

SPATIAL PATTERNS IN NEARSHORE JUVENILE FISH ABUNDANCE THROUGHOUT THE CALIFORNIA NETWORK OF MARINE PROTECTED AREAS AS REVEALED BY SEABIRD FORAGING RATES

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ABSTRACT

The successful adaptive management of marine protected areas (MPAs) requires knowledge of spatial variability in the rates of juvenile fish recruitment to recovering fish populations. We used the foraging rates of two piscivorous seabirds (Brandt's cormorant and pelagic cormorant) to index juvenile fish abundance at 46 sites throughout California's MPA network. We used mixed effects negative binomial regression to develop models relating seabird foraging rates to coastal geography and annual upwelling strength and variability. The best models for both species included upwelling variability among years (i.e., persistent versus pulsed upwelling). The effects of upwelling variability differed depending on coastal geography. In the lees of headlands, foraging rates were highest and more stable with respect to upwelling variability. For all other coastal configurations, pulsed upwelling was associated with higher foraging rates. Thus, periods of relaxation in upwelling appear to be important for these sites. Our results suggest that coastal geography should be considered when establishing realistic expectations for the performance of individual MPAs.

INTRODUCTION

In 2012, the State of California finished implementing a network of 124 marine protected areas (MPAs) throughout state waters (Kirlin et al. 2013). One goal for resource managers is to adaptively manage the network in order to recover fish populations that have been depressed by intensive historic fishing throughout California (see Ainley et al. 2018 for an overview of California's fishing history and management actions taken to rebuild stocks). Successful adaptive management of the network will require establishing realistic expectations for the performance of individual MPAs as not all MPAs are equal in their potential for population recovery rates. In other words, managers need to be able to distinguish between an individual MPA that is underperforming versus one that needs more time. The network itself resides within the California Current System, an eastern boundary current where high interannual variability in wind-driven coastal upwelling leads to high

variability in primary productivity and the survival of early-life stages of many fish species (Ryckaczewski and Checkley 2007). As a result, the growth of nearshore fish populations within the CCS tends to be recruitment-limited (Morgan et al. 2011). Thus, variability in the strength of juvenile recruitment is an important determinant of recovery rates for fish populations protected within California MPAs.

The placement of individual MPAs along California's geographically complex coastline has direct implications for establishing expectations about variability in recruitment rates. The California coastline is dotted with headlands that create eddies in their lee during coastal upwelling events and influence the distribution of fish larvae at scales of 10–100 km (Sponaugle et al. 2002). Several studies over the past 25 years have demonstrated that these coastal headlands accumulate larvae and enhance year class recruitment to leeward habitats (e.g., Wing et al. 1998). Most of these studies have investigated individual headlands and have not looked at interactions between coastal geography and coastal upwelling by comparing multiple headlands throughout California.

Here, we investigate the role of coastal upwelling and coastal geography in determining spatiotemporal variability in community-level juvenile fish recruitment throughout California's MPA network and whether the effects of upwelling differ among sites with different coastal geographic characteristics. We define recruitment as the settlement of juvenile age classes into adult habitat. We target the community of fishes that have pelagic egg and larval stages that can be redistributed by ocean currents and that can settle as juveniles into a variety of nearshore habitats (e.g., kelp forest, sandy bottom, rocky reef) within one km of shore (e.g., many species of rockfishes, *Sebastes* sp., and sanddabs, *Citharichthys* sp.; see Robinette et al. 2018). We investigate juvenile fish abundance within one km of shore because this is the extent of our visual shore-based surveys. However, our results can be used to infer patterns of relative juvenile fish abundance within several km (but likely <10 km) of shore.

We used the foraging rates of two coastally breeding seabirds, Brandt's cormorant (*Phalacrocorax penicillatus*) and pelagic cormorant (*Phalacrocorax pelagicus*), to index

relative juvenile fish abundance at 46 sites throughout California's MPA network using data collected over nine years. While both species can take a variety of prey from nearshore habitats, studies have shown that relatively few species dominate the diets of each species (Ainley et al. 1981; Elliott et al. 2018). Pelagic cormorants feed heavily on post-settlement age juvenile fishes in mostly rocky habitats and, while Brandt's cormorants can prey heavily on schooling fishes in pelagic environments, they also take post-settlement age juvenile fishes from habitats associated with both rocky and soft bottom substrates. We use foraging behavior to identify when the cormorants are taking post-settlement age fishes in midwater and bottom habitats as those are the fishes we consider recruited into the nearshore habitats protected by MPAs. Both species are pursuit divers and can easily access all depths of the water column found within one km of shore. As such, they are good at sampling juvenile fish abundance throughout a variety of nearshore habitats.

Numerous studies conducted over the past four decades have shown that seabirds respond predictably to changes in prey abundance and can thus be used as reliable indicators of change in prey populations (see Cairns 1992; Hatch and Sanger 1992). Seabirds are highly visible and easily enumerated and many of the coastally breeding species (e.g., Brandt's and pelagic cormorants) prey heavily on juvenile age classes of multiple fish species. The use of seabirds to index temporal variability in juvenile fish abundance has been well established (e.g., Mills et al. 2007; Roth et al. 2007). More recently, seabirds have been used to investigate spatial variability in juvenile fish abundance on scales relevant to MPA management. Robinette et al. (2007) used measures of seabird diet, fish larval abundance, and coastal upwelling to compare juvenile sanddab recruitment in the lee of a coastal headland to that at an exposed site. Recruitment to the leeward site was overall greater and less variable among years than at the exposed site. Robinette et al. (2012) investigated foraging rates of four juvenile-fish-eating seabird species around the same headland over six years and found that all four species consistently foraged in the lee of the headland where juvenile fish recruitment was presumably higher. In addition, Robinette et al. (2018) compared seabird foraging rates to independent measures of juvenile fish abundance in kelp forests at 11 sites within three distinct regions of the Southern California Bight. Seabird and fish distributions were similar at the regional scale but less similar at the site-specific scale. At the site level, seabirds were sampling a broader array of habitats than the kelp forest fish surveys and thus providing an index of community-level juvenile fish abundance over multiple habitats within a site. Here, we use seabird foraging rates as a proxy for juvenile fish abundance in midwater and bottom habitats. While there are

many post-settlement factors (e.g., predation on juveniles) that dictate the recruitment of individuals into adult fish populations, understanding the conditions that lead to high juvenile fish abundance will allow MPA managers to better understand where fish recruitment is likely to occur in a given year.

Spatiotemporal variability in juvenile fish abundance is largely determined by survival at the early larval stage (Rothschild 2000). Wheeler et al. (2016) found that even subtle changes in larval condition can lead to orders-of-magnitude differences in year-class strength. Coastal upwelling plays a significant role in larval survival as it is a major source of variability in both primary productivity and the offshore distribution of larvae (Rykaczewski and Checkley 2007). The offshore advection of surface waters that drives coastal upwelling can also displace larvae from important nearshore settlement habitat. In fact, studies have shown that juvenile recruitment can be higher during periods of relaxation in upwelling when larvae are distributed more onshore (Wing et al. 1995a, 1995b; Ottman et al. 2018). However, results from other studies on the advection of larvae have been less convincing (e.g., Wilson et al. 2008) and some have shown no relationship between coastal upwelling and larval distribution (e.g., Kinlan and Gaines 2003; Morgan et al. 2009, 2018). These studies attribute the lack of clear relationships between upwelling and larval distribution to ontogenetic and species-specific differences in larval behavior and vertical distribution allowing larvae to take refuge from offshore surface currents. These differing responses of larvae to coastal upwelling make it challenging to understand the impacts of upwelling on fish recruitment at the community level and at spatial scales relevant to MPA management.

Despite the varying responses of different ages and species of larvae to coastal upwelling, multiple studies have consistently shown that eddies formed in the lee of headlands accumulate larvae and their planktonic prey, thereby increasing larval survival and juvenile recruitment to these habitats (Wing et al. 1998; Roughan et al. 2005; Mace and Morgan 2006a, 2006b; Morgan et al. 2011). This retention creates recruitment hot spots and appears to happen in the lee of both large headlands (e.g., Wing et al. 1998) and small headlands (e.g., Roughan et al. 2005; Mace and Morgan 2006a), though the role of headland size and shape in creating retention has not been thoroughly investigated. Understanding how coastal upwelling and coastal geography interact to impact larval survival and distribution will allow MPA managers to make basic predictions about the conditions under which individual MPAs are likely to experience high recruitment events. This, in turn, will allow managers to establish realistic expectations for the performance of individual MPAs.

Here, we ask 1) what is the role of coastal upwelling in determining annual juvenile fish abundance in nearshore habitats, 2) does the size and shape of a headland determine its impact on annual juvenile fish abundance, and 3) does the effect of coastal upwelling differ with respect to coastal geography? We test the hypotheses that 1) variability in upwelling (i.e., more periods of relaxation in upwelling) will have a greater impact on annual juvenile fish abundance than overall upwelling strength, 2) larger, pointier headlands will have a greater impact on annual juvenile fish abundance than smaller, broader headlands, and 3) the impacts of coastal upwelling on annual fish recruitment will vary among exposed, windward, and leeward stretches of coast. We test for both linear and curvilinear impacts of upwelling and headland characteristics. Additionally, in an effort to better understand the mechanisms for how upwelling impacts juvenile fish recruitment, we compared results using two different upwelling indices: 1) Coastal Upwelling Transport Index (CUTI) and 2) Biologically Effective Upwelling Transport Index (BEUTI). The CUTI estimates vertical transport and is a good measure of the potential for offshore transport during upwelling (Jacox et al. 2018). The BEUTI estimates vertical nitrate flux due to upwelling and is a good measure of the potential biological response (e.g., primary productivity) to upwelling (Jacox et al. 2018). Finally, we compare our foraging observations to upwelling during both the current year when juvenile fish have already settled into adult habitats and the year prior to our foraging observations when the fish are newly hatched larvae in order to understand when in the early fish life history stage upwelling is having the biggest impact on juvenile fish abundance.

METHODS

Indicator Species

We used the foraging rates of Brandt's and pelagic cormorants to index relative juvenile fish abundance at individual sites throughout the MPA network. Pelagic cormorants breed in small groups (often <100 individuals) usually on ledges of coastal cliffs and take mostly juvenile bottom fishes in rocky reef habitats, though they will also take bottom fishes from flat sand and mud habitats (Hobson 2013). In California, Ainley et al. (1981), found the dominant prey of pelagic cormorants to be sculpins (family Cottidae) and various species of nearshore rockfishes. Brandt's cormorants breed in large colonies (100s to 1,000s of individuals) usually on offshore rocks. The feeding niche of Brandt's cormorants is broader in both diet and foraging habitat than that of pelagic cormorants, taking approximately equal biomass of schooling fishes (e.g., anchovies and pre-

settlement rockfishes) and midwater and bottom fishes (e.g., post-settlement rockfishes and sanddabs; Ainley et al. 1981; Elliott et al. 2015). In our study, we distinguish between birds forming large flocks to forage on schooling fishes versus isolated dives by individual birds foraging on post-settlement juvenile fishes in midwater and bottom habitats (Thiebault et al. 2014) as we are interested only in the latter (see section on Seabird Foraging Surveys below). In central California, Elliott et al. (2015) found that Brandt's cormorants can switch dominant prey types between years, foraging heavily on either anchovies, rockfishes, or sanddabs in a given year. At the southern California islands, Ainley et al. (1981) found that anchovies were again the dominant schooling prey while rockfishes and blacksmith (*Chromis punctipinnis*) were the dominant midwater prey. Robinette (unpublished data) found that, in addition to anchovies and rockfishes, sanddabs and sculpins were the dominant bottom prey at a mainland southern California colony. Thus, while there is some overlap in the niches of Brandt's and pelagic cormorants, they are also sampling different components of the ecosystem. Our sampling approach therefore provides broad sampling coverage over multiple components of nearshore fish communities.

Survey Site Characteristics

We conducted seabird foraging surveys at 46 sites throughout the California MPA network (table 1, figs. 1 and 2). We divided the network into four bioregions to control for known latitudinal gradients in marine community composition. We used the geographic boundaries used by Blanchette et al. (2008) but included an additional break at Cape Mendocino as studies have shown this to be a biogeographic barrier (Sivasundar et al. 2010). However, we did not divide the Southern California Bight at Santa Monica bay as was done in Blanchette et al. (2008) due to a low representation of sites throughout the bight. Thus, our four bioregions are 1) North (north of Cape Mendocino), 2) North Central (between Cape Mendocino and Monterey Bay), 3) South Central (between Monterey Bay and Point Conception), and 4) South (south of Point Conception). The majority of sites were included in baseline monitoring programs for California's Marine Life Protection Act Initiative and were surveyed for two consecutive years (table 1). In addition, we surveyed six sites within South Central for seven to eight years (2007–14) as part of a long-term coastal seabird monitoring project. We controlled for differences among years surveyed in our statistical models.

We defined coastal geography around each site in three ways. First, we categorized each site as located along an exposed section of coast (exposed), within 30 km windward of a headland (windward), or within

TABLE 1
 Names, years surveyed, coastal geography categories, length of nearest headland, and coastal direction
 of the 46 sites surveyed throughout the four bioregions of coastal California. Site codes are used in Figures 1 and 2.
 Coastal direction values of 66° to 134° represent south-facing coastlines, values of 135° to 224° represent
 west-facing coastlines, and values of 225° to 277° represent north-facing coastlines.

Bioregion	Survey Site (site codes)	Survey Years	Coastal Geography	Headland Length (km)	Coastal Direction (Deg)
North					
	Pyramid Point (py)	2014–15	Windward	6.8	184
	Crescent City (cc)	2014–15	Exposed	6.8	160
	Patrick's Point (pp)	2014–15	Exposed	5.5	174
	Trinidad Bay (tb)	2014–15	Leeward	5.5	141
	South Cape Mendicino (sc)	2014–15	Exposed	3.0	169
	Devil's Gate (dg)	2014–15	Leeward	3.0	169
North Central					
	Kibesillah (ki)	2014–15	Exposed	0	173
	Ten Mile (tm)	2014–15	Exposed	0	173
	Point Cabrillo (ca)	2014–15	Exposed	0	162
	Mendocino Headlands (mh)	2014–15	Exposed	0	162
	Bodega SMCA (bc)	2010–11	Exposed	3.7	147
	Bodega SMR (br)	2010–11	Exposed	3.7	147
	McClure's Beach (mb)	2010–11	Windward	15.4	153
	Point Reyes (po)	2010–11	Leeward	15.4	96
	Drakes Bay (db)	2010–11	Leeward	15.4	110
	Miller Point (mi)	2010–11	Leeward	15.4	141
	Montara (mr)	2010–11	Exposed	5.0	151
	Pillar Point (pi)	2010–11	Exposed	5.0	151
	Pescadero (pe)	2010–11	Windward	6.7	186
South Central					
	La Cruz Rock (lc)	2011–12	Exposed	5.9	137
	Pt Piedras Blancas (pb)	2011–12	Exposed	5.9	178
	San Simeon (ss)	2011–12	Leeward	5.9	119
	Cayucos Point (cp)	2011–12	Leeward	6.7	87
	Spooner's Cove (sp)	2011–12	Windward	12.5	200
	PG&E Trail (pg)	2011–12	Exposed	12.5	143
	Fossil Point (fp)	2011–12	Leeward	12.5	104
	Dinosaur Caves (dc)	2011–12	Leeward	12.5	74
	Lion's Head (lh)	2007–12	Leeward	5.3	128
	Purisima Colony (pr)	2007–14	Leeward	3.0	150
	Cabrillo Beach (cb)	2007–14	Leeward	3.0	150
	Lompoc Landing (ll)	2009–14	Leeward	3.0	150
	Vantage Point (vp)	2007–14	Exposed	9.1	143
	Boathouse (bh)	2007–14	Exposed	9.1	96
	Sudden Ranch (su)	2007–14	Leeward	9.1	121
South					
	Northwest Point (nw)	2012–13	Windward	10.4	277
	Painted Cave (pc)	2012–13	Windward	10.4	277
	Scorpion (sc)	2012–13	Windward	10.4	232
	Scorpion SMR (sr)	2012–13	Windward	10.4	265
	South Beach (sb)	2012–13	Exposed	10.4	124
	Gull Island (gi)	2012–13	Exposed	10.4	66
	Point Vicente (pa)	2012–13	Exposed	17.9	159
	White Point (ps)	2012–13	Exposed	17.9	114
	North La Jolla (ln)	2012–13	Windward	6.2	267
	South La Jolla (ls)	2012–13	Exposed	6.2	143
	Sunset Cliffs (sn)	2012–13	Exposed	6.2	184
	Cabrillo Monument (cm)	2012–13	Exposed	6.2	161

30 km in the lee of a headland (leeward). We categorized sites that were on the tips (west-facing portion) of headlands as exposed. Second, we defined the coastal orientation of a site by measuring coastal direction which we defined as the direction (degrees) of a straight line drawn

parallel to the coast in the poleward direction. Coastal direction values ranged from 66° to 277° with smaller values (66° to 134°) representing south-facing coastlines, intermediate values (135° to 224°) representing west-facing coastlines, and larger values (225° to 277°) repre-

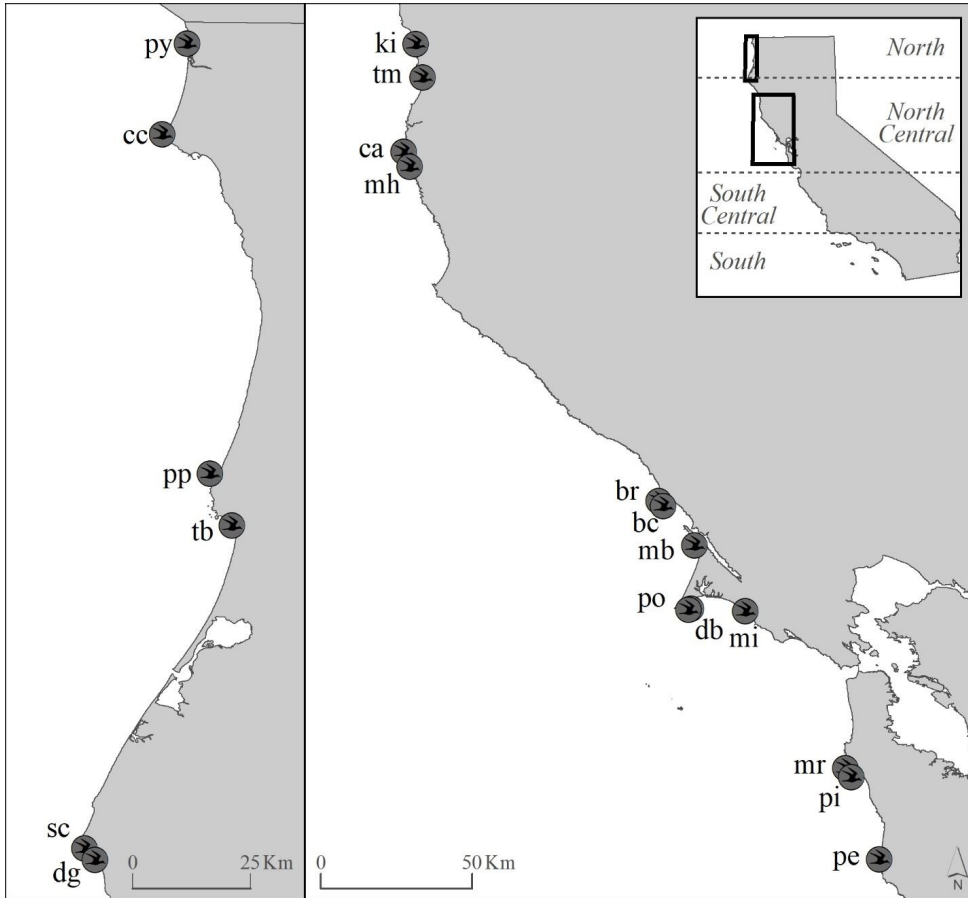


Figure 1. Locations of seabird foraging survey sites within the North and North Central bioregions of California. See Table 1 for site code definitions and years surveyed.

senting north-facing coastlines. Finally we defined the size and shape of the nearest headland to a given site. We used existing literature on nearshore larval retention (e.g., Mace and Morgan 2006a; Wing et al. 1995a) to define a headland as any coastline that projects into the ocean at least three km but less than 20 km and distinguish headlands from the two large capes along California's coast (Cape Mendocino and Point Conception) which project approximately 35–40 km into the ocean. Capes influence ocean currents on large scales and can create breaks in biogeography (Sivasundar et al. 2010). They can also create eddies but these tend to influence large areas and lead to latitudinal rather than nearshore retention (Sponaugle et al. 2002). Additionally, we treated Santa Cruz Island as a headland for the purposes of our analysis. For each headland, we measured headland size, headland length, and headland aspect ratio. We measured headland size as the distance the headland projects into ocean. If there was no headland within 30 km (e.g., at some exposed sites), then headland size was equal to zero. We calculated headland width as the linear along-shore distance from where a headland begins to project into the ocean to where it returns to the predominant

direction of the coast. We used aspect ratio (headland size divided by headland length) to define the overall shape of a headland, with larger values indicating a more abrupt or “pointy” change in coastline.

Finally, we measured a site's distance to the nearest headland in order to investigate whether proximity to a headland impacted fish recruitment rates. We measured this as the straight-line distance from the survey site to the nearest tip of the nearest headland. We recorded distances measured from sites windward of a headland as negative values and distances from sites leeward of a headland as positive values. We recorded distance as zero for sites on the west-facing portion of a headland. For island sites, we measured the distance from the site to the nearest western tip of the island. For sites farther than 30 km from a headland, we recorded a maximum distance of 30 km as these were considered exposed and likely not influenced by the headland.

Seabird Foraging Surveys

We conducted weekly seabird foraging surveys from April through July at each of the 46 sites during the years listed in Table 1. We conducted surveys during one

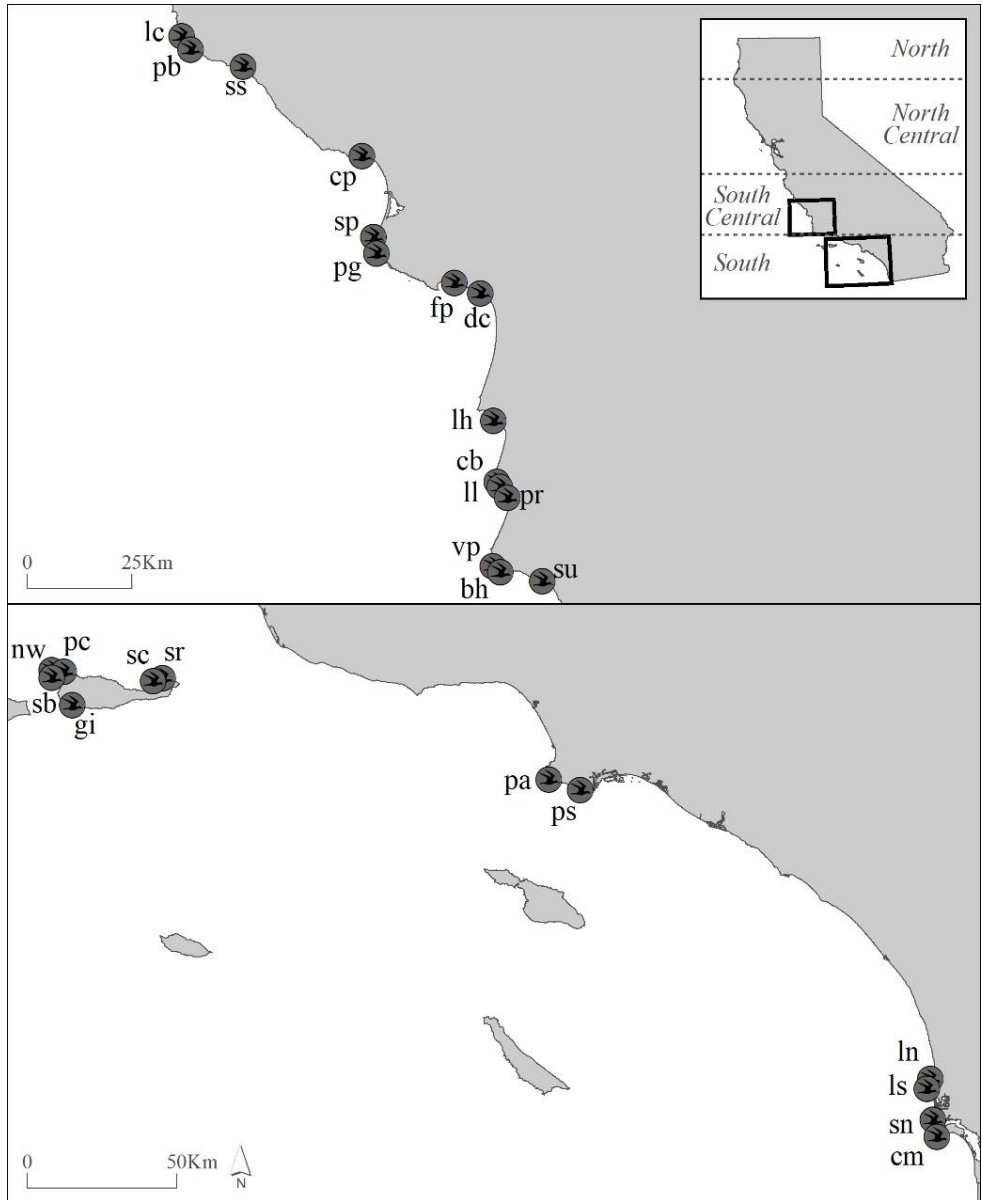


Figure 2. Locations of seabird foraging survey sites within the South Central and South bioregions of California. See Table 1 for site code definitions and years surveyed.

of the following time periods: 0600–0900, 0900–1200, 1200–1500, or 1500–1800, rotating sites among the four time periods per week to develop a complete 12-hour assessment of foraging activity. We made observations from a single observation point, using binoculars and a 20–60x spotting scope. We divided each three-hour period into 15-minute blocks. During each 15-minute block, we scanned all water within a one-kilometer radius of our observation point and recorded the numbers of actively diving individuals for all seabird species. We collected data on birds foraging in flocks separately from birds foraging independently in order to distinguish the general prey types (i.e., schooling and pre-settlement juvenile fishes versus post-settlement juvenile fishes)

being taken. We defined a foraging flock as an aggregation of five or more birds foraging on an aggregation of prey (e.g., a shoal of anchovies). We defined independent foragers as birds that were not aggregated and not diving for aggregated prey. Thus, there could be more than five individual foragers within our one km radius, but they were all foraging independent of one another. In this study, we use only data on independent foragers as that behavior indicates foraging on non-schooling juveniles that have settled into adult habitat. We recorded only birds that were observed actively diving as foraging. We calculated a foraging rate by averaging all 15-minute blocks over the three-hour survey to produce the mean number of diving birds per survey. Thus, our sample unit

is each three-hour survey, and our total sample size for all sites and years is 1,797 surveys. We did not pool data from multiple years for a given site. Rather, we treated site-year as a random effect in order to control for correlated responses among surveys within a site, within a year, and allow the models to assess interannual and spatial variability in juvenile fish abundance.

Data Analysis

We used mixed effects negative binomial regression to investigate how coastal geography and coastal upwelling contributed to annual variability in the foraging rates of Brandt's cormorants and pelagic cormorants, our proxies for juvenile fish abundance, using Stata 14 (StataCorp. 2015). We analyzed six variables describing coastal geography and four variables describing coastal upwelling to generate statistical models accounting for variability in foraging rates. Site-year was treated as a random effect.

In addition, we used bioregion, time of day, season, local breeding population size, and percent rocky bottom substrate to control for variation in foraging rates not related to coastal geography and/or upwelling. We did not include wind speed, wave height, or tide as control variables as we found that those variables did not significantly affect cormorant foraging rates (see Robinette et al. 2012). Categories for biogeography are defined above. Time of day is the three-hour period during which observations were made (integer ranging from 1 to 4) and season is the week during which observations were made (integer ranging from 14 to 35); we fit both as polynomials up to second order. Breeding population size is the number of birds for either Brandt's or pelagic cormorants breeding within 10 km of our foraging observation site. Both species typically forage within 10 km of their breeding sites (Kotzerka et al. 2011; Peck-Richardson et al. 2018). We used annual breeding population numbers recorded during ground-based surveys conducted as part of the same monitoring projects contributing the foraging data, ln-transformed. Percent rocky bottom substrate is the percentage of our foraging observation area (1 km radius from our observation site) that contained rocky bottom substrate. We obtained bottom substrate data from California Department of Fish and Game (ftp://ftp.dfg.ca.gov/R7_MR/HABITAT/) and calculated percent rocky bottom using ArcGIS 10.5.1.

Calculations of Indices Used in the Models We used geographic category, coastal direction, headland size, headland length, headland aspect ratio, and distance to headland as defined above for our coastal geography variables. For coastal upwelling, we calculated annual upwelling strength and variability across the settlement season (April through August) separately for the CUTI and BEUTI indices. We obtained monthly values for both indices from the M. Jacox website (<http://mjacox.com/upwelling-indices/>).

We calculated annual upwelling strength as the sum of monthly upwelling values across all five months and annual upwelling variability as the standard deviation in monthly values across all five months. We calculated upwelling strength and variability for the year during which observations were made (current year) to define oceanographic conditions when the seabirds were foraging and for the year prior to when observations were made (year-1) to define oceanographic conditions during the period when their prey were likely developing from larvae into juveniles and settling into nearshore habitats. We calculated values for all four coastal upwelling variables separately for each of the two upwelling indices. We tested linear and quadratic relationships for all non-categorical variables except coastal direction.

Mixed Effects Models For each seabird species, we created two separate base models—one using the CUTI values for coastal upwelling and the other using the BEUTI values. For each model, we used a backwards stepwise approach to select the best model describing variability in foraging rate. We loaded each model with all the variables and removed non-significant ($p > 0.05$) variables from model iterations, one at a time, to produce a model containing only significant variables ($p < 0.05$). The exception was that linear terms were included if the quadratic term was significant.

We then tested for interactions between coastal geographic category (windward, exposed, or leeward) and coastal upwelling variables to determine if the effect of these variables differed by coastal geographic category. We did this using only the BEUTI base models as initial model results for both indices were similar, and the BEUTI model was the superior predictive model. We used likelihood ratio tests (LRTs) to test for differences among models containing or not containing interactions; the likelihood ratio statistic (LRS) provides a measure of the variation in the dependent variable accounted for by a single variable or an entire model. We first examined interactions one at a time, and then considered models with two interactions. Where models were not nested, we used Akaike information criterion (AIC) to select the best model with interactions.

We used AIC to confirm that all variables in the final models should be retained. Note that main effects were always included if the respective interaction was included.

RESULTS

CUTI and BEUTI Models without Interactions

Brandt's Cormorants Table 2 shows the variables that had significant relationships with Brandt's cormorant foraging rate in the initial CUTI and BEUTI models. The results from the CUTI model were similar to

TABLE 2

Best models describing variability in Brandt's cormorant foraging rates using either the CUTI or BEUTI index to quantify upwelling strength and variability. Each model was selected using a backwards stepwise approach. The table shows only variables that were significant ($p < 0.05$) and therefore included in the model. Dashed lines identify variables that were not included in a given model. Linear and quadratic expressions are delineated by "L" and "Q", respectively. For categorical variables (Cat), each category listed is being compared to a base category (North category for Region and Windward category for Geography). Likelihood ratio statistics (LRS) are shown for each model.

Factor	CUTI		BEUTI	
	Coeff	p	Coeff	p
CUTI AIC = 5782.60 LRS(15) = 129.09 n = 1,797, $p < 0.001$				
BEUTI AIC = 5781.47 LRS(18) = 144.66 n = 1,797, $p < 0.001$				
<i>Control Variables</i>				
Region (Cat)				
North Central	-0.737	0.034	1.389	<0.001
South Central	1.121	0.006	1.030	0.004
South	1.286	0.006	0.693	0.125
Time of Day (L)	0.459	<0.001	0.441	<0.001
Time of Day (Q)	-0.084	<0.001	-0.080	<0.001
Within Season (L)	-0.113	0.007	-0.119	0.005
Within Season (Q)	2.8 e-3	0.002	2.9 e-3	0.001
Population (L)	—	—	0.0003	0.006
<i>Coastal Geography</i>				
Geography (Cat)				
Exposed	0.202	0.294	0.068	0.500
Leeward	0.606	0.009	0.471	0.010
Headland Size (L)	0.396	<0.001	0.198	0.001
Headland Size (Q)	-0.012	0.002	-0.007	0.011
Headland Length (L)	-0.036	0.009	—	—
Headland AR (L)	-2.863	<0.001	—	—
<i>Upwelling</i>				
Cumulative (L)	—	—	-0.001	0.001
Stan Dev (L)	—	—	0.139	0.005
Cumulative Y-1 (L)	—	—	-0.003	<0.001
Cumulative Y-1 (Q)	—	—	7.0 e-7	<0.001
Stan Dev Y-1 (L)	-2.218	0.059	0.348	0.001
Stan Dev Y-1 (Q)	-2.406	0.037	-0.010	0.001

those from the BEUTI model, but the BEUTI model was substantially superior to the CUTI model (AIC = 5781.47 vs AIC = 5782.60, respectively). Thus, while we continue to compare both models in this section, we only show model outputs for the superior BEUTI model when illustrating relationships between foraging rate and upwelling and coastal geography variables.

Both models showed significant relationships for all control variables except local breeding population size. Only the BEUTI model included a significant relationship between foraging rate and population size. There were differences in mean foraging rate among bioregions, curvilinear relationships between foraging rate and time of day and season, and a linear relationship between foraging rates and local population size (BEUTI model only). There was no significant relationship between foraging rates and bottom substrate for either model. Additionally, both models showed differences among geographic categories, with mean foraging rates highest at leeward sites (fig. 3).

Both CUTI and BEUTI models showed curvilinear relationships between foraging rates and headland size, with foraging rates increasing with headland size and plateauing as headland size increased past 10 km (fig. 4). The CUTI model also showed linear relationships between foraging rate and headland length and headland aspect ratio. Coastal direction and distance to headland did not make significant contributions to either model. Both models showed curvilinear relationships between foraging rates and prior year upwelling variability, with an intermediate maximum. Only the BEUTI model showed curvilinear relationship with prior year upwelling strength, with an intermediate maximum, and linear relationships with current year upwelling strength and upwelling variability. We explore these relationships further in the interactions section below.

Pelagic Cormorants Table 3 shows results from the initial CUTI and BEUTI models for pelagic cormorants. As with Brandt's cormorants, the CUTI model was similar to the BEUTI model, but the BEUTI model

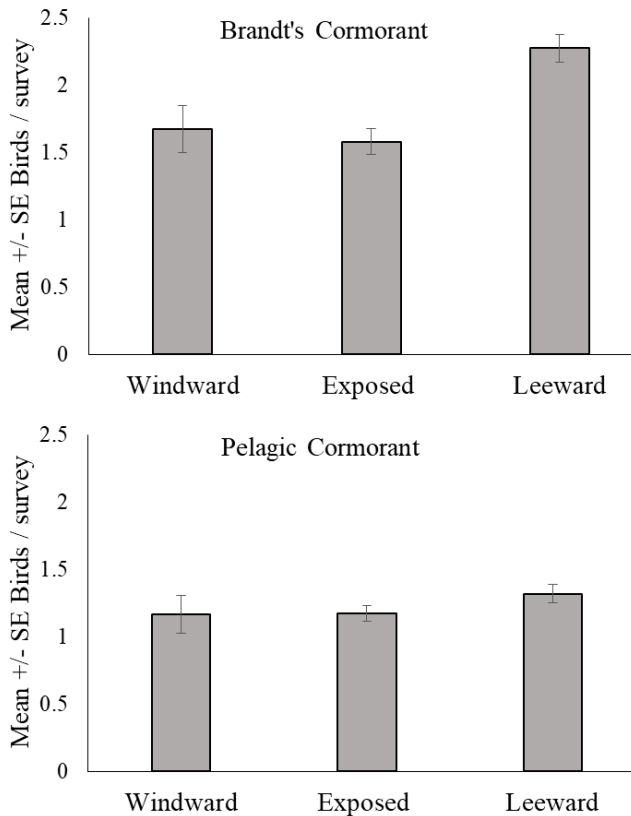


Figure 3. Mean +/- Standard Error (SE) foraging rates for Brandt's cormorants and pelagic cormorants for three categories of coastal geography: windward, exposed, and leeward.

was substantially superior to the CUTI model (AIC = 4457.09 vs AIC = 4461.34, respectively). We therefore only show model outputs for the superior BEUTI model when illustrating relationships between foraging rate and upwelling and coastal geography variables.

There were no differences in mean foraging rates among bioregions and curvilinear relationships between

foraging rates and time of day, season, and local breeding population size. Similar to Brandt's cormorants, there was no significant relationship between foraging rate and bottom substrate with either model.

Unlike Brandt's cormorants, mean foraging rates for pelagic cormorants were only slightly higher at leeward sites (fig. 3) and only the BEUTI model showed significant differences among coastal geography categories. Both models showed a curvilinear relationship between foraging rates and headland length, with very short and very long headlands leading to higher foraging rates (fig. 4). Additionally, both models showed a linear relationship between foraging rates and coastal direction, with lower coastal direction values (i.e., south-facing coastlines) leading to higher foraging rates (fig. 4). Both models showed curvilinear relationships between foraging rates and current year upwelling strength and prior year upwelling variability, with intermediate maximums. We explore these relationships further in the interactions section below.

Interactions between Coastal Upwelling and Coastal Geography

Brandt's Cormorant For the Brandt's cormorant BEUTI model, we found significant interactions between geography category and upwelling strength, upwelling variability, and prior year upwelling variability, considered one at a time. Both upwelling strength and upwelling variability interactions were significant when included in a single model as were upwelling strength and prior year upwelling variability interactions. However, the interaction with upwelling variability was not significant when the interactions with upwelling strength and prior year upwelling variability were included in the model. AIC showed that the model including interactions with upwelling strength and prior year upwelling variability was superior to a model that included

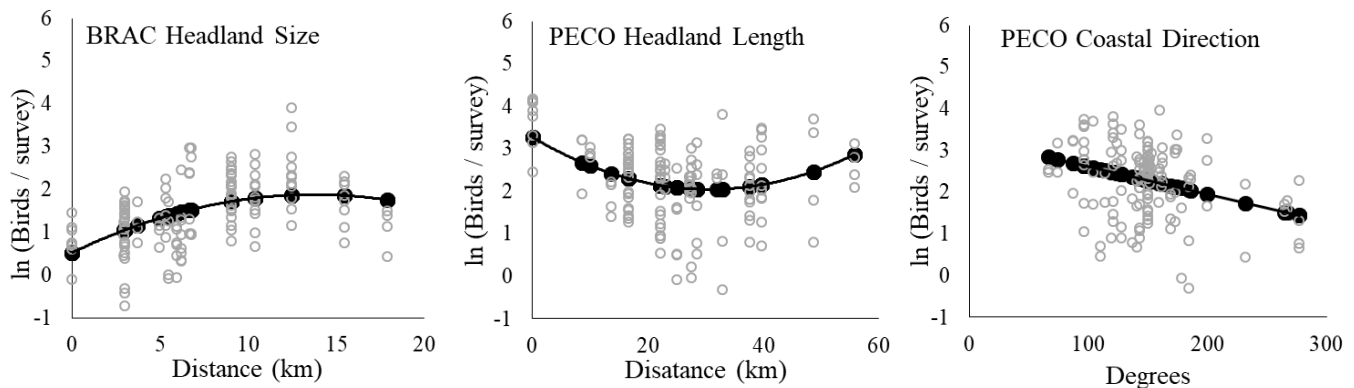


Figure 4. Effects of headland size on Brandt's cormorant (BRAC) foraging rates and the effects of headland length and coastal direction on pelagic cormorant (PECO) foraging rates. Black points represent predicted values based on BEUTI model outputs and open gray circles represent raw observations for a given site from a given year controlled for the effects of all independent variables except that displayed on the x-axis. Controlled raw observations were derived by removing the effects of all independent variables used in the BEUTI model except the variable displayed on the x-axis.

TABLE 3

Best models describing variability in pelagic cormorant foraging rates using either the CUTI or BEUTI index to quantify upwelling strength and variability. Each model was selected using a backwards stepwise approach.

The table shows only variables that were significant ($p < 0.05$) and therefore included in the model.

Dashed lines identify variables that were not included in a given model. Linear and quadratic terms are delineated by “L” and “Q”, respectively. For categorical variables (Cat), each level listed is being compared to a base level (Windward category for Geography). Likelihood ratio statistics (LRS) are shown for each model.

Factor	CUTI		BEUTI	
	Coeff	p	Coeff	p
CUTI AIC = 4461.34 LRS(15) = 192.17 n = 1,797, $p < 0.001$				
BEUTI AIC = 4457.09 LRS(15) = 209.21 n = 1,797, $p < 0.001$				
<i>Control Variables</i>				
Time of Day (L)	0.641	<0.001	0.650	<0.001
Time of Day (Q)	-0.126	<0.001	-0.128	<0.001
Week (L)	-0.267	<0.001	-0.275	<0.001
Week (Q)	5.4 e-3	<0.001	5.6 e-3	<0.001
Population Size (L)	0.009	<0.001	0.008	<0.001
Population Size (Q)	-3 e-5	0.001	-2 e-5	0.004
<i>Coastal Geography</i>				
Geography (Cat)				
Exposed	-0.488	0.100	-0.537	0.059
Leeward	0.039	0.900	-0.062	0.834
Coastal Direction (L)	-0.007	0.004	-0.007	0.003
Headland Length (L)	-0.059	0.004	-0.080	<0.001
Headland Length (Q)	0.001	0.002	0.001	0.001
<i>Upwelling</i>				
Cumulative (L)	0.109	0.009	0.002	0.001
Cumulative (Q)	-4 e-4	0.012	-9 e-7	<0.001
Stan Dev Y-1 (L)	9.729	0.009	0.245	<0.001
Stan Dev Y-1 (Q)	-5.467	0.036	-0.004	0.033

TABLE 4

Comparison of two models for Brandt’s cormorants with interactions between geography category and upwelling variables: in addition, interaction results from the best model as determined by AIC (model including interactions between geography category and upwelling strength and prior year upwelling variability).

Model	AIC			
Cum BEUTI & Std Dev BEUTI Year -1	5769.23			
Cum BEUTI & Std Dev BEUTI	5770.26			
Cum BEUTI & Std Dev BEUTI Year-1: LRS (24) = 180.53, n = 1,797, $p < 0.001$				
	Coeff	Std Error	P	
Cum BEUTI (linear)	Windward	8.9 e-4	8.0 e-4	0.268
	Exposed	-9.2 e-4	4.7 e-4	0.049
	Leeward	-2.0 e-3	4.6 e-4	<0.001
Std Dev BEUTI Year -1 (linear)	Windward	-0.129	0.166	0.437
	Exposed	0.311	0.104	0.003
	Leeward	0.319	0.119	0.007
Std Dev BEUTI Year -1 (quadratic)	Windward	-2.2 e-3	4.1 e-3	0.593
	Exposed	-0.010	3.0 e-3	0.001
	Leeward	-9.2 e-3	4.1 e-3	0.023

interactions with upwelling strength and upwelling variability (table 4). Likelihood ratio tests confirmed the significance of the interaction with prior year upwelling variability, when the interaction with upwelling strength was included (LRS = 9.91, $df = 4$, $p = 0.042$), and conversely, the significance of the interaction with upwelling strength, when the interaction with prior year upwell-

ing variability was included (LRS = 12.87, $df = 2$, $p = 0.002$). The final model with interactions for upwelling strength and prior year upwelling variability showed significant relationships between foraging rates and both upwelling variables for exposed and leeward sites, but not for windward sites (table 4). Foraging rates showed negative linear relationships with upwelling strength at

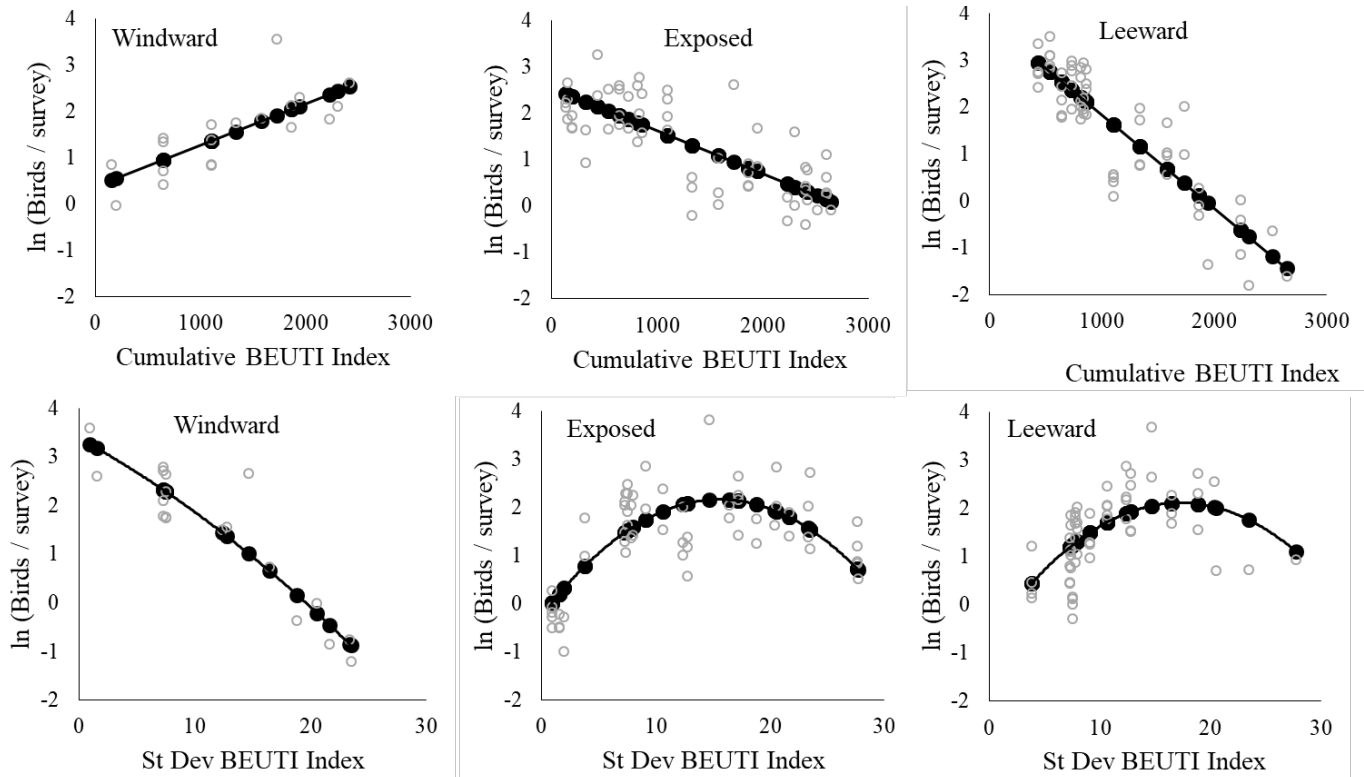


Figure 5. Effects of upwelling strength and prior year upwelling variability on Brandt's cormorant foraging rates at windward, exposed, and leeward study sites. Black points represent predicted values based on BEUTI model outputs and open gray circles represent raw observations for a given site from a given year controlled for the effects of all independent variables except that displayed on the x-axis. Controlled raw observations were derived by removing the effects of all independent variables used in the BEUTI model except the variable displayed on the x-axis.

exposed and leeward sites, though foraging rates were more variable at leeward sites (fig. 5). Furthermore, foraging rates were highest at exposed and leeward sites with intermediate values of prior year upwelling, though foraging rates at leeward sites were less variable overall.

Pelagic Cormorant For pelagic cormorant BEUTI models, we found significant interactions between geography category and upwelling strength and prior year upwelling variability. However, the interaction with upwelling strength was not significant when the interaction with prior year upwelling variability was included in the model. AIC showed that the model including the interaction with prior year upwelling variability was an improvement over the model including the interaction with upwelling strength (table 5). A likelihood ratio test showed that this model differed significantly from the model that did not include interactions (LRS = 28.04, df = 4, p < 0.001). The final model with interaction for prior year upwelling variability showed significant relationships between foraging rates and upwelling for windward and exposed sites, but not for leeward sites (table 5). Foraging rates at the windward sight peaked at intermediate values of prior year upwelling variability and then decreased slightly (fig. 6). Foraging rates at the

exposed sights plateaued at higher values of prior year upwelling variability and did not decrease.

DISCUSSION

We found that the effects of coastal upwelling on seabird foraging rates differed by coastal geography. This was especially true for prior year upwelling. Foraging rates were higher at exposed sites when prior year upwelling was more variable. This is likely because variability in upwelling reduces offshore transport thereby increasing retention of larvae to nearshore habitats where they settle as juveniles into midwater and bottom habitats. Ainley et al. (1993) found similar results when using the common murre (*Uria aalge*) to sample juvenile rockfish abundance within the Gulf of the Farallones, with pelagic juvenile rockfish more abundant within the gulf in years when upwelling was pulsed during the rockfish larval stage. Foraging rates at leeward habitats were more stable and did not change drastically with changes in prior year upwelling variability. These results are supported by Wing et al. (1995b) who reported continuous post-larvae settlement in the lee of Point Reyes in central California compared to more episodic settlement at exposed habitats.

TABLE 5
 Comparison of two models for pelagic cormorants with interactions between geography category and upwelling variables: in addition interaction results from the best model as determined by AIC (model including interactions between geography category and prior year upwelling variability).

Model		AIC		
Std Dev BEUTI Year -1		4437.05		
Cum BEUTI		4440.96		
Std Dev BEUTI Year -1: LRS (19) = 210.86, n = 1,797, p <0.001				
		Coeff	Std Error	P
Std Dev BEUTI Year -1 (linear)	Windward	0.587	0.171	0.001
	Exposed	0.370	0.068	<0.001
	Leeward	0.073	0.076	0.338
Std Dev BEUTI Year -1 (quadratic)	Windward	-0.017	5.7 e-3	0.003
	Exposed	-6.8 e-3	2.0 e-3	0.001
	Leeward	-6.9 e-3	2.7 e-3	0.796

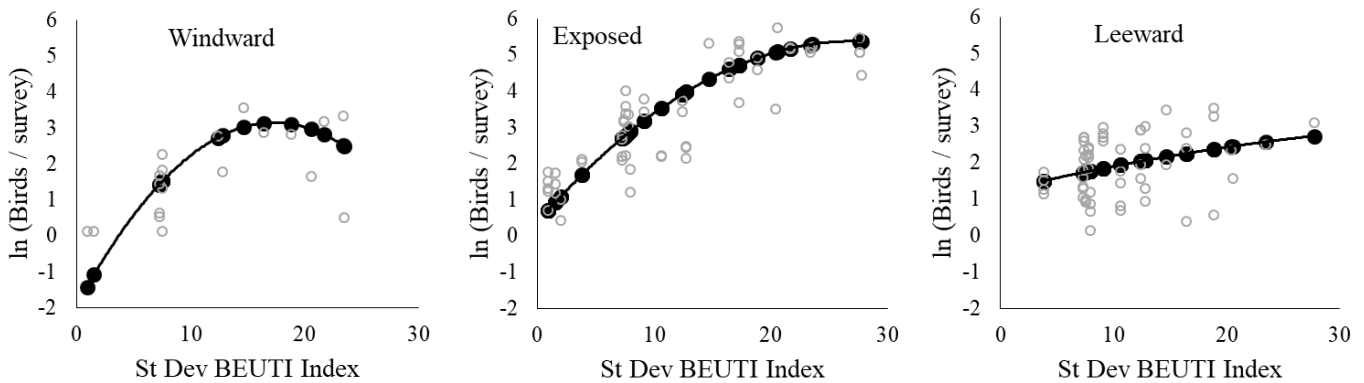


Figure 6. Effects of prior year upwelling variability on pelagic cormorant foraging rates at windward, exposed, and leeward study sites. Black points represent predicted values based on BEUTI model outputs and open gray circles represent raw observations for a given site from a given year controlled for the effects of all independent variables except that displayed on the x-axis. Controlled raw observations were derived by removing the effects of all independent variables used in the BEUTI model except the variable displayed on the x-axis.

In contrast to what we expected, Brandt’s cormorant foraging rates were lower at exposed and leeward habitats when current year upwelling was more intense. This may be more of a result of prey switching in Brandt’s cormorants as current year upwelling conditions change rather than an indicator of juvenile fish abundance at exposed and leeward habitats. Brandt’s cormorants regularly switch from midwater and bottom fishes to anchovies when anchovy favorable conditions occur (Elliott et al. 2015, 2016; Warzybok et al. 2018). Intense coastal upwelling supports blooms of the larger phytoplankton species that northern anchovies prey upon (Rykaczewski and Checkley 2007). Furthermore, there is evidence that intense upwelling causes swarming behavior in schooling fishes that would make them more available to cormorants, whereas these species are more dispersed and less available during relaxation in upwelling (Benoit-Bird et al. 2018). Thus, Brandt’s cormorants may be foraging more on anchovies away from shore during intense upwelling years. Diet studies of pelagic cormorants have shown that they are likely not switching to pelagic prey like anchovies (Ainley et al. 1981).

We found that the overall relationship between cormorant foraging rates and prior year upwelling variability was not linear but curvilinear. Foraging rates were overall higher with intermediate values of prior year upwelling variability. Thus, there appears to be an optimal window of coastal upwelling conditions that increases larval survival and leads to peak juvenile fish abundance. Cury and Roy (1989) found a curvilinear relationship between upwelling strength and larval survival that suggests larval survival is highest with intermediate levels of coastal upwelling. Roy et al. (1992) described an “optimal environmental window” of wind speeds that promote larval survival. If upwelling is too weak, there is not enough primary productivity to support larval survival. However, if upwelling is too strong, larval mortality can occur as larvae are displaced from water masses favorable to larval survival. Our results showing that BEUTI-based models were superior to CUTI-based models suggest that larval survival due to increased primary productivity is also important as the delivery of larvae to nearshore habitats in determining juvenile fish abundance. Finally, Robinette et al. (2007)

found that upwelling variability was more important than upwelling strength in determining regional survival and delivery to nearshore habitats. Our results here support that conclusion and the idea of an optimal environmental window for larval survival. Intermediate variability in coastal upwelling allows for primary productivity to support larval survival but reduces offshore transport away from nearshore habitats. Ultimately, upwelling variability translates into more relaxation events that allow larvae to return to exposed and windward habitats. Retention of larvae in the lee of headlands can provide more stable recruitment rates among years by decreasing the advection of larvae during years of persistent upwelling.

We found evidence that the size and shape of headlands can impact cormorant foraging rates. There was some evidence that headlands projecting further into the ocean lead to higher juvenile fish abundance as indicated in the Brandt's cormorant models. Additionally, the pelagic cormorant models indicated that both long and short headlands lead to higher juvenile fish abundance. The longer headland length may indicate that very large headlands enhance larval retention while the shorter headland length may indicate that pointier headlands with higher aspect ratios also enhance larval retention. Additionally, coastal orientation was an important determinant of juvenile fish abundance as indicated by pelagic cormorants regardless of whether a headland was present. Pelagic cormorant foraging rates were higher at south-facing coasts than other coastal orientations. Offshore advection due to coastal upwelling is not as strong along south-facing coasts and eddies can form in the lee of the south facing coasts of embayments (e.g., Graham and Largier 1997).

Understanding the mechanisms that dictate larval survival and distribution along the coast and having a cost-effective means by which to measure the abundance of juveniles settling into nearshore habitats will allow managers to set realistic expectations for the performance of individual MPAs. Seabirds can help determine when and where larval accumulation and juvenile settlement are likely to occur and whether recruitment hot spots are being adequately represented within the MPA network. For example, MPAs that are not in the lees of coastal headlands or not along southward-facing sections of coastline may not receive similar numbers of juvenile recruits as those in leeward habitats, especially if multiple years of persistent upwelling have pushed fish larvae away from these MPAs. These MPAs may never achieve the same fish population levels as MPAs in leeward habitats. Managers should therefore establish unique expectations for individual MPAs based on their potential for juvenile fish recruitment. Additionally, seabirds offer a community-level perspective of juvenile fish recruitment

because each species samples multiple fish species across multiple habitats. Finally, using multiple seabird species that differ in their diet and foraging habitat use will provide a broad community-level perspective (see Robinette et al. 2018).

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