



# Differential response of seabird species to warm- and cold-water events in a heterogeneous cross-shelf environment in the Gulf of Alaska

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**ABSTRACT:** We used seabird surveys and concurrent oceanographic observations in the Northern Gulf of Alaska during spring 1998–2019 to evaluate how seabirds responded to temperature variability, including a protracted marine heatwave, in a highly heterogeneous ecosystem. We examined temporally changing distributions of seabirds along the Seward Line, a 220 km transect across the shelf and slope, and evaluated relationships between water-mass properties and seabird abundance. Environmental factors associated with abundance include depth, water-column temperature and salinity, and surface-current velocities. Environmental responses of alcids and gulls contrasted with those of procellariiform (tubenose) seabirds, and their trajectories suggest a possible shift in community composition under future climate warming. Changes in seabird distribution and abundance associated with a shift from cold to warm conditions were especially pronounced over the middle- and outer-shelf domains, which are transitional between coastal and oceanic water masses. The abundance of tubenoses increased during and after the heatwave, whereas alcids and gulls shifted inshore, exhibited reproductive failures, and experienced mass mortalities due to starvation. Tubenoses appear well-adapted to periods of lower productivity during warming events because of their flight efficiency, allowing them to search widely to locate prey patches. In contrast, alcids, which forage by diving and have energetically expensive flight, appear sensitive to such conditions.

**KEY WORDS:** Seabird · Marine heatwave · Climate change · Habitat use · Oceanography · Gulf of Alaska · Alcidae · Laridae · Procellariiformes

## 1. INTRODUCTION

In subarctic marine ecosystems, upper trophic level predators such as seabirds confront a shifting mosaic of physical and biological conditions that are undergoing both interannual variability and long-term change. Seabirds possess numerous adaptations to dynamic ocean environments, and differences among species in habitat use and foraging strategies can affect their responses to environmental perturbations

(Oedekoven et al. 2001, Cushing et al. 2018). We analyzed 2 decades of seabird surveys and concurrent oceanographic observations along a coast-to-basin transect in the northern Gulf of Alaska (NGA) to evaluate responses of an ecologically diverse suite of seabird species to warm- and cold-water events, including a protracted marine heatwave.

Across the continental shelf and slope, the transition from coastal to oceanic waters manifests as strong gradients in physical and chemical proper-

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ties that can be examined to better understand biological responses to environmental variability. The NGA has a deep continental shelf (often exceeding 200 m) with complex, glacially sculpted bathymetry (Carlson et al. 1982). Near the coast, the fresh-water-fed Alaska Coastal Current (ACC) forms a westward-flowing advective corridor with associated eddies and meanders arising from frontal dynamics and interactions with the seafloor topography (Royer 1982, Weingartner et al. 2005, Stabeno et al. 2016). The distribution of coastal and oceanic waters across the shelf varies seasonally and interannually (Coyle & Pinchuk 2005, Sousa et al. 2016). Offshore, the Alaska Current flows southwestward, beyond the shelf-break (Reed 1984, Stabeno et al. 2004). Long-lived mesoscale eddies intermittently move westward along the continental slope, entraining and mixing neritic and oceanic waters (Okkonen et al. 2003). In high-nitrate, low-chlorophyll oceanic waters of the NGA, production by large phytoplankton often is often limited by iron (Martin et al. 1989). Eddy-induced mixing of low-salinity, iron-rich shelf water with high-salinity, high-nitrate/low-iron oceanic water generates patches of enhanced primary productivity (Stabeno et al. 2004, Coyle et al. 2012).

This dynamic spatial heterogeneity is overlaid by changes in weather and climate. The NGA coastal shelf waters have warmed by  $0.22 \pm 0.10^\circ\text{C decade}^{-1}$  since the 1970s (Danielson et al. 2022), with atmospheric warming contributing to increased glacial ablation (Jacob et al. 2012, Hill et al. 2015), causing long-term freshening of near-surface shelf waters (Royer & Grosch 2006). Perturbations from storms to El Niño–Southern Oscillation (ENSO) cycles are superimposed on climate change, leading to unprecedented warming of the North Pacific Ocean during the 2014–2016 Pacific marine heatwave (Di Lorenzo & Mantua 2016), when water-temperature anomalies exceeded the estimated range of preindustrial variability (Walsh et al. 2018, Litzow et al. 2020).

Spatiotemporal variability in physical forcing affects the distributions and abundance of organisms at lower trophic levels (Waite & Mueter 2013, Sousa et al. 2016), thereby altering the prey base for higher trophic levels (Sousa 2011). The 2014–2016 marine heatwave was a major perturbation of the NGA ecosystem, resulting in abrupt changes in phytoplankton and zooplankton communities (Suryan et al. 2021) and simultaneous declines of multiple species of forage-fish prey of piscivorous seabirds (Arimitsu et al. 2021).

The NGA hosts a diverse avifauna that employs a range of foraging strategies and consumes a variety of large zooplankton and small nekton, including fish, squid, and crustaceans (Hunt et al. 2005, Day 2006). Species with estimated breeding populations >250 000 within the Gulf of Alaska include 5 species of alcids (Alcidae; Stephensen & Irons 2003, Piatt et al. 2007), 1 species of gull (Laridae), and 3 species of tubenoses (Procellariiformes). Tubenoses also are the most abundant non-breeding summer migrants, in that short-tailed shearwaters *Ardeanna tenuirostris* and sooty shearwaters *A. grisea* breed in Oceania during the austral summer, then migrate to the North Pacific and the Pacific Arctic during the boreal summer (Gabrielson & Lincoln 1959). The NGA also hosts 3 species of albatrosses (Diomedidae) that breed in the tropical and subtropical Pacific.

Seabird taxonomic lineages possess suites of phenotypic traits, such as wing morphologies, diving abilities, and foraging methods, that are adaptive for ocean environments that differ in productivity and prey assemblages. In lower-productivity environments, species with efficient flight (e.g. most tubenoses) are favored due to their ability to locate dispersed prey patches, whereas competition operates as an increasingly important selective force in high-productivity environments, favoring species (e.g. diving alcids) able to exploit dense prey patches (Balance et al. 1997). However, most diving seabirds have energetically expensive flight due to morphometric tradeoffs between aerial and aquatic locomotion (Elliott et al. 2013) and are thus constrained largely to highly productive environments (Ainley 1977). Consequently, seabird species may differ in sensitivity to changes in ecosystem productivity, based on diets and adaptations related to foraging and mobility.

Long-term observation programs can provide insights into ecological responses to variability in environmental forcing (Lindenmayer et al. 2012, Jones & Driscoll 2022). We surveyed seabirds at sea as part of long-term oceanographic observations along transects crossing the continental shelf and slope in the NGA from 1998 to 2019. Here, we examined the responses of ecologically diverse seabird species to physical-oceanographic parameters in the NGA during the spring. We sought to understand how seabirds responded to temperature fluctuations in a dynamic and heterogeneous environment in which other factors also may have affected their distribution and abundance. Our objectives were to (1) describe spatial (cross-shelf) and temporal (interannual) patterns of seabird abundance and community

composition during spring, (2) describe how these patterns related to warming and cooling events, and (3) evaluate relationships between water-mass properties and seabird abundance. We examined the responses of these seabird species to warming events to better understand the potential for changes in this community under anticipated future warming.

## 2. MATERIALS AND METHODS

### 2.1. Seward Line

The Seward Line is a 220 km cross-shelf transect in the NGA (Fig. 1) that was sampled repeatedly during late spring (typically early May) from 1998 to 2019. This line comprises 13 primary stations, each spaced ~18 km apart (range: 16–20 km), from the mouth of Resurrection Bay across the continental shelf to deep oceanic waters. Water depth is 270 m at the innermost station (GAK1), but the shallowest portion (150 m) is in the middle of the shelf, near GAK5; the shelf-break occurs ~150 km from shore, near GAK9 (280 m), beyond which depths rapidly increase to >2000 m at GAK13. Hereafter we refer to stations GAK1–3 as the inner shelf, GAK4–6 as the middle shelf, GAK7–9 as the outer shelf, and GAK10–13 as the slope (Fig. 1).

### 2.2. Data collection and processing

#### 2.2.1. Water-mass properties

We collected conductivity–temperature–depth profiles at stations with a Sea-Bird SBE 911plus CTD system, with sensors calibrated annually at the factory. For each profile ( $n = 282$ ), we calculated depth-averaged values for temperature ( $^{\circ}\text{C}$ ) and practical salinity (dimensionless) of the upper 100 m of the water column. We also calculated an index of upper water column stratification (Brunt-Väisälä frequency,  $\text{s}^{-1}$ ; Gill 1982) and the mixed layer depth (m) by using a density threshold of  $0.2 \text{ kg m}^{-3}$  relative to the value measured at 5 m.

We extracted zonal (east–west) and meridional (north–south) surface-current velocities (Absolute Geostrophic velocity plus Ekman velocity;  $\text{m s}^{-1}$ ) from the Copernicus Marine Services Global Total Surface and 15 m Current data product (MULTIOBS\_GLO\_PHY\_REP\_015\_004; Rio et al. 2014; [https://resources.marine.copernicus.eu/product-detail/MULTIOBS\\_GLO\\_PHY\\_REP\\_015\\_004/INFORMATION](https://resources.marine.copernicus.eu/product-detail/MULTIOBS_GLO_PHY_REP_015_004/INFORMATION); accessed

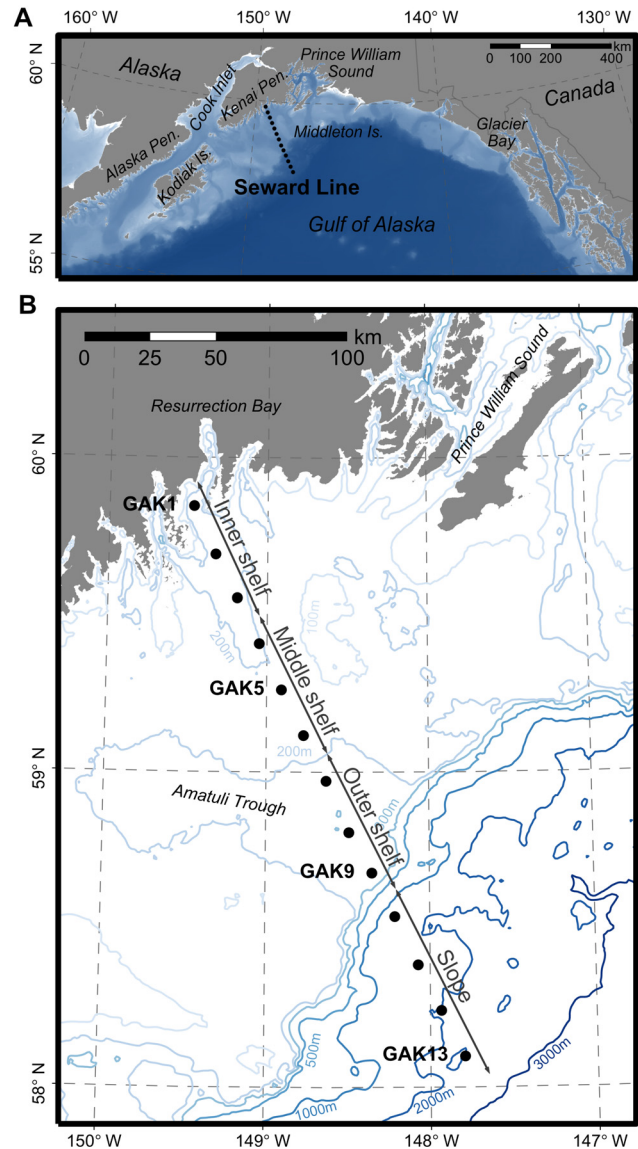


Fig. 1. The Seward Line in the northern Gulf of Alaska. Dots indicate locations of sampling stations (GAK1–13), and arrows demarcate the shelf/slope domains

22 October 2020). This multi-observation data product uses satellite altimetric and *in situ* observations and models a  $1/4^{\circ}$  latitude  $\times$   $1/4^{\circ}$  longitude grid. We used mean monthly values for May of each year, corresponding to the location of each station; all stations except GAK12 and GAK13 were in separate grid cells. We used a bathymetric digital elevation model with a  $1 \text{ km}^2$  grid (Alaska Region Digital Elevation Model v2.0; Danielson et al. 2015; <https://portal.aos.org/models-grids.php#module-metadata/0f2c570e-a3b8-11e3-a3d5-00219bfe5678/6743fe72-13f3-49f4-a044-20d7d17b00dc>; accessed 12 December 2018) to obtain a nominal depth at each station.

### 2.2.2. Seabird abundance

We conducted at-sea surveys for seabirds during 18 spring cruises between 1998 and 2019. No seabird surveys occurred during cruises in 2004–2006 and 2010, and the line was surveyed only partially in 2008 and 2012. Seabird surveys were conducted during daylight hours while the vessel was underway between stations and during longer transits. An observer searched a 90° arc from bow to beam and within 300 m on one side of the vessel. Sightings were identified to the lowest possible taxonomic level with 10 × 42 binoculars. Birds on the water were recorded continuously, whereas flying birds were recorded by instantaneous scans to minimize bias due to rapid movement of flying birds (Tasker et al. 1984, Gould & Forsell 1989).

Some aspects of data collection varied among years. Seabird surveys during 1998–2003 used consecutive 5 or 10 min count periods; 5 min counts typically were 1.5–1.7 km in length, whereas 10 min counts typically were ~3.2 km in length. During 1998–2000, data were recorded on data sheets, with geographic coordinates, time, and environmental conditions recorded at the beginning of each period, and coordinates then interpolated for each observation (Day 2006). During 2001–2003, data were recorded with custom software that associated coordinates and time with each observation (Sousa 2011); some count periods were <5 min, with new periods initiated if survey conditions changed. From 2007 to 2019, surveys were continuous transects with data recorded by the program dLog (R. G. Ford Consulting, Portland, OR) that logged the time and coordinates of each sighting and environmental conditions. Continuous transects were then subdivided into segments with a maximal length of 3 km, with the centroid used as the location of the segment. Additional details regarding survey methods are provided by Day (2006), Kuletz et al. (2008), and Sousa (2011).

Seabird data were processed consistently across years. For each cruise, we associated each transect segment or count period with the closest station, using a distance cutoff of 10 km from stations (half of the maximal distance between stations) for inclusion of survey data. Once all segments were associated with a station, we summed the count for each species or taxon, summed the area surveyed, and calculated the density (birds km<sup>-2</sup>). Over the study, the area of included surveys totaled 1426 km<sup>2</sup>.

For data summaries, we included phalaropes (*Phalaropus* spp.) and sea ducks as seabirds but excluded other shorebirds, waterfowl, landbirds, and raptors. For analysis, we selected 8 common and ecologically

diverse focal species, plus combined totals for 3 higher taxa: family Alcidae (murrelets, puffins, murrelets, auklets, guillemots; hereafter, alcids), family Laridae (gulls and terns; hereafter, gulls), and order Procellariiformes (albatrosses, storm-petrels, fulmars, and shearwaters; hereafter, tubenoses). The 8 focal taxa we examined were murrelets (combined common and thick-billed murrelets, *Uria aalge* and *U. lomvia*), tufted puffin *Fratercula cirrhata*, black-legged kittiwake *Rissa tridactyla*, glaucous-winged gull *Larus glaucescens*, black-footed albatross *Phoebastria nigripes*, fork-tailed storm-petrel *Hydrobates furcatus*, and shearwaters (combined short-tailed and sooty shearwaters). Murrelets and shearwaters were combined within genera due to low rates of species identification within these taxa in some years (Table 1); we refer to both as species.

### 2.3. Statistical analysis

For each of the 8 species and 3 higher taxonomic groups, we used generalized additive models (GAMs; Wood 2011) to evaluate relationships between physical–environmental variables and densities of seabirds. Functional responses of organisms to environmental gradients are expected to be non-linear, non-monotonic, and multivariate (Whittaker 1965, ter Braak & Prentice 1988). GAMs allow for estimation of non-linear relationships between species abundances and environmental attributes, with relationships between predictor and response estimated via smooth functions (Wood 2017). Each station–year combination was treated as a sample. We used  $n = 255$  station–year samples with both seabird survey and oceanographic data. We fit a GAM for each species or group, using the Tweedie distribution for the response variable (seabird density), with a logarithmic link between the response and the predictor (Wood 2017). Predictors included water depth (at stations), temperature of the upper 100 m, salinity of the upper 100 m, strength of stratification, mixed layer depth, and zonal and meridional surface-current velocities, all of which were modeled with smooth functions using penalized thin-plate regression splines. In addition, we included year as a random-intercept effect. Water depth and stratification were log-transformed to avoid highly leveraged values due to skewed distributions. Models were fit with a double-penalty approach (Marra & Wood 2011) that allowed terms to be shrunk to zero and, thus, to be effectively removed from the model during the fitting process. Model adequacy was assessed with standard diagnostics such as quantile–

Table 1. Mean at-sea densities (birds km<sup>-2</sup>) of seabirds along the Seward Line during May 1998–2019. Only selected species in the families Anatidae (sea ducks) and Scolopacidae (phalaropes) were counted as seabirds

Order	Family	English name	Scientific name	Mean density	
Anseriformes	Anatidae	Common eider	<i>Somateria mollissima</i>	0.017	
		White-winged scoter	<i>Melanitta deglandi</i>	0.006	
		Black scoter	<i>Melanitta americana</i>	0.005	
		Long-tailed duck	<i>Clangula hyemalis</i>	0.016	
		Unid. goldeneye	<i>Bucephala</i> spp.	0.002	
Charadriiformes	Scolopacidae	Red-necked phalarope	<i>Phalaropus lobatus</i>	0.233	
		Red phalarope	<i>Phalaropus fulicarius</i>	0.138	
		Unid. phalarope	<i>Phalaropus</i> spp.	0.083	
	Stercorariidae	Pomarine jaeger	<i>Stercorarius pomarinus</i>	0.013	
		Parasitic jaeger	<i>Stercorarius parasiticus</i>	0.003	
		Long-tailed jaeger	<i>Stercorarius longicaudus</i>	0.004	
	Alcidae	Common murre	<i>Uria aalge</i>	1.010	
		Thick-billed murre	<i>Uria lomvia</i>	0.004	
		Unid. murre	<i>Uria</i> spp.	0.050	
		Pigeon guillemot	<i>Cepphus columba</i>	<0.001	
		Marbled murrelet	<i>Brachyramphus marmoratus</i>	0.084	
		Kittlitz's murrelet	<i>Brachyramphus brevirostris</i>	0.014	
		Unid. <i>Brachyramphus</i> murrelet	<i>Brachyramphus</i> spp.	0.029	
		Ancient murrelet	<i>Synthliboramphus antiquus</i>	0.062	
		Unid. murrelet	<i>Brachyramphus</i> or <i>Synthliboramphus</i> spp.	0.002	
		Cassin's auklet	<i>Ptychoramphus aleuticus</i>	0.011	
		Parakeet auklet	<i>Aethia psittacula</i>	0.012	
		Least auklet	<i>Aethia pusilla</i>	0.002	
		Crested auklet	<i>Aethia cristatella</i>	0.001	
		Rhinoceros auklet	<i>Cerorhinca monocerata</i>	0.024	
		Horned puffin	<i>Fratercula corniculata</i>	0.045	
		Tufted puffin	<i>Fratercula cirrhata</i>	0.763	
		Unid. puffin	<i>Fratercula</i> spp.	<0.001	
	Unid. alcid	Alcidae spp.	0.012		
	Laridae	Black-legged kittiwake	<i>Rissa tridactyla</i>	0.609	
		Sabine's gull	<i>Xema sabini</i>	0.003	
		Short-billed gull	<i>Larus brachyrhynchus</i>	0.002	
		California gull	<i>Larus californicus</i>	0.001	
		Herring gull	<i>Larus argentatus</i>	0.069	
		Glaucous-winged gull	<i>Larus glaucescens</i>	0.387	
		Glaucous gull	<i>Larus hyperboreus</i>	0.005	
		Unid. gull	<i>Larus</i> spp.	0.042	
		Arctic tern	<i>Sterna paradisaea</i>	0.069	
Unid. tern		<i>Sterna</i> or <i>Onychoprion</i> spp.	0.022		
Gaviiformes		Gaviidae	Red-throated loon	<i>Gavia stellata</i>	0.003
			Pacific loon	<i>Gavia pacifica</i>	0.046
	Yellow-billed loon		<i>Gavia adamsii</i>	<0.001	
	Unid. loon		<i>Gavia</i> spp.	0.002	
Procellariiformes	Diomedidae	Laysan albatross	<i>Phoebastria immutabilis</i>	0.076	
		Black-footed albatross	<i>Phoebastria nigripes</i>	0.402	
		Short-tailed albatross	<i>Phoebastria albatrus</i>	0.004	
	Hydrobatidae	Fork-tailed storm-petrel	<i>Hydrobates furcatus</i>	2.936	
		Leach's storm-petrel	<i>Hydrobates leucorhous</i>	0.034	
		Unid. storm-petrel	<i>Hydrobates</i> spp.	0.006	
	Procellariidae	Northern fulmar	<i>Fulmarus glacialis</i>	0.855	
		Mottled petrel	<i>Pterodroma inexpectata</i>	0.006	
		Unid. petrel	<i>Pterodroma</i> spp.	0.002	
		Buller's shearwater	<i>Ardenna bulleri</i>	0.001	
		Short-tailed shearwater	<i>Ardenna tenuirostris</i>	1.278	
		Sooty shearwater	<i>Ardenna grisea</i>	0.492	
		Unid. shearwater	<i>Ardenna</i> spp.	0.524	
	Unid. procellariid	Procellariidae spp.	0.002		
	Suliformes	Phalacrocoracidae	Brandt's cormorant	<i>Urile penicillatus</i>	0.002
Red-faced cormorant			<i>Urile urile</i>	0.002	
Pelagic cormorant			<i>Urile pelagicus</i>	0.016	
Pelagic or red-faced cormorant			<i>Urile pelagicus</i> or <i>urile</i>	0.002	
Double-crested cormorant			<i>Nannopterum auritum</i>	0.004	
<b>Total seabirds</b>				<b>10.549</b>	

quantile plots of model residuals. When indicated by diagnostics, the basis dimension of a smooth term ( $k$ , which controls the maximal possible degrees of freedom) was increased from an initial value of 8 up to a maximum of 20. GAMs were fit with the R package 'mgcv' 1.8-33 (Wood 2020) in R version 4.0.2 (R Core Team 2020); the 'select' argument in the 'mgcv' function 'gam' was used to implement the double-penalty approach. We also compared densities (on the  $\log_{10}$  scale) of total seabirds, total surface foragers (Ashmole 1971), and total divers by domain. We calculated the median densities with 95% CIs and judged medians with non-overlapping CIs to significantly differ (Krzywinski & Altman 2014).

The densities of seabirds at any given location or time are likely affected by processes operating on scales ranging from local conditions at the time of sampling to long-term demographic trends. To determine whether any taxa underwent changes in abundance over the study that were not accounted for by the environmental predictors in the GAMs, we conducted simple linear regression analyses that used the random-effects estimates for the year terms as the response variables.

To determine whether variability in surface currents over the continental slope were associated with eddy activity, we evaluated sea surface height anomalies in the vicinity of the Seward Line (within a box bounded by 57.125–58.625° N and 148.88–146.62° W) in all years of the satellite record and identified the presence/absence of anticyclonic sea surface height ridges and cyclonic troughs based on a  $\pm 12$  cm sea surface height anomaly threshold. We then conducted linear regression analyses, with the zonal and meridional velocity components at stations GAK9–12 as a function of presence of eddy ridge (or trough) and station. We also evaluated whether anticyclonic eddy ridges were present in each case in which reversals of the mean flow field occurred.

### 3. RESULTS

#### 3.1. Water-mass properties

Early May mean temperatures of the upper 100 m of the water column were highly synchronous across the length of the Seward Line (Fig. 2A). The sampling period 1998–2006 was characterized by shifts between warm and cool upper-ocean temperatures associated with ENSO variability, including a strong El Niño event that began in 1997 and persisted through spring 1998, immediately followed by a strong La Niña that

persisted through spring 2001. Apart from 2010, cool conditions predominated during 2007–2013 (Janout et al. 2010, Danielson et al. 2022). Warm upper-ocean temperatures dominated during 2014–2019, beginning with the onset of the Pacific marine heatwave in 2014–2016 (Bond et al. 2015, Di Lorenzo & Mantua 2016), with some cooling in 2017 and then warming again in 2018–2019 (Danielson et al. 2022). Across all years, the coolest mean early May upper water column temperatures occurred at GAK1, with mean temperatures gradually increasing offshore to peak at GAK7, then decreasing farther offshore.

Upper water column salinities had substantial spatial structure and temporal variability (Fig. 2B). Salinities were lowest in the ACC and generally increased offshore, with the steepest rate of increase over the inner shelf defining the ACC baroclinic jet (Weingartner et al. 2005). There was less synchrony in salinity fluctuations across the shelf than was seen for temperature, with differences among domains evident in some years. The upper water column was characterized by shallower average mixed layer depths and stronger stratification in the ACC-influenced waters of the inner shelf than in the other domains; offshore of the inner-shelf domain, stratification weakened over the study period (Fig. 2C,D).

Surface currents at station GAK1 were characterized by strong westward and weak southward velocities (Fig. 2E,F), with a mean vector speed of  $0.31 \text{ m s}^{-1}$  to the west-southwest. Surface-current speeds decreased offshore across the inner shelf and were weak over the middle shelf (mean vector speed  $0.05 \text{ m s}^{-1}$  to the west-northwest). Flows over the outer shelf and slope showed high spatial and inter-annual variability; the mean vector speed was  $0.08 \text{ m s}^{-1}$  to the southwest, with intermittent flow reversals, and the mean scalar speed was  $0.14 \text{ m s}^{-1}$ . Analysis of sea surface height anomaly fields near the Seward Line indicated that the presence of anticyclonic eddies was significantly associated with increased eastward ( $p = 0.006$ ) and northward ( $p < 0.001$ ) flows over the shelf-break and slope, whereas the presence of cyclonic eddies was significantly associated with increased westward flows ( $p = 0.002$ ). Flow reversals detected when eddies were absent (e.g. 2006, 2010) probably were meanders of the slope current.

#### 3.2. Abundance and environmental relationships of seabirds

We observed 47 species of seabirds on-transect during the 18 cruises (Table 1). The mean density of

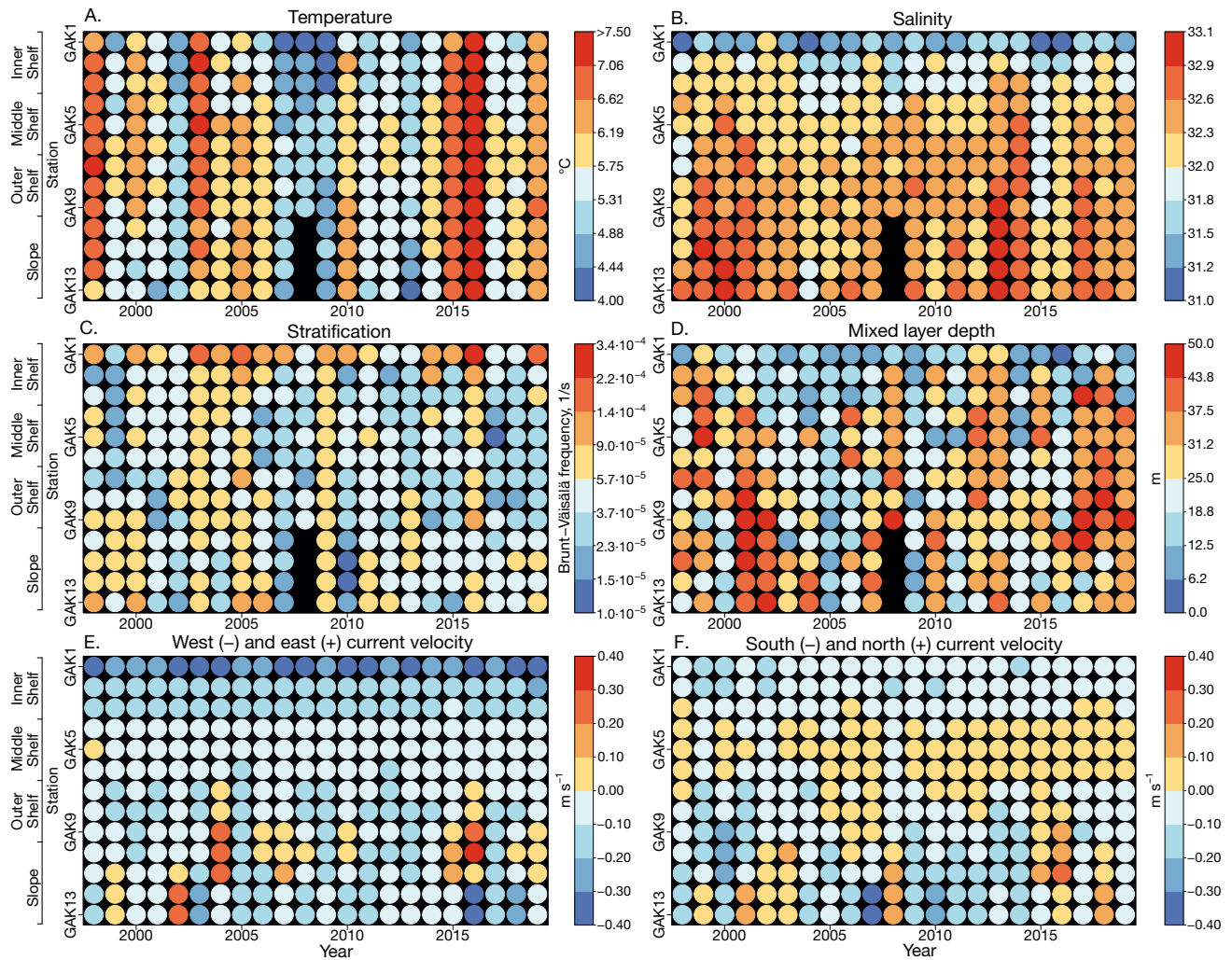


Fig. 2. Water-mass characteristics along the Seward Line, May 1998–2019. (A–D) Hydrographic parameters calculated from conductivity–temperature–depth (CTD) profiles of the upper 100 m of the water column during cruises. Black indicates stations that were not sampled. (E–F) Zonal and meridional surface-current velocities calculated from satellite altimetry with monthly values for May, with values at stations extracted from a  $1/4^\circ$  latitude  $\times$   $1/4^\circ$  longitude grid (EU Copernicus Data)

all seabirds combined across all samples (station–year combinations) was  $10.5 \text{ birds km}^{-2}$  (median  $9.8$ ; interannual range  $3.2$ – $25.8 \text{ birds km}^{-2}$ ). The mean densities of alcids, gulls, and tubenoses were  $2.1$ ,  $1.2$ , and  $6.6 \text{ birds km}^{-2}$ , respectively. Other seabird taxa included phalaropes (*Phalaropus* spp.;  $0.5 \text{ birds km}^{-2}$ ) and several groups with  $<0.1 \text{ birds km}^{-2}$ , including loons (Gaviidae), jaegers (Stercorariidae), cormorants (Phalacrocoracidae), and sea ducks (selected species of Anatidae).

Higher taxonomic groups had different patterns of cross-shelf (spatial) and temporal distributions (Fig. 3), as did individual species (Fig. 4). GAMs explained an average of 47% of the deviance in densities of the 3 highest taxonomic groups (range 43–52%; Table 2) and an average of 55% of the de-

viance in densities of the 8 focal species (range 38–73%). Significant predictors of densities in most of the models were depth, temperature, salinity, and zonal (east–west) surface-current velocity (Table 2). Meridional (north–south) surface-current velocity was significant in 3 models, mixed layer depth was significant in 2 models, and stratification strength was not significant in any model. Standard deviations of the random-year effects were higher for all tubenoses than for any of the alcids or gulls (Table 2), indicating that the tubenoses had more interannual variability in densities that was not explained by the predictors included in the GAMs. One species, tufted puffin, had a significant long-term abundance trend (see Section 3.2.1); linear regressions for the other species and groups were not significant.

Fig. 3. At-sea densities (birds km<sup>-2</sup>) of numerically dominant seabird taxonomic groups along the Seward Line, May 1998–2019. Black indicates no seabird surveys were conducted; no data were collected in 2004–2006 and 2010, and the line was only partially surveyed in 2008 and 2012. Density values are averaged from all surveys within 10 km of each of the 13 sampling stations that compose the Seward Line

### 3.2.1. Alcids

The abundance of all alcids combined was highest over the inner and middle shelves (Fig. 3A). Alcids were positively associated with depths <300 m (i.e. over the shelf) and lower salinities (i.e. in or near the ACC; Fig. 5).

Murres (*Uria* spp.) were the most abundant alcids, composing 52% of total alcids (Table 1). Overall, 96% of murres were identified to species and most (>99%) were common murres. Murres decreased in abundance over the middle shelf and became concentrated over the inner shelf after about 2015, around the beginning of the heatwave (Fig. 4A). Their abundance decreased with warmer temperatures and increased with lower salinities, westward-flowing surface currents, and water depths <300 m (i.e. in the ACC; Fig. 6).

Tufted puffins composed 37% of total alcids (Table 1) and were most abundant over the middle shelf (Fig. 4B). Puffin abundance was highest at

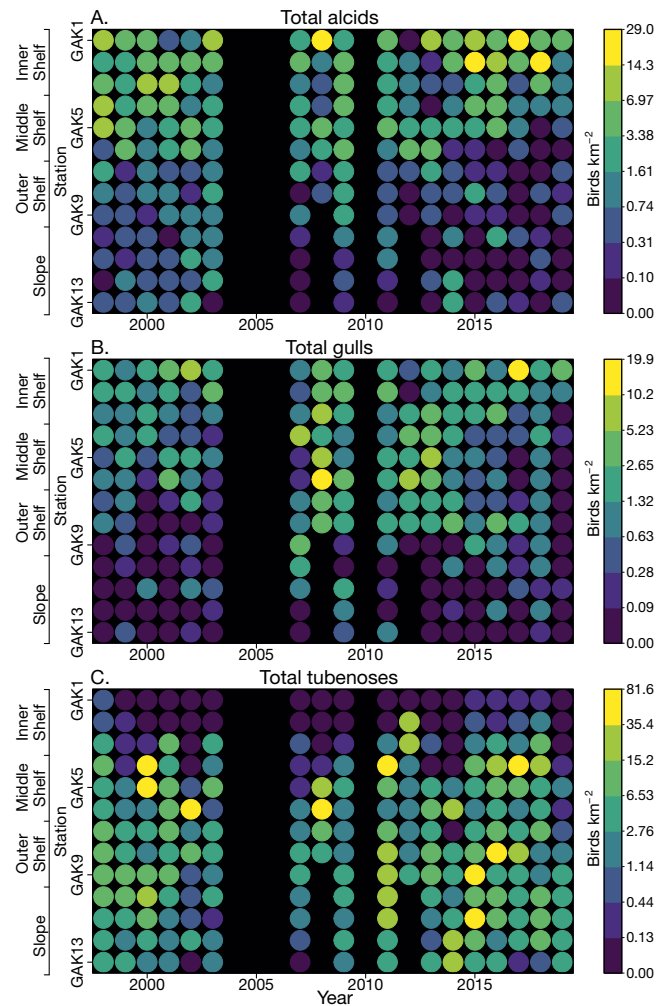


Table 2. Effects of depth and water-mass characteristics on the abundance of seabirds during May 1998–2019. Effects were estimated with generalized additive models, with abundance dependent on smooth functions of the predictors. Statistically significant effects were characterized as generally positively (+) or negatively monotonic (-); unimodal (U), with underlying increase (U+) or decrease (U-); or bimodal (B/B+/B-). Empty cells indicate non-significant effects. Stratification strength was not significant in any model so is not shown here. Zonal surface-current velocity is scaled west (negative) to east (positive), and meridional surface-current velocity is scaled south (negative) to north (positive). Effects are graphically presented in Figs. 5–15

Species	Depth	Temperature	Salinity	Mixed layer depth	Zonal velocity	Meridional velocity	Random year SD	Deviance explained (%)
Murres	-	-	-				0.44	59.7
Tufted puffin	B-		+				0.60	37.6
Black-legged kittiwake	-	U-		B		U+	0.55	57.4
Glaucous-winged gull	-	U-	-		U+		0.37	41.6
Black-footed albatross	U+	+	+		U+	B-	1.03	72.9
Fork-tailed storm-petrel		+	B		+		1.05	53.7
Northern fulmar		+	+		+	-	1.02	60.8
Shearwaters			U+				1.67	57.7
<b>Taxonomic groups</b>								
Alcids	B-		-				0.21	43.6
Gulls	-	U-	-		B-	U+	0.27	46.4
Tubenoses		+	+	U	+		0.71	51.6



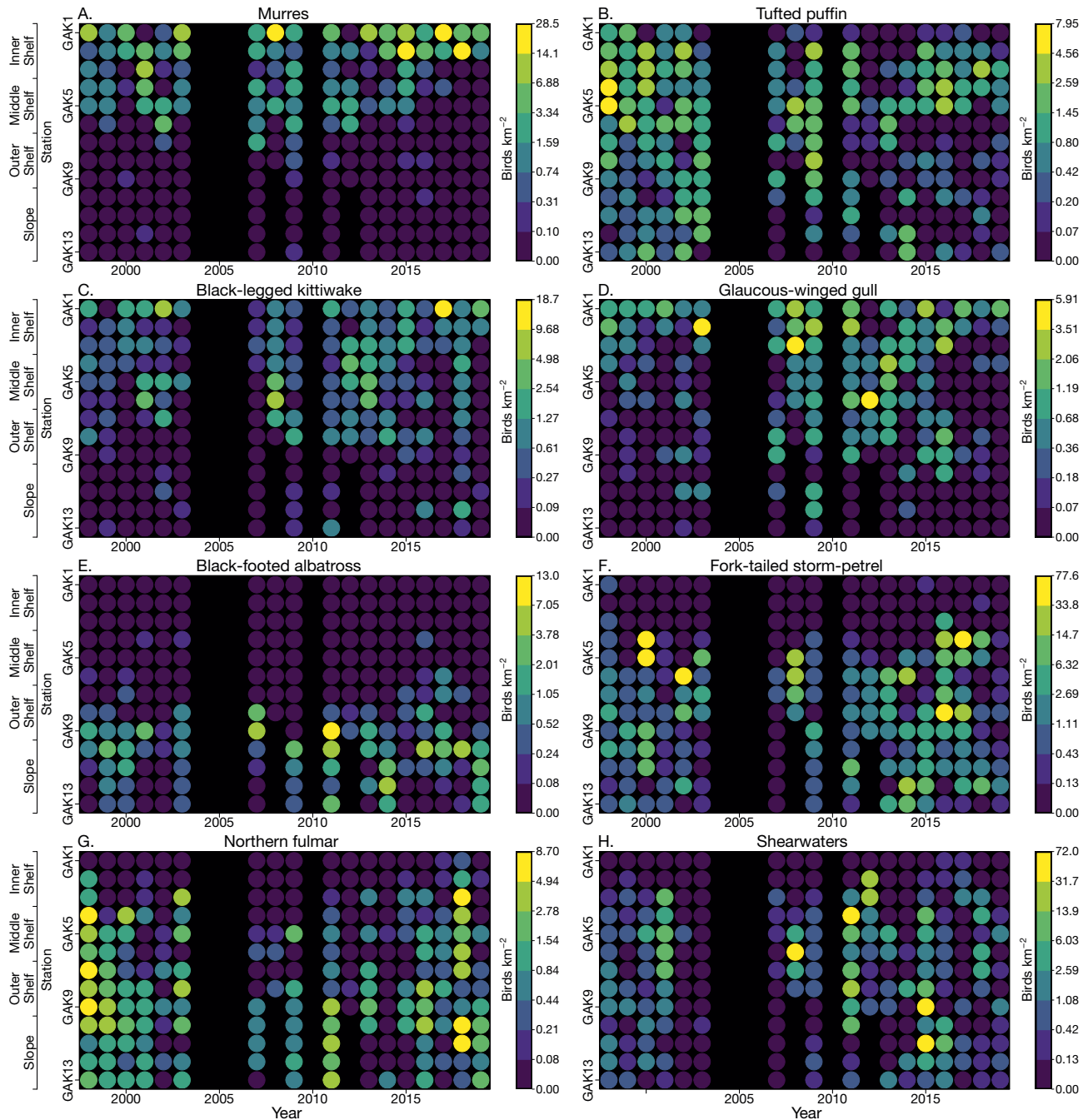


Fig. 4. Densities (birds km<sup>-2</sup>) of seabird species and species groups, as in Fig. 3

depths <300 m and lowest near the shelf-break; it was also positively associated with salinity (Fig. 7). There was a significant negative linear trend in the random-year coefficients from the fitted GAM ( $p = 0.004$ ), meaning that after accounting for the effects of environmental predictors, densities decreased over time. Their densities decreased at an estimated rate of 4.8% yr<sup>-1</sup> (95% CI: 2.1–7.6%), with a cumulative decline of 64.8% (95% CI: 35.4–80.9%).

### 3.2.2. Gulls

Gulls occurred widely over the shelf but were less abundant over the slope (Fig. 3B). The abundance of gulls was higher over the middle and outer shelves during the cool period (2007–2013) than during the preceding or subsequent periods. Gulls were positively associated with fresher water, shallower depths, and westward- and northward-

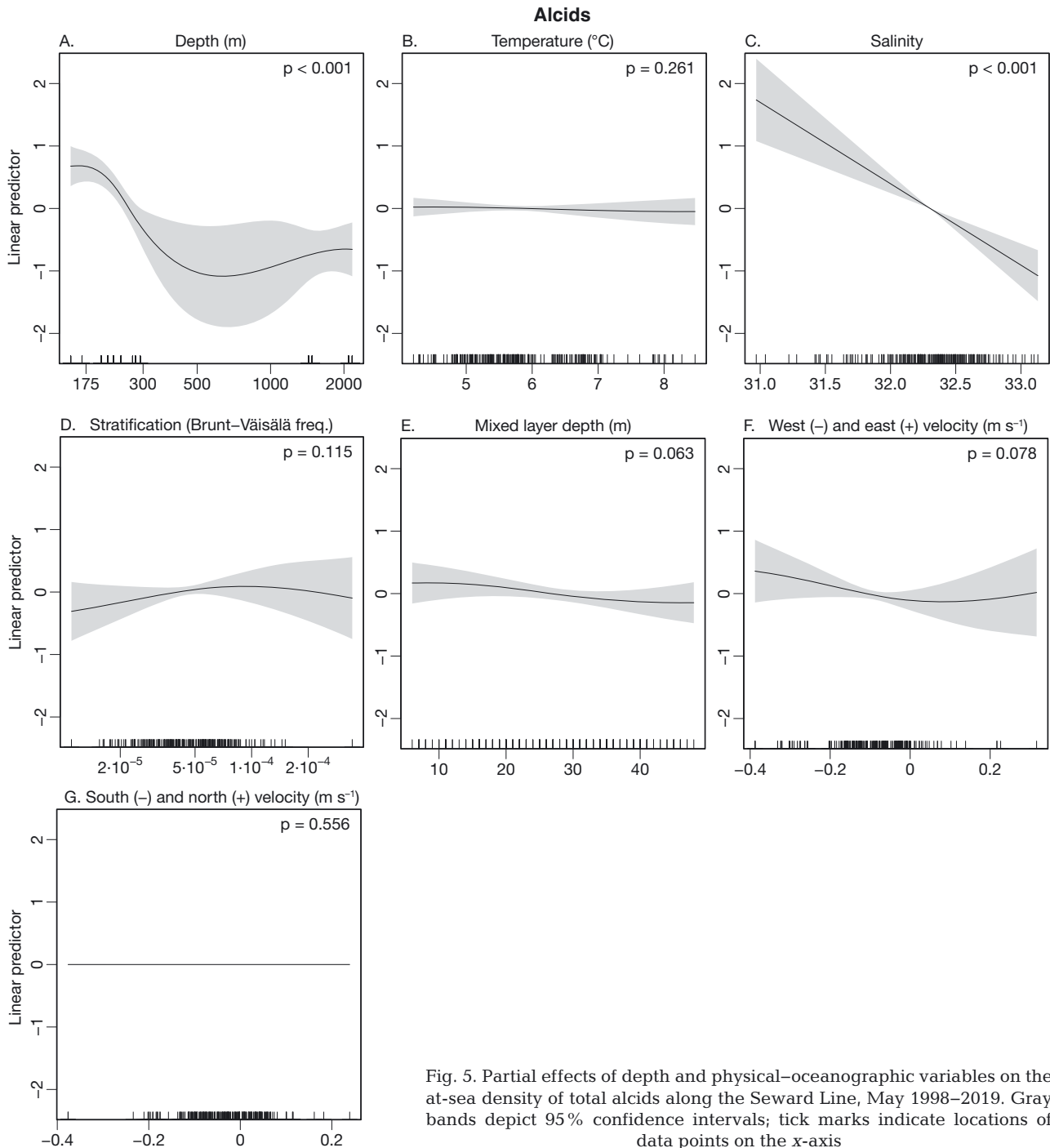


Fig. 5. Partial effects of depth and physical-oceanographic variables on the at-sea density of total alcids along the Seward Line, May 1998–2019. Gray bands depict 95% confidence intervals; tick marks indicate locations of data points on the x-axis

flowing surface currents (Fig. 8). They were negatively associated with water-column temperatures across the range of most temperature observations but had average abundances at temperature extremes.

Black-legged kittiwakes composed 50% of total gulls (Table 1). They were most abundant over the inner and middle shelves but varied over time in

their use of these habitats (Fig. 4C). Kittiwakes were positively associated with shallow depths, intermediate mixed layer depths, cool water-column temperatures, and stronger westward- and northward-flowing surface currents (Fig. 9). Kittiwakes were negatively associated with warm temperatures across the range of most temperature observations. However, they were also negatively associated

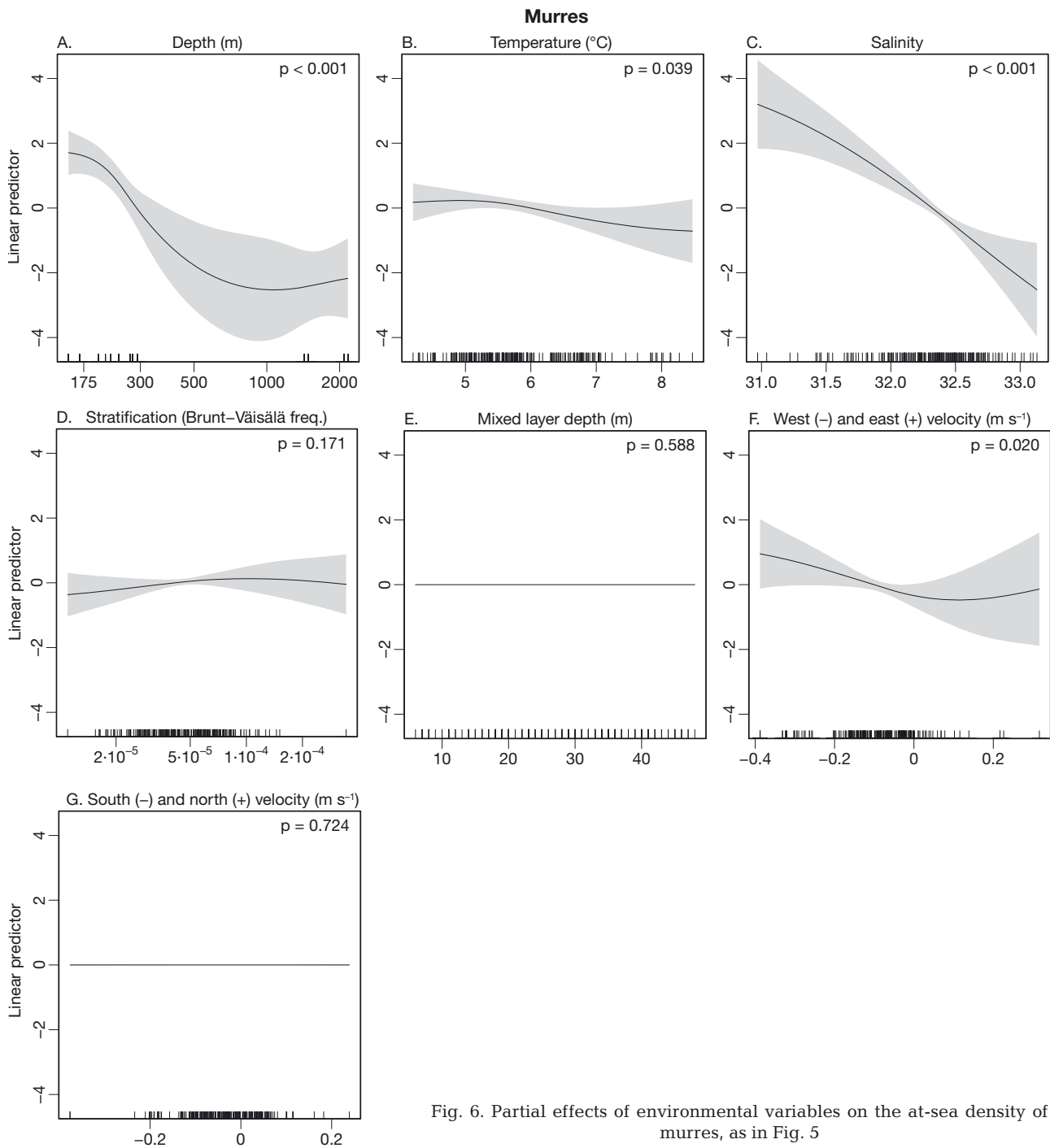


Fig. 6. Partial effects of environmental variables on the at-sea density of murres, as in Fig. 5

with temperatures  $< 4.5^{\circ}\text{C}$  (Fig. 9), which occurred primarily on the inner shelf during 2007–2009 (Fig. 2A), when kittiwakes were more abundant on the cool middle shelf than on the cold inner shelf (Fig. 4C).

Glaucous-winged gulls were the second-most-abundant gull species, composing 32% of total gulls (Table 1). They occurred consistently near the coast

but were also widely distributed across the shelf during ~2009–2015 (Fig. 4D). Glaucous-winged gulls were positively associated with fresh and shallow waters and cool water-column temperatures and were negatively associated with warm temperatures across most of the observed temperature range; however, they increased in abundance in the warmest temperatures (Fig. 10).

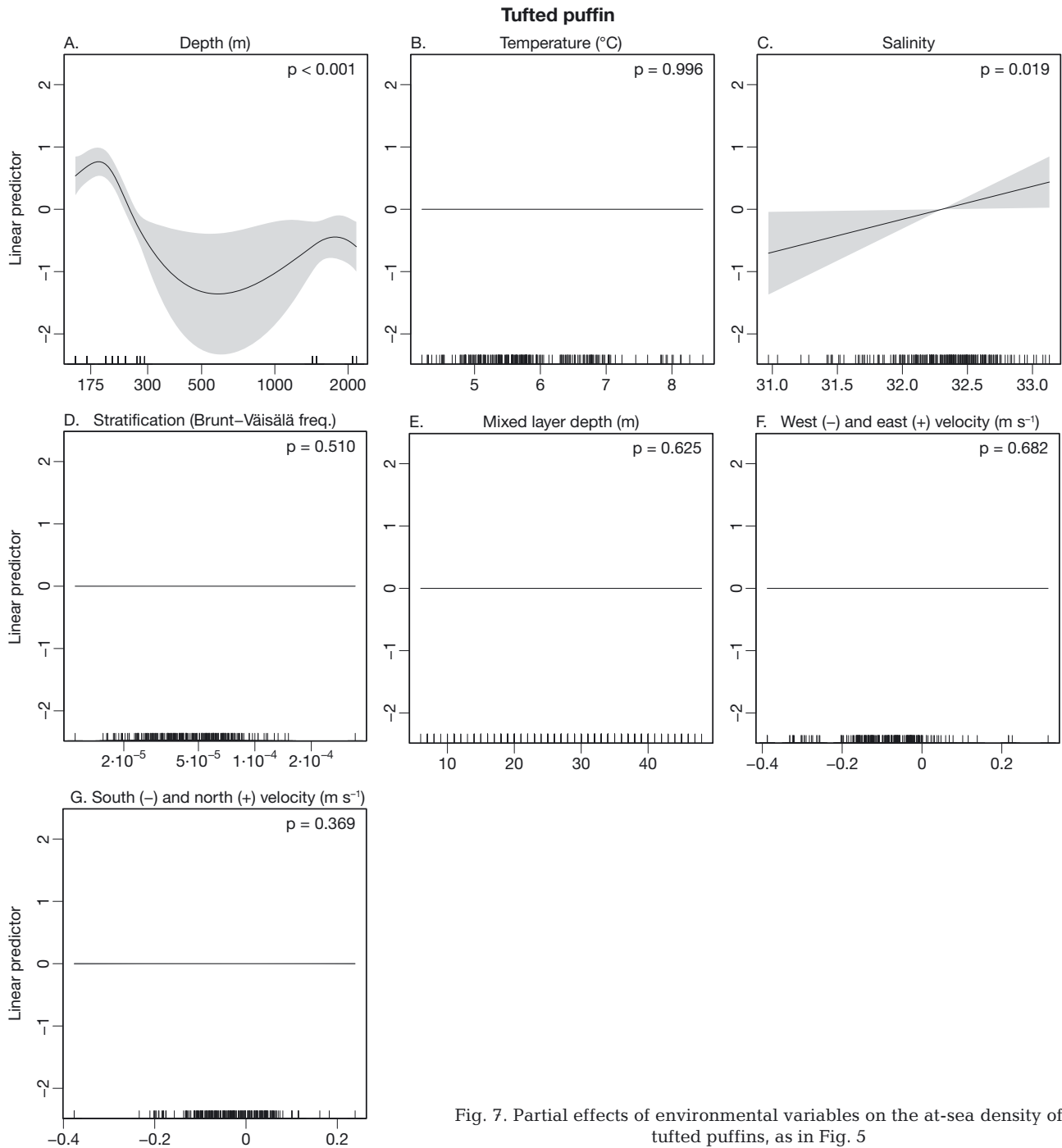


Fig. 7. Partial effects of environmental variables on the at-sea density of tufted puffins, as in Fig. 5

### 3.2.3. Tubenoses

Tubenoses composed the majority (63%) of total seabirds (Table 1). They were most abundant from the middle shelf to the continental slope and were rare or absent on the inner shelf; their overall abundance also fluctuated interannually (Fig. 3C). Tubenoses were negatively associated with cold tempera-

tures and low (<32.0) salinities (Fig. 11). They were also positively associated with eastward-flowing surface currents, which intermittently occurred during reversals of the mean westward flow over the outer shelf and continental slope, and with intermediate mixed layer depths.

Black-footed albatrosses composed 6% of total tubenoses (Table 1). They rarely occurred on the

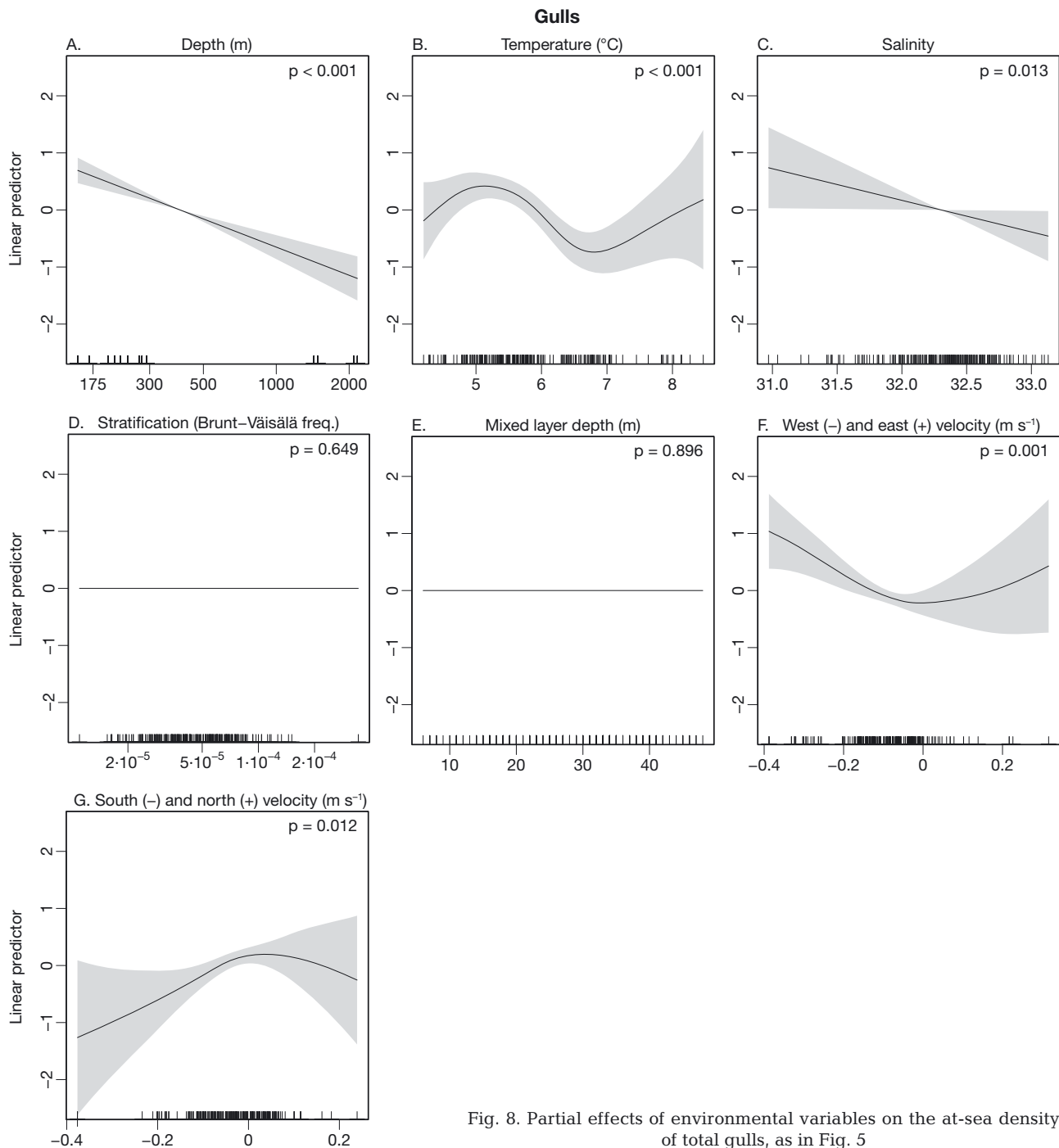


Fig. 8. Partial effects of environmental variables on the at-sea density of total gulls, as in Fig. 5

middle and inner shelves, were most abundant near the shelf-break, and decreased in densities farther offshore (Fig. 4E). During and after the heatwave, they shifted inshore, with abundance peaking over the outer shelf. They were more abundant with depths >300 m (abundance peaked at ~500 m), increasing upper water column salinity, warmer water-column temperatures, and east-

ward- and southward-flowing surface currents (Fig. 12).

Fork-tailed storm-petrels were the most abundant species of seabird (28% of total seabirds; Table 1) and composed 44% of total tubenoses. They were widely distributed from the middle shelf to the slope (Fig. 4D), with concentrations occurring irregularly over the middle and outer shelves. Their

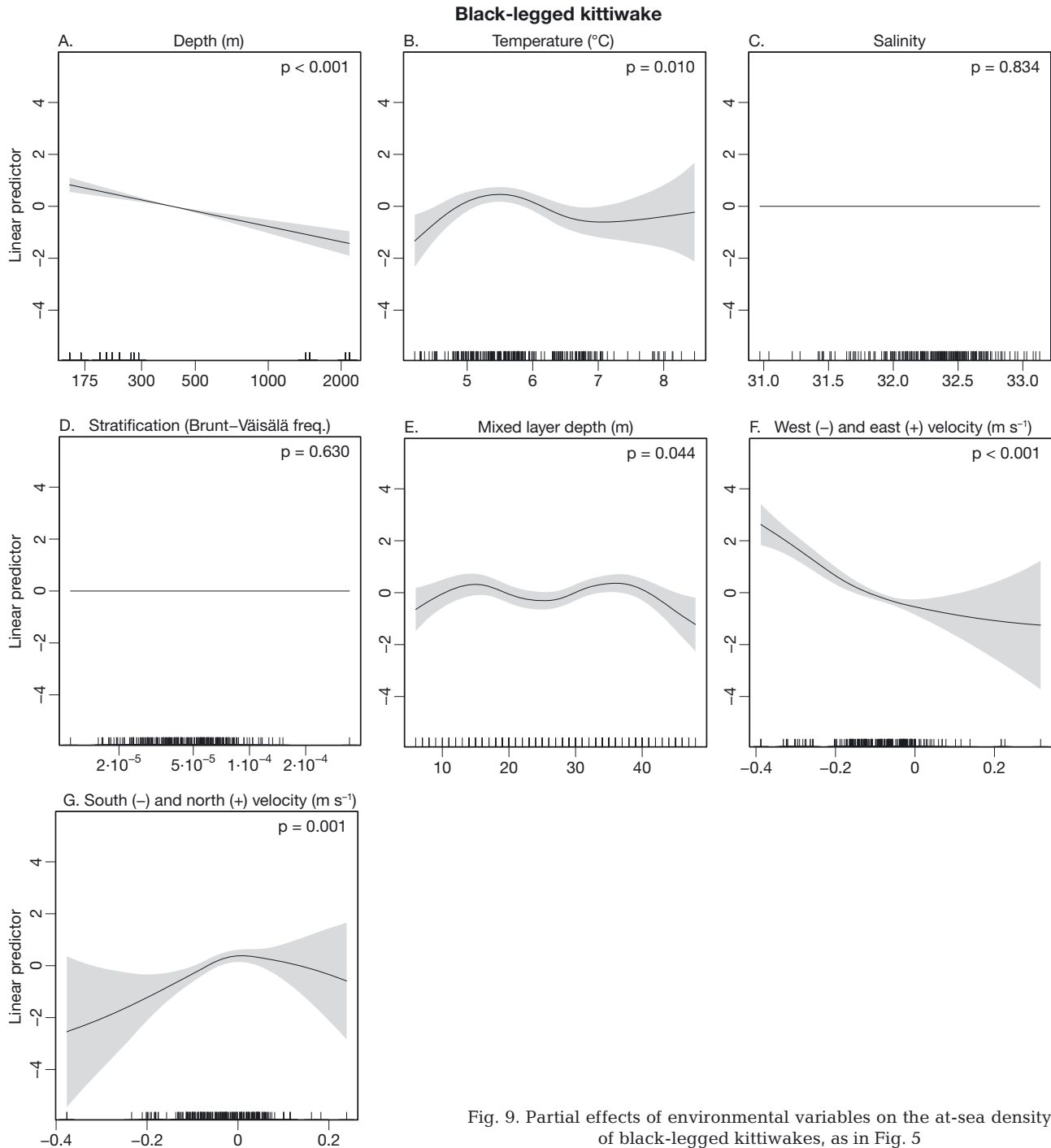


Fig. 9. Partial effects of environmental variables on the at-sea density of black-legged kittiwakes, as in Fig. 5

abundance increased with higher water-column temperatures, higher upper water column salinities (>32.0), and neutral or eastward-flowing surface currents (Fig. 13).

Northern fulmars *Fulmarus glacialis* composed 13% of total tubenoses (Table 1). They were widely distributed but were most abundant near the shelf-

break and least abundant near the coast (Fig. 4E). Fulmars were positively associated with temperature and salinity and with faster eastward- and southward-flowing surface currents (Fig. 14).

Shearwaters (*Ardenna* spp.) were the second-most-abundant tubenoses, composing 35% of total tubenoses. We identified 77% of observed shearwaters to

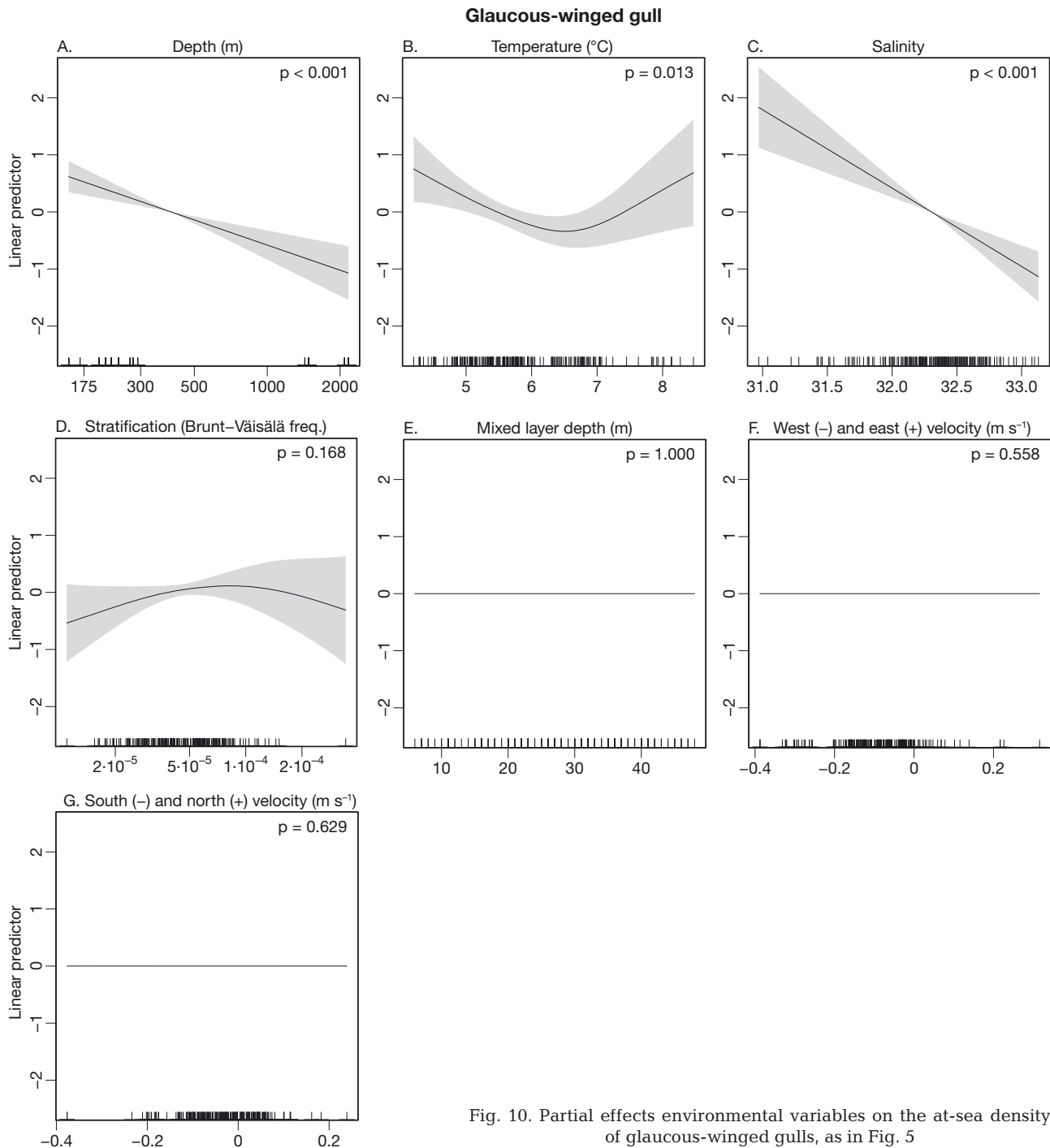


Fig. 10. Partial effects environmental variables on the at-sea density of glaucous-winged gulls, as in Fig. 5

the species level; of these, 72% were short-tailed and 28% were sooty shearwaters, with a single observation of a Buller's shearwater *A. bulleri*. The abundance of shearwaters was lowest near the coast and highest over the middle and outer shelves (Fig. 4F). Shearwaters were positively associated with salinities  $>32.0$  and with eastward-flowing surface currents (Fig. 15).

#### 3.2.4. Summary of patterns

Although each focal species was characterized by a unique suite of environmental responses, several patterns emerged across species and higher taxa (Table 2). Total alcids, total gulls, and 2 of the 4 focal species were associated with lower-salinity waters; however, one of the alcids (tufted puffin) was associ-

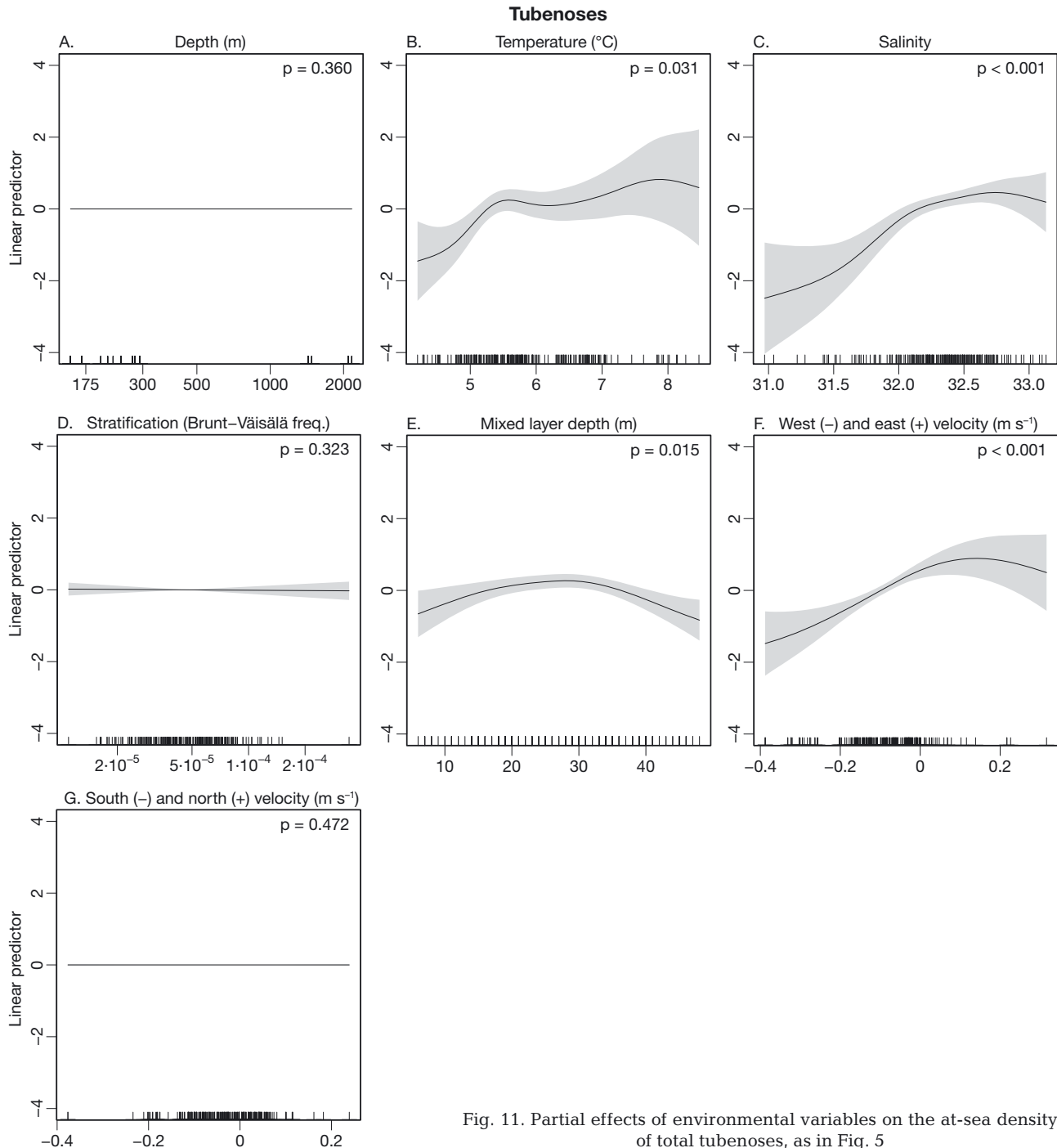


Fig. 11. Partial effects of environmental variables on the at-sea density of total tubenoses, as in Fig. 5

ated with higher-salinity waters. Total tubenoses and all 4 focal species were associated with higher-salinity waters, and 3 of the 4 focal species were positively associated with higher upper water column temperatures. In contrast, among alcids, the abundance of murres was positively associated with cooler temperatures, whereas among gulls, black-legged kittiwakes and glaucous-winged gulls were positively

associated with cooler temperatures and negatively associated with warmer temperatures across most of the temperature range.

Responses to depth and surface currents also differed among taxa. Gulls preferred shallower water, whereas alcids preferred moderate depths. Most tubenoses had no relationship with depth, although black-footed albatrosses were associated with the



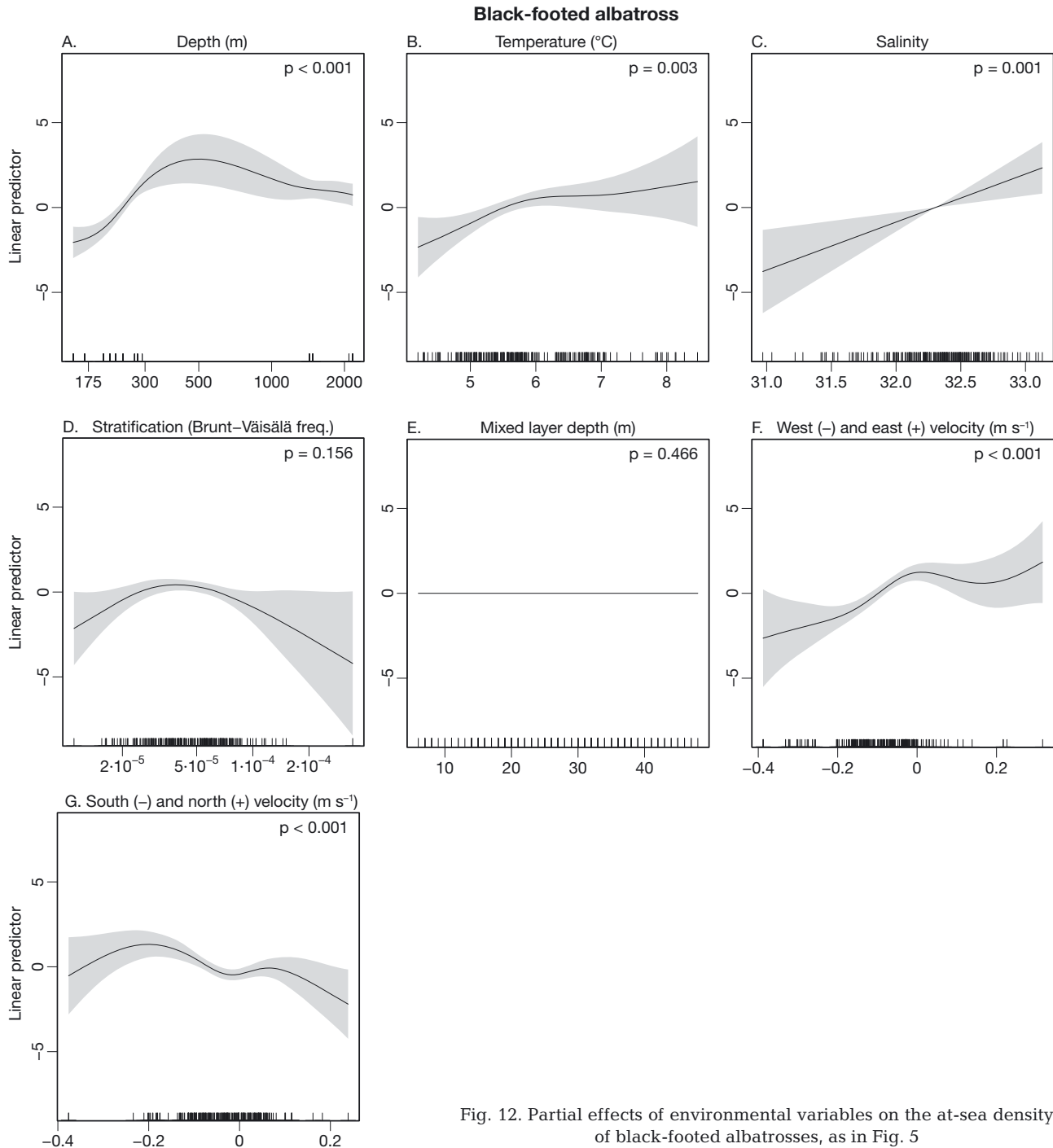


Fig. 12. Partial effects of environmental variables on the at-sea density of black-footed albatrosses, as in Fig. 5

shelf-break. All tubenoses had positive relationships with eastward-flowing surface currents, indicating an association with eddy-induced flow reversals. In contrast, 1 alcid taxon (murre) and 1 gull (black-legged kittiwake) were associated with stronger westward-flowing surface currents typical of the ACC. The abundance of 3 species and 1 taxonomic

group was also affected by meridional surface-current velocity. Mixed layer depth was a significant predictor in few models, and stratification strength was never significant (Table 2).

The median density of total seabirds was significantly higher over the shelf than over the slope (Fig. 16A). The median density was highest on the

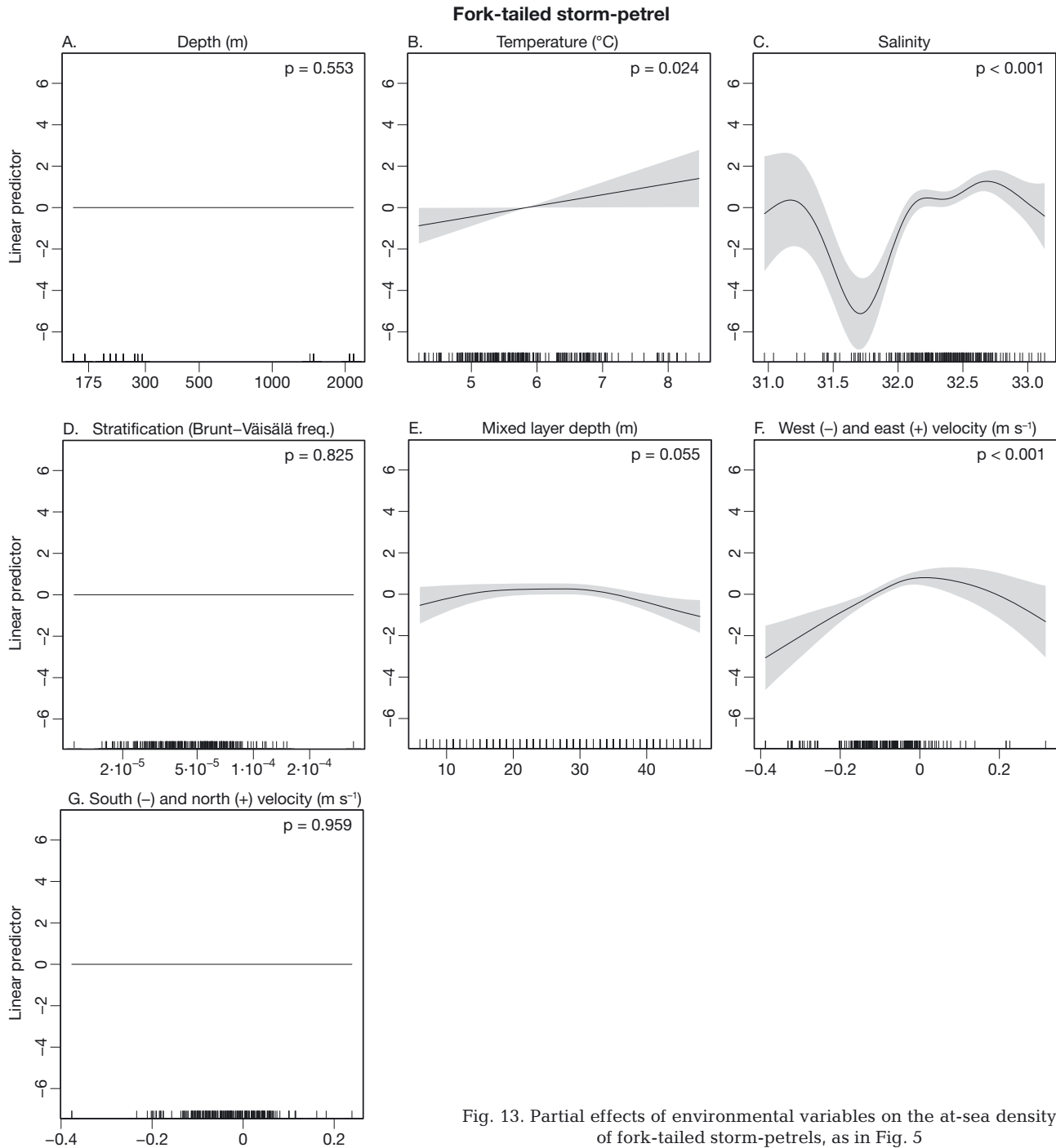


Fig. 13. Partial effects of environmental variables on the at-sea density of fork-tailed storm-petrels, as in Fig. 5

middle shelf, but confidence intervals for median values overlapped among the inner, middle, and outer shelves. The median total density of surface-foraging taxa was significantly lower on the inner shelf than in other domains (Fig. 16B). In contrast, the median total density of divers was significantly higher over the inner and middle shelves than in outer-shelf and slope domains (Fig. 16C).

## 4. DISCUSSION

### 4.1. Marine-habitat relationships of seabirds

Patterns of distribution, abundance, and species composition of seabirds along a standardized cross-shelf transect over 2 decades were linked to both spatial and temporal variability in physical oceanog-

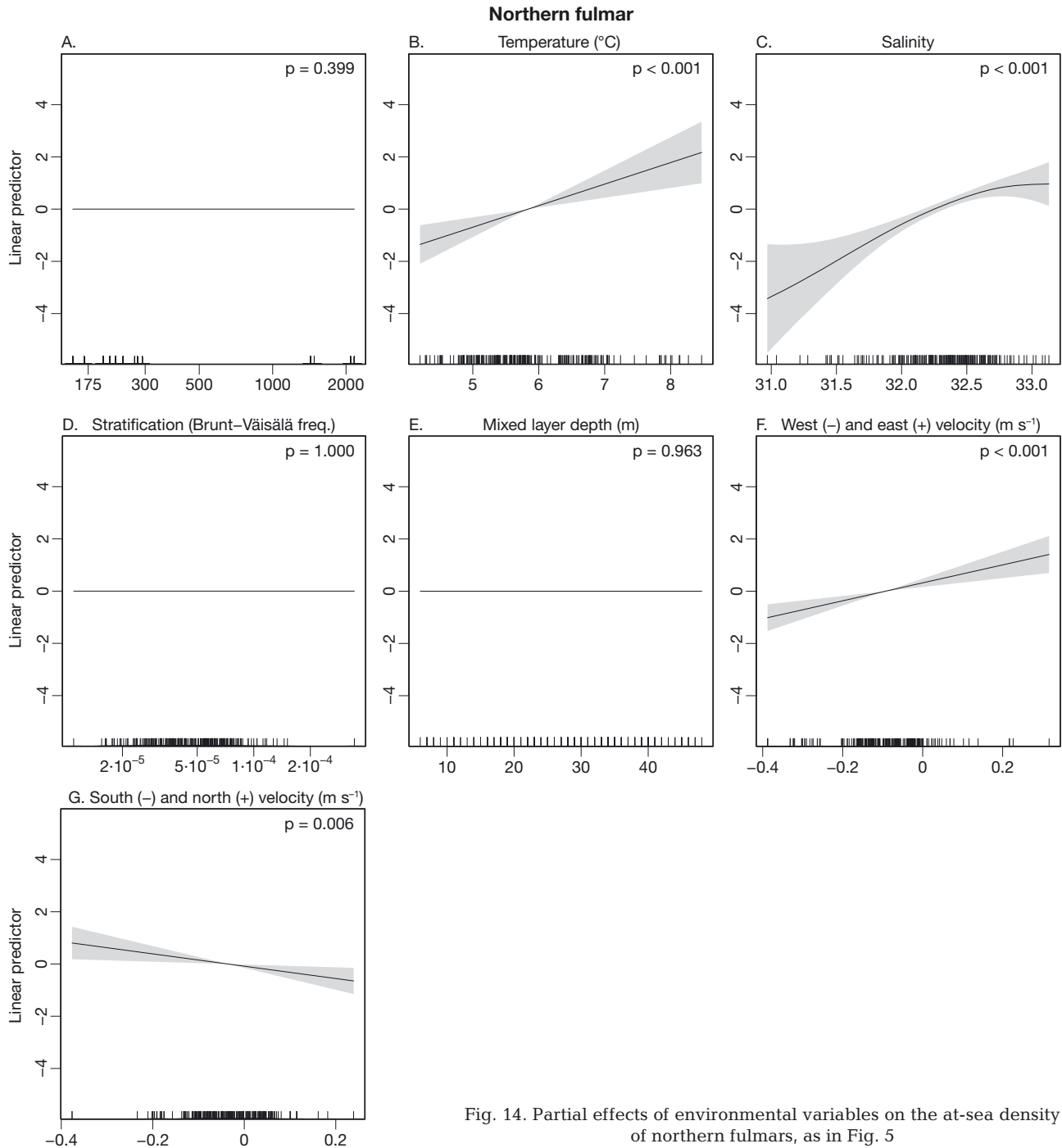


Fig. 14. Partial effects of environmental variables on the at-sea density of northern fulmars, as in Fig. 5

raphy. Mesoscale (10s–100s of km) zonation of seabird communities has been related to bathymetric features and boundaries between water masses that differ in salinity, temperature, stability, and velocity (Hunt et al. 2014, Force et al. 2015). Most of the seabird taxa we evaluated were characterized by shoreward or seaward limits beyond which individuals rarely occurred. However, onshore–offshore shifts

occurred over time within these limits that generally fell between the outer edge of the ACC and the shelf-break. The cross-shelf distributions of seabirds reflected the physical characteristics of water masses, paralleling patterns previously observed in lower trophic levels (Sousa et al. 2016). Environmental factors regulating the distribution and abundance of seabirds along the Seward Line during spring

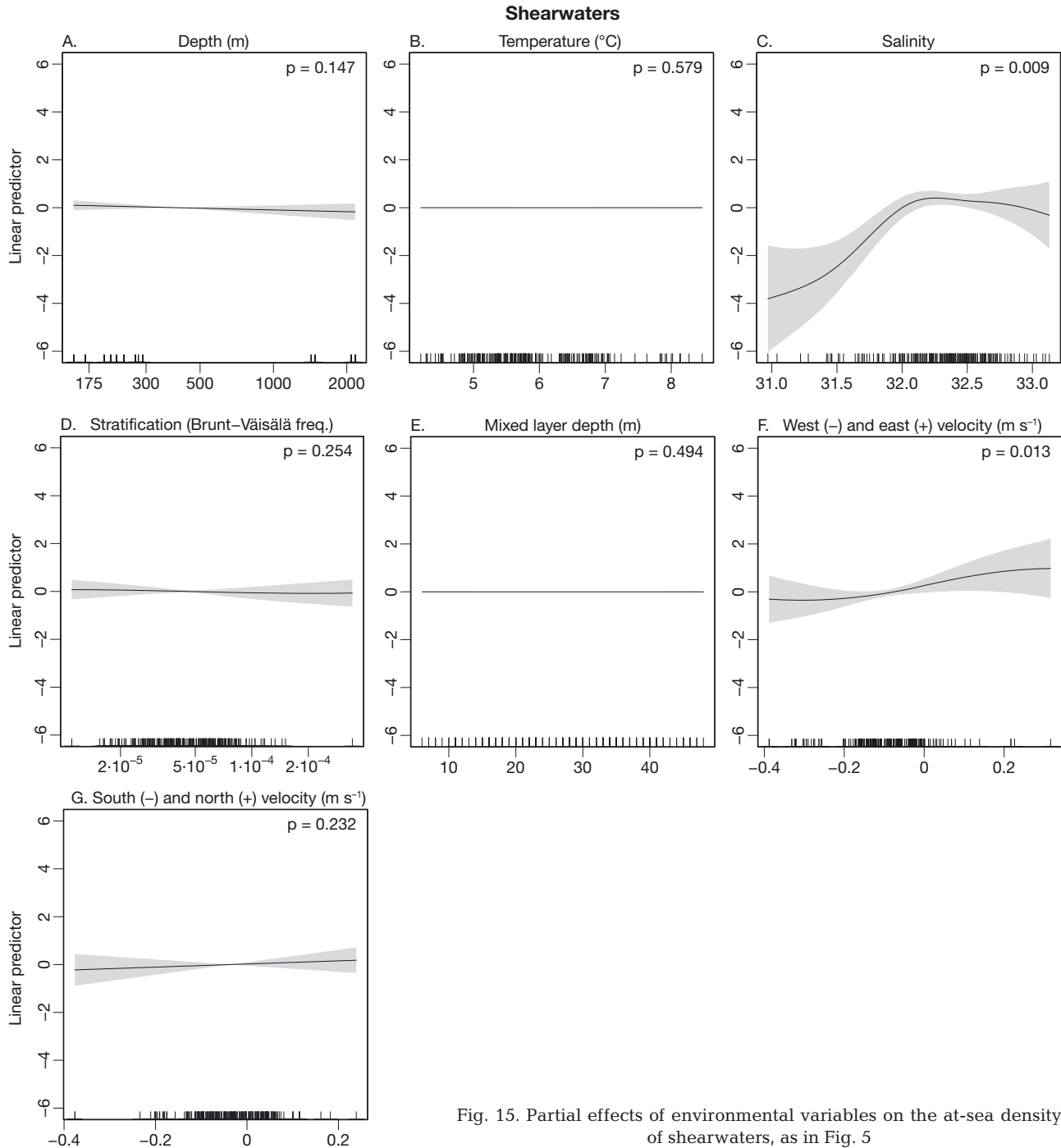


Fig. 15. Partial effects of environmental variables on the at-sea density of shearwaters, as in Fig. 5

included water depth, fluctuations in water-column temperatures, the distribution of high- and low-salinity waters, and variability in surface-current velocities related to movement of mesoscale eddies along the continental slope. Taxonomic groups and species were characterized by different responses to environmental gradients, presumably reflecting contrasting ecological niches and distinct suites of adaptations to features of dynamic ocean environments.

#### 4.1.1. Relationships between distributions and hydrographic features

The ACC is the dominant hydrographic feature of the inner shelf. Piscivorous murre (*Uria* spp.), black-legged kittiwakes, and glaucous-winged gulls were correlated with characteristics of the inner shelf, including low salinities (murre, glaucous-winged gulls), moderate depths (all 3 species), and fast west-

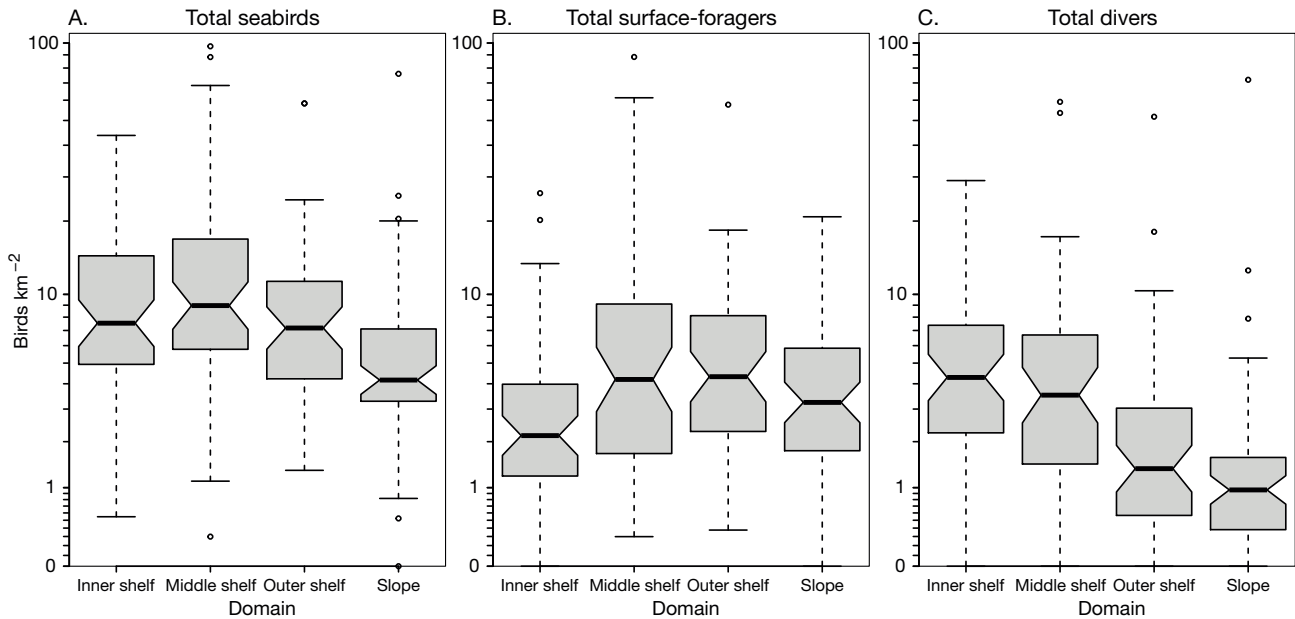


Fig. 16. At-sea densities of seabirds along the Seward Line, May 1998–2019, on the  $\log_{10}$  scale, grouped by domain. The lower and upper box boundaries depict 1<sup>st</sup> and 3<sup>rd</sup> quartiles, respectively. **Bold** horizontal lines inside boxes are medians, with approximate 95% confidence intervals depicted by notches. Whiskers delimit minimal and maximal values excluding outliers, and outliers (points  $>1.5 \times$  the interquartile range below the 1<sup>st</sup> quartile or above the 3<sup>rd</sup> quartile) are indicated by circles. Surface-foragers include phalaropes, gulls, terns, albatrosses, storm-petrels, and fulmars. Divers include sea ducks, alcids, loons, shearwaters, and cormorants

ward currents (murres, kittiwakes). Similarly, in the Bering Sea, a subarctic shelf system sharing similar species assemblages with the NGA and linked to it via advection, piscivorous seabirds were more abundant in near-coastal water masses influenced by large freshwater inputs (Elphick & Hunt 1993, Piatt & Springer 2003). The inner-shelf domain of the NGA is characterized by steep gradients in salinity, stratification, and current velocities that create numerous fronts at which convergent flow can aggregate prey and, thus, provide efficient foraging opportunities for seabirds. The use of fronts by foraging seabirds has been well-studied in the southeastern Bering Sea, where foraging murres have been associated with tidal fronts, at which prey biomass tends to be high and predictable (Decker & Hunt 1996, Suryan et al. 2016). Strong fronts are also associated with larger seabird foraging aggregations than are those with weak fronts (Schneider et al. 1987); strong gradients may increase prey concentrations and predictability (Hunt et al. 1999).

The middle shelf is a transitional domain, with interannual variability in the extent and mixing of coastal and oceanic waters and zooplankton (Coyle & Pinchuk 2005, Sousa et al. 2016). The Seward Line becomes shallower over the middle shelf as it crosses over a 150 m deep ridge before dropping into the deep Amatuli Trough over the outer shelf. Primary

production is enhanced over this mid-shelf ridge during the spring (Coyle et al. 2019); it is also where the highest mean densities of seabirds occurred. Canyons are conduits of slope water, nutrients, zooplankton, and larval fish onto the shelf, with advected water supplied to adjacent banks via tidal mixing (Stabeno et al. 2016, Mordy et al. 2019). In Amatuli Trough, warm surface temperatures are correlated with enhanced supply of cool and salty bottom waters ( $>200$  m) onto the outer shelf (Danielson et al. 2022); an implication of this is increased advection of oceanic organisms in these deep waters onto the shelf in warm years. The transitional and variable nature of the middle- and outer-shelf environments was reflected in high variability in the total abundance and species composition of the seabirds that occurred there, especially during periods of cooler or warmer water-column temperatures.

High-salinity, oceanic water masses were preferred by all 4 tubenose species. The productivity of oceanic waters offshore of the shelf break is estimated to be about one-third lower than that on the adjacent shelf (Coyle et al. 2019). In these waters, the availability of iron limits the production of large diatoms, which are associated with more efficient trophic transfer of energy than are smaller phytoplankton (Boyd et al. 2005, Strom et al. 2006). The slope in this area has enhanced eddy activity during

winter and spring (Ladd 2007), with upwelling occurring between the southwestward-flowing shelf-break frontal jet and northeastward-flowing near-shore edge of anticyclonic eddies (Okkonen et al. 2003); shelf water also is drawn offshore along the trailing edge of anticyclonic eddies (Janout et al. 2009). All tubenoses were positively associated with eastward-flowing surface currents, and 2 were also associated with southward-flowing currents. Eastward flows occur on the northern edge of anticyclonic eddies, downstream of upwelling occurring near the shelf break at the leading (western) flank, and within a zone of mixing between shelf and basin waters, whereas southeastward flows occur at the trailing edge of these eddies, where water is drawn offshore. Seabirds in other ecosystems use mesoscale eddies for foraging (e.g. Nel et al. 2001, Cotté et al. 2007). The positive association of all 4 tubenose species with eddy-associated flow patterns reflects enhanced foraging opportunities associated with these important, but intermittent, phenomena in lower-productivity environments.

Coastal–oceanic gradients occur across trophic levels in the NGA and include primary-producer biomass and size composition (Strom et al. 2006) and the metazooplankton and forage-fish communities eaten by seabirds (Coyle & Pinchuk 2005, Sousa et al. 2016, McGowan et al. 2019). Although we evaluated relationships between seabird distributions and physical oceanography, a limitation of our analysis is that it did not incorporate information on their prey. Marine-habitat characteristics affect the distribution and abundance of seabirds because these characteristics influence the availability of various marine organisms that are food for birds and because the physical environment provides cues used by foraging birds to locate prey patches. In the California Current system, the most important predictors of seabird distributions are distance to fronts, salinity, chlorophyll concentrations, and different size classes of plankton and nekton (Ainley et al. 2005). Similarly, in Glacier Bay, Alaska, both physical and biological factors are important predictors of seabird distributions (Renner et al. 2012). These studies support our assertion that the physical environment shapes seabird distributions both indirectly and directly.

#### 4.1.2. Relationships between distributions and adaptations of species

Coastal–oceanic gradients in ecosystem productivity and prey-field characteristics are linked to differ-

ent suites of adaptations among the seabird species within these environments. Seabird species that forage by diving are restricted largely to cool, productive ecosystems such as upwelling boundary currents and subarctic-shelf systems (Ainley 1977). Although diving provides the ability to exploit prey occurring within the water column, it is also energetically expensive (Cairns et al. 1990). Additionally, alcids incur high energetic flight costs due to morphometric tradeoffs (Pennycuick 1987, Elliott et al. 2013) and, consequently, have high metabolic rates (Ellis & Gabrielsen 2002) and high food requirements (Piatt et al. 2020). We found that divers were less abundant over oceanic waters of the slope than over most of the shelf, consistent with previous observations (Gould 1983, Hunt et al. 2005) and explained by the observation that the competitive abilities and energetic requirements of diving seabirds favor the use of highly productive habitats. During our May surveys, the highest abundance of diving seabirds occurred over the inner and middle shelves, whereas Sousa (2011) found that diving seabirds during March and early April were most abundant over the middle and outer shelves. This seasonal inshore movement of divers from late winter to spring is consistent with constraints due to flight costs as locally breeding birds return to their colonies, albeit with less restriction of their foraging range than during summer.

Most tubenoses that inhabit the NGA are surface feeders, with the exception of the shearwaters (*Ardenna* spp.), which either forage at the surface or dive for prey. Their wing morphology enables efficient flight (Pennycuick 1987), and they can harness kinetic energy from wind-shear gradients above the ocean surface and updrafts created by waves (Richardson 2011). Breeding tubenoses can travel thousands of km during foraging trips (Edwards et al. 2013). Tubenoses also have an acute olfactory sense that enables them to locate dispersed and unpredictable prey patches (Nevitt 2008). Both fork-tailed storm-petrels and northern fulmars breed in the NGA. Of the 4 focal tubenose species, the shearwaters (which can forage by diving) had the most-inshore distribution, whereas surface-feeding tubenoses were preponderant in less productive offshore waters.

Another important group of surface feeders are gulls, which typically use flapping flight to cover distance but can glide at low speeds and are highly maneuverable (Pennycuick 1987); they forage by circling, hovering, and dropping from the air onto prey. These flight attributes facilitate visual searching behavior and surface foraging in productive coastal

marine environments. Gulls cover distance more efficiently than alcids but more slowly than most comparably sized tubenoses. The 2 focal gulls both breed at coastal sites in the NGA, and their highest abundance occurred at GAK1, near breeding colonies. Gulls used the middle and outer shelf more than alcids, presumably reflecting their more efficient flight and, hence, their ability to forage over larger areas. The distribution of total surface feeders during March and early April was similar to the distribution during early May, without the seasonal inshore shift exhibited by divers (Sousa 2011).

#### 4.2. Responses of seabirds to cold- and warm-water events and changes in prey

The Pacific marine heatwave of 2014–2016 was one of the most extreme and persistent marine heatwaves recorded to date (Hobday et al. 2018). Peak temperature anomalies during this heatwave exceeded 3°C across much of the Gulf of Alaska, and anomalies >2°C persisted through 2 winters (Di Lorenzo & Mantua 2016). Surface-water chlorophyll concentrations decreased, as did the mean cell size of phytoplankton (Suryan et al. 2021), resulting in longer food chains with less efficient transfer of energy to higher trophic levels (Ruiz-Cooley et al. 2017, Armengol et al. 2019). Concurrently, the abundance of small, warm-water copepods increased (Ducklow et al. 2022), whereas the abundance of cool-water copepods was variable among species, and the abundance of cool-water euphausiids declined (Arimitsu et al. 2021, Suryan et al. 2021). The abundance and/or nutritional quality of forage fishes on the continental shelf, including capelin *Mallotus catervarius*, sandlance *Ammodytes personatus*, and herring *Clupea pallasii*, decreased during and after this heatwave (Arimitsu et al. 2021). Responses of piscivorous seabirds to the simultaneous reduction in availability and quality of multiple forage-fish species included reproductive failures of murres and kittiwakes (Piatt et al. 2020, Suryan et al. 2021, Schoen et al. 2022, this Theme Section) and the starvation of common murres in winter 2015–2016 (Piatt et al. 2020).

We observed changes in the distribution and abundance of species within all 3 major taxonomic groups during and after this heatwave. Murres concentrated near the coast and decreased their use of the middle shelf. Black-legged kittiwakes and glaucous-winged gulls, both of which increased in abundance over the middle and outer shelves during the 2007–2013 cold

period, also moved inshore. Fork-tailed storm-petrels became more abundant, especially over the middle and outer shelves, and black-footed albatrosses and northern fulmars used shelf habitats more commonly. Fluctuations in the abundance of murres and kittiwakes in Prince William Sound have previously correlated with ocean-climate variability (Cushing et al. 2018); for example, an influx of these species during the 1993 El Niño event was also associated with a mass mortality of common murres (Piatt & Van Pelt 1997). In addition to the redistribution of murres, kittiwakes, and other seabirds along the Seward Line during the Pacific marine heatwave, murres increased in Prince William Sound and along the coastline of the Alaska Peninsula before the winter 2015–2016 mass-starvation event (Arimitsu et al. 2021), and anomalous concentrations of murres were observed nearshore during the 2 subsequent summers (B. Robinson et al. unpubl.). Kittiwake densities also increased in summer along the coastline of Kenai and Alaska Peninsulas following the onset of this heatwave (B. Robinson et al. unpubl.), indicating that distributional shifts were widespread in the NGA.

Movement of piscivorous seabirds such as gulls and murres into coastal waters during these large-scale warming events in the NGA was probably caused by a reduction in the abundance of their prey on the continental shelf (Arimitsu et al. 2021). During and after this heatwave, black-legged kittiwakes breeding at Middleton Island reduced their use of the middle and outer shelves near that island (Osborne et al. 2020), where capelin had consistently occurred in prior years (McGowan et al. 2020), and instead foraged farther from their colony, making greater use of both the mainland coast and the continental slope. Concurrently, the frequency of capelin in kittiwake chick diets decreased, and the frequency of herring increased (Arimitsu et al. 2021), reflecting greater use of more distant, coastal resources. The frequency of mussels and chitons increased in diets of omnivorous glaucous-winged gulls during the heatwave (Suryan et al. 2021), indicating increased use of intertidal prey due to the reduction in forage-fish availability. Similar patterns have been seen in the California Current, where murres and shearwaters moved inshore and switched to alternative prey during warm conditions (Oedekoven et al. 2001) and where gulls made longer foraging trips and used nearshore and terrestrial habitats more during a marine heatwave (Cimino et al. 2022). These results suggest that switching between prey that differ in spatial distributions and environmental responses is a prevalent strategy by

which seabirds, including alcids, gulls, and shearwaters, buffer climate-linked variability in food resources. Inshore movements of seabirds suggest that coastal ecosystems, with their diversity of species and trophic pathways, may offer greater foraging opportunities than shelf waters during warming events. Prior to the Pacific marine heatwave, forage fishes in the NGA showed contrasting population responses to warmer and cooler periods, buffering their overall availability to mobile pelagic predators such as seabirds (Arimitsu et al. 2021). However, the reproductive failures of murres and kittiwakes and the mass starvation of murres there show that redistribution and prey-switching were insufficient to mitigate the effects of an extreme, protracted warming event.

Phenological shifts are an alternate explanation to consider for the inshore redistribution of alcids and gulls during the spring pre-breeding period in warm years. During the heatwave, the timing of the spring bloom was earlier (Litzow et al. 2020), and some zooplankton and ichthyoplankton taxa showed earlier phenology (McKinstry et al. 2022). If seabirds advanced their seasonal timing in response to shifts in the phenology of their prey, this could result in earlier seasonal redistribution closer to coastal breeding sites. However, studies of the reproductive timing of kittiwakes and murres in the NGA argue against this explanation: earlier laying dates of kittiwakes at Middleton Island were correlated with the negative (cool) phase of the Pacific Decadal Oscillation (Wheeler et al. 2022), and laying dates of murres and kittiwakes in lower Cook Inlet were later in warmer years with lower prey availability (Shultz et al. 2009).

In contrast to the lack of forage fishes and consequent negative effects on seabirds in the NGA during this heatwave, some other taxa responded positively to warming (Suryan et al. 2021). In nearshore waters, the heatwave had a mix of neutral and positive effects on benthivorous marine birds and their invertebrate prey (B. Robinson et al. unpubl.). In pelagic waters, the mean biomass of large calanoid copepods in spring 2015–2018 exceeded the long-term average (R. R. Hopcroft unpubl. data); we concurrently recorded high densities of fork-tailed storm-petrels over the middle and outer shelves. Crustacean zooplankton, including copepods, amphipods, euphausiids, and decapods, are major storm-petrel prey, especially during spring and early summer; juvenile sablefish *Anoplopoma fimbria*, myctophid fishes, and squid also are important, especially during chick-rearing (Boersma & Silva 2021). Although fork-tailed storm-petrel diet time series from the NGA are unavailable, frequencies of inver-

tebrates and young-of-year sablefish increased in diets of Middleton Island kittiwakes during this heatwave, whereas the proportion of forage fishes declined (Zador et al. 2019). Strong sablefish year-classes also occurred during the heatwave (Hanselman et al. 2019). Although information about changes in the distribution or abundance of mesopelagic fish and squid that are prey for many tubenose seabirds in the NGA is sparse, the increase in densities of tubenoses that we observed during warmer conditions may be indicative of increases in their prey. Such increases were observed in the California Current ecosystem, where contributions of offshore taxa to pelagic macrozooplankton and micronekton communities increased during the heatwave (Brodeur et al. 2019). Among these changes was an increase in gelatinous zooplankton (Brodeur et al. 2019), similar to observations during warm events in other high-latitude systems (Yaragina et al. 2022), including the NGA (R. R. Hopcroft unpubl. data). Gelatinous zooplankton are consumed by a variety of seabirds (Harrison 1984); however, they are of lower energy density than crustaceans and fish (Schaafsma et al. 2018). An environment with a preponderance of low-energy prey should favor seabird species with lower energy requirements, such as surface-foraging tubenoses, rather than those with higher metabolic energy requirements, such as alcids.

Finally, we note that tubenoses can cover thousands of km during extended foraging trips (Edwards et al. 2013). Although densities of tubenoses along the Seward Line increased during warming events, fully understanding the scale and likely mechanisms involved in these distributional shifts requires synthesis efforts encompassing the NGA and adjacent Large Marine Ecosystems.

### 4.3. Long-term community reorganization

Although common murres experienced a mass mortality event during the Pacific marine heatwave (Piatt et al. 2020), the long-term decline of tufted puffins is also of concern. Other studies also suggest declines of tufted puffins in the NGA. Based on monitoring at colonies, Goyert et al. (2017) estimated that populations of tufted puffins declined by 47% in the Gulf of Alaska from 1991 to 2013—within the 35–81% overall decline we estimated. The abundance of puffins has also declined in Prince William Sound (Cushing et al. 2018), lower Cook Inlet (Arimitsu et al. 2023), and in the California and Oyashio



Current systems, suggesting a broad, northward contraction in range (USFWS 2020).

The contrasting responses of tubenoses versus alcids and gulls to warm-water events suggest changes in species composition of the NGA seabird community under future climate warming, especially over the continental shelf. In the southern California Current System, warming has been accompanied by declining ecosystem productivity and lower abundance of seabirds, with fewer diving seabirds and more surface-feeding and plunge-diving seabirds (Hyrenbach & Veit 2003). Changes in seabird taxa associated with the shift from cool to warm conditions during our study were especially pronounced over the middle and outer shelves, which is an area that is transitional between coastal and oceanic water masses. During and after the heatwave, most tubenoses increased in abundance on the middle and outer shelves, whereas alcids and gulls moved inshore. These spring at-sea observations were concurrent with, or preceded, reproductive failures of murre and kittiwakes and the mass mortality of murre during the heatwave. Tubenoses may be especially well adapted to periods of low availability and energetic quality of prey on the shelf during warming events because of their adaptations, such as efficient flight, to low-productivity oceanic environments. In contrast, alcids, which forage by diving and have energetically costly flight, appear to be especially sensitive to such conditions. The only tubenoses not positively associated with temperature were shearwaters, which can forage both at the surface and via diving. Consequently, warmer projected ocean temperatures in the NGA may result in more surface-feeding tubenoses such as fulmars and storm-petrels and fewer diving-feeders such as murre and puffins.

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