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Effects of currents and temperature on ecosystem productivity in Unimak Pass, Alaska, a premier seabird and biodiversity hotspot

William J. Sydeman [a,*], Sarah Ann Thompson [a], Marisol García-Reyes [a], Caitlin Kroeger [a], Brian Hoover [a], Sonia D. Batten [b], Nora A. Rojek [c]

[a] Farallon Institute, 101 H St., Ste. Q., Petaluma, CA 94952, USA
[b] North Pacific Marine Science Organization (PICES), 9860 West Saanich Road, BC V8L 4B2, Canada
[c] U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, 95 Sterling Highway, Suite 1, Homer, AK 99603, USA

ABSTRACT

Understanding bio-physical relationships for areas of high biodiversity in marine systems can illuminate potential impacts of environmental change on concentrations of marine life. A biodiversity hotspot of singular significance in the North Pacific Ocean is Unimak Pass, Alaska, where millions of seabirds, hundreds of cetaceans, and thousands of pinnipeds concentrate each summer to forage on rich zooplankton and forage fish resources. We synthesized a large number of disparate datasets from different sources to examine the effect of current flows and temperature on productivity across trophic levels in Unimak Pass on the seasonal time scale. Our results verify the importance of these factors. This study is one of few to investigate how seabird reproductive success may vary relative to ocean currents, and corroborates other studies showing trait-mediated responses of seabirds to variation in oceanographic conditions, but at the local scale of an Aleutian pass. Somewhat surprisingly, seabird species with larger foraging ranges appeared to respond most to variability in ocean parameters at the seasonal scale. Our hypothesis that spring conditions promote summer productivity was not supported. Instead, contemporaneous conditions in summer had more and stronger effects on seabird production and foraging density. An important caveat of our study is that these relationships remain mechanistically poorly understood due to a lack of data on lower trophic levels and corresponding information on prey use and other aspects of trophic ecology across species. Nonetheless, we have shown that the breeding success of some seabird species on Aiktak Island, as well as seasonal average foraging densities of migratory shearwaters and other species, track currents and temperature variability in Unimak Pass, and may thus be useful as ecological indicators to the robustness of local pelagic food webs, and therefore ecosystem status assessments, in the region.

1. Introduction

Understanding the role of seasonal environmental variation on mesoscale sites where marine organisms concentrate to forage or reproduce (i.e., so-called “hotspots”) is an important topic in ecosystem ecology (e.g., Cury et al., 2008; Santora et al., 2017) and conservation (e.g., Piatt et al., 2006; Game et al., 2009; Briscoe et al., 2016). While many previous studies have focused on determining the locations of biodiversity hotspots in time and space (e.g., Nur et al., 2011), far fewer have investigated how local oceanographic conditions drive ecosystem function and productivity through time (reviewed by Hazen et al., 2013). From a conservation standpoint, the spatial overlap between biological hotspots and human uses of the ocean can be used to develop risk assessments and thereby manage living marine resources in a spatial context (e.g., Santora et al., 2017), but understanding how ecosystem productivity varies under differing oceanographic conditions is a requisite first step (Cashion et al., 2020).

One of the premier biodiversity sites in the subarctic North Pacific Ocean is Unimak Pass, Alaska (54°20′01″N 164°55′14″W), a narrow (16–18 km) and shallow (~70–160 m) waterway in the eastern Aleutian Archipelago that connects the northwestern Gulf of Alaska (GoA) with the southeastern Bering Sea (Stabeno et al., 2002; Fig. 1A). Unimak Pass is situated along the great circle shipping route from western North America to Asia, and > 5000 container ships and bulk carriers move through the pass annually, making this site and its ecosystem vulnerable to shipping-related accidents (Renner and Kuletz, 2015). The combination of oceanographically dynamic conditions, including strong tidal flows, shallow sea floor passes, and wind-driven geostrophic currents, characterize Unimak Pass and other Aleutian passes (Stabeno et al., 2005a; Ladd et al., 2005), and they are highly productive in terms of trophic transfer (Eddy et al., 2021). Current flows through Aleutian passes are thought to enhance ocean mixing, nutrient input, and entrainment in the euphotic zone, thereby promoting primary productivity (Mordy et al., 2005; Stabeno et al., 2005b). Moreover, the

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[*] Corresponding author.
E-mail address: wsydeman@faralloninstitute.org (W.J. Sydeman).

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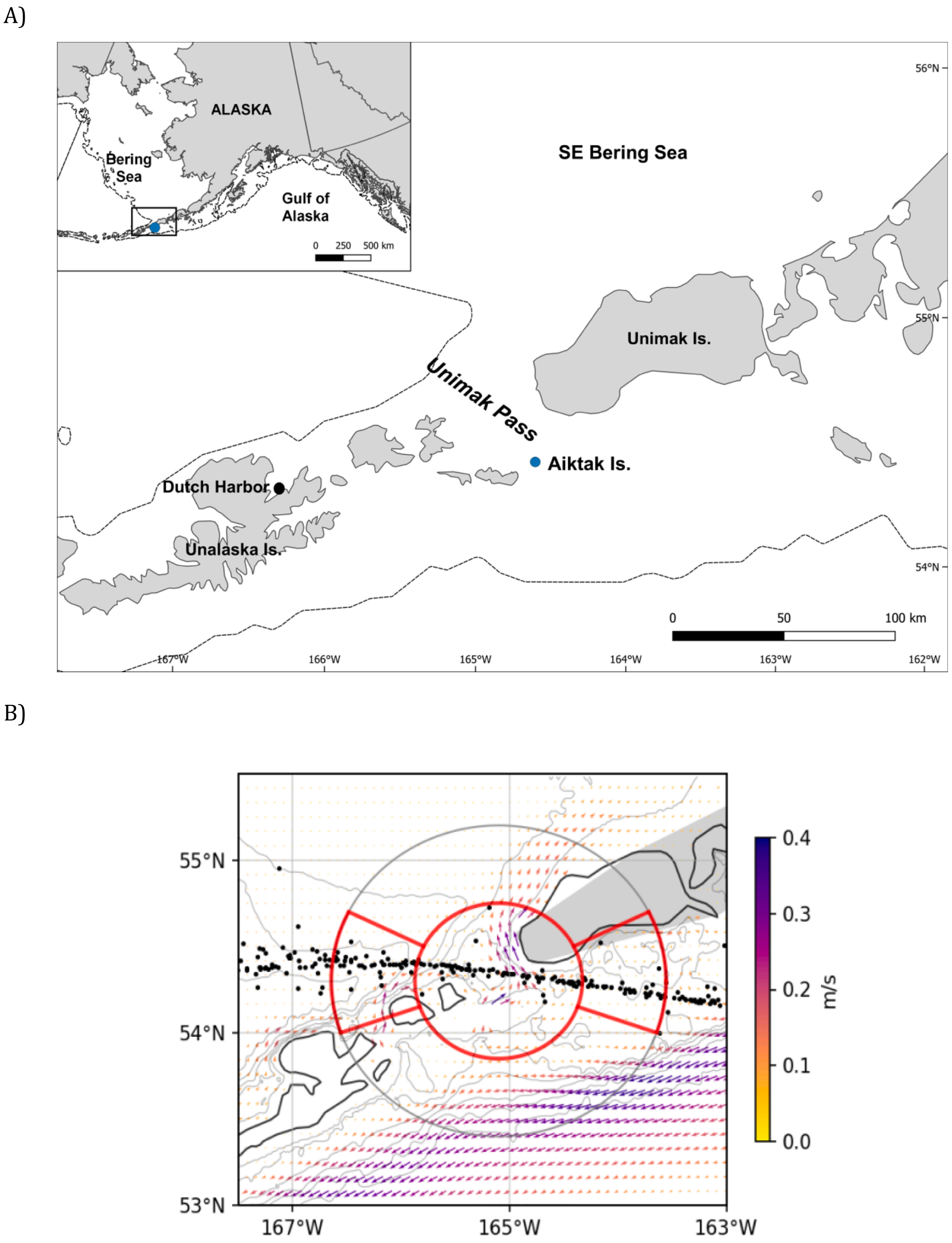

Fig. 1. (A) Location of the Unimak Pass study area in the North Pacific. Aiktak Island is shown with the blue point. The dashed line indicates the 200-m isobath. (B) May–August climatology of surface currents in three sub-regions (“candy-wrapper”) of Unimak Pass where data were averaged and synthesized using Principal Components Analysis. Surface current velocities are shown by arrow length and color (m/s). Black dots represent zooplankton (Continuous Plankton Recorder) sample locations (2001–2020). Seabird transects are not shown on this figure for clarity.

Table 1
Sea surface temperature (°C) characteristics in the Unimak Pass study area for late winter-spring (February–April) and summer (May–August), including differences in absolute values between the east and west (E/W) sub-regions.

	Spring	Summer
Mean (standard deviation)	3.5 (0.1)	7.5 (0.5)
Minimum/Maximum	1.5/5.2	5.9/10.2
Mean difference E/W regions	0.3	1.0
Max. difference E/W regions	0.7	1.7
Min. difference E/W regions	0.02	0.5

numerous sills and narrow boundaries within Aleutian passes produce fine-scale currents that create fronts where zooplankton are concentrated and become available to marine consumers, including fish (Logerwell et al., 2007), seabirds (Hunt et al., 1998; Jahncke et al., 2005; Ladd et al., 2005; Renner et al., 2008), pinnipeds (Ream et al., 2005), and cetaceans (Barrett-Lennard et al., 2011; Kennedy et al., 2014; Wright et al., 2018). In Unimak Pass specifically, major concentrations of seabirds, including millions of shearwaters from the southern hemisphere, forage in this region during the summer (Jahncke et al., 2005; Shaffer et al., 2006; Renner et al., 2008). At least 58 species of breeding and non-breeding seabirds, representing an estimated 7–10 million individuals, may reside in the pass during the summer foraging season (Smith et al., 2014). Renner et al. (2008) showed that the density of seabirds in the central Unimak Pass area was 1–2 times and 5–10 times greater in summer and winter, respectively, than densities measured for other Aleutian passes. Given these concentrations, Unimak Pass is considered an Important Bird Area (IBA) by the U.S. National Audubon Society, i.e., a key site for birds that is worthy of recognition and protection (Smith et al., 2014). Oceanographically, a unique feature of Unimak Pass is that it provides the first major connection between the narrow shelf of the northwestern GoA and the SE Bering Sea shelf as one moves southwest along the Alaska Peninsula. Therefore, some species (e.g., Pacific sand lance *Ammodytes hexapterus*) may play a larger ecological role in Unimak Pass than in other Aleutian passes without such an extensive connection to shelf habitats in both ocean basins.

Despite the fact that Unimak Pass is well known as essential habitat for foraging seabirds, whales, and other marine predators, the influence of oceanographic variability on its ecosystem has yet to be quantified across trophic levels on seasonal to interannual time scales. In this paper, we examine variability in key oceanographic processes and biotic attributes of Unimak Pass to test the hypothesis that stronger currents and warmer temperatures are positively related to greater productivity during the summer, defined as May–August. We examined zonal and meridional current flows into the pass because these factors describe flow along the Aleutian Islands (zonal), and from the GoA into the Eastern Bering Sea (EBS) (meridional). Meridional flows have previously been related to seabird densities (Renner et al., 2008) and foraging ecology in the region (Hunt et al., 1998; Jahncke et al., 2005; Ladd et al., 2005). We hypothesized that warmer temperatures and stronger currents promote greater primary and secondary productivity by enabling earlier and faster growth of planktonic organisms, such that warmer spring temperatures will lead to a more productive summer in the region.

To test this hypothesis, we examine relationships between currents, temperature, and indicators for primary through tertiary productivity using time series of NASA satellite remote-sensing of chlorophyll-a (surface concentration, which is a proxy for phytoplankton biomass at the sea surface), the North Pacific Continuous Plankton Recorder (CPR) program (Hoover et al., 2021; Batten et al., 2022), the Alaska Maritime National Wildlife Refuge (AMNWR) seabird monitoring program (e.g., Dragoo et al., 2017; data used in this paper from Youngren et al., 2022), and the North Pacific Pelagic Seabird Database (NPPSD; Drew and Piatt, 2005). This research may have implications for ecosystem monitoring and place-based management if changes in these parameters can be used to track fundamental oceanographic drivers of ecosystem change (e.g., shifts in the Pacific Decadal Oscillation (PDO)).

2. Methods

2.1. Study area

Environmental data were obtained for different regions of Unimak Pass as shown in Fig. 1B: i) the central area of Unimak Pass, roughly 50 km in radius from a point at 54.3°N, 165.1°W, and ii) two wedge-shaped areas east and west of the central area and extending another 50 km from the edge of the central sub-region. We refer to this as the "candy-wrapper" Unimak Pass study area. The central circle is meant to capture currents and biological observations from the main portion of Unimak Pass (Fig. 1B) where most of the zooplankton sampling and seabird observations were obtained. We also designed the central region partly to restrict the extent of the east and west regions, so as not to capture currents that are not directly impactful to zooplankton or birds. We could have used square-shaped sub-regions, but the candy-wrapper design evolved from a desire to have two concentric circles representing the inner and outer parts of the pass, and in the end was the best shape to capture both the CPR and at-sea seabird observations without mismatch to the physical data.

2.2. Physical data

Surface ocean currents (m/s) data were obtained from the Mercator GLORYS Global Reanalysis (Version 12 V1; Lellouche et al., 2018), from the EU Copernicus Marine Service Information. GLORYS is a 4-D ocean product from an assimilative numerical model with a 1/12-degree spatial resolution. In this study we used monthly zonal (u) and meridional (v) components of surface flow (0 m depth) over the period 1992–2019.

Sea surface temperature data (SST; °C) were obtained from the Optimum Interpolation Sea Surface Temperature (OISST), based on AVHRR-Only, Version 2 (Reynolds et al., 2008) from the National Oceanic and Atmospheric Administration (NOAA). Data were available from 1982 to 2020, with a spatial resolution of 0.25° and a daily temporal resolution. Sea surface temperatures were higher and more variable in summer, defined here as May–August, and differences among regions were larger in this season as well (Table 1).

2.3. Biological data

2.3.1. Lower trophic level productivity

Chlorophyll-a concentration data (chl-a; mg/m^3) were obtained from the Ocean Colour dataset v4.2 from the European Space Agency (ESA) Centre for Environmental Data Analysis (Sathyendranath et al., 2020). Data had a 0.04-degree spatial resolution at a monthly temporal resolution and were available from 1998 to 2019. Zooplankton data were obtained for the study region from the PICES North Pacific Continuous Plankton Recorder Program, 2001–2020. Zooplankton crustaceans were consolidated into broad categories for analysis: euphausiids, "small" copepods, and "large" copepods (e.g., *Neocalanus* spp.). Mean count data were natural log-transformed (ln(+1)) prior to analysis.

2.3.2. Upper trophic level productivity

Seabird productivity data in Unimak Pass came from long-term monitoring by AMNWR at Aiktak Island (Fig. 1A; Youngren et al., 2022). Seabird productivity often reflects prey availability in a region (Cury et al., 2011), and therefore may illustrate interannual variation in both the abundance and accessibility of large mesozooplankton and forage fish (e.g., euphausiid crustaceans and juvenile pollock) during the breeding season of May through August each year. The species studied included common and thick-billed murres; ancient murrelets; tufted and horned puffins; fork-tailed and Leach's storm-petrels; and red-faced,

Table 2

Foraging and primary dietary characteristics for focal seabird species used in this study. Foraging depth is defined as subsurface (>10 m) and surface (≤10 m). Typical foraging range is distance (km) from breeding colonies based on ship-board and tracking observations interpreted by the authors to reflect primary foraging ranges; non-breeders are migratory in the study area. Omnivorous species consume zooplankton, ichthyoplankton, fish, and squid.

Common name	Scientific name	Foraging depth	Foraging range (km)	Diet
Common murre	*Uria aalge*	Sub-surface	10–100	Omnivorous
Thick-billed murre	*Uria lomvia*	Sub-surface	10–100	Omnivorous
Ancient murrelet	*Synthliboramphus atiquus*	Sub-surface	10–100	Planktivorous
Horned puffin	*Fratercula corniculata*	Sub-surface	10–50	Piscivorous
Tufted puffin	*Fratercula cirrhata*	Sub-surface	10–50	Piscivorous
Fork-tailed storm-petrel	*Hydrobates furcata*	Surface	50–300	Planktivorous
Leach's storm-petrel	*Hydrobates leucorhoa*	Surface	50–300	Planktivorous
Short-tailed shearwater	*Puffinus tenuirostrus*	Sub-surface	Non-breeder	Omnivorous
Sooty shearwater	*Ardenna grisea*	Sub-surface	Non-breeder	Omnivorous
Red-faced cormorant	*Urile urile*	Sub-surface	0–20	Piscivorous
Pelagic cormorant	*Urile pelagicus*	Sub-surface	0–20	Piscivorous
Double-crested cormorant	*Nannopterum auritus*	Sub-surface	0–30	Piscivorous

pelagic, and double-crested cormorants (Table 2). These species vary in their foraging and dietary attributes (Table 2). For example, ancient murrelets are planktivorous, feeding on zooplankton and meroplankton in the coastal-pelagic zone, whereas cormorants are piscivorous and forage in the nearshore coastal domains. At Aiktak Island, fork-tailed storm-petrels feed primarily on krill and secondarily on larval fish, and Leach's storm-petrels primarily on gammarid amphipods and krill (Youngren et al., 2022).

Variation in the species foraging ecology and diet is expected to affect their responses to variation in ocean conditions, including current flows and temperature (e.g., Sydeman et al., 2021).

Annual productivity was assessed as the mean number of chicks fledged per breeding pair for each species, based on replicate checks of individual nest sites. For cormorants, productivity was proxied as the mean number of large chicks observed per nest site as it was not possible to monitor these species to when chicks departed each nest (fledged). The productivity metric we used for murres, puffins, and storm-petrels was "maximum potential reproductive success", which assumed that all chicks still alive when researchers left the island in late summer survived to fledge (Youngren et al., 2022). This variable is highly correlated (Spearman rho = 0.9) with the measurements of reproductive success determined at the time of personnel departure, which excluded the late breeding pairs that were not monitored until the end of the breeding success. Given this correlation we expected and found no difference in models using either variable.

We collated long-term breeding success data on the ten locally breeding species shown in Table 2. For each species, years in which fewer than five nests were monitored were coded as missing for analyses. Due to overall similarities in the foraging ecology of congeneric species (diet, foraging range), as well as some limitations in species-specific annual sample sizes, we averaged across species for each year to also examine productivity at the genus level of "murres" (*Uria* spp.), "puffins" (*Fratercula* spp.), "storm-petrels" (*Hydrobates* spp.), and "cormorants" (*Urile* spp. and *Nannopterum*). Ancient murrelets were analyzed separately; furthermore, murrelet productivity increased significantly through time (rho = 0.55), thus we removed the linear trend in this time series to isolate the interannual variation prior to regression against oceanographic conditions.

Prey use for the piscivorous and omnivorous breeding seabirds was proxied by examining the offspring diet composition for tufted puffins. Prey use was characterized by long-term sampling of fish delivered to puffin nest sites using the "burrow screening" technique (see Hatch and Sanger, 1992). In brief, small screens were placed in the front of puffin nesting burrows, which caused provisioning parents to drop prey at the burrow entrance where they could be collected and later analyzed by researchers. The use of select species of forage fish in Unimak Pass each year was assessed as the percent biomass of Pacific sand lance and age-0 walleye pollock (*Gadus chalcogrammus*) in the puffin chick diet (see also Sydeman et al., 2017; Piatt et al., 2018; Thompson et al., 2019; Sydeman et al., 2022). The use of Pacific sand lance and age-0 pollock by puffins is pertinent to other seabirds in this study, particularly murres and cormorants, that are also known to forage on these prey items (Youngren et al., 2022). Moreover, the use of age-0 pollock by puffins is related to spawning stock biomass of walleye pollock in northwestern Gulf of Alaska (Sydeman et al., 2022).

2.4. Foraging density

We assessed the use of Unimak Pass as foraging habitat by seabirds to determine if foraging densities were also affected by changes in currents and temperature. Observations of seabirds at sea were obtained from the North Pacific Pelagic Seabird Database (NPPSD; updated v.3; Drew and Piatt 2005), and filtered for the study area delineated in Fig. 1B. Briefly, seabirds foraging in the region were visually identified and counted by trained ornithologists on ships of opportunity (e.g., Hyrenbach et al., 2007) or government research vessels transiting the realm. Observers used hand-held binoculars to aid in species identifications; birds were counted in a 300-m strip transect on the side of the vessel with the best viewing conditions (i.e., minimal glare) while the ships were underway at speeds > 5 kt. Counts were placed into 3-km bins, and the series of bins along the survey track were considered transects. Virtually all of the observations used in this study were obtained from large to very large vessels, including a series of surveys conducted from bulk transport carriers ("container ships") from June 2002–March 2007 (99.9% of all transects). We excluded seabirds in flight from density estimations because these birds may have been migrating through the area and not actively searching for or obtaining food. Moreover, both the "continuous" (38.8% of all transects) and "snapshot/scan" method (Tasker et al., 1984) were used in the area to account for birds in flight, but the snapshot/scan method was used almost exclusively after 2005, resulting in a systematic bias in these data. The continuous survey method is known to result in over-counts of flying seabirds relative to the snapshot method (e.g., Arimitsu et al., 2023), and rather than attempting to correct for this bias for birds that may or may not have been foraging, we simply omitted these counts from on-the-water density estimates. Another consideration is that some sitting birds may not be actively foraging, but for our purposes we assumed that sitting birds were either actively foraging or were resting on the water before or after foraging. This assumption, however, may not be entirely appropriate for all species examined, as some species may rest after foraging more so than others. Therefore, similar to our anticipated responses in breeding productivity, we expected that species would show varied responses to seasonal ocean conditions due to differences in habitat associations or foraging behaviors.

A total of 4,318 transects (mean area = 0.79 km^2) were obtained for analysis over the period 1991–2018; 1994 and 1997 were omitted from

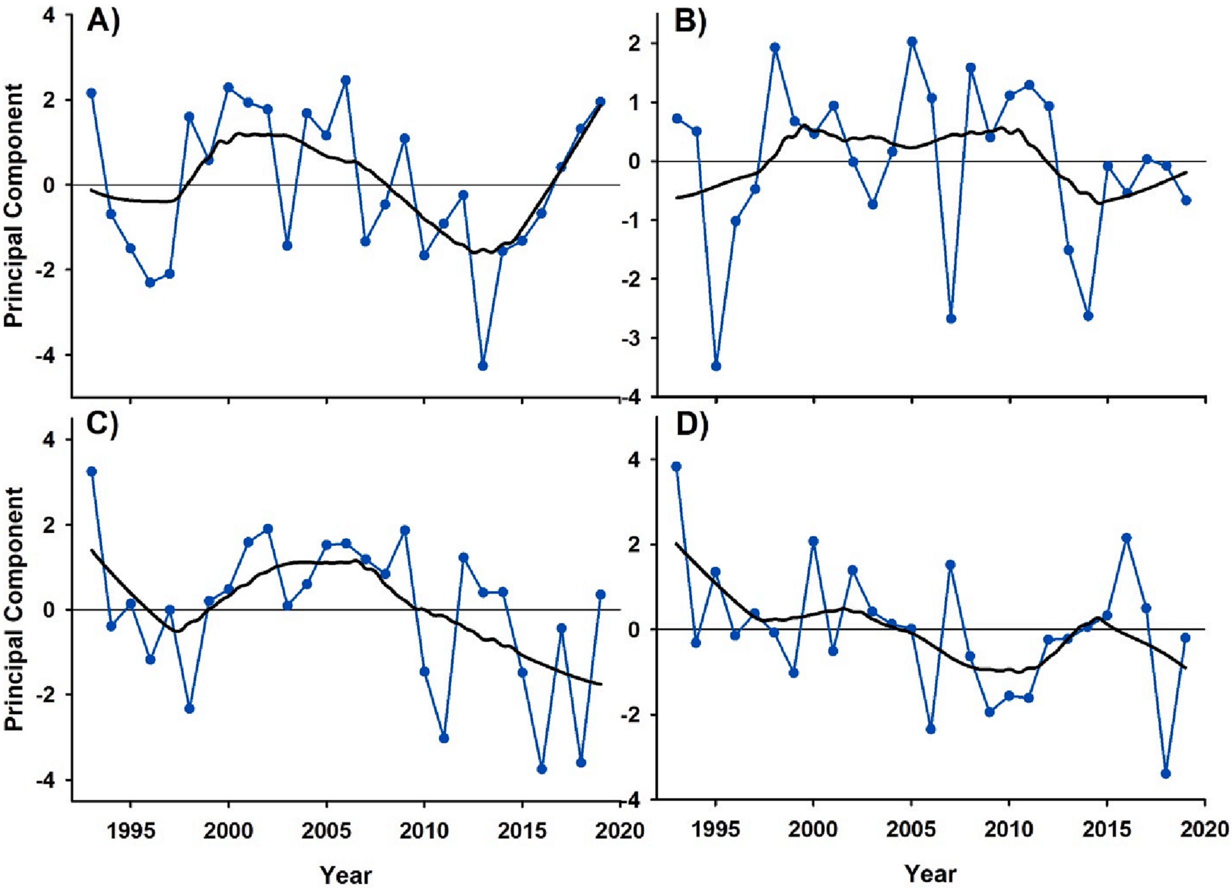

Fig. 2. Time series results of PCA on currents, 1993–2019. (A) Spring zonal currents ($PC1_{spring}$), (B) summer zonal currents ($PC2_{summer}$), (C) summer meridional currents ($PC1_{summer}$), and (D) spring meridional currents ($PC2_{spring}$). Black line indicates Loess smoothing function. Note the y-axis scale varies between panels.

Table 3

Principal component analysis (PCA) results for currents in A) spring (February–April) and B) summer (May–August). Input variables were zonal and meridional winds in the center, east, and west areas of the overall "candy-wrapper" study region.

A)			
Component	Eigenvalue	Proportion	Cumulative
1	3.0597	0.5100	0.5100
2	2.2410	0.3735	0.8834
3	0.3835	0.0639	0.9474
Eigenvectors/Components			
Variable	1	2	3
Zonal, center	0.4996	−0.2971	−0.1861
Zonal, east	0.4023	−0.4598	−0.0667
Zonal, west	0.4813	0.2238	−0.6190
Meridional, center	0.2379	0.5598	0.0927
Meridional, east	0.4958	−0.0836	0.7464
Meridional, west	0.2333	0.5743	0.1099
B)			
Component	Eigenvalue	Proportion	Cumulative
1	2.9742	0.4957	0.4957
2	1.8782	0.3130	0.8087
3	0.5973	0.0995	0.9083
Eigenvectors/Components			
Variable	1	2	3
Zonal, center	−0.2921	0.5728	−0.3724
Zonal, east	−0.5172	0.2811	−0.1303
Zonal, west	0.3672	0.4573	−0.4630
Meridional, center	0.4329	0.3465	0.2559
Meridional, east	−0.3416	0.4165	0.7016
Meridional, west	0.4564	0.3002	0.2690

Table 4

Principal component analysis (PCA) results for sea surface temperature (SST) in the center, east, and west study regions in A) spring (February–April) and B) summer (May–August).

A)			
Component	Eigenvalue	Proportion	Cumulative
1	2.9500	0.9833	0.9833
2	0.0443	0.0148	0.9981
Eigenvectors/Components			
Variable	1	2	
Center	0.5811	−0.0133	
East	0.5756	−0.7001	
West	0.5753	0.7139	
B)			
Component	Eigenvalue	Proportion	Cumulative
1	2.9271	0.9757	0.9757
2	0.0568	0.0189	0.9946
Eigenvectors/Components			
Variable	1	2	
Center	0.5811	−0.1353	
East	0.5743	0.7669	
West	0.5766	−0.6273	

analysis due to low sample size ($n < 10$ transects per year). Overall densities were derived by averaging counts across all transects for the period 1 May through 31 August each year. These months corresponded with the breeding season for breeding species on Aiktak Island, as well as the period of peak local presence in the study area by migratory species, especially shearwaters (July and August). To estimate densities of the

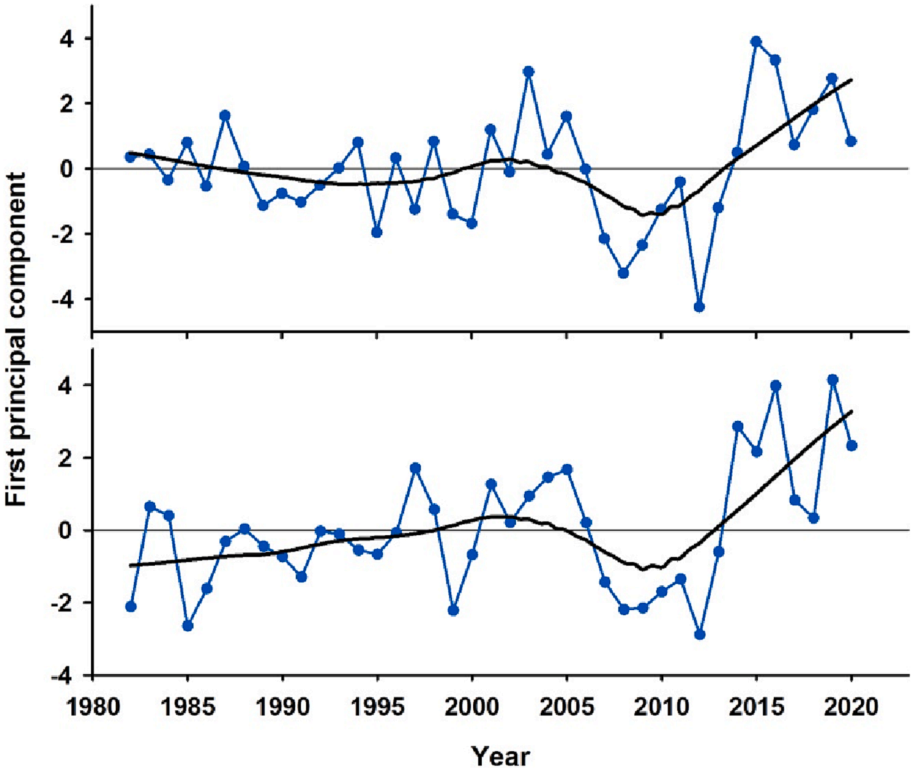

Fig. 3. Time series results of Principal Component Analysis (PCA) for SST, 1982–2020. First principal component (PC1) in spring (top) and summer (bottom). Black line indicates Loess smoothing function.

Table 5
Principal component analysis (PCA) results for chlorophyll-a concentration in the center, east, and west study regions in A) spring (February–April) and B) summer (May–August).

A)			
Component	Eigenvalue	Proportion	Cumulative
1	2.0398	0.6799	0.6799
2	0.8600	0.2867	0.9666
Eigenvectors/Components			
Variable	1	2	
Center	0.6784	−0.0961	
East	0.6148	−0.4685	
West	0.4022	0.8782	
B)			
Component	Eigenvalue	Proportion	Cumulative
1	2.0324	0.6775	0.6775
2	0.8494	0.2831	0.9606
Eigenvectors/Components			
Variable	1	2	
Center	0.6771	−0.0761	
East	0.5947	−0.5293	
West	0.4335	0.8450	

seabird community we summed data for all seabird species, but due to the large numbers of dark shearwaters in the dataset (primarily short-tailed shearwaters (*Puffinus tenuirostrus*) but also sooty shearwaters (*Ardenna grisea*)) which overwhelmed community effects in our analyses, we created a separate variable for all species minus dark shearwaters. Additionally, we examined dark shearwater, ancient murrelet, and tufted puffin densities alone. We selected murrelets and puffins as they were relatively abundant in the at-sea dataset, and are also part of our data on seabird productivity. Unfortunately, there was insufficient data on murres, storm-petrels, and cormorants to conduct analyses on these species. Densities were $\log_{10}(+1)$ transformed prior to analysis. Densities for i) all species minus dark shearwaters (rho = -0.53), ii) ancient murrelet (rho = -0.43), and iii) tufted puffin (rho = -0.58) showed significant negative trends through time, thereby violating an assumption of stationarity for these data in regression analyses. Therefore, density values of these species were detrended using linear regression prior to analysis with ocean variables. As for productivity, this de-trending process isolated the interannual changes in density from long-term trends, facilitating analyses on the annual time scale of interest.

2.5. *Seasonal oceanographic indicators*

Surface current flow, SST, and chl-concentrations were obtained for each of the three sub-regions of the Unimak Pass study area and averaged for two seasonal periods: February–April (“spring”) and May–August (“summer”). Subsequently, for each season, we developed indices of current flows, SST, and chl-a abundance by implementing Principal Component Analysis (PCA) on each parameter-subregion. Zonal and meridional currents were analyzed together because the directionality of currents within the Unimak Pass region is related to each other by winds (Stabeno et al., 2002). Therefore, PCA on current flows was run on a matrix containing six variables (zonal and meridional currents in three sub-regions) over 27 years (1993–2019). PCA on SST and chl-a was implemented on matrices of three variables (one per sub-region) by 39 years (1982–2020) and 22 years (1998–2019), respectively, and there was one PCA for each season.

2.6. *Regression analysis*

To test the importance of both leading and concurrent oceanographic conditions on chl-a (as a proxy for primary productivity), zooplankton abundance, and seabird productivity, diet, and density at sea, we included both spring and summer oceanographic variables (e.g.,

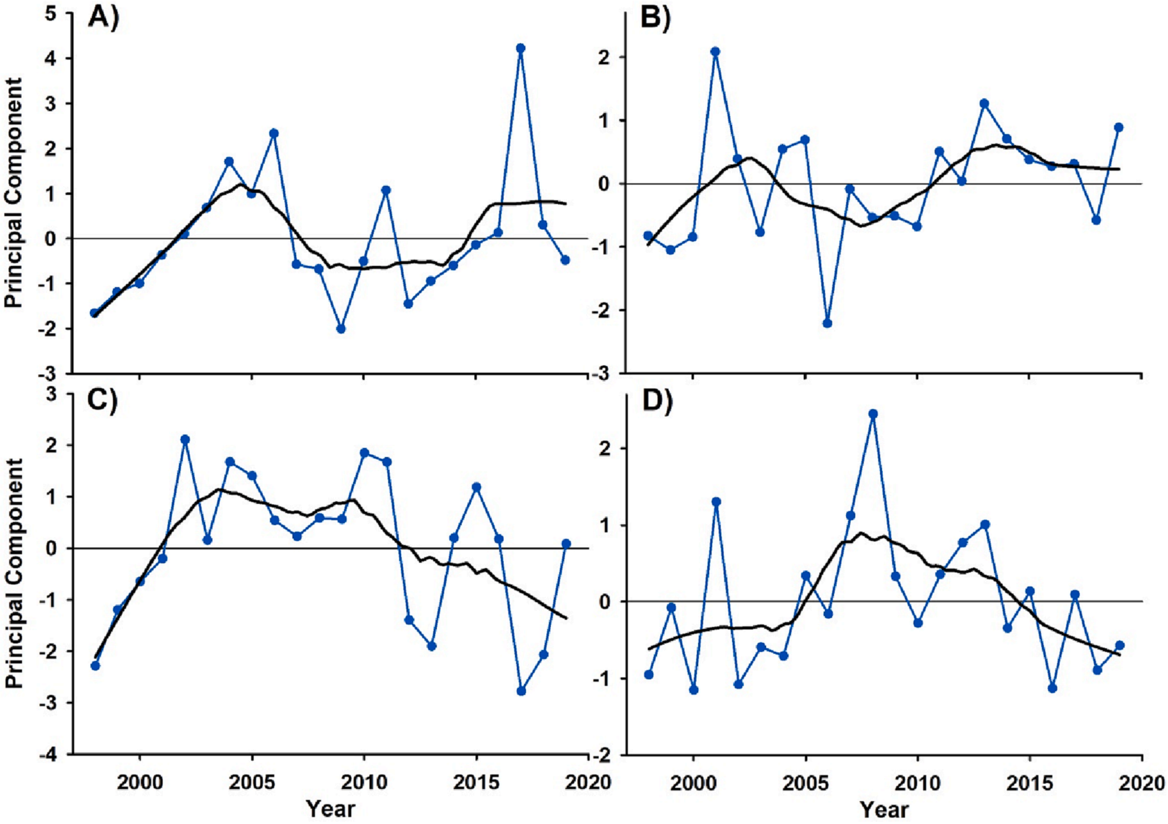

Fig. 4. Time series results of Principal Component Analysis (PCA) on chlorophyll-a concentrations, 1998–2019. (A) $PC1_{spring}$, (B) $PC2_{spring}$, (C) $PC1_{summer}$, and (D) $PC2_{summer}$. Black line indicates Loess smoothing function. Note the y-axis scale varies between panels.

Table 6

Results of forward stepwise regression on seasonal, regional chlorophyll-a concentration (represented by principal components; see Table 5) predicted by currents and SST with p-value entered = 0.1. Spring chlorophyll concentration was predicted by spring currents and SST; spring and summer environmental predictors were included for summer chlorophyll concentration. Current variables included zonal and meridional components. SST was represented by the first principal component (see Table 4).

Region	Predictor	N (years)	Coefficient	p-value	Model R^2
Center/east, spring	SST, spring	22	0.2386	0.099	0.13
West, spring	none				
Center/east, summer	none				
West, summer	SST, spring	22	−0.2092	0.021	0.24

principal components) in regression models using a forward stepwise variable selection procedure in Stata v. 11.1 (StataCorp, 2009). In brief, variables were entered sequentially in the model starting with the one that was the most highly predictive of the response variable (entered at p-value < 0.05). In models where chl-a was the dependent variable, we used $p < 0.1$ to infer marginal significance because of the lower sample sizes of this variable as well as our interest in comparing effect sizes across trophic levels. Additional variables were added sequentially if they were significantly related to a response variable after the inclusion of variables entered earlier in the stepwise process. We implemented these models on seabird breeding success (ten species and four species groups, $n = 14$ models), seabird density at sea (four species and two species groups, $n = 6$ models), forage fish availability (two species, $n = 2$ models), zooplankton density (three species groups, $n = 3$ models), and chl-a (two regional groups resulting from PCA, $n = 2$ models). Chl-a was used as both a response and predictor variable. In one set of regressions, current and SST PCA-based indicators were used as predictors. In the next set of models, we used currents, SST, and chl-a; owing to the fact that the chl-a time series available was five years shorter than that for currents and SST we refer to this approach as the “reduced model”. We

Table 7

Results of forward stepwise regression on zooplankton abundance (ln(mean count)) predicted by currents and SST in the spring and summer with p-value entered = 0.1. Current variables included zonal and meridional components. SST was represented by the first principal component (see Table 4).

Zooplankton	Predictor	N (years)	Coefficient	p-value	Model R^2
Euphausiids	none	12			
Small copepods	SST, spring	12	0.5400	0.061	0.31
Large copepods	Zonal currents, summer	12	−0.4097	0.064	0.30

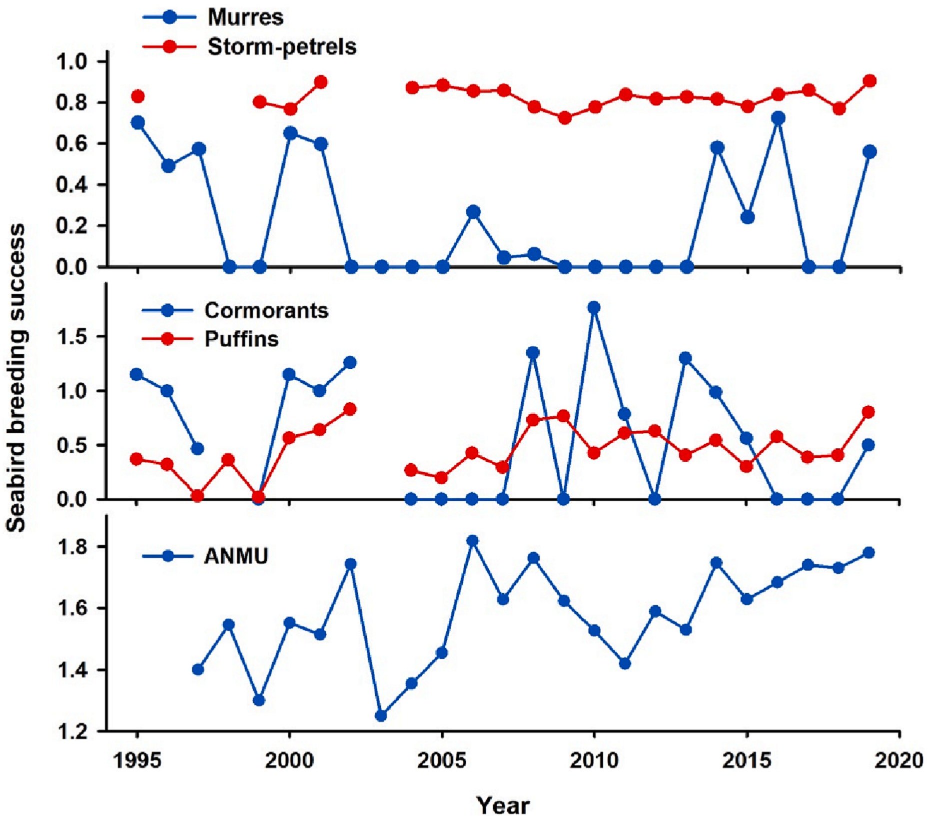

Fig. 5. Seabird breeding success, 1995–2019, for pelagic foraging murres and storm-petrels (two species in each group; top), neritic foraging cormorants (three species) and coastal-pelagic puffins (two species; upper center), and ancient murrelets (ANMU; bottom). See Table 2 and text for additional details on species.

compared the results of these analyses to determine whether chl-a played a role in determining higher trophic level responses, as well as which models were most robust to changes in time series length (i.e., sample size, see Discussion).

3. Results

3.1. Currents and temperature

PCA revealed changes in currents in Unimak Pass through time (Fig. 2). The dominant mode of variability in spring, shown as PC1 (Fig. 2A), explained 51% of the variation in spring currents, and is interpreted as mostly reflecting zonal currents (Table 3A). PC2 explained 37% of the variation in spring currents, and is interpreted as mostly reflecting meridional currents (Table 3A). The dominant mode of variability in summer, PC1 (Fig. 2C), explained 50% of the variance in summer currents, and was interpreted as mostly reflecting meridional currents (Table 3B). PC2 in summer (Fig. 2B) explained 30% of the variation, and is interpreted as mostly reflecting zonal currents (Table 3B). $PC1_{spring}$ (zonal currents) was high during the late 1990s and early 2000s (Fig. 2A) and low in 2013, but increased in the latter years of the time series. $PC2_{summer}$ (zonal currents) showed low values in 1995, 2007, and 2013–2014 (Fig. 2B). $PC1_{summer}$ (meridional currents) showed high values in the mid-2000 s and low values at the end of the time series (Fig. 2C). $PC2_{spring}$ (meridional currents) showed a nonsignificant declining trend (rho = -0.23, p = 0.25), with a low value in 2019 (Fig. 2D).

PCA revealed significant variation in SST. Only one PC was needed for each season to characterize interannual variation in SST; $PC1_{spring}$ and $PC1_{summer}$ explained 98% of the variation in each season (Table 4). $PC1_{spring}$ and $PC1_{summer}$ were correlated (rho = 0.677, $p < 0.0001$); each showed weak interannual variability in the early part of the time series, followed by a “stanza” of cooler SST in 2007–2013 (spring mean SST = 2.65 °C, summer mean SST = 6.73 °C), followed by a stanza of warmer than average SST in 2014–2020 (spring mean SST = 4.33 °C, summer mean SST = 8.63 °C; Fig. 3). The trend in $PC1_{spring}$ SST was not significant (rho = 0.15, p = 0.34), but $PC1_{summer}$ SST increased through time (rho = 0.362, p = 0.024). Interannual variability in temperature appeared to increase through time, and was greater after 2000 (spring CV = 12%, summer CV = 7% from 1982 to 2000; spring CV = 25%, summer CV = 12% from 2001 to 2020).

3.2. Chlorophyll-a

PCA revealed two modes of variability in chl-a concentration in each season (Table 5). $PC1_{spring}$ chl-a explained 68% of the variation (Fig. 4A). $PC1_{summer}$ chl-a also explained 68% of the variation, and was characterized by low values at the beginning and end of the time series (Fig. 4C). $PC2_{spring}$ and $PC2_{summer}$ explained 28% of the variation (Table 5). For both seasons, we interpret PC1 as chlorophyll concentration in the center and east sub-regions and PC2 as chl-a concentration in the western sub-region (Table 5).

Stepwise regression showed that seasonal, regional chl-a was positively related to SST (Table 6). At $p < 0.1$, center/east chl-a in the spring ($PC1_{spring}$) was predicted by spring SST. Chl-a in the western sub-region in the summer ($PC2_{summer}$) was predicted by spring SST (p = 0.021).

3.3. Zooplankton abundance

None of the zooplankton species groups that we modeled in the summer months (euphausiids, small copepods, and large copepods) revealed significant relationships with seasonal currents or temperature in Unimak Pass at $p < 0.05$, however, small copepods were positively correlated with spring SST and large copepods were positively correlated with summer zonal currents at $p < 0.1$ (Table 7).

Table 8

Results of forward stepwise regression on seabird breeding success predicted by A) currents and SST in spring and summer and B) currents, SST, and chlorophyll-a concentration (chl-a) in spring and summer with p-valued entered = 0.05. Current variables included zonal and meridional components. SST was represented by the first principal component (see Table 4). Chlorophyll-a variables included concentration in the east/center regions (PC1; see Table 5) and the western region (PC2). Species were grouped by averaging. *Detrended variable.

A)

Species	Predictor	N (years)	Coefficient	p-value	Model R^2
Common murre (COMU)	None	15			
Thick-billed murre (TBMU)	SST, summer	17	0.1642	0.001	0.58
	SST, spring		−0.1045	0.022	
Murres	SST, summer	20	0.0593	0.027	0.46
	Meridional currents, spring		0.0754	0.049	
Fork-tailed storm-petrel (FTSP)	Meridional currents, spring	20	0.0223	0.04	0.22
Leach's storm-petrel (LHSP)	SST, summer	20	0.0149	0.008	0.33
Petrels	SST, summer	20	0.0117	0.022	0.26
Horned puffin (HOPU)	None	18			
Tufted puffin (TUPU)	None	24			
Puffins	None	24			
Double-crested cormorant (DCCO)	None	12			
Red-faced cormorant (RFCO)	None	13			
Pelagic cormorant (PECO)	None	13			
Cormorants	None	18			
Ancient murrelet (ANMU)*	Zonal currents, spring	23	0.033	0.042	0.18

B)

Species	Predictor	N (years)	Coefficient	p-value	Model R^2
Common murre (COMU)	SST, summer	12	0.0781	0.035	0.37
Thick-billed murre (TBMU)	SST, summer	14	0.0593	0.007	0.83
	Zonal currents, spring		0.077	0.002	
	Meridional currents, spring		0.0774	0.009	
Murres	SST, summer	17	0.0757	0.004	0.44
Fork-tailed storm-petrel (FTSP)	None	19			
Leach's storm-petrel (LHSP)	SST, summer	19	0.0148	0.01	0.33
Petrels	SST, summer	19	0.0118	0.024	0.26
Horned puffin (HOPU)	None	18			
Tufted puffin (TUPU)	None	21			
Puffins	None	21			
Double-crested cormorant (DCCO)	None	12			
Red-faced cormorant (RFCO)	Chl-a (east/center), spring	12	−0.2676	0.043	0.35
Pelagic cormorant (PECO)	None	11			
Cormorants	None	15			
Ancient murrelet (ANMU)*	Zonal currents, spring	22	0.0347	0.045	0.19

3.4. *Seabird breeding success*

Breeding success of planktivorous storm-petrels at Aiktak Island was relatively consistent through time, but the breeding success of all other species was highly variable (Fig. 5). Murres showed higher productivity at the beginning and end of the time series, and generally failed to produce young from 2002 to 2013 (Fig. 5). Tufted puffin breeding success was variable, with low breeding success in 1995–1998, 2005, 2007, 2015, and 2017 (Fig. 5). The breeding success of cormorants was also highly variable with multi-year periods of apparent failure (Fig. 5). In contrast, the breeding success of ancient murrelets increased through time (rho = 0.551, p = 0.006) with no years of breeding failure (Fig. 5). To reiterate, the positive trend in ancient murrelet breeding success was removed and only the interannual variability in this time series was included in models below.

Forward stepwise regression demonstrated significant effects of currents and temperature in both spring and summer on the breeding success of murres, murrelets, and storm-petrels, but not puffins and cormorants (Table 8A). The best models were for murres: temperature and spring meridional currents explained 58% of the variation in thick-billed murre breeding success and 46% of the variation in the breeding success of both murre species combined, which undoubtedly is related to the oceanographic effects on thick-billed murres. Notably, the effect of temperature on thick-billed murre breeding success varied in sign by season, with a positive effect of summer temperature and a weaker negative effect of spring temperature (Table 8, Fig. 6A and B). For combined murres, the effect of spring meridional currents was weaker than the effects of temperature (Table 8, Fig. 6C and D). Similarly, but with less variance explained, summer temperature and spring meridional currents related to the breeding success of storm-petrels, with explanatory power varying from 22 to 33% (Table 8, Fig. 6E–G). Zonal currents in spring also related to the breeding success of ancient murrelets, but explained only 18% of the variance (Table 8, Fig. 6H).

Adding chl-a as a predictor variable improved the explanatory power of some of the models and confirmed the selected predictors (Table 8B), but chl-a concentration did not improve most models, and was unexpectedly included as a negative influence on the breeding success of red-faced cormorants. The reduced dataset, however, resulted in a very large improvement in the model for thick-billed murres, with 83% of the variance explained.

3.5. *At sea density*

The density of dark shearwaters was noticeably high in the period 2003–2005, but decreased thereafter to a low point in 2016 (Fig. 7). The density of all other species (excluding dark shearwaters) declined significantly from 1990 to 2019 (rho = -0.53, p = 0.006). Seasonal density of seabirds in Unimak Pass was affected by currents and temperature (Table 9). Models included positive relationships with meridional currents in summer, explaining 18% of the variance in all species, and 16% of the variance in the density of dark shearwaters in the region (Table 9A, Fig. 8). Models also included negative effects of increasing summer zonal currents on ancient murrelet (26% of the variance explained) and increasing spring temperature on tufted puffin (17% of

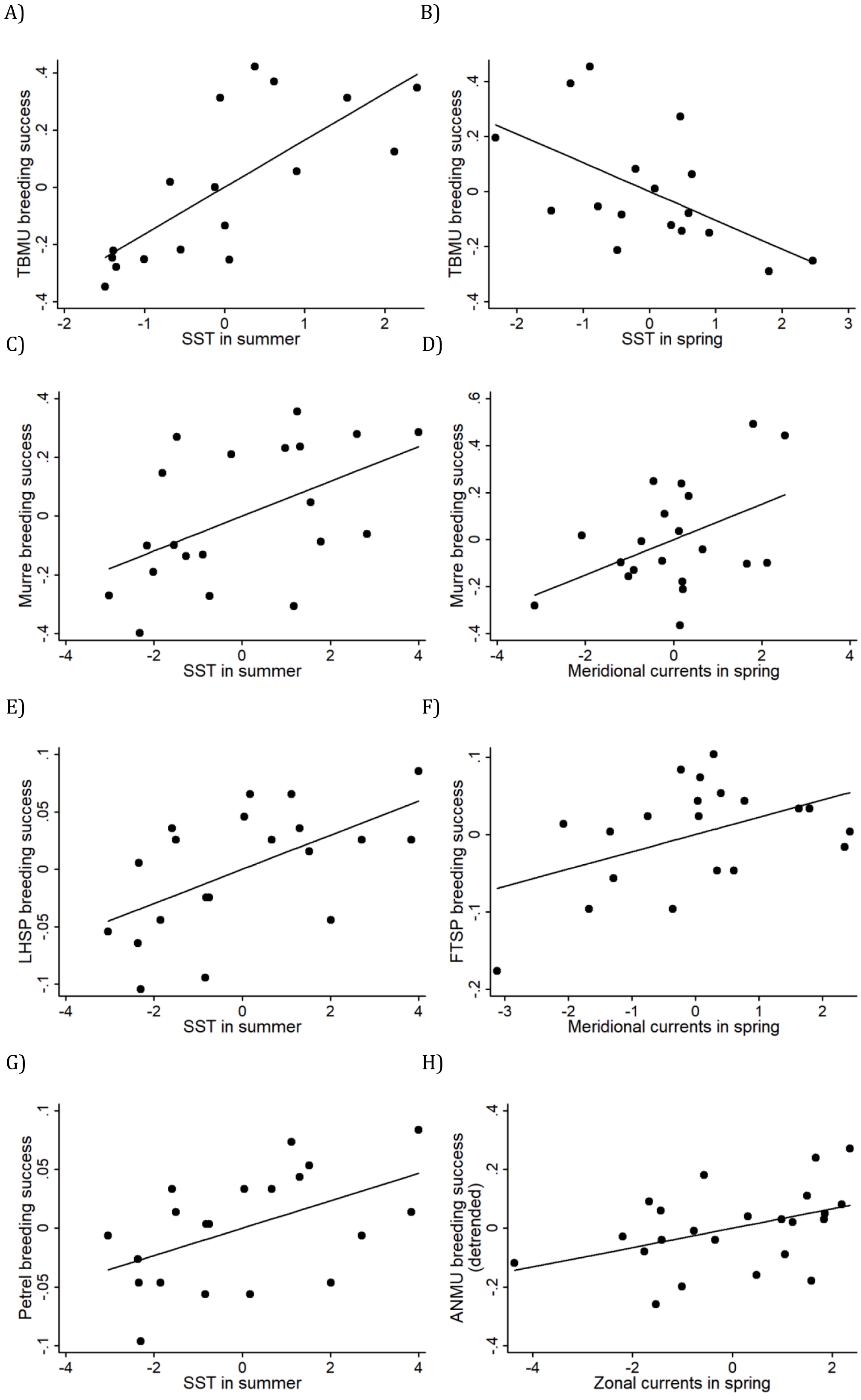

Fig. 6. Multiple (added) variable plots of seabird breeding success as a function of currents and SST (chl-a concentration was not included in these models). Thick-billed murres (TBMU) as predicted by A) summer SST and B) spring SST. Murre breeding success (both species combined) as predicted by C) summer SST and D) spring meridional currents ($PC2_{spring}$). E) Leach's storm-petrel (LHSP) breeding success predicted by summer SST. F) Fork-tailed storm-petrel (FTSP) breeding success as predicted by spring meridional currents ($PC2_{spring}$). G) Storm-petrel (both species combined) breeding success predicted by summer SST. H) Ancient murrelet (ANMU; detrended) breeding success as predicted by spring zonal currents ($PC1_{spring}$). SST was represented by the first principal component (see Table 4).

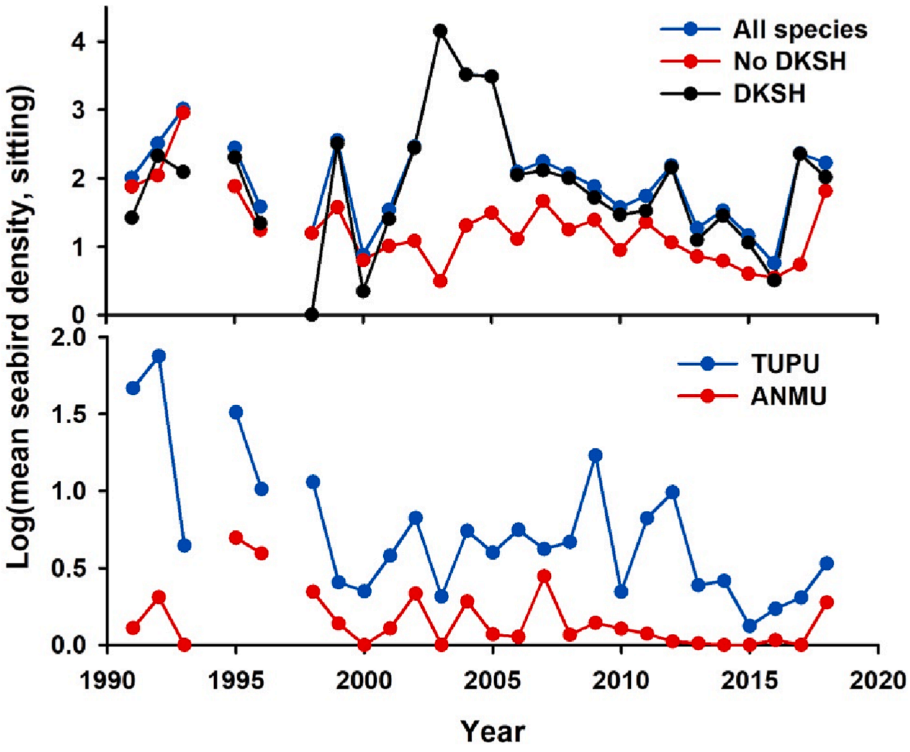

Fig. 7. Time series of seabird foraging density (birds/km^2; sitting birds only) within the Unimak Pass study area, 1991–2018. Top: all species, all species without dark shearwaters (no DKSH) and dark shearwaters (DKSH). Bottom: tufted puffin (TUPU) and ancient murrelet (ANMU).

Table 9

Results of forward stepwise regression on seabird mean density at sea, sitting birds only, predicted by A) currents and SST in spring and summer and B) currents, SST, and chlorophyll-a concentration (chl-a) in spring and summer with p-value entered = 0.05. Current variables included zonal and meridional components. SST was represented by the first principal component (see Table 4). Chlorophyll-a variables included concentration in the east/center regions (PC1; see Table 5) and the western region (PC2). *Detrended variables.

A) Species	Predictor	N (years)	Coefficient	p-value	Model R^2
All birds	Meridional currents, summer	24	0.1968	0.039	0.18
Birds, no dark shearwaters*	None				
Dark shearwaters (DKSH)	Meridional currents, summer	24	0.2159	0.049	0.16
Ancient murrelet (ANMU)*	Zonal currents, summer	24	−0.0625	0.01	0.26
Tufted puffin (TUPU)*	SST, spring	24	−0.0621	0.049	0.17

B) Species	Predictor	N (years)	Coefficient	p-value	Model R^2
All birds	None				
Birds, no dark shearwaters*	Meridional currents, spring	21	−0.1579	0.007	0.32
Dark shearwaters (DKSH)	None				
Ancient murrelet (ANMU)*	None				
Tufted puffin (TUPU)*	Meridional currents, spring	21	−0.0913	0.047	0.19

the variance explained). Using the reduced time series that included chl-a (Table 9B), we found negative effects of springtime meridional currents on densities of all species excluding dark shearwaters (32% of the variance explained; Fig. 9) and tufted puffin (19% of the variance explained).

3.6. Prey use

Prey use varied on multiple time scales. The proportion of Pacific sand lance and walleye pollock in tufted puffin diet was inversely related (rho = -0.46, p = 0.013; Fig. 10). Pollock was more abundant in the diet in the early years of our time series, generally lower in the middle period, and then higher again after 2012 (Fig. 10). Pacific sand lance, on the other hand, showed the opposite pattern. Due to this relationship, the other fish species in tufted puffin diet were also included in the stepwise regression models (e.g., Pacific sand lance as a predictor for pollock; Table 10). Model results showed that the use of Pacific sand lance by tufted puffins was positively related to spring zonal currents, negatively related to the use of walleye pollock, and also negatively related to summer meridional currents; this model explained 55% of the variation (Table 10A, Fig. 11 A–C). Tufted puffin use of pollock was negatively related to the use of sand lance, explaining 22% of the variation (Table 10A, Fig. 11D). Including chl-a as a predictor did not improve these models (Table 10B).

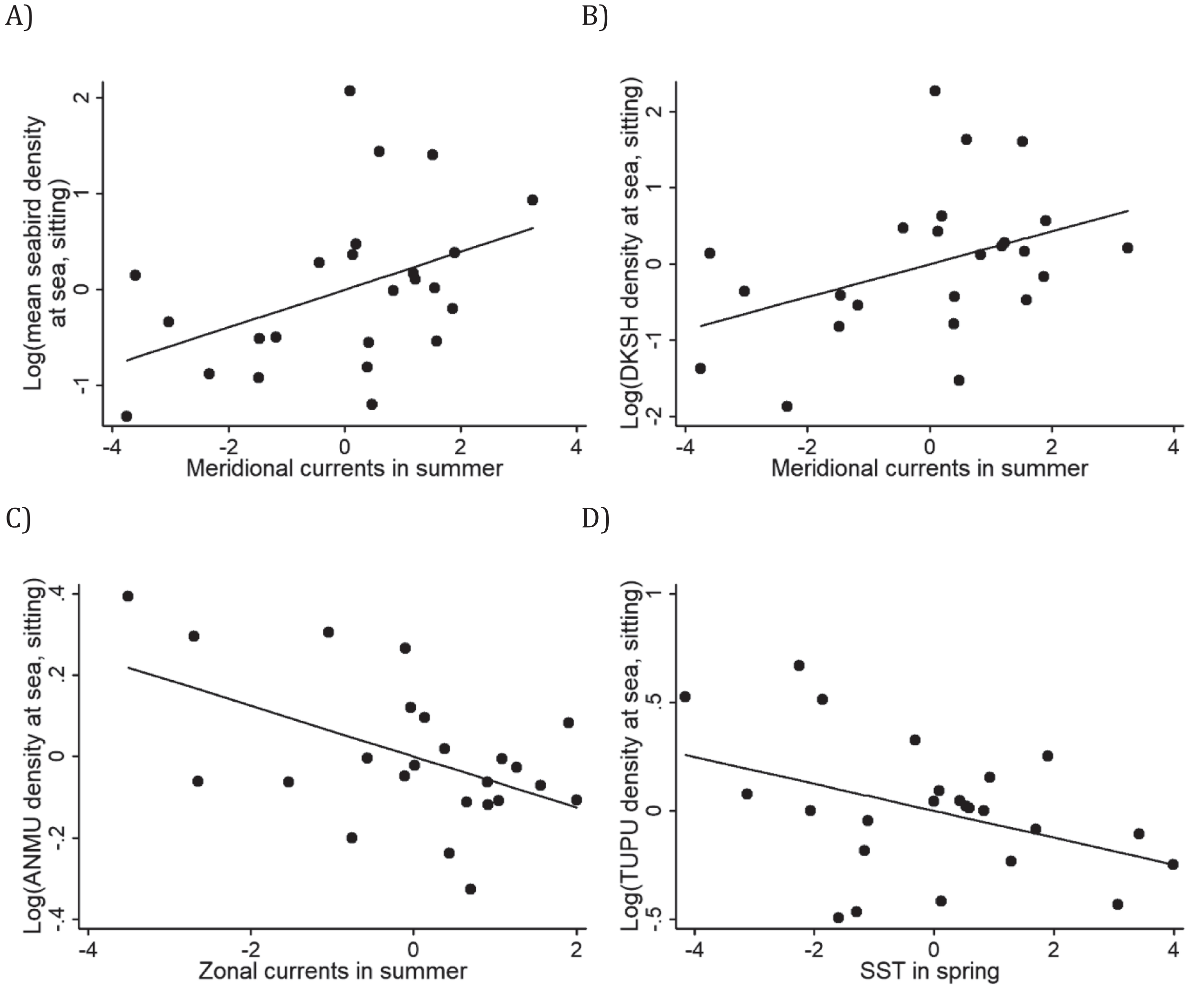

Fig. 8. Multiple (added) variable plots for seabird foraging density within Unimak Pass as a function of currents and SST. A) Overall seabird density at sea predicted by summer meridional currents ($PC1_{summer}$). B) Density of dark shearwaters (DKSH) at sea predicted by summer meridional currents ($PC1_{summer}$). C) Ancient murrelet (ANMU) density at sea predicted by summer zonal currents ($PC2_{summer}$). D) Tufted puffin (TUPU) density at sea predicted by spring SST. SST was represented by the first principal component (see Table 4).

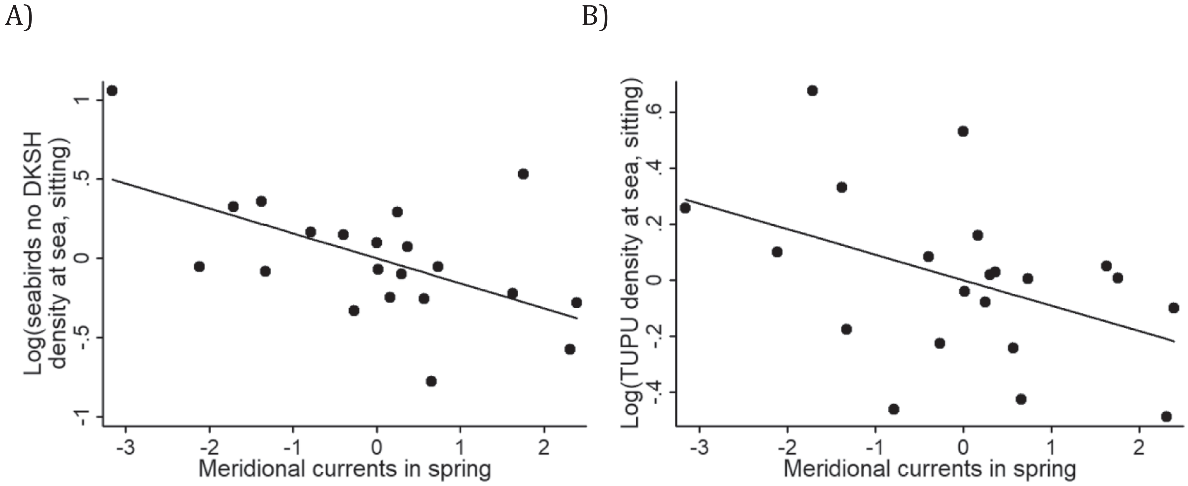

Fig. 9. Multiple (added) variable plots for seabird mean density at sea, sitting birds only, in a model containing currents, SST, and chlorophyll-a as predictors. A) Seabird species excluding dark shearwaters (no DKSH) density at sea predicted by spring meridional currents ($PC2_{spring}$). B) Tufted puffin (TUPU) density at sea predicted by spring meridional currents ($PC2_{spring}$).

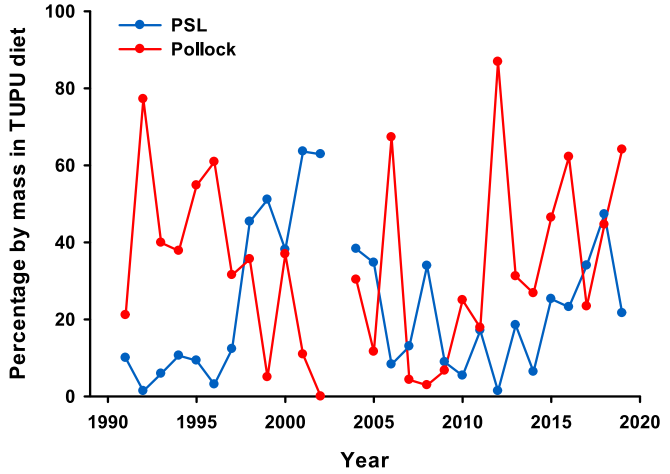

Fig. 10. Percent by biomass of Pacific sand lance (PSL) and walleye pollock in tufted puffin (TUPU) diet at Aiktak Island, 1991–2019.

Table 10

Results of forward stepwise regression on Pacific sand lance (PSL) and walleye pollock proportion in tufted puffin diet predicted by A) currents, SST, and the other fish species (e.g., PSL or walleye pollock) in spring and summer and B) currents, SST, chlorophyll-a concentration (chl-a), and the other fish species in the spring and summer, with p-value entered = 0.05. Current variables included zonal and meridional components. SST was represented by the first principal component (see Table 4). Chlorophyll-a variables included concentration in the east/center regions (PC1; see Table 5) and the western region (PC2).

A)

Species	Predictor	N (years)	Coefficient	p-value	Model R^2
PSL	Zonal currents, spring	26	6.1138	0.001	0.55
	Pollock		−0.4279	0.002	
	Meridional currents, summer		−3.7055	0.033	
Pollock	PSL	26	−0.5802	0.016	0.22

B)

Species	Predictor	N (years)	Coefficient	p-value	Model R^2
PSL	Zonal currents, spring	21	5.6813	0.008	0.44
	Pollock		−0.3414	0.022	
Pollock	None	21			

4. Discussion

Many biological hotspots in pelagic environments have been identified on the basis of persistent oceanographic conditions that create and maintain habitat features, such as fronts or eddies, which in turn promote and concentrate food resources (e.g., Palacios et al., 2006; Arrigo et al., 2015; Nishino et al., 2016) and generate persistent aggregations of foraging marine consumers (Yen et al., 2004, 2006; Block et al., 2011; Wingfield et al., 2011; Louzao et al., 2012; Santora and Veit, 2013; Thiers et al., 2014). Rarely, however, have the physical and biological attributes of a particular hotspot been examined over long time scales to determine interannual dynamics relative to oceanographic drivers of lower trophic level productivity. In this paper, we used long-term biological and oceanographic data sets to test the hypothesis that stronger currents and warmer temperatures are positively related to greater productivity across trophic levels of the Unimak Pass ecosystem in summer (defined as May–August). We found that current flows and temperature in the study area were unrelated. We expected that stronger regional meridional currents from the GoA would bring warmer waters into the study region, but this was not observed. Instead, while temperature varied substantially by season, interannual variation in temperature appeared to be determined primarily by large- to basin-scale features, such as the PDO (Mantua et al., 1997) which has been in a warm state over the past decade (Werb and Rudnick, 2023). We therefore developed separate seasonal indicators for currents and temperature using PCA scores, and then used these physical indicators to model biological responses.

4.1. Effects of currents

In general, the effects of large-scale circulation on seabird density at sea and breeding success are not well known. In our study, both zonal and meridional currents within the Unimak Pass study area were related to breeding and other foraging seabirds (e.g., shearwaters) in the region. Zonal current flows were unrelated to chl-a, but were negatively related to zooplankton (large copepods, $R^2 = 0.30$), and even more strongly and positively related to the use of Pacific sand lance by breeding tufted puffins at Aiktak Island ($R^2 = 0.55$). Zonal currents were also positively related to the breeding success of ancient murrelets ($R^2 = 0.18$), but, in contrast, were negatively related to the density of foraging murrelets in the region ($R^2 = 0.26$). Ancient murrelets take their tiny, flightless chicks to sea usually within 2–3 days of hatching, where the parents then rear them to independence (Gaston, 2003). The apparently contradictory findings above concerning zonal currents therefore reflects the proportion of eggs hatched, rather than the success of murrelets in rearing offspring to independence. The evident negative relationship between zonal currents and at sea density of murrelets may reflect movements of birds outside of our study region in years of higher hatching success. Ancient murrelets are consumers of zooplankton (mainly euphausiids) and larval sand lance, with fish taken more frequently later in each breeding period (Sealy, 1975). At Aiktak Island specifically, the diet of ancient murrelets is not well known but probably contains euphausiids and sand lance. It is plausible that the positive effects of zonal currents on the take of Pacific sand lance (as proxied by puffin diet), and ancient murrelet success are causally related, but we did not find a direct relationship between these variables. This could be due to differences in the size/age of sand lance targeted by these species; we assume that murrelets target generally smaller sand lance than puffins, given the inclusion of larval sizes (Sealy, 1975; Gaston, 1992). While puffins can also consume larval size classes, they mostly use larger individuals (Thompson et al., 2019; Piatt and Kitaysky, 2020; Thompson et al., unpublished data). Another factor could be differences in the timing of breeding; murrelets breed considerably earlier each year than puffins (Youngren et al., 2022), and this timing may correspond to the availability of younger/smaller size classes of sand lance.

Models revealed increases in seabird breeding success and at sea density with increasing meridional currents, in both spring and summer. The breeding success of murres (both species combined) and fork-tailed storm-petrels were positively related to spring meridional flows in Unimak Pass. Murres are the latest breeders at Aiktak Island, with average chick hatching dates in mid-August, and the average hatching date of fork-tailed storm-petrels is mid-July (Youngren et al., 2022). Summer meridional currents were also positively related to the density of seabirds at sea in the study area (all species and dark shearwaters alone). We expected to see relationships between seabirds and meridional currents as these currents may create oceanic structures (e.g., fronts) that may be used as foraging habitat by the birds (e.g., Hunt et al., 1998).

4.2. Effects of temperature

Increasing summer temperatures were positively related to thick-billed murre, murre (both species combined), Leach's storm-petrel, and storm-petrel (both species combined) breeding success. These models indicate apparently linear relationships (Fig. 6), which may, in part, be related to using PCA-derived current and temperature indices.

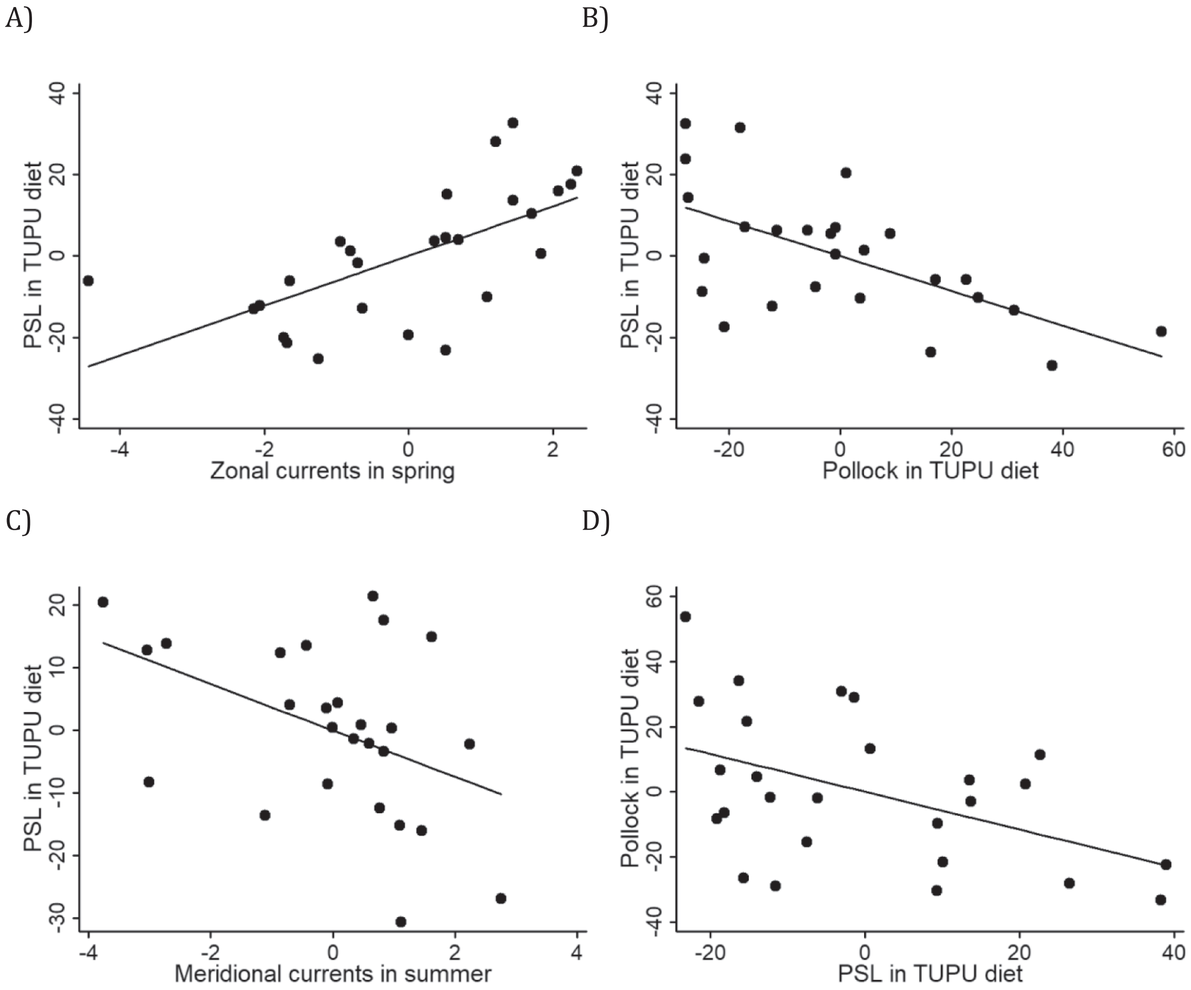

Fig. 11. Multiple (added) variable plots for Pacific sand lance (PSL) and walleye pollock in tufted puffin (TUPU) diet as a function of currents and SST. Pacific sand lance in the diet was predicted by (A) spring zonal currents ($PC1_{spring}$), (B) walleye pollock in tufted puffin diet, and (C) summer meridional currents ($PC1_{summer}$). (D) Walleye pollock in tufted puffin diet was predicted by Pacific sand lance in the diet.

The model developed for thick-billed murre, including a positive effect of summer temperature and a negative effect of spring temperature, explained nearly 60% of the variation in their breeding success after removing years of no or failed breeding from the time series.

Using the reduced data set that included chl-a, the explained variation increased to 83%. Spring temperature was weakly positively related to spring chl-a ($R^2 = 0.13$), but more strongly to the abundance of small copepods ($R^2 = 0.31$), suggesting connectivity between temperature and zooplankton productivity. Diet of thick-billed murres at Aiktak Island is not well known, but sampling from the Pribilof Islands in the Eastern Bering Sea indicates they primarily consume gadids, such as age-0 pollock, as well as euphausiids (Tanedo et al., 2019; Mayer et al., 2020), and on Bogoslof Island they also forage extensively on squids (Dragoo et al., 2011). Thus, the varied responses of thick-billed murres to seasonal temperatures may be related to the diversity of their diet, if certain prey species are more (less) available during times of warmer (cooler) temperatures. Additionally, as noted above, the murres failed breeding in many years. In comparison with other murre colonies in Alaska, the Aiktak murre colony is relatively small, which may result in loss of some of the benefits of their colonial nesting strategy (e.g., for finding food and protection from predators), making them more susceptible to failure due to various causes. More work is needed to disentangle these complex effects of temperature.

4.3. Species variation

There were clear differences between seabird species in their responses to variation in current flows and especially temperature. It is generally believed that dietary specialists, often species with more limited foraging ranges, are most sensitive to changes in local food resources (Furness and Tasker, 2000), hence variation in ocean conditions. Our models revealed few effects of ocean conditions on cormorants and puffins, species that forage on diverse forage fish prey in neritic to coastal-pelagic habitats of Unimak Pass (Table 1). In contrast, storm-petrels, which may forage upwards of hundreds of kilometers from breeding colonies, and murres, which are capable of 100-km foraging trips, showed the strongest responses to variation in currents and temperature. This indicates that foraging range may be a key trait affecting species responses to large-scale, seasonal variation in currents and temperature. Murres and storm-petrels also may forage beyond the boundaries of our "candy-wrapper" Unimak Pass study area, but nonetheless the study area we defined appears to have been large enough to capture some of the dynamics important to these species. Another important caveat to these interpretations is that the oceanographic data used in our study are limited to surface measurements, whereas subsurface data may be needed to better understand seabird responses to variation in currents and temperature. Thus, future comparative studies exploring seabird response to ocean conditions over depth are warranted, and may provide greater insight into variation in species responses.

4.4. *Trophic amplification*

We found few relationships between currents, temperature, chl-a concentrations, and zooplankton relative abundance. The lesser effects on lower trophic levels may be due to the shorter time series we used for these analyses, or that seabirds, as upper trophic level consumers, amplify oceanographic signals operating across trophic levels (Lotze et al., 2019; Hazen et al., 2019). The CPR-based zooplankton time series we used was relatively sparse in length (only 13 years of data), whereas we used 18–24 years for seabird productivity (depending on species-group), and 26 years for seabird density at sea. The CPR samples at a relatively shallow depth of 7 m, and the data are therefore strongly affected by vertically-migrating zooplankton. Because of this, and because we used corresponding data on seabird densities obtained during CPR sampling of the region, we filtered our data on CPR samples to daytime, further limiting the data available for this study. Remotely sensed chl-a data were obtained for 20 years, which may represent an adequate time scale for establishing biophysical relationships with temperature (e.g., Dunstan et al., 2018), and possibly currents. We are therefore more confident in concluding lack of relationships with chl-a concentration, as a proxy for phytoplankton abundance. Remotely-sensed chl-a, however, does not provide information on phytoplankton species, which may be important to food web dynamics in the study area, and as mentioned previously, is measured only at the surface.

5. Summary and conclusion

Consistency in trophic dynamics within specific sites or regions of interest has been proposed as a mechanistic explanation for biodiversity hotspot formation and persistence (Sydeman et al., 2006; Suryan et al., 2012; Wingfield et al., 2011; Santora et al., 2017; reviewed by Hazen et al., 2013), but this mechanism has rarely been tested using long-term observations because at least decadal-scale data on oceanographic conditions and biology for ecosystem hotspots of interest is required, and these data are uncommon. In this paper, we examined the hypothesis that stronger current flows in this region, coupled with warmer ocean conditions in spring, enhance local primary and secondary productivity within Unimak pass, thereby affecting the at-sea foraging density and breeding success of seabirds on Aiktak Island (within the pass) in summer. Using multi-decadal data, we found partial support for this hypothesis in that stronger meridional flows correlated positively with the breeding success of seabirds that forage in more pelagic habitats (murres and storm-petrels), but surprisingly, few relationships were found for more neritic-foraging species (cormorants and puffins). Similarly, we found support that stronger current flows have a positive effect on the at-sea densities of shearwaters from the southern hemisphere that visit the area to forage, but little support that current flows increase foraging density of locally breeding puffins or murrelets. Stronger zonal currents correlated positively to the use of Pacific sand lance in offspring provisioning by puffins, suggesting a possible link between alongshore transport and sand lance availability. In contrast to our hypothesis, warmer spring conditions had negative effects on seabird productivity and foraging densities. Currents and temperature variation were weakly related to primary and secondary productivity (proxied by chlorophyll-a concentrations and Continuous Plankton Recorder-based zooplankton abundance). This study extends earlier work on short-term, fine-scale foraging ecology of seabirds in Aleutian passes by showing the importance of currents and temperature on seabird productivity on seasonal time scales.

Data availability

GLORYS Dataset: GLOBAL_MULTIYEAR_PHY_001_030. https://doi.org/10.48670/moi-00021. [Accessed July 2021]. Sea surface temperature: see Reynolds et al. (2008). Chlorophyll-a: see Sathyendranath et al. (2020). Zooplankton data are available from the Continuous Plankton Recorder program. At-sea seabird data are available from the North Pacific Pelagic Seabird Database (https://data.usgs.gov/datacatalog/data/USGS:ASC29). See Youngren et al. (2022) for seabird breeding success data and tufted puffin diet data.

CRediT authorship contribution statement

William J. Sydeman: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Supervision, Supervision. **Sarah Ann Thompson:** Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Marisol García-Reyes:** Conceptualization, Methodology, Software, Data curation, Writing – review & editing, Visualization. **Caitlin Kroeger:** Methodology, Software, Formal analysis, Data curation, Writing – review & editing. **Brian Hoover:** Methodology, Software, Formal analysis, Data curation, Writing – review & editing. **Sonia D. Batten:** Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing. **Nora A. Rojek:** Methodology, Investigation, Data curation, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

We include a Data Availability Statement in the text; all data are freely available from original sources.

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