, source	ζ_m	19.1	-5306.67	0.714	
1	Fisheries survey	year, source	ω	17.9	-9276.2	0.700	
2	Fisheries survey	year, source	ζ_m	21.8	-9104.94	0.664	
Pacific herring (Gulf of Alaska)							
1	Integrated	year, source	ω	31.8	-12515.6	0.832	
2	Integrated	year, source	ζ_m	32.5	-11894.8	0.829	
1	Seabird diet	year, source	ω	17.8	-4709.1	0.759	
2	Seabird diet	year, source	ζ_m	18.2	-4701.03	0.653	
1	Groundfish diet	year, source	ω	20.6	-1067.71	0.779	
2	Groundfish diet	year, source	ζ_m	21.2	-1148.07	0.768	
1	Fisheries survey	year, source	ω	27	-6589.5	0.657	
2	Fisheries survey	year, source	ζ_m	27.2	-6504.39	0.642	
Sand lance (Gulf of Alaska)							
1	Integrated	year, source	ω	40.9	-18811	0.886	
2	Integrated	year, source	ζ_m	45.2	-18058.5	0.877	
1	Seabird diet	year, source	ω	25.5	-11102	0.775	
2	Seabird diet	year, source	ζ_m	29.8	-10979.7	0.696	
1	Groundfish diet	year, source	ω	32.5	-4308.57	0.812	
2	Groundfish diet	year, source	ζ_m	35.8	-4091.2	0.804	
1	Fisheries survey	year, source	ω	41.9	-2612.57	0.886	
2	Fisheries survey	year, source	ζ_m	42.3	-2572.78	0.886	

Table S 3.2: Summary of model selection for spatio-temporal models. The fixed effects and random effects columns represent the model structure. Random effects in the models include a spatial effect (ω), spatio-temporal effect (ε) and spatially-varying catchability effect (ζ_m). Predictors include the fixed effects of data source and climate stanza. Within-sample performance metrics include the percent deviance explained. Out-of-sample performance metrics for model comparison from cross-validation results are presented in the last three columns. The sum log likelihood (SLL) is the sum across all withheld (testing) data across eight cross-validation folds. A more positive SLL indicates a better model performance. The more positive SLL of the four models is bolded. Positive-definite Hessian (P Hess) is the number of folds (eight folds total) that converged (i.e., Hessian was invertible). Cases where the Hessian was not invertible for the model fit to each fold are in red. Area under the curve (AUC) is the discriminative ability of the model as averaged across models fit to the cross-validation folds, where an AUC closer to 1 has a better model performance.

Model #	Data type	Fixed effects	Random effects	% Dev exp	SLL	AUC	P Hess (#/8)
Pacific capelin (Bering Sea)							
1	Integrated	source	ζ_m	59.2	-15167.3	0.908	8
2	Integrated	source, stanza	ζ_m	60.2	-15094.1	0.914	8
3	Integrated	source, stanza	ω, ε	59.9	-14743.8	0.915	8
4	Integrated	source, stanza	ζ_m, ε	60.8	-14599.6	0.914	8
1	Groundfish diet	source	ζ_m	27.3	-4503.36	0.756	8
2	Groundfish diet	source, stanza	ζ_m	28	-4483.42	0.789	8
3	Groundfish diet	source, stanza	ω, ε	30.3	-4383.54	0.881	8
4	Groundfish diet	source, stanza	ζ_m, ε	30.2	-4390.53	0.845	8
1	Fisheries survey	source	ζ_m	40.8	-10525.2	0.631	8
2	Fisheries survey	source, stanza	ζ_m	43.2	-10445.2	0.559	8
3	Fisheries survey	source, stanza	ω, ε	42.4	-10035	0.553	7
4	Fisheries survey	source, stanza	ζ_m, ε	43.9	-10002.2	0.593	8
Pacific herring (Bering Sea)							
1	Integrated	source	ζ_m	53.2	-13924.8	0.927	8
2	Integrated	source, stanza	ζ_m	53.8	-13848.2	0.934	8
3	Integrated	source, stanza	ω, ε	54.3	-13600.7	0.923	8
4	Integrated	source, stanza	ζ_m, ε	54.7	-13566.5	0.929	8
1	Groundfish diet	source	ζ_m	8.7	-3514.74	0.599	8
2	Groundfish diet	source, stanza	ζ_m	11.9	-3418.28	0.71	8
3	Groundfish diet	source, stanza	ω, ε	13	-3385.2	0.775	8
4	Groundfish diet	source, stanza	ζ_m, ε	11.8	-3453.56	0.739	8
1	Fisheries survey	source	ζ_m	22.4	-10507.3	0.560	8
2	Fisheries survey	source, stanza	ζ_m	23.1	-10481.3	0.578	8
3	Fisheries survey	source, stanza	ω, ε	24.5	-10273.6	0.630	8
4	Fisheries survey	source, stanza	ζ_m, ε	25	-10243.8	0.574	8

Table S 3.2 cont.

Sand lance (Bering Sea)							
1	Integrated	source	ζ_m	41.3	-11796.8	0.817	8
2	Integrated	source, stanza	ζ_m	41.9	-11703.4	0.824	8
3	Integrated	source, stanza	ω, ε	42.3	-11528	0.792	8
4	Integrated	source, stanza	ζ_m, ε	42.5	-11404.8	0.797	8
1	Groundfish diet	source	ζ_m	41.1	-8419.6	0.837	8
2	Groundfish diet	source, stanza	ζ_m	41.8	-8353.24	0.839	8
3	Groundfish diet	source, stanza	ω, ε	43.2	-8104.13	0.920	8
4	Groundfish diet	source, stanza	ζ_m, ε	42.9	-8019.58	0.896	8
1	Fisheries survey	source	ζ_m	36.3	-2893.48	0.712	6
2	Fisheries survey	source, stanza	ζ_m	37.1	-2884.68	0.691	3
3	Fisheries survey	source, stanza	ω, ε	35.9	-2792.84	0.672	6
4	Fisheries survey	source, stanza	ζ_m, ε	37.2	-2816.65	0.643	6
Pacific capelin (Gulf of Alaska)							
1	Integrated	source	ζ_m	25.2	-21682.3	0.768	8
2	Integrated	source, stanza	ζ_m	28.8	-21154.1	0.796	8
3	Integrated	source, stanza	ω, ε	29.3	-21715.8	0.798	8
4	Integrated	source, stanza	ζ_m, ε	31.2	-21054.6	0.793	8
1	Groundfish diet	source	ζ_m	23.2	-4740.63	0.704	8
2	Groundfish diet	source, stanza	ζ_m	25.9	-4558.38	0.743	8
3	Groundfish diet	source, stanza	ω, ε	29.2	-4363.19	0.881	8
4	Groundfish diet	source, stanza	ζ_m, ε	31.7	-4199.94	0.870	8
1	Fisheries survey	source	ζ_m	18.3	-7423.18	0.691	8
2	Fisheries survey	source, stanza	ζ_m	18.9	-7395.16	0.696	8
3	Fisheries survey	source, stanza	ω, ε	19.8	-7524.62	0.720	8
4	Fisheries survey	source, stanza	ζ_m, ε	20.7	-7308.42	0.704	8
Pacific herring (Gulf of Alaska)							
1	Integrated	source	ζ_m	33.1	-9905.61	0.852	8
2	Integrated	source, stanza	ζ_m	34.4	-9772.83	0.848	8
3	Integrated	source, stanza	ω, ε	35.8	-9986	0.834	8
4	Integrated	source, stanza	ζ_m, ε	36.3	-9659.49	0.839	8
1	Groundfish diet	source	ζ_m	17.2	-1078.41	0.758	8
2	Groundfish diet	source, stanza	ζ_m	18.9	-1048.98	0.781	8
3	Groundfish diet	source, stanza	ω, ε	22	-992.317	0.869	8
4	Groundfish diet	source, stanza	ζ_m, ε	23.7	-1042.57	0.828	8
1	Fisheries survey	source	ζ_m	27.8	-5226.72	0.640	8
2	Fisheries survey	source, stanza	ζ_m	28.4	-5195.52	0.643	8
3	Fisheries survey	source, stanza	ω, ε	31.4	-5174.11	0.716	8
4	Fisheries survey	source, stanza	ζ_m, ε	31.2	-5111.11	0.685	8
Sand lance (Gulf of Alaska)							
1	Integrated	source	ζ_m	41.6	-17602.1	0.843	8

Table S 3.2 cont.

2	Integrated	source, stanza	ζ_m	45.5	-16914.4	0.866	8
3	Integrated	source, stanza	ω, ε	43.7	-17528	0.859	8
4	Integrated	source, stanza	ζ_m, ε	46.9	-16793	0.857	8
1	Groundfish diet	source	ζ_m	30.6	-3606.3	0.723	8
2	Groundfish diet	source, stanza	ζ_m	33.7	-3437.2	0.794	8
3	Groundfish diet	source, stanza	ω, ε	37.7	-3290.07	0.919	8
4	Groundfish diet	source, stanza	ζ_m, ε	38.7	-3098.98	0.908	8
1	Fisheries survey	source	ζ_m	39.3	-2549.76	0.864	8
2	Fisheries survey	source, stanza	ζ_m	41.4	-2514.49	0.877	8
3	Fisheries survey	source, stanza	ω, ε	42	-2499.26	0.879	8
4	Fisheries survey	source, stanza	ζ_m, ε	42.4	-2492.63	0.881	8

Table S 3.1: Results of latitudinal and longitudinal center-of-gravity (COG) analysis by species and region across decadal climate stanzas. Includes estimated center of gravity (COG) and change in COG from prior decadal stanza (Δ), where a decrease from the prior stanza (i.e. southern or western shift) is differentiated by red text.

Species	Region	Decadal stanza	Longitude		Latitude	
			COG	Δ	COG	Δ
Pacific capelin	Gulf of Alaska	1977 - 1988	-154.38		57.669	
		1989 - 1998	-153.929	0.45	57.711	0.042
		1999 - 2005	-153.505	0.425	57.849	0.138
		2006 - 2013	-153.694	-0.189	57.794	-0.055
		2014 - 2019	-154.53	-0.836	57.655	-0.139
	Bering Sea	1980 - 1988	-168.321		60.229	
		1989 - 1998	-167.917	0.404	60.270	0.041
		1999 - 2005	-167.696	0.221	60.592	0.321
		2006 - 2013	-167.892	-0.196	60.431	-0.161
		2014 - 2019	-167.869	0.023	60.402	-0.028
Pacific herring	Gulf of Alaska	1977 - 1988	-151.021		58.912	
		1989 - 1998	-149.651	1.37	59.297	0.385
		1999 - 2005	-150.411	-0.76	59.043	-0.254
		2006 - 2013	-149.799	0.611	59.262	0.219
		2014 - 2019	-151.358	-1.559	58.725	-0.536
	Bering Sea	1980 - 1988	-167.755		59.878	
		1989 - 1998	-167.622	0.134	60.421	0.543
		1999 - 2005	-167.5	0.121	60.316	-0.105
		2006 - 2013	-168.218	-0.717	60.723	0.407
		2014 - 2019	-168.485	-0.267	60.724	0.001
Sand lance	Gulf of Alaska	1977 - 1988	-156.281		56.852	
		1989 - 1998	-155.803	0.479	57.035	0.183
		1999 - 2005	-155.888	-0.086	57.039	0.004
		2006 - 2013	-156.373	-0.485	56.838	-0.201
		2014 - 2019	-156.396	-0.023	56.890	0.052
	Bering Sea	1980 - 1988	-165.124		59.670	
		1989 - 1998	-164.239	0.885	59.267	-0.403
		1999 - 2005	-164.684	-0.445	59.005	-0.262
		2006 - 2013	-164.827	-0.143	59.573	0.568
		2014 - 2019	-165.251	-0.424	60.075	0.502

3.9.2 Supplementary Figures

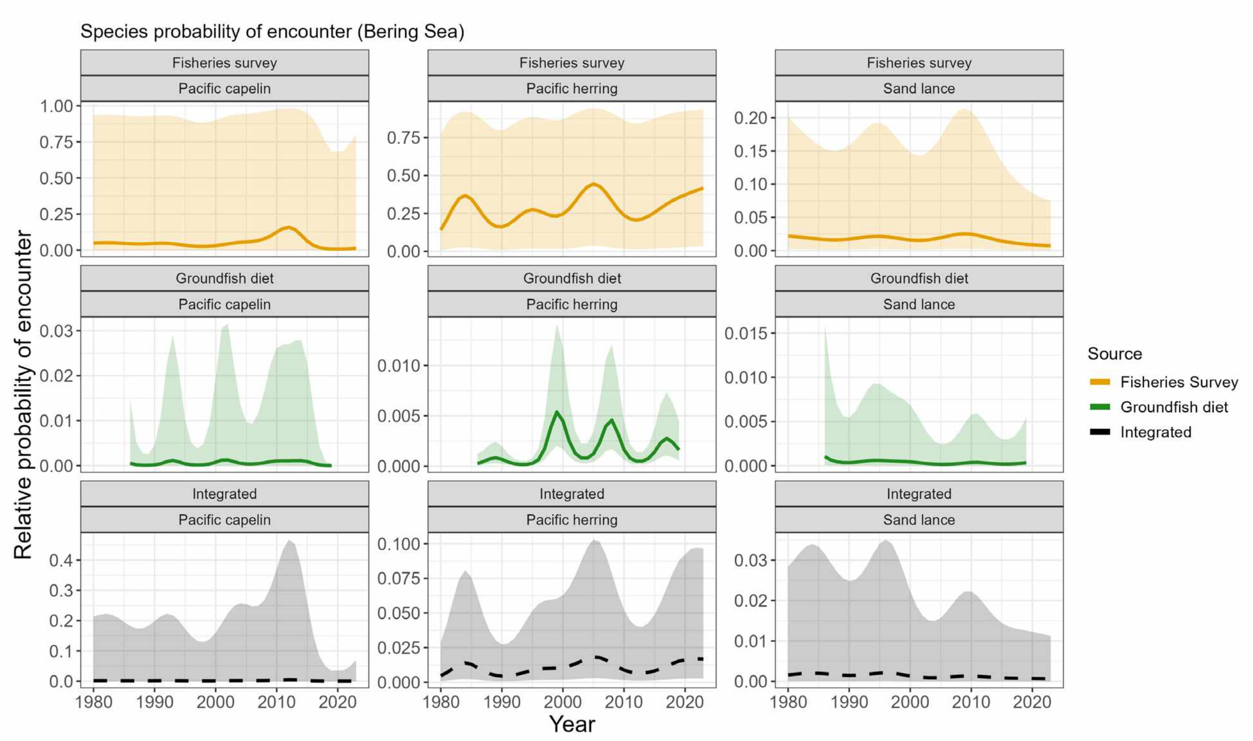

Figure S 3.1: Estimated probability of encounter in the Bering Sea from models fit to fisheries survey data (gold), groundfish diet data (green), and combined data sources (black) with 95% confidence intervals for each region and species.

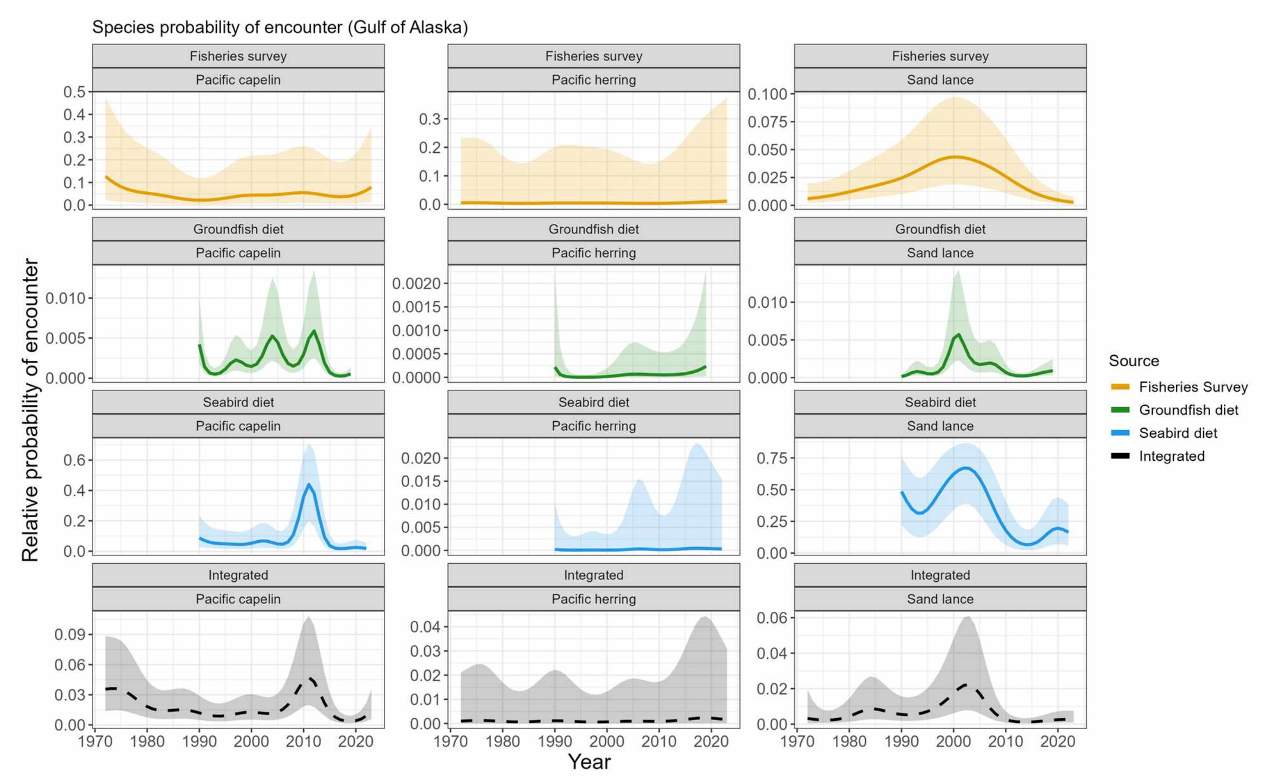

Figure S 3.2: Estimated probability of encounter in the western-central Gulf of Alaska from models fit to fisheries survey data (gold), groundfish diet data (green), seabird diet data (blue), and combined data sources (black) with 95% confidence intervals for each region and species.

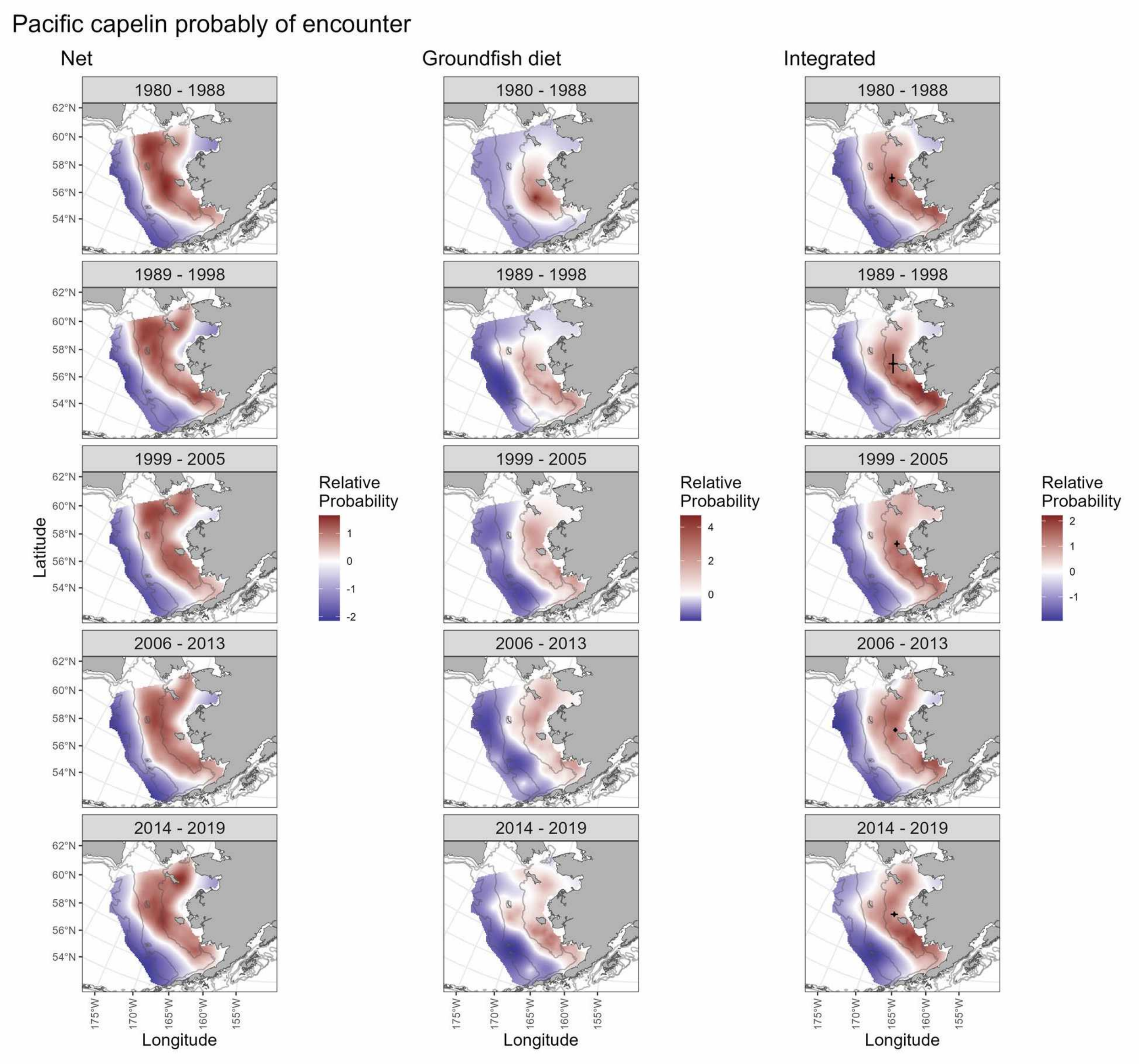

Figure S 3.3: Distribution of Pacific capelin in the Bering Sea estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

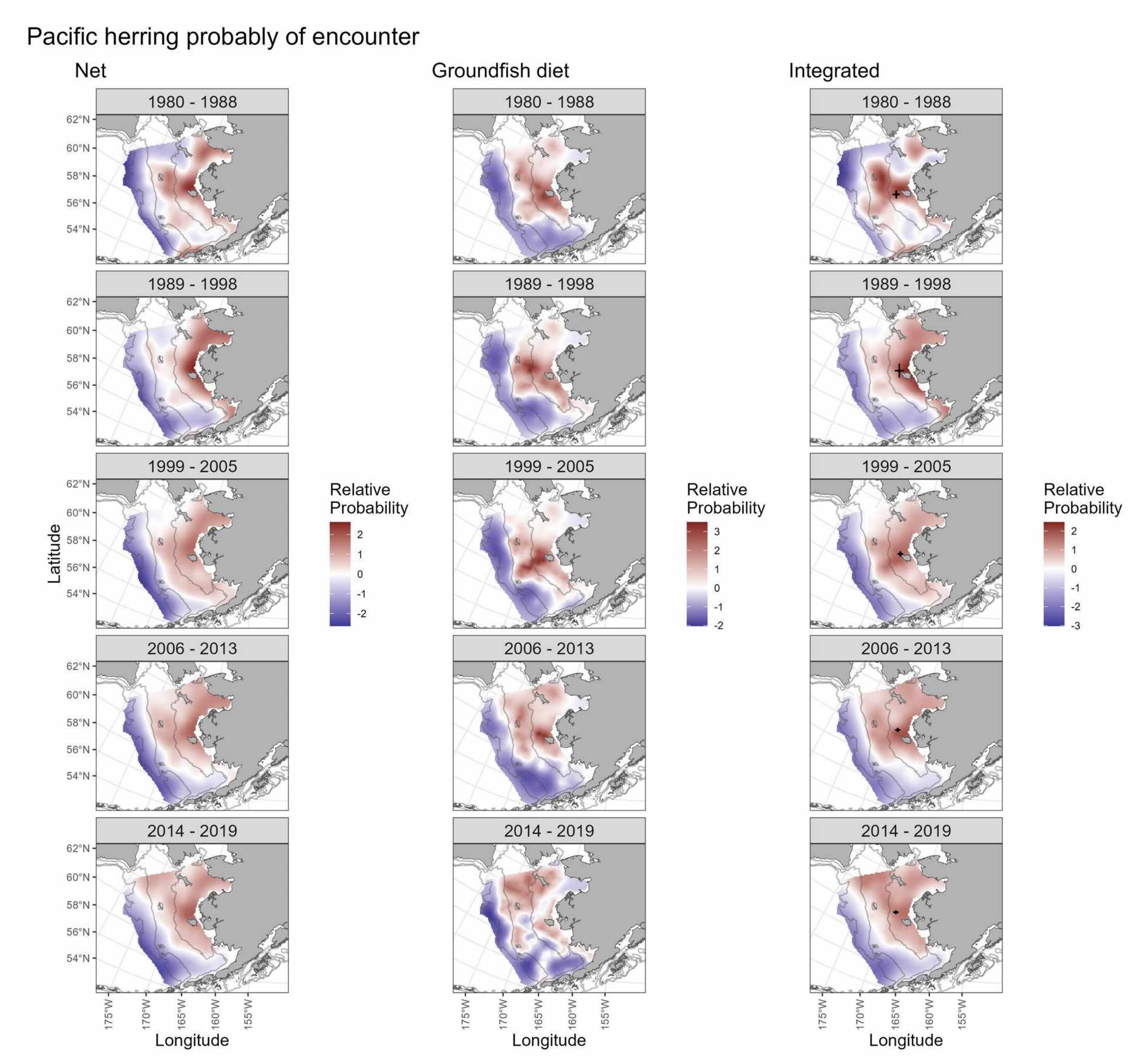

Figure S 3.4: Distribution of Pacific herring in the Bering Sea estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

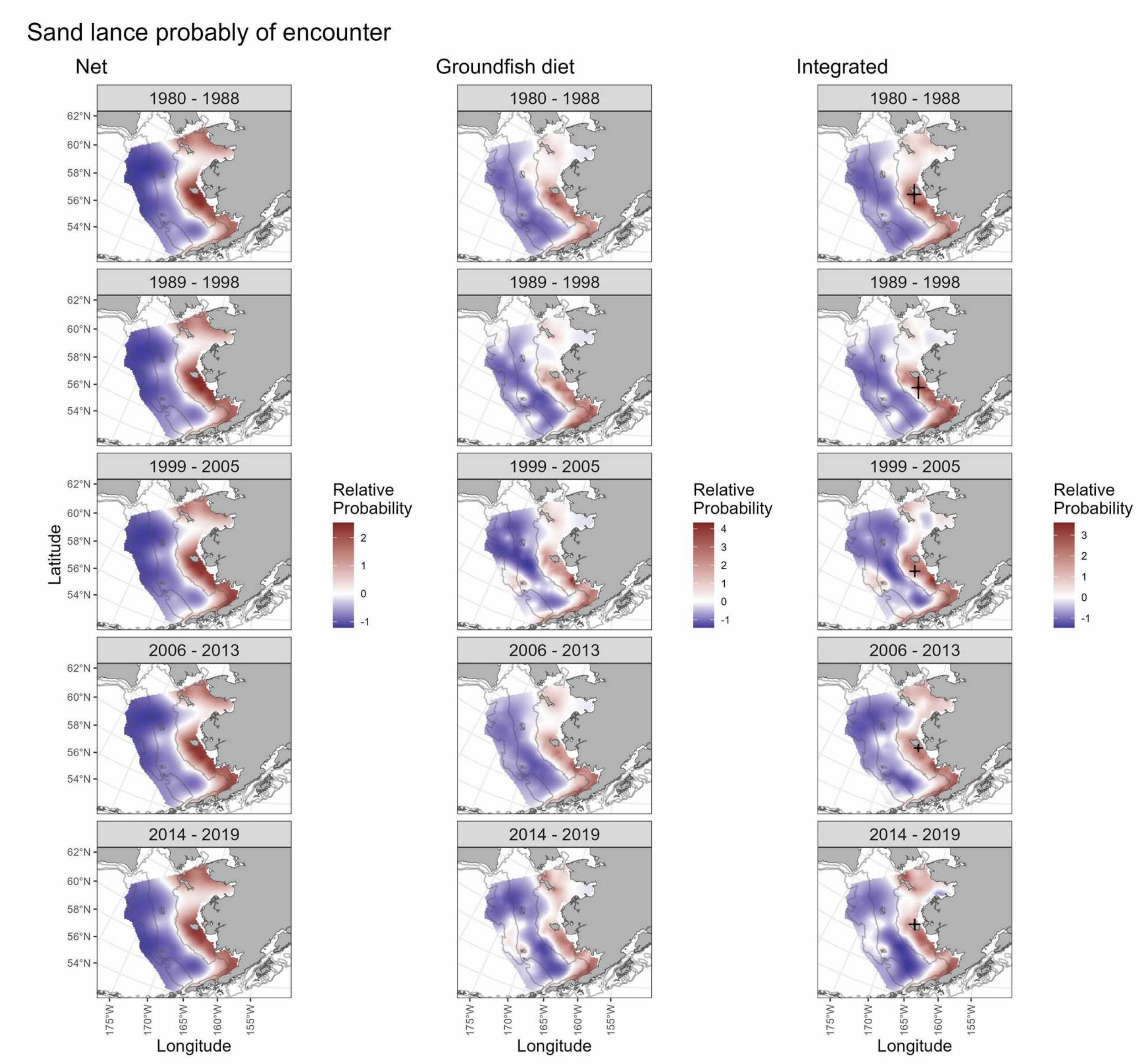

Figure S 3.5: Distribution of sand lance in the Bering Sea estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

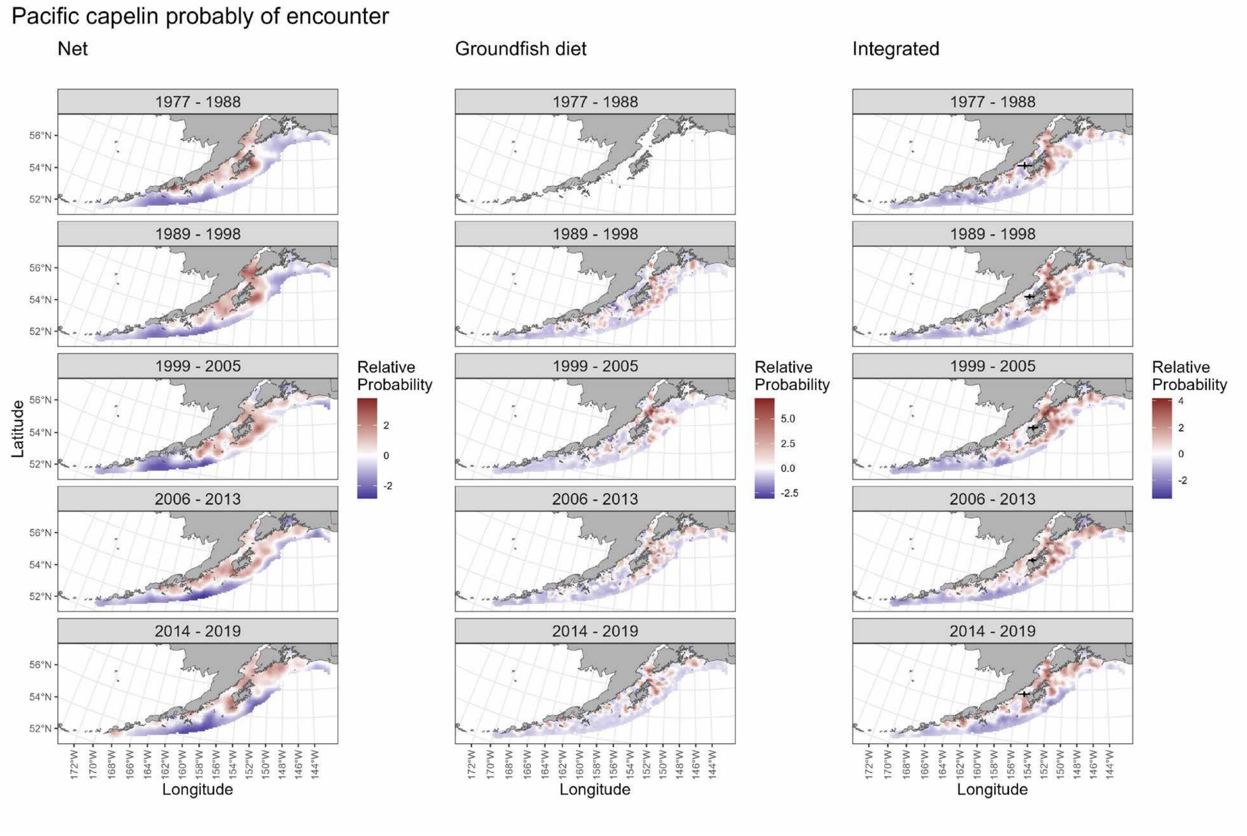

Figure S 3.6: Distribution of Pacific capelin in the Gulf of Alaska estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

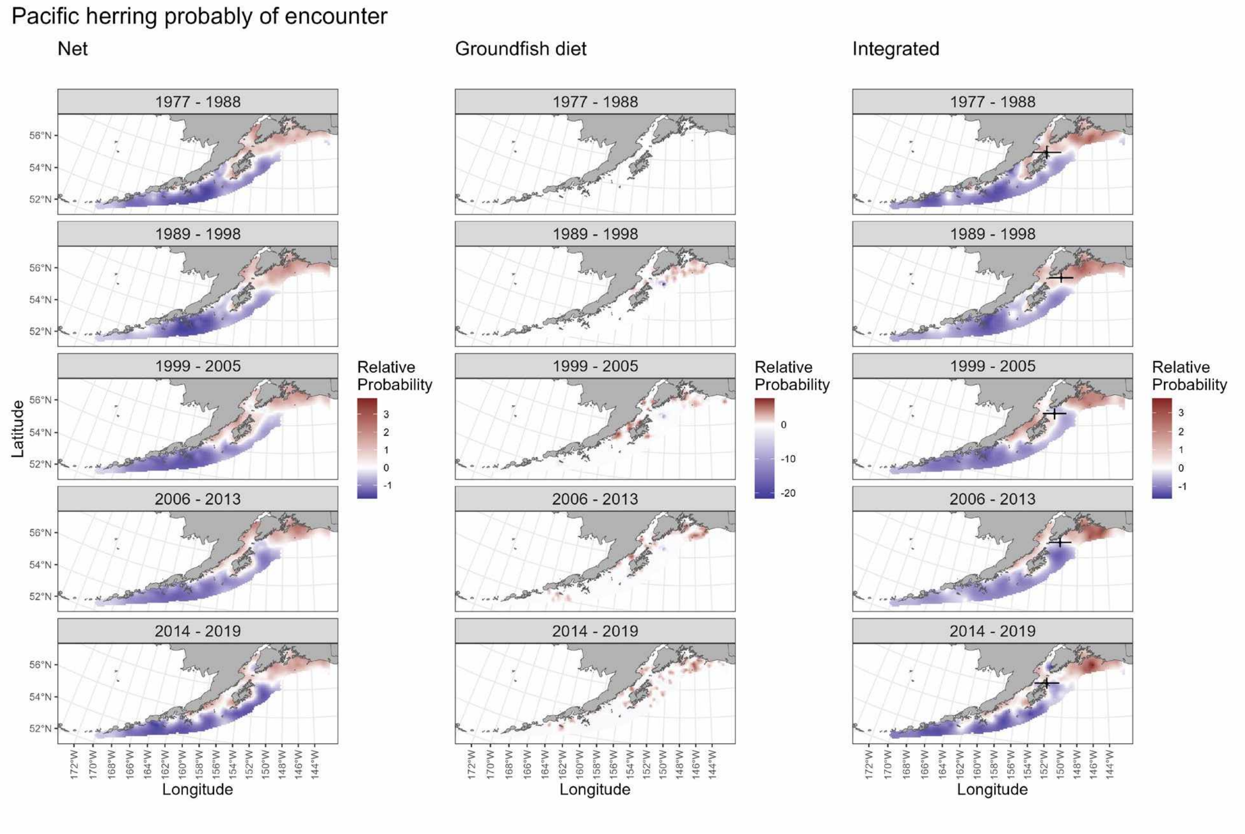

Figure S 3.7: Distribution of Pacific herring in the Gulf of Alaska estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

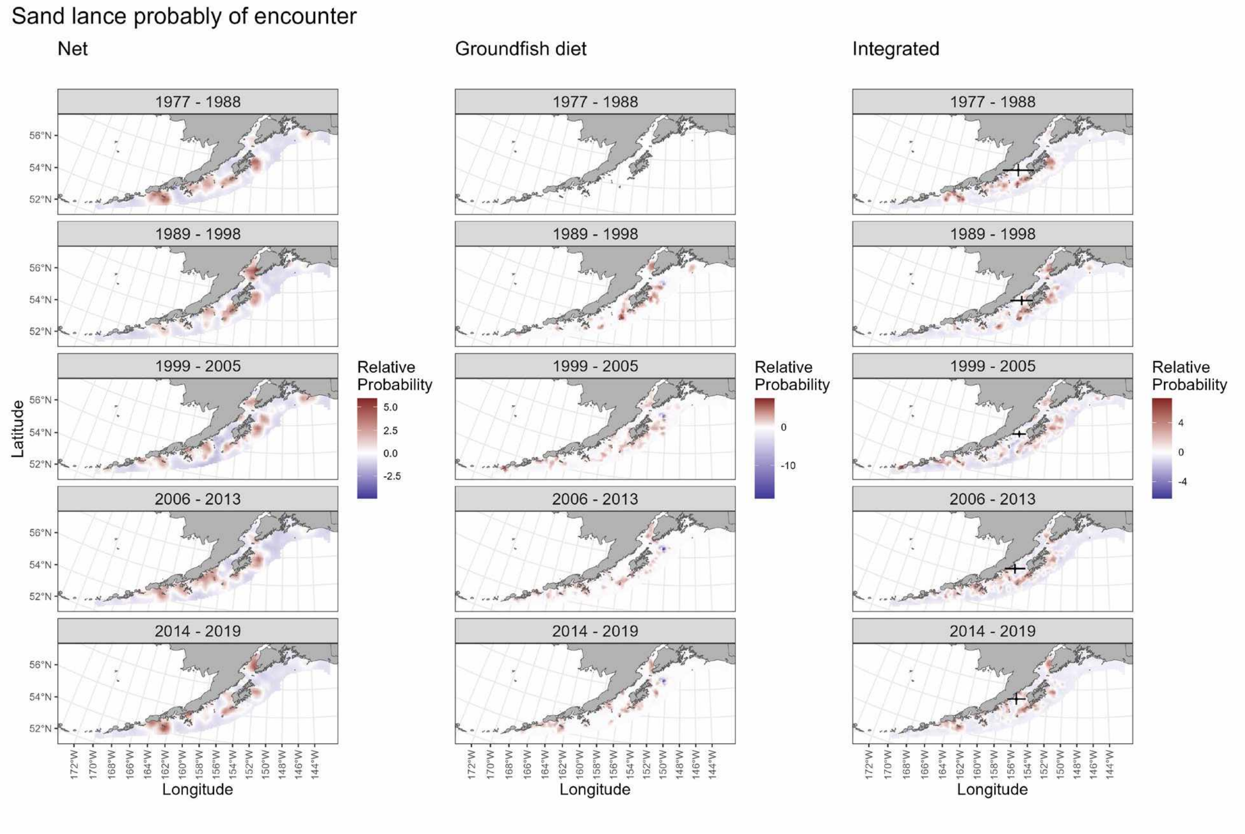

Figure S 3.8: Distribution of sand lance in the Gulf of Alaska estimated from models fit to fisheries survey data, groundfish diet data, and combined data sources. Logit transformed probability of encounter is scaled across space within each stanza to a mean of 0 and SD of 1. Red-blue gradient color indicates a high to low probability of encounter, with white representing the mean. Black points indicate the COG calculated in the decadal stanza, with bars showing the SE.

Chapter 4: General Conclusions

Forage species are nutrient rich small pelagic fish, juvenile fish, and invertebrates (henceforth referred to as forage fish) that feed on lower trophic levels (e.g. zooplankton) and transfer energy up to commercially and culturally important marine predators. As such, forage fish support Alaska's ecosystems and fisheries through their role as abundant prey species, and as the basis for commercial and subsistence harvest in the case of Pacific herring. To improve understanding of Alaskan forage fish populations and their spatial dynamics and responses to climate regime shifts, I compiled available forage fish occurrence and abundance data from a wide variety of data sources including fisheries-independent surveys in nearshore and offshore regions employing a diversity of gear types, and seabird and groundfish predator diets. In doing so, my intent was to explore the extent to which different sources of information on forage fish encounter rate could provide common inference about species-specific trends through time, distribution across space, and spatio-temporal changes following climate regime shifts, despite differences in survey sample design, survey gear, frequency and spatial coverage, and the use of predators as opportunistic samplers of the target forage species.

In collaboration with multiple agencies who lead field data collection efforts, I published the Alaska Forage Fish Database (AFFD), which provides researchers with a novel data repository for analysis of forage fish demography. Thanks to the immense contributions from agencies such as the NOAA Alaska Fisheries Science Center, Alaska Department of Fish and Game, USGS Alaska Science Center, US Fish and Wildlife Service Alaska Maritime National Wildlife Refuge, Gulf Watch Alaska, this project has become largest Alaska forage fish database to date. The data and metadata are published and publicly available as part of a US Geological Survey (USGS) Alaska Science Center data release (Turner et al., 2024). Through the compilation of disparate data sources on Alaskan forage fish occurrence, the AFFD includes abundance and effort information from 461,449 sampling events at 105,420 unique sites from the years 1953 – 2023. Chapter 2 of this thesis describes the spatial and temporal coverage of these data, highlights gaps in forage fish data availability across seasons and regions and discusses the benefits and limitations of the available data within each region.

In the third chapter of this thesis, I utilized the forage fish occurrence data available from the AFFD to inform broad-scale analysis of forage fish population and spatial dynamics in the Bering Sea and Gulf of Alaska. Specifically, I quantified how Alaskan forage fish have responded to climate regime shifts, and the extent to which different data sources including fisheries independent surveys (pelagic and benthic trawls, beach seines) and predator diets (groundfish and seabird diets), described similar or differing spatial and temporal responses. My research assessed occurrence trends and distribution shifts for three species, Pacific capelin (*Mallotus catervarius*), Pacific herring (*Clupea pallasii*) and sand lance (*Ammodytes* spp.), across regions of Alaska.

I examined the differences in interannual trends and response to regime shifts when using fisheries independent surveys or predator diets to estimate forage fish encounter and distribution. While the interannual trends in forage fish encounter probability estimated based on different sources of information (e.g., fisheries surveys vs. predator diets) differed on shorter-time scales (1-5 years), coherent responses by species to rapid bio-physical environmental change, in part due to decadal oscillations (such as ENSO, PNA patterns, and PDO), were detected independent of data source. Asynchronous temporal patterns in predicted encounter probability between models fit to differing data sources exhibited greater synchrony during the most recent heatwave (2014-2016). Despite the observation of some synchrony in predicted trends across time and space, it should be noted that model estimates based on predator diets may be confounded by ontogenetic shifts, diet preferences and prey availability, but our results support previous findings that rapid changes can be detected through the increase or decrease of prey presence in diets (Gunther et al., 2023; Hatch, 2013; Hatch & Sanger, 1992; Piatt et al., 2018; Sydeman et al., 2017)

Findings regarding the temporal trends of forage fish emphasize the importance of long-term datasets in understanding the shifting baseline that occurs when limited by the temporal scale of specific surveys or data sources. An integral part of my analysis came from the inclusion of small-mesh shrimp trawl survey conducted by NOAA and the Alaska Department of Fish and Game in the Gulf of Alaska, which was available from 1953 – 2022 but was consistent in sampling location and survey design from 1972 onward. By integrating the small-mesh shrimp trawl survey data with other survey data sources in my analysis, I demonstrated the persistent impacts of the major regime shift that occurred in 1976/1977 that resulted in a decline in smaller pelagic species. The influence of this post-1976 regime shift on the forage fish species considered was especially apparent for Pacific capelin within the Gulf of Alaska; while research has generally pointed to the 2007-2013 period as a major increase in capelin encounter rate in response to cooler temperatures, the context of early 1970's data suggests that capelin never truly recovered from prior declines. The expanded temporal assessment contextualizes the impact of rapid ecosystem change and recovery time of forage fish.

The general spatial distributions estimated for capelin, herring, and sand lance match expectations based on habitat preferences and previous literature. Overall, predicted distribution among climate stanzas when models were fit to diet or fisheries survey data identified the same primary habitats occupied by each forage fish. However, estimates of encounter probability within primary habitats varied, leading to discrepancies in predicted latitudinal and longitudinal shifts across climate stanzas. When models were fit to the integrated data, estimated forage fish occurrence and distribution differed between the relatively warm period (1999-2005) and the more recent marine heatwave (2014-2019). During the anomalously high temperatures of 2014-2019, capelin shifted inshore in the Bering Sea and Gulf of Alaska, corresponding with a declining encounter probability, while sand lance encounter probability increased in the Northern Bering Sea. Further research is needed to parse out which dynamics are driving these major population changes given the co-occurring effects of abiotic (such as temperature, acidity and low oxygen) and biotic (such as food limitations and predation) factors during each regime shift (Hauri et al., 2024; McGowan et al., 2019; Olsen et al., 2024). Recent literature has emphasized the synergy of abiotic and biotic effects as an influence of the circumstances that led to the dramatic shift in populations after the marine heatwave (Hauri et al., 2024). As extreme events in the marine ecosystem increase in frequency and intensity, the continued exploration of forage fish responses to environmental conditions is crucial for informing sustainable and climate-adaptive management strategies for these important species. My research provides a broad scale assessment of forage fish distribution and encounter, presenting novel results in the Gulf of Alaska that can facilitate a greater understanding of forage fish dynamics and trophic processes in marine ecosystems in response to a rapidly changing climate.

4.1 References

Gunther, K., Baker, M., & Aydin, K. (2023). Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea. Marine Ecology Progress Series, SPF2. https://doi.org/10.3354/meps14389

Hatch, S. A. (2013). Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. Marine Ecology Progress Series, 477, 271–284. https://doi.org/10.3354/meps10161

Hatch, S., & Sanger, G. (1992). Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Marine Ecology Progress Series, 80, 1–14. https://doi.org/10.3354/meps080001