

Biogeography of pelagic food webs in the North Pacific

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Abstract

The tufted puffin (*Fratercula cirrhata*) is a generalist seabird that breeds throughout the North Pacific and eats more than 75 different prey species. Using puffins as samplers, we characterized the geographic variability in pelagic food webs across the subarctic North Pacific from the composition of ~10,000 tufted puffin meals (~56,000 prey items) collected at 35 colonies in the Gulf of Alaska (GoA) and Aleutian Archipelago. Cluster analysis of diet species composition suggested three distinct forage fish communities: (i) in the northern GoA, multiple age-classes of coastal and shelf residents such as capelin, sand lance and herring dominated the food web, (ii) in the western GoA to eastern Aleutians, the shelf community was dominated by transient age-0 walleye pollock, and (iii) in the western Aleutians, shelf-edge and mesopelagic forage species such as squid, lanternfish, and Atka mackerel were prevalent. Geographic patterns of abundance of capelin and sand lance in tufted puffin diets were corroborated by independent research fisheries and diets of piscivorous fish, indicating that puffin diets reflect the local abundance of forage species, not just selection of favored species. Generalized additive models showed that habitat characteristics predict, in a non-linear fashion, forage species distribution and abundance across two large marine ecosystems. We conclude that major biogeographic patterns in forage fish distribution follow gradients in key habitat features, and puffin diets reflect those patterns.

KEYWORDS

Alaska, Aleutian Islands, cluster analysis, ecological indicators, forage fish, generalized additive model, Gulf of Alaska, habitat, North Pacific, pelagic food web, puffins, seabirds

1 | INTRODUCTION

Understanding spatial and temporal variability in pelagic food webs and predator-prey interactions sits at the nexus of ocean resource management and ecosystem oceanography (Cury et al., 2000, 2008; Hunsicker et al., 2011; Link, 2010). However, in many (if not most) marine ecosystems, knowledge of the distribution and abundance of the key mid-trophic-level species that pass energy and carbon from primary producers (phytoplankton) to higher trophic level consumers (large fish, seabirds, and marine mammals) is fragmentary, unless the

species of interest are the subject of directed fisheries (e.g., clupeids worldwide). Even for commercially-harvested forage fish species, however, studies of distribution and abundance are challenging owing to patchiness and difficulties in sampling at the proper temporal and spatial scales (Freon et al., 2005). For species that are not fished, there is often little support to fund studies of their populations, even though they may play a crucial role in the functioning of marine ecosystems and the production of commercial groundfish and marine wildlife.

In some marine ecosystems, seabirds have been put forth as reliable indicators of forage fish abundance and community structure

(Cairns, 1987; Piatt, Sydeman, & Wiese, 2007; Sydeman et al., 2017a,b). While most seabirds breed on land, they obtain virtually all their food from the sea. Many aspects of seabird ecology directly reflect the ecology and dynamics of forage fish populations and communities, and indirectly reflect climatic factors and the marine environment as those influence forage fish (Piatt et al., 2007; Sydeman et al., 2015). This is significant from the perspective of ocean resources and ecosystem oceanography because seabirds are usually much easier to study than the forage fish they consume, and thus may provide valuable information about forage nekton that is difficult to obtain using traditional fisheries methods. There are caveats to this approach, such as species and size selectivity or foraging limitations that may limit the value of seabirds as forage fish indicators. Overall, however, seabirds can provide data that are potentially of great value to ocean and fisheries management (e.g., Cairns, 1992; Einoder, 2009; Zador, 2015; Zador & Yasumiishi, 2016).

North Pacific seabirds consume a variety of forage fish species, including Pacific sand lance (*Ammodytes personatus*, hereafter sand lance), capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*), and lanternfish (esp. Myctophidae). Of these, only one (herring) is fished commercially, and aside from a few studies based largely on sampling focused on other species (e.g., Anderson & Piatt, 1999; Ormseth, 2012; Parker-Stetter et al., 2013), the remainder are poorly documented throughout the region. North Pacific seabirds also consume juvenile age-classes (0–1 year) of larger commercial species including walleye pollock (*Gadus chalcogrammus*), Atka mackerel (*Pleurogrammus monopterygius*), and rockfish (*Sebastes* spp.), and juveniles of other forage nekton such as squid and octopus (Cephalopoda). These age classes are not well sampled by any traditional sampling methods in the region (Hinckley, Hermann, Mier, & Megrey, 2001; Springer & Speckman, 1997). Because seabirds specifically target these taxa and age classes for food, seabird “sampling” of the North Pacific prey base can complement traditional methods to inform us about fluctuations in fish stock abundance (e.g., Mills, Laidig, Ralston, & Sydeman, 2007; Renner, Mueter, Drummond, Warzybok, & Sinclair, 2012; Sydeman et al., 2017a), age structure and year class strength (e.g., Barrett, 2002; Hatch & Sanger, 1992; Miller & Sydeman, 2004), and geographic patterns of distribution (e.g., Springer, Piatt, & van Vliet, 1996; Thayer et al., 2008). When synthesized, this information may be used to better understand regional coastal pelagic food webs.

We hypothesize that geographic variability in coastal pelagic food webs, as proxied by seabird diets, may be explained by physical and biological habitat characteristics across the region, from the Gulf of Alaska (GoA) to the western Aleutian Islands. To test this hypothesis, we analyzed a large data set of tufted puffin (*Fratercula cirrhata*) diet samples (for details on the database see Sydeman et al., 2017a). Briefly, puffins forage 50–100 km from their breeding colonies and deliver fresh, intact, and easily identifiable forage fish to chicks in their burrows. Adults making deliveries can be blocked at the burrow entrance and the meals can be collected (Hatch & Sanger, 1992; Thayer et al., 2008). Puffins are flexible in selection of prey, but an important criterion is size, and most of the forage fish returned to

the colonies are ca. 40–200 mm in length (Piatt, 1990; Piatt & Kitaysky, 2002a,b; Sanger, 1986; Van Pelt, Piatt, Lance, & Roby, 1997). Because tufted puffins may dive to depths of 135 m to capture prey (calculated from Piatt & Nettleship, 1985), they are capable of sampling most pelagic fish populations on continental shelves.

To analyze forage fish community structure relative to habitat characteristics, we compared communities to local habitat measurements made within the typical foraging ambit (ca. 50-km radius) of the bird colonies. We selected a few key habitat variables which previous studies indicated would likely influence distribution and abundance of forage nekton, including shelf slope, depth, and distance to the shelf break (Hollowed, Wilson, Stabeno, & Salo, 2007; Logerwell et al., 2005; Springer et al., 1996), winds, primary productivity, water temperature (Abookire, Piatt, & Robards, 2000; Abookire & Piatt, 2005; Speckman, Piatt, Mintevera, & Parrish, 2005; Borstad, Crawford, Hipfner, Thomson, & Hyatt, 2011;), and tides (tidal mixing) (Drew, Piatt, & Hill, 2013; Hollowed et al., 2012). We also modeled the distribution of forage fish in the puffin diet as a function these habitat characteristics, as well as latitude and longitude. To corroborate our findings, we compared the distribution of forage fish predicted from our puffin samplers to distributions obtained independently by more traditional methods: bottom trawl surveys, beach seine sets, and the diets of large piscivorous fish. From these analyses of forage community structure and habitat use, we identified three fundamentally different types of coastal/shelf pelagic food webs in the region that are shaped by local to regional oceanographic processes. As far as we know, the biogeography of forage fish communities in the North Pacific has never been framed in this way.

2 | MATERIALS AND METHODS

2.1 | Puffin diets

We compiled data from 10,514 chick meals (food loads) representing 76 different species. Meals were collected between 1978 and 2013 at 35 colonies dispersed over 3,700 km of coastline (Figure 1) from the northeastern Gulf of Alaska to the western Aleutian Islands. Details of methods for the collection of puffin chick meals are described elsewhere (Hatch & Sanger, 1992), but the usual procedure was to place small wire-mesh screens over the entrance of puffin burrows so that adults returning with food could not enter their burrows, and subsequently dropped the food at the burrow entrance. In this manner, samples were collected in summer (mid-July to early September) during one to three day visits to the colony. Sampling at Middleton, Amatuli, Suklik, Midun, Aiktak, and Buldir islands was more frequent as field crews were stationed there for weeks at a time. Approximately half (16/35) of the sites were sampled in more than 1 year (Table S1).

Chick meals typically consist of “bill loads” containing single or multiple prey items caught by parent puffins and brought back to the colonies to provision developing offspring. To describe geographic patterns and model changes in composition among sites and

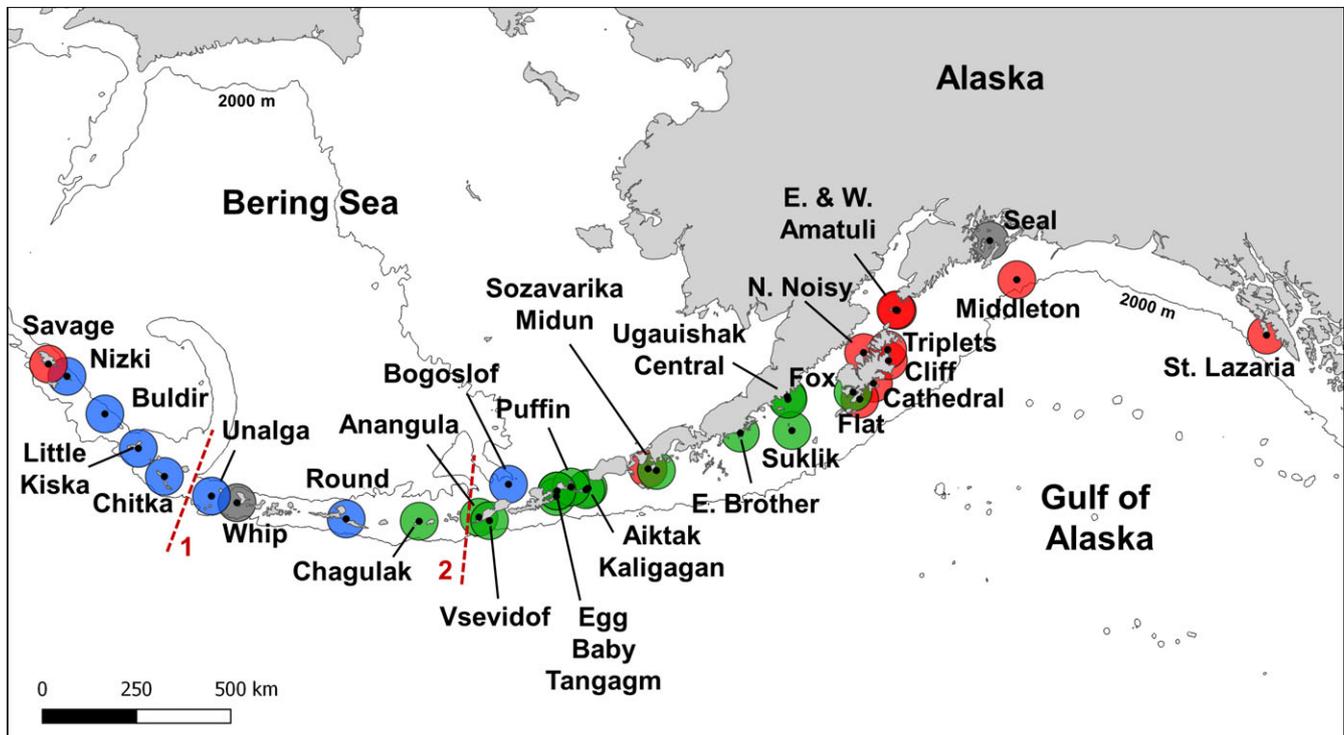


FIGURE 1 Colonies of tufted puffins in Alaska (black dots) where diet samples were collected. Colonies are ringed with a colored circle (50 km radius) in which habitat characteristics were measured. Colors represent different diet community types and were assigned by cluster analysis of diet composition (Red—Coastal residents; Green—Shelf transients; Blue—Oceanic; see text for details). Two passes in the Aleutian Islands are indicated by red dashed lines: (1) Amchitka Pass and (2) Samalga Pass

habitats, we summarized data by “bill load” rather than individual prey items, because prey types in each meal cannot be assumed to be independent from one another (Thayer et al., 2008). The summary statistic we used was the mean % number of prey items per bill load by site. Most bill loads consisted of fish, while zooplankton and other planktonic invertebrates were sometimes important (Table S2); most of the zooplankton were collected at the Semidi Islands and consisted largely of *Thysanoessa* spp. euphausiids. While numerically abundant, euphausiids comprised a negligible proportion of chick diets by mass (ca. 0.5%) and were excluded from our analysis, which was focused on geographic patterns in fish and cephalopods. We also excluded “other” ($n = 172$) and “unidentified” ($n = 1,055$) fish (<2% total number) from the analysis, as these provide no useful information for assessing spatial patterns in forage fish communities. Thus, while 62,376 individual prey items were tallied overall, 56,095 individual prey items were used in pattern description and models.

To investigate spatial variability in forage fish communities, we condensed the dietary data containing 80 different species or higher taxa into 15 taxonomic groups (Table S2). Many nekton were from large families with similar species, and often in larval or small juvenile stages, so identification was often made to taxonomic classifications higher than species. Forage fish analyzed at the species level included Pacific herring, capelin, sand lance, sablefish (*Anoplopoma fimbria*), prowlfish (*Zaprora silenus*), and Pacific sandfish (*Trichodon trichodon*). “Mesopelagic” fishes were primarily (97%) identified to the

Family Myctophidae (all *Stenobrachius* spp.), but also included Bathylagidae. All “salmon” included fish identified to the genus *Oncorhynchus* or Family Salmonidae; most were pink (59%, *O. gorbuscha*) or sockeye (39%, *O. nerka*) salmon. The “gadid” group was primarily (90%) walleye pollock and (9%) Pacific cod (*Gadus macrocephalus*). “Rockfish” contained *Sebastes* spp., mostly *S. aleutianus* (75%), or prey identified as Family Scorpaenidae. “Hexagrammids” were mostly greenling (*Hexagrammos* spp. (88%), which was primarily comprised of kelp greenling *H. decagrammus*) and Atka mackerel (11%). “Sculpins” comprised all sculpins, including the species *Phallogcottus obtusus* (55%) and *Hemilepidotus jordani* (18%), and other fish from the families Cottidae, Hemitripterae, and Psychrolutidae. The group “flatfish” were mainly arrowtooth flounder (*Atheresthes stomias*, 72%), but also contained a variety of sole, halibut, and turbot. The “octopus” group included prey only identified as Order Octopoda. Most “squid” were identified as belonging to the Family Gonatidae or Superorder Decabrachia.

2.2 | Comparing puffin diets with other indices of forage fish abundance

To test whether tufted puffins were collecting forage fish species in the same proportions as they occurred in waters around colonies, we focused on two species: capelin and sand lance. Both are among the most important prey for puffins and both are widely distributed in Alaskan waters (Mecklenburg, Mecklenburg, & Thorsteinson,

2002; Piatt & Kitaysky, 2002a,b). Puffins and large predatory fish eat the same age-classes of capelin and sand lance, so diet composition (calculated here as % number) can be compared directly. In contrast, puffins consume only age-0 pollock whereas large predatory fish also consume older age-classes, which have considerably larger mass. This would bias numerical comparisons, so we did not attempt to conduct an analysis for pollock.

Obtaining independent (non-puffin sampler) data on the distribution and abundance of capelin or sand lance is problematic because: (i) there is no directed fishery for either species in Alaska, (ii) directed research studies with appropriate small-mesh gear are scarce, and (iii) both species can be abundant near shore but difficult to sample with offshore trawl gear (Abookire & Piatt, 2005; Arimitsu et al., 2008; Robards, Piatt, Kettle, & Abookire, 1999). Therefore, we compiled data from three "imperfect sampler" sources to create independent indices of abundance for these species. The first was NOAA Groundfish Survey data on the incidental catch of forage species in groundfish research trawls ($n = 20,231$) in the study area. Data were collected during standard bottom trawl surveys conducted in the summers of alternate years between 1990 and 2012 in the Aleutian Islands and GoA. The large-mesh nets used in these trawls are poor quantitative samplers of small forage species because these fish usually pass through them. However, small fish do get swept up with larger species and/or get snagged on net rope. Capelin and sand lance catch per unit effort was measured as kg caught per hectare of substrate trawled. Second, we used NOAA Nearshore Fish Atlas data (Johnson, Neff, Thedinga, Lindeberg, & Maselko, 2012) from beach seine catches ($n = 3,684$ hauls) of forage fish conducted during summer (May–September) between 1995 and 2013. Beach seine data were compiled from surveys conducted by NMFS and USGS in the GoA and eastern Aleutian Islands using similar gear and methods (Arimitsu et al., 2008; Johnson et al., 2012; Robards, Piatt, Kettle, et al., 1999). Beach seines have a small mesh and are effective at catching forage fish, but sample only a small swath of shallow nearshore waters. Rate of fish capture was calculated as number of fish per haul. The third imperfect sampler data set was NOAA Resource Ecology and Ecosystem Modeling groundfish diet data, including diet composition of large predatory gadids and flounders ($n = 32,357$ fish), which can offer unique insight into population distribution and trends of forage species (e.g., Zador & Yasumiishi, 2016). Diets reflect more than local prey abundance, however, as each predatory fish species has its own diet preferences, and prey choice varies as predatory fish grow (Aydin, Gaichas, Ortiz, Kinzey, & Friday, 2007). We did not include predatory fish smaller than 20 cm in length in our analysis, as a piscivorous diet is much less common below that size. The predatory fish we included in our query were Alaska plaice (*Pleuronectes quadrituberculatus*), arrowtooth flounder (*Atheresthes stomias*), Atka mackerel, flathead sole (*Hippoglossoides elassodon*), Greenland turbot (*Reinhardtius hippoglossoides*), Pacific cod, Pacific halibut (*Hippoglossus stenolepis*), rock sole (*Lepidopsetta bilineata*), sablefish, walleye pollock, and yellowfin sole (*Limanda aspera*). Stomachs were collected at sea during groundfish surveys (during dates described above) and additional NMFS surveys, and

frozen/preserved in 10% buffered formalin. Stomach contents were later identified and counted in the lab. Larger predatory fish can eat more prey, although stomach fullness in wild-caught fish varies not only with size, but also among species and with temperature, prey abundance, and predator activity (Aydin et al., 2007). To standardize among samples for the size of predators in the sample, we assumed a linear relationship between predator size and quantity of prey consumed, and calculated numbers of prey per cm of predator length.

We compared the relative abundance of capelin and sand lance in puffin diets (arcsine of % composition by number) at each colony to the local abundance of sand lance and capelin estimated independently from trawls, beach seines, and groundfish diets, as described above. We drew a 100-km radius circle (approximate maximum foraging range) around each of the 35 puffin colonies and identified the bottom trawl ($n = 17,983$), seine haul ($n = 2,633$), and groundfish stomach ($n = 29,212$) samples that fell within those areas. Beach seine data were only available near 15 puffin colony sites, and were notably absent from sites in the western Aleutians. Using Spearman rank correlation coefficient, we then tested a matrix of associations between relative capelin and sand lance abundance determined from puffin diets and indices of abundance obtained from the other imperfect samplers of forage fish.

Additionally, we ranked rates of prey capture as none, low, medium, and high on a scale geared to each of the above methods, and then combined sample ranks from all sources to estimate relative abundance of forage in spatial bins of 50×50 km. Data were averaged per grid cell, then based on the distribution of those values, and with a desire to have a rank that pooled the highest (top 10%) of extreme values and equal division for all remaining moderate (45%) or low (45%) abundance cell values, each grid cell was ranked from 0 to 3, with 3, 2, and 1 representing the top 10%, middle 45%, and bottom 45%, respectively, of non-zero data values per cell. Grid cells where the prey type was never encountered were assigned 0 to clearly distinguish cells with complete absence of prey. For capelin and sand lance, ranks per grid cell were averaged ($n = 1, 2, \text{ or } 3$ ranks per cell). We measured the Spearman rank correlation between the puffin diet prey index and the combined index of relative forage fish abundance from other imperfect samplers.

2.3 | Analyses of spatial distribution and habitat use

Puffin diet data (average percent composition of bill load by site) were arcsine-transformed to normalize the distribution and variance. We then employed a hierarchical cluster analysis on these data from 35 puffin sites to describe food web structure. Clusters were amalgamated using average linkages weighted by bill load sample sizes (to minimize impact of small sample sizes from some colonies); distances were computed using one minus the Pearson product-moment coefficient for each pair of objects. We used the Root Mean Square Standard Deviation (RMSSTD) Index to identify likely clusters in the data, and the Pseudo T-square Index to further

evaluate whether more than one clustering pattern emerges from the hierarchical clustering arrangements (Systat, 2013).

Using the literature to inform which habitat variables are likely to affect forage fish distribution and availability to puffins (e.g., Abookire & Piatt, 2005; Abookire et al., 2000; Afonso, McGinty, & Machete, 2014; Borstad et al., 2011; Drew et al., 2013; Hinckley, Bailey, Picquelle, Schumacher, & Stabeno, 1991; Hollowed et al., 2007, 2012; Logerwell et al., 2005; Speckman et al., 2005; Springer et al., 1996), we selected monthly values of sea surface temperature (SST), chlorophyll-*a*, slope of the sea floor, distance to the 2,000-m isobath (a proxy for continental slope edge), tide range, and U- and V-wind vectors at 10 m. Sources for all habitat data are provided in Table 1. We dropped bottom depth from the analysis because it was linearly related to slope with $r^2 = .90$, and was therefore redundant with other bathymetric variables. We used GIS to average values of each variable within a 50-km study radius (max. area = 7,854 km²) centered on each colony (land area removed). NOAA Pathfinder SST data at 4-km pixel resolution were extracted for each site and then averaged over the months May–August and the years 1982–2009. Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua chlorophyll-*a* data at 4-km pixel resolution were extracted for these same months and years. We used earth topography ETOPO1 global relief model data to derive our bathymetric variables. First, we extracted depth data within each study area and then used GIS to calculate average slope of the sea floor and the minimum distance of each colony from the 2,000-m isobath. We obtained maximum tidal ranges at each colony from NOAA predicted tide tables. Finally, mean U- (east-west) and V-wind (north-south component) speed vectors were obtained from the North American Regional Reanalysis Quick Scatterometer (NARR QuikSCAT) database and calculated over the months of May–August for the years 1979–2008. Due to multicollinearity in the habitat variables, we simplified the habitat dimensions by reducing the marine habitat variables to their shared principal components (PC_{habitat}) based on the correlation matrix (Systat, 2013). The relative importance of each habitat variable was assessed from factor loadings on the primary principal component.

We used Generalized Additive Models (GAM) with the *mcgv* package (Wood, 2011) in R V 3.1.2 (R Development Core Team, 2014) to model habitat associations and produce smoothed maps of spatial variability in forage fish availability. For modeling purposes, the response variable was defined as the site- and species-specific catch per unit effort (CPUE; total number of fish delivered divided by the total number of bill loads sampled at a site). We used a negative binomial distribution for these models, using fish count data with the total number of bill loads as the offset, and a log-link function. The habitat analysis used smooth terms for PC1 and PC2 in the full model, and reduced models were fit by sequentially dropping predictors. The best model was chosen on the basis of lowest Akaike Information Criterion (AIC); only the best AIC model is shown in the results. For the smoothed maps, we used a single smoothing term for latitude x longitude. Model predictions were made at 10-km grid resolution within 100 km of a line drawn between the colonies.

TABLE 1 Resolution and source of habitat data associated with tufted puffin colonies

Variable	Resolution		Data source
	Spatial	Temporal	
SST (°C)	4 km	Monthly, 1982–2009	NOAA Pathfinder Version 5.0 and 5.1 cloud-screened SST http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/
Chl- <i>a</i> (mg/m ³)	4 km	Monthly, 1982–2009	MODIS Aqua http://oceancolor.gsfc.nasa.gov/
Bathymetry	0.017 deg	NA	ETOPO1, http://ngdc.noaa.gov/mgg/global/
Derivative variables			
Dist2K (km)		NA	(Minimum distance from a colony to the 2,000-m isobath)
Slope (degrees)		NA	
Tide (m)	Point	Daily	NOAA tide tables. http://tidesandcurrents.noaa.gov/tide_predictions.html
10-m wind speed (m/s)	0.189 deg	Monthly, 1979–2008	North American Regional Reanalysis http://nomads.nccdc.noaa.gov/dods/NCEP_NARR-A_MONTHLY
Research trawl CPUE	Point	Monthly, 1982–2013	NOAA Groundfish Survey Data https://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm
Beach seine CPUE	Point	Monthly, 1995–2013	NOAA Nearshore Fish Atlas of Alaska http://www.alaskafisheries.noaa.gov/habitat/fishatlas/
Groundfish stomach contents	Point	Monthly, 1982–2013	NOAA Resource Ecology and Ecosystem Modeling—Groundfish Diet Data https://access.afsc.noaa.gov/REEM/WebDietData/DietDataIntro.php

3 | RESULTS

3.1 | Geographic variability in forage fish availability

Five taxa/taxonomic groups accounted for more than 90% of overall forage fish in puffin diets: sand lance, capelin, gadids, hexagrammids, and squids (Table 2). These taxa were not uniformly distributed across the 3,700-km study arc (Figure 2). Hexagrammids and squids were common only in the central and western Aleutians, gadids were common in the northwestern GoA and across the eastern and central Aleutians, and capelin and sand lance were most common in the GoA. Other relatively common taxa groups varied in similar ways, with some more abundant in the GoA (e.g., salmon,

Pacific sandfish, sablefish, and Pacific herring) and others more abundant in the Aleutians (e.g., mesopelagics, rockfish; Figure S1). Very few species were found to be distributed in similar frequency throughout the entire study area (e.g., prowlfish).

Cluster analysis revealed three groupings of forage fish availability based on puffin diets (Figure 1). These clusters resembled those for individual taxa described above. Sites with puffin diets dominated by sand lance and capelin (Table 2) are clustered in the northern GoA (Figure 1, red circles), with one exception along the Alaska Peninsula (Sozavarika Island), and one in the far western Aleutians (Savage Island). Sites dominated by gadids formed a second geographic cluster from the northwestern GoA through the eastern Aleutians (Figure 1, green circles). The third major cluster, found mostly in the central and western Aleutians, included sites dominated (variably) by three taxa: squids, hexagrammids, or gadids (Figure 1, blue circles). Two sites were so different from the clusters that they stood alone: Seal Island in the northern GoA (Figure 1) was dominated by herring and lacked sand lance (Figure 2, Table S1), and Whip Island in the western Aleutians was dominated by hexagrammids (mostly Atka mackerel) and gadids (Figures 1 and 2).

3.2 | Forage fish habitat association

PC1_{habitat} explained 64% of the variance in habitat measurements, and PC2_{habitat} explained another 14% (Table 3). All habitat variables loaded heavily on PC1 (Table 3), particularly tide, alongshore winds (U-component, east-west), SST, and distance to the shelf edge. Only sea floor slope and meridional winds (V-component, north-south)

had higher loadings on PC2 than PC1 (Table 3). A plot of PC1 versus PC2 (Figure 3) revealed a gradient in site habitats along each axis. Sites of +PC1 are positioned on a shelf, distant from the shelf edge, where the tidal range is large, winds are predominately easterly in summer, sea surface temperatures tend to be relatively warm, and chlorophyll-*a* production is higher. Sites of -PC1 lie closer to a shelf edge where tidal range is small, winds are predominately westerly in summer, sea surface temperatures are cooler, and chlorophyll-*a* production is lower. Segregation on the PC2 axis was pronounced, reflecting more (+PC2) or less (-PC2) sea floor slope around colonies and stronger (-PC2) or weaker (+PC2) southerly winds.

The forage availability clusters based on puffin diets can be visualized with respect to habitat characteristics (Figure 3). The continental shelf in the northern GoA becomes increasingly narrow along the Alaska Peninsula, a pattern which continues into the eastern Aleutians until the shelf is so narrow that shelf break/slope habitats become part of the average foraging ambit of puffins (~50 km). Except for wind vectors, all the other variables track, and/or are influenced by, the reduction in amount of shelf habitat. The gradual transition in forage fish availability from sand lance/capelin to gadids to squid/hexagrammids corresponds well with east-to-west changes in PC1_{habitat} (Figure 3).

PC1_{habitat} explained 59% to 85% of the deviance in the availability of five forage taxa (Table 4). GAM curves illustrate that forage fish respond differently to habitat measurements (Figure 4). Both sand lance and capelin are associated with warmer, productive, shelf-based habitats, but sand lance appears to occur at all but the most extreme shelf break/slope-dominated sites (PC1_{habitat} < -2).

TABLE 2 Overall composition of tufted puffin diets in each of three clusters of colonies (blue, green, and red, Figure 1) with similar diet composition

Taxonomic group	Cluster									All areas		
	Blue			Green			Red					
	No.	% No.	Avg. %	No.	% No.	Avg. %	No.	% No.	Avg. %	No.	% No.	Avg. %
Pacific herring	0	0.00	0.00	37	0.08	0.03	493	9.37	5.47	530	0.94	1.89
Mesopelagic	209	7.99	2.40	48	0.10	1.24	4	0.08	0.04	261	0.47	1.10
Capelin	27	1.03	2.55	2249	4.66	6.10	1640	31.18	20.15	3916	6.98	10.11
Salmon	1	0.04	0.11	51	0.11	0.47	51	0.97	1.68	103	0.18	0.80
Gadid	852	32.57	18.03	28721	59.56	61.27	836	15.90	12.32	30409	54.21	34.61
Rockfish	12	0.46	0.13	557	1.16	0.90	12	0.23	0.04	581	1.04	0.43
Sablefish	31	1.19	0.15	82	0.17	0.14	33	0.63	0.95	146	0.26	0.42
Hexagrammid	99	3.78	18.70	1568	3.25	3.58	18	0.34	1.66	1685	3.00	6.38
Sculpin	104	3.98	3.02	276	0.57	0.68	4	0.08	0.04	384	0.68	1.00
Prowlfish	29	1.11	1.02	395	0.82	1.63	77	1.46	1.79	501	0.89	1.55
Pacific sandfish	3	0.11	0.46	74	0.15	0.17	37	0.70	2.79	114	0.20	1.14
Pacific sand lance	207	7.91	2.20	11744	24.36	17.98	1895	36.03	50.83	13846	24.68	25.64
Flatfish	81	3.10	5.56	724	1.50	0.93	17	0.32	0.07	822	1.47	1.69
Octopus	7	0.27	0.05	292	0.61	0.58	15	0.29	0.15	314	0.56	0.31
Squid	954	36.47	45.62	1402	2.91	4.29	127	2.41	2.02	2483	4.43	12.95

No., number of prey items; %No., percentage of total identified large nekton from all colonies combined; Avg. %, average of percentages of prey in meal loads at each colony (i.e., standardized for effort). Bold percentages are those with values greater than 5% of total. (See Section 2 for details.)

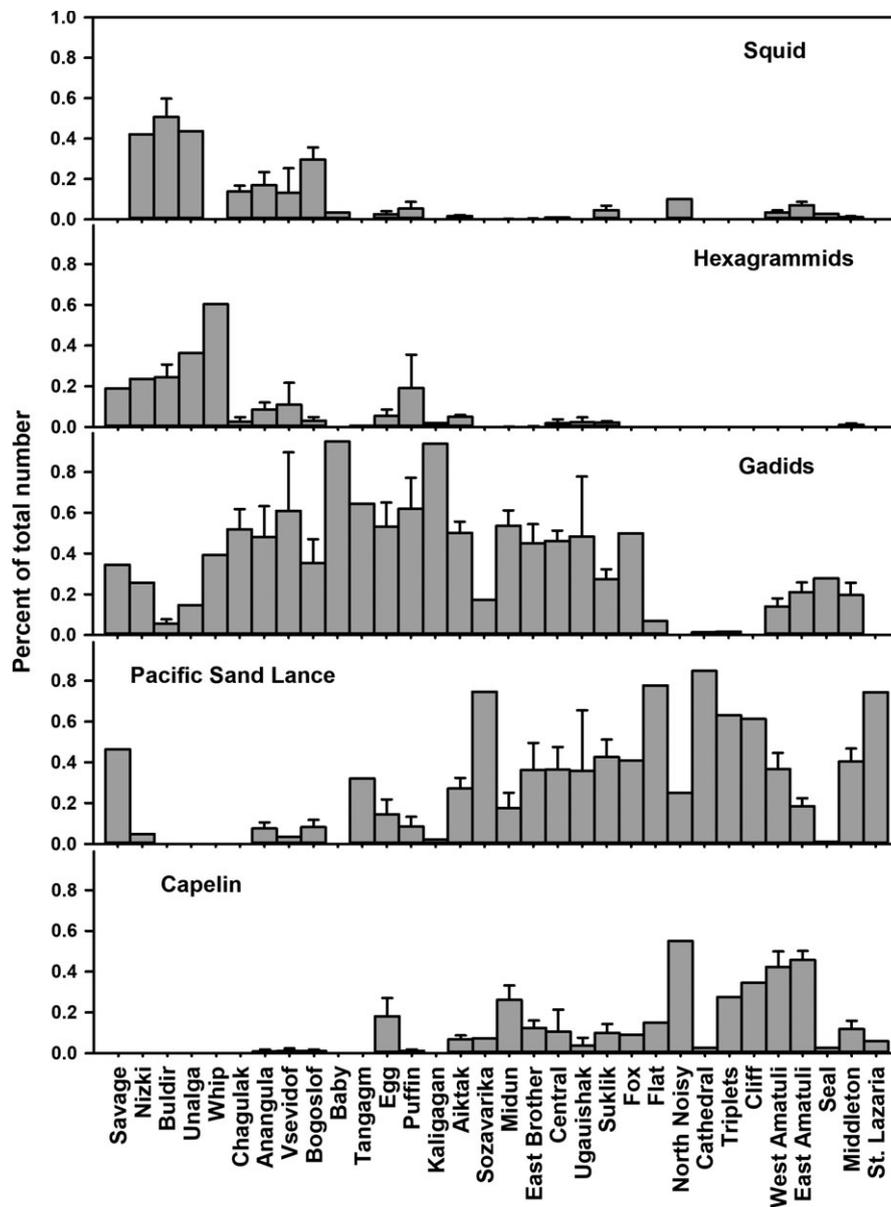


FIGURE 2 Percentages of different prey taxa in the diet of tufted puffins at individual colonies (see Figure 1) sampled from the far western Aleutians (left) to the eastern Gulf of Alaska (right). Standard error bars are shown for colonies with sampling in multiple years (Table S1). See methods for composition of taxonomic groupings

Capelin declined steadily with decreasing $PC1_{\text{habitat}}$, i.e., less shelf habitat ($PC1_{\text{habitat}} < 1$; Figure 4). In contrast, both squid ($PC1_{\text{habitat}} < -1$) and hexagrammids ($PC1_{\text{habitat}} < 1$) are more available at sites with more shelf break/slope-type habitat. Gadids appear to occupy sites with both shelf and shelf-edge habitats, but not the northern shelf with high $PC1_{\text{habitat}}$ scores (>1) characterized by very large tides and great distance from the shelf edge.

3.3 | Modeling geographic structure

Geographic structuring by habitat is evident in models of the five primary forage fish as a function of latitude and longitude (54%–96% of the deviance; Table 4). Using these simple models, we made predictive maps of forage fish availability and distribution throughout

the study area (Figure 4). Two of these maps (capelin, sand lance) compare favorably with distributions estimated independently by other imperfect samplers, i.e., by net fishery and predatory fish diet data collected within the vicinity (<100 km) of puffin diet sample sites (Figure 5). The proportion of capelin and sand lance in puffin diets was well correlated with some of the independent indices of abundance of these forage fish (Table 5), and with the overall combined index ($r = 0.79$ and 0.50 , respectively).

4 | DISCUSSION

In this study we showed that tufted puffins are good indicators of the geographic structure of forage fish communities across a wide

TABLE 3 Results of principal component analysis of puffin habitat variables

Parameter	Principal component (PC)			
	PC1	PC2	PC3	PC4
Eigenvalue	4.457	0.945	0.658	0.495
Proportion of variance	0.637	0.135	0.094	0.071
Cumulative proportion	0.637	0.772	0.866	0.936
Habitat variable	Abbreviation	Loading		
		PC1	PC2	
Minimum distance to 2,000-m contour	Dist2K	0.829	-0.329	
Average slope of sea floor	Slope	-0.671	0.652	
Average chlorophyll- <i>a</i> concentration	Chl- <i>a</i>	0.754	0.066	
Average summer sea surface temperature	SST	0.861	0.180	
East-west (U) wind vector	U-wind	-0.899	-0.005	
North-south (V) wind vector	V-wind	-0.613	-0.592	
Maximum tidal range	Tide	0.909	-0.154	

TABLE 4 Generalized additive models of geographic structure (latitude [Lat.] and longitude [Long.]) and habitat distribution (PC1) of forage taxa eaten by tufted puffins in Alaska

Model	Taxa	edf	χ^2	Prob.	r^2	Dev. expl. (%)
Lat., Long.	Sand lance	9.86	46.3	<0.0001	0.94	86.7
	Capelin	7.16	31.2	<0.001	0.57	83.4
	Gadid	14.95	135.9	<0.0001	0.99	95.6
	Squid	2	28.46	<0.0001	0.133	54.4
	Hexagrammid	2	33.1	<0.0001	0.65	77.1
PC1	Sand lance	6.46	44.5	<0.0001	0.95	85.4
	Capelin	3.11	43.1	<0.0001	0.498	80.7
	Gadid	2.29	11.5	<0.01	0.91	75.2
	Squid	2.48	34.99	<0.0001	0.02	59.1
	Hexagrammid	2.24	43.4	<0.0001	0.74	83.5

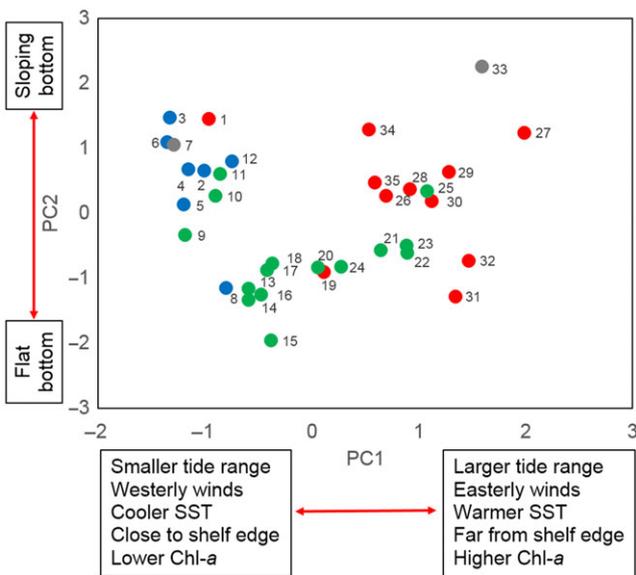


FIGURE 3 Biplot of the first two principal components (PC) resulting from an ordination of puffin colony habitat characteristics within a 50-km radius of each colony. Numbers correspond to colonies in order from west (#1) to east (#35) in Figure 1; see also Table S1. Colors correspond to those in Figure 1, with each color representing a different cluster of islands with similar diet composition. Habitat variables with high loadings on PC1 and PC2 are listed in rank order, top to bottom, below each axis

range of the North Pacific. We validated their reliability by showing that fish distributions revealed by puffin diets were corroborated independently by research fisheries and diets of large piscivorous fish. As we hypothesized, geographic structure in forage fish distributions was well explained by changing habitat characteristics from east to west. However, fish distributions appear as gradients in

abundance with serial replacement (Figure 2), not thresholds in distributions as might be predicted from sharp oceanographic boundaries and topography alone (Ladd, Hunt, Mordy, Salo, & Stabeno, 2005).

4.1 | Habitat associations

We used tidal range, wind, SST, chlorophyll production, and bathymetry to calculate a principal component index ($PC1_{\text{habitat}}$) that accounted for 64% of spatial variability in habitat characteristics from east to west. Given the important role these environmental factors play in shaping spawning and foraging habitats at local spatial scales (e.g., Abookire et al., 2000; Borstad et al., 2011; Hollowed et al., 2007, 2012; Renner, Drummond, Benson, & Paredes, 2014; Robards, Piatt, & Rose, 1999; Robards, Piatt, Kettle, et al., 1999; Speckman et al., 2005; Wilson, 2009), it is not surprising that $PC1_{\text{habitat}}$ explained a high proportion of the deviance in spatial distribution of the dominant forage species (Table 4), especially sand lance and capelin, which are local resident species in summer (Abookire & Piatt, 2005), and juvenile pollock, a transitory species in the region (Hinckley et al., 1991). In the western Aleutians, hexagrammids are patchy and associated with epibenthic characteristics (e.g., kelp, rocky substrates) that we did not measure, and deep-water squid may be less connected to shelf features (Logerwell et al., 2005), explaining why the habitat characteristics we analyzed did not account as well for their distributions.

4.2 | Oceanography and coastal pelagic food webs

Based on spatial clustering of puffin diet composition and associations with ocean habitats, we propose three unique pelagic food webs in the region. These are: (i) a “Type I” community, comprised of coastal resident forage species such as capelin and sand lance in the east, (ii) a “Type II” community, comprised of some resident species but dominated by age-0 gadids, especially pollock, which are

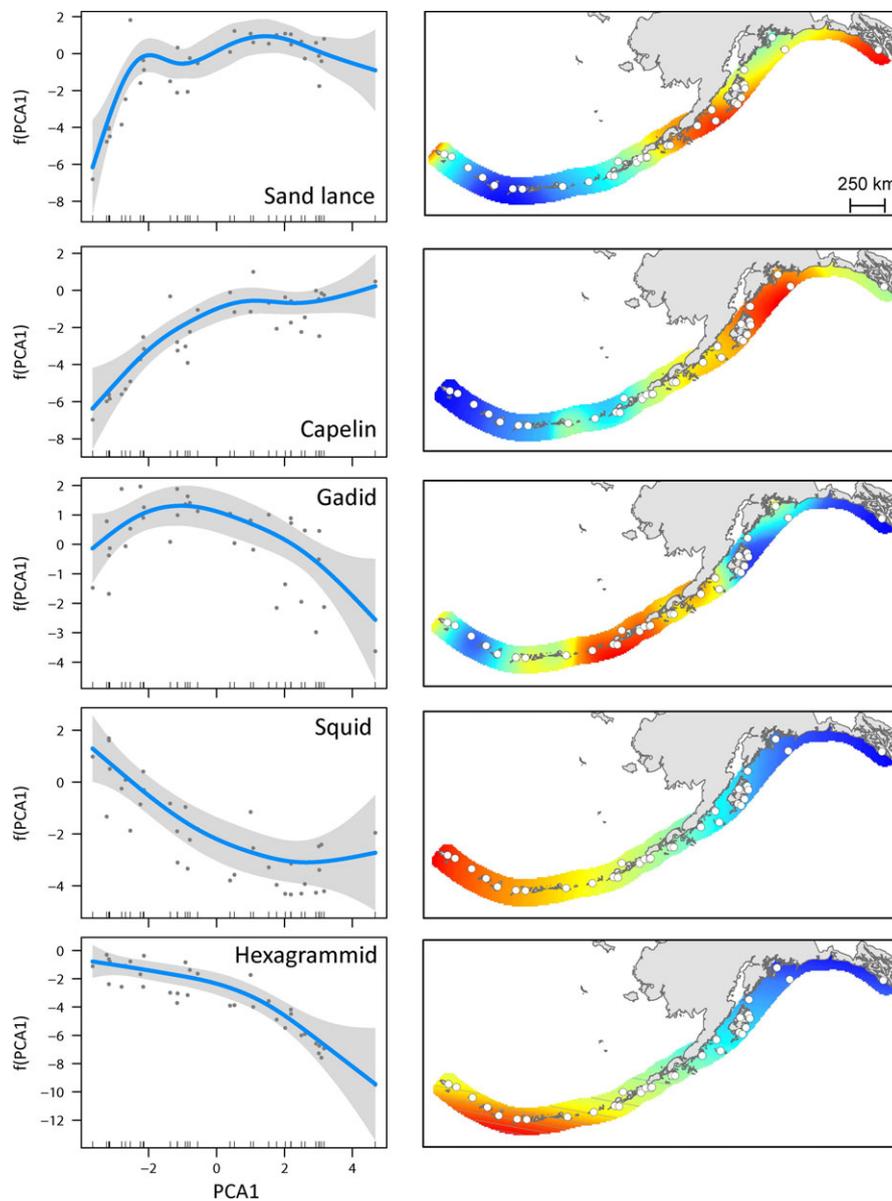


FIGURE 4 Left: Generalized additive model fit (blue line) and 95% confidence interval (grey) of relative forage fish abundance in tufted puffin diet as a function of colony $PC1_{\text{habitat}}$ scores. Right: Generalized additive model predictions of relative forage fish abundance in tufted puffin diets as a function of latitude and longitude, with higher predicted relative abundance shown in warmer colors. Colony locations are indicated by white circles

transported over the shelf by currents along the Alaska Peninsula and into the eastern Aleutians, and (iii) a “Type III” community comprised of mesopelagic, shelf-edge and oceanic species in the west. These three communities are discussed below in more detail.

4.2.1 | Type I: Coastal residents food web

Cluster analysis identified the area of the northern Gulf of Alaska as a region where puffin diets were comprised largely of resident coastal forage species including sand lance (51%) and capelin (20%; Table 2). Small and planktivorous throughout their lifetimes, and seasonally rich in high-energy lipids, they are quintessential forage fish species (Smith et al., 2011). They tend to form dense schools

(Speckman, 2004) and are preferentially consumed by many species of fish, seabirds, and marine mammals (Springer & Speckman, 1997). Other prey taxa in this food web include energy-rich Pacific herring, Pacific sandfish, and juvenile salmon, all of which are linked with coastal and shelf features (Abookire & Piatt, 2005; Johnson et al., 2012). Age-0 walleye pollock comprised about 10% of puffin diets in this region, but are largely transient shelf species (below). Few shelf-edge or oceanic taxa are present in the puffin diets in the northern GoA.

Fishery data on northern GoA forage fish are relatively sparse, but also suggest that sand lance and capelin are the dominant pelagic forage fishes on the northern shelf (Ormseth, 2012). The long-term importance of capelin in this region is probably underestimated

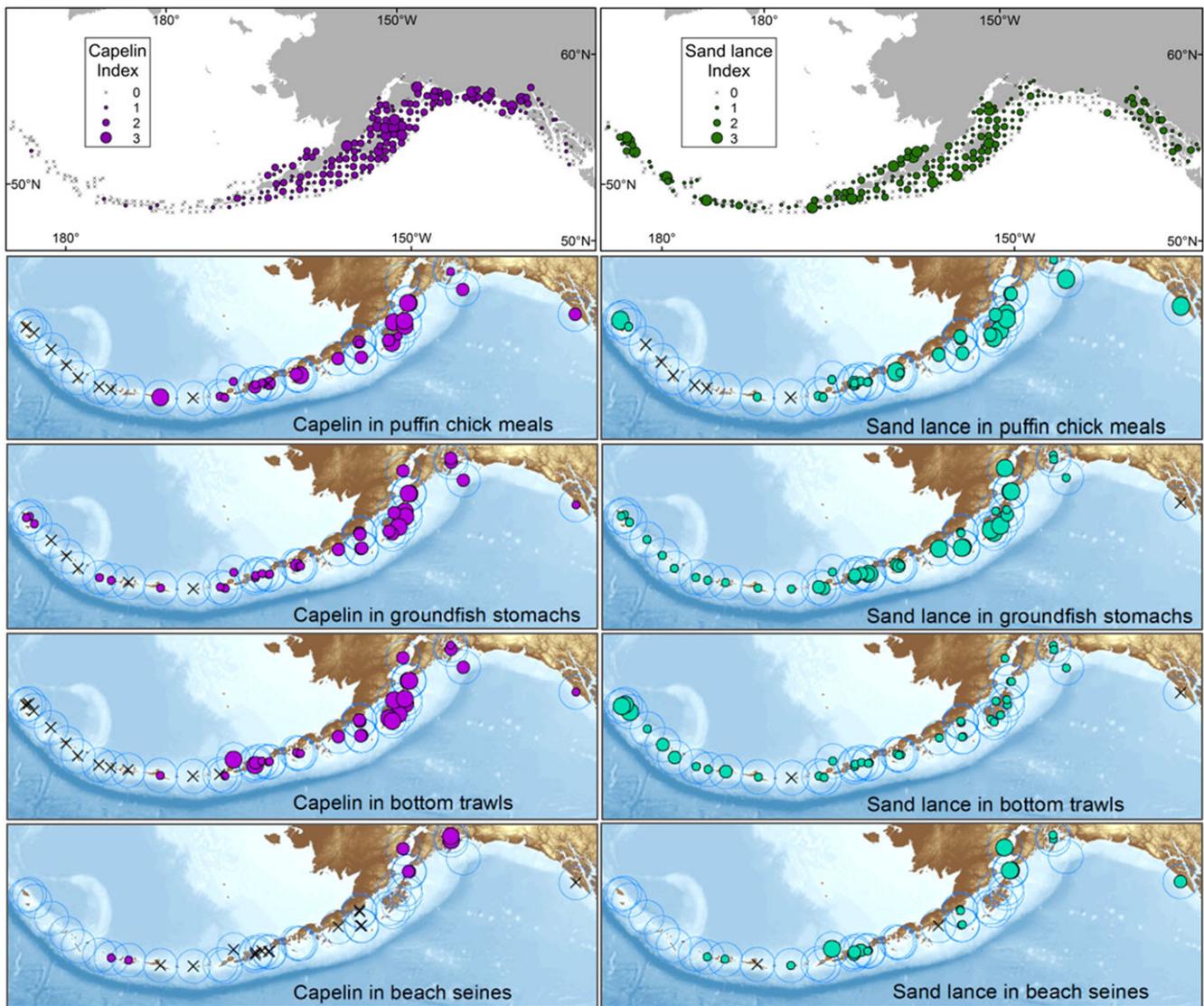


FIGURE 5 Distribution and index of relative abundance of sand lance and capelin in the study area (top) developed by combining abundance estimates from trawl and seine CPUEs, and predatory fish stomach contents (see Section 2). The relative abundance of capelin or sand lance within a 100 km radius circle (blue) around each puffin colony is mapped for capelin (purple dots) and sand lance (green dots). Presence of X indicates sampling was conducted but no fish were caught. Absence of both X and colored dot indicates that no sampling occurred around that colony

by recent fishery data because, historically, they were the most common prey for piscivorous seabirds in the GoA (Piatt and Anderson, 1996), and were also prevalent in the diet of Steller sea lions (*Eumetopias jubatus*) (Sinclair & Zeppelin, 2002). Capelin and sand lance both require sandy substrates for nearshore spawning on beaches or banks (Arimitsu et al., 2008; Robards, Piatt, Rose, 1999), which may explain the strong associations with shallow banks and coastal sites far from the shelf edge. Outside of spawning, capelin tend to be found in deeper waters (30–100 m) than sand lance and are associated with colder waters found in glacially modified fjords and in areas of strong upwelling (Abookire & Piatt, 2005; Arimitsu et al., 2008). Sand lance schools occupy depths of 0–30 m (when not burrowed in sand) throughout the shelf, and have a wider range of preferred temperatures (Speckman et al., 2005). Additionally, their

distribution is restricted by the location of sandy benthic substrates they can use for refuge from predators (Robards, Piatt, Rose, 1999).

The importance of habitat quality over location is highlighted by the observation of high sand lance abundance in puffin meals and bottom trawls in the Near Island group of the far western Aleutians (Figure 5) despite being relatively scarce throughout most of the Aleutian chain. This anomaly was noted previously when red-faced cormorant (*Phalacrocorax urile*), tufted puffin, common and thick-billed murre (*Uria aalge* and *U. lomvia*, respectfully), and black-legged kittiwake (*Rissa tridactyla*) diets revealed marked geographic differences between the Near Islands shelf (mostly sand lance, some pollock) and Buldir Island, a lone volcanic seamount to the east where diets were dominated by oceanic prey such as lanternfish, squid, and other invertebrates (Springer et al., 1996). This was attributed to the

TABLE 5 Spearman correlations among forage fish abundance indices derived from several “imperfect” forage fish samplers in the vicinity of 35 puffin colonies in Alaska

	Puffin	Trawl	Groundfish	Seine
Capelin				
Bottom trawl	0.64			
Groundfish	0.76	0.87		
Beach seine	0.19	0.23	0.46	
Combined index	0.79	0.82	0.96	0.34
Sand lance				
Bottom trawl	0.00			
Groundfish	0.48	0.08		
Beach seine	0.22	0.31	0.17	
Combined index	0.50	0.45	0.63	0.42

Indices derived from tufted puffin chick meals (Puffin), research trawls for large bottom fish (Trawls), stomach contents of large predatory fish (Groundfish), and beach seine hauls for nearshore fishes (Seine). An index using combined data from trawls, seines and groundfish was also developed to compare with puffin estimates of prey abundance. Significance of correlations: $p < 0.01$ in bold.

presence of a relatively large, shallow, and sandy shelf surrounding the Near Islands that provides optimal habitat for coastal/shelf species such as sand lance (Springer et al., 1996).

4.2.2 | Type II: Shelf transients food web

The second food web encompassed sites along the Alaska Peninsula and into the eastern Aleutians to about Samalga Pass (Figure 1). Dominant forage in this web were gadids, comprised largely of juvenile walleye pollock (91%) and Pacific cod (8%). While juvenile age-classes of gadids form large schools that are attractive to predators, they are not as dense as those formed by capelin or sand lance (Speckman, 2004) and they do not offer the same energy yield (Van Pelt et al., 1997) or nutritional benefits (Romano, Piatt, & Roby, 2006; Rosen & Trites, 2000; Whitfield, 2008). Furthermore, gadid recruitment is episodic (Bailey, Ciannelli, Bond, Belgrano, & Stenseth, 2005), making their year-to-year availability to predators unpredictable. In contrast to the coastal resident food web, the gadid-dominated food web of the central portion of the study area is transient in nature, characterized by seasonal movements related to large-scale circulation over the continental shelf, and these species are available for consumption by puffins as age-0 fish (although larger seabirds eat some age-1 pollock; e.g., Renner et al., 2014).

The major spawning center for walleye pollock in the Gulf of Alaska is located in Shelikof Strait between the Kodiak Archipelago and the Alaska Peninsula (Figure 1). Pollock spawn in deep waters of the strait in late March and April. Larvae hatch at depth, then rise to concentrate in the surface layer where they are advected southwest by the Alaska Coastal Current (Brodeur, Frost, Hare, Francis, & Ingraham, 1996; Hinckley et al., 1991). By late June and July, the center of distribution of age-0 larval and juvenile (50+ mm) pollock comprises a large zone between the Semidi and Shumagin islands, and

by late July and August, juvenile pollock appear to be well distributed over the southwestern GoA shelf (Figures 2 and 4). The exact timing and spatial extent of this advection of larvae and juveniles varies from year to year (Hinckley et al., 1991; Wilson, 2009), but generally coincides with the 40- to 60-day chick-rearing period for tufted puffins breeding throughout this region (Hatch & Sanger, 1992; Piatt & Kitaysky, 2002a). Variability in phenology of spawning by pollock and breeding by puffins undoubtedly accounts for some of the spatial variability in distribution and abundance detected by our study (Hatch & Sanger, 1992), but the broad scale of juvenile distribution is also well established by pollock research surveys (e.g., Bailey et al., 2005; Wilson, 2009). By the fall some juvenile pollock have been transported onto the eastern Aleutian shelf, where they are the most abundant forage fish; probably originating from multiple stocks in the GoA, southeast Bering Sea, and around Bogoslof Island (Barbeaux, Ianelli, & Palsson, 2013).

Given these dynamics of pollock life history and regional habitat features, the entire (ca. 700 km) Alaska Peninsula shelf west of Kodiak and the eastern Aleutian shelf becomes a giant nursery area for transient age-0 pollock through summer and fall, with circulation being a primary structuring mechanism (Hinckley et al., 2001; Wilson, 2009). Despite the lower energy content of pollock, predators can compensate by consuming more individual fish (although this also has physiological costs; Rosen & Trites, 2000; Kitaysky, Romano, Piatt, Wingfield, & Kikuchi, 2005; Romano et al., 2006). Notably, the largest populations of tufted puffins in the North Pacific are found in the western GoA and eastern Aleutians, so clearly Type II forage communities dominated by juvenile gadids are more than adequate to sustain puffins.

Movements and spawning areas of Pacific cod are not as well known as those of walleye pollock. Juvenile cod (age-0) in the GoA, and to a lesser extent the Aleutians, have been found in greatest abundance near the shoreline in coastal embayments, sometimes in association with marine macrophytes, and rarely over deeper waters on the continental shelf (Abookire, Duffy-Anderson, & Jump, 2006; Hurst, Cooper, Duffy-Anderson, & Farley, 2015). Large scale transport is probably not as important for age-0 Pacific cod as it is for pollock, which is a topic deserving further research (Abookire et al., 2006).

While gadids dominated the food web in this part of the GoA, sand lance and capelin were also found in some abundance (Figures 2 and 4). The habitat features favored by sand lance and capelin (described above) are also found on the Alaska Peninsula shelf. However, this is a transitional area; the shelf narrows steadily from east to west toward the Aleutians, the Alaska Stream accelerates to greater speeds over the shelf (favoring the rapid transport of gadid larvae and juveniles to the southwest), winds diminish in strength and become more southwesterly, and surface chlorophyll-*a* levels decline (Brodeur et al., 1996; Hinckley et al., 1991; Wilson, 2009; Wilson, Jump, & Duffy-Anderson, 2006). Accordingly, other coastal species such as herring, sandfish, and juvenile salmon that were fairly common in the northern GoA were also present but diminished along the Alaska Peninsula and eastern Aleutians (Figures 2 and S1).

In contrast, and in keeping with our description of serial replacement of food web constituents, some shelf-edge and/or Aleutian species became more frequent in puffin diet samples from the Peninsula shelf (e.g., hexagrammids, sculpins, rockfish, and cephalopods; Figures 2 and S1).

4.2.3 | Type III: Oceanics food web

The third food web was largely restricted to the central and western Aleutians, dominated by oceanic squids and nearshore hexagrammid species (mostly kelp greenling and Atka mackerel) associated with deep, mixed waters around the islands (Tables 2 and S1). At a few islands (e.g., Bogoslof, Chagulak), significant proportions of puffin diets were comprised of mesopelagic fish (Myctophidae). Adult pollock stocks in the western Aleutians are relatively small, use deep-water spawning habitat, and eat more oceanic prey than pollock in the eastern Aleutians or southeast Bering Sea (Barbeaux et al., 2013). Juvenile pollock may also be considered part of this oceanic food web in the western Aleutians. These results corroborate an earlier study (Springer et al., 1996) that identified the importance of shelf edge/oceanic habitat in shaping both predator diets and predator community composition in the western Aleutians.

Notably, the sites in the central and western Aleutians are, on average, only 30 km from the 2,000-m isobath, providing puffins easy access to oceanic species. Factors influencing the spatial distribution and abundance of juvenile squid, hexagrammids, and myctophids are poorly known. Hexagrammids may prefer to forage in the transition zones between stratified and mixed waters in the straits between islands (Rand & Lowe, 2011). While kelp greenling (shallow, rocky coastal habitat) and Atka mackerel (<200 m, rocky habitats with strong tidal currents) are widely distributed in Alaska and are generally considered coastal or nearshore species, they are particularly abundant in the western Aleutians (Logerwell et al., 2005), where adults feed heavily on oceanic prey such as squid, calanoid copepods, and myctophids (Barbeaux et al., 2013; Mecklenburg et al., 2002; Rand & Lowe, 2011). Squid and myctophids may gather along current boundaries or shelf-edge transition zones between shelf and oceanic waters (Sinclair & Stabeno, 2002). Deep-water habitat for vertically migrating species is relatively stable and may provide shelter beyond the direct influence of the shallower Alaska Stream or Aleutian North Slope Current (Sinclair & Stabeno, 2002).

4.3 | Implications for predators

In our study, tufted puffins exploited differing suites of forage species associated with the habitat features found within each food web domain. Similarly, Steller sea lion diets in Alaska (Sinclair, Johnson, Zeppelin, & Gelatt, 2013; Sinclair, Moore, Friday, Zeppelin, & Waite, 2005), exhibited clusters of diet similarity in the western GoA and the eastern and western Aleutian Islands, and demonstrated serial replacement of coastal to shelf to oceanic food webs from the Alaska Peninsula to the western Aleutians. Large demersal fish and

their prey in the Aleutians also exhibit similar biogeographic patterns (Logerwell et al., 2005).

The transitional use of these food webs has implications for the interpretation of marine predator population dynamics and reproductive biology (Dragoo, Renner, & Kaler, 2017; Hatch, 2013; Renner et al., 2014; Sinclair et al., 2013). It may well be the reason, for example, why common murrens have for the past couple decades been rapidly increasing in the western Aleutians while demonstrating the opposite (declining) trend in the eastern Aleutians (Dragoo et al., 2017). Similarly, increases in prey species diversity and frequency of occurrence since the 1990s in the western GoA are associated with a stronger recovery of Steller sea lions in this domain than in the western Aleutians, where prey diversity has changed little, and sea lion populations remain depressed (Sinclair et al., 2013).

These geographic asymmetries in biology may be correlated with ecoregional differences in diet composition, but that may be more a symptom than a cause. If we hope to understand how environmental change affects predator populations in an area, then we need to identify the mechanisms by which it alters the dominant food web operating in that domain. Conversely, it could be enlightening to learn more about predator or prey taxa that show synchrony in production or population trends across food web domains, in spite of the differences among them (e.g., synchrony in sand lance population abundance across the entire Aleutians and GoA; Sydeman et al., 2017b). Either way, the role of marine climate and circulation in driving variation in these coastal pelagic food webs should be further examined by integrating oceanographic models with predator diets in each region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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