Patterns of distribution, abundance, and change over time in a subarctic marine bird community

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ABSTRACT

Over recent decades, marine ecosystems of Prince William Sound (PWS), Alaska, have experienced concurrent effects of natural and anthropogenic perturbations, including variability in the climate system of the northeastern Pacific Ocean. We documented spatial and temporal patterns of variability in the summer marine bird community in relation to habitat and climate variability using boat-based surveys of marine birds conducted during the period 1989–2012. We hypothesized that a major factor structuring marine bird communities in PWS would be proximity to the shoreline, which is theorized to relate to aspects of food web structure. We also hypothesized that shifts in physical ecosystem drivers differentially affected nearshore-benthic and pelagic components of PWS food webs. We evaluated support for our hypotheses using an approach centered on community-level patterns of spatial and temporal variability. We found that an environmental gradient related to water depth and distance from shore was the dominant factor spatially structuring the marine bird community. Responses of marine birds to this onshore-offshore environmental gradient were related to dietary specialization, and separated marine bird taxa by prey type. The primary form of temporal variability over the study period was monotonic increases or decreases in abundance for 11 of 18 evaluated genera of marine birds; 8 genera had declined, whereas 3 had increased. The greatest declines occurred in genera associated with habitats that were deeper and farther from shore. Furthermore, most of the genera that declined primarily fed on pelagic prey resources, such as forage fish and mesozooplankton, and few were directly affected by the 1989 *Exxon Valdez* oil spill. Our observations of synchronous declines are indicative of a shift in pelagic components of PWS food webs. This pattern was correlated with climate variability at time-scales of several years to a decade.

1. Introduction

Patterns of species distribution, abundance, and composition are often associated with gradients, along which multiple environmental characteristics change in tandem (Whittaker 1956, 1967). Ecological communities are also shaped, however, by biotic interactions and by disturbance (Beals, 1984). Marine ecosystems of the northern Gulf of Alaska (GoA) have experienced major natural and anthropogenic perturbations over recent decades (Spies, 2007). Over that period, dramatic population changes have occurred in numerous marine taxa (Anderson and Piatt, 1999). In this paper, we asked whether temporal patterns of change in abundance and community composition differed along environmental gradients in a GoA marine bird community.

Coherence between climate variability and fluctuations in marine populations have been observed across vast spatial scales in the Pacific

Ocean (Francis et al., 1998; Chavez et al., 2003). Climate forcing and ecosystem response can operate at different time-scales, however, making the resulting time-series out of phase. One proposed explanation for low-frequency fluctuations in marine biological time-series is cumulative integration of stochastic climate variability (Di Lorenzo and Ohman, 2013). Oceanic integration of high-frequency atmospheric variability over time can produce physical ocean time-series characterized by low-frequency fluctuations (Hasselmann, 1976; Hsieh et al., 2005). In biological time-series, such low-frequency variability can be further enhanced, if the rate of population change is forced by the environment, but damped across the time-scale (such as generation time) over which the population responds to the environmental forcing (Di Lorenzo and Ohman, 2013). This damped, autoregressive forcing-response relationship is expected to result in stronger and smoother fluctuations in the biological time-series (i.e. greater low-frequency

power), relative to the fluctuations of the physical environmental drivers themselves.

Two primary modes of low-frequency atmospheric-oceanic variability have been characterized in the northeastern Pacific Ocean (Chhak et al., 2009). The Pacific Decadal Oscillation (PDO; Mantua et al., 1997; Zhang et al., 1997) is in part related to variability in the Aleutian Low pressure system (Graham, 1994; Bond et al., 2003). In the coastal GoA, the positive phase of the PDO corresponds to warm coastal water column temperatures, increased runoff, and increased alongshore advection (Royer, 2005). The North Pacific Gyre Oscillation (NPGO) corresponds to atmospheric forcing by the North Pacific Oscillation (Di Lorenzo et al., 2008). The positive phase of the NPGO is associated with strengthening of the Alaska Coastal Current and associated fluctuations in sea surface temperature (Di Lorenzo et al., 2008). Physical forcing influences the coastal ecosystems of the northern GoA in several ways. Variability in temperature affects growth and development of invertebrates and fish (Mackas et al., 1998; von Biela et al., 2016a). Freshwater runoff and advection of low-salinity water along the coast by the Alaska Coastal Current influences water column stability, which in turn affects the amount and timing of primary production by phytoplankton (Royer et al., 2001; Eslinger et al., 2001). Variable exchanges of both surface and deep waters (including nutrients and organisms) occur between fjord systems such as PWS and the adjacent GoA, and these processes are influenced by variability in physical forcing (Cooney et al., 2001; Halverson et al., 2013).

The 1989 *Exxon Valdez* oil spill (EVOS) was a notable anthropogenic perturbation of ecosystems in the northern GoA, especially in PWS where the spill originated. The EVOS had immediate acute effects on marine organisms, as well as biological effects that persisted for a decade or more (Peterson et al., 2003; Esler et al., this issue). Some species associated with nearshore sediments have experienced chronic oil exposure (Trust et al., 2000; Golet et al., 2002; Esler et al., 2010), which affected population recovery from losses due to acute mortality (Iverson and Esler, 2010). PWS marine communities have thus experienced concurrent effects of anthropogenic disturbance and a variable physical environment.

Studies of top marine consumers can provide insights into processes of ecosystem change (Reid and Croxall, 2001; Fredericksen et al., 2006). Marine birds are a relatively conspicuous group of species in ocean environments, where many organisms are difficult to observe because they are underwater (Piatt et al., 2007a). While they possess adaptations to buffer moderate variability in their food supply, vital rates of marine birds are sensitive to large fluctuations in prey availability (Cairns, 1987; Piatt et al., 2007b; Cury et al., 2011). Marine birds are relatively long-lived organisms, with delayed maturity, low reproductive rates, and high adult survivorship (Lack, 1967). Fluctuations in marine bird populations are therefore expected to most directly correspond to environmental variability over response time-scales from several years to decades. As long-lived upper-trophic consumers that can buffer moderate variability, changes in marine bird populations can be indicative of important ecosystem perturbations (Irons et al., 2008). For example, Agler et al. (1999) concluded that, coincident with climate fluctuations that affected forage fish abundance, abundance of piscivorous taxa of marine birds declined more than non-piscivorous taxa in PWS between the early 1970s and the early 1990s.

Marine birds of PWS constitute an ecologically diverse group of species that are adapted to habitats ranging from the intertidal to the open ocean, habitats that differ dramatically in food web structure (Lack, 1967; Isleib and Kessel 1973; Schreiber and Burger, 2001). In offshore waters, for example, primary production is generated by phytoplankton (Parsons, 1986), while in intertidal and shallow nearshore waters, most intrinsic primary production is generated by macrophytes, sea grasses, and benthic microalgae (Mann, 2000). Pelagic and nearshore-benthic food webs are linked, however, via consumption of phytoplankton by benthic filter-feeders (Newell and Shumway, 1993), and by consumption of macroalgae-derived suspended

particulate matter by organisms feeding in the water column (Kaehler et al., 2006; von Biela et al., 2016b). In nearshore areas, both kelp- and phytoplankton-derived carbon are assimilated by benthic invertebrates and fish, as well as by avian consumers of both prey types (Duggins et al., 1989; Fredriksen, 2003; von Biela et al., 2016b). The strength of benthic-pelagic coupling weakens along a spatial gradient from the coast to offshore (Fredriksen, 2003; Kopp et al., 2015).

While physical environmental drivers clearly affect organisms in both nearshore-benthic and pelagic systems, we expected that environmental fluctuations would result in greater variability in the pelagic food web for several reasons. First, the primary autotrophs in the offshore pelagic system (phytoplankton) are characterized by low biomass and high annual turnover (Mann, 2000), with each year's production strongly linked to physical processes in the atmosphere and ocean (Eslinger et al., 2001). In addition, the crucial role played by a small number of species of schooling planktivorous fishes in transferring energy to higher trophic levels makes the pelagic food web vulnerable to sudden shifts (Bakun, 2006). In contrast, in the nearshore-benthic system, the primary autotrophs (macrophytes and seagrasses) are characterized by high biomass and relatively low annual turnover (Mann, 2000). Nearshore-benthic systems exist at an ecological boundary, and receive allochthonous carbon inputs from pelagic, terrestrial, and riverine sources (Tallis, 2009; von Biela et al., 2013). We considered that these diverse pathways of energy flow may increase stability of the nearshore-benthic food web.

Here, we investigate the relationship between spatial and temporal patterns of variability within a diverse group of marine bird taxa using boat-based surveys of marine birds conducted in PWS during the summers of 1989–2012. We hypothesized that a major factor structuring marine bird communities in PWS would be proximity to the shoreline, which is theorized to relate to aspects of food web structure, and was incorporated into our sampling design (via stratification) at the onset of our study. We also hypothesized that shifts in physical ecosystem drivers such as the PDO and the NPGO differentially affected nearshore-benthic and pelagic components of PWS food webs. Given their ecological diversity, we predicted that responses of regionally sympatric marine bird taxa to environmental perturbations would vary based on their use of resources and habitats.

We evaluated support for our hypotheses using an approach centered on community-level patterns of spatial and temporal variability. First, we examined spatial patterns of community composition and the relationship between community composition and habitat. Our use of the term "community" follows the concrete community concept (McCune and Grace, 2002), and refers to the organisms that occur within a specific location in space and time. By "community composition" we refer to the abundances of taxa in a location. Second, we evaluated population- and community-level changes over time, and determined whether community-level changes correlated with climate variability. Third, we evaluated the relationship between temporal changes and spatial patterns of marine bird community composition. Synchronous population changes among co-occurring taxa would suggest common extrinsic agents of change, linked to the same factors that spatially structure the community.

2. Methods

2.1. Marine bird surveys

PWS is a subarctic estuarine fjord system (~9000 km²) that is separated from the northern GoA by several large islands (Niebauer et al., 1994; Fig. 1). We conducted boat-based surveys of marine birds throughout PWS in 12 different years within the period of 1989–2012. Surveys were conducted during the breeding season, in July, and were originally designed to assess effects of the EVOS on marine birds in PWS (Klowsiewski and Laing, 1994). Our study employed a stratified-randomized sampling design, based on proximity to the shoreline (Agler
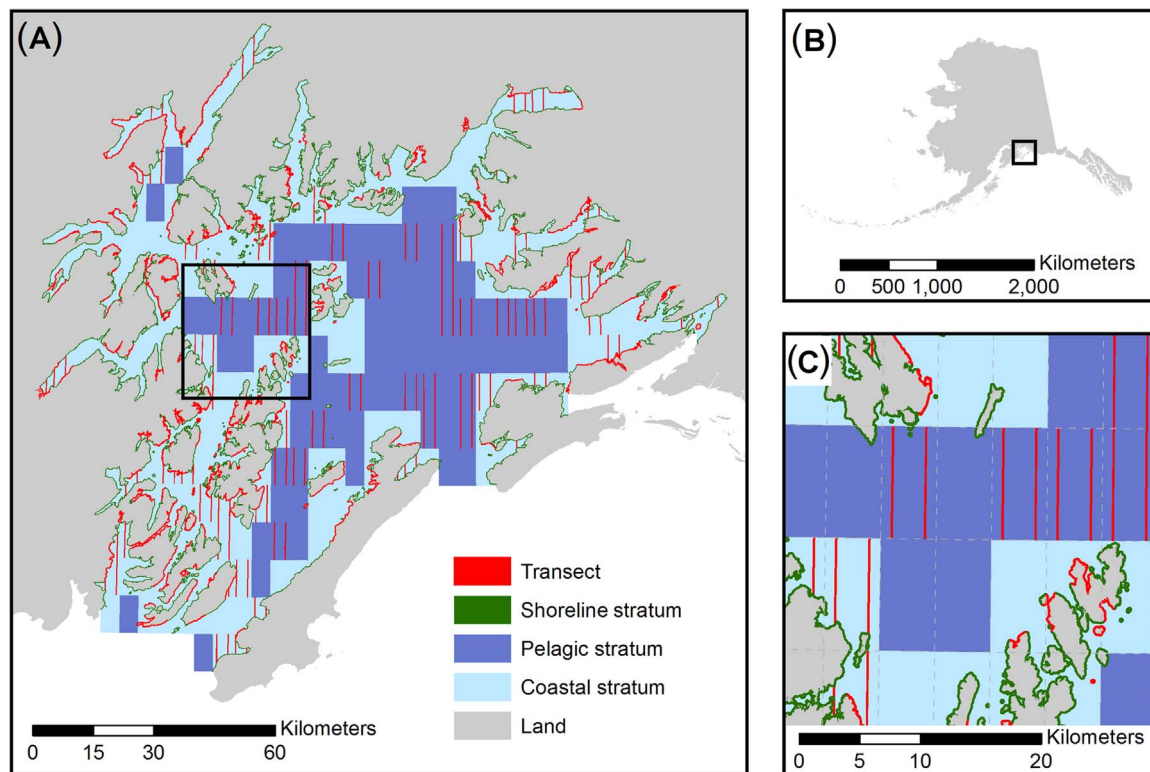
Fig. 1. Study area and sampling design. (A) Location of sampling strata and transects within the study area in Prince William Sound, Alaska. (B) Geographic location of Prince William Sound within the state of Alaska. (C) Detailed view illustrating sampling design.

et al., 1999; Kuletz et al., 2011; Fig. 1). The shoreline stratum comprised waters within 200 m of shore and land within 100 m of the waterline. This stratum was subdivided into 742 transects of unequal length (mean = 5.5 km), defined by prominent geographic features. We further subdivided the shoreline stratum into two substrata, Eastern PWS and Western PWS, with slightly different sampling intensities, and randomly selected a total sample of 212 shoreline transects from the 742 transects available.

Waters greater than 200 m from shore were divided into 5-minute latitude by 5-minute longitude blocks, with small areas isolated by complex topography merged with adjacent blocks. Blocks containing greater than 1.8 km (1 nautical mile) of coastline were categorized as "coastal", because a substantial portion of the block was close to the shore, and the remaining blocks as "deep-water"; 44 out of 206 "coastal" blocks and 29 out of 86 "deep-water" blocks were randomly selected, and transects were systematically placed in each block along north-south lines. We treated all transects nested within each block as a single sample unit. The same set of shoreline, coastal, and deep-water transects were surveyed each year.

Surveys were conducted from 7.6-m boats traveling at speeds of 10–20 km h^{-1}, with three survey vessels operating simultaneously. On each vessel, two observers, aided by the boat operator, counted all birds detected within 100 m on either side of, ahead of, or above the vessel, using binoculars to aid in identification. During shoreline surveys, the sampling area included waters within 200 m of the shore and land within 100 m of the shoreline. Observers were trained in distance estimation, and radar and rangefinders were used to maintain vessel distance from shore. Most surveys were conducted when mean wind-wave heights were less than 30 cm. No surveys where wind-wave heights were greater than 60 cm were retained during analysis. In total, our analysis incorporated 3313 surveys totaling approximately 24,000 linear km, during which we observed over 330,000 individual birds.

Observers identified birds to the lowest possible taxonomic level. As some bird species are quite similar in appearance, it was not possible for observers to identify all observed birds to the level of species. For some taxonomic groups, the possibility of both spatially and temporally varying species ratios and rates of species identification posed challenges for species-level analyses (see Kuletz et al., 2011; Hodges and Kirchhoff, 2012; Kuletz et al., 2013). We sought to include numerous taxa with diverse ecological characteristics in our analysis, which was primarily focused on community-level patterns. Consequently, we aggregated bird observations at the taxonomic level of the genus, where identification rates and reliability were very high (Table 1). We defined our community of interest as comprising taxa generally considered seabirds, shorebirds, waterbirds, and waterfowl (orders Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Suliformes, Anseriformes, and Charadriiformes). We collectively refer to these taxa as "marine birds," as they utilize marine food resources and occur within the marine environment, where we surveyed their abundance. Unless evaluating species richness, community analyses often benefit from removal of very rare species (McCune and Grace, 2002). We used two criteria to select genera for inclusion in our analyses. First, we excluded genera that did not occur in every survey year. Second, we excluded genera that did not occur at least once in at least 5% of the sample units within at least one of the primary strata. Application of these criteria resulted in the inclusion of 18 genera with diverse ecological characteristics (Table 1).

For comparative purposes, we classified the EVOS impact category of each genus of marine bird in PWS, using impact determinations published by the *Exxon Valdez* Oil Spill Trustee Council, a consortium of federal and state agencies charged with restoration of injured resources (*Exxon Valdez* Oil Spill Trustee Council, 2010). We also classified the primary prey types utilized by genera of marine birds based on species accounts in Rodewald (2015) as either Pelagic (e.g. forage fishes, squid, euphausiids, copepods), Benthic (e.g. demersal fishes, bivalves, gastropods, worms, small crabs), or Both Pelagic and Benthic (Table 2).

Table 1

Species composition of 18 evaluated genera of marine birds from Prince William Sound, Alaska.

Genus name	Species name	Common name	Percent of genus
Gavia	*Gavia stellata*	Red-throated loon	13.3
	Gavia pacifica	Pacific loon	21.2
	Gavia immer	Common loon	61.8
	Gavia adamsii	Yellow-billed loon	3.7
Oceanodroma	*Oceanodroma furcata*	Fork-tailed storm-petrel	99.8
	Oceanodroma leucorhoa	Leach's storm-petrel	0.2
Phalacrocorax	*Phalacrocorax auritus*	Double-crested cormorant	6.1
	Phalacrocorax urile	Red-faced cormorant	9.9
	Phalacrocorax pelagicus	Pelagic cormorant	84.0
Ardea	*Ardea herodias*	Great blue heron	100.0
Histrionicus	*Histrionicus histrionicus*	Harlequin duck	100.0
Melanitta	*Melanitta perspicillata*	Surf scoter	54.7
	Melanitta fusca	White-winged scoter	39.9
	Melanitta americana	Black scoter	5.4
Bucephala	*Bucephala albeola*	Bufflehead	2.6
	Bucephala clangula	Common goldeneye	45.0
	Bucephala islandica	Barrow's goldeneye	52.4
Mergus	*Mergus merganser*	Common merganser	95.0
	Mergus serrator	Red-breasted merganser	5.0
Haematopus	*Haematopus bachmani*	Black oystercatcher	100.0
Larus	*Larus canus*	Mew gull	16.3
	Larus argentatus	Herring gull	0.6
	Larus glaucescens	Glaucous-winged gull	83.1
Chroicocephalus	*Chroicocephalus philadelphia*	Bonaparte's gull	100.0
Rissa	*Rissa tridactyla*	Black-legged kittiwake	100.0
Sterna	*Sterna paradisaea*	Arctic tern	100.0
Stercorarius	*Stercorarius pomarinus*	Pomarine jaeger	49.3
	Stercorarius parasiticus	Parasitic jaeger	45.6
	Stercorarius longicaudus	Long-tailed jaeger	5.1
Uria	*Uria aalge*	Common murre	97.3
	Uria lomvia	Thick-billed murre	2.7
Cepphus	*Cepphus columba*	Pigeon guillemot	100.0
Brachyramphus	*Brachyramphus marmoratus*	Marbled murrelet	95.2
	Brachyramphus brevirostris	Kittlitz's murrelet	4.8
Fratercula	*Fratercula corniculata*	Horned puffin	22.0
	Fratercula cirrhata	Tufted puffin	78.0

2.2. Spatial patterns of marine bird community composition

We evaluated spatial patterns of marine bird community composition using ordination, which is a family of statistical methods used to extract common signals from correlated multivariate data, such as the abundances of organisms within samples (McCune and Grace, 2002). In general, ordination arranges objects (e.g. study plots or transects) on axes or dimensions based on the overall similarity or resemblance of each object to all the others, extracting the strongest independent patterns. In particular, we used Nonmetric Multidimensional Scaling (NMS; Kruskal, 1964; Mather, 1976), which is regarded as the most effective ordination method for analysis of community data (McCune and Grace, 2002). Before performing this analysis, we first calculated mean density (birds km^{-2}) of each of the 18 focal genera of marine birds, averaged across all 12 years when surveys were conducted, within each sample unit (transect or block; n = 282). We then applied the transformation $\log_{10}(x + 1)$, which retains zero values, an important feature of community data (McCune and Grace, 2002). We used the Bray-Curtis distance metric (Bray and Curtis, 1957; Faith et al., 1987) to calculate the compositional similarity between each pair of transects. The Bray-Curtis distance metric can be thought of as the

proportion of the abundance of different taxa shared between objects (McCune and Grace, 2002). We performed NMS using program PC-ORD 6.07 (McCune and Mefford, 2011), with sample units (transects or blocks) ordered on axes based on similarity in community composition. The resulting ordination had two orthogonal axes, or independent spatial patterns of marine bird community composition, which we refer to as S-NMS1 and S-NMS2. Next, we calculated the weighted average position, or center of mass, for each genus on each resulting axis. The weighted average positions can be thought of as representing optima of different genera along the gradients of community composition. To examine how spatial patterns of community composition were related to foraging strategies, we generated plots depicting the positions of genera, classified based on prey type, within the community ordination space. Additional statistical details regarding ordination and weighted averaging procedures are provided in Appendix A.

2.3. Temporal changes in abundance and patterns of community composition

To evaluate temporal population- and community-level changes, we first estimated annual abundance within the entire study area for each genus. Annual abundance estimates for each genus were calculated separately within each stratum, and then summed for all strata. Within strata, abundance estimates were calculated as total count divided by surveyed area multiplied by total area of the stratum. Standard errors and confidence intervals (CI) were calculated via bootstrap resampling (Manly, 2007), with 10,000 bootstrap iterations for each group, stratum, and year. Abundance estimates were uncorrected for detection probability, and thus likely under-estimate actual abundance. Given the constant sampling design, however, annual estimates generated from replicated surveys over time represent indices of abundance, which are useful for evaluating temporal changes.

Rates of change in abundance over time were estimated using weighted nonlinear regression (Bates and Watts, 1988). We weighted each annual estimate by the inverse of its variance. We used exponential models, and initiated the optimization using the 1989 annual estimate for the intercept parameter, and 1.0 for the rate parameter, using function nls in program R 3.1.0 (R Core Team, 2014).

We used NMS ordination to evaluate temporal change in the community as a whole. In this analysis, years were objects that were compared based on overall similarity in community composition. The resulting patterns were then plotted in relation to time. These patterns of change over time could conceivably take any form. We performed a $\log_{10}$ transformation of the abundance values, and then performed a NMS ordination (n = 12 years) using the Bray-Curtiss distance metric. We termed the two resulting axes or temporal patterns of community composition T-NMS1 and T-NMS2. We then calculated weighted average positions, or center of mass, for each genus on the two axes. Additional analytical details are provided in Appendix A.

2.4. Relationships between spatial patterns of community composition and habitat

We evaluated relationships between spatial patterns of community composition (S-NMS1 and S-NMS2) and six environmental variables: water depth (m), distance to shore (m), mean sea surface salinity (SSS; practical salinity units [psu]), mean sea surface temperature (SST; ˚C), shoreline wave exposure, and shoreline substrate composition. We measured SST and SSS during surveys (Appendix B), we acquired bathymetric data from Caldwell et al. (2009), and we acquired shoreline data from ADNR (1998) and Harney et al. (2008); data sources and processing are described in detail in Appendix B. We used generalized additive models (GAMs; Wood, 2011) to identify environmental gradients within the community ordination space. We first calculated standardized anomalies for each environmental variable. We then fit GAMs using package mgcv in program R 3.1.0. For shoreline wave

exposure and shoreline substrate models, we only included transects from the shoreline stratum, where these variables were measured. Models used standardized anomalies as the response variable, with a two-dimensional isotropic smoothing term estimated as a function of the coordinates of sample units on S-NMS1 and S-NMS2. Smoothing parameters were optimized via generalized cross-validation. We then used the fitted model to predict response values using a grid of coordinates over the community ordination space, after first removing grid cells supported by only a few data points.

2.5. Relationships between temporal patterns of community composition and climate

We used the PDO and the NPGO as proxies for broad-scale atmospheric-oceanic variability. Changes in marine bird populations due to increases or decreases in productivity, recruitment, and survivorship are generally expected to take place over periods of years. We therefore anticipated that responses of marine bird populations to climate variability would follow a damped autoregressive forcing-response relationship, with higher-amplitude, lower-frequency population fluctuations, as described by Di Lorenzo and Ohman (2013). To elucidate the relationship between temporal patterns of change in community composition and physical variability, we calculated the Pearson correlation coefficient between T-NMS1 and T-NMS2 and the PDO and NPGO indices. The indices were transformed by equation (2) of Di Lorenzo and Ohman (2013), using damping timescale (τ_{bio}) values from one to 10 years, representing annual to decadal response time-scales. We also calculated direct correlations with July PDO and NPGO index values, without integration, representing linear responses to environmental forcing at a monthly timescale.

2.6. Relationships between temporal and spatial patterns

We used variance weighted multiple linear regression to determine whether estimated rates of change in abundance of genera were predicted by their positions on S-NMS1 and S-NMS2. Similarly, we fit multiple linear regression models for T-NMS1 and T-NMS2, with the temporal coordinates of genera as the response, and the spatial coordinates of groups as the predictors. Models were fitted using function lm in program R 3.1.0.

3. Results

3.1. Spatial patterns of community composition

The majority (86.9%) of the variability in marine bird community composition among transects were accounted for by the two orthogonal axes, S-NMS1 and S-NMS2 (Fig. 2). The gradients in community composition represented by these two axes corresponded to "onshore-offshore" and "marine-estuarine" environmental gradients, respectively (Fig. 3). Coordinates of transects (points) on these two axes represented 72.4% and 14.5% of compositional variability among transects. Therefore, most of the variability in marine bird community composition was explained by distance from shore and depth, while more than half of the remaining unexplained variability was explained by gradients of decreasing salinity and shoreline exposure from outer Sound marine habitats to freshwater-dominated estuarine habitats.

Marine bird genera that feed on different prey resources were separated along the onshore-offshore axis (S-NMS1), with only a small amount of overlap among Benthic, Pelagic and Both feeding categories (Fig. 2). A cluster of four intertidal and benthic-feeding marine bird genera had the lowest mean positions on this axis: black oystercatcher (genus *Haematopus*), great blue heron (genus *Ardea*), harlequin duck (genus *Histrionicus*) and goldeneyes (genus *Bucephala*, primarily Barrow's and common goldeneyes, with an occasional bufflehead; Table 1). Similarly, the genera with the highest positions on the onshore-offshore

axis were pelagic feeders: storm-petrels (genus *Oceanodroma*, nearly all of which were fork-tailed storm-petrels), puffins (genus *Fratercula*, about 80% tufted puffins and 20% horned puffins), murres (genus *Uria*, primarily common murres), jaegers (genus *Stercorarius*, mostly parasitic and pomarine jaegers, with ca. 5% long-tailed jaeger), murrelets (genus *Brachyramphus*, mostly marbled murrelet, with ca. 5% Kittlitz's murrelet), and black-legged kittiwake (genus *Rissa*). Intermediate along this axis (S-NMS1) were the feeders in the Both category: mergansers (genus *Mergus*, mostly common mergansers), cormorants (genus *Phalacrocorax*, most of which were pelagic cormorants, with smaller numbers of double-crested and red-faced cormorants), Bonaparte's gull (genus *Chroicocephalus*), pigeon guillemot (genus *Cepphus*), loons (genus *Gavia*, of which most were common loons, followed in abundance by Pacific loons, red-throated loons, and yellow-billed loons), and *Larus* gulls (genus *Larus*, mostly glaucous-winged gulls, with moderate numbers of mew gulls and small numbers of herring gulls). Interspersed with these were benthic-feeding scoters (genus *Melanitta*, primarily surf and white-winged scoters, and ca. 5% black scoters) and pelagic-feeding arctic terns (genus *Sterna*).

There was less separation of genera along the marine-estuarine axis (S-NMS2), and there was no discernable separation by feeding type (Benthic, Pelagic, Both) along this axis (Fig. 2). Cormorants had the lowest position on the marine-estuarine axis, indicating that this group was the most restricted to marine waters along exposed coastlines, and the positions of black oystercatcher, pigeon guillemot, and puffins were lower than average on this axis. Bonaparte's gull had the highest position on axis 2, followed by arctic tern, indicating that these genera were more restricted to sheltered, estuarine waters. Positions of loons, goldeneyes, mergansers, and scoters were also higher than the average along the marine-estuarine axis.

3.2. Relationships between spatial patterns of community composition and habitat

Spatial ordination axis 1 (S-NMS1) represented a gradient in marine bird community composition that corresponded to an onshore-offshore environmental gradient, from benthic-feeding specialists, such as goldeneyes and harlequin duck, to pelagic-feeding specialists, such as storm-petrels and puffins. Sampling strata were separated along axis 1, from shoreline, to coastal, to deep-water, with small amounts of overlap (Fig. 2). The two shoreline substrata (Eastern PWS and Western PWS), however, were similar in community composition (Fig. 2). The transects with the lowest positions on axis 1 were shallow shorelines characterized by landforms such as tidal flats, moraines, and gravel bars (Fig. 3). Intermediate on axis 1 were steeper shorelines, followed by coastal transects in bays and passages. Transects in the central basin of PWS had the highest positions on axis 1. GAMs indicated that both distance from shore (Fig. 4A, $p < 0.001$, $r^2 = 0.79$) and depth (Fig. 4B, $p < 0.001$, $r^2 = 0.55$) were strongly related to the onshore-offshore gradient represented by axis 1.

Spatial ordination axis 2 (S-NMS2) represented a second spatial gradient in marine bird community composition that corresponded to a marine-estuarine environmental gradient, with marine genera such as cormorants, black oystercatcher, and pigeon guillemot on one end of the gradient, and estuarine genera such as to Bonaparte's gull, arctic tern, and mergansers on the other. Axis 2 did not discernably separate sampling strata; however, sample units in the deep-water stratum showed little variability along the marine-estuarine gradient compared to other strata, while coastal transects were intermediate and shoreline transects showed the greatest variability along axis 2 (Fig. 2). The transects with the lowest positions on axis 2 (most marine) were exposed capes and sea cliffs that were located in central PWS and near ocean entrances (Fig. 3). In contrast, transects with the highest positions on axis 2 (most estuarine) were located in mainland bays and fjords that receive substantial freshwater input from rivers and glaciers. GAMs indicated that SSS was strongly related to the marine-estuarine
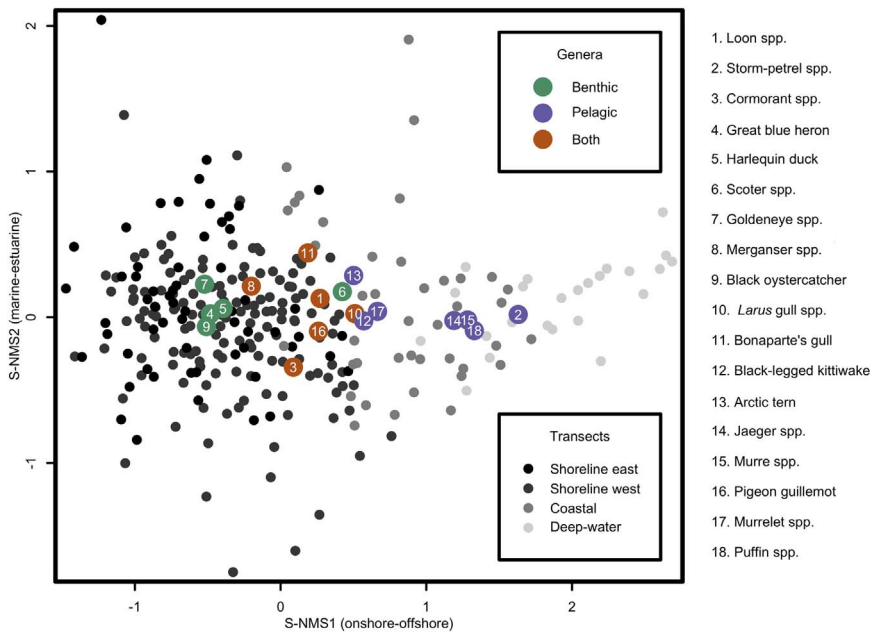
Fig. 2. Nonmetric Multidimensional Scaling (NMS) ordination representing spatial variability in marine bird community composition among transects in Prince William Sound, Alaska. Small grey points represent sample units (transects or blocks), and are shaded by sampling stratum. Axis coordinates of points are determined based on similarity of community composition; transects with greater similarity are closer together, and those with greater dissimilarity are farther apart. The two plot axes, S-NMS1 (onshore-offshore gradient) and S-NMS2 (marine-estuarine gradient), represent independent (orthogonal) patterns of variability in community composition. The large colored points represent weighted average positions (i.e. centers of mass, or optima) of taxonomic groups (genera) of marine birds on S-NMS1 and S-NMS2, with points colored by feeding category (Benthic, Pelagic, Both).

gradient of axis 2 (Fig. 4C, p < 0.001, r^2 = 0.53) and shoreline exposure to wave energy also had a moderately strong relationship to axis 2 (Fig. 4E, p < 0.001, r^2 = 0.33).

GAMs indicated shoreline substrate composition was related, with moderate strength, to both axes (Fig. 4F, p < 0.001, r^2 = 0.26), as was SST (Fig. 4D, p < 0.001, r^2 = 0.20). Thus, these habitat variables were significantly, but only moderately, associated with the gradients represented by spatial axes 1 and 2.

3.3. Temporal changes in abundance and patterns of community composition

We found that three of the 18 evaluated genera of marine birds significantly increased in abundance over the study period 1989–2012, while eight genera significantly declined in abundance (Table 2; Fig. 5). The three genera that significantly increased were cormorants, great blue heron, and harlequin duck. The eight genera that declined significantly over the study period were storm-petrels, scoters, Bonaparte's gull, arctic tern, jaegers, pigeon guillemot, murrelets, and puffins. Cumulative declines for these eight genera were in most cases substantial: abundance of six genera decreased by at least two-thirds over the study
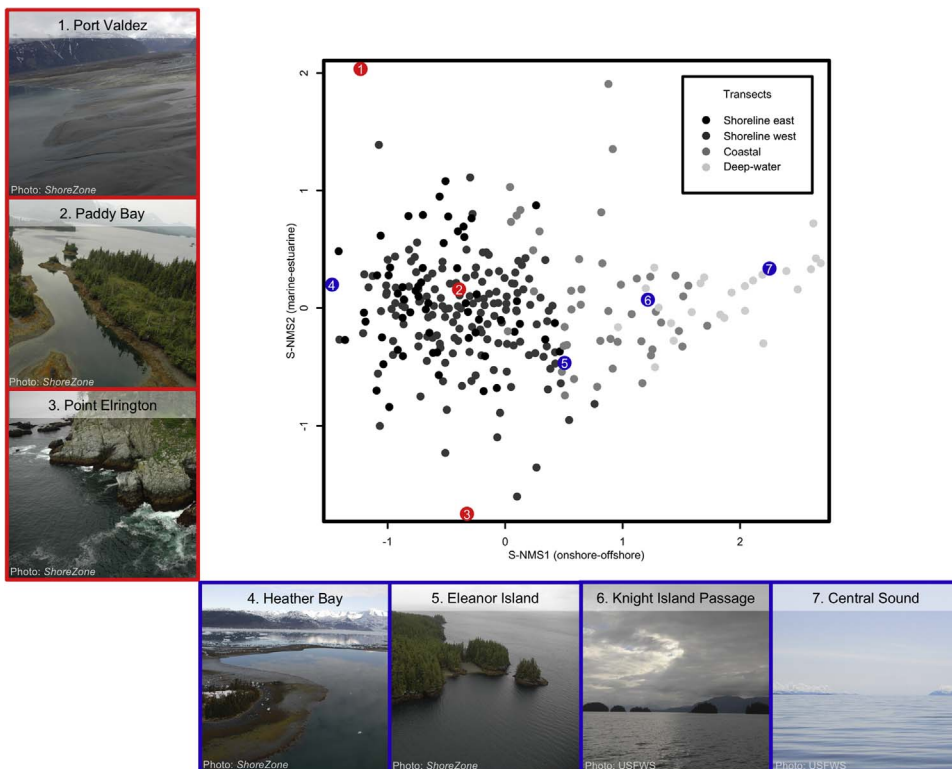

Fig. 3. Nonmetric Multidimensional Scaling (NMS) ordination depicting spatial variability in marine bird community composition among sample units (transects or blocks) in Prince William Sound, Alaska. Points represent transects; positions are based on similarity in community composition. Photos depict habitat characteristics at specific transects indicated on the plot by corresponding numbered and colored points. Shoreline habitat photos courtesy of *ShoreZone* coastal habitat mapping program, www.shorezone.org.
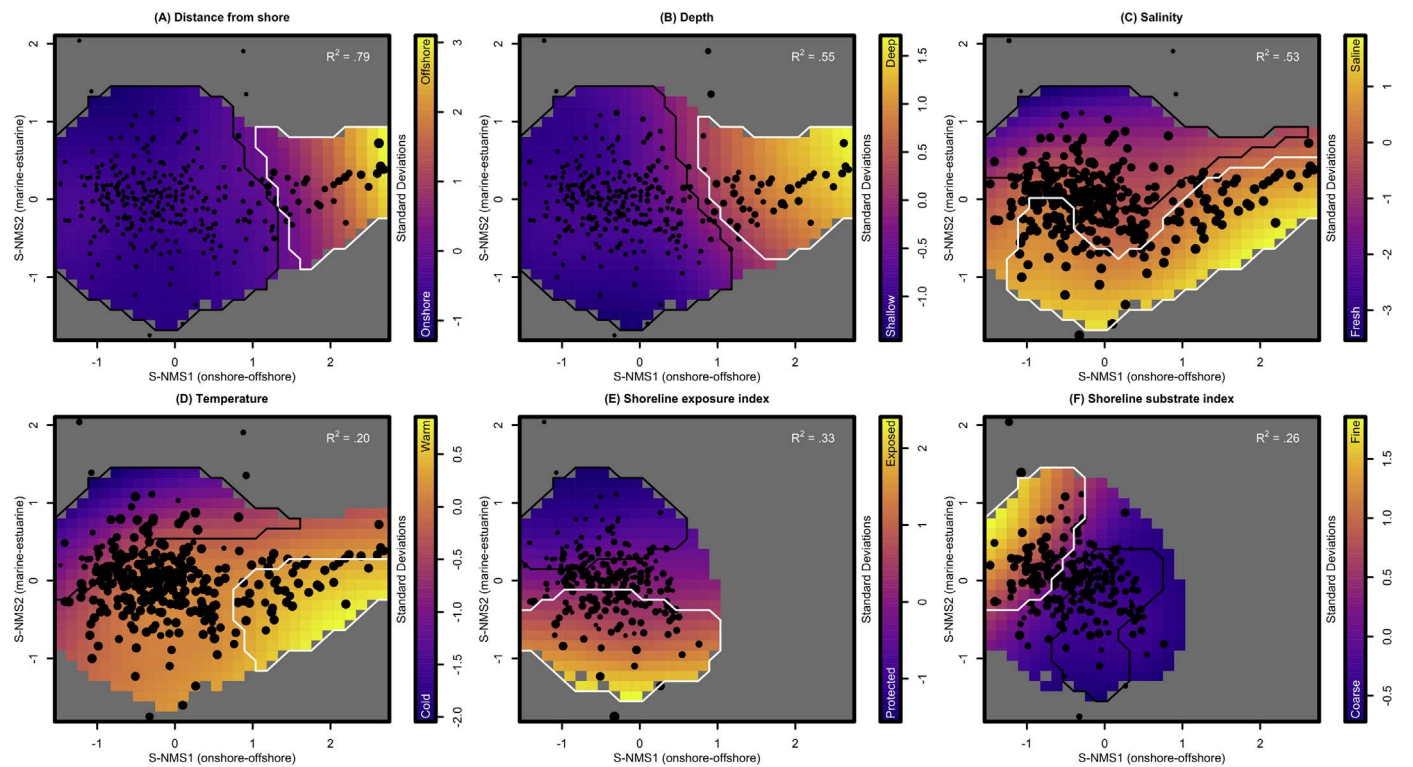
Fig. 4. Relationships between spatial patterns of marine bird community composition in Prince William Sound, Alaska, represented by Nonmetric Multidimensional Scaling (NMS) ordination, and habitat variables. Points represent transects, with coordinates based on similarity in community composition. Point size is proportional to measured values of habitat variables. Colored overlays represent predicted values from Generalized Additive Models (GAMs) relating habitat variables to plot coordinates. White (black) contours enclose plot areas where 95% prediction intervals are greater (less) than mean habitat values. Panels E and F display only shoreline sample units, as these habitat variables were measured only for shoreline strata.

period. There was a clear pattern of greater proportional declines among genera that were classified as Pelagic feeders, compared with than those that were classified as Benthic feeders or both Benthic and Pelagic feeders (Table 3). There was also a pattern of greater proportional declines among genera that were classified as "not injured" by the EVOS compared to those that were classified as "injured" (Table 3).

Nearly all the variability in marine bird community composition among years (93.8%) was accounted for by two temporal gradients, represented by ordination axes T-NMS1 and T-NMS2; the first temporal gradient (T-NMS1) was approximately monotonic, suggesting steady increases and or decreases in abundance over the study period, and the

second temporal gradient (T-NMS2) was characterized by population fluctuations during the study period (Fig. 6). Axis 1 represented 82.4% of variability in marine bird community composition among years, indicating that the vast majority of the temporal change in marine bird abundance during the study period was consistent with a nearly constant rate of change on the original scale (Fig. 6A). Annual abundance values of eight genera were significantly correlated with axis 1: storm petrels ($r = 0.91$, $p < 0.001$), arctic tern ($r = 0.86$, $p < 0.001$), puffins ($r = 0.74$, $p = 0.006$), Bonaparte's gull ($r = 0.71$, $p = 0.009$), jaegers ($r = 0.68$, $p = 0.016$), murrelets ($r = 0.65$, $p = 0.021$), pigeon guillemot ($r = 0.59$, $p = 0.041$), and harlequin duck ($r = -0.65$, $p =$

Table 2
Mid-summer abundance trends over the period 1989–2012, prey group classification, and *Exxon Valdez* oil spill (EVOS) population injury classification for 18 evaluated genera of marine birds from Prince William Sound, Alaska.

| Genus	Common name	Annual rate of change (%)	95% CI	p	Conclusion	Prey group	EVOS injury
Gavia	Loon spp.	−1.7	−4.4, 1.0	0.250	No change	Benthic & pelagic	Yes
Oceanodroma	Storm-petrel spp.	−15.5	−18.8, −12.1	< 0.001	Declined	Pelagic	No
Phalacrocorax	Cormorant spp.	7.4	2.8, 12.3	0.010	Increased	Benthic & pelagic	Yes
Ardea	Great blue heron	5.4	2.0, 9.0	0.011	Increased	Benthic	No
Histrionicus	Harlequin duck	2.7	0.6, 4.8	0.028	Increased	Benthic	Yes
Melanitta	Scoter spp.	−4.0	−7.3, −0.7	0.040	Declined	Benthic	No
Bucephala	Goldeneye spp.	−1.6	−4.8, 1.6	0.340	No change	Benthic	Yes
Mergus	Merganser spp.	−0.6	−2.4, 1.3	0.561	No change	Benthic & pelagic	No
Haematopus	Black oystercatcher	−0.8	−0.7, 2.4	0.319	No change	Benthic	Yes
Larus	*Larid* gull spp.	1.2	−0.3, 2.6	0.142	No change	Benthic & pelagic	No
Chroicocephalus	Bonaparte's gull	−4.7	−8.3, −1.1	0.031	Declined	Benthic & pelagic	No
Rissa	Black-legged kittiwake	−1.3	−3.9, 1.4	0.365	No change	Pelagic	No
Sterna	Tern spp.	−7.5	−9.4, −5.7	< 0.001	Declined	Pelagic	No
Stercorarius	Jaeger spp.	−9.0	−16.1, −1.3	0.046	Declined	Pelagic	No
Uria	Murre spp.	4.1	−2.3, 10.9	0.243	No change	Pelagic	Yes
Cepphus	Pigeon guillemot	−2.3	−4.0, −0.5	0.023	Declined	Benthic & pelagic	Yes
Brachyramphus	Murrelet spp.	−5.2	−7.1, −3.2	< 0.001	Declined	Pelagic	Yes
Fratercula	Puffin spp.	−5.6	−7.6, −3.6	< 0.001	Declined	Pelagic	No
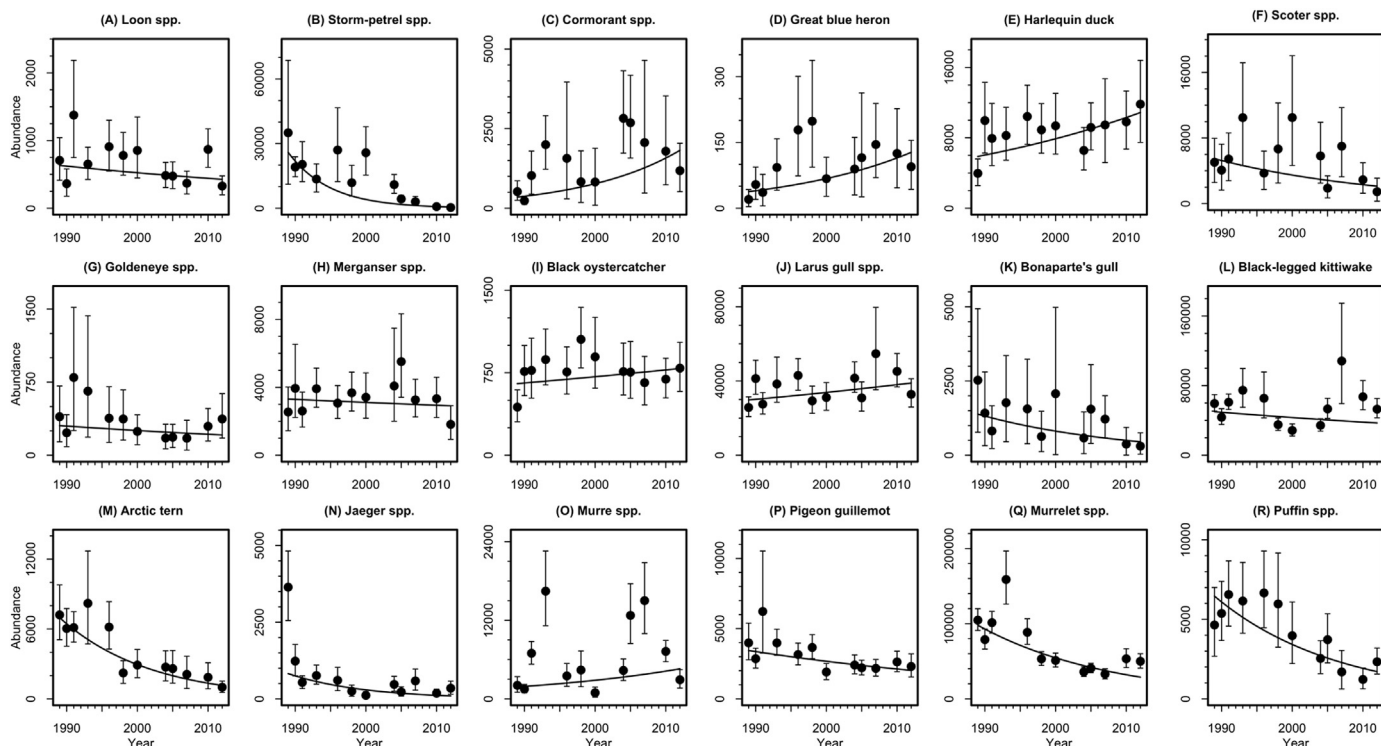
Fig. 5. Changes in mid-summer abundance of 18 genera of marine birds in Prince William Sound, Alaska, over the period 1989–2012. Points represent annual abundance estimates, with 95% confidence intervals indicated by bars. Curves represent exponential abundance trends, estimated using weighted nonlinear regression. Confidence intervals and statistical significance of each abundance trend are provided in Table 2.

Table 3
Number of evaluated marine bird genera from Prince William Sound, Alaska, that significantly increased, significantly declined, or did not change in abundance over the period 1989–2012, in relation to primary prey type and *Exxon Valdez* oil spill (EVOS) population injury classification.

Group	Number of genera	Percent increased	Percent stable	Percent declined	Average annual rate of change (%)
Prey group					
Benthic	5	40.0	40.0	20.0	0.7
Benthic & pelagic	6	16.7	50.0	33.3	−0.1
Pelagic	7	0.0	28.6	71.4	−5.7
EVOS group					
No Injury	10	10.0	30.0	60.0	−4.2
Injury	8	25.0	50.0	25.0	0.1

0.023). This list includes 8 of the 11 genera that were determined to have significantly increased or decreased during the study period, based on weighted nonlinear regression analysis. Unlike the nonlinear regression analysis, the ordination analysis that generated temporal axis 1 (T-NMS1) did not assume any specific functional form of change over time. Nonetheless, this analysis identified monotonic changes in abundance as the dominant form of temporal variability within the marine bird community of PWS during the study period.

Temporal axis 2 (T-NMS2), which was characterized by fluctuations over shorter time-scales of one to several years, only represented an additional increment of 11.4% of the temporal variability in marine bird community composition (Fig. 6B). Abundance patterns of three genera were significantly correlated with axis 2: murres (r = 0.92, p < 0.001), black-legged kittiwakes (r = 0.72, p = 0.008), and cormorants (r = 0.63, p = 0.030). Thus, axis 2 represents synchronized short-term fluctuations in the abundance of these three genera within PWS.

3.4. Relationships between temporal patterns of community composition and climate

Temporal axis 1 (T-NMS1), which was characterized by a monotonic pattern of increase or decrease in abundance of genera during the study period, was significantly correlated with physical variability, especially the PDO, at time-scales of several years to a decade. The correlation between axis 1 and the integrated PDO was significant at time-scales of three or more years, with the highest correlation (r = 0.77, p = 0.004) at a time-scale of six years (Fig. 6D). The correlation between axis 1 and the integrated NPGO was significant at time-scales of nine or more years, with the highest correlation (r = −0.58, p = 0.046) at 10 years (Fig. 6G). Direct correlations between axis 1 and corresponding July values of the PDO (r = 0.43, p = 0.116) and NPGO (r = −0.54, p = 0.070) were non-significant and weaker than correlations with integrated values, though only slightly so in the case of the NPGO.

Temporal axis 2 (T-NMS2), a pattern of short-term population fluctuations, was correlated with physical variability at short time-scales; the strongest relationship was the direct correlation with the PDO index values for July, the month of the surveys (i.e. no integration). The direct correlation between temporal axis 2 and the corresponding July PDO index values (r = −0.75, p = 0.005) was stronger than with integrated PDO values, which were not significant at any time-scale (Fig. 6E). Axis 2 was significantly correlated with the integrated NPGO index at a time-scale of one year (r = 0.61, p = 0.035), and the correlation progressively weakened at longer time-scales (Fig. 6H). For the NPGO, direct correlation with July index values was weaker and nonsignificant (r = 0.46, p = 0.128) compared with the integrated values.

3.5. Relationships between temporal and spatial patterns

Offshore-associated genera (i.e. storm-petrels, puffins, jaegers) tended to decrease in abundance over the study period, while onshore-associated genera (e.g. harlequin duck, great blue heron) tended to
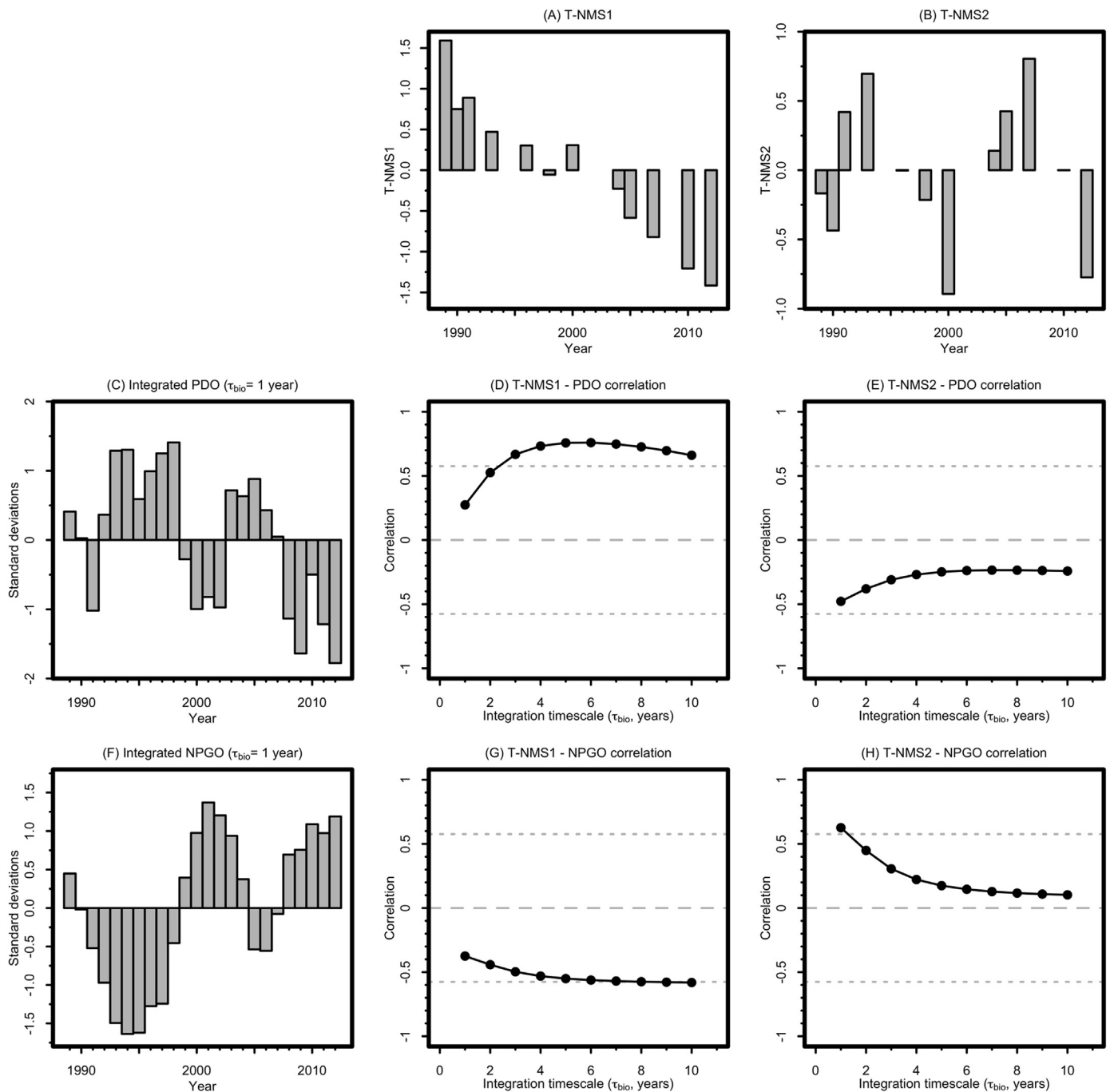
Fig. 6. Temporal patterns of marine bird community composition in Prince William Sound, Alaska, represented by Nonmetric Multidimensional Scaling (NMS) ordination, and correlation between ordination axes and modes of atmospheric-oceanic variability. First (A) and second (B) temporal ordination axes (T-NMS1 and T-NMS2, respectively), representing variability in marine bird community composition among years. Pacific Decadal Oscillation (PDO; C) and North Pacific Gyre Oscillation (NPGO; F) indices, transformed using equation (2) of Di Lorenzo and Ohman (2013) with a biological integration time-scale (τ_{bio}) of one year. (D, E, G, H) Depict correlations between T-NMS1 and T-NMS2 and integrated PDO and NPGO indices at τ_{bio} values from 1 to 10 years, representing annual to decadal time-scales of biological integration of atmospheric-oceanic variability. The correlation significance threshold ($\alpha = 0.05$) is indicated by dashed lines at $+/- 0.576$.

increase in abundance over the study period. In a multiple regression model, mean positions of genera along the onshore-offshore gradient and the marine-estuarine gradient (Fig. 2) accounted for 56% of the variability in rates of change in abundance (Fig. 7). Higher mean position on spatial axis 1 (i.e. more offshore) was associated with decreased abundance over time, and the converse was also true (p = 0.002). There was only moderate evidence that mean position of genera on spatial axis 2, representing the marine-estuarine gradient, was associated with rates of change in abundance over time (p = 0.041); higher position on axis 2 (i.e. more estuarine) was associated with

decreased abundance over time, and the converse was also true (p = 0.041). In other words, after accounting for relationships between onshore-offshore gradients and trends, genera associated with more protected, freshwater-influenced habitats, such as Bonaparte's gull and arctic tern, tended to decline, while genera such as cormorants, which were associated with exposed coastlines influenced by higher-salinity ocean waters, tended to increase.

Because temporal axis 1 (T-NMS1) represented monotonic changes in abundance over the study period, its relationships with the onshore-offshore gradient (S-NMS1) and with the marine-estuarine gradient (S-
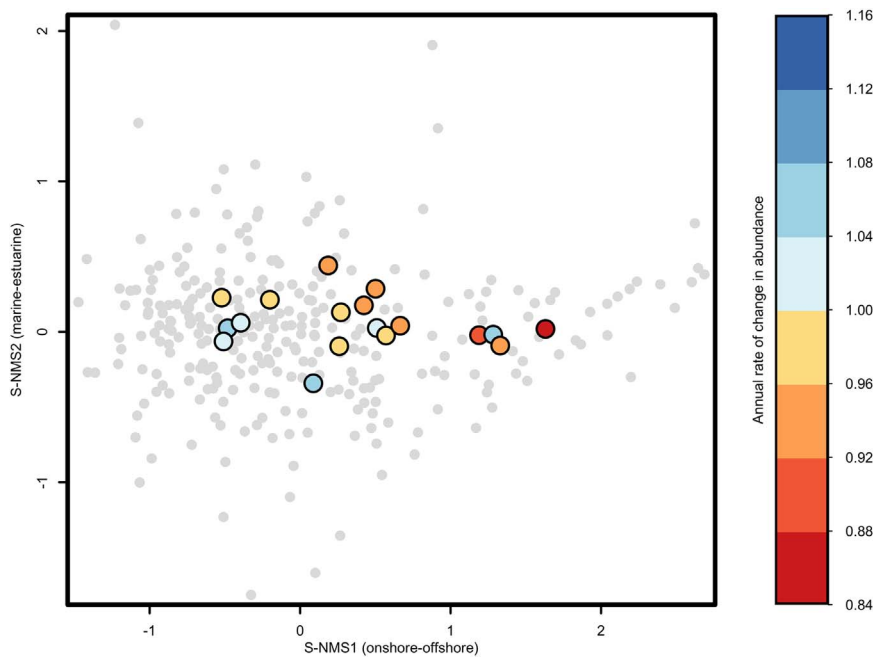
Fig. 7. Relationship between positions of 18 genera of marine birds in Prince William Sound, Alaska on axes from Nonmetric Multidimensional Scaling (NMS) ordination of community compositional similarity among transects, and annual rates of change in abundance over the period 1989–2012. Small grey points represent transects. Large colored points represent weighted average positions of genera (i.e. centers of mass, or optima) on the two axes, S-NMS1 and S-NMS2. S-NMS1 and S-NMS2 correspond to onshore-offshore and marine-estuarine environmental gradients, respectively (Figs. 2–4). Colors depict estimated rates of change in abundance over time (Table 2). Rates of change differed based on both S-NMS1 (p = 0.002) and S-NMS2 (p = 0.041), based on a multiple regression model (r² = 0.56).

NMS2) were the same as previously described for abundance trends. There was strong evidence that mean position of a genus on the onshore-offshore gradient (S-NMS1) was associated with mean position of that genus on T-NMS1 (p = 0.004). There was only moderate evidence that mean position of a genus on the marine-estuarine gradient (S-NMS2) was associated with position on temporal axis 1 (T-NMS1; p = 0.014). Thus, genera that were associated with more offshore habitats tended to decrease in abundance at a constant rate during the study period, while genera that were associated with more estuarine habitats also tended to decrease in abundance at a constant rate during the study period.

The responses of genera to onshore-offshore and marine-estuarine environmental gradients were not associated with the pattern of shorter-term fluctuations represented by axis 2 of the temporal ordination (T-NMS2). The coordinates of genera on the onshore-offshore gradient (S-NMS1) and the marine-estuarine gradient (S-NMS2) accounted for little (12%) of the variability in the position of genera along temporal axis 2 (T-NMS2). There was no evidence that the coordinates of genera on temporal axis 2 were associated with coordinates on either the onshore-offshore gradient (S-NMS1; p = 0.451) or the estuarine-marine gradient (S-NMS2; p = 0.243). Thus, genera of marine birds that were associated with more offshore habitats did not tend toward short-term fluctuations in abundance more than those associated with onshore habitats. Similarly, groups of marine birds that were associated with more estuarine habitats did not tend toward short-term fluctuations in abundance more than those associated with more marine habitats.

4. Discussion

4.1. Spatial patterns of community composition and relationships with habitat

Onshore-offshore gradients in the distribution and abundance of marine birds are typical of shelf regions (Hunt, 1990). In both the GoA and the southeastern Bering Sea, onshore-offshore gradients in marine bird communities are related to species-specific foraging strategies, with greater use of inshore waters by subsurface-feeders, and greater use of offshore waters by surface-feeders (Hunt et al., 2005; Hunt et al., 2014). In the GoA, cross-shelf gradients have been described for

physical and chemical properties, phytoplankton community structure and function, and the composition of zooplankton communities (Coyle and Pinchuk, 2005; Strom et al., 2006).

As with studies in shelf systems, we found that the strongest gradient in community composition corresponded to an onshore-offshore environmental gradient and was related to foraging mode and dietary specialization. In PWS, benthic-foraging specialists, pelagic-foraging specialists, and mixed benthic/pelagic-foraging generalists tended to use habitats that differed in water depth and proximity to the shoreline. Relationships between habitat use and foraging adaptations have been observed elsewhere in the coastal GoA. In Glacier Bay, a fjord system about 600 km southeast of PWS, Drew et al. (2013) found that habitat use of most marine bird species was related to water depth and current speed, with differential habitat use by foragers that specialized on bottom, mid-water, or surface prey. Combined, these studies underscore the linkages between an intertidal-neritic-oceanic environmental gradient, food web structure, and foraging adaptations of marine birds.

Several other studies have linked marine-estuarine environmental gradients to community composition in the northern GoA. In Cook Inlet, a large tidal estuary about 200 km west of PWS, Speckman et al. (2005) determined that zooplankton and forage fish communities were strongly related to marine-estuarine environmental gradients. Similarly, in glacial fjord systems in the northern GoA, multiple studies have found that upper- and mid-trophic level communities were structured by glacial meltwater, which affects photic depth, salinity, and temperature gradients (Arimitsu et al., 2012; Renner et al., 2012; Stephensen et al., 2016). Similarly, we found that the composition of the marine bird community of PWS varied in relation to salinity and exposure to wave energy. These two habitat characteristics tend to co-vary in PWS because salinity is lowest where rivers and glaciers meet the sea in the protected inner reaches of bays and fjords.

We found that shoreline substrate was weakly but significantly related to both gradients in community composition (onshore-offshore and marine-estuarine). This suggests that, at the spatial scale used in our surveys (shoreline transects averaged 5.5 km in length), substrate was in and of itself a relatively minor driver of variation in marine bird communities, with effects likely interrelated with those of water depth and wave exposure. Similarly, fine-scale habitat use studies (400-m shoreline segments) of harlequin duck and Barrow's goldeneye in PWS also found that the effects of shoreline substrate were equal to or less

than effects of several other environmental variables (Esler et al., 2000a, 2000b). For example, Esler et al. (2000b) reported that the best model for densities of wintering Barrow's goldeneye included a relatively large effect for distance to stream, and smaller effects for both wave exposure and substrate composition.

4.2. Temporal changes in abundance and community composition in relation to climate variability

We found that the primary form of temporal change in marine bird community composition (T-NMS1) was largely monotonic, and related to sustained increases or decreases in abundance of some genera of marine birds over the interval between 1989 and 2012. Our abundance trend analyses indicated that few marine bird genera in PWS (three of 18) increased during this period, while eight of the 18 genera declined, plus the magnitude of cumulative changes in abundance for a number of genera were large and biologically significant. We found that temporal axis 1 (T-NMS1) was correlated with climate variability (integrated PDO and NPGO) at time-scales of 3–10 years. Di Lorenzo and Ohman (2013) suggested that the strength of correlation of biological time-series with physical forcing is not likely to be sensitive to different response time-scales within the expected lifespan of the organism. This is supported by our analysis; marine birds generally do not reach reproductive maturity until several years old, and life-spans of many species exceed a decade (Schreiber and Burger, 2001). The strong correlation we observed between rates of change in the marine bird community and the PDO at correlation time-scales that corresponded to those of demographic processes indicates climate forcing is a plausible explanation for the observed changes in abundance during the study period.

We also found that short-term fluctuations in the composition of the marine bird community (T-NMS2) in PWS were correlated with climate variability at shorter time-scales; the strongest relationship was the direct correlation with the PDO index value during the month of the surveys. This suggests that short-term fluctuations in abundance were the result of immediate responses to environmental variability. While marine bird populations can experience rapid losses during mass-mortality events (Bailey and Davenport, 1972), intrinsic rates of population increase are nevertheless limited. This suggests that the fluctuations we observed must be due, at least in part, to movement of birds between PWS and the adjacent GoA. Movement in response to environmental variability is consistent with a short correlation time-scale.

Several studies provide evidence suggesting that these short-term fluctuations in local abundance in PWS may be related to foraging conditions. Two of the genera characterized by such fluctuations were murres and kittiwakes; substantial breeding populations of both common murres and black-legged kittiwakes are present in the GoA (Goyert et al., 2017), and provide a large pool of individuals that could potentially move among locations, especially non-breeders or failed-breeders. Warm, PDO-positive years during which relatively high local abundances of murres and kittiwakes occurred in PWS were associated with decreased prey availability elsewhere in the northern GOA (Piatt and Van Pelt, 1997; Hatch, 2013). In 1993, a PDO-positive year, widespread starvation of murres occurred across the northern GoA, combined with redistribution of murres from offshore to inshore waters (Piatt and Van Pelt, 1997). Based on multi-decade studies of kittiwakes breeding at Middleton Island, located about 100 km south of PWS near the shelf-break in the GoA, Hatch (2013) found that PDO-positive conditions were correlated with reduced occurrence of capelin (*Mallotus villosus*) in kittiwake diets, as well as decreased reproductive output. In contrast, cold, PDO-negative years during which Middleton kittiwakes obtained more capelin and had high reproductive success, such as the year 2000, were associated with fewer kittiwakes and murres in PWS. We infer that interannual movements of marine birds probably occurred between PWS and the GoA, and were likely short-term responses to climate-linked ecosystem fluctuations as they affected prey availability.

Studies of physical ecosystem drivers and lower trophic levels provide additional insights into climate-ecosystem linkages in PWS and the northern GoA. Over the past several decades, the physical environment of PWS and the adjacent GoA has been characterized by long-term trends, overlaid with substantial interannual variability (Campbell, this issue). In PWS, water temperatures have increased at most depths. Vertical salinity gradients have steepened, and mixed layer depths have become shallower. Such physical changes are expected to affect primary and secondary production. Batten et al. (this issue) investigated interannual variability in phytoplankton and zooplankton abundance and community composition on the GoA shelf during 2000–2015, and found that temperature and water column stability influenced the quantity and timing of phytoplankton production, which in turn affected the biomass and size composition of the mesozooplankton. There is also evidence of long-term variation in secondary production in the pelagic system of PWS. Based on spring zooplankton samples collected during 1981–1998, zooplankton biomass declined by 50% after 1991 (Eslinger et al., 2001). In turn, the characteristics of the mesozooplankton production affected early marine survival of juvenile pink salmon (*Oncorhynchus gorbuscha*) and overwinter survival of juvenile Pacific herring (*Clupea pallasi*; Cooney et al., 2001).

4.3. Relationships between spatial and temporal patterns

We found that the primary patterns of marine bird community composition across space and time were related. Synchronous changes in the abundance of co-occurring genera provide evidence that the factors that caused the changes were correlated with the same processes that spatially organize the community. Half of the variability in rates of change in abundance over time was explained by the responses of species groups to environmental gradients, the strongest of which was related to depth and proximity to the shoreline. We also found that most of the species groups that significantly declined in abundance primarily feed on pelagic prey, while those that primarily feed on benthic prey or that feed on both pelagic and benthic prey types experienced fewer declines. Thus, whether viewed through the lens of habitat (declines of offshore-associated genera) or the lens of diet (declines of genera that specialize on pelagic prey), we observed a high degree of synchrony in population changes within the marine bird community of PWS. The hypothesis that climate variability has differentially affected benthic and pelagic components of PWS food webs, including marine birds, is a parsimonious explanation for our observations.

Studies of pigeon guillemots breeding at the Naked Island Group in central PWS provide additional information regarding changes in prey availability to marine birds. Pigeon guillemots forage in nearshore environments, and provision their young with both demersal fishes such as blennies and sculpins, and schooling pelagic fishes such as Pacific sand lance (*Ammodytes hexapterus*) and herring (Ewins, 1993). In this study, we categorized the dietary group of pigeon guillemots as both benthic and pelagic. As a species that uses both prey types, guillemot diets may provide a good indicator of relative prey availability. Compared to the late 1970s, guillemots delivered proportionally fewer high-lipid schooling forage fishes and more demersal fishes to their nestlings during the 1990s and 2000s. (Golet et al., 2002; Bixler, 2010). At the same time as this shift in chick diet, there were declines in adult body mass and condition, chick growth rate, and overall productivity (Golet et al., 2002; Bixler, 2010). Supporting the causal link between diet and reproductive output, guillemot pairs that delivered a greater proportion of high-lipid forage fish to their nestlings had higher reproductive success, and their chicks grew at faster rates (Golet et al., 2000). While the decline we observed in abundance of pigeon guillemots in PWS was substantial, the rate of decline of guillemots, which forage in the nearshore on a wide range of prey taxa, was smaller than that of several of the genera that specialize in pelagic prey.

4.4. Conservation implications

The rapid local declines in abundance we observed in several different genera of marine birds are of sufficient magnitude that if they occurred across entire species populations or significant subpopulations they would warrant conservation concern. For example, there is evidence of widespread declines of tufted puffins in the northeastern Pacific (Piatt and Kitaysky, 2002; Gaston et al., 2009; Hanson and Wiles, 2015; Goyert et al., 2017). We estimated that abundance of puffin species in PWS declined by 74% between 1989 and 2012, and most (78%) of the puffins we observed during surveys were tufted puffins. Declines of both tufted and horned puffins have also been observed at PWS breeding colonies (Bixler, 2010). At GoA colonies outside of PWS, tufted puffins declined by an estimated 47% between 1990 and 2013 (Goyert et al., 2017). There is also evidence of declines of tufted puffin populations and abandonment of breeding sites along the west coast of North America (Piatt and Kitaysky, 2002; Gaston et al., 2009; Hanson and Wiles, 2015).

Declines of Brachyramphus murrelets have also been geographically widespread (Burger, 2002; McShane et al., 2004; Piatt et al., 2007c; Miller et al., 2012). We estimated that Brachyramphus murrelets declined by a cumulative total of 71% in PWS, and 95% of the murrelets that we identified to species during surveys were marbled murrelets. Declines of marbled murrelets have occurred in a substantial portion of the species' range (Piatt et al., 2007c; Miller et al., 2012), and, due to population losses, the species is legally protected under conservation laws in British Columbia, Canada, and in and the conterminous United States (Burger, 2002; McShane et al., 2004). Our results provide further evidence of geographically widespread declines of tufted puffins and Brachyramphus murrelets. The cumulative declines we observed in other genera in PWS were also substantial; abundance of pigeon guillemots declined by 41%, scoters by 61%, Bonaparte's gulls by 67%, arctic terns by 84%, and storm-petrels by 98%. Our results underscore the importance of assessing population changes for these birds at other locations in the GoA.

Many of the marine bird taxa included in our study are known to have experienced direct harmful effects caused by the EVOS (Table 2; Exxon Valdez Oil Spill Trustee Council, 2010). Diving species suffered the most pronounced acute oiling effects, while surface-feeding species are thought to have had a greater ability to avoid acute oil exposure (Piatt et al., 1990). In some locations, oil persisted in nearshore sediments for more than a decade after the spill (Short et al., 2004; Michel et al., 2010), and in those areas, some benthic-foraging species experienced chronic oil exposure in PWS (Trust et al., 2000; Golet et al., 2002; Esler et al., 2010) and associated demographic effects (Iverson and Esler, 2010).

Population trajectories of the eight evaluated genera that were classified as injured by the EVOS were variable. We found that, over the study period, two had increased in abundance, two had decreased, and four had not changed significantly (Tables 2 and 3). Thus, while two genera, harlequin ducks and cormorants, underwent increases in abundance in PWS, consistent with recovery from population injury, six other injured genera did not increase, including nearshore-associated benthic-feeders such as black oystercatcher and goldeneyes.

On average, the rate of change of the genera that were classified as injured by the EVOS was 0.1% per year, suggesting a very slow rate of recovery (Table 3). In contrast, the average rate of change of the non-injured group was −4.2% per year. The non-injured group included more pelagic-specialists (50%) than did the injured group (25%), perhaps due in part to shorter oil retention time in offshore habitats compared to shoreline habitats. Most of the pelagic-feeders that we evaluated declined, likely due to changes in the pelagic ecosystem, and this was apparently the primary driver of the difference in average population trajectories between the injured and non-injured genera.

There is evidence that some of the population declines we observed began prior to 1989, the year of the EVOS. Agler et al. (1999) concluded

that, within PWS, piscivorous marine bird taxa declined more than non-piscivorous taxa between 1972 and the early 1990s. Similarly, we found that the greatest declines over the period 1989–2012 occurred among genera that specialized on pelagic prey such as forage fishes and mesozooplankton.

Marine birds are not the only taxa to have decreased in abundance within PWS in recent decades. Of particular note, the PWS stock of Pacific herring, an important mid-trophic level species, collapsed in the early 1990s (Hulson et al., 2008). Additionally, two piscivorous marine mammals, Pacific harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*), have experienced population declines in PWS (Frost et al., 1999; Trites et al., 2007), and elsewhere in the western GoA. Decreases in numbers of Steller sea lions wintering in PWS were correlated with declines in indices of herring abundance (Thorne and Thomas, 2008). In contrast, numbers of humpback whales (*Megaptera novaeangliae*) have increased in the northeastern Pacific, including PWS, following the end of commercial whaling (Teerlink et al., 2015). Humpback whales are a major consumer of herring, and predation by humpback whales may now be of sufficient magnitude to affect the PWS herring stock (Moran et al., this issue).

The proximate and ultimate causes of population changes in GoA marine taxa remain subject to debate. Our observations of large declines among many different marine birds that specialize in pelagic prey provide important context for population changes within this system. Our results support ecosystem-level hypotheses regarding causes of population declines, rather than hypotheses unique to the biology of individual taxa. We observed strong correlations between changes in marine bird community composition and the PDO at both short-term (monthly) and long-term (years to decades) time-scales. The parsimonious explanation for the observed population changes is bottom up alteration of the pelagic food webs of PWS resulting from broad-scale changes in the atmospheric-oceanic systems of the northeastern Pacific Ocean.

While the most dramatic changes we observed in the marine bird community appear to be related to shifts in the pelagic system, we also observed a secondary pattern, with declines of estuarine-associated taxa. The importance of salinity in structuring upper-trophic level coastal communities suggests that changes in freshwater inputs due to altered precipitation or glacial recession have the potential to alter marine bird communities in coastal areas of the GoA. There is evidence that increased meltwater inputs have affected the hydrography of bays and fjords along the margins of PWS (Campbell, this issue).

5. Conclusions

Over the 24-year period evaluated in this study, major changes occurred within the marine bird community of PWS. Our results indicated that there were strong spatial and temporal patterns of community composition and that they were related. We found that the primary spatial pattern of community organization, an onshore-offshore environmental gradient related to dietary specialization, separated marine bird taxa by prey type, from benthic- and intertidal-feeders such as the harlequin duck, to mixed benthic/pelagic-feeding generalists such as gulls, to pelagic-feeding specialists such as the puffins. We also found that the dominant form of variability in community composition among years was a pattern of monotonic trends in abundance of genera over time, with more declines than increases. This temporal pattern most strongly correlated with physical variability, primarily the PDO, over time-scales of 3–10 years. Finally, the positions of genera along an onshore-offshore environmental gradient were strongly related to rates of change in abundance of over time. The response of birds to an onshore-offshore environmental gradient predicted rates of change in abundance, and the greatest declines occurred in genera associated with offshore habitats. Birds associated with these offshore habitats primarily feed on pelagic prey types. Our observations of synchronous declines are indicative of a pronounced shift in the

pelagic food web of PWS.

Appendix A. Nonmetric Multidimensional Scaling analysis

We evaluated spatial and temporal patterns of marine bird community composition using Nonmetric Multidimensional Scaling (NMS), which is an iterative, nonparametric ordination method based on ranked dissimilarities (Kruskal, 1964; Mather, 1976). For our analysis of spatial patterns of marine bird community composition, we first calculated mean density (birds km^{-2}) of each of the 18 focal genera of marine birds, within each sample unit (transect or block) and across all survey years. We then applied the transformation $log_{10}(x + 1)$, which retains zero values, an important feature of community data (McCune and Grace, 2002). We performed NMS ordination, with sample units (n = 282) ordinated on axes based on similarity in community composition. We performed the ordination using the program PC-ORD 6.07 (McCune and Mefford, 2011) and the Bray-Curtis distance metric (Bray and Curtis, 1957; Faith et al., 1987), a random starting configuration, 1000 real runs, 1000 randomized runs, an instability criterion of 10^{-8}, and a maximum of 500 iterations. We selected a two-axis solution based on scree plots and a Monte Carlo test. The final run used the lowest stress prior result as the starting configuration, and reached convergence (instability $< 10^{-8}$) in 68 iterations, with a final stress value of 17.42. We rotated the final ordination by orthogonal principal axes. To determine the percent of variance in the distance matrix represented by the ordination, we calculated r^2 between the Bray-Curtis distance values among transects and the Euclidian distances among points in the ordination space (McCune and Grace, 2002).

For each ordination axis, we calculated the weighted average position p on ordination axis i of genus j,

$$p_{ij} = \frac{\sum_{i=1}^{n} c_{ik} a_{jk} w_k}{\sum_{i=1}^{n} a_{jk} w_k}, \tag{1}$$

where c_{ik} is the coordinate on ordination axis i of sample unit k, a_{jk} is the density value for genus j in sample unit k, and w_k is the stratum weight for sample unit k, calculated as the area of the corresponding stratum divided by the total area of all strata. This equation is conceptually the same as that provided by McCune and Grace (2002; page 150-1), with the addition of the w_k term to account for the stratified sampling design. This calculation can be thought of as determining the center of mass for each genus along each axis.

We also used NMS ordination to evaluate temporal change in the community as a whole. We performed a log_{10} transformation of annual abundance values for each genus within the entire study area (see Methods section for details), and then performed a NMS ordination (n = 12 years) using the same distance measure and analytical settings as in the previous spatial community ordination. We selected a two-axis solution based on scree plots and a Monte Carlo test. The final run reached convergence in 32 iterations, with a stress value of 6.98, and we performed a rotation by orthogonal principal axes. We calculated the weighted average ordination axis position of each genus (i.e. center of mass), using Eq. (1) with genus j, and years k and omitting the stratum weights, which were not needed as the calculation of annual abundance estimates for the study area accounted for the stratified sampling design.

Appendix B. Habitat data sources and processing

We obtained habitat data from several sources described below. For each transect, we calculated mean values for four variables: water depth (m), distance from shore (m), sea surface salinity (SSS; practical salinity units [psu]), and sea surface temperature (SST; °C). For shoreline transects, we calculated mean values for two additional variables: substrate composition and exposure to wave energy (see below). We processed geospatial data using the program ArcMap 10.0 (ESRI, 2011). We calculated mean transect water depth using an 8/3 arc-second bathymetric–topographic digital elevation model for PWS (Caldwell et al., 2009), after removing positive elevation values (i.e., offshore rocks, shorelines). We calculated mean transect distance from shore using a 1:63,360 Alaska coastline layer (ADNR, 1998).

We obtained geospatial data on shoreline substrate and sediment composition and shoreline exposure to wave energy from the *ShoreZone* Coastal Habitat Mapping Program (Harney et al., 2008), which mapped shoreline habitat using low-altitude aerial imagery collected during negative tidal elevations. The alongshore units of the *ShoreZone* geodatabase were smaller than our marine bird transects. Based on substrate and sediment data in the *ShoreZone* variable "BC Class", we generated a continuous index of transect substrate and sediment type, with a value of 1.0 corresponding to rock substrate with no overlying sediment, and a value of 8.0 corresponding to sedimentary substrate overlaid with organic sediments (Appendix C). The *ShoreZone* variable "Biological Wave Exposure" categorized the wave exposure of alongshore units using the wave energy tolerance of indicator species and biobands. Biological Wave Exposure was classified into six levels, which we converted to a continuous index from 1.0 (Very Protected) to 6.0 (Very Exposed).

During marine bird surveys, we measured SSS and SST (1-m depth) at the beginning of each transect. SSS was measured to the nearest 0.1 psu during eight of the 12 survey years, beginning in 1996, using YSI model 63 digital meters. SST was measured to the nearest 0.1 °C during all 12 survey years, using either YSI model 63 digital meters or thermometers. We averaged SSS and SST values within each sample unit across all measured years.

Appendix C. Categorization of substrate and overlying sediments for shoreline transects in Prince William Sound, Alaska.

Substrate	Sediment	Code	Percent of sample
Rock	None	1	9.2
Rock and Sediment	Gravel	2	15.4
Rock and Sediment	Sand and Gravel	3	26.7
Rock and Sediment	Sand	4	0.0
Sediment	Gravel	5	2.6
Sediment	Sand and Gravel	6	35.1
Sediment	Sand and Mud	7	3.0
Sediment	Organics	8	7.3
Anthropogenic	Anthropogenic	NA	0.4
Channel	Current	NA	0.1
Glacier	Ice	NA	0.1

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