



# Brandt's cormorant diet (1994–2012) indicates the importance of fall ocean conditions for northern anchovy in central California

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## ABSTRACT

Effective ecosystem-based management requires a comprehensive understanding of the functional links in the system. In many marine systems, forage species constitute a critical link between primary production and upper trophic level marine predators. As top predators, seabirds can be indicators of the forage species they consume and the ocean processes that influence these populations. We analyzed the diet and breeding success for the years 1994, 2003, 2005, and 2007–2012 of the Brandt's cormorant (*Phalacrocorax penicillatus*), a piscivorous diving seabird, breeding in central California, to evaluate the extent to which cormorant diet composition relates to prey availability, and how diet composition relates to breeding success and ocean conditions. Cormorant diet was primarily composed of young-of-the-year (YOY) northern anchovy (*Engraulis mordax*), YOY rockfish (*Sebastes* spp.), and several species of small flatfish (order Pleuronectiformes). YOY rockfish consumption was positively related to their abundance as measured in a late spring pelagic midwater trawl survey. Northern anchovy appeared to be the most important prey as its consumption was positively related to cormorant breeding success. More northern anchovy were

consumed in years where warm-water conditions prevailed in the fall season before cormorant breeding. Thus, warm ocean conditions in the fall appear to be an important contributing factor in producing a strong year-class of northern anchovy in central California and consequently a strong-year class of Brandt's cormorant on the Farallon Islands.

**Key words:** California Current, *Engraulis mordax*, Farallon Islands, *Phalacrocorax penicillatus*, rockfish, seabirds as indicators, *Sebastes*

## INTRODUCTION

Marine systems are under increasing stress from anthropogenic activity (e.g., fishing, nutrient input, pollution, and climate change; Teck *et al.*, 2010). As a result, there is increasing demand for ecosystem-based management approaches that account for the combined impacts of exploitation on multiple components of complex systems (Lester *et al.*, 2010; Teck *et al.*, 2010). In order to practice a more holistic approach to managing ocean resources, it is important to develop an understanding of marine ecosystem functions and the mechanistic links between abiotic conditions (e.g., sea surface temperature), biotic responses at multiple trophic levels (e.g., fish and seabirds; Borstad *et al.*, 2011), and competitive and facilitative relationships (Ainley *et al.*, 2009; Ainley and Hyrenbach, 2010).

In upwelling-dominated systems, a critical intermediate trophic link is occupied by small, schooling, pelagic fish (i.e., forage fishes; Brodeur *et al.*, 2005; Ralston *et al.*, 2015). Typically, a relatively few number of species serve as the primary energy transfer between lower trophic (e.g., plankton) and upper trophic level predators (e.g., salmon, tuna, and seabirds), which has led to a growing concern over the consequences of large-scale fisheries on forage species to the rest of the food web (Smith *et al.*, 2011; Ainley *et al.*, 2015). Moreover, it has long been recognized that the annual abundance of many forage species is subject to high interannual or interdecadal variability, often driven by changes in ocean conditions (Miller

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and Sydeman, 2004; Lindegren *et al.*, 2013) and influenced by competitive forces (Ainley *et al.*, 2009; Ainley and Hyrenbach, 2010). Therefore, understanding the mechanisms that influence the abundance of these important forage species is a critical step in moving toward multispecies and ecosystem-based management.

One of the challenges to effective ecosystem-based management of pelagic ecosystems is the difficulty involved in assessing the abundance of highly mobile, pelagic forage fish. Seabirds have often been mentioned as potentially good indicators of the marine environment: they are relatively easy to study, and their breeding success is often linked to changes in ocean conditions and prey availability (Boehelheide and Ainley 1989; Thayer and Sydeman, 2007). Furthermore, the diet of seabirds has been shown to be strongly correlated with the availability of their prey (Ainley *et al.*, 1993; Miller and Sydeman, 2004). Information on changes in seabird diet has proven useful in understanding fish recruitment and has been used in models that have informed fisheries management (Field *et al.*, 2007; Roth *et al.*, 2007). With recent increased interest in ecosystem-based management in the California Current, considerations related to seabirds are now being included in management plans, both with respect to their role as consumers, as well as competitors with humans (Field *et al.*, 2010; Smith *et al.*, 2011). There is a need for indicators and metrics of ecosystem function, and seabirds are well suited to provide information on forage species (Ainley *et al.*, 2015; Lyday *et al.*, 2015). By examining the relationships between seabird diet and prey, and prey and ocean climate, we can better understand the links between climate and upper trophic level predators. If changes in diet accurately reflect changes in prey availability, diet information could be used alone or in concert with other fisheries catch data to make inferences about the consequences of changes in forage species abundance over time (e.g., Roth *et al.*, 2007).

In this paper, we use data collected on the Brandt's cormorant (*Phalacrocorax penicillatus*) breeding on Southeast Farallon Island (SEFI), California. The Brandt's cormorant is of particular interest because their breeding success fluctuates dramatically, and at times out of sync with other seabirds in the area (Schmidt *et al.*, 2014). This has been apparent in recent years as central California Brandt's cormorant populations suffered several years of very poor breeding success, whereas other species were experiencing high productivity (Capitolo *et al.*, 2014; Schmidt *et al.*, 2014). In addition, recent findings comparing Brandt's

cormorants at the offshore SEFI site and the nearshore Point Arguello site showed different diets and contrasting productivity; however, both colonies showed similar trends in the occurrence of certain prey species in the diets (Elliott *et al.*, 2015), suggesting the greater importance of particular forage species to the offshore SEFI cormorants. These contrasting responses suggest Brandt's cormorants are not only dependent on different prey than other seabirds, but their prey may be responding differently to ocean conditions than other forage fish in the area. For this paper, we aim to address three questions: (i) What are the most important prey affecting breeding success in the Brandt's cormorant on SEFI?; (ii) Does the Brandt's cormorant diet composition match the prey abundance measured by trawl sampling in the region?; and (iii) Do ocean conditions influence the most important prey species in the cormorant diet? By analyzing the relationships between diet, prey availability, breeding success, and ocean conditions, we will gain valuable insight into how important forage fish respond to ocean conditions in central California.

## METHODS

### *Study area*

The Farallon Islands (37°42'N, 122°60'W), are located 48 km west of San Francisco along the central California coast (Fig. 1a). They are the largest seabird colony in the continental United States and have historically hosted the single largest Brandt's cormorant colony in the world, with the cormorant population ranging from 1250 to 24 000 breeding birds (Wallace and Wallace, 1998).

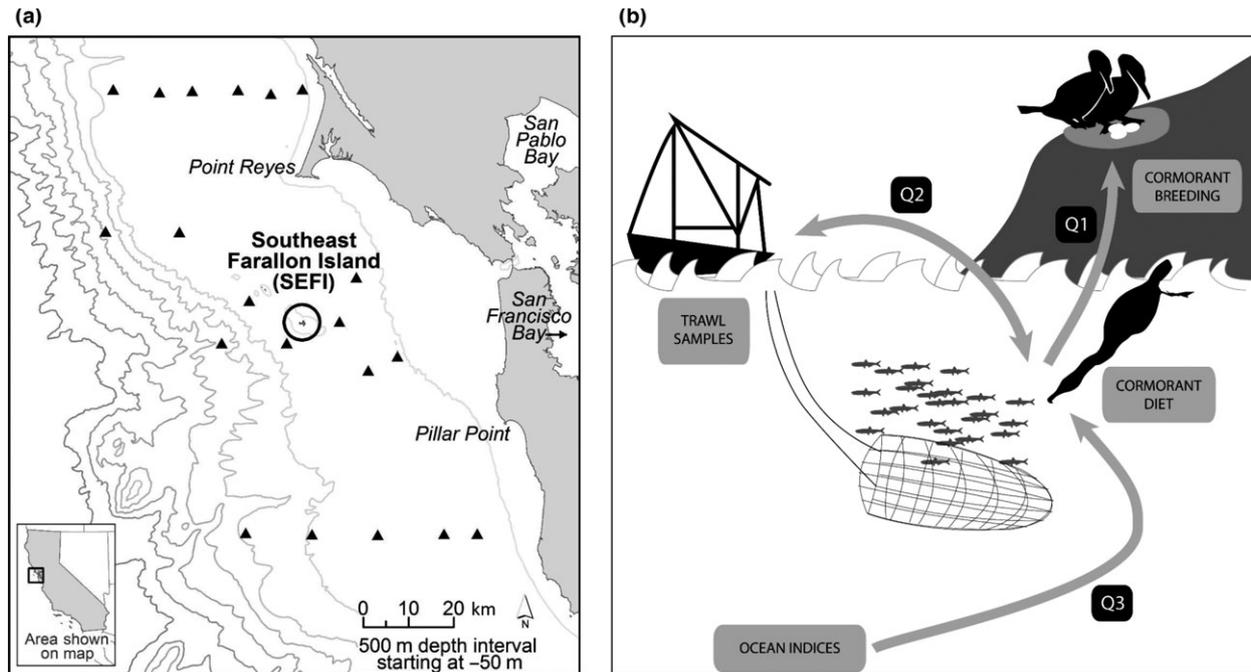
### *Brandt's cormorant breeding success*

A minimum of 60 Brandt's cormorant nests were monitored each year on SEFI from 1971 to 2012 to determine the annual mean breeding success. Nest contents were recorded every 5 days from blinds using binoculars and 20–60× spotting scopes from late March through to July. Breeding success (number of chicks fledged per pair) was based on nests in which at least one egg was produced and determined for all attempts (including first attempts and relays). We considered chicks fledged if they reached at least 25 days and were wandering from the nest (crèched).

### *Brandt's cormorant diet*

We collected regurgitated pellets from several Brandt's cormorant breeding areas on SEFI at the end of the breeding season. In most years, we

**Figure 1.** (a) Map showing the location of Southeast Farallon Island in central California, United States. (b) Diagram of the study system and our questions. Arrows and black boxes indicate questions explored. Q1: What are the most important prey affecting breeding success in Brandt's cormorants?; Q2: Does the Brandt's cormorant diet composition match the prey abundance (as measured by trawl sampling)?; Q3: Do ocean conditions influence the most important prey species in the cormorant diet?



attempted a stratified sampling approach by collecting from 3 to 7 different subcolonies, although only one subcolony was sampled in 2003. Pellets are produced daily and are regurgitated by adults and subadults (i.e., an age when young cormorants learn to fly; Wallace and Wallace, 1998), and their contents have been used to provide a quantitative index of diet composition (Barrett *et al.*, 2007). The time of the pellets' deposition was unknown, so it is assumed that they could have been deposited it at any point during the breeding season (which can vary but is roughly March–August). However, most pellets collected were likely deposited later in the season (June–August), as they have not been subjected to trampling or other degradation. All pellets were frozen for later processing. For analysis, each pellet was soaked in water with detergent (to suppress further enzyme action and further erosion of contents), then rinsed through a 0.5-mm sieve. We examined contents under a dissecting microscope. All sagittal otoliths and pre-opercle spines were removed and identified to the lowest taxonomic level possible (Wyllie Echeverria, 1987; Harvey *et al.*, 2000; Yakich, 2005; Lowry, 2011). While cephalopod beaks were also removed and identified from

samples, they only constituted 1% of the prey items identified; therefore, this study focuses on the fish species consumed. We enumerated the number of prey in each taxonomic group by using the higher number of left and right otoliths. To estimate the size of prey, the lengths of intact otoliths that were not very eroded were measured with an ocular micrometer to the nearest 0.1 mm. Species-specific regression equations, from the literature or created from our otolith reference collection, were used to estimate fish length and mass from otolith size (Table S1). Cumulative prey curves were created for each year to determine if a sufficient number of samples had been analyzed (Ferry and Caillet, 1996).

We used two measures of diet: the average individual length per species/group per sample, and the Geometric Index of Importance (GII; Assis, 1996). For the most common prey species/group, we estimated fish length based on measured otoliths and calculated the mean of the estimated fish length in each sample, then calculated an annual average. Unmeasurable yet identifiable otoliths (i.e., broken or eroded, but still identifiable to a prey group) were excluded from this metric.

To understand the importance of the different prey in the diet of the Brandt's cormorant, we calculated an annual GII for important prey groups (Assis, 1996; Brown *et al.*, 2012). The GII uses three metrics for the following calculation:

$$\text{GII} = (\%N + \%M + \%FO) / \sqrt{3}$$

where %N represents the percent by number, %M is the percent by mass, and %FO is the percent frequency of occurrence; this sum is then divided by the square root of the number of variables used, which is three in this study. As we could not estimate the mass of all prey consumed, we adjusted our GII calculations to be the percent by number (%N) and the percent by mass (%M) of species/groups for which we had size estimates (see Table S1). %FO was calculated as the percent of samples these prey were present in for a given year. Unidentifiable prey (i.e., otoliths that were too broken or eroded to identify to a prey group) were excluded from prey calculations. To ensure sufficient sample sizes to characterize diet, we only used data from years in which >20 pellets were collected and analyzed: 1994, 2003, 2005, and 2007–2012 (9 yr total).

#### Fish trawl data

Data on fish abundances were derived from a trawl monitoring survey covering much of the potential foraging area for cormorants conducted by the National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS). The NMFS trawl surveys used in our study were conducted annually in central California in May through to mid-June starting in 1983 (Sakuma *et al.*, 2006). Standardized nighttime midwater trawls to survey young-of-the-year (YOY) rockfish (*Sebastes* spp.), other groundfish, and other epipelagic/mesopelagic species were conducted at a set of fixed stations in the core area between Monterey Bay and Point Reyes, with the survey area expanded to the entire California coast beginning in 2004 (Sakuma *et al.*, 2006; Ralston *et al.*, 2013). For the purposes of this paper, we used data from stations near SEFI, which included all stations in the core area except the stations in and just north of Monterey Bay (see Sakuma *et al.*, 2006; Fig. 1) from 1990 to 2012. The NMFS trawls captured a number of species, many of which were not potential prey items to Brandt's cormorants based on their size and depth range (Ralston *et al.*, 2015). Also, size information (standard length) was only available for select species and life history stages.

We limited our analysis to likely cormorant prey items based on previously published information on the diet of SEFI Brandt's cormorants (Ainley *et al.*, 1981). Catch data for these fish were summed by haul then log-transformed to adjust for the high variability in catches. The log-transformed counts were then averaged over each cruise (4–6 weeks in May–June) to provide an annual estimate of prey abundance in the region.

#### Ocean conditions

We used several indices at both local and regional scales to quantify ocean conditions (Table S2). As an indicator of local upwelling, we used local sea surface temperature (SST) measured daily at SEFI [see Abraham and Sydeman (2004) for collection details]. Upwelling in the region has a distinct seasonal cycle, so we calculated seasonal means for SST using the definitions provided in Largier *et al.* (1993), which are the spring upwelling season (April–July), the fall low-upwelling or 'relaxation' season (August–November), and the winter 'storm' season (December–March). Previous studies indicated that conditions prior to the breeding season are important to seabird prey (Ainley *et al.*, 1993; Abraham and Sydeman, 2004), so we calculated the mean SST during the fall and winter seasons prior to the breeding season of interest, as well as the spring upwelling season during the breeding season. To quantify regional, low frequency variability in ocean conditions, we calculated annual averages (August–July) starting with the fall (August) prior to the breeding season for the following indices: the Multivariate ENSO Index (MEI), Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO). The MEI index characterizes variability in the El Niño Southern Oscillation (ENSO; Wolter and Timlin, 1998). The PDO is an index of SST in the North Pacific basin, with positive values typically indicating reduced productivity in the California Current (Mantua *et al.*, 1997; Mantua and Hare, 2002). NPGO indicates changes in the circulation of the North Pacific gyre and is associated with variation in nutrients and primary production in the Northeast Pacific (Di Lorenzo *et al.*, 2008). These environmental variables were chosen because they have been previously shown to be important predictors of the regional marine ecosystem (Ainley *et al.*, 1993; Thayer and Sydeman, 2007; Ralston *et al.*, 2013). We standardized all ocean variables to have a mean of zero and unit variance before analysis. Pairwise Pearson's correlation coefficients were calculated for all ocean and climate indices to identify highly correlated variables.

### Regression analyzes

We used simple linear regressions to address the three questions (Fig. 1b, Table S3). Because our sample was limited to 9 yr of cormorant diet data, we did not consider models with multiple variables or complex non-linear relationships, although such models could be explored as the time series becomes longer. To test that breeding success varied with diet composition, we modeled the mean number of chicks fledged per pair as a function of the GII values calculated for the dominant species/groups found in the cormorant diet. We tested the second question (Brandt's cormorant diet composition reflects regional prey abundance) by modeling the importance of the same dominant species/groups as a function of the annual mean of the log-transformed catches in the midwater trawl survey; additional analyzes of prey groups were further broken down into species and age classes when possible. Once the prey species influencing breeding success were identified (from question 1), we modeled the GII values for these species/groups as a function of each of the ocean and climate indices for each season to test the third question (ocean conditions influence diet composition). Residuals were plotted and examined for obvious deviation from normality and Shapiro–Wilk

W tests for normality were performed; if residuals deviated significantly from normal, we transformed variables or added a quadratic term, and the normality of residuals was re-tested. Statistical analyzes were performed in Stata (StataCorp, 2007) and R (R Development Core Team, 2013).

## RESULTS

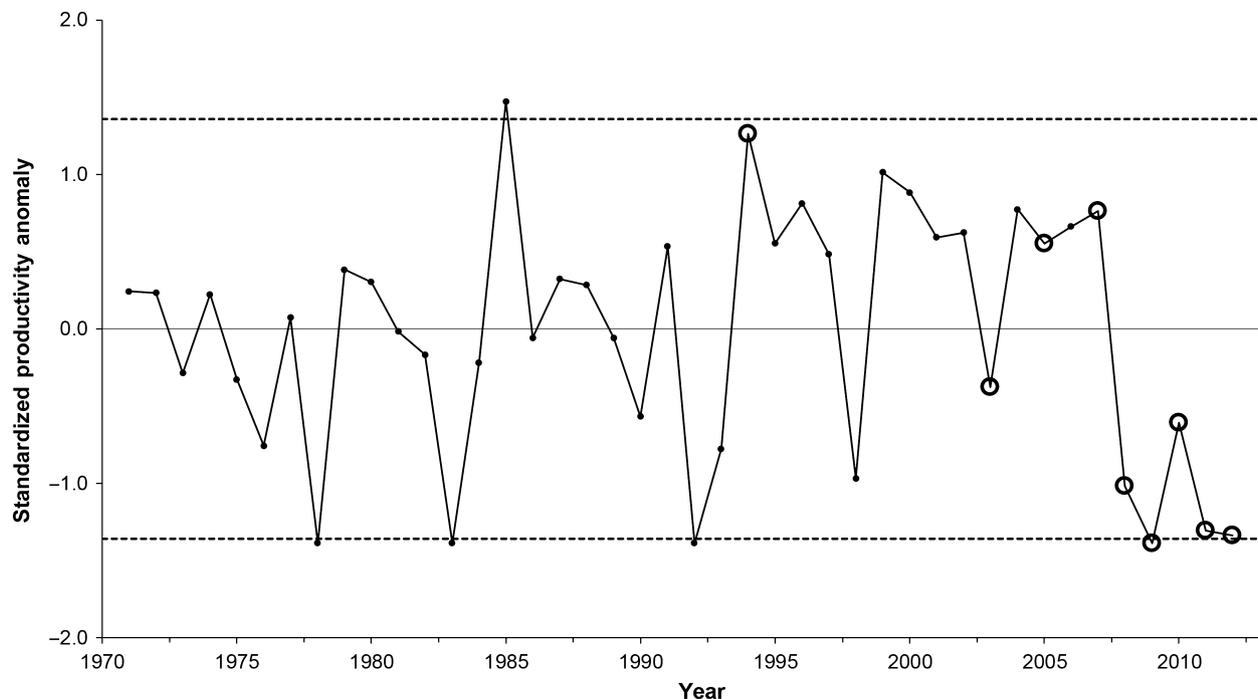
### Breeding success

The breeding success of Brandt's cormorants on SEFI was highly variable, with particularly low breeding success in some years (Fig. 2). Before 2008, most reproductive failures occurred in isolation, typically bracketed by average or above average reproduction. However, breeding success from 2008 to 2012 was exceptionally poor.

### Diet

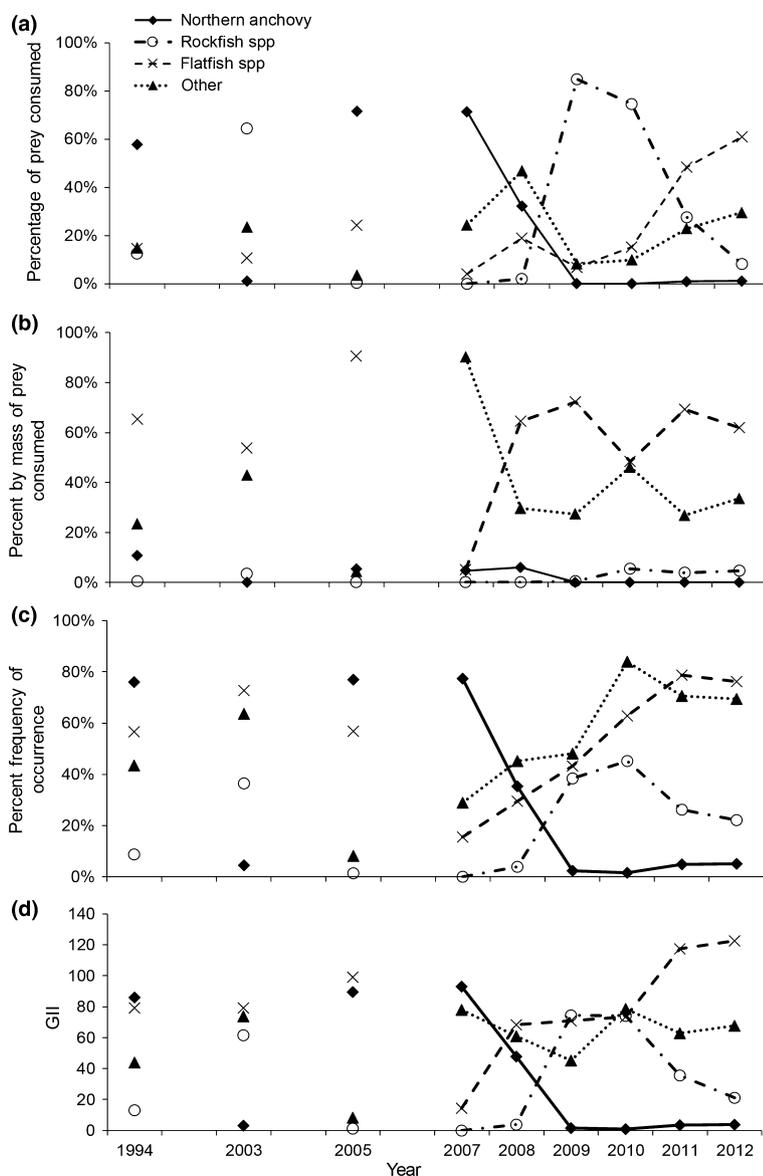
A total of 646 regurgitated pellets analyzed contained otoliths and were used in this analysis (Table 1). Seven species/groups comprised ~90% of the cormorant diet and the three most common prey groups consumed were flatfish species (order Pleuronectiformes), YOY rockfish (*Sebastes* spp.), and northern anchovy (*Engraulis mordax*; Fig. 3a). The 'other'

**Figure 2.** Standardized productivity anomalies for Brandt's cormorants breeding on Southeast Farallon Island, 1971–2012. The zero-line represents the long-term mean productivity; the dashed lines represent the 90% forecast interval around the long-term mean; and the open circles are the years for which diet data exist.



**Table 1.** Samples containing otoliths and corresponding collection information by year.

Year	Number of samples analyzed	Proportion of analyzed samples that contained otoliths	Dates collected	Number of subcolonies represented
1994	46	0.96	17, 22, 23 August	3
2003	22	1.00	14 September	1
2005	74	0.85	8, 9, 14 September	3
2007	97	0.52	16 July; 13 August; 1, 14, 16 September	2 (and one roosting area)
2008	101	0.64	20, 23 September; 2 October	3
2009	124	0.79	29 July; 5–7 August	3
2010	62	1.00	15–16 September; 17 October	3
2011	61	0.98	8, 23 September	4
2012	59	0.98	13–14 August	1
Total	646			



**Figure 3.** Different measures of common prey species/groups in Brandt's cormorant diet on Southeast Farallon Island: (a) percent by number; (b) percent by mass; (c) percent frequency of occurrence; and (d) Geometric Index of Importance (GII).

category contains the remaining four species/groups: Pacific tomcod (*Microgadus proximus*), white croaker (*Genyonemus lineatus*), plainfin midshipman (*Porichthys notatus*), and sculpin species [family Cottidae, with Pacific staghorn sculpin (*Leptocottus armatus*) being the most abundant]. Northern anchovy, YOY rockfish, and flatfish made up 85% of the diet; these were the only species/groups considered in the subsequent regression analysis.

The average individual size of different prey species per sample declined through time, with 2007–09 being a period of significant change in the cormorant diet. The average standard length of flatfish per sample was 154.8 mm  $\pm$  37.2 SD before 2007, then declined to 124.8 mm  $\pm$  33.1 SD in 2007–08, and decreased again to 114.8 mm  $\pm$  32.9 SD in 2009–12. Northern anchovy consumed declined in size over time, with the average standard length of 80.3 mm  $\pm$  7.2 SD before 2007 and 41.6 mm  $\pm$  1.6 SD from 2009 to 10. The average total length of YOY rockfish per sample was 84.4 mm  $\pm$  66.3 SD before 2007, then declined (70.1 mm  $\pm$  44.3 SD) during 2009–12.

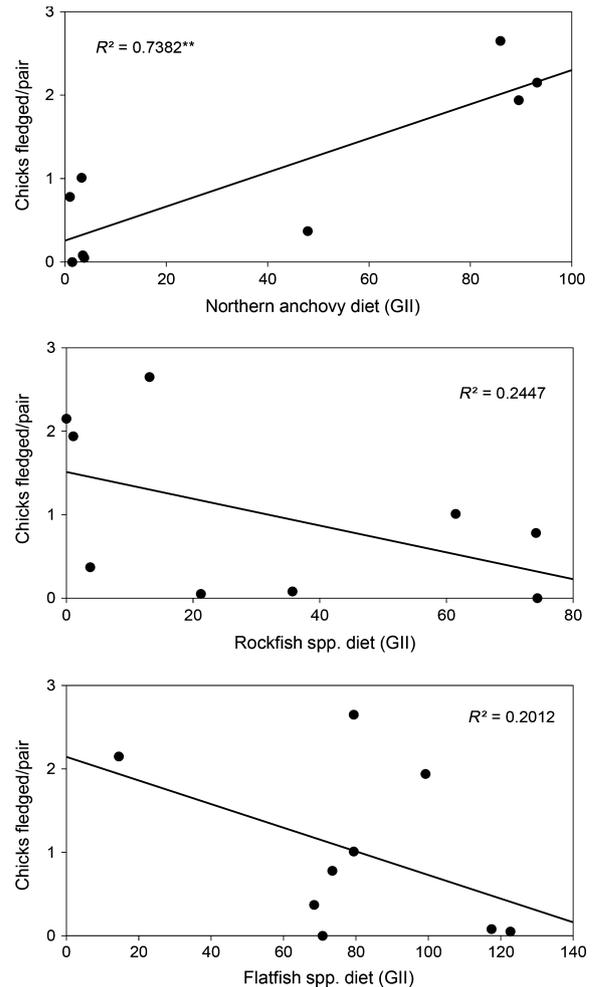
Trends in percent frequency of occurrence were similar to the annual percentages of prey (Fig. 3a,c); however, percent by mass remained low for rockfish and northern anchovy, whereas flatfish and other prey were more variable (Fig. 3b). Northern anchovy appeared in diet samples more frequently in earlier years (e.g., 1994, 2005, 2007; Fig. 3c), coinciding with increased GII values for this species (Fig. 3d). Flatfish species had the highest GII scores in 5 of 9 yr (highest in 2011–12) and only 1 yr where GII was very low (2007; Fig. 3d). YOY rockfish were the most important prey in only 1 yr, 2009.

#### Climate, breeding success, diet, and trawls

Brandt's cormorant breeding success on SEFI covaried positively with the importance (GII) of northern anchovy in the diet ( $R^2 = 0.7382$ ,  $P = 0.003$ ; Fig. 4). There was a slight negative trend in breeding success with increasing importance of YOY rockfish and flatfish in the diet, but neither relationship was significant (Fig. 4).

Changes in diet composition tracked changes in catch composition in the NMFS trawls with the GII values of northern anchovy, rockfish, and flatfish in cormorant diet samples increasing as their relative abundance in the trawls increased (Fig. 5). However, residuals and Shapiro–Wilk test results ( $W = 0.771$ ,  $P = 0.0096$ ) indicated the relationship for anchovy might be curvilinear; therefore, GII values for northern anchovy were log-transformed, and normality of residuals improved ( $W = 0.884$ ,  $P = 0.1749$ ). Only

**Figure 4.** Relationships between the importance (GII) of the three dominant species/groups in Brandt's cormorant diet and the mean number of chicks fledged per breeding pair (\*\* $P < 0.01$ ).

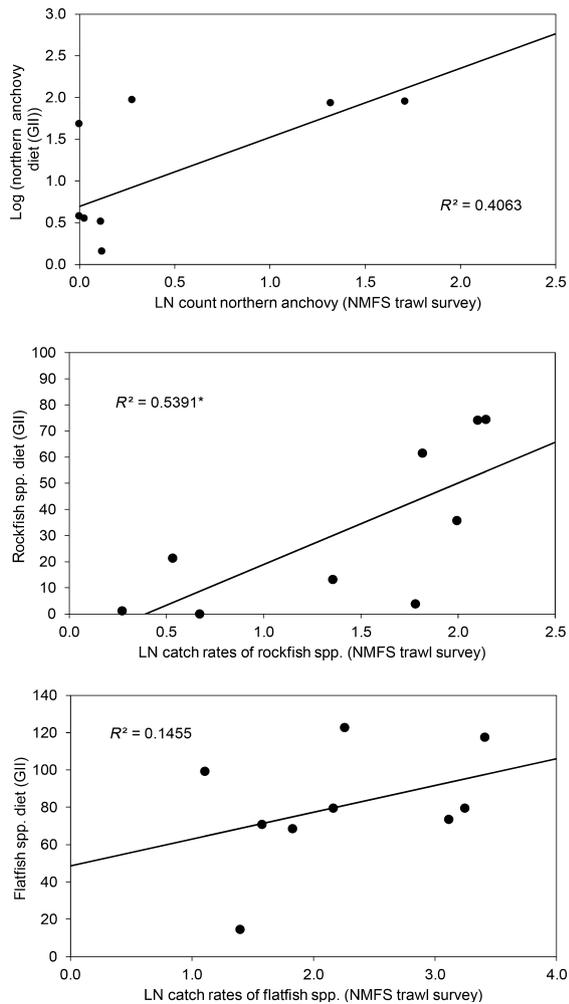


the relationship with YOY rockfish ( $R^2 = 0.5391$ ,  $P = 0.024$ ) was significant.

We further examined relationships between different flatfish species. English sole (*Parophrys vetulus*), Pacific sanddab, speckled sanddab, and unidentified sanddab species (*Citharichthys* spp.) were the most common flatfish species in the cormorant diet. As English sole was not frequently caught by the NMFS survey, we tested for a relationship between the importance of sanddabs (Pacific sanddab, speckled sanddab, and unidentified sanddab species) in the cormorant diet with the abundance of sanddabs in the NMFS trawl samples, but the relationship was not significant.

There were also size and age class information to consider for further analyzes. NMFS surveys primarily

**Figure 5.** Relationships between mean log-transformed catch rates in the NMFS trawl samples and Geometric Index of Importance (GII) values in Brandt's cormorant diet (relationships shown only for the three dominant fish species/groups found in cormorant diet; \* $P < 0.05$ ).



collect age 1+ northern anchovy, but also catch late larval and early juvenile (age 0) life history stages of anchovy. Therefore, catch rates of age 0 northern anchovy (i.e., size classes consumed by the cormorants) in NMFS surveys were also calculated and tested separately with log-transformed diet results (Shapiro–Wilk  $W = 0.897$ ,  $P = 0.2363$ ), but no significant relationship was observed.

In general, climate and ocean variables indicated warmer conditions in the earlier years of our study (through 2005), then a transition to cooler, more productive conditions in the latter years (Fig. 7). Significant correlations were found among the environmental variables (Table 2): these include PDO and MEI (for basin- and global scale variables);

SST values for storm and upwelling periods (for local variables); and NPGO and relaxation period SST, and PDO and storm period SST values for basin and local scales comparisons. These correlations highlight the influence of large-scale forces on smaller scales, and how local conditions during the storm period are associated with upwelling period conditions. We focused our analyzes for our third question on northern anchovy in the diet (GII) in relation to ocean and climate variables. Residuals for the test with NPGO were not normal (Shapiro–Wilk  $W = 0.828$ ,  $P = 0.0426$ ); a quadratic relationship appeared to be a better fit, and residuals for this test improved normality (Shapiro–Wilk  $W = 0.942$ ,  $P = 0.6083$ ). Northern anchovy was only significantly related to NPGO (negative;  $R^2 = 0.7740$ ,  $P = 0.012$ ) and SST (positive;  $R^2 = 0.5035$ ,  $P = 0.032$ ) in the fall season before the cormorant breeding season (Fig. 6). Residuals for the test with MEI (Shapiro–Wilk  $W = 0.852$ ,  $P = 0.0793$ ) and SST during the upwelling season were not normally distributed (Shapiro–Wilk  $W = 0.823$ ,  $P = 0.0388$ ); however, we observed no discernible relationship, so no data transformations or additional tests were performed.

## DISCUSSION

The presence or absence of particular forage fish in the cormorant diet may be influenced by both prey preference and prey availability (Ainley and Boehelheide, 1990; Mills *et al.*, 2007). Cormorant diet composition reflected the availability of northern anchovy and YOY rockfish, but only the rockfish relationship was significant. The positive but non-significant relationship between the importance of northern anchovy in the diet and abundance in trawls may reflect the fact that they appear to be sampling different size/age classes (YOY in cormorant diet compared to age 1+ in the trawls). It may also indicate that northern anchovy is a preferred prey item, and cormorants will at times consume them in higher relative proportion to their availability in the environment. Nevertheless, Brandt's cormorants do appear to consume YOY rockfish in proportion to their relative abundance in NMFS trawls, indicating that cormorant diet can be a useful indicator of the availability of these important forage fish.

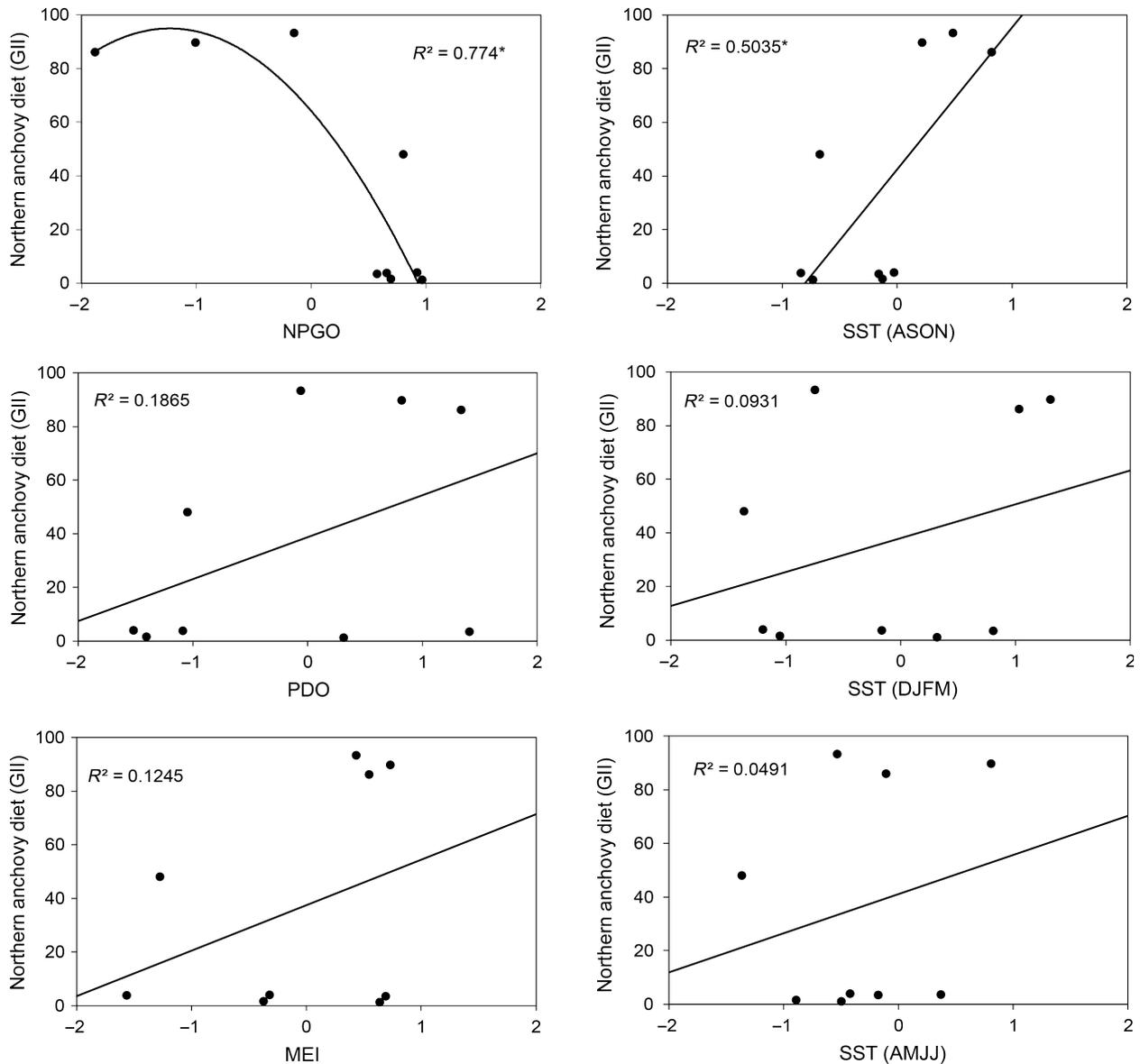
The strong positive relationship between breeding success and northern anchovy in the diet after the early 1990s indicates the importance of this prey when it is available. Northern anchovy is a lipid-rich prey species and contains twice the energy (per unit of mass) as a similarly-sized YOY rockfish (Becker *et al.*,

**Table 2.** Pairwise Pearson's correlation coefficients and significance values for ocean and climate variables.

	PDO	NPGO	MEI	SST (relaxation)	SST (storm)	SST (upwelling)
PDO	–	0.0654	<b>0.0123</b>	0.2032	<b>0.0014</b>	0.2304
NPGO	–0.6363	–	0.1962	<b>0.0084</b>	0.0636	0.1887
MEI	<b>+0.7847</b>	–0.4751	–	0.0855	0.0593	0.4412
SST (relaxation)	+0.4687	<b>–0.8079</b>	+0.6031	–	0.3954	0.5778
SST (storm)	<b>+0.8866</b>	–0.6397	+0.6477	+0.3237	–	<b>0.0200</b>
SST (upwelling)	+0.4447	–0.4822	+0.2949	+0.2154	<b>+0.7496</b>	–

PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation; MEI, Multivariate ENSO Index; SST, sea surface temperature. Numbers below diagonal line are Pearson's correlation coefficients, and numbers above diagonal line are *P*-values. Significant results (*P* < 0.05) are in bold.

**Figure 6.** Relationships between the Geometric Index of Importance (GII) for northern anchovy in Brandt's cormorant diet and ocean indices (\**P* < 0.05; \*\**P* < 0.01).



2007). When this energy-rich species is abundant and close to the breeding colony, it may provide ample energy for relatively little foraging effort. Past research of SEFI Brandt's cormorants has linked poorer breeding success to increased foraging effort during the nestling period (Ainley and Boehelheide, 1990). The decline in the numbers and sizes of northern anchovy could indicate that northern anchovy were no longer readily available to sustain Brandt's cormorants and their chicks during the energy-demanding breeding season. The cormorants then consumed mostly YOY rockfish. The decreased availability of both northern anchovy and YOY rockfish in the later years may have then been even more detrimental to the cormorant colony, causing the switch to other prey (e.g., flatfish species). Flatfish species in the cormorant diet settle at various sizes [ $<25$  mm for English sole (Krygier and Percy, 1986);  $>30$  mm for Pacific and speckled sanddabs (Sakuma and Larson, 1995)], and the sizes observed in the diet suggest that Brandt's cormorants are likely taking settled flatfish, which may be less energetically efficient for cormorants to catch and digest. The years when flatfish dominated cormorant diet were associated with unprecedented low breeding success, indicating they may only forage on these species when other high-value prey are unavailable.

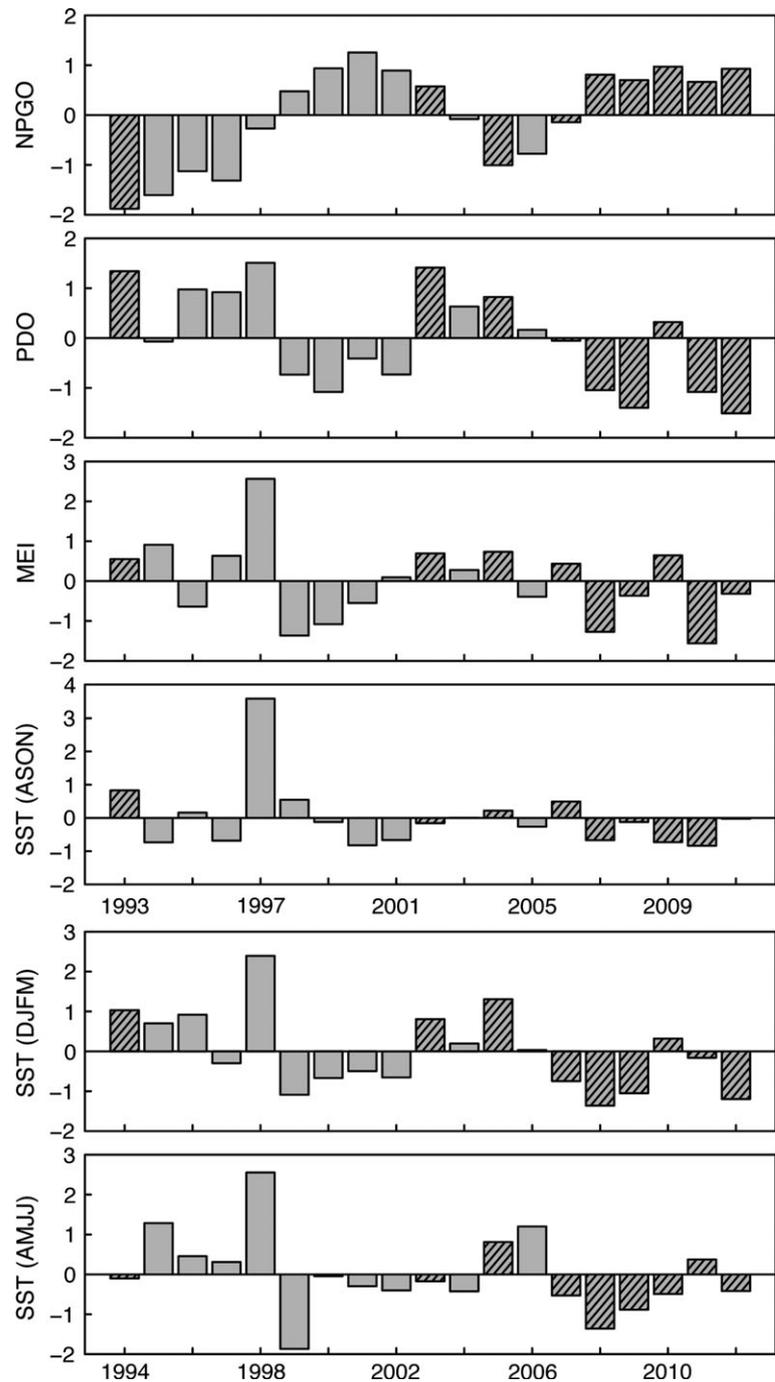
Variability in the abundance of northern anchovy in central California may be explained by variability in spawning production and survival of young in the local area, changes in the distribution of individuals produced elsewhere, and other food web dynamics not addressed here, such as changes in the abundance of anchovy predators. Here, too, the signal might be difficult to disentangle, as some predator populations have declined in recent years [e.g., salmon (*Onchorhynchus* species); O'Farrell *et al.*, 2013], whereas others [e.g., California sea lion (*Zalophus californianus*), humpback whale (*Megaptera novaeangliae*)] have increased substantially (Carretta *et al.*, 2015). Surprisingly, the increased importance of northern anchovy in the diet was associated with warmer ocean conditions (i.e., negative NPGO values, positive SST values) during the fall before the breeding season. Previous studies have indicated anchovy prefer cool conditions (Chavez *et al.*, 2003; but see Santora *et al.*, 2014) and also indicated stronger upwelling and cooler conditions in the winter as an important precursor of summertime productivity in the California Current (Black *et al.*, 2010, 2011). In contrast, our results indicate low upwelling, warmer conditions in the fall before breeding were associated with more northern anchovy in cormorant diet, and consequently higher breeding success (Figs 4 and 7). The significant correlation

between NPGO and fall SST suggests the large-scale forcing behind NPGO is influencing local conditions more during the fall than at other seasons.

The fall period is also when stratification of the surface water in central California is strongest (McGowan, 1986; Palacios *et al.*, 2004). Adult and larval northern anchovy prefer stratified water conditions, which include less wind, less upwelling, and less turbulent mixing (Lasker, 1975; Peterman and Bradford, 1987). These conditions increase survival of northern anchovy larvae by maintaining high concentrations of food (Peterman and Bradford, 1987). Negative NPGO values are also associated with weaker upwelling favorable winds and later onset of upwelling in the spring that can contribute to greater overall stratification (Di Lorenzo *et al.*, 2008; Chenillat *et al.*, 2012).

The northern anchovy found in the SEFI cormorant diet were estimated to be primarily YOY ( $<100$  mm, most northern anchovy reach  $\sim 90$  mm in length at 1 yr; Butler, 1989). Cohort strength of fish populations is determined by spawning output as well as larval survival, so favorable ocean conditions during and after the spawning period for northern anchovy would presumably result in larger and more abundant YOY fish during the cormorant breeding season (Peterman and Bradford, 1987). The northern anchovy that occur in central California may either be from the central or northern subpopulations (Vrooman *et al.*, 1981). The central subpopulation primarily spawns January–April in southern California (Hunter and Macewicz, 1980). This period overlaps with our definition of the winter season (December–March), which was not significant (Fig. 6). However, the spawning of northern anchovy in San Francisco Bay peaks in June–August with peak larval abundance in August–September (McGowan, 1986); this corresponds with the fall season in our analysis and may indicate SEFI cormorants are foraging on anchovy produced within the San Francisco Bay.

The decrease in the size of northern anchovy consumed may indicate a change in the spawning time of northern anchovy. Beginning in 2009, cormorants were consuming northern anchovy nearly half the size (42 mm) of anchovy consumed in the earlier years (80 mm). Northern anchovy that are 80 and 40 mm in length are approximately 7 and 2.5 months old, respectively (Butler, 1989). Assuming pellets represent consumption in June–August, the significant change in size suggests older northern anchovy (spawned during the fall/winter before the breeding season) were eaten in earlier years whereas younger northern



**Figure 7.** Standardized annual means (calculated from August year  $t-1$  to July year  $t$ ) for the North Pacific Gyre Oscillation (NPGO), Pacific Decadal Oscillation (PDO), Multivariate ENSO Index (MEI), and standardized seasonal sea surface temperature (SST) anomalies, 1993–2012. Year on  $x$ -axis for annual indices and fall SST (ASON) is labeled for year  $t-1$ . Diagonal shading denotes years used in the analysis.

anchovy (spawned during the spring) were consumed in later years. In fact, to the south of this region, there has been an observed decline in winter anchovy egg and larval abundances relative to spring since 2000, and a later spawning season was one reason considered for this (MacCall *et al.*, 2015).

The decrease in size may also be related to shifts in the at-sea foraging distribution of cormorants. Past

(Ainley and Boehelheide, 1990) and recent (McGowan *et al.*, 2013) studies confirm higher numbers of Brandt's cormorants foraging near SEFI and in near-shore areas. As larger age classes of northern anchovy became scarce near SEFI, cormorants may be expending more energy traveling to nearshore areas to forage on the smaller, younger age classes of northern anchovy, in addition to the other fish of lower

energetic value (e.g., flatfish, particularly English sole). English sole and speckled sanddabs are known to inhabit nearshore waters and settle in estuaries [Boehlert and Mundy, 1987; Sakuma and Larson, 1995; T. Laidig (NOAA/NMFS), personal communication], areas that are either undersampled or not sampled by the NMFS survey owing to bottom depth constraints.

Our results on the diet and breeding success of the Brandt's cormorant on SEFI demonstrate how this top marine predator can provide information on forage fishes. While YOY rockfish have previously been shown to be important prey to this colony (Ainley and Boehlert, 1990; Nur and Sydeman, 1999), we document for the first time the importance of northern anchovy for this population's breeding success and the importance of warm local fall conditions for YOY northern anchovy production. Brandt's cormorants may be foraging in nearshore waters at the mouth of San Francisco Bay, an area not sampled by the midwater trawls, making for complex diet-trawl comparisons. Nonetheless, this type of information on ecosystem food web linkages can provide increasingly valuable information as we strive to move towards more ecosystem-based management.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Equations used to relate otolith size to fish size, and fish size to fish weight.

**Table S2.** Sources of climate and ocean indices.

**Table S3.** Regression results for relationships between Brandt's cormorant productivity, diet, and environmental variables.