Contribution to the Theme Section 'Small pelagic fish: new research frontiers'

Using predator diets to infer forage fish distribution and assess responses to climate variability in the eastern Bering Sea

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ABSTRACT: Forage fishes comprise an integral part of marine food webs in the highly productive ecosystems of the North Pacific. However, significant knowledge gaps exist related to the status of forage fish, their life histories, and how populations may react to future climatic shifts. Standardized bottom trawl surveys are critical to the stock assessment of groundfish but lack the gear and protocols to quantitatively evaluate small pelagic forage fish. Where diet data are available, predators may be used as an indirect method of collecting data on forage fish distribution and relative abundance. We used stomach contents data to infer predator–prey interactions in the eastern Bering Sea and to analyze the distribution of 5 forage taxa over a 34 yr time series (1985–2019). Using 4 dominant groundfish predators, we constructed forage fish and predator depth and temperature habitat profiles and used center of gravity (COG) analysis and global index of collocation to examine predator–prey overlap. Results provide insight on the habitat partitioning and competitive interactions between forage species and the dynamics between predators and prey. Interannual COG analyses indicated recent periods of cooling (2007–2013) and warming (2014–2019) had significant effects on the distribution of forage fish, and suggest differences in the relative resilience of forage fish populations to climate change in this region. Population shifts were particularly evident in recent periods of anomalous warming, highlighting the need to understand how future periods of prolonged warming may affect predator–prey dynamics. Results also demonstrate the importance of predator diet time series and how these data might inform multi-species models and management strategies.

KEY WORDS: Predator–prey dynamics · Diet analyses · Species distribution models · Climate regime · Surveys · Groundfish · Pacific herring · Pacific sand lance · Eulachon · Capelin

1. INTRODUCTION

Small pelagic fish (i.e. forage fish) play important ecological roles in marine ecosystems (Pikitch et al. 2014, Peck et al. 2021) but are poorly understood, particularly in North Pacific ecosystems (Baker & Siddon 2021, Boldt et al. 2022). Population dynamics and distributions of these species are often highly variable (Szuwalski et al. 2019), and accurately assessing these populations and understanding the pro-

cesses that drive changes in stock productivity and distribution remain a challenge. Further insight into their dynamics may enhance science-based advice to fisheries management, not only relevant to forage species (Kaplan et al. 2016) but also informative to the management of their predators (Engelhard et al. 2014, Holsman & Aydin 2015) and ecosystem-based approaches to management (Whitehouse et al. 2021).

Assessing and managing data-limited fish stocks are a critical challenge (Quinn et al. 2016). Forage

fish in the highly productive North Pacific marine ecosystem comprise an integral part of the marine food web (Rice 1995, Cury et al. 2000). Despite their importance to understanding trophic interactions in the Bering Sea (Aydin & Mueter 2007, Aydin et al. 2007), there is minimal survey effort dedicated to estimating their abundance and distribution. Standardized bottom trawl survey protocols for abundance estimates involving fishery-dependent data and catch per unit effort (CPUE) indices are critical to the stock assessment of groundfish but lack the gear and protocols necessary for evaluating forage fish populations. Significant knowledge gaps exist related to the status of forage fish populations in Alaska, their distribution, and how populations may react to future climatic shifts (Brooker et al. 2007).

Monitoring pelagic forage fish abundance and distribution is complicated by multiple factors; these populations are difficult to sample, undergo large fluctuations in abundance, and are prone to density-dependent and environmentally driven range shifts (Fréon et al. 2005). Thus, monitoring requires creative approaches to sampling and assessment methods. In most traditional fishery-independent surveys, gear used and habitats surveyed are not optimized for capturing forage species. Challenges to effective sampling include habitat constraints and limits to availability (Baker et al. 2019b) as well as gear constraints and issues related to selectivity (De Robertis et al. 2023). New and innovative methods and approaches are often required to survey and assess forage fishes (Boldt et al. 2017, Baker et al. 2021). Predator diets offer a useful tool for assessing these populations (Yang 1993, Yang et al. 2005, Grüss et al. 2020) and may also provide insight into shifts in distribution and abundance in response to environmental change (Holsman & Aydin 2015). Using predator–prey interactions also allows us to derive valuable insight into ecological interactions and the consequences of environmental change on food webs, which are not readily apparent from traditional survey methods.

High-latitude areas such as the North Pacific and Pacific Arctic gateway regions are particularly sensitive to warming (Danielson et al. 2020), and the North Pacific appears to be in a period of intense and substantial climate transformation (Huntington et al. 2020), with long-term projections for continued increases in temperature (Hermann et al. 2019, Ruela et al. 2020). Ecological responses to a warming climate, such as shifts in community composition and distribution of marine species, have been documented in the northeastern Pacific (Overland et al. 2010, Baker & Hollowed 2014, Li et al. 2019) as well

as other regions (Nye et al. 2009, Pinsky et al. 2013). Shifts in the eastern Bering Sea (EBS) have been documented and projected for marine fish and fisheries (Hollowed et al. 2013), including groundfish distribution (Baker 2021a, Rooper et al. 2021). Increasing temperatures and associated changes such as stratification, prey densities, and system phenology may induce differing responses among marine taxa, with implications for predatory and competitive interactions. Both climate and demography influence the strength of predator–prey overlap (Hunsicker et al. 2013), and shifting fish distributions have been shown to impact predation intensity (Goodman et al. 2022). As climate change is anticipated to shift the spatial overlay of trophically interacting species (Schweiger et al. 2008), it is important to predict habitat shifts not only for top predators (Hazen et al. 2013) but also for prey (Rijnsdorp et al. 2009).

Our analysis used a comprehensive dataset on predator–prey interactions in the EBS to analyze the distribution of 4 forage species over a 34 yr time series (1985–2019) via data gathered from predator diet samples. We assessed the diets of 4 abundant and commercially important groundfish predators: walleye pollock *Gadus chalcogrammus*, Pacific cod *G. macrocephalus*, Pacific halibut *Hippoglossus stenolepsis*, and arrowtooth flounder *Atheresthes stomias*, to give insight into the distribution and habitat preferences of 4 forage fish species complexes: sand lance *Ammodytes* spp., capelin *Mallotus villosus*, eulachon *Thaleichthys pacificus*, and herring *Clupea pallasii*, as well as the smelt family Osmeridae spp. Unique differences exist among our 4 predator species including distinct pelagic versus demersal life histories, thermal preference, historic latitudinal ranges, and depth preferences as well as feeding strategies. By comparing and aggregating forage fish consumption trends across these 4 predators, we diversify the range of marine habitat sampled in the EBS.

2. METHODS

2.1. Study system

The EBS is a wide boreal continental shelf extending 500 km from the coast to the continental slope. This shelf is often split into 3 bathymetric zones: an inner domain along the mainland coast (0–50 m), a middle domain (50–100 m), and an outer domain (100–200 m). Physical attributes such as temperature, stratification, and sea ice coverage are highly dynamic and variable between years and as a conse-

quence of recent warming (Overland & Stabeno 2004, Stabeno & Bell 2019). During winter, ice forms and extends from the Bering Strait to the Alaska Peninsula. The extent and duration of ice in winter has a strong effect on the size and extent of the cold pool (bottom temperatures <2°C) that results from melted ice and usually persists throughout the summer. The cold pool typically covers waters in the middle domain, while the inner and outer domain waters at the same latitude to the east and west of the cold pool may be much warmer (Baker et al. 2020b). Sea ice coverage and the extent of the cold pool are primarily determined by atmospheric forcing, water temperature, and strong northerly winds that cool the water column and drive ice southward (Stabeno & Bell 2019).

The cold pool acts as a thermal barrier that affects ecological community structure (Baker & Hollowed 2014), including the distribution of forage fish (Hollowed et al. 2012) and groundfish predators (Duffy-Anderson et al. 2003, Ciannelli & Bailey 2005, Stevenson & Lauth 2019). In recent years, the EBS has experienced warmer than average climate conditions, characterized by a small cold pool and poleward range expansion of subarctic groundfish species (Eisner et al. 2020, Baker 2021a).

Since the start of annual survey data collection (1982), the climate regime of the EBS has transitioned from a pattern of high interannual variability to alternating cold (2007–2013) and warm (2001–2005, 2014–2019) phases (Stabeno et al. 2012, Baker et al. 2020b). Recent studies have used these unprecedented cold and warm phases to explore how climate conditions might influence species distribution and interactions (Baker 2021a, Baker et al. 2022, 2023a). Similarly, this study aims to explore how data derived from a 34 yr time series of predator diets might inform forage fish distribution and predator–prey interactions in the context of climate change. Cumulative distribution functions were constructed to characterize forage fish and predator habitat preferences in relation to depth and temperature. Comparisons between broad temperature regimes are a central point of interest for the ecosystem-based management of these species. Therefore, we present interannual center of gravity (COG) analyses and comparisons of shifts in mean distribution during warm and cold phases to provide insight on how forage fish distributions may be expected to shift in response to continued prolonged periods of extreme climate anomalies. COG latitudes and forage fish areal coverage were regressed against the cold pool index as a complementary analysis to the broad tem-perature regime comparisons to assess the strength of the cold pool as a physical barrier. Global index of collocation (GIC) approaches were used to determine extent overlap and partitioning in predator–prey distributions. Results demonstrate the importance of predator diet data time series and how we might expand the use of these data to inform multi-species models and management strategies.

2.2. Forage fish distributions

Data used in these analyses were collected from 1987 to 2019 in summer bottom trawl surveys of the EBS continental shelf conducted by the NOAA Alaska Fisheries Science Center (AFSC) Groundfish Assessment Program (GAP) (Lauth et al. 2019). Surveys were generally conducted between late May and early August over a standard area of the EBS continental shelf (≤200 m depth) at 376 standardized sampling stations located according to a fixed 20 × 20 nautical mile (37 × 37 km) grid. Trawl duration at each station is 30 min (for an average swept area of ~0.05 km^2), and depth and temperature are recorded in real time. The northern Bering Sea (NBS) survey is conducted over 144 sampling stations based on an extension of the EBS grid. Details of the survey design, sampling gear, and sampling methods are described by Stauffer (2004), Lauth (2011), and Markowitz et al. (2022).

2.3. Predator diets

The most comprehensive dataset on EBS predator–prey interactions is available through the Resource Ecology and Ecosystem Modeling (REEM) program food habits database at NOAA-AFSC (Livingston et al. 2017). This database includes detailed quantitative information on the stomach contents of fish species collected during annual bottom trawl surveys of the EBS between 1985 and 2019. NBS survey data were also included in distribution and consumption maps. Although the NBS has only been sampled in recent years (2010 and 2017–2019), these data are valuable for visualization of the northward movement of species. Collections are designed to sample a suite of common fish predators in each survey. Most fish stomachs were collected during summer months aboard standardized fishery-independent bottom trawl surveys, following a length-stratified sampling scheme containing 3 to 4 length classes, depending on the species. Stomach samples are col-

lected at sea and returned to NOAA-AFSC, where each sample is weighed, and all prey are identified to species level when possible (dependent on digestion stage). Piscivorous prey are counted and weighed, and length is measured when possible. Percentage composition by weight of prey in diet samples is a common metric used to describe and evaluate diet data. Percent weight of forage fish prey is calculated by dividing the mass of a prey species identified in a sample by the total mass of the stomach sample and multiplying by 100. Complete bottom trawl survey methods are detailed in Lauth (2011).

This study focuses on stomach samples from Pacific cod, Pacific halibut, arrowtooth flounder, and walleye pollock. These species are the dominant piscivorous fishes in the EBS and the most consistently surveyed predators over the time series. In the EBS, cod and large flatfish such as arrowtooth and halibut are dominant consumers (Aydin & Mueter 2007). Pollock maintain a central role in the EBS food web as both intermediate predators and prey for all 4 species of groundfish, including pollock (i.e. cannibalism; Aydin & Mueter 2007, Spencer et al. 2016, Livingston et al. 2017). Stomach contents from these 4 species were considered in our analyses for the following reasons: (1) consistency of stomach sample collections over space and time; (2) clearly established evidence for their nodal roles in northeastern Pacific ecosystems (Aydin & Mueter 2007, Gaichas & Francis 2008); and (3) differences in diet, life history, thermal preference, and geographic range among these predators, which diversify the span of marine habitat that we are able to sample via diet analysis.

Four forage fish species (sand lance, capelin, herring, eulachon) and the smelt (Osmeridae) family were considered in this analysis. These species make up most of the forage fish community in the North Pacific and are responsible for much of the energy transferred from lower to higher trophic levels. The family complex Osmeridae was included in the analysis in consideration of the limitations of identifying partially or extensively digested forage fishes to species from solely morphological identification methods (Paquin et al. 2014). Our purpose for including this family was to fully utilize the diet database for representation of forage fish distributions.

2.4. Identification of cold and warm periods

There has been a series of distinct thermal phases in the EBS (Stabeno et al. 2012, Baker et al. 2020b). Following a period of high interannual variability

(1982–2000), the system transitioned into multi-year stanzas of warm (2000–2005, 2014–2019) and cold (2007–2013) periods. These trends are also evident in the western Bering Sea (Khen et al. 2013, Kivva et al. 2021) and in the NBS (Baker 2021b). Table 1 lists which years of data were assigned to each general climate category (i.e. cold, average, warm) for these analyses.

2.5. Spatial analysis

To examine the relationship between predator distributions, prey distributions, and how these may shift interannually and with the climate regime, consumption maps were constructed for each predator and prey combination over the full length of the time series. Percent weight of forage fish recorded in the diet samples of predators was represented by the size of the circle used to mark that coordinate position. This visual aid allows us to see predator distributions and patterns associated with their consumption of forage fishes overall. Additionally, the same dataset is presented in an alternative way by mapping the consumption patterns of each forage fish by all predators considered in this survey.

The center of distribution for each forage fish species was calculated annually and comprehensively following protocols from Nye et al. (2009) and Baker (2021a). We also used spatial metrics (Ciannelli et al. 2008, Carroll et al. 2019) to describe the distribution of each species and quantify the spatial overlap among species.

The COG represents the mean spatial location of the sampled population. The COG for each forage fish species was calculated by using the biomass-weighted mean for latitude (X_{lat}, °N) and longitude (X_{long}, °W) using Eqs. (1) & (2):

$$\bar{X}_{lat} = \frac{\sum_{i=1}^{n}(N_i \times lat_i)}{\sum_{i=1}^{n} N_i} \tag{1}$$

$$\bar{X}_{long} = \frac{\sum_{i=1}^{n}(N_i \times long_i)}{\sum_{i=1}^{n} N_i} \tag{2}$$

where N_i is the percent weight of forage fish in stomach samples at a particular location i for the species and years of interest.

Comprehensive COG coordinates are presented on the forage fish consumption maps. Annual COG latitudes are reported in a line graph and overlaid with the cold pool index. The use of a weighted mean center of distribution for geographic latitude and lon-

Table 1. Years categorized by their average climate conditions used in these analyses. Gathered from various publications (Wyllie-Echeverria & Wooster 1998, Brodeur et al. 1999, Stabeno et al. 2001, 2012, Aydin & Mueter 2007, Hollowed et al. 2012, Holsman & Aydin 2015, Baker et al. 2020b)

Warm years	Average years	Cold years
1987	1985	1986
1989	1988	1992
1993	1990	1995
1996	1991	1997
1998	1994	1999
2001–2005	2000	2007–2013
2014–2019	2006	

gitude has been used in many studies to determine preferred location and habitat conditions of different stocks (Perry et al. 2005, Nye et al. 2009, Pinsky et al. 2013, Baker 2021a). Maps were made in Rstudio primarily using the package 'ggplot2' (Wickham et al. 2016).

COG latitude was calculated annually for each forage fish species, and a COG coordinate for the consumption of each forage fish species as aggregated by climate regime was calculated and displayed on the consumption maps of forage fish by groundfish predators. COG latitude and the areal extent of forage fish were regressed against the cold pool index to assess the effect of the cold pool as a direct physical barrier to fish populations. The cold pool index is defined as the area of the EBS bottom trawl survey with bottom temperatures less than or equal to 2°C, in square kilometers. Cold pool index data were gathered in Rstudio from the 'coldpool' package (Rohan et al. 2022) as given in the AFSC GAP Survey Data Products github repository (https://github.com/afsc-gap-products). Regression statistics were calculated in Excel (Analysis Toolpak) and are displayed in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m14389_supp.pdf.

Inertia (I) is the variance of the location of individuals in the sampled population and describes dispersion of the population around its COG:

$$I = \sum_{i=1}^{N} \left(\frac{\sum_{i=1}^{n} (x_i - \text{COG})^2}{\sum_{i=1}^{N}} \right) \qquad (3)$$

To evaluate the spatial overlap between forage fish species and to examine the shifts in distribution within each individual forage species in response to the distinct climate regimes, we used the GIC (Renard et al. 2023, RGeostats: The Geostatistical R

Package. Version 21, http://cg.ensmp.fr/rgeostats). The GIC is a spatial statistic that captures the extent to which 2 populations are geographically distinct by comparing the distance between their centers of gravity and their inertias (Woillez et al. 2007, 2009, Petitgas et al. 2017). A GIC was calculated from the percent weight of forage fish in each predator diet sample and associated with the given coordinates where that predator was sampled. GIC measures range from 0 to 1, where 0 indicates each population is concentrated on a single but different location (no individuals of either species co-occurred at any site), and 1 indicates where the centers of gravity coincide:

$$\text{GIC} = 1 - (\Delta \text{COG2} / \Delta \text{COG2} + I1 + I2) \qquad (4)$$

where ΔCOG is the distance between the centers of gravity of 2 populations with densities $z1(x)$ and $z2(x)$ at point x, and $I1$ and $I2$ are their respective inertias.

Spatial metrics were calculated using the 'RGeostats' package (Renard et al. 2023) in R (R Core Team 2022, version 4.2.2). ANOVA and Tukey-Kramer ($\alpha < 0.05$) approaches were used to compare weighted annual mean latitudes and longitudes among species and among climate regimes within species, using the 'Real Statistics Resource Pack' add-in for Excel (Zaiontz 2020, see www.real-statistics.com).

2.6. Cumulative distribution functions

To better understand species habitat preferences as they relate to depth and temperature, we compared the cumulative distribution of the observation of these variables in the EBS habitat over the entire time series with the cumulative distribution of the mass of forage fish found in the diets of predators sampled during the bottom trawl survey. This approach has 3 steps that were described by Perry & Smith (1994). First, we characterize the general frequency distribution of the habitat variable (depth or temperature) by constructing its cumulative distribution function using Eq. (5):

$$f(t) = \sum_i \frac{1}{n} I(x_i) \qquad (5)$$

with the indicator function $I(x_i)$,

$$I(x_i) = \begin{cases} 1, & if \ x_i \le t \\ 0, & otherwise \end{cases} \qquad (6)$$

where t represents an index variable ranging from the lowest to highest value of the habitat variables

assessed. Eq. (5) was calculated over all values of t for each measurement of the habitat (x_i).

Second, we associated the mass of a particular species of prey forage fish found in the diet samples of predators with the habitat conditions at that location set as a weighted value in the form $g(t)$:

$$g(t) = \sum_i \frac{1}{n} \frac{W_i}{W} I(\mathbf{x}_i) \tag{7}$$

where W_i is the mass of the species caught at a specific habitat condition, and W is the total mass of a species caught over the survey area. Therefore, $g(t)$ gives the cumulative frequency of a species found at the habitat value being tested. Weighting the habitat variable (depth or temperature) cumulative distribution function by fish mass results in curves that increase at a faster rate (relative to the unweighted cumulative distribution function) where fish are abundant and at a slower rate where rare. A $g(t)$ equal to 1 indicates that 100% of fish were found at or below the habitat variable value (x_i).

Finally, to determine the strength of the association between catch and the habitat variable, we assess the degree of difference between the 2 curves $g(t)$ and $f(t)$. This is done by calculating the maximum absolute vertical distance between $g(t)$ and $f(t)$:

$$\max|g(t) - f(t)| = \max | \sum_i \frac{1}{n} \left(\frac{y_i - \overline{y_t}}{\overline{y_t}} \right) I(x_i) \tag{8}$$

where $| g(t)$ and $f(t) |$ indicate the absolute value of the difference between $g(t)$ and $f(t)$ at any point $t.$ We applied the Kolmogorov-Smirnov test to assess goodness of fit. We also applied the Anderson-Darling test of goodness of fit, which may perform with higher power when comparing 2 distributions that (1) vary in shift only, (2) vary in scale only, (3) vary in symmetry only, or (4) have the same mean and SD but differ on the tail ends only (Engmann & Cousineau 2011). We are interested in identifying differences at the extremes of the distributions as a means of depicting critical thresholds; the Anderson-Darling test provides additional weight to the tails and is therefore a useful alternative method alongside the Kolmogorov-Smirnov test. These goodness of fit tests were completed using the 'Real Statistics Resource Pack' add-in for Excel (Zaiontz 2020, see www.real-statistics.com).

We plot and evaluate the value of the variables at which $\max | g(t) - f(t) |$ is greatest. This was determined by calculating the top 5% of the distribution of $\max | g(t) - f(t) |$ for each cumulative distribution frequency plot. The top 5% maximum difference values for each species distribution curve and the range of depths and bottom temperatures associated with

maximum difference are reported in Tables S1 and S2. These values represent the strongest association between the environmental variable and the abundance of fish (Tseng et al. 2013).

3. RESULTS

3.1. Predator distributions and habitat profiles

Cumulative distribution functions show that predator distributions varied by species and by climate regime in the Bering Sea and provide important insights into predator distribution by depth and temperature (Figs. 1 & 2). All Kolmogorov-Smirnov and Anderson-Darling goodness of fit tests between the cumulative distribution frequency of predator ranges and the distribution of temperature and depth ranges across the Bering Sea returned significant test statistics (p < 0.001), demonstrating predators show preferences for specific ranges of depth and temperature within the environment. Pollock distributions were found at shallow depths, reflecting a life history characterized by ontogenetic shifts that occur as pollock move sequentially deeper into the EBS with age (Fig. 1a). Cod and halibut had similar depth distributions (Fig. 1b,c). All 3 of these predators were widely distributed across the available depth gradients on the EBS continental shelf. In contrast, arrowtooth are nearly exclusively distributed at greater depth in the outer shelf. The max $| g(t) - f(t) |$ for arrowtooth distribution was greatest from 88 to 95 m depth (Fig. 1d). The values and overall shape of the cumulative distribution function of pollock most closely match those of the habitat. Pollock were found at temperatures as low as –2.1°C, and the temperatures where max $| g(t) - f(t) |$ was highest were between 4.0 and 4.3°C (Fig. 2a). Cod were also present at the coldest temperatures (–2.1°C), and the max $| g(t) - f(t) |$ between the distribution of cod and the habitat was greatest between –0.7 and 0.7°C, the coldest max $| g(t) - f(t) |$ among the fish in this analysis (Fig. 2b). The cumulative distribution curve for arrowtooth has a steep slope between the temperatures of 2 and 4°C, indicating a strong preference for relatively warm water temperatures (Fig. 2d). Similarly, halibut distributions showed a preference for warmer waters; max $| g(t) - f(t) |$ was greatest between 1.2 and 2.9°C (Fig. 2c).

Viewed spatially, the most widespread predators, cod and pollock, were found in bottom trawl surveys throughout the EBS survey grid (Fig. 3, '+' marks predator distribution) and were also found in a large
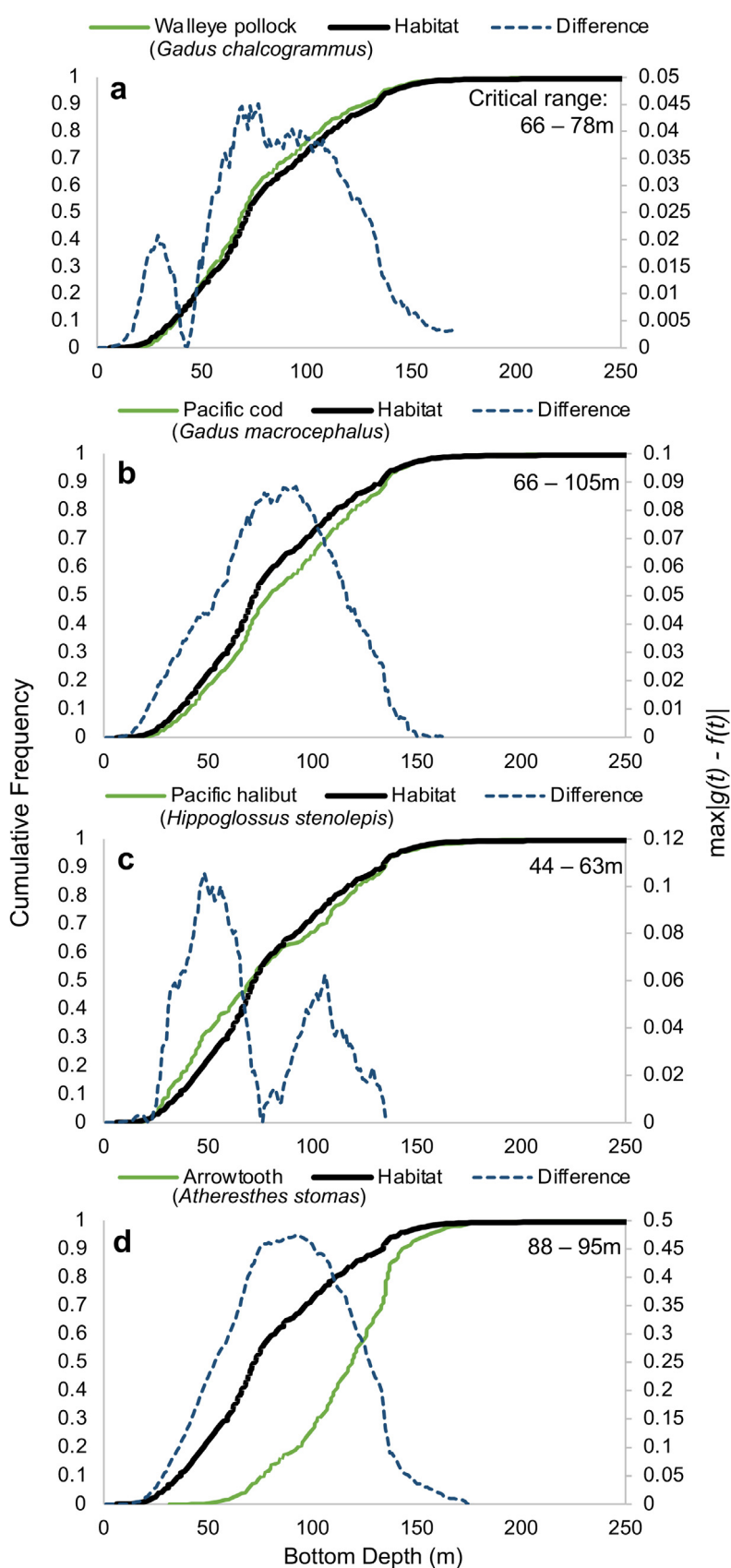
section of the NBS. Halibut distribution was mostly restricted to the EBS, south of the 62nd parallel, present only in a few locations in the NBS (Fig. 3c). Halibut were also more commonly distributed in the inner shelf; more halibut were found in the inner domain (waters <50 m) than any other predator (Fig. 1c). Arrowtooth distribution was the most restricted among predators, with the majority of occurrences in the outer domain (100–200 m depth); arrowtooth were also generally absent in the NBS and concentrated south of 60° N (Fig. 3d). This preference for deeper and warmer waters was mirrored in the cumulative distribution function; 80% of arrowtooth were found at depths >100 m and waters warmer than 2°C (Figs. 1d & 2d).

3.2. Prey distributions and habitat profiles

Kolmogorov-Smirnov and Anderson-Darling goodness of fit tests were assessed for each forage fish cumulative distribution against the cumulative distribution function of all haul locations across the survey area. Each comparison showed that these distributions were significantly different (p < 0.001) from the distribution of depths and bottom temperatures throughout the habitat, indicating that species distributions reflect a habitat preference.

Sand lance distribution was concentrated nearshore between Nunivak Island and the Alaska Peninsula. Most occurrences of sand lance in predator

Fig. 1. Cumulative distribution functions of the bottom depths (m) occupied by each predator compared to the function of all bottom depths surveyed in the Bering Sea. (a) Walleye pollock, (b) Pacific cod, (c) Pacific halibut, (d) arrowtooth. The values with the largest degree of difference (max | $g(t) - f(t)$ |) between these distributions, as shown by the blue line and secondary axis, represent the preferred habitat range of the populations. The range of depth values in the top 5% of max | $g(t) - f(t)$ | are listed on each graph in the upper right corner
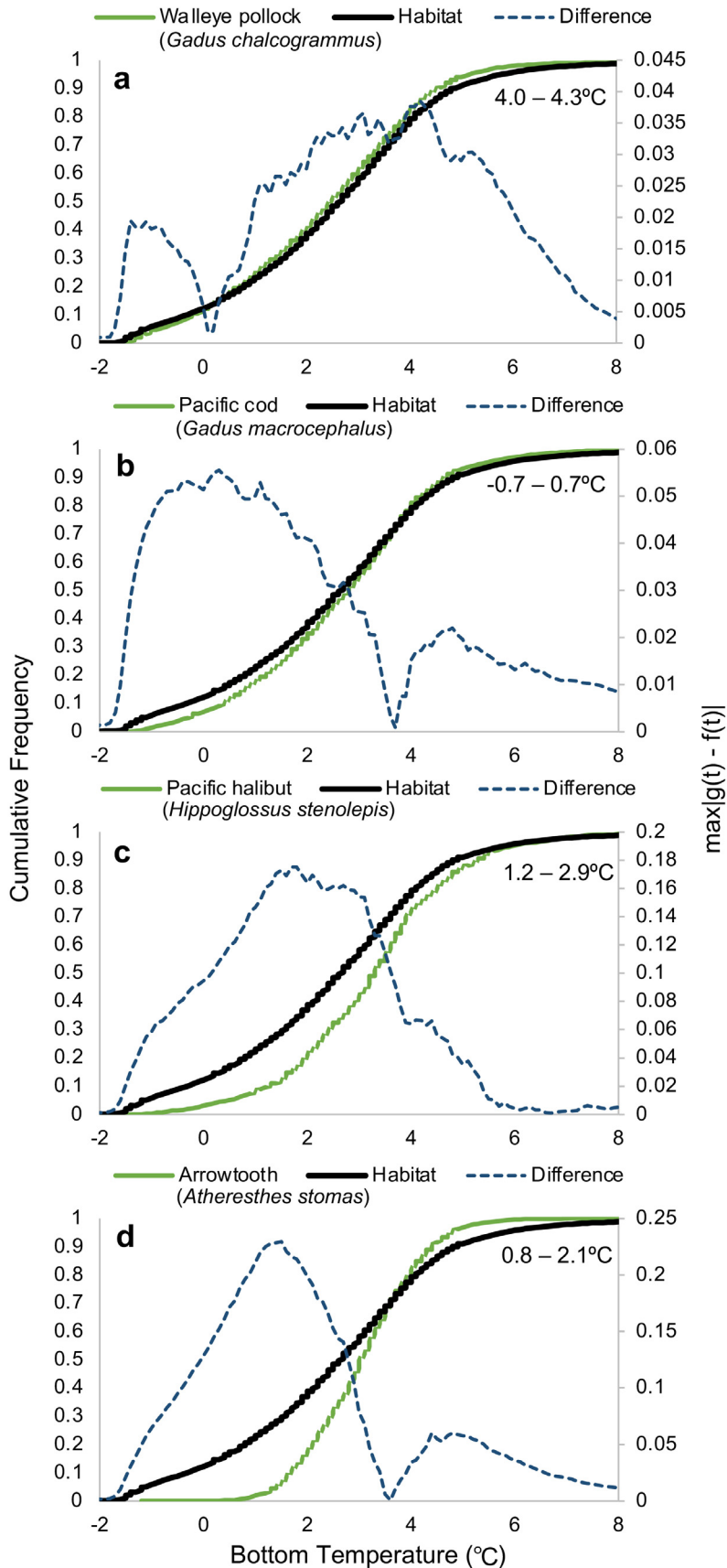
diet samples occurred in the inner domain, and a small cluster was located near the Pribilof Islands. Sand lance were found in shallow waters; the steep cumulative distribution function shows that 80% of the population was found in waters ≤53 m (Fig. 4a). Cumulative distributions show that this species had one of the warmest bottom temperature profiles among forage fishes; 80% of sand lance were found in waters exceeding 2.6°C, and the temperature values where max $|g(t) - f(t)|$ was greatest fell between 2.5 and 3.8°C (Fig. 5a).

Cumulative distributions for bottom depth were similar between capelin and sand lance, with 80% of capelin found in waters ≤44 m (Fig. 4b). Unlike sand lance, capelin range spread further west into the middle domain (50–100 m) of the EBS shelf (Fig. 3e–h). Capelin also had a lower incidence of occurrence in Bristol Bay and nearshore to the Alaska Peninsula compared to sand lance. The max $|g(t) - f(t)|$ was greatest for capelin between 2.7 and 3.8°C; however, they could be found in waters as cold as −1.6°C (Fig. 5b).

Herring were the most widespread among the forage fish in this study. Herring were distributed across depths with low max $|g(t) - f(t)|$ values (<0.14), indicating little preference for any specific bathymetric range (Fig. 4c), but preferred much colder waters compared to the other forage fish species (Fig. 5c). Half of all herring were found in waters 1.8°C or colder, in contrast to 3.5°C (capelin, eulachon, smelt) and 3.9°C

Fig. 2. Cumulative distribution function of the bottom temperature (°C) occupied by each predator compared to the cumulative distribution frequency of bottom temperatures surveyed in the Bering Sea. (a) Walleye pollock, (b) Pacific cod, (c) Pacific halibut, (d) arrowtooth. The values with the largest degree of difference (max $|g(t) - f(t)|$) between these distributions, as shown by the blue line and secondary axis, represent the preferred habitat range of the populations. The range of temperature values in the top 5% of (max $|g(t) - f(t)|$) are listed on each graph in the upper right corner
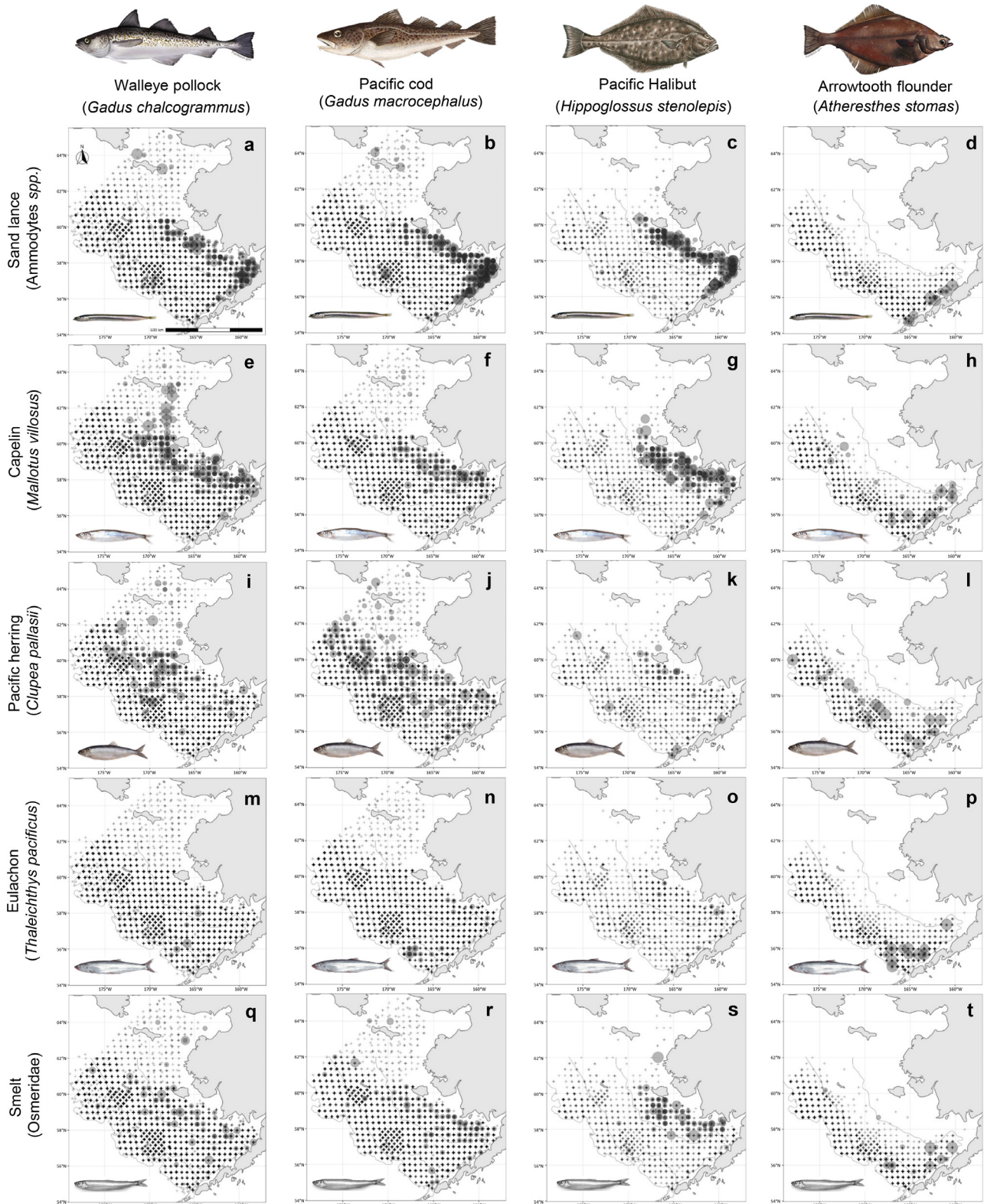
Fig. 3. Consumption maps for each predator and forage prey combination for all years of the time series (1985–2019). (a,e,i,m,q) Walleye pollock, (b,f,j,n,r) Pacific cod, (c,g,k,o,s) Pacific halibut, (d,h,l,p,t) arrowtooth flounder. Grey lines denote domain boundaries. Each + represents the location of a haul where predators were caught but no forage fish were found in diet samples. Each circle represents the location of a forage fish sampled by a predator, and the size of the circle corresponds to the percent weight of that sample, with larger circles indicating a higher percent weight of prey in the sample. Darker symbols (+ or circles) indicate multiple years of data layered on the same location
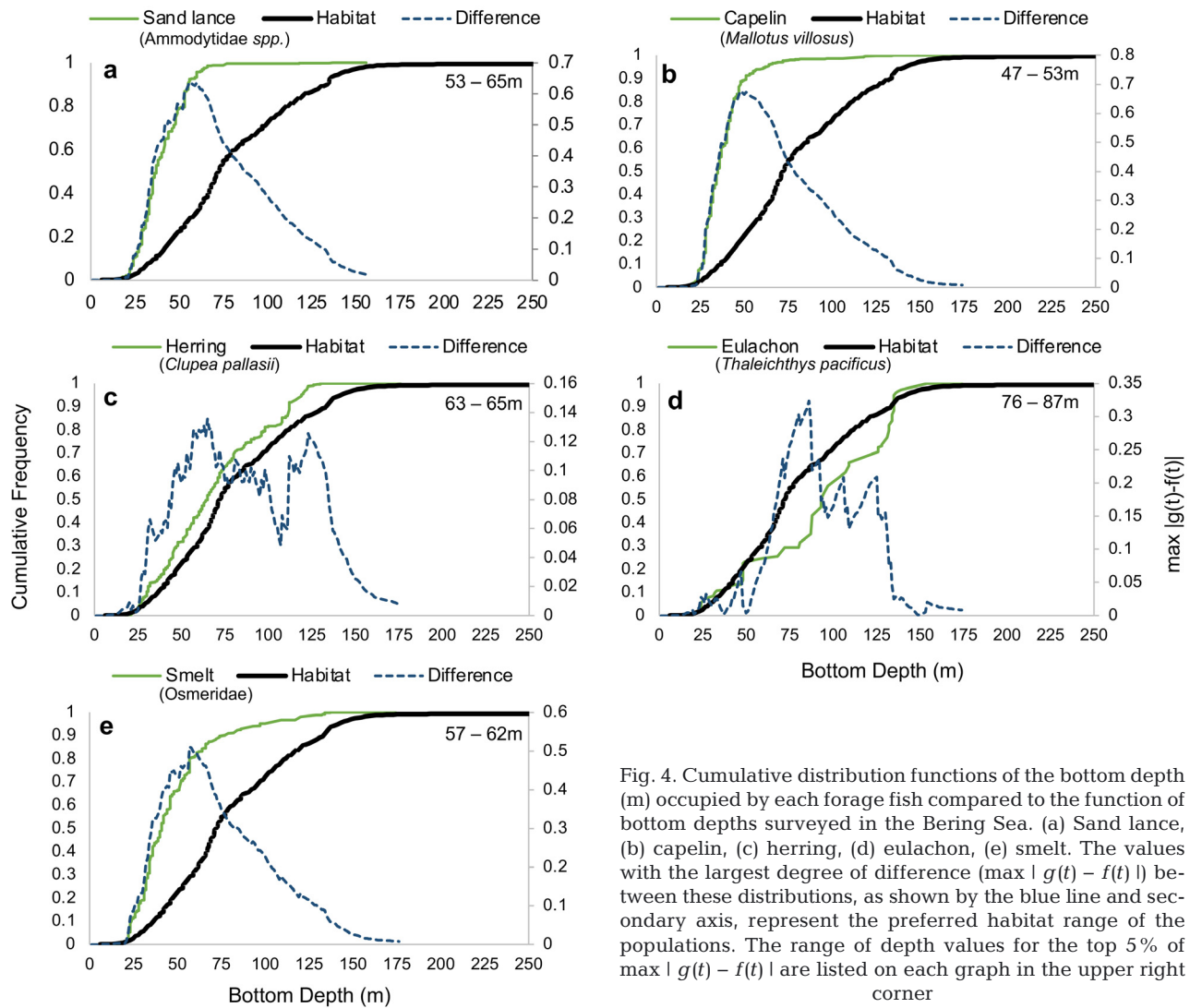
Fig. 4. Cumulative distribution functions of the bottom depth (m) occupied by each forage fish compared to the function of bottom depths surveyed in the Bering Sea. (a) Sand lance, (b) capelin, (c) herring, (d) eulachon, (e) smelt. The values with the largest degree of difference (max | $g(t) - f(t)$ |) between these distributions, as shown by the blue line and secondary axis, represent the preferred habitat range of the populations. The range of depth values for the top 5% of max | $g(t) - f(t)$ | are listed on each graph in the upper right corner

(sand lance) for 50% cumulative frequency thresholds in other forage species. The greatest values of max | $g(t) - f(t)$ | of herring were between 0.5 and 2.0°C.

Eulachon were distributed deeper than the other forage fishes, with 50% of the population in waters ≥93 m and highest max | $g(t) - f(t)$ | values from 76 to 87 m (Fig. 4d). Eulachon also tended to occupy warmer waters compared to other forage fishes; 80% of eulachon were found in waters ≥2°C, with greatest max | $g(t) - f(t)$ | values corresponding to the range of 2.3 to 3.3°C (Fig. 5d). Eulachon were concentrated in the middle and outer domains in the southwestern section of the EBS, with a few records in the inner domain between Nunivak Island and the Alaska Peninsula (Fig. 3m–p).

Smelt were mostly found in the inner domain, with some observations reaching into the middle and even

outer (100–200 m) domains. Smelt preferred shallower waters, with 80% of the population at a depth ≤41 m (Fig. 4e). The greatest values of max | $g(t) - f(t)$ | for bottom temperature occurred at 3.4 to 4.9°C, the warmest range among the forage fishes analyzed (Fig. 5e).

3.3. Patterns of consumption

Halibut consumed the largest percent weight of forage fish (6.32%) among predators, with the largest portion composed of sand lance (2.92%), followed closely by capelin (2.30%; Table 2). Arrowtooth consumed the second highest percent weight of forage fish at 2.37% of its total diet, while cod and pollock consumed the lowest amounts of forage fish. Eulachon was the least consumed forage fish among all preda-
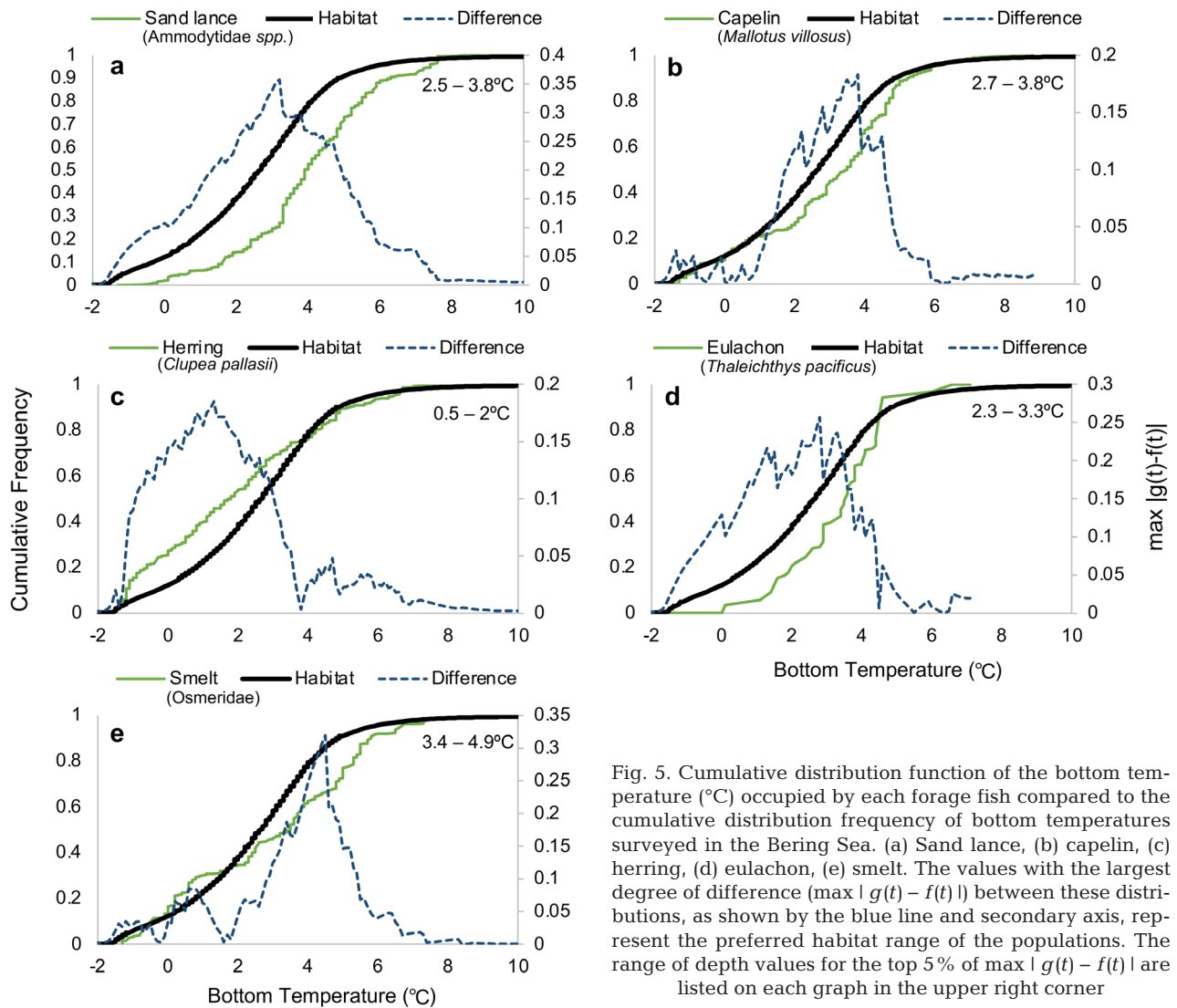
Fig. 5. Cumulative distribution function of the bottom temperature (°C) occupied by each forage fish compared to the cumulative distribution frequency of bottom temperatures surveyed in the Bering Sea. (a) Sand lance, (b) capelin, (c) herring, (d) eulachon, (e) smelt. The values with the largest degree of difference (max | $g(t) - f(t)$ |) between these distributions, as shown by the blue line and secondary axis, represent the preferred habitat range of the populations. The range of depth values for the top 5% of max | $g(t) - f(t)$ | are listed on each graph in the upper right corner

tors except arrowtooth, with percent weights totaling <0.1% of their diet. Arrowtooth diet samples also contained the largest percent weight of herring among the 4 predators. The species of forage fish with largest percent weight in cod diets was sand lance (0.97%).

The species of forage fish with the largest percent weight in pollock diets was capelin (0.67%).

Pairwise comparison of annual weighted mean latitudes (Table 3) between species showed that most combinations of species were significantly different

Table 2. Percent weight of forage fish consumed by predators in the eastern Bering Sea from 1987−2019. N: total number of predators sampled

	Walleye pollock (N = 76968)	Pacific cod (N = 49213)	Pacific halibut (N = 7071)	Arrowtooth flounder (N = 9288)
Total forage fish	1.78	2.04	6.32	2.37
Sand lance	0.44	0.97	2.92	0.33
Capelin	0.67	0.28	2.30	0.51
Pacific herring	0.47	0.62	0.37	0.72
Eulachon	0.03	0.04	0.05	0.52
Smelt	0.17	0.13	0.68	0.29

Table 3. ANOVA and Tukey-Kramer test for weighted mean pairwise comparison of annual center of gravity between forage fish species. Shifts between species in latitude to the north are indicated by positive difference values and to the south by negative difference values; shifts in longitude to the west (offshore) are indicated by positive values and to the east (inshore) by negative values. ** $p < 0.05$, *** $p < 0.001$

Species 1	Species 2	Difference	95% CI	Significance (adjusted p)
Latitude (° N) (ANOVA, $F_{4,155} = 26.6$, $p < 0.001$)				
Herring	Sand lance	−1.1	(0.3–1.8)	***
Herring	Eulachon	−2.7	(1.9–3.5)	***
Herring	Capelin	−0.3	(−0.4 to 1.0)	0.769
Herring	Smelt	−0.6	(−0.2 to 1.3)	0.197
Sand lance	Eulachon	−1.6	(0.9–2.4)	***
Sand lance	Capelin	0.8	(0.0–1.5)	0.040 **
Sand lance	Smelt	0.5	(−0.3 to 1.2)	0.373
Eulachon	Capelin	2.4	(1.6–3.2)	***
Eulachon	Smelt	2.1	(1.3–2.9)	***
Capelin	Smelt	−0.3	(−0.5 to 1.0)	0.854
Longitude (° W) (ANOVA, $F_{4,155} = 27.2$, $p < 0.001$)				
Herring	Sand lance	−6.1	(4.5–7.7)	***
Herring	Eulachon	−3.1	(1.3–4.8)	***
Herring	Capelin	−3.5	(1.8–5.1)	***
Herring	Smelt	−3.2	(1.6–4.9)	***
Sand lance	Eulachon	3.0	(1.3–4.8)	***
Sand lance	Capelin	2.6	(1.0–4.3)	***
Sand lance	Smelt	2.9	(1.2–4.5)	***
Eulachon	Capelin	−0.4	(−1.4 to 2.2)	0.971
Eulachon	Smelt	−0.2	(−1.6 to 1.9)	0.999
Capelin	Smelt	0.2	(−1.4 to 1.9)	0.995

(Tukey-Kramer, p < 0.04), with the exceptions of herring and capelin (Tukey-Kramer, 95% CI = −0.4–1° N, p = 0.769), herring and smelt (Tukey-Kramer, 95% CI = −0.2–1.3° N, p = 0.197), sand lance and smelt (Tukey-Kramer, 95% CI = −0.3–1.2° N, p = 0.373), and capelin and smelt (Tukey-Kramer, 95% CI = −0.5–1° N, p = 0.854). There were also significant differences between the annual weighted mean longitude of forage fish species consumed by predators across the time series (ANOVA, $F_{4,155} = 27.2$, p < 0.001). Pairwise comparison of annual weighted mean latitudes between species showed that most combinations of species were significantly different (Tukey-Kramer, p < 0.001), with the exceptions of eulachon and capelin (Tukey-Kramer, 95% CI = −1.4–2.2° N, p = 0.971), eulachon and smelt (Tukey-Kramer, 95% CI = −1.6–1.9° N, p = 0.999), and capelin and smelt (Tukey-Kramer, 95% CI = −1.4–1.9° N, p = 0.995). Capelin and smelt had non-significant differences between both annual weighted mean latitude and longitude over the time series, indicating there is a high degree of overlap between these 2 distributions.

Sand lance consumption among all predators was concentrated in the inner domain (0–50 m) from Nuni-

vak Island to the coast of the Alaska Peninsula (Fig. 3a–d). Arrowtooth consumption of sand lance is restricted to coastal waters near the Alaska Peninsula, with an outlier near the Pribilof Islands (Fig. 3d). Relatively few instances of sand lance consumption were found in the NBS; however, those that do occur there were from diet samples of pollock and cod (Fig. 3a,b).

Capelin consumption patterns are closely aligned with those of sand lance (Fig. 3e–h). However, the distribution stretches farther west and north than sand lance, with fewer instances of consumption along the coast of the Alaska Peninsula. Notably, pollock consumption of capelin stretches from Nunivak Island up to St. Lawrence Island in the NBS (Fig. 3e), a unique pattern in comparison to cod, the other widespread generalist predator, which provided only a few instances of capelin consumption in the NBS (Fig. 3f).

Herring consumption was widespread throughout the Bering Sea (Fig. 3i–l). Consumption occurred in all domains for cod, pollock, and halibut. Arrowtooth consumption of herring also occurred more frequently in waters farther offshore than any other forage fish (Fig. 3l).

Eulachon consumption was the lowest in comparison to all other forage fish (Table 2, Fig. 3m–p). Most instances of consumption occurred in the southwestern portion of the EBS, south of 56° N (Fig. 3m–p). There are a small number of instances of predation on eulachon outside of this concentration, occurring mostly in the inner domain. There were no occurrences north of Nunivak Island (60° N).

Smelt consumption by pollock and cod was widespread, reaching into all domains and north of 64° N (Fig. 3q–t). The occurrence of smelts in halibut diets was mostly restricted to the inner domain between Nunivak Island and Bristol Bay (Fig. 3s). Arrowtooth diets containing smelts were mostly found south of the 55th parallel, near the Alaska Peninsula (Fig. 3t).

3.4. Patterns of predation in warm and cold years

Pollock were more widely distributed across the EBS shelf in warm years than cold years, and those trends were particularly notable in the NBS, with rel-

atively few pollock in the NBS in cold years and concentrated in the inner domain (Fig. 6a−c). Pollock predation rates on forage fishes in warm years were highest in the inner EBS, Bristol Bay, Pribilof Islands, and St. Matthews Island and throughout the NBS (Fig. 6a). In cold years, predation on forage fishes was more narrowly distributed, with high concentrations in the areas north and south of Nunivak Island, possibly reflecting increased overlap with capelin populations (Fig. 6c).

Pacific cod distributions in the EBS in cold and warm years were similar, but cod populations ranged further north and throughout the NBS shelf in warm years in contrast to cold years (Fig. 6d−f). Patterns of cod predation on forage fishes were also similar in cold and warm years, though, like pollock, there was reduced predation on forage fishes in Bristol Bay and along the Alaska Peninsula in cold years (Fig. 6f).

Pacific hailbut had similar distributions during cold and warm years in the EBS (Fig. 6g−i). Patterns of predation on forage fishes appeared relatively constant across climates. Halibut were largely absent in the NBS except for a few instances in Norton Sound and the area around St. Lawrence Island.

Arrowtooth distribution differed more dramatically as a function of climate (Fig. 6j−l). In warm years, arrowtooth distributions extended further north and east onto the shelf and into the middle domain (Fig. 6j). Arrowtooth were virtually absent in the middle domain in cold years (Fig. 6l). Patterns in forage fish predation also differed notably between warm and cold phases in arrowtooth. Predation was concentrated almost exclusively along the Alaska Peninsula in cold years (Fig. 6l) but extended throughout the middle domain in warm years (Fig. 6j). Arrowtooth were not present in the NBS (north of 60° N) in any year.

3.5. COG analysis in warm and cold climate phases

There were significant differences in the distribution of forage fishes between climate phases. The distributional COG coordinates for each forage fish species aggregated by climate regime are listed in Table 4. Significant differences were found in weighted mean latitude (Table 5) for the distribution of sand lance (ANOVA, $F_{2,777}$ = 5.3, p < 0.005), capelin (ANOVA, $F_{2,487}$ = 8.2, p < 0.001), and smelt (ANOVA, $F_{2,256}$ = 10.8, p < 0.001) between climates. No significant differences were found in weighted means of latitude for eulachon (ANOVA, $F_{2,48}$ = 1.0, p = 0.358) or herring (ANOVA, $F_{2,379}$ = 2.5, p = 0.086).

Pairwise comparison of weighted means between climate phases (Table 6) showed that latitudinal distribution of sand lance varied significantly between average climate years and warm years (Tukey-Kramer, 95% CI = 0.07−0.72° N, p = 0.012) and between cold years and warm years (Tukey-Kramer, 95% CI = 0.02−0.54° N, p = 0.035). Sand lance COG moved 0.28 to 0.40° further north (95% CI = 0.02−0.72° N) in warm years (Table 4, Fig. 7a). Latitudinal distribution of capelin varied significantly between average and cold years (Tukey-Kramer, 95% CI = 0.31−1.19° N, p < 0.001) and between average and warm years (Tukey-Kramer, 95% CI = 0.05−0.93° N, p = 0.024) but did not vary significantly between cold and warm years (Tukey-Kramer, 95% CI = −0.03−0.56° N, p = 0.096). Latitudinal distribution of smelt varied significantly between cold and warm years (Tukey-Kramer, 95% CI = 0.45−1.39° N, p < 0.001). Smelt COG moved 0.92° further north in warm years (Fig. 7j). A significant difference between climate phases was found in weighted mean longitude for the distribution of herring (ANOVA, $F_{2,379}$ = 3.3, p < 0.040; Table 5). Pairwise comparison of weighted means between climate phases showed that the longitudinal distribution of herring (Table 6) varied significantly between average and warm climate years (Tukey-Kramer, 95% CI = 0.12−3.06° N, p = 0.030); however, no significant differences were detected between average and cold years or cold and warm years.

Distinct trends were noted in COG analyses among forage fish distributions (Fig. 7). In warm years, sand lance were found at greater concentration in the Pribilof and St. Matthews regions as well as St. Lawrence Island and demonstrated an overall higher prevalence in the NBS (Fig. 7a). In warm years, capelin were more widely distributed, including into the middle domain of the EBS (Fig. 7d), but had notable reduced concentration in the Norton Sound region of the NBS, relative to cold years (Fig. 7f). Herring were also more broadly distributed across the shelf in warm years and had greater concentrations in the NBS in warm years (Fig. 7g). In warm years, herring were spread across all 3 domains and from the northern areas of the NBS survey to the southern portions of the EBS in a patchy distribution pattern. In cold and average climates, herring distribution appears to cluster more in the inner and middle domain areas, with a few records of herring north of St. Lawrence Island in the NBS during cold years (Fig. 7i). Comparisons of eulachon distributions in cold versus warm years showed no distinct trends, though the northernmost records for eulachon were
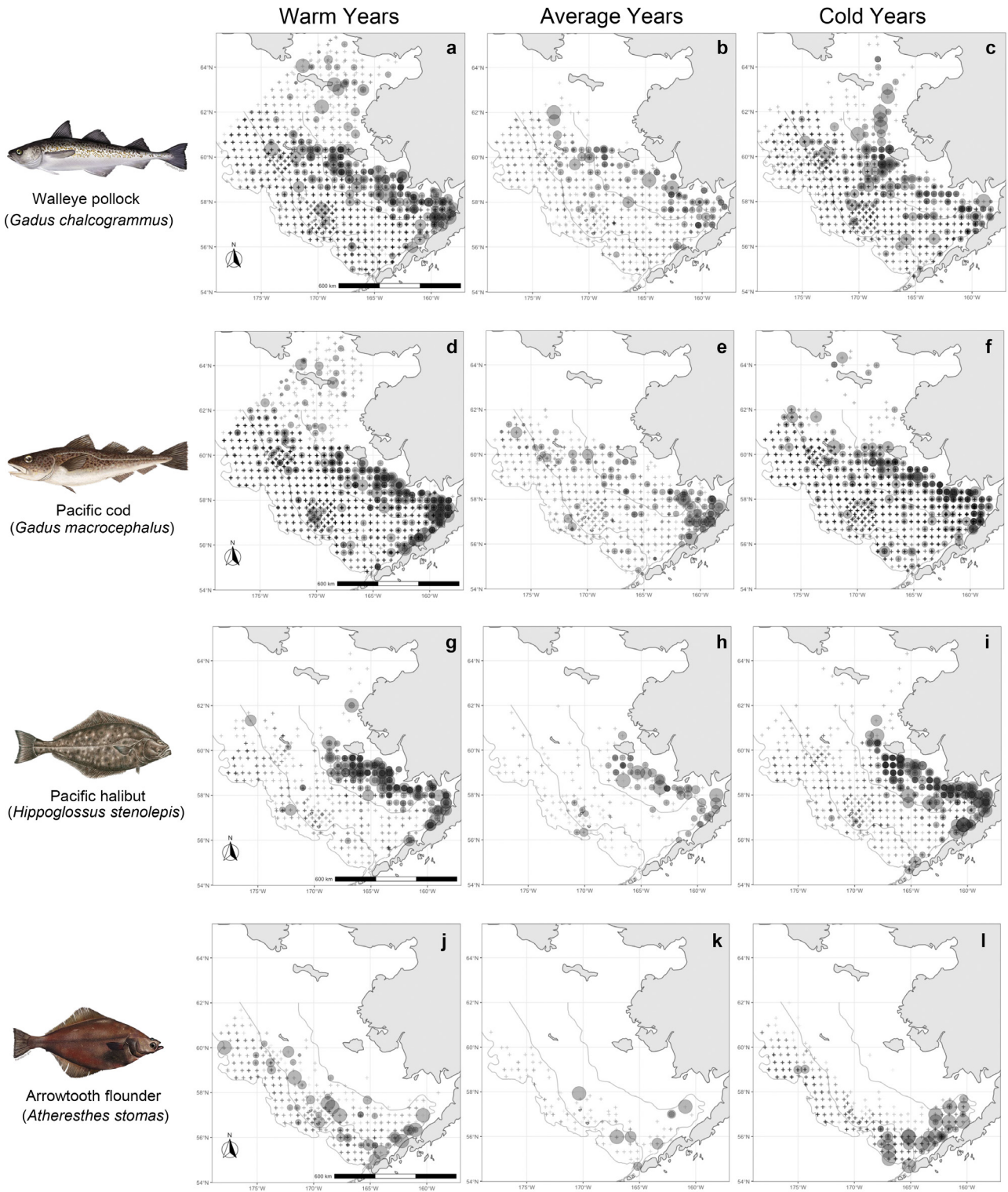
Fig. 6. Consumption of all forage fish by each predator aggregated by climate conditions. (a,d,g,j) Warm years, (b,e,h,k) average years, (c,f,i,l) cold years. Each + represents the location of a haul where predators were caught but no forage fish were found in diet samples. Each circle represents the location of a forage fish sampled by a predator, and the size of the circle corresponds to the percent weight of that sample, with larger circles indicating a higher percent weight of prey in the sample. Darker symbols (+ or circles) indicate multiple years of data layered on the same location

Table 4. Weighted mean latitude and longitude of each forage fish species in warm, average, and cold years. Also marked (triangle symbol) on maps in Fig. 7 as 'COG'

	Warm years	Average years	Cold years
Latitude (°N) (weighted mean ± SD)			
All forage fish	58.5 ± 1.7	58.2 ± 1.4	58.4 ± 1.7
Sand lance	58.2 ± 1.7	57.8 ± 1.0	57.9 ± 1.2
Capelin	58.7 ± 1.3	58.2 ± 1.1	58.9 ± 1.6
Pacific herring	58.8 ± 2.0	59.4 ± 1.7	59.1 ± 1.8
Eulachon	56.3 ± 2.1	56.6 ± 0.9	55.9 ± 0.8
Smelt	59.0 ± 1.8	58.4 ± 3.1	58.1 ± 1.6
Longitude (°W) (weighted mean ± SD)			
All forage fish	−164.6 ± 4.3	−164.3 ± 4.8	−164.6 ± 4.2
Sand lance	−162.3 ± 3.6	−161.4 ± 2.8	−161.7 ± 2.9
Capelin	−164.8 ± 3.5	−164.4 ± 3.7	−164.4 ± 3.6
Pacific herring	−168.3 ± 4.5	−169.9 ± 4.2	−168.7 ± 3.8
Eulachon	−166.1 ± 2.7	−164.0 ± 3.8	−165.3 ± 2.0
Smelt	−165.5 ± 3.7	−165.8 ± 11.6	−164.7 ± 3.7

in warm years as far north as 65° N (Fig. 7j). In all 3 temperature regimes, the 2 primary areas of eulachon concentration were in the outer domain between the Alaska Peninsula and the Pribilof Islands and in the inner shelf of the EBS. In warm years, smelt distributions shifted north and offshore, with multiple records of smelt in the NBS in warm phases (Fig. 7m).

Regressions of latitudinal COG for each forage fish species were run against the cold pool index (Fig. S1). We found that shifts in the COG related to the cold pool index were significant only for capelin (R^2 = 0.20, p = 0.008). An examination of forage fish distributional extent demonstrated that distributions did not vary significantly with the cold pool index.

3.6. Trends in movement north

Trends in movement were also analyzed on an annual basis to examine sequential shifts across the available time series and to visualize trends across warm and cold periods (Fig. 8). Both sand lance and herring showed consistent trends in movement north in warm periods (Fig. 8a,c). In the case of herring, there was also substantial movement south during the second half of the 2006–2013 cold phase. Capelin demonstrated inconsistent trends over most of the timeframe analyzed (Fig. 8b) but clear movement north in the latest warm phase (2014–2019). Smelts were similar to capelin, with inconsistent trends for most of the time series but dramatic movement north

in the latest warm phase (2014–2019) (Fig. 8e). Eulachon showed no clear trends in shifts in the latitude of distribution during the timeframe analyzed (Fig. 8d). Overall, forage fish appear to move north in periods of warming; this trend is particularly notable in the latest warm phase, which includes the last 5 yr of the analyzed time series (Fig. 8f).

3.7. GIC

GIC analyses showed that the COG varied between species (Table S3); however, variation within a population between climate types was minimal (Table S4). The largest degree of variation occurred between sand lance and herring (GIC = 0.414), sand lance and eulachon (GIC = 0.56), and herring and eulachon (GIC = 0.55). The species determined to have the highest degree of collocation were capelin and smelts (GIC = 0.99) and, to a lesser degree, sand lance and capelin (GIC = 0.78). This is likely because capelin could comprise a sizable proportion of the unidentified smelts from stomach samples, where prey are difficult to identify due to digestion state. The largest degree of variation found between climate types occurred between the centers of gravity for eula-

Table 5. ANOVA using weighted means for pairwise comparisons of latitude and longitude for forage fish in warm, cold, and average climate years. No significant differences in distribution were noted across climate phases for eulachon. No significant differences were noted in latitude for herring; however, we note that herring had the only significant difference in longitude among these forage fish. **p < 0.05, ***p < 0.001

	F	p
Latitude (°N)		
Sand lance	$F_{2,777}$ = 5.3	0.005**
Capelin	$F_{2,487}$ = 8.2	***
Herring	$F_{2,379}$ = 2.5	0.086
Eulachon	$F_{2,48}$ = 1.0	0.358
Smelt	$F_{2,256}$ = 10.8	***
Longitude (°W)		
Sand lance	$F_{2,777}$ = 2.9	0.058
Capelin	$F_{2,487}$ = 0.7	0.506
Herring	$F_{2,379}$ = 3.3	0.040**
Eulachon	$F_{2,48}$ = 1.8	0.177
Smelt	$F_{2,256}$ = 1.6	0.209

Table 6. Tukey-Kramer conducted after ANOVA (Table 5) using weighted means for pairwise comparisons of latitude and longitude for forage fish in warm, cold, and average climate years. Shifts in latitude to the north are indicated by positive values and to the south by negative values; shifts in longitude to the west (offshore) are indicated by positive values and to the east (inshore) by negative values. No significant differences in distribution were noted across climate phases for eulachon. No significant differences were noted in latitude for herring; however, we note that herring had the only significant difference in longitude among forage fish. $^{**}p < 0.05$, $^{***}p < 0.001$

	Difference	95% CI	Significance (adjusted p)
Latitude (°N)			
Sand lance			
Average–cold	0.1	(−0.2 to 0.4)	0.681
Average–warm	0.4	(0.1–0.7)	0.012**
Cold–warm	0.3	(0.0–0.5)	0.035**
Capelin			
Average–cold	0.8	(0.3–1.2)	***
Average–warm	0.5	(0.1–0.9)	0.024**
Cold–warm	−0.3	(0.0–0.6)	0.096
Smelt			
Average–cold	−0.3	(−0.6 to 1.2)	0.685
Average–warm	0.6	(−0.3 to 1.5)	0.275
Cold–warm	0.9	(0.4–1.4)	***
Longitude (°W)			
Herring			
Average–cold	−1.2	(−0.3 to 2.7)	0.144
Average–warm	−1.6	(0.1–3.1)	0.030**
Cold–warm	−0.4	(−0.7 to 1.5)	0.643

chon in average years versus those in warm years (GIC = 0.727). Some variation was noted for eulachon between average and cold (GIC = 0.854) and cold and warm (GIC = 0.899) years. GIC analysis of all other forage fish species between climate phases showed very little variation (GIC > 0.9).

4. DISCUSSION

This study provides insight into the uses and limitations of predator diet data in the spatial assessment of forage fishes not typically targeted by monitoring surveys. The results indicate there are shifts in the spatial distribution of these populations in response to changes in climate conditions, and these shifts have intensified for some species in recent years. Species overlap and interactions may also change, with the potential to create new trends in competition between forage fish species and foraging habits of large predators.

4.1. Predators as a distribution sampling method

Upper trophic level consumers are often used as sentinels of ecosystem conditions (Hazen et al. 2019). As a consequence of their position at the top of the trophic web, changes in groundfish populations and diet compositions may occur in response to shifts in abundance and distribution of the prey populations they consume (Young et al. 1993). By monitoring changes to predator diets over time, we can assess the status of other marine populations and effects of ecosystem conditions (Rovellini et al. in press) and improve models of ecosystem dynamics and interactions (Gaichas et al. 2010, 2018).

The primary method of collecting fishery-independent indices of distribution and abundance over the vast area of the EBS is the standardized bottom trawl survey conducted by NOAA-AFSC. This 34 yr time series of annual monitoring data is critical to annual assessments and evaluating long-term changes in groundfish populations but is limited in sampling small pelagic species. Bottom trawl nets sample the seafloor to the height of the headrope of the trawl net and do not sample pelagic or surface-dwelling populations (Kotwicki et al. 2015). Since the goal of these surveys is to evaluate populations of commercially fished groundfish species, the net mesh size (1.25–4 inches, 3–10 cm) is not designed to retain small pelagic or juvenile fishes (Stauffer 2004). Analysis of predator diets offers an indirect method of sampling forage fish (Zador et al. 2011, Rohan & Buckley 2017, Piatt et al. 2018).

There are limitations and biases associated with using predators as forage fish samplers that are important to consider when interpreting the results of our analyses. This study uses cumulative distribution functions from the mass of forage fish sampled by predators to better understand habitat preferences. However, the conditions where a predator was caught in a bottom trawl are not necessarily representative of the temperatures or vertical position in the water column occupied by the forage fish that were consumed. The forage fish may have been consumed some distance away from the trawl location or higher in the water column, where temperatures may have been different. There are also limitations to weight data when considering the digestion states of diet samples. While these limitations are worth noting, they should not greatly impact the overall conclusions of the results.

Predators themselves are not unbiased samplers, especially when their distributions may be shifting (Baker 2021a), and they may not consume prey in
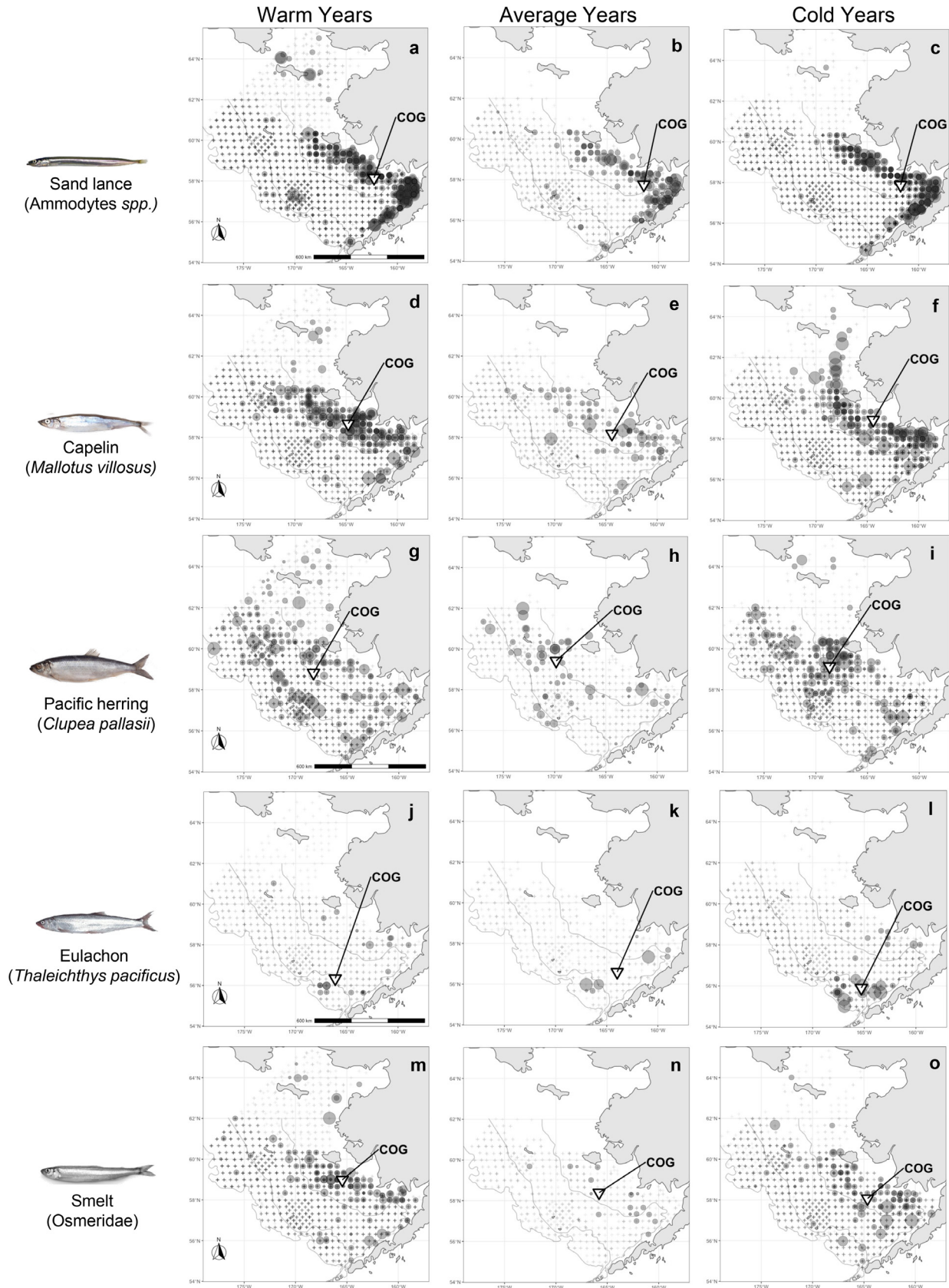
Fig. 7. Predation distribution maps of each forage fish aggregated by climate conditions. (a,d,g,j,m) Warm years, (b,e,h,k,n), average years, (c,f,i,l,o) cold years. Each + represents the location of a haul where predators were caught but no forage fish were found in diet samples. Each circle represents the location of forage fish consumed by predators, and the size of the circle corresponds to the percent weight of that sample, with larger circles indicating a higher percent weight of prey in the sample. Darker symbols (+ or circles) indicate multiple years of data layered on the same location. COG: center of gravity
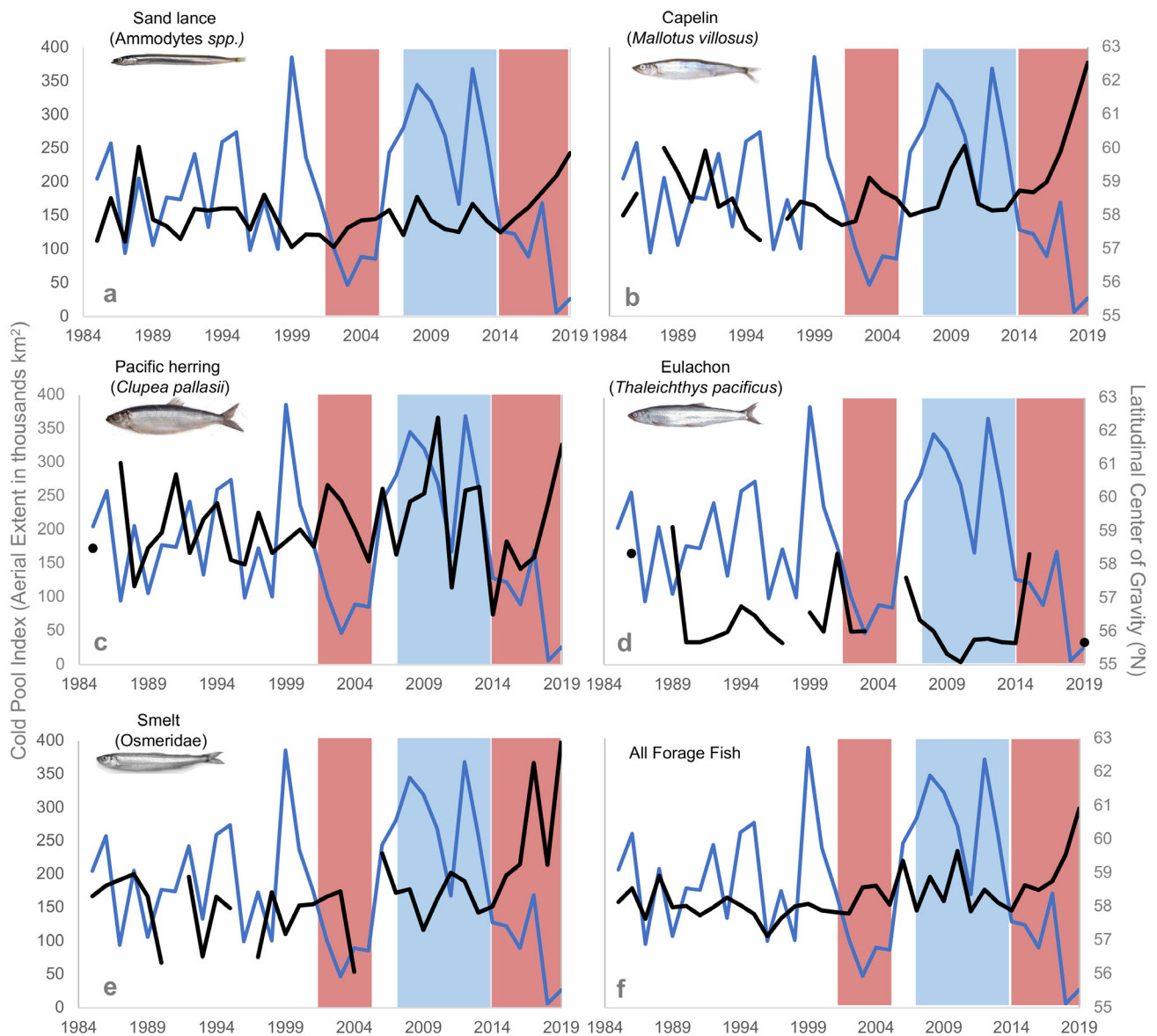
Fig. 8. Interannual center of gravity analyses of latitude for forage fish species as sampled by all 4 dominant predators overlaid with cold pool index data for the entire time series (1985–2019). (a) Sand lance, (b) capelin, (c) Pacific herring, (d) eulachon, (e) smelt, (f) all forage fish (all forage species data aggregated). Primary *y*-axis units are displayed as the areal extent of the cold pool in thousands of square kilometers, shown with the blue line. The secondary *y*-axis displays the latitudinal center of gravity in decimal degrees, as shown in black. Recent periods of warm and cold years are highlighted in red and blue, respectively

proportion to their availability. Our approach of using multiple predators to evaluate forage fish populations helps to reduce sampling bias related to differing availability to or preference for specific prey species in comparison to using a single predator species. This also allowed us to compare and contrast predator diets and foraging patterns. Spatial segregation across the shelf, in response to both temperature and depth gradients, appears to influence predator–prey overlap and predation rates.

4.2. Foraging patterns in predator species

Arrowtooth flounder, the most spatially constrained predator species analyzed, appears to access small pelagic species that occupy deeper areas (e.g. eulachon, herring) but not those occupying mostly cool (capelin) or shallow (e.g. sand lance) waters. Arrowtooth consume very little sand lance compared to the other predators (Table 2) and more eulachon than the other predators (Fig. 3p, Table 2). Cumulative distri-

bution functions for arrowtooth and eulachon exhibit a shared preference for warmer and deeper waters (Figs. 1d, 2d, 4d & 5d) and therefore a high level of overlap in the southwestern corner of the EBS. While all 4 predator species are also found in this region, arrowtooth rely more on eulachon compared to the other 3 predators. Thermal constraints in arrowtooth (Zador et al. 2011, Baker & Hollowed 2014) result in an avoidance of the cold pool and distribution limited to the outer shelf, especially in cold climate phases (Fig. 6l). Other diet analyses of arrowtooth show the consumption of mostly pelagic prey, including forage fish, shrimp, and euphausiids (Yang 1993, Doyle et al. 2018) and, at large sizes, herring and pollock (Lang & Livingston 1996, Doyle et al. 2018).

Pacific cod patterns contrast to the spatially constrained arrowtooth. As generalist benthivores (Yang 1993, Cooper et al. 2023), cod consume large amounts of invertebrates and benthic fishes, as well as pelagic species (Lang & Livingston 1996), and therefore less forage fish than halibut or arrowtooth (Table 2). Cod are tolerant of multiple temperatures and depth gradients and therefore are widespread in the EBS, although cod experience thermal constraints related to the cold pool when this barrier is strong (Overland & Stabeno 2004, Baker & Hollowed 2014, Baker 2021a). Our results corroborated the results from previous studies; cod were found throughout the NBS in warm years and appear to be more restricted to southern and nearshore waters during cold and average years (Fig. 6d–f). The spatial overlap between cod and sand lance in the inner domain may explain why this forage fish was consumed by cod more than others. Capelin also occupy these shallow nearshore waters, so we may expect cod consumption of these 2 forage fishes to be more similar; however, sand lance and capelin have differing preference for cold water. Cumulative distribution curves based on bottom temperature (Figs. 2b & 5a,b) showed that capelin occupy colder waters than sand lance and cod. Capelin niche preference for cold temperatures allows their distribution to extend farther offshore and into colder, deeper waters than sand lance, providing refuge from thermally restricted predators.

Walleye pollock had the lowest percent weight of forage fish in their diet among the analyzed groundfish predators (Table 2). Diet analyses of pollock from the Gulf of Alaska reported diets consisting mainly of euphausiids and shrimp; however, forage fishes were also important, especially capelin, at nearly 13% weight of their total diet (Yang 1993). Adult pollock are known to avoid the cold pool (Duffy-Anderson et al. 2003, Stevenson & Lauth 2019, Stevenson et al.

2022), whereas juvenile pollock (age-0 to age-2) tolerate colder temperatures and are found within and inshore of the cold pool (Wildes et al. 2022). Duffy-Anderson et al. (2003) found age-2 pollock distribute higher in the water column than age-1 and adult pollock. Due to their thermal niche, nearshore distribution, and pelagic stratification high in the water column, age-2 pollock have a high degree of distributional overlap with capelin; as a result, pollock consumption of capelin was higher than pollock consumption of other forage fishes (Table 2).

Pacific halibut diets consist mainly of crabs and fishes (Brodeur & Livingston 1988). Half of all fish consumed were pollock, with notable proportions of herring, sand lance, and Pacific cod (Livingston et al. 1993). Halibut are also known to feed in shallow nearshore environments during the summer before migrating to deeper spawning grounds near the edge of the EBS shelf in the Bering and Pribilof canyons (Dunlop et al. 1964, St. Pierre 1984). Our study marked a relatively large consumption rate of sand lance and capelin by halibut (Table 2), likely due to a combination of their piscivorous diet and cohabitation of shallow nearshore waters in the inner domain of the EBS.

4.3. Ontogenetic considerations

Ontogenetic shifts in diet and distribution are well documented among all analyzed predators (Yang 1993, Yang & Nelson 2000, Duffy-Anderson et al. 2003, Yang et al. 2006, Knoth & Foy 2008, Boldt et al. 2012, Barbeaux & Hollowed 2018, Stevenson et al. 2022). As was briefly discussed for pollock, ontogenetic differences in size, spatial distribution, and thermal preference influence evolving foraging strategies within the lifetime of a species. Although the age classes of predators were not separated for the analyses of this paper, this is an important dynamic that should be considered as context for the results of this study.

The diet composition of pollock evolves from one dominated by copepods and mysids in small pollock to a higher reliance on euphausiids among large pollock in the southeastern area of the EBS shelf and higher reliance on fishes and shrimp in the northeastern areas of the shelf (Buckley et al. 2016). Cannibalism is one of the most important controlling mechanisms over pollock population dynamics and may be a driver of density dependence (Wespestad et al. 2000, Boldt et al. 2012). It is important to note that juvenile and young-of-year pollock are among the most abundant sources of forage fish for preda-

tors in the Bering Sea (Lang et al. 2000, Wespestad et al. 2000, Wilson et al. 2006, Sigler & Csepp 2007, Hurst et al. 2021). Walleye pollock is one of the largest single-species fisheries in the world (Fissel et al. 2015); therefore, sufficient funding and research have been allocated to understanding this population. Due to their extensive coverage by existing literature, we excluded analyses of pollock as a forage population in our study.

Pacific cod and Pacific halibut have similar ontogenetic patterns of migration (Barbeaux & Hollowed 2018). Juveniles are found in shallow nearshore waters and spread offshore and into deeper waters across the shelf as they grow (Bailey et al. 1999). Midsized fish were the most mobile and generally shifted to deeper southern waters in cold years. Juvenile cod (<50 mm) have diets composed largely of calanoid copepods, amphipods, euphausiids, and fish larvae (Lee 1985). Ontogenetic differences in diet among halibut are comparable to those of cod; small halibut have a much more diverse diet than adults, consisting of smaller fishes and invertebrates (Livingston et al. 1993). This is likely due to a combination of gape limitation and the spatial overlap of predators and prey.

It is hypothesized that the adult population of arrowtooth in the southwestern portion of the Bering Sea may arise in part from larval transport of individuals from spawning areas in the Gulf of Alaska via the Aleutian Island passes (Doyle et al. 2018, Gibson et al. 2022). This connectivity was noted in pollock populations with spawning areas near the Shumagin Islands in the Gulf of Alaska and nursery habitat in the outer domain of the southeastern Bering Sea shelf (Parada et al. 2016, Gibson et al. 2022). Juveniles feed primarily on euphausiids and copepods, midsized individuals increasingly rely on forage fishes (e.g. smelts and capelin) and shrimps, and adult diets are composed mainly of larger fish (e.g. pollock, pleuronectids, and herring; Doyle et al. 2018). Smelts comprise a larger percentage of small arrowtooth diets, whereas herring and pollock are more important in large arrowtooth diets (Doyle et al. 2018). It has been noted that the size of prey items (mainly pollock and herring) increases with arrowtooth size (Yang et al. 2006).

4.4. Forage fish distributions in the EBS

Our maps of forage fish distributions, derived solely from the stomachs of large groundfish predators, correlate closely with previously published research on distributions and preferences of forage fishes in the Bering Sea derived from bottom trawl and surface trawl surveys (Ormseth & Yasumiishi 2021).

Sand lance distributions in the EBS, as identified by presence in bottom trawl surveys, show highest concentrations nearshore in the inner domain of the EBS shelf (<50 m; Ormseth & Yasumiishi 2021, their Fig. 12). Information on this species is lacking. Sand lance are difficult to retain in nets (Baker et al. 2022, Levine et al. 2023), exhibit diel vertical migration between benthic substrates and the water column (Sisson & Baker 2017, Baker et al. 2023b), and are highly associated with specific sediments, typically described as fine gravel and sand (Greene et al. 2020, Baker et al. 2021), resulting in patchy distributions. Additionally, sand lance become dormant in winter, to reduce their metabolic rate and conserve energy stores until prey abundance returns to optimal levels in the spring (Baker et al. 2019a). All of this presents challenges to effective sampling of this species. Evidence suggests that juveniles occupy beach sites or nearshore habitat and shift to deepwater benthic habitats at maturity (Baker et al. 2019a), reaching maturity in their second year and returning to spawn once a year in subtidal and intertidal waters in winter (Matta & Baker 2020, Zhukova & Baker 2022). These patterns in distribution match patterns in predator diets presented in our results (Figs. 3a–d & 7a–c).

Fluctuations in the abundance and distribution of capelin have been correlated with temperature variability and climate perturbations (Anderson & Piatt 1999, Huse & Ellingsen 2008). Capelin sampled in the EBS bottom trawl survey occur primarily in the inner domain at depths of approximately 50 m, but distribution extended beyond 100 m depths into the middle domain (Ormseth & Yasumiishi 2021). Surface trawl surveys found capelin distribution to be farther north compared to the bottom trawl survey (Yasumiishi et al. 2017, Ormseth & Yasumiishi 2021, their Fig. 4). Interestingly, consumption patterns of capelin presented in our results simultaneously reflect distributions of capelin separately recorded in the bottom trawl in the inner domain of the EBS and surface trawl surveys in the NBS (Figs. 3e–h & 7d–f).

Eulachon tend to be associated with deeper waters and are therefore sampled more efficiently in bottom trawl surveys than other forage fishes (Ormseth & Yasumiishi 2021). Eulachon was our most data-limited species, yet distribution in predator diets correlated well with distribution descriptions from bottom trawl surveys (Figs. 3m–p & 7j–l). Eulachon in the

EBS have been shown to concentrate around the west end of the Alaska Peninsula and north towards the Pribilof Islands (Brodeur et al. 1999, Ormseth & Yasumiishi 2021, their Fig. 8). This region corresponds to habitat preferences for waters >100 m and 3 to 6°C (Figs. 4d & 5d; Brodeur et al. 1999).

Pacific herring are an abundant and widespread forage fish in the EBS. Spawning occurs in nearshore areas in the spring followed by migration to overwintering grounds in the outer domain; evidence suggests water temperature influences the migration route and spawning date of this population (Tojo et al. 2007). Herring distribution in the EBS is more variable than the other forage fishes discussed above. In the EBS bottom trawl survey, herring occurred at depths ranging from 0 to >100 m (Ormseth & Yasumiishi 2021). The CPUE data from the bottom trawl survey (Ormseth & Yasumiishi 2021, their Fig. 17) and the consumption patterns reported in this paper (Fig. 7g–i) are consistent with movement patterns reported by Tojo et al. (2007, their Fig. 6).

Smelts represent a data-poor group. Rainbow smelt are the most prominent member within the complex of smelts analyzed. Although rainbow smelt were rarely caught in the EBS bottom trawl survey, surface trawl surveys report their abundance to be highest in the northeastern Bering Sea, especially in Norton Sound (Ormseth & Yasumiishi 2021, their Fig. 11); nearshore studies also note large numbers of rainbow smelt in Bristol Bay. The smelt family also includes capelin and eulachon; these are identified to the family level of smelt in stomach samples, where a species level identification cannot be determined due to digestion state. Our results show distributions primarily concentrated in the inner domain, with increased concentration in the Bristol Bay area during cold years (Fig. 7m–o).

4.5. Distribution shifts and recent warming periods

Our results suggest that forage fish populations experience spatial distribution shifts in response to changes in climate conditions, and these shifts have intensified for some species in recent years (Fig. 8). The annual COG shifted markedly for sand lance, capelin, herring, and smelts during the most recent phase of warm climate conditions from 2014 to 2019. For capelin and smelts, the latitudinal COG in 2019 was farther north than previously recorded (Fig. 8b,e). This trend was also apparent when data for all forage fish were analyzed in aggregate. However, it should be noted that the sampling scheme could bias this

result since NBS surveys were only conducted in 2010, 2017, and 2019.

For the purposes of the analysis, we utilized 2 different metrics to detect differences in spatial distribution between climate phases. An ANOVA test was performed (Table 5) on the latitudinal and longitudinal COG, and a GIC statistic (Table S4) was calculated. Regressions of latitudinal COG and the cold pool index as well as forage fish extent and cold pool index were run and displayed in Fig. S1. The combination of pairwise test statistics on broad temperature conditions across the ecosystem with regressions targeting the direct effect of the cold pool as a discrete barrier provides complementary perspectives of thermal impacts. Using multiple tools to assess the difference in results and why they might arise can be a useful strategy for understanding complicated processes and interactions.

In general, species are expected to shift poleward to higher latitudes during warm years (Rooper et al. 2021, Baker et al. 2023a, Levine et al. 2023). Due to the location and shape of the cold pool, however, temperature gradients do not necessarily correlate directly with latitude. Therefore, distribution shifts tracking thermally optimal habitats by marine species in the Bering Sea may not present as a straightforward northern shift. By using ANOVA concurrently with GIC analyses, we were able to distinguish cross-shelf or longitudinal movement from latitudinal movement.

Our results suggest the longitudinal COG for herring was significantly different between climate phases (Table 5). The distribution of herring consumption during warm climate years was more diffuse and marked increased herring presence in the NBS, Pribilof Islands region, and southern region of the EBS (Fig. 7g). In cold years, herring consumption was concentrated mostly in the inner and middle domains near Nunivak Island (Fig. 7i). The distribution of herring consumption in warm years correlates well with later stages of herring migration to their overwintering grounds in the outer domain near the Pribilof Islands and the southwestern corner of the EBS survey area. Likewise, the distribution of herring consumption in cold years is more compact in the middle domain near Nunivak Island, pointing to an earlier stage in the migratory route. The discrepancy in distribution may be due to fluctuating spawning dates with thermal conditions and is consistent with results from Tojo et al. (2007).

GIC analyses did not detect much discrepancy in population distribution between climate phases for any of the forage fish populations assessed (GIC > 0.93),

except for eulachon (GIC = 0.727−0.899) (Table S4). However, ANOVA and Tukey-Kramer pairwise comparison tests of the latitudinal COG between climate phases indicated there are significant differences for sand lance, capelin, and smelt (Tables 5 & 6).

Sand lance latitudinal COG was significantly different between cold and warm climate regimes (Tukey-Kramer, 95% CI = 0.02−0.54° N, p = 0.035; Table 6). Environmental effects have been shown to influence condition and timing of winter dormancy in sand lance populations of the North Pacific (Baker et al. 2019a). Recently, records of sand lance as far north as the Canadian Arctic Archipelago have increased substantially (Falardeau et al. 2017), indicating an expansion of range from waters south of the Bering Strait to northern waters in the Chukchi Sea, Beaufort Sea, and throughout the Arctic (also see Baker et al. 2022, where models indicate latitude is not a limiting factor when thermal conditions are met). Although our data are limited to predation records from the EBS and NBS surveys, we did find a significant northward shift in warm climate years as expected. It should be noted that NBS survey years were limited (2010, 2017, 2019), and 2 of 3 of these surveys occurred in warm climate years.

Our observations of capelin distribution are consistent with shifts recorded during warm and cold climate states in previous studies (Ciannelli & Bailey 2005, Andrews et al. 2016). Predation of capelin was constrained to the inner domain, east of the approximate area of the cold pool in cold years (Fig. 7f). Concentrations of predation during cold years appear to increase in the southeastern Bering Sea region near Bristol Bay and north of Nunivak Island. In warm years, the thermal barrier of the cold pool is reduced and was associated with increased consumption of capelin within the middle domain and a greater concentration of consumption in the northeastern Bering Sea, just south of Nunivak Island. Additionally, we found significant (R^2 = 0.20, p = 0.008) shifts in capelin latitudinal COG as it relates to the cold pool index across the time series (Fig. S1). Research on the dynamic effects of the cold pool on forage fish shows that bathymetry, bottom temperature, and frontal zones form boundaries between different populations (Hollowed et al. 2012). Research by Ciannelli & Bailey (2005) suggested that capelin distribution in the inner domain is a predator avoidance strategy which normally protects capelin from predation by thermally restricted species (Pacific cod, arrowtooth). Thus, the reduction of cold pool coverage is increasing the overlap between groundfish predators and capelin and increasing offshore predation in warm climate years.

Eulachon was the most limited species in our dataset; hence, it is not surprising that ANOVA and pairwise comparison of distributions in cold and warm phases returned insignificant values. There is limited research into projected distributional shifts of eulachon under climate change. In general, eulachon are known to return to rivers in the early spring to spawn; therefore, summer distribution in any year is likely limited by the distance from spawning grounds. Eulachon populations throughout the North Pacific are experiencing drastic declines (Hay & McCarter 2000) likely due to climate effects and other factors (e.g. habitat degradation, changes in predation).

Smelt latitudinal COG was significantly different between cold and warm climate regimes (Tukey-Kramer, 95% CI = 0.4−1.4° N, p < 0.001; Table 6). The difference between the consumption distribution of smelts in cold and warm climate years provides further evidence for the influence of the thermal barrier created by the cold pool (Fig. 7m,o). In cold years, predators are restricted in their distribution; therefore, we see increased consumption of smelts in the southeastern area of the Bering Sea. In warm years, predators have access to waters previously excluded to them, and we note increased consumption of smelts in the northern areas of the EBS.

4.6. Potential climate impacts on trophic webs

Our results suggest that continued prolonged periods of warming will lead to shifts in species distributions, which may alter the overlapping ranges of groundfish predators and small pelagic prey. Interspecific interactions are likely to change due to these distribution shifts (Hollowed et al. 2012, Selden et al. 2018). Examining the impact of warming on interactions between species is crucial for improving our understanding of biodiversity in climate projections (Kortsch et al. 2015, Selden et al. 2018).

Projected warming climate conditions (IPCC 2022) predict shifts in the timing and extent of seasonal sea ice that will result in warmer water temperatures and a smaller cold pool in the EBS. The timing of sea ice retreat is linked with the oceanographic conditions and timing of pulses in primary production and resultant effects on the composition of zooplankton communities (Hunt et al. 2011, Eisner et al. 2014). Late ice retreat in cold conditions results in a higher abundance of medium and large lipid-rich copepods with higher nutritional value to forage species and stronger energy transfer to upper trophic levels. Early ice retreat in warm conditions promotes a

higher abundance of smaller copepods of less nutritional value, with implications for energetics that may propagate up the food chain (von Biela et al. 2019). When warming is persistent over several years, (e.g. 2014–2019, Baker et al. 2020b), there may be both bottom-up (Hunt et al. 2011) and top-down (Aydin & Mueter 2007) pressures on forage species. Capelin and herring data from differing climate conditions show that warm years have significantly lower catch rates than cold years (Andrews et al. 2016), evidence that food sources were limited and predation pressures increased for these species in warm climates.

4.7. Movement north and implications for competitive and predatory interactions

Climate influences many aspects of marine populations, including fecundity and recruitment (Pörtner et al. 2001), growth (Huang et al. 2021), and distribution (Takasuka 2018). On a global scale, striking cyclical patterns characterize many small pelagic populations. Oscillating dominance between populations of sardine *Sardinops* spp. and anchovy *Engraulis* spp. is a well-known example (Chavez et al. 2003, Takasuka 2018). During the 1970s, the Pacific shifted from a colder anchovy regime to a warmer sardine regime and then back in the late 1990s. Such large-scale shifts are important to note when considering the impacts of climate and ecosystem approaches to fisheries management (Link et al. 2020). In both the Arctic and Antarctic, climate-related shifts to sea ice phenology, duration, and extent may also shift the timing of peak primary productivity and impact pelagic fish populations in polar regions (e.g. Antarctic silverfish *Pleuragramma antarcticum*, La Mesa & Eastman 2012, Ross et al. 2014; Arctic cod *Boreogadus saida*, Levine et al. 2023; mackerel *Scomber scombrus* and capelin *Mallotus villosus*, Heide-Jørgensen et al. 2023).

Locally, climatic shifts may alter barriers to movement in the EBS ecosystem. The cold pool has long served as a thermal barrier limiting northward migration of subarctic groundfish (De Robertis & Cokelet 2012, Stevenson & Lauth 2019, Baker et al. 2020b). Groundfish predators are likely to shift distributions under warming climate conditions (Baker 2021a), although shifts are not strictly latitude dependent (Pinsky et al. 2013). Our results suggest that distributional overlap is a determining factor in the importance, or absence, of prey in a predator's diet (Silva et al. 2021).

Years with reduced cold pool extent are hypothesized to increase the spatial overlap of outer domain groundfish and inner domain forage fish (Hollowed et al. 2012), creating a stronger predation relationship between these fishes and limiting zooplankton and forage fish availability to marine birds and mammals (Siddon et al. 2020). Recent analysis of multiple climate models shows that depth and bottom temperature were the most important variables when determining species distribution shifts for pollock, cod, and arrowtooth (Thorson 2019, Rooper et al. 2021). These groundfish exhibit the potential to shift or expand their range to waters in the middle domain when the cold pool is absent (Ciannelli & Bailey 2005, Spencer 2008, Zador et al. 2011, Baker 2021a). Our results lend further evidence that distributional shifts in predators will result in changes to predation of forage fish and competitive interactions between forage fish.

Shifts in arrowtooth populations to the middle domain have been shown to be related to the reduction of cold pool waters during warm years (Spencer 2008). Predation data show arrowtooth consume forage fish at higher latitudes and farther east, over the middle domain, in warm years (Fig. 6j), whereas predation is restricted to southern waters in cold years (Fig. 6l). Comparison of arrowtooth predation distribution (Fig. 6j–l) and forage fish consumption patterns (Fig. 7) in warm years clearly shows increased predation occurring between arrowtooth and herring. Spatial partitioning that normally occurs between these species is reduced in the absence of a thermal barrier, and the importance of herring as a prey resource for arrowtooth increases (Spencer 2008).

Ciannelli & Bailey (2005) hypothesized that capelin usage of the inner domain, east of the cold pool, provides a refuge from predation by cod. In the absence of this thermal barrier, cod have greater access to middle and inner domain waters, and their predation of capelin increases. This was further supported by Hollowed et al. (2012). These trends were also evident in our results comparing cod predation patterns (Fig. 6d–f) with consumption patterns of capelin (Fig. 7d–f). In warm years, the spatial overlap of these species increases in the middle domain, indicating the lack of a thermal barrier that would typically create a refuge area for capelin. Additionally, Silva et al. (2021) found that increased overlap between cod and sand lance was a determining factor in the abundance of sand lance found in cod diets. Similar increases in sand lance predation by cod could occur in the EBS if cod distributions shift further nearshore in the absence of thermal barriers.

Competitive interactions between forage fish species also have the potential to change with shifting distributions. Age-1 pollock exhibit spatial partitioning strategies in concert with capelin (Hollowed et al. 2012). By tolerating cold bottom temperatures, age-1 pollock maintain physical separation from groundfish predators and reduce competitive interactions with capelin populations in the inner domain. Hollowed et al. (2012) found evidence for reduced competitive interactions between age-1 pollock and capelin during warm years, since age-1 pollock were more broadly dispersed across the middle and outer domains in warm years, reducing their co-occurrence with capelin in the inner shelf. Similarly, competition between sand lance and capelin may be reduced in warm years. Capelin distribution could extend further offshore if thermal barriers buffering groundfish predation are absent, though both capelin and sand lance appear to display significant potential for latitudinal shift north in warm years (Table 6, Figs. 7 & 8; Baker et al. 2022).

Although NBS data are highly limited compared to the EBS time series, evidence suggests several subarctic species migrate north of 60° N in warm conditions (Stevenson & Lauth 2019, Baker et al. 2020a, Baker 2021a). By including NBS consumption data from groundfish predators, we highlight that this shift is occurring not only for pollock, cod, and halibut but also for sand lance, capelin, herring, and smelt. At least 1 instance of predation occurred for these forage fish north of St. Lawrence Island in both warm (2017, 2019) and cold (2010) years (Fig. 7). Predicting distributional shifts and species interactions in the Arctic is a rapidly expanding area of research, with many scenarios proposed and complex dynamics to be explored (Huntington et al. 2020, Mueter et al. 2021, Baker et al. 2023a).

4.8. Implications for informing management and future research

Climate impacts on the distribution and abundance of forage fish populations and/or predator populations in the EBS could lead to shifts in predator–prey relationships and may affect management decisions for commercial stocks (Mueter et al. 2021). More research is needed to increase the understanding of each of these forage fish species in the context of recent climate shifts and projected conditions. The role of ontogeny in predation of forage fish should also be explored. Identifying the life history stages where forage fish are most important to predators

and assessing changes in predation rates by these age groups over time may provide greater insight on predator–prey dynamics.

We used a COG analysis method to estimate shifts in distribution over time. While this is a trusted method used in many studies to demonstrate distributional shifts (Perry et al. 2005, Pinsky et al. 2013), other approaches, such as using multi-model inference to estimate species distribution functions and occupancy, are also useful and may be relevant when combining data from multiple sampling methods (Thorson et al. 2016). Future research might explore the potential to combine diet data with data from traditional sampling methods such as bottom trawl and midwater trawl using species distribution models. Similarly, spatio-temporal models facilitate the use of environmental covariates to relate physical habitat conditions to biomass and distribution estimates. Research suggests that spatio-temporal models can improve the precision of abundance indices and distribution shift estimates (Thorson et al. 2016, Thorson & Barnett 2017). Future research may expand upon ideas presented in this study, using diet data to estimate abundance and distribution of forage fishes with spatio-temporal modeling such as the 'Vector Autoregressive Spatio-Temporal' package (Thorson 2019). Ultimately, a combination of qualitative and quantitative assessments is necessary to understand forage fish in the Bering Sea (Zador et al. 2017).

Development and investigation of predator diet datasets could be expanded to assist in more comprehensive forecasting and management of pelagic stocks in the North Pacific and other marine ecosystems. Recently, an open-access salmon diet database for the North Pacific Ocean was built by Graham et al. (2020) to compile, centralize, and make available salmon diet data across open ocean regions, providing important insights on open water pelagic food webs and dynamics related to offshore and mesopelagic prey populations (e.g. squid, myctophids). Maintaining, compiling, expanding, integrating, and mining these predator diet datasets are crucial to understanding and managing target or predator populations, expanding understanding of ecosystem dynamics, and providing important metrics to better characterize population distributions, abundance, and dynamics of prey and data-poor stocks, including many small pelagics.

Our findings in the EBS suggest that forage fish populations experience distributional shifts related to climate change. Understanding the pattern and magnitude of these shifts will help inform how climate change might affect trophic food webs and

commercially fished stocks. Results also highlight the utility of diet data and their potential to inform future models and ecosystem-based management decisions both in the Bering Sea and with important insights into such efforts elsewhere.

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