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Ocean-influenced estuarine habitat buffers high interannual variation in seabird reproductive success

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ABSTRACT: Seabirds in more variable habitats generally live longer and more readily forgo or reduce breeding investments in poor resource seasons to maximize their overall lifetime fitness. Their breeding success is dependent on factors including diet, prey availability, and proximity to foraging habitat. Furthermore, seabird colonies in upwelling ecosystems are subject to interannual variation in oceanic conditions that drive bottom-up processes. Adjacent estuarine ecosystems, while less affected by upwelling, are also influenced by freshwater input and may experience less interannual variation in seabird prey resources. Here, we compare the breeding ecology and diet of pigeon guillemots *Cephus columba* from an estuarine colony (Alcatraz Island, California) and an isolated offshore colony (Southeast Farallon Island, California) from 2015 to 2017 to understand how habitat location and surrounding environment differentially influence diet and reproduction. Breeding phenology in pigeon guillemots was similar between colonies, but reproductive success was higher and more stable at the estuarine site than at the offshore colony, where productivity was explained primarily by ocean conditions. Interannual and estuarine/offshore variability in chick diet composition was partially explained by upwelling and the influence of freshwater inputs. Variation in offshore pigeon guillemot productivity was related to the prey species composition. With increasingly variable conditions offshore in the California Current, the availability of alternative estuarine and nearshore breeding sites inshore may become increasingly important for the regional pigeon guillemot population and other seabirds capable of exploiting nearshore prey resources.

KEY WORDS: Alcatraz Island · Southeast Farallon Island · Pigeon guillemot · *Cephus columba* · California Current · Estuary · Seabird colony · Breeding ecology

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1. INTRODUCTION

Seabird populations generally exhibit some variation in reproductive success and survivorship across

their range (Stearns 1992). This may be a function of variation in habitat quality, resource availability, predation pressure, competition, climate, or other factors (Boyce et al. 2006). Furthermore, each of these forces

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may vary at different sites in different years (or seasons), adding both spatial and temporal variation in breeding success and other population level parameters (Cayuela et al. 2019). Life history theory predicts that species or populations living in more variable environments, where resources may be lower in some years than others, will favor survivorship over reproductive success ('bet-hedging') to maximize overall reproductive output over a lifetime (Stearns 1992, Roff 2002, Simons 2011). While there is limited direct evidence for bet-hedging between species utilizing habitats of differing variability (Simons 2011), there is even less for intraspecific bet-hedging. Nonetheless, black-browed albatross *Thalassarche melanophrys* populations feeding from more variable oceanic habitats have higher adult survival and lower reproductive success (Nevoux et al. 2010) and European storm petrels *Hydrobates pelagicus melitensis* skip breeding under strong climate variations (Soldatini et al. 2016). Thus, within-species strategies for maximizing lifetime reproductive success may vary depending on habitat variability and determining intraspecific variation in reproductive success related to temporal habitat stability is the first hurdle in this assessment. Conversely, species may not be 'bet-hedging' and are rather maximizing fecundity each year, regardless of environmental conditions.

Reproductive success in upper trophic level marine predators in eastern boundary currents is strongly influenced by interannual variability in prey availability driven by regional and proximate oceanographic conditions (García-Reyes & Sydeman 2017). Favorable coastal upwelling conditions and subsequent nitrate availability foster primary production which builds a robust spring and summer food web, exploited by upper trophic level predators including seabirds, marine mammals, fishes, and sharks (Bakun 1996). This link between oceanography and seabird prey availability in the upwelling dominated California Current System (CCS) has been well established (Black et al. 2010). Depending on the life history, prey selection, and foraging strategy of species, they may experience years of extraordinary productivity or near complete breeding failure (Ainley & Boekelheide 1990, Sydeman et al. 2001, Warzybok et al. 2014). Much of this variation is explained by annual or decadal changes in coastal upwelling and nutrient input related to oceanographic processes such as the El Niño-Southern Oscillation (ENSO) (Ainley & Boekelheide 1990), the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997), and the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008, Schmidt et al. 2014).

Species that rely on prey supported by favorable oceanographic conditions (upwelling), may experience more interannual variability in breeding success due to variation in prey resources. For example, Brandt's cormorants *Phalacrocorax penicillatus* in coastal California colonies are partially buffered from interannual oceanographic variation affecting prey resources (specifically juvenile rockfish availability) compared to the offshore colony at the Farallon Islands (Elliott et al. 2015). Both Brandt's cormorants and western gulls *Larus occidentalis* had higher productivity over a 5 yr period at the estuarine colony on Alcatraz than on the Farallon Islands. This is likely related to more consistent and available prey that is easily accessible and ample benthic foraging habitat near the nesting colony on Alcatraz (Saenz et al. 2006).

For colonies and individual seabirds foraging within estuaries, prey availability may not only be driven by the effects of oceanographic variation on prey species that move between estuary and ocean, but also the interplay between freshwater input and tidal influences from the adjacent ocean (Cloern & Jassby 2012). Fish abundance and species composition in San Francisco Bay (SFB) are correlated with marine conditions (Cloern & Jassby 2012, Feyrer et al. 2015), as there are strong associations of outer SFB lower and mid-trophic species with long-term oceanographic NPGO conditions (Cloern & Jassby 2012). Specifically, between 1980 and 2010, as the NPGO strengthened, flatfish, sculpin, shrimp, and phytoplankton increased dramatically. This is likely due to increased production of these species in the near-shore coastal ocean during favorable conditions and movement of juveniles into the bay (Cloern et al. 2010, Cloern & Jassby 2012). There is also interplay between oceanic influences and freshwater input, both of which often covary with oceanographic conditions. Much of the variation in SFB estuarine community composition is explained by the spatial expression of the salinity gradient which is chiefly controlled by changes in freshwater inputs (Feyrer et al. 2015). Density gradients generally create a lens of low salinity water floating over denser saltier waters. This allows waters near the mouths of the estuaries to be subjected to strong tidal action, delivering ocean-sourced water with higher salinities at depth, regardless of interannual variability in freshwater input. For example, locations near the mouth (within ~20 km) of SFB still maintain salinities >20 ppt near the estuary floor during extreme freshwater inflow (Cloern et al. 2017). Thus, the estuary floor communities near bay mouths may be somewhat buffered from periodic or even persistent freshwater intrusions.

Importantly, SFB prey resources may be less variable on an annual basis since they track a longer-term average of offshore conditions. Estuarine seabird prey, including English sole *Parophrys vetulus*, Pacific staghorn sculpin *Leptocottus armatus*, plainfin midshipman *Porichthys notatus* and blacktail bay shrimp *Crangon nigricauda*, complete their life cycles using both SFB and the nearshore ocean (Raimonet & Cloern 2017). Favorable ocean conditions (upwelling) benefit these species offshore, but positive and negative population effects are not immediately manifested and lag for 3 to 5 yr within the San Francisco Estuary (Raimonet & Cloern 2017). Further, since the estuarine response integrates offshore conditions over several years, amplitudes will be dampened, suggesting a more consistent interannual prey base available to seabird predators. Of course, with long-term poor ocean conditions, these estuarine resources may decline, but the interannual fluctuations should still be tempered. While inshore environments may offer a more stable prey base for seabirds, offshore environments provide prey species richness, which is important during years of variable conditions when prey-switching is critical for survival (Thayer & Sydeman 2007).

Within this broad pattern of oceanographic forcing driving annual reproductive success, seabird colonies closer to the mainland and within estuaries have shown higher reproductive success than their offshore counterparts, regardless of oceanographic conditions. For example, herring gull *Larus argentatus* (Hunt 1972), common murre *Uria aalge* (Davoren & Montevecchi 2003), and common tern *Sterna hirundo* (Hall & Kress 2004) colonies in the Gulf Stream Current exhibit higher average productivity nearshore. Reproductive success between colonies may be influenced by foraging distances, which tend to be lower nearshore and higher offshore (Hall & Kress 2004). Longer foraging distances result in lower prey delivery rates and increased exposure time for eggs and chicks to predators (Davoren & Montevecchi 2003, Hall & Kress 2004).

The pigeon guillemot *Cepphus columba* is a widely distributed Alcid, ranging from the Kuril Islands in Russia to north of the Bering Strait, and through the Aleutian Chain to western Alaska and down the Pacific Coast to the Point Conception area in Southern California (Ewins 2021). The global population of pigeon guillemots is approximately 470 000 individuals (del Hoyo et al. 1996) and they are categorized as a species of Least Concern on the IUCN Red List (BirdLife International 2021). Although pigeon guillemot populations are stable across their range

(BirdLife International 2021), disturbance, predation, pollution events, and fishing practices may threaten populations at a local level (Ewins 2021).

Pigeon guillemots nest in rock cavities, burrows along cliffs, or human-made structures such as buildings, piers, and artificial nest boxes (Drent 1965). While the variability in the timing of breeding is low among pigeon guillemot populations, the egg-laying stage can be protracted, skewing the mean date when eggs are laid (Ainley & Boekelheide 1990). Pigeon guillemots lay 1 or 2 eggs, with 2 egg clutches more common, especially in productive years (Ainley & Boekelheide 1990). If nests fail early in incubation, pigeon guillemots may lay a second clutch. Born semi-precocial, chicks hatch 1 to 2 d apart (Drent 1965, Ainley & Boekelheide 1990). Both parents participate in incubation, brooding, and food provisioning of chicks. Fledging occurs between 29 and 43 d (Drent 1965, Ainley & Boekelheide 1990, Vermeer et al. 1993) and chicks are independent after leaving the nest site.

Pigeon guillemots are benthic pursuit-diving foragers in the neritic zone, feeding on fish and invertebrates (Drent 1965, Ainley & Boekelheide 1990, Vermeer et al. 1993, Litzow et al. 1998, Warzybok et al. 2014). Diet appears to be somewhat opportunistic and flexible, with the constraint that they generally take most prey near or at the estuary or sea floor; schooling fishes in the water column are also taken in some areas (Ainley & Boekelheide 1990, Litzow et al. 2002). Sculpin (Cottidae) and blennies were the main prey items delivered to chicks on Mandarte Island, British Columbia (Drent 1965), while gunnel (Pholidae) and prickleback *Lumpenus* spp. were main prey items delivered to chicks on Haida Gwaii, British Columbia (Vermeer et al. 1993). There is generally an absence or low abundance of crustaceans fed to pigeon guillemot chicks (Drent 1965, Ainley & Boekelheide 1990); however, hermit crabs *Pagurus* spp. made up a significant proportion of pigeon guillemot diets in Kachemak Bay, Alaska colonies in 1997 (Litzow et al. 1998). On Southeast Farallon Island (SEFI), juvenile rockfish *Sebastes* spp. have dominated the pigeon guillemot chick diets since 1972, with sculpin substituted in years of low rockfish abundance (Ainley & Boekelheide 1990, Sydeman et al. 2001, Warzybok et al. 2014).

As shallow divers foraging within 7 km of colonies (Golet et al. 2000, Ewins 2021), shorter foraging trips allow pigeon guillemots to deliver prey at higher rates required to provision 2-chick broods (Emms & Verbeek 1991). Furthermore, as single-prey loaders, pigeon guillemots may be constrained to a foraging

range near the colony (McLeay et al. 2009a,b), and shorter foraging trips compensate for the decrease in food provisioning from only carrying 1 prey at a time to chicks (Gaglio et al. 2018). This foraging constraint and the need to provision multiple chicks for up to 29–43 d until fledging increases pigeon guillemot sensitivity to prey variability (McLeay et al. 2009b).

Oceanic conditions affecting food availability for seabirds leading to periods of extraordinary productivity or complete breeding failure in populations are well documented on SEFI, the latter having occurred in pigeon guillemot populations on SEFI in 1983, and to a lesser extent in 1978 and 1998 (Ainley & Boekelheide 1990, Warzybok et al. 2014). A strong ENSO event, warming the surface layers in the eastern and central equatorial Pacific Ocean due to weakening trade winds, occurred in 2014–2016; peaking in November 2015 and concluding in June 2016 (Rupic et al. 2018). This ENSO was similar to strong events in 1982–1983 and 1997–1998, but its physical forcings made it the strongest event on record (Rupic et al. 2018). A highly anomalous warm ocean state in 2015 (designated as a ‘marine heatwave’), together with the 2014–2016 ENSO, contributed to negative impacts on marine productivity and upper trophic level predators (Jacox et al. 2016, 2019) that continued into 2017 and 2018 (Thompson et al. 2018).

Here, we expand the comparisons of reproduction in pigeon guillemots in more and less variable habitats to the California Current System (SEFI) and the adjacent San Francisco Bay (Alcatraz), by investigating whether the spatially and temporally variable influences of ocean and estuarine environments, and their subsequent effects on prey availability, are differentially related to the reproductive success of pigeon guillemots at the SEFI (oceanic) and Alcatraz (estuarine) colonies. We collected pigeon guillemot chick diet and reproductive success data from 2015 to 2017 at a colony at Alcatraz Island in SFB and SEFI, 48 km to the west at the edge of the continental shelf. Based on the temporal dampening of oceanographic influences on seabird prey within SFB (Cloern et al. 2017), we predicted that the SFB pigeon guillemot colony would have (1) less interannual variation in chick diet and reproductive success (measured via fledging success), and (2) higher overall reproductive success. To understand the reproductive and environmental data for the study period in the context of longer-term patterns, we also analyzed the long-term (1988 to 2018) relationship between ocean conditions and pigeon guillemot reproduction at SEFI.

2. MATERIALS AND METHODS

2.1. Study areas

Alcatraz Island (37.8267° N, 122.4233° W) is in central SFB, approximately 2 km from the San Francisco mainland (Fig. 1). The island is 8.9 ha and supports 9 species of seabirds, including the largest nesting colony of pigeon guillemots in SFB with 50 breeding pairs in 2016 (Seher 2016). Alcatraz is a US National Park site in an urban estuary, and experiences nearby marine traffic, aircraft overflights, and over 1.4 million annual visitors (National Park Service 2014) (Fig. 1). Seasonally closed areas on Alcatraz are designed to protect breeding birds from island-based disturbances, but off-island activities such as marine vessels, aircraft, and, more recently, unmanned aerial systems (drones) may have negative impacts (Saenz et al. 2006). A recommended 100 m buffer zone around the island (through placement of buoys and outreach education) reduces proximity of near-shore vessels by an unknown extent. SFB, with water depths of approximately 10 to 20 m, has 52 potential benthic habitat types mapped, a higher diversity than in the offshore areas (Greene et al. 2013). Late spring and summer bay surface temperatures are influenced by ocean waters from tidal action, and average 12 to 14°C (<https://tidesandcurrents.noaa.gov/>). The pigeon guillemot population on Alcatraz is poorly studied and while some breeding population estimates are available, breeding phenology, reproductive success, impacts from predation, and food habits are largely unknown for this estuarine population.

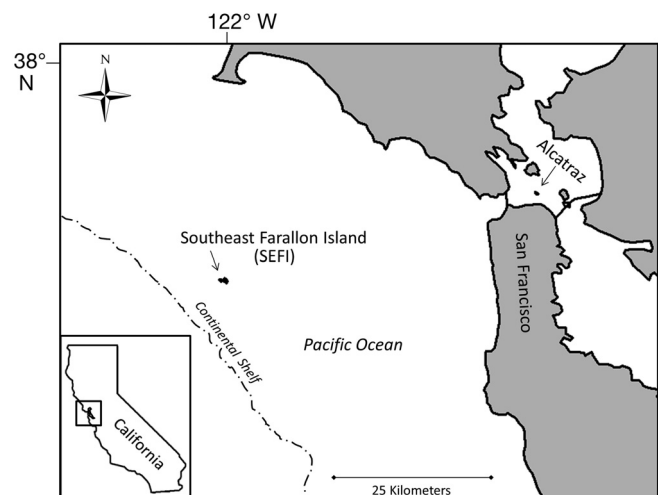


Fig. 1. Alcatraz Island and Southeast Farallon Island (SEFI), San Francisco County, California. SEFI is at the edge of the shelf-break within the California Current System and Alcatraz is inside San Francisco Bay

SEFI is located in the Northeast Pacific Ocean (37.7249° N, 123.0303° W), approximately 48 km west of San Francisco at the edge of the continental shelf (Fig. 1). SEFI is part of the Farallon Islands National Wildlife Refuge, managed by the US Fish and Wildlife Service (USFWS). It also sits within the Greater Farallones National Marine Sanctuary and is surrounded by a no-take State Marine Reserve and a Special Closure Area that prohibits vessels within 100 m of the island during the breeding season (Mach et al. 2017). The 38.8 ha island is minimally developed and closed to public access. SEFI April to June sea surface temperatures over the past several decades generally range from approximately 10.5 to 13.5°C, with extremes from approximately 9.5 to 15.2°C, and with generally strong, upwelling favorable winds from the NW during that time (Bakun 1996). SEFI is at the edge of the continental shelf (on the western edge), with surrounding depths near the islands rapidly descending to 100–150 m towards the east, and down to 3500–4000 m to the west off the shelf break. SEFI is surrounded by the nutrient-rich and productive waters of the California Current, supporting the largest US colony of seabirds south of Alaska (USFWS 2005). Pigeon guillemot monitoring on SEFI began in 1971 and the breeding ecology is well understood (Johns & Warzybok 2018). Prey availability can be high, but temporally variable depending on environmental conditions (Thayer & Sydeman 2007). The pigeon guillemot breeding population on SEFI varied between approximately 1000 and 1500 breeding pairs during the study period (Warzybok et al. 2018).

While oceanographic variability is a dominant driver of prey availability (Sydeman et al. 2014), improved fisheries management actions since around 2001 have had a positive impact on many seabird prey species (Bellquist & Semmens 2016). Importantly for pigeon guillemots, rockfish and flatfish populations are showing an increase in larger fish (Bellquist & Semmens 2016). There is no significant recreational or commercial take of sculpin, but bay shrimp is commercially harvested in SFB (Leet et al. 2001).

2.2. Data collection

Nest monitoring began prior to egg laying between 27 April and 5 May during the study period (2015–2017) and monitoring protocols were similar on both Alcatraz and SEFI, with sites checked every 5 d to record phenology and breeding performance. To minimize disturbance, site checks occurred in the afternoons when adults were less likely to be pres-

ent. If adults were present, nest sites were not disturbed, and nest contents went unrecorded. On SEFI, eggs were marked, and chicks were weighed, measured, and banded. On Alcatraz, only visual inspections occurred, and no eggs or chicks were handled. Sheer inaccessible cliffs on the west side of Alcatraz severely limited the number of nest sites monitored (14 to 16 nest sites), unlike on SEFI (78 to 86 nest sites) where sites are largely accessible to researchers.

In addition to site checks, we installed video surveillance systems on Alcatraz on 11 active sites (with eggs or chicks) in 2015, 15 active sites in 2016, and 10 sites in 2017 (no sites on SEFI were under video surveillance) to record phenology, reproduction, diet, and potential predation. Systems included bullet-shaped (Day Night Mini Lipstick camera with invisible 950 nm IR LED, 3.6 mm lens; EZ Spy Cam) and dome shaped (Outdoor Indoor Day Night 700TVL camera with IR LED, 3.6 mm lens; Zmodo Technology) cameras connected to digital video recorder (DVR) systems using either BNC or Cat5e power cables. DVR systems included 4 Zmodo 8CH HDMI 960H (Zmodo Technology) and 1 AV Tech 4CH H.264 (AV Tech) with WD Green 2 TB Desktop Hard Drives (3.5 inch, SATA III, 64 MB Cache) installed for recording. When feasible, installation of cameras occurred before birds visited nest sites to avoid disturbance, and equipment remained in the field until all chicks fledged. The cameras used infrared lights and sensors inside the dark interior of cavities and nest boxes, thus producing black and white images. Most DVRs were on island-based direct power, with some remote areas requiring batteries. We set DVRs to record 24 h d⁻¹ at 15 frames s⁻¹. Systems were checked every 5 d to clean camera lenses and ensure recording. Following the monitoring protocol used on SEFI (Johns & Warzybok 2018), we considered nest sites successful if at least 1 chick fledged after 35 d and was fully feathered.

For diet composition on Alcatraz, we used recorded video from nest cameras. We recorded each visible prey delivery that occurred during daylight hours when adults were most active from the date chicks hatched to the date chicks fledged for each nest site. Prey were identified to the lowest taxonomic level possible and categorized as unknown if items were unidentifiable due to poor image quality, immediate ingestion, small size, or lack of identifiable features. In 2017, 2 hard drives failed, resulting in a small sample size (n = 2 nest sites). Diet data collection methods differed on SEFI, where prey deliveries were observed in the field between 07:00 and 11:00 h at 2 rotating sites, every 3 d. Observations were made by

a 3-person team, with 2 observers using binoculars or spotting scopes to identify prey delivered to nest sites. The configuration of nesting cavities on Alcatraz allowed most pigeon guillemots to deliver prey undetected by video surveillance, therefore this study does not address delivery or provisioning rates.

2.3. Environmental data

Three *a priori* oceanographic or estuarine indices were selected to describe ocean conditions and variability: Biologically Effective Upwelling Transport Index (BEUTI), Multivariate Ocean Climate Index (MOCI), and San Francisco Bay outflow. The mean April to June BEUTI index at 38° N (Jacox et al. 2018) was used to represent annual variation in upwelling and nitrate conditions at SEFI. The MOCI used the annual spring values that also represent April to June each year (García-Reyes & Sydeman 2017). The MOCI integrates several oceanographic parameters and generally predicts population dynamics and diets of many marine organisms in the California Current, including pigeon guillemots (Sydeman et al. 2014, García-Reyes & Sydeman 2017). San Francisco Bay outflow was defined as the average rainfall of watersheds draining to SFB each water year (October to September) (Cloern & Jassby 2012). We did not investigate ENSO, PDO, NPGO, and other available indices (1) to avoid spurious correlations and (2) because the BEUTI and MOCI are mechanistically and statistically linked, and therefore correlated to most other local and basin-wide ocean indices (Jacox et al. 2018). Specifically, while the NPGO affects ocean conditions as well as prey composition and abundance in SFB (Raimonet & Cloern 2017), it is closely related to the BEUTI, with positive phases of the NPGO associated with increased upwelling (Jacox et al. 2018).

2.4. Statistical analyses

We investigated reproductive success (probability of fledging at least 1 chick after 35 d, fully feathered) of each colony using binomial generalized linear models (GLM) to explore *a priori* models composed of combinations of year, colony, BEUTI, MOCI, and SFB outflow. While pigeon guillemots may fledge up to 2 chicks when environmental conditions are favorable, only 7 nests (4 on SEFI and 3 on Alcatraz) fledged more than 1 chick during the study period (see Table 1). Therefore, the number of fledges was

not analyzed. We ranked breeding success models using the corrected Akaike's information criterion for small sample sizes (AIC_c) (Burnham & Anderson 2002) to select the most parsimonious models, and investigated residuals for heteroscedasticity and overdispersion. Exploratory analyses adding nest type (natural cavity vs. artificial) as a covariate increased AIC_c values (>2 units and $p > 0.8$) of the best fitting models and were not further investigated. To avoid overfitting and confounding variables, BEUTI and MOCI were not used in the same candidate models, since they have some common and correlated components (e.g. upwelling indices). Random effects (hierarchical models) using specific nest sites as a random effect were explored, but generally resulted in non-identifiable matrices and subsequent lack of error estimates due to lack of repeated data at many nests. Random effects (GLMM) models with site (SEFI or Alcatraz) as a random effect to control for differences in sample sizes were also run on the same set of candidate models. In addition, we graphically present the long-term (1988–2018) relationship between BEUTI and pigeon guillemot reproduction at SEFI.

To assess any potential bias due to the longer chick prey observation period at Alcatraz, we compared the proportional composition of 5 species groupings (flatfish, sculpin, shrimp, goby, and other) between morning (07:00–11:00 h) and afternoon (11:01–21:00 h) samples during 2016 and 2017. Chick diet composition (frequency of prey item groups) at each nest for each year and site was analyzed using non-metric multidimensional scaling (MDS) (Oksanen et al. 2020) to investigate community dissimilarities related to (1) nest success and (2) colony, year, BEUTI, MOCI, and SFB outflow for both SEFI and Alcatraz. We then implemented a permutational multivariate analysis of variance in the vegan package (Oksanen et al. 2020) to test for differences in chick diet composition between these covariates. Competing models were ranked by AIC_c . All analyses were done in R version 4.1.1 (R Core Team 2021).

3. RESULTS

3.1. Reproductive success

Between 14 and 16 active sites containing eggs and chicks were monitored on Alcatraz each year. The number of active sites with 2 eggs increased from 57% in 2015 to 94 and 86% in 2016 and 2017, respectively (Table 1). The number of active sites that fledged at least 1 chick increased from 71% in 2015

Table 1. Clutch size and number of fledged chicks from active sites on Alcatraz and SEFI from 2015 through 2017

	Total sites w/eggs	Clutch size		Fledged chicks	
		One egg	Two eggs	One chick	Two chicks
Alcatraz					
2015	14	6	8	10	0
2016	16	1	15	11	1
2017	14	2	12	9	2
SEFI					
2015	83	12	71	49	2
2016	86	18	68	24	1
2017	78	35	43	44	1

to 75 % in 2016 and to 79 % in 2017 (Table 1). We only documented 1 re-lay attempt on Alcatraz during the 3 yr study. Brood reduction (number of sites fledging just 1 chick divided by number of sites where 2 chicks hatched) was high in all 3 years on Alcatraz, with 86 % brood reduction in 2015, 67 % in 2016, and 78 % in 2017 (Table 2). In all 2-chick sites monitored using video cameras, beta chicks died from apparent starvation, not siblicide.

Between 78 and 86 sites were active at SEFI during the study period. The number of sites with 2 eggs decreased from 86 % in 2015 to 79 % in 2016 and 55 % in 2017 (Table 1) and those that fledged at least 1 chick decreased from 61 % in 2015 to 29 % in 2016, but increased to 58 % in 2017 (Table 1). There were 2 re-lay attempts in 2015, 4 in 2016, and none in 2017. Brood reduction was also high at SEFI with 81 % in 2015, 31 % in 2016 and 79 % in 2017 (Table 2). Although brood reduction decreased in 2016, the overall failure rate was high at 67 %.

Within the 3 yr study period, fledging success was best explained by the interaction between BEUTI and colony (0.49 ± 0.26 SE, $z = 1.86$) with generally stable fledging on Alcatraz over the study period, while SEFI reproductive success increased with in-

Table 2. Brood reduction from active sites on Alcatraz and SEFI from 2015 through 2017

	Clutch size	Brood size	Fledged chicks
	Two eggs	Two chicks	One chick
Alcatraz			
2015	8	7	6
2016	15	9	6
2017	12	9	7
SEFI			
2015	71	53	43
2016	68	51	16
2017	43	28	22

creasing BEUTI (Table 3, Fig. 2A). Models that included SFB outflow or MOCI had an increase in ΔAIC_c score of at least 3.5 points but both were positively associated with breeding success on SEFI, presumably because all 3 (BEUTI, MOCI, and SFB outflow) indices are associated.

The 1988–2018 time series showed spring BEUTI and annual SEFI pigeon guillemot productivity to be highly variable. Spring BEUTI and SEFI pigeon guillemot productivity were positively related (linear model: $\beta_1 = 0.04 \pm 0.01$ SE, $t = 2.9$, $p < 0.01$; residuals well distributed) from 1988–2018 and the productivity during 2015 and 2017 were near the long term mean of 0.74 (range 0.05–1.45) fledges per nest, while 2016 was 1 of the 4 lowest productivity years (1990, 1998, 2006; Johns & Warzybok 2018). The April to June BEUTI was at a low point in 2016 (Fig. 2B), concurrent with the largest asymmetry in productivity between Alcatraz and SEFI. Random-effects (GLMM) models with site (SEFI or Alcatraz) as a random effect were not used since some models had singularity problems (within group variances close to zero). Nevertheless, they reported essentially identical model results and model rankings to standard fixed-effects GLMs.

3.2. Chick diet

On Alcatraz, an increase in artificial nest box use by pigeon guillemots and improved video camera placement increased the number of nest sites ana-

Table 3. ΔAIC_c and Akaike weights (ω) of negative binomial GLM models explaining reproductive success (≥ 1 fledge) at SEFI and Alcatraz from 2015–2017. Out: annual SFB outflow; Site: Alcatraz or SEFI; K: number of parameters

Model	K	ΔAIC_c	ω	r^2
BEUTI \times Site	4	0.0	0.56	0.13
BEUTI + Site	3	1.5	0.26	
Out + BEUTI + Site	4	3.5	0.10	
Out:Site + BEUTI:Site	5	4.7	0.05	
Out:Site + MOCI:Site	5	4.8	0.05	
MOCI \times Site	4	13.4	0	
MOCI + Site	3	13.7	0	
BEUTI	2	15.6	0	
Site	2	20.3	0	
Year \times Site	3	22.0	0	
Out + Site	3	22.3	0	
Year + Site	4	23.5	0	
Out \times Site	4	23.9	0	
MOCI	2	27.1	0	
Year	2	34.7	0	
Out	2	34.9	0	

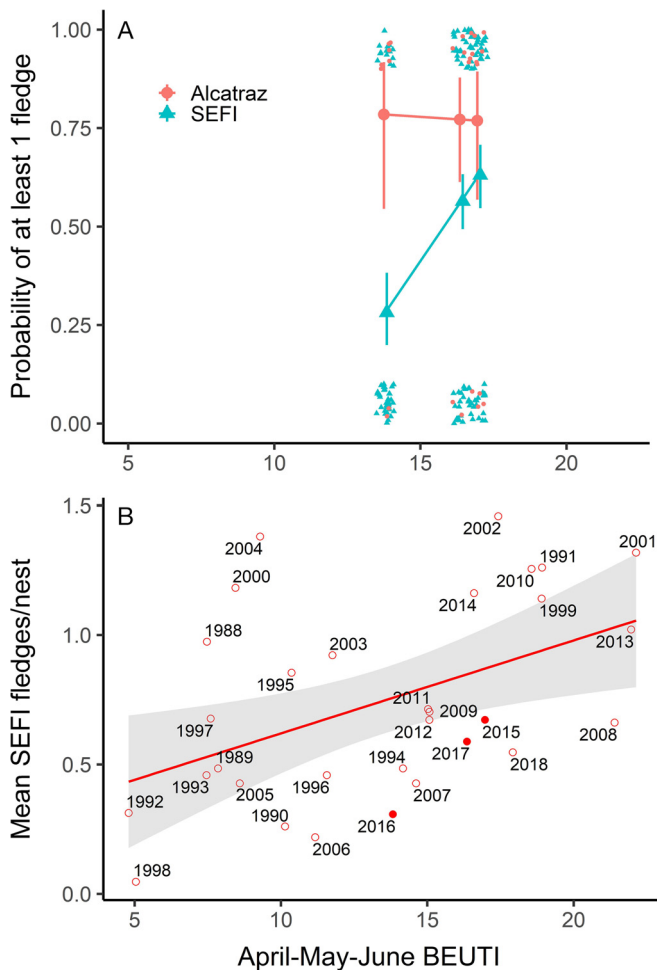


Fig. 2. (A) Logistic GLM relationship between the April to June BEUTI and probability of a nest producing fledges at SEFI and Alcatraz. Points (jittered) represent individual successful (1) and unsuccessful (0) nests each year and points with 95 % errors represent model estimates. (B) Relationship between the April to June BEUTI and reproductive success for SEFI from 1988–2018 ($\beta_1 = 0.04 \pm 0.01$ SE, $t = 2.9$, $p < 0.01$). (Red line) Linear fit with 95 % CIs (gray). Filled circles are from this study. SEFI fledge data from Johns & Warzybok (2018). Note different but correlated measures of reproductive success between plots

lyzed from 7 in 2015 to 11 in 2016, totaling 2345 individual prey items for both years. In 2017, most of the video footage was lost after the nesting season due to failed hard drives, and therefore only 313 prey items from 2 nest sites were identified. On SEFI, 128 nest sites were analyzed in 2015, 74 nest sites in 2016, and 102 nest sites in 2017, totaling 4866 individual prey items for all years. Over the 3 years, 13 different prey types were identified on Alcatraz and 16 prey types at SEFI. On Alcatraz, sculpin, flatfish, and shrimp were the main prey items delivered to chicks, with the dominant prey item shifting from flatfish (41 %) in

2015 to sculpin in 2016 (58 %) and 2017 (69 %) (Fig. 3). Pigeon guillemot diets on SEFI were dominated by juvenile rockfish, sculpin, and flatfish, with rockfish being the main prey item in 2015 and 2016 (49 %) and sculpin (41 %) in 2017 (Fig. 3). Although brown rockfish *Sebastes auriculatus* are found in SFB, only 4 rockfish deliveries were recorded on Alcatraz. Despite a low abundance of crustaceans found in chick diets in previous studies (Drent 1965, Ainley & Boekelheide 1990, Vermeer et al. 1993), shrimp were an important food source and the third most frequent prey item in Alcatraz diets. The proportional composition of 5 species groupings (flatfish, sculpin, shrimp, goby, and other) were delivered in the same proportions for both time periods (07:00–11:00 and 11:01–21:00 h) for all data summed in 2016 and 2017, varying by at most 0.02 for species by time (not shown).

Successful nests on Alcatraz and SEFI had a different diet composition to unsuccessful nests ($p < 0.001$, $df = 183$); however, this difference explained only 19 % of the overall variation when also considering site differences (Fig. 4A). Nonetheless, SEFI nests within and between years that were delivered a more diverse diet poorer in sculpin and rockfish were more likely to fledge chicks, and this weak pattern was consistent within each year from 2015–2017 (Fig. 4A). There were only 3 unsuccessful nests on Alcatraz, so we do not interpret fledge-diet differences at that site. Models including additive and interaction effects of the environmental covariates BEUTI, colony, and year explained the most variation in chick diet ($\Sigma\omega = 0.93$; Table 4). These top models were approximately 3 AIC_c units better than models containing other covariates. As SFB outflow increased, estuarine species such as flatfish, goby, shrimp, and crab were more common in chick diets, and increased BEUTI shifted diets to more pelagic species such as squid and anchovy (Fig. 4B). Overall, Alcatraz chicks relied more on flatfish and sculpin while SEFI chicks were additionally fed rockfish over the study period (Figs. 3 & 4).

4. DISCUSSION

Consistent with our predictions, we found that intra-specific reproductive success in pigeon guillemots was higher and exhibited lower variability between years at the estuarine colony with less temporal variation in prey availability than at SEFI. While buffered against the dramatic oceanographic effects of the 2015 marine heatwave and 2014–2016 ENSO,

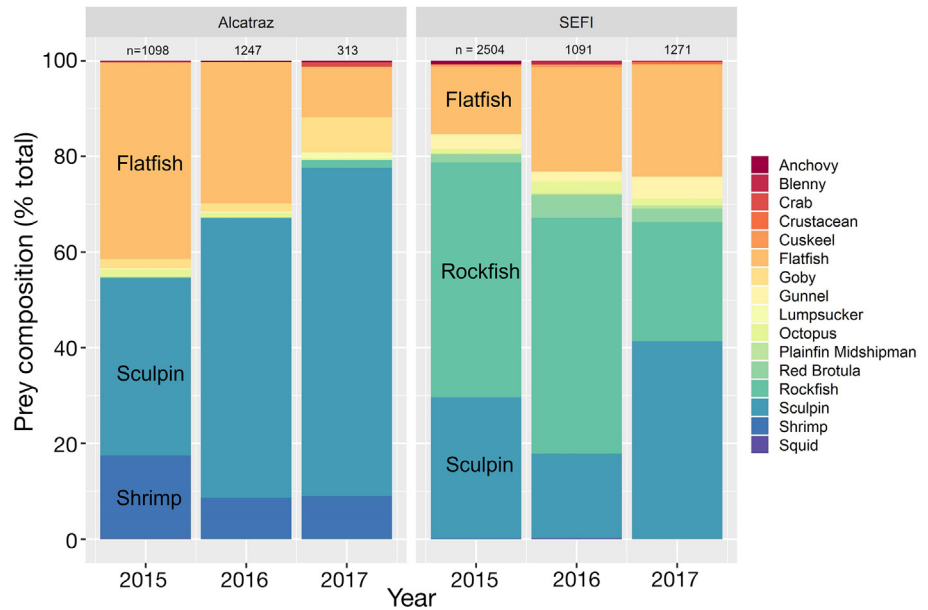


Fig. 3. Diet composition of prey delivered to pigeon guillemot chicks on Alcatraz and SEFI from 2015–2017. Sample size (n) above each bar. On Alcatraz, the number of nest sites with prey deliveries were 7 in 2015, 10 in 2016, and 2 in 2017. The number of nest sites with prey deliveries on SEFI were 123 in 2015, 65 in 2016, and 98 in 2017

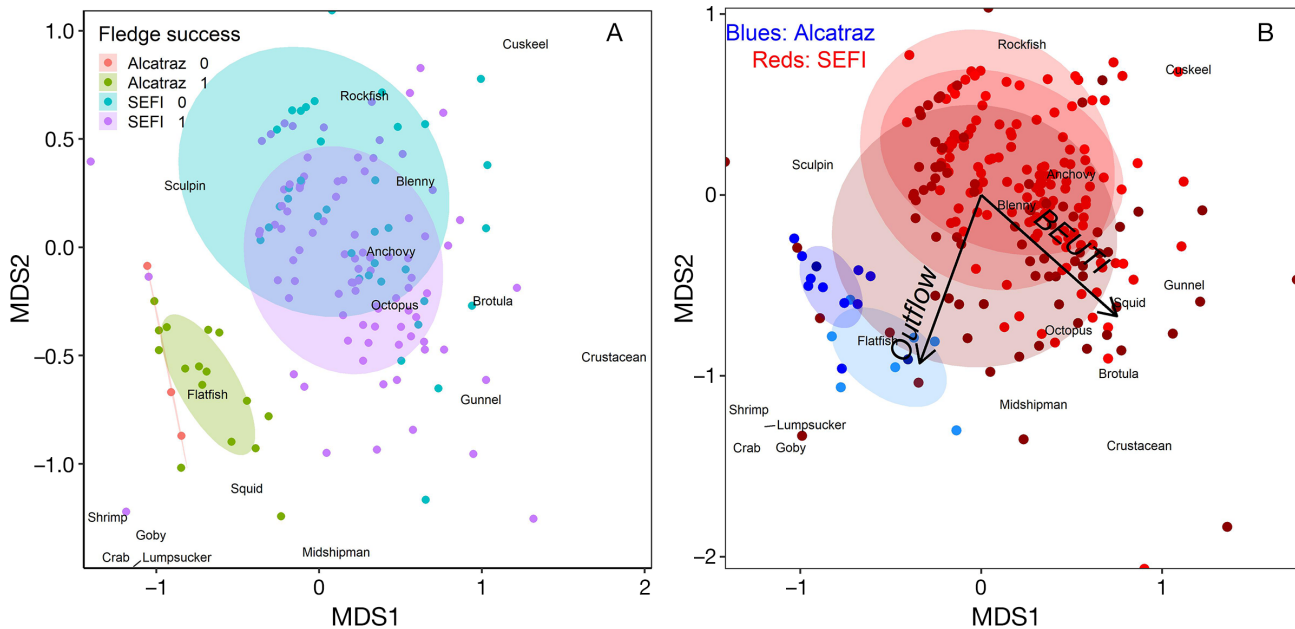


Fig. 4. Non-metric multidimensional scaling (MDS) plot of (A) chick diet composition for successful (1) and unsuccessful (0) nests on Alcatraz and SEFI and (B) estimated diet composition of prey delivered to pigeon guillemot chicks/nests on SEFI and Alcatraz from 2015–2017. Each point represents the composition of prey items ($n = 7542$) brought to a specific nest ($n = 423$) in a specific year and some points overlap. Ellipses (50% CIs) represent different years. There were only 2 nests with chick diet data on Alcatraz in 2017 and therefore no ellipse is shown. Prey species names represent location where predicted chick diet is predominantly that species or a mixture of nearby species. Arrows represent strength of relationship between SFB annual outflow or oceanic BEUTI and composition of prey items brought to the nest (Table 4). For example, during increased SFB outflow, species such as goby, shrimp, and flatfish were more commonly represented. Note that the MDS solutions (species locations) are different for each panel due to differing model data (i.e. A only has data from nests where fledge status was determined)

the stable estuarine environment may have provided other benefits such as shorter foraging distances and a more reliable prey source. Previous studies on other seabird species nesting in SFB that have also

shown higher breeding success may be viewed in the context of the relative resource stability of the bay. From 1989–1990, double-crested cormorants *Phalacrocorax auritus* nesting on the Richmond-San

Table 4. Permutational multivariate analysis of variance model rankings and Akaike weights (ω) for chick diet species composition. Out: annual SFB outflow; Site: SEFI or Alcatraz; p-values on top model were: Out < 0.01, Site < 0.01, BEUTI < 0.01, Out:Site < 0.07, Site:BEUTI < 0.06

Model	ΔAIC_c	ω
Out \times Site \times BEUTI	0.0	0.27
Out + Site	0.4	0.22
Out \times Site	1.0	0.16
Year + Site	1.0	0.16
Year \times Site	1.6	0.12
MOCI + Site	4.4	0.03
MOCI \times Site	5.0	0.02
BEUTI + Site	7.6	0.01
BEUTI \times Site	7.9	0.01
Site	8.6	0.00
Out \times BEUTI	21.7	0.00
Year	23.3	0.00
MOCI	25.9	0.00
BEUTI	28.9	0.00

Rafael Bridge had higher nesting success and fledged more chicks than those nesting on SEFI in 1989 and 1990 (Stenzel et al. 1995). Those nesting in SFB foraged closer to breeding colonies, which may have resulted in higher provisioning rates and therefore more successfully fledged chicks (Stenzel et al. 1995). On Alcatraz, despite higher rates of human activity and potential disturbance, productivity of Brandt's cormorants was higher than that of populations on SEFI between 1997 and 2002 (Saenz et al. 2006). The availability of benthic habitat in SFB, and the flexibility of cormorants in consuming both pelagic and benthic prey, may have influenced their higher breeding success on Alcatraz. This suggests prey availability is more stable in the estuary, and this area is perhaps even more amenable overall to successful reproduction, notwithstanding potential predation and disturbance pressures.

While it is not uncommon for pigeon guillemots to raise 2 chicks (Litzow & Piatt 2003), only 7 of 291 pairs fledged both chicks during this study. Brood reduction is often correlated with prey availability in *Cephus* (Cook et al. 2000). Specifically, Litzow et al. (2002) found higher frequency of brood reduction in chicks fed a low-lipid diet and during periods of low demersal fish abundance. In Kachemak Bay, Alaska, chicks fed high-lipid fish experienced only 3% brood reduction, while those provisioned with low-lipid demersal fish experienced 36% brood reduction, with brood reduction increasing over 300% during years of below average demersal abundance (Litzow et al. 2002). In contrast, brood reduction was high at SEFI and Alcatraz in all 3 years, suggesting the low-

lipid diets of both SEFI and Alcatraz chicks may have been insufficient for most pairs to fledge 2-chick broods.

During years when preferred prey species are absent or less available, alternative prey sources become important. Many seabirds, including pigeon guillemots, exhibit a precipitous decline in productivity when their primary prey resources are below a threshold of approximately one-third their historical maximum (Cury et al. 2011). Plasticity was evident on SEFI when pigeon guillemots switched prey in 2017, from a rockfish- to a sculpin-dominated diet, perhaps in response to a reduction in numbers or decline in nutritional value of rockfish. No evidence of prey switching occurred on Alcatraz, but chicks demonstrated plasticity in prey consumption.

Shrimp, delivered 1 at a time, were a primary food source on Alcatraz, comprising over 10% in 2015 and 2016, and 18% in 2017. While crustacean predation can be a response to low abundance of high-lipid schooling fish (Litzow et al. 1998), the shrimp in Alcatraz diets could suggest an abundant and easy prey source in SFB, allowing pigeon guillemots to maximize energy budgets. Video footage frequently recorded chicks rejecting shrimp and returning to begging behavior, but ultimately eating the shrimp after the adult left the site. This behavior of rejecting food deliveries was only observed with shrimp or fish too large for chicks to swallow.

Despite strong support for critical thresholds of primary prey species in relation to reproduction (Cury et al. 2011), along with the fact that chick diets had similar rockfish frequencies in 2015 and 2016, pigeon guillemot reproductive success on SEFI was low in 2016. Additional factors of prey quality and delivery rates may also be important. Thayer & Sydeman (2007) compared diet and breeding success of rhinoceros auklets *Cerorhinca monocerata* colonies on Año Nuevo and SEFI, and found that chick survival depended more on prey mass delivered to chicks than diet composition. Similarly, Golet et al. (2000) found prey size, rather than delivery rates, contributed to higher breeding success in pigeon guillemots that specialized when selecting prey. Finally, during the Pacific marine heatwave of 2015, von Biela et al. (2019) found a significant decline in nutritional value of Pacific sand lance, a key forage fish for seabirds during the breeding season. This disruption to the food web in the Gulf of Alaska, along with a subsequent increase in seabird breeding failures, may explain the lower reproductive success on SEFI. With similar prey composition in 2015 and 2016, the higher breeding failures may have been the result of

a change in prey condition during the marine heatwave.

With similar diet composition on SEFI in 2015–2016, a decrease in the nutritional value, size, or abundance of prey items may explain the lower reproductive success on SEFI in 2016. There was no evidence of prey switching in 2016 as a response to a possible lower prey abundance, suggesting alternative prey were in low abundance or unavailable (Warzybok et al. 2016). Unlike SEFI in 2015–2016, the dominant prey item delivered to chicks changed between years on Alcatraz, from flatfish to sculpin, with no apparent effect on fledging. Thus, while the long-term offshore relationships between critical prey species and productivity are well supported, they are not the same for estuaries (Cloern & Jassby 2012).

The effect of the 2015 marine heatwave and the 2014–2016 ENSO event appeared to affect reproductive success at SEFI more than Alcatraz. Elevated temperatures strongly impacted common murres, causing major declines in reproduction during this time at the Farallones with temperatures 2 to 3 SD above average (Piatt et al. 2020). Piatt et al. (2020) propose that an ‘ectothermic vise’ may impact seabird reproduction and survival during these warm-water events. This proceeds via ectothermic seabird competitors requiring additional calories to maintain higher metabolism in warmer waters, while forage fishes are less nutrient rich due to their own higher metabolism in warmer waters. Thus, there are fewer, and less nutritious prey available to seabirds, which is consistent with the pattern we show for SEFI pigeon guillemots and evidence that the Alcatraz birds were buffered from the marine heatwave. Similarly, Hodder & Graybill (1985) found no impact on reproductive success of pigeon guillemots nesting in Coos Bay, Oregon during the 1982–1983 ENSO, with benthic fish likely buffered from primary productivity loss. While there was some interannual variability in chick diet composition, these differences were only partially explained by oceanographic variables correlated with chick diet, and therefore variation in offshore pigeon guillemot productivity may be mostly related to the quantity, availability, and quality of the prey, rather than the specific species composition. The April to June BEUTI was at a low point in 2016, concurrent with the largest divergence in fledging success between Alcatraz and SEFI. Further, extending the long-term relationship between spring BEUTI and SEFI pigeon guillemot productivity from 1988–2018 is consistent with the 2015–2017 fledging success for Alcatraz. However, all 3 of the

years in this study were relatively poor reproductive years at SEFI (Fig. 2B) and additional data are needed before generalizing these patterns to higher productivity years. Ainley & Boekelheide (1990) found smaller clutch sizes during past ENSO events (which affect BEUTI), and suspected that the age of breeding birds or prey availability for breeding females may also influence clutch size. Similarly, Nevoux et al. (2010) found that while overall black-browed albatross breeding success was higher in more stable environments, much of this effect was due to less experienced breeders. The number of breeding pairs on Alcatraz increased in 2016 from 42 to 50 pairs. A similar increase occurred following the 1998 ENSO, where nest sites increased from 14 to 22 (Saenz et al. 2006). Ocean conditions may have decreased recruitment of first-time breeders at SEFI in favor of areas inshore with more stability, higher prey density, and smaller transit distances to bring prey to chicks.

5. CONCLUSIONS

Breeding productivity of pigeon guillemots at nearshore and estuarine seabird colonies, including Alcatraz Island in San Francisco Bay, generally had less annual variation and higher average reproductive success than an offshore colony, consistent with a more stable and predictable estuarine prey base (Davoren & Montevecchi 2003) buffered from the marine heatwave and ENSO event. Yet, this stability may come at the cost of higher potential disturbance and predation pressure. Certainly, the added benefits of high-productivity boom years from superabundant prey resources under favorable oceanographic conditions can also support long-term persistence and larger populations of most offshore colonies. The weak but significant connection of chick diet composition to pigeon guillemot productivity nonetheless indicate that additional data on prey quality and prey delivery rates, and/or a longer time series are needed to fully investigate these connections. With increasingly variable conditions in the California Current (Feyrer et al. 2015), the availability of alternative breeding sites inshore may become more important for the regional pigeon guillemot population. We also predict growing nearshore colonies may attract more predators, possibly counterbalancing some advantages in fecundity. Thus, a diversity of habitats available to seabirds is likely important for natural long-term population processes and population resiliency.

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