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Can nearshore seabirds detect variability in juvenile fish distribution at scales relevant to managing marine protected areas?

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Abstract

Juvenile recruitment is an important determinant of change within marine protected areas (MPAs). Understanding spatio-temporal variability in recruitment rates will help managers set realistic expectations for rates of population and community level change within individual MPAs. Here we ask whether seabird foraging rates can be used as a proxy for juvenile fish recruitment at spatial scales relevant to MPA management. We investigated the foraging rates of six piscivorous seabirds inside and outside of three island and four mainland MPAs in Southern California and compared these rates to estimates of juvenile fish density from kelp forest surveys conducted at the same sites during the same 2 years (2012 and 2013). Juvenile fish communities at island and mainland sites were dominated by three families, Embiotocidae, Labridae and Pomacentridae, in both years. Additionally, there was an influx of young-of-the-year rockfishes (family Sebastidae) at most sites in 2013. Seabird and fish distributions were similar at the regional (approximately 15–30 km) scale, but less similar at the site-specific scale. Site-specific differences reflected differences in the diet and foraging habits of individual seabird species. While fish surveys were specific to the kelp forest habitat, seabirds were sampling multiple habitats (i.e. multiple water depths over multiple bottom substrates) within a given site. Our results suggest that integrating seabird data with data on juvenile fish abundance can produce a more holistic index to proxy spatio-temporal variability in juvenile fish recruitment. In other words, seabird studies can provide additional information not captured by fish surveys and help resource managers better understand local patterns of fish recruitment at the community level. This will help resource managers establish realistic expectations for how quickly fish populations should change within individual MPAs.

KEYWORDS

Brandt's cormorant, California least tern, Caspian tern, double-crested cormorant, Embiotocidae, juvenile fish recruitment, Labridae, marine protected area, pelagic cormorant, pigeon guillemot, Pomacentridae, seabird foraging, Sebastidae

1 | INTRODUCTION

Seabirds are long-lived species (often living >20 years; Clapp, Klimkiewicz, & Kennard, 1982) that produce few offspring and provide a large amount of parental care compared to most marine species. During the breeding season, seabirds are central place foragers, returning to the nesting colony throughout the day to incubate eggs and provision young. Thus, seabirds can benefit from protections enacted adjacent to breeding colonies. Marine protected areas (MPAs) can have both direct and indirect benefits to seabird populations (Tasker et al., 2000). Direct benefits include (i) reduced disturbance to breeding and roosting sites and (ii) decreased human interaction (e.g. bycatch, light attraction, gear entanglement) at foraging sites. Indirect benefits include (i) reduced competition with humans for food resources and (ii) greater prey supplies resulting from increased prey production. Seabirds can also provide valuable information on the populations of prey species to help improve the adaptive management of MPAs. Seabirds have proven to be reliable, cost-effective indicators of change in the marine environment (Piatt, Sydeman, & Wiese, 2007). In fact, several studies conducted over the past 40 years 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 & Sanger, 1992). Multiple coastally breeding seabird species depend on juvenile age classes of nearshore fishes for prey and studies have shown these species to be good indicators of temporal variability in juvenile fish recruitment (Mills, Laidig, Ralston, & Sydeman, 2007; Roth, Mills, & Sydeman, 2007; Thayer & Sydeman, 2007). It is this aspect of seabird biology that we investigate herein.

The recovery rate of populations released from fishing pressure (e.g. as a result of MPA establishment) will be largely determined by the degree to which new individuals recruit to MPAs (Warner & Cowen, 2002). The majority of fish species within the nearshore habitats of Southern California have pelagic larval stages. For these species, recruitment will be largely dependent on (i) the number of larvae produced in a given year, (ii) the survival of those larvae to settlement age, and (iii) delivery of those larvae to adult habitat (Jenkins & Black, 1994; Levin, 1996; Wing, Largier, Botsford, & Quinn, 1995). The first two conditions are greatly affected by regional oceanographic conditions while the third condition is greatly affected by nearshore ocean currents and larval behavior. As a result, fish recruitment can be highly variable both temporally due to oceanographic conditions and spatially due to larval delivery mechanisms (Caselle, Kinlan, & Warmer, 2010). Thus, not all MPAs are equal in their potential to receive recruits to fish populations. This is an important aspect of fish population dynamics that MPA managers must consider if they are to set realistic expectations for how quickly fish populations will recover within individual MPAs.

While there have been many studies demonstrating how seabirds can be used to measure temporal variability in fish recruitment, few have demonstrated their use as indicators of spatial variability in fish recruitment. Understanding spatial variability in fish recruitment is necessary for assessing the effectiveness of individual MPAs. In California, Robinette, Howar, Sydeman, and Nur (2007) investigated sanddab (*Citharichthys* spp.) recruitment around a mainland MPA and illustrated how seabird diet can be integrated with estimates of regional larval abundance and upwelling to investigate spatio-temporal variability in recruitment. They found that regional larval sanddab abundance was highest when upwelling was persistent. They also showed that recruitment of sanddabs differed on opposing sides of a coastal promontory, with leeward recruitment strongest during persistent seasonal upwelling and windward recruitment strongest during variable upwelling. Dispersal patterns of planktonic larvae are often influenced by the phasing and amplitude of coastal upwelling, showing offshore transport during periods of persistent upwelling and onshore transport during periods of relaxation (Sakuma & Larson, 1995; Sakuma & Ralston, 1995; Wing, Largier, et al., 1995). Several studies throughout Central California have found persistent, predictable retention areas in the lees of coastal promontories that could explain these recruitment patterns (Wing, Botsford, Largier, & Morgan, 1995; Wing et al. 1998, Graham & Largier, 1997; Mace & Morgan, 2006a,b). Robinette, Nur, Brown, and Howar (2012) investigated the foraging distribution of multiple seabird species around the same promontory as Robinette et al. (2007) and showed that foraging distributions were consistent over a 6-year period. Seabird species that feed on juvenile fishes foraged mostly in the lee of the promontory. However, Robinette et al. (2012) were not able to confirm that foraging seabirds were responding to an abundance of juvenile fishes. This is an important connection to make if seabird foraging rates are to be used to index fish recruitment.

In this study, we ask the question: do spatial differences in seabird foraging rates reflect spatial differences in juvenile fish densities? We test the hypothesis that seabirds can be used as indicators of fish recruitment by comparing seabird foraging distribution to juvenile fish distribution inside and outside of seven Southern California MPAs. Our goal is not to establish whether MPAs are causing higher recruitment rates in Southern California. Rather, we are asking whether variability in seabird foraging rates can be used as a proxy for juvenile fish recruitment to nearshore habitats at different spatial scales. Thus, the presence or absence of an MPA will not affect our results and we do not emphasize differences between MPA and reference sites in this paper.

2 | METHODS

2.1 | Study area

All data were collected as part of the baseline monitoring program for the South Coast Study Region (SCSR) of California's Marine Life Protection Act Initiative (MLPAI). The SCSR baseline program surveyed multiple ecosystem components within MPA and reference sites throughout the Southern California Bight (SCB). The SCB resides at the southern end of the California Current, an eastern boundary current that supports some of the most productive marine ecosystems on the planet (Ainley, Sydeman, & Norton, 1995). The SCB is also at the intersection between the equatorward California Current and the poleward Southern

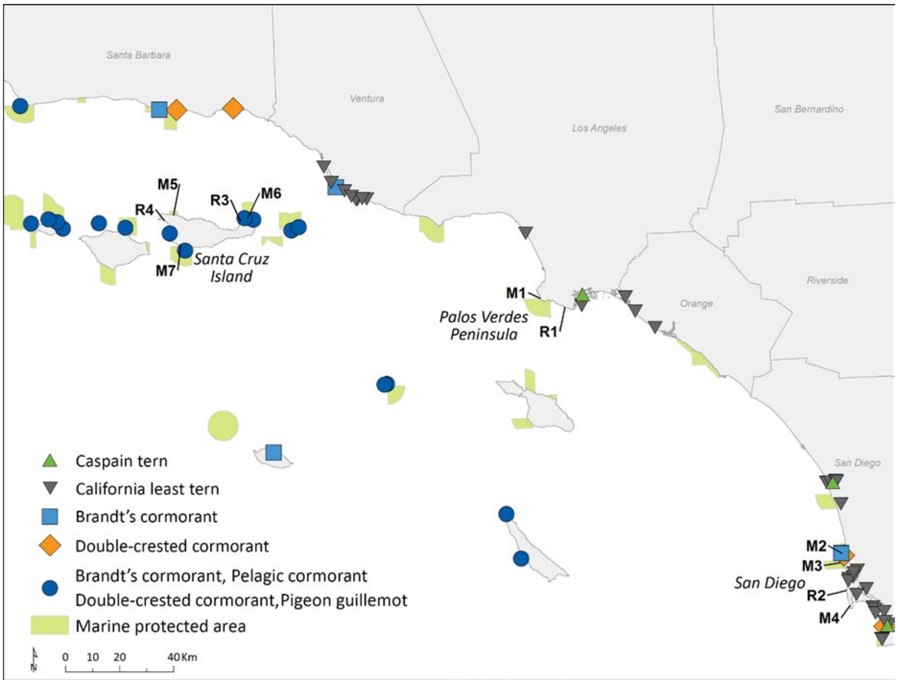

FIGURE 1 Map showing the location of the marine protected area (MPA) sites (M1 through M7) and reference sites (R1 through R4) within the two island and two mainland regions. Also shown are all southern California MPAs and the distribution of breeding colonies for the six focal seabird species: Caspian tern (CATE), least tern (LETE), Brandt's cormorant (BRAC), double-crested cormorant (DCCO), pelagic cormorant (PECO), and pigeon guillemot (PIGU)

California Counter Current (Hickey, 1992). These intersecting currents create a gradient of near surface temperatures throughout the bight with colder temperatures in the northwest and warmer temperatures in the southeast (Pondella, Gintert, Cobb, & Allen, 2005). Annual variability in the strength of these currents and the magnitude of coastal upwelling can impact annual primary and secondary (e.g. fish larvae) productivity for the region (Anderson, Brzezinski, Washburn, & Kudela, 2006). Island and mainland regions of the SCB also differ in the habitats available for fish communities, with approximately 75% of the total island coastline containing nearshore rocky reefs compared to approximately 25% for the total mainland coast (Pondella et al., 2015).

The distribution of breeding seabird colonies within the SCB is similar to that of fish habitat, with rocky coast breeders found mostly at the islands and sandy coast breeders limited to the mainland (Figure 1). We used data from the six species that were consistently observed during foraging surveys: pigeon guillemot (*Cepphus columba*), Brandt's cormorant (*Phalacrocorax penicillatus*), pelagic cormorant (*Phalacrocorax pelagicus*), double-crested cormorant (*Phalacrocorax auritus*), California least tern (*Sternula antillarum browni*) and Caspian tern (*Hydroprogne caspia*). Pigeon guillemots and pelagic cormorants breed only at the islands while least terns and Caspian terns breed only along the mainland. Brandt's cormorants are most abundant at the islands with only three small breeding colonies along the mainland, including one within the San Diego (SD) region of our study. Double-crested cormorants are also most abundant at the islands with four small breeding colonies along the mainland, including two within the SD region.

We used data from 11 sites where both kelp forest fish and seabird foraging surveys were conducted (Table 1). Six of these sites were along the mainland and five were at Santa Cruz Island (Figure 1). Along the mainland, two sites (one MPA and one reference) were within the Palos Verdes Peninsula (PVP) region and four (three MPAs and one reference) were within the SD region. We divided Santa Cruz Island into two regions: North Santa Cruz Island (SCI-N) and South Santa Cruz Island (SCI-S). We used data from three sites (two MPAs and one reference) at SCI-N and two sites (one MPA and one reference) at SCI-S. Percent sand cover was estimated for each site within the areas sampled for fish as a proxy for bottom habitat type. The remaining proportion of bottom habitat was composed of some form of rocky habitat. Table 1 shows the estimated percent sand cover for each site. The SD sites had the highest percent sand cover (mean ± *SD* [*n*] = 12.90 ± 0.09 [4]) while the PVP, SCI-N and SCI-S sites were more similar in percent sand cover (3.85 ± 0.04 [2], 2.23 ± 0.01 [3], 3.30 ± 0.02 [2], respectively).

2.2 | Data collection

Baseline kelp forest fish surveys were conducted in 2011 and 2012 while baseline seabird foraging surveys were conducted in 2012 and 2013. Additionally, kelp forest fish surveys were conducted at four locations, R3 and M6 at SCI-N and M1 and R1 at PVP, in 2013 as part of ongoing long-term monitoring programs. As a result, we were able to make direct comparisons between fish and seabird data sets for 2012 and limited comparisons between data sets for 2013. Seabird foraging surveys were conducted almost weekly (see seabird foraging methods below) at each site from April through July of each year. Fish surveys were conducted once at each site between August and December of each year.

2.3 | Kelp forest fish surveys

At each monitoring site, visual transect surveys by SCUBA divers were used to quantify the species composition, size structure and

TABLE 1 Estimates of percent sand cover for each of the 11 sites surveyed

Region	Site	Sand cover (%)	2012 sample size	2013 sample size
PVP	C1	1.2	14	17
	R1	6.5	14	17
SD	R2	21.8	17	16
	C2	16.1	17	15
	R3	12.1	18	17
	R4	1.6	18	15
SCI-N	R5	1.1	14	16
	C3	3.1	5	15
	R6	2.5	9	18
SCI-S	R7	1.9	14	17
	C4	4.7	12	18

PVP, Palos Verdes Peninsula; SD, San Diego; SCI-N, North Santa Cruz Island; SCI-S, South Santa Cruz Island.

Also shown are sample sizes used to calculate mean seabird foraging rates for each site in 2012 and 2013. M and R in the site name denotes whether the site was inside a marine protected area site or a reference site, respectively.

density of fish populations. Visual transects were 30 m long × 2 m tall × 2 m wide and were stratified across the face of the reef (alongshore and cross-shore) and vertically through the water column. Within each cross-shore ‘zone’, three to four randomly located transects were sampled along isobaths parallel to shore. The zones at each site were stratified to encompass the offshore edge of the reef, the middle of the reef and as shallow inshore as practical. For example, for a reef with a maximum depth of 25 m the target depths for the zones would be 5, 10, 15 and 25 m. If no appreciable depth stratification was present, stratification was based on proximity to the outer edge of the reef and the shore.

Three portions of the water column (bottom, midwater and canopy) were sampled by two divers along each transect. Bottom transects sampled the bottom 2 m of the water column, contiguous with the reef surface, and the midwater transect was located above the bottom transect. The height of the midwater transect varied as a function of bottom depth (4–6 m above the bottom for bottom depths of 10 m or greater, 2–4 m above the bottom for bottom depths of 6 m or less). Bottom and midwater transects were sampled simultaneously by two divers. After completion of bottom and midwater transects, divers moved up to the canopy and, moving in the opposite direction, counted fish in the top 2 m of the water column only. Both divers in the team identified, counted and sized (total length to the nearest cm) all conspicuous fishes on each transect.

2.4 | Seabird foraging surveys

Seabird foraging surveys were conducted during the following time periods, 06:00–09:00, 09:00–12:00, 12:00–15:00 or 15:00–18:00, with sites rotated among the four time periods each week to develop complete 12-hr assessments of foraging activity. Mainland sites were surveyed once a week while Santa Cruz Island sites were surveyed twice every 3 weeks from April through July. For each survey, all observations were made from a single observation point, using binoculars and a 20–60× spotting scope. Each 3-hr period was divided into 15-min blocks. During each 15-min block, one observer scanned all water within a 1-km radius of the observation point and recorded the numbers of actively foraging individuals for all seabird species.

2.5 | Data analysis

The overarching goal of our analysis was to compare spatial patterns in the fish data to those in the seabird data. We analysed fish and seabird data at two spatial scales: (i) regional (comparing SCI-N, SCI-S, PVP and SD) and (ii) study site (comparing individual MPA and reference sites). While we were not testing the impacts of MPAs on seabird foraging behavior, we maintained the MPA and reference site designations so that we could present our results within the context of MPA management. We used descriptive statistics to characterize juvenile fish (<20 cm total length) community composition (at the family level) and densities for the four families with the highest densities (see Results below) and seabird species composition and foraging rates at the two different spatial scales mentioned above. The four fish families with the highest densities are also known to be important prey for multiple seabird species (see Discussion below). The sample unit for fish data was one complete site survey. We averaged fish densities over all transects for a given survey to produce a single value for each family that characterized density throughout the water column and across isobaths. Thus, we had a sample size of one for each site in a given year. The sample unit for seabird data was a single 3-hr period. We averaged all 15-min blocks over a given 3-hr period. If 100% of the study area was not visible (e.g. due to fog, sun glare) during two or more 15-min blocks for a given hour, that hour was not included in our analysis. Sample sizes for each site are shown in Table 1. We were unable to perform tests of significance to assess differences in fish densities among sites and years due to insufficient sample sizes. We used analysis of variance (ANOVA) to compare mean seabird foraging rates between years, among regions

TABLE 2 Mean densities (fish/m^2) for all fish families representing potential seabird prey observed at all 11 sites surveyed in 2012 and the four sites revisited in 2013

	2012						**2013**	
Mainland families	**M1**	**R1**	**M2**	**M3**	**R2**	**M4**	**M1**	**R1**
Atherinopsidae	0.1	4.2	0.0	0.0	15.8	1.1	0.0	0.0
Bathymasteridae	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Carangidae	4.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Clinidae	0.0	0.3	0.0	0.0	0.1	0.0	0.0	0.1
Embiotocidae	11.4	28.1	17.5	4.2	7.6	0.7	9.6	14
Gobiidae	0.9	0.0	0.0	1.1	5.3	0.0	0.9	2.9
Hexagrammidae	1.0	0.6	0.0	0.0	0.2	0.1	1.0	1.8
Kyphosidae	0.0	0.3	0.0	0.4	0.4	0.0	0.2	0.1
Labridae	3.2	16.8	42.3	18.5	33.3	8.5	39.0	49.4
Pomacentridae	4.8	4.0	48.5	14.8	13.1	13.8	111.3	3.8
Sebastidae	9.2	0.1	0.0	1.0	0.8	0.1	37.3	1.3
Serranidae	0.1	1.8	4.0	1.5	0.8	0.3	0.1	0.7

	2012					**2013**	
Island families	**M5**	**R3**	**M6**	**M7**	**R4**	**R3**	**M6**
Atherinopsidae	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Aulorhynchidae	0.0	0.0	0.0	0.0	4.5	0.0	0.0
Clinidae	0.1	0.0	0.9	0.2	1.5	0.1	0.0
Embiotocidae	11.1	5.4	27.7	6.9	9.4	4.8	33.8
Hexagrammidae	6.5	7.4	4.2	5.8	4.6	4.6	2.4
Labridae	16.2	17.6	14.2	58.2	11.7	20.4	21.9
Labrisomidae	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Pomacentridae	21.3	17.1	15.6	13.3	6.0	32.4	26.8
Scombridae	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Scorpaenidae	1.3	0.8	1.0	0.3	0.8	0.0	0.0
Sebastidae	14.9	7.6	1.1	16	4.9	25.3	44.5
Serranidae	0.0	0.1	2.2	0.0	0.0	1.0	5.6

M and R in the site name denotes whether the site was inside a marine protected area or a reference site, respectively.

and among sites. Not all seabirds foraged in all regions. We therefore used only the regions where a given species was observed foraging in our analyses. We used PVP, SD and SCI-S for our analysis of double-crested cormorant foraging rates; PVP, SCI-N and SCI-S for pelagic cormorants and pigeon guillemots; and PVP and SD for Caspian terns and least terns. We used all four regions for Brandt's cormorants. Finally, we used Spearman's rank correlation analysis on the 2012 data to compare mean seabird foraging rates to mean fish densities at the regional and study site scales.

3 | RESULTS

3.1 | Community composition of juvenile fishes

Fish family composition was similar between the two mainland regions and between the two island regions, but less similar across mainland versus island regions. There was a total of 12 families observed within the island regions (Table 2). Seven of these families were common to all island sites. The three most abundant families were Embiotocidae (surfperches), Labridae (wrasses) and Pomacentridae (damselfishes). Rockfishes (family Sebastidae) were one of the most abundant families in 2013. Likewise, there were 12 families observed within the mainland regions, eight of which were the same as those in the island regions. Only four families were common to both mainland regions, and the same four families were the only families common to all mainland sites. Additionally, rockfishes were common to all mainland sites but M2. As with the island regions, surfperches, wrasses and damselfishes were the three most abundant families observed.

Patterns of juvenile fish abundance were similar across regions and indicated higher fish recruitment in 2013 compared to 2012, although we caution that fewer sites were sampled in 2013 than 2012 and sample sizes were not adequate to perform tests of significance. Within SCI-N, there was an overall eightfold increase in mean rockfish density from 2012 to 2013 (Table 1). The increase was threefold at R3 and 40-fold at M6. There was a twofold increase in damselfishes in 2013 and no noticeable change in wrasse or surfperch densities among years. Within PVP, there were increases in damselfish and wrasse densities in 2013, but not in surfperch densities. Wrasses increased twofold while damselfishes increased threefold. Rockfishes increased 10-fold and were one of the most abundant families in 2013.

3.2 | Regional and site-specific differences in seabird foraging rates

Table 3 shows the results of ANOVA tests on seabird foraging rates. All six species showed significant differences in mean foraging rates among sites, although differences for Caspian terns were marginally significant. We considered results marginally significant at $p < .01$. Brandt's cormorants, pelagic cormorants and Caspian terns showed significant differences in mean foraging rates among regions and Brandt's cormorants and pigeon guillemots showed significant differences between years. Double-crested cormorants and Caspian terns showed marginally significant differences in mean foraging rates between years. There was a significant year × region interaction for Brandt's cormorants and a marginally significant year × region interaction for pigeon guillemots. There were significant year × site interactions for pelagic cormorants, pigeon guillemots and least terns, and a marginally significant year × site interaction for Brandt's cormorants. Specific differences are discussed in the sections below as they relate to observed variability in regional and site-specific fish densities.

TABLE 3 Results of analysis of variance tests comparing mean foraging rates between years, among regions and among sites for each seabird species

	Year	Region	Site	Year × region	Year × site
Brandt's cormorant					
F	**14.66**	**5.33**	**6.86**	**8.12**	*8.12*
df	**1, 310**	**1, 310**	**10, 310**	**3, 310**	*7, 310*
p	**<.001**	**.022**	**<.001**	**<.001**	*.066*
Pelagic cormorant					
F	1.63	**40.65**	**12.15**	0.86	**6.20**
df	1, 185	**2, 185**	**5, 185**	2, 185	**4, 185**
p	.203	**<.001**	**<.001**	.425	**<.001**
Pigeon guillemot					
F	**6.72**	0.60	**15.78**	*2.74*	**18.67**
df	**1, 185**	2, 185	**5, 185**	*2, 185*	**4, 185**
p	**.010**	.549	**<.001**	*.067*	**<.001**
Double-crested cormorant					
F	*3.05*	2.32	**3.97**	1.62	1.10
df	*1, 238*	2, 238	**5, 238**	2, 238	5, 238
p	*.082*	.101	**.002**	.201	.362
Caspian tern					
F	*3.46*	**5.54**	*2.27*	2.24	1.26
df	*1, 183*	**1, 183**	*4, 183*	1, 183	4, 183
p	*.064*	**.020**	*.063*	.137	.289
Least tern					
F	1.45	0.01	**2.49**	0.00	**3.73**
df	1, 183	1, 183	**4, 183**	1, 183	**4, 183**
p	.231	.929	**.045**	.993	**.006**

Also shown are results for year × region and year × site interactions. Significant differences/interactions are shown in bold while marginally significant ($p < .1$) differences/interactions are shown in italics.

3.3 | Regional comparisons of seabird and juvenile fish

Juvenile fish densities and seabird foraging rates showed similar patterns at the regional scale, with fish densities and seabird foraging highest in SD, followed by SCI-S, then SCI-N and finally PVP (Figure 2). Combined foraging rates for all six seabirds was positively correlated with combined densities of the four common fish families (Table 4 and Figure 3). However, most correlations between individual seabird species and fish families were not significant. Species/family-specific correlations were only significant between Brandt's cormorants and rockfishes and between pelagic cormorants and rockfishes. Both of these correlations were positive.

The lack of significant correlations between specific seabird species and fish families is likely due to region-specific differences in seabird species and fish family composition. While total densities for the four common fish families were similar among SD, SCI-N and SCI-S, densities for individual families varied among regions (Figure 2). Total juvenile fish density for the four common families in 2012 was lowest at PVP, although this region showed the highest density of surfperches. Damselfishes showed the highest density at SD while wrasses showed the highest density at SCI-S. Densities for the four families appeared evenly distributed at SCI-N. Similarly, differences in species composition of foraging seabirds was most prominent between the island and the mainland in 2012 while differences within island and mainland regions were more subtle (Figure 2). Both island regions were dominated by Brandt's and pelagic cormorants. On the mainland, PVP was the only region where all six species were observed foraging. However, all six species showed their lowest foraging rates at PVP compared to other regions. Within PVP, Brandt's cormorants, double-crested cormorants and Caspian terns showed the highest foraging rates of all species. Brandt's cormorants, double-crested cormorants, Caspian terns and least terns all foraged within SD, with the highest rates observed for Brandt's cormorants and Caspian terns.

Among-year patterns in fish densities and seabird foraging rates were also similar at the regional scale. Fish densities were higher at PVP and SCI-N in 2013 than in 2012. Caspian terns showed higher rates at PVP in 2013 compared to 2012 and Brandt's cormorants and pigeon guillemots showed higher foraging rates at SCI-N in 2013. While foraging rates for Brandt's cormorants, double-crested cormorants and Caspian terns were higher in 2012 than 2013 at SD,

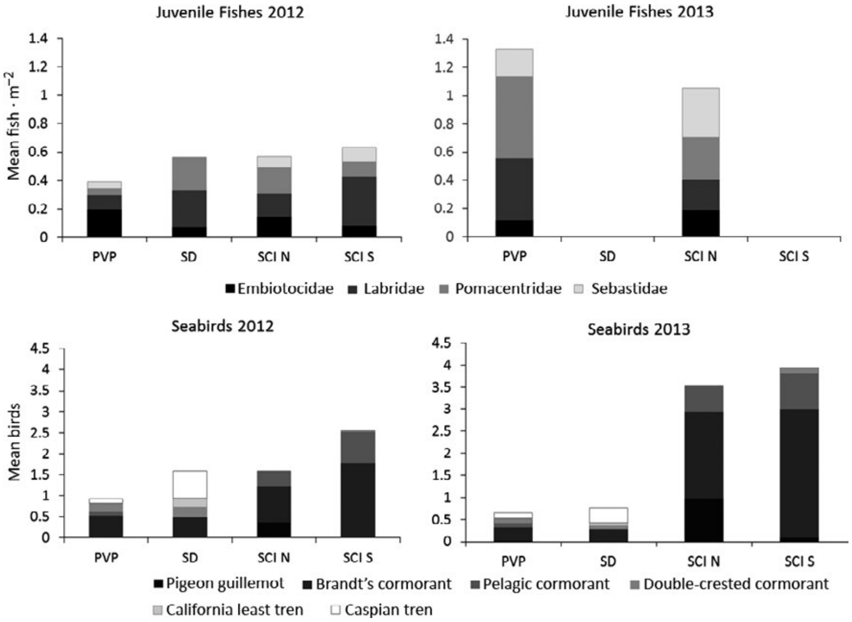

FIGURE 2 Mean juvenile fish densities and mean seabird foraging rates for each of the four regions in 2012 and 2013. Absence of bars for SD and SCI-S in 2013 are due to an absence of data for those regions in 2013. PVP, Palos Verdes Peninsula; SD, San Diego; SCI-N, North Santa Cruz Island; SCI-S, South Santa Cruz Island. See Table 4 for definitions of seabird and fish codes

we have no fish data for SD in 2013 and do not know if temporal trends in seabird foraging reflect similar trends in fish abundance. Our seabird foraging results suggest that densities of juvenile fishes at SD were likely higher in 2012 than in 2013. Similarly, there were no fish surveys conducted at SCI-S in 2013, but higher foraging rates of Brandt's cormorants and double-crested cormorants in 2013 suggest that densities of juvenile fishes were higher there in 2013 than 2012. Additionally, results for rockfishes and Brandt's cormorants and pigeon guillemots support the correlations observed in 2012 as all three groups showed greater increases at SCI-N in 2013.

3.4 | Site-specific comparisons of seabird and juvenile fish

Fish and seabird data were less complementary at the site-specific scale than the regional scale. There were no significant correlations for the island sites (Table 4). For the mainland sites, combined seabird rates were positively correlated with wrasse densities and Caspian tern foraging rates were negatively correlated with surfperch densities (Figure 4). Both Caspian terns and least terns are plunge divers and can penetrate <0.5 m of the water column. The negative correlation between Caspian tern foraging rates and surfperch densities may indicate an avoidance of kelp forest habitat where fish can easily hide from plunge divers and less easily hide from pursuit divers like cormorants and guillemots that can swim throughout the water column.

Despite the overall lack of correlation between juvenile fish densities and seabird foraging rates, there were definite similarities that are noteworthy within the island (Figure 5) and mainland (Figure 6) regions. Within SCI-S, wrasse and rockfish densities were highest at M7 where Brandt's cormorants also showed their highest foraging rates. Pelagic and double-crested cormorants showed similar rates for M7 and R4 indicating that densities for other juvenile fishes may have been similar between the two sites in 2012. Within SCI-N, surfperch densities were highest at M6 while damselfish and wrasse were more evenly distributed among sites. Pigeon guillemots also showed high foraging rates at M6, while Brandt's cormorant foraging rates were similar among sites. For the two SCI-N sites surveyed for fish in 2013 (R3 and M6), Brandt's cormorant foraging rates were highest at M6 where wrasse and damselfish densities showed the highest increases. Within PVP, fish densities were low and spread evenly among sites in 2012. Foraging rates for Caspian terns and least terns were also low at PVP sites. The most abundant fishes at PVP in 2012 were surfperches. Double-crested cormorants, a surfperch predator, showed relatively high foraging rates at the PVP sites in 2012. Additionally, both surfperch densities and double-crested cormorant foraging rates decreased at PVP sites in 2013. Finally, within SD Brandt's cormorant foraging rates were highest at M2 where wrasse and damselfish densities were also highest.

4 | DISCUSSION

Our results showed that spatio-temporal trends in fish densities and seabird foraging rates were similar at the regional scale, but less similar at the site-specific scale. The lack of similarity at the site-specific scale is likely because fish and seabird survey methods measure different components of the nearshore ecosystem. In fact, combining fish and seabird monitoring efforts likely presents a more holistic approach to nearshore fish recruitment. The fish surveys were designed to sample kelp forests and focused on fish species associated with rocky reef habitat. While the seabird surveys were located at the same sites as fish surveys, seabird surveys sampled all habitats within a 1-km radius of the observation point. The seabirds in our study take prey from both rocky reef and soft bottom habitats. Additionally, these species will take pelagic prey, including young-of-the-year (YOY) rockfish that have not settled into adult habitat, and anchovies (family Engraulidae). The availability of pelagic YOY rockfish and anchovies is seasonally variable, with shoals congregating in

TABLE 4 Results of Spearman's rank correlation analyses of seabird foraging rates versus juvenile fish densities

	EMB	LAB	POM	SEB	Total fish
Regional scale					
PIGU	0.40	0.00	−0.20	0.80	0.60
	0.60	1.00	0.80	0.20	0.40
BRAC	0.20	0.40	−0.40	**1.00**	0.80
	0.80	0.60	0.60	**<0.01**	0.20
PECO	0.20	0.40	−0.40	**1.00**	0.80
	0.80	0.60	0.60	**<0.01**	0.20
DCCO	−0.40	0.00	0.20	−0.80	−0.60
	0.60	1.00	0.80	0.20	0.40
Total seabirds	−0.40	0.80	0.20	0.80	**1.00**
	0.60	0.20	0.80	0.20	**<0.01**
Island sites					
PIGU	0.70	−0.40	060	−0.60	−0.10
	0.19	0.50	0.29	0.29	0.87
BRAC	−0.60	0.30	−0.80	0.30	0.00
	0.29	0.62	0.10	0.62	1.00
PECO	−0.70	0.10	−0.50	0.10	−0.60
	0.19	0.87	0.39	0.87	0.28
DCCO	−0.30	−0.10	−0.60	0.40	−0.10
	0.62	0.87	0.29	0.50	0.87
Total seabirds	−0.60	0.30	−0.80	0.30	0.00
	0.28	0.62	0.10	0.62	1.00
Mainland sites					
BRAC	0.71	0.03	0.03	−0.55	0.26
	0.11	0.96	0.96	0.26	0.62
DCCO	−0.26	−0.03	−0.31	0.75	−0.03
	0.62	0.96	0.54	0.08	0.96
LETE	−0.67	0.03	−0.05	0.46	−0.20
	0.15	0.96	0.91	0.36	0.70
CATE	**−0.83**	0.20	0.54	−0.20	−0.26
	0.04	0.70	0.27	0.70	0.62
Total seabirds	−0.14	**0.83**	0.71	−0.67	0.60
	0.79	**0.04**	0.11	0.15	0.21

BRAC, Brandt's cormorant; CATE, Caspian tern; DCCO, double-crested cormorant; EMB, Embiotocidae (surfperches); LAB, Labridae (wrasses); LETE, California least tern; PECO, pelagic cormorant; PIGU, pigeon guillemot; POM, Pomacentridae (damselfishes); SEB, Sebastidae (rockfishes).

For each pair, the top value is the correlation co-efficient (rho) and bottom number is the significance (*p*-value). Significant correlations are shown in bold. LETE and CATE were not included in regional scale analysis because they did not breed or forage at the two island areas and, thus, the sample size was too small to perform the analysis.

nearshore habitats during spring and summer months (Kucas, 1986; Stein & Hassler, 1989). The timing of shoal formation is also highly variable. Thus, it is possible that diver surveys underestimate these species or miss them altogether. Finally, it is noteworthy that spatial trends in fish densities and seabird foraging rates differed the most at SD. The SD sites had the highest percent of sand coverage of all 11 sites. It is likely that seabirds foraging at SD were targeting more soft bottom and pelagic fishes than rocky reef fishes.

Ultimately, using multiple sampling approaches should produce a more holistic picture of recruitment to nearshore habitats. This approach has been well illustrated in a series of three studies that integrated fish and seabird metrics to investigate temporal variability in first annual juvenile rockfish abundance and then annual adult salmon abundance. Adult salmon are trophic equivalents to many seabird species as both salmon and seabirds prey heavily on juvenile rockfish. Thayer and Sydeman (2007) showed significant co-variation in sea surface temperatures, independent measures of juvenile rockfish abundance, and seabird diet, validating the ability of seabirds to index prey abundance as well as oceanographic parameters influencing prey abundance. Mills et al. (2007) integrated the diets of three seabird species and adult salmon with independent net samples of juvenile rockfish to produce multivariate indices of juvenile rockfish abundance explaining more of the inter-annual variability than any individual metric. Finally, Roth et al. (2007) developed models that integrated seabird and salmon metrics that successfully forecasted salmon abundance in a given year. The seabird models explained up to an additional 54% of the variation in salmon abundance compared with traditional jack-based models used by fisheries managers. These results illustrate how developing indices through the integration of fish and seabird data can potentially improve sampling schemes by providing information on difficult-to-measure biological as well as physical variation acting on juvenile fish populations.

In 2012, surfperches, wrasses and damselfishes were the most abundant families in the fish surveys at all the sites. While seabirds are known to take these prey, they are taking other species as well. Of the six seabird species in our study, pelagic cormorants are the most obligate to rocky reef habitats (Ainley, Anderson, & Kelly, 1981). Pelagic cormorants have been poorly named as their diet consists primarily of non-schooling, rocky reef fishes such as sculpins (family Cottidae) and settled rockfish, although they will take pre-settled YOY rockfish if abundant (Hobson, 2013). Brandt's cormorants, double-crested cormorants and pigeon guillemots are the most general of the six species and will take fishes from both rocky and soft bottom habitats and throughout all depths of the water column. At the Southern California islands, Ainley et al. (1981) found that Brandt's cormorants preyed heavily on damselfishes, wrasses, rockfishes and anchovies. At a mainland Southern California site during the same years as this study, Brandt's cormorants took mainly flatfish in 2012 and took more anchovies, rockfish and sculpins in 2013 (D. P. Robinette, unpublished data). A long-term study in Central California found that Brandt's cormorants will readily switch prey items, preying heavily on anchovies in some years and rockfish and flatfish in others (Elliott, Bradley, Robinette, & Jahncke, 2015). Double-crested cormorants typically forage more inshore than Brandt's cormorants (Dorr, Hatch, & Weseloh, 2014), taking schooling fishes such as silverside smelt (family Atherinopsidae) and anchovies,

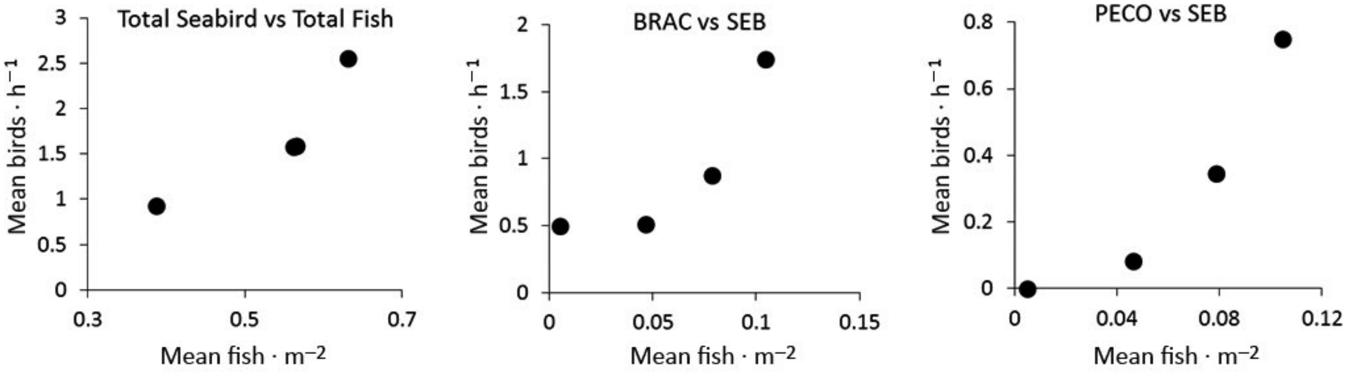

FIGURE 3 Plots of mean seabird foraging rates versus mean juvenile fish densities for 2012 correlations with significant outcomes at the regional scale (Table 4). Each point represents a study area (i.e., PVP, SD, SCIN, or SCI-S). BRAC, Brandt's cormorant; SEB, Sebastidae (rockfishes); PECO, pelagic cormorant

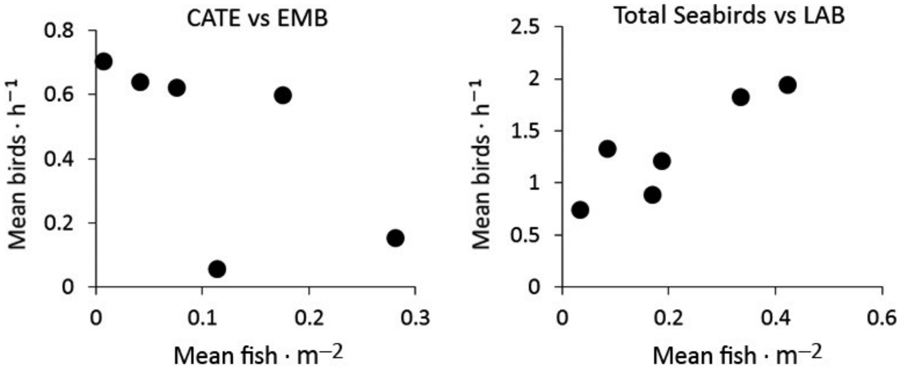

FIGURE 4 Plots of mean seabird foraging rates versus mean juvenile fish densities for 2012 correlations with significant outcomes at the island study site scale (Table 4). Each point represents an individual island study site. CATE, Caspian Tern; EMB, Embiotocidae (surfperches); LAB, Labridae (wrasses)

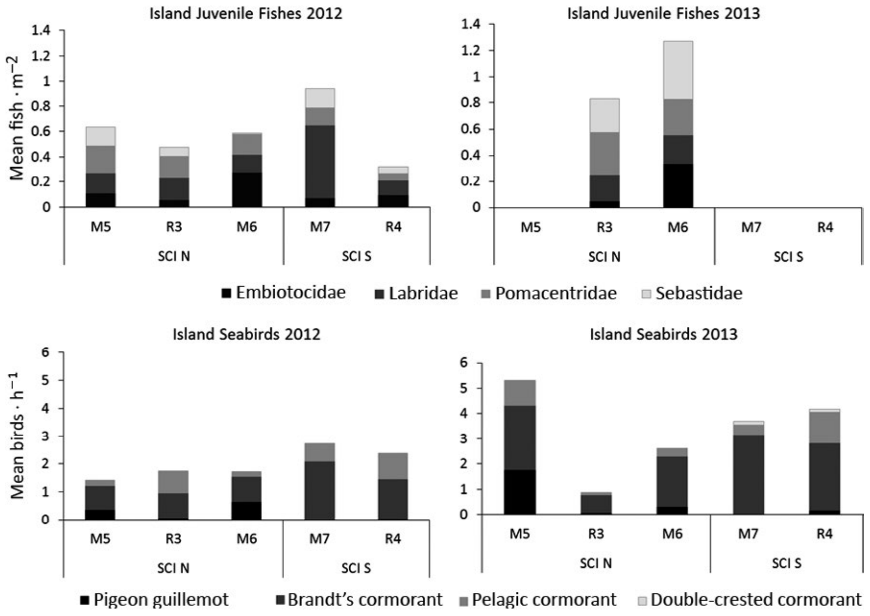

FIGURE 5 Mean juvenile fish densities and mean seabird foraging rates for island study sites in 2012 and 2013. Absence of bars for M5, M7, and R4 in 2013 are due to an absence of data for those sites in 2013. See Table 4 for definitions of seabird and fish codes

as well as non-schooling fishes like croakers (family Sciaenidae), midshipman (family Batrachoididae) and surfperches (Ainley et al., 1981). Pigeon guillemots have a short foraging range and diet often reflects habitat types adjacent to the breeding colony (Ewins, 1993). Diets of guillemots breeding within 2 km of each other can vary substantially (e.g. Robinette et al., 2007). Sanddabs (family Paralychthyidae), sculpins and midshipman were important prey at a mainland Central California site (Robinette et al., 2007) while rockfish were important at Southeast Farallon Island off Central California (Ewins, 1993). Caspian terns are similar to

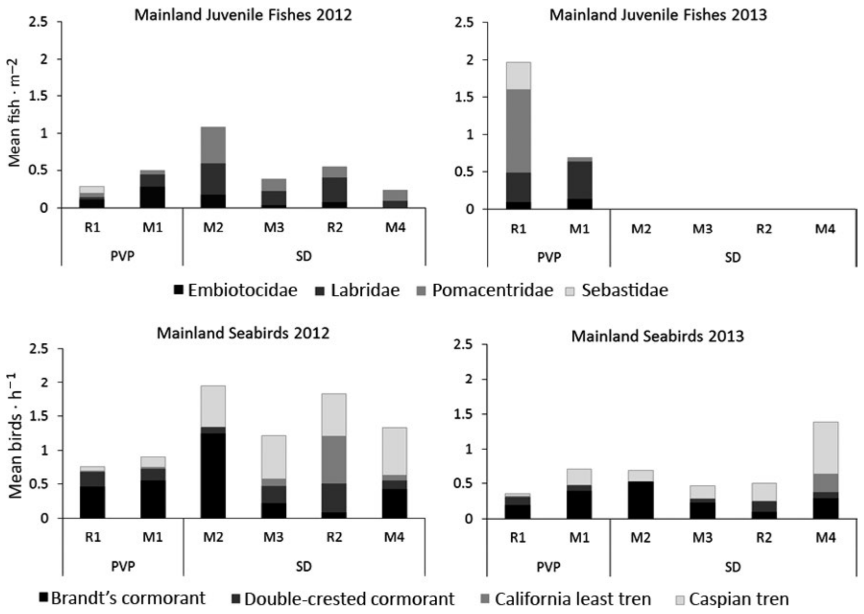

FIGURE 6 Mean juvenile fish densities and mean seabird foraging rates for mainland study sites in 2012 and 2013. Absence of bars for M2, M3, R2, and M4 in 2013 are due to an absence of data for those sites in 2013. See Table 4 for definitions of seabird and fish codes

double-crested cormorants with their inshore foraging habits, taking mostly croakers, silverside smelt and anchovies in one Southern California study (Robinette, 2003) in addition to surfperch and sculpins in other California studies (Cuthbert & Wires, 1999). Least terns also forage mostly inshore, preying heavily on anchovies, silverside smelt (Robinette, 2003) and pre-settled YOY rockfish (D. P. Robinette, unpublished data).

Fish survey results indicate that rockfish recruitment was higher in 2013 than in 2012 as the densities of juvenile rockfish were higher at all four sites surveyed in 2013. The seabird results indicate that juvenile rockfish densities were likely higher at the island than the mainland as all island foraging species showed higher foraging rates at the island in 2013 than 2012. Additionally, data on Brandt's cormorant reproductive success show that success was much higher in 2013 at SCI and higher in 2012 at SD (Robinette, Howar, Elliott, & Jahncke, 2014). Oceanographic conditions during our study were cool and productive, the results of an overall negative state of the Pacific Decadal Oscillation that has persisted since 2007 and above average upwelling conditions in 2012 and 2013 (Wells et al., 2013). These conditions generally favor species like rockfishes and anchovies. However, the offshore advection created during intense upwelling may have pushed the larvae and juveniles of these species further offshore. Upwelling conditions relaxed in the summer of 2013, and anchovy and YOY rockfish abundance increased in trawl surveys (PaCOOS 2013) and in the diet of least terns at many Southern California breeding colonies (Robinette et al., 2014). Additionally, El Niño-like conditions developed in spring and summer of 2012, but then dissipated by fall. While these conditions had no apparent impact on sea surface temperatures (likely due to the above average upwelling), they may have contributed to the low YOY rockfish abundance and low seabird reproductive success observed in 2012.

Our results highlight the complexities of understanding recruitment, especially for multi-species assemblages and under variable oceanographic conditions. We propose that the best way to understand these mechanisms is to take a two-pronged approach, looking at (i) broad-scale oceanographic conditions to understand variability in regional larval production and (ii) fine-scale tracking of how larvae are delivered to MPAs and areas outside MPA boundaries. Seabirds can provide information for both of these approaches. Monitoring seabird breeding population sizes and reproductive success can complement indices of ocean climate to track inter-annual variability in ocean productivity while monitoring seabird diet and foraging can complement fish surveys to provide information on spatio-temporal variability in fish recruitment. Ideally, data on all of the above metrics could be combined to produce an region-, and maybe even site-, specific index of annual fish recruitment that will help explain rates of change observed within individual MPAs. Integrating fish data and seabird data into one multivariate index would provide a more holistic approach to assessing the recruitment of multiple fish species inside and outside of MPAs. Understanding and tracking recruitment will then allow managers to set realistic expectations for how quickly change should occur within individual MPAs and the MPA network as a whole.

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