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Changes in forage fish community indicated by the diet of the Brandt's cormorant (*Phalacrocorax penicillatus*) in the central California Current

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ABSTRACT

The population, productivity and diet of two Brandt's cormorant (*Phalacrocorax penicillatus*) colonies located in the central California Current were compared. The offshore colony on Southeast Farallon Island has experienced a declining population over time and anomalously low productivity in recent years. The nearshore colony near Point Arguello has been increasing and its productivity has remained stable. The diets of cormorants at the two colonies elucidated by analysis of regurgitated pellets, while different, have shown similar decreases in the consumption of northern anchovy (*Engraulis mordax*) since 2008, followed by increased consumption of rockfish (*Sebastes* spp.) and flatfish (order Pleuronectiformes). By using the diet results from another seabird nesting in central California, the rhinoceros auklet (*Cerorhinca monocerata*), and one from which whole fish can be obtained, we found that the rockfish species assemblage has changed with offshore rockfish species decreasing while nearshore ones have increased. This change in the rockfish species has negatively impacted Brandt's cormorants at the offshore colony by forcing them to make longer foraging trips to meet energy needs of themselves and their chicks; this has led to low breeding success and a declining population at this site. On the other hand, the nearshore colony has abundant nearby food resources, and it has prospered. These results underscore the value of using seabird data from multiple colonies to better understand changes occurring in the marine environment.

1. Introduction

There is increasing emphasis on managing our marine resources through ecosystem-based fisheries management (EBFM) as opposed to the historical single-species management approach. Though currently subject to much discussion (Link, 2002), in general, the overall goal of EBFM is to sustain healthy marine ecosystems, including its fisheries, with specific objectives to prevent ecosystem degradation, maintain species assemblages and ecosystem processes, preserve long-term benefits to people, and understand the processes of the ecosystem to recognize the impacts of humans (Pikitch et al., 2004).

Forage fish are an important part of the marine food web, being prey to many higher-trophic level organisms. Modeling exercises have been used to explore interactions between forage species and their predators (Cury et al., 2000; Field et al., 2010), and the abundance and composition of forage fishes are known to fluctuate on various time scales based on ocean and climate conditions (Chavez et al., 2003; Schwartzlose et al., 1999). Continued research and monitoring in the California Current and elsewhere are necessary to understand these interactions for effective EBFM.

The Brandt's cormorant (*Phalacrocorax penicillatus*) is a large, colonial nesting seabird that breeds along the west coast of North America (Wallace and Wallace, 1998). This mostly piscivorous species forages mainly on or near the benthos (Ainley et al., 1981), and diet information on this species and other seabirds has been used as an indicator of changes in forage fish populations (Piatt et al., 2007a, 2007b).

For the purposes of this paper, we will be comparing two colonies of Brandt's cormorants in the central portion of the California Current System (CCS): Southeast Farallon Island (SEFI) and Vandenberg Air Force Base (VAN) at Point Conception. SEFI is located in north-central California at the outer edge of the continental shelf; this site hosts the largest Brandt's cormorant colony in the world, and it has been monitored for over 40 years (Ainley and Boekelheide, 1990; Capitolo et al., 2014). VAN, located ~400 km southeast of SEFI, is located on a rock just a few hundred meters off the mainland coast where Brandt's cormorants have been monitored since 2000 (Point Blue, unpublished data).

With population size, reproductive success, and diet data collected from these two colonies, we aim to answer three questions: 1) are Brandt's cormorants from SEFI and VAN consuming the same prey species, 2) are any differences in the diet driven by changes in prey availability, and 3) are contrasting trends in population and productivity related to differences in prey availability and therefore diet?

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2. Materials and methods

2.1. Study sites

SEFI (37°42′ N, 122°60′W) is located 30 miles west of the Golden Gate Bridge, San Francisco, on the outer edge of the continental shelf (Fig. 1). It is the largest seabird colony in the contiguous United States and is included in the Farallon Islands National Wildlife Refuge with the surrounding waters under partial management by the Gulf of the Farallones National Marine Sanctuary. Seabirds have been studied at the Farallones continuously since 1970. Data from 13 species includes population, phenology, reproductive success, and diet (see Ainley and Boekelheide, 1990).

VAN is located just north of Point Conception (34°34′ N, 120°39′W; Fig. 1). VAN hosts six species of seabirds (including the Brandt's cormorant), and Brandt's cormorants were first observed breeding here in 1995; monitoring of this colony began in 2000 (Robinette and Howar, 2013). Brandt's cormorants breed primarily on two mainland points: Point Arguello and North Rocky Point.

2.2. Brandt's Cormorant population size

For the Farallon Islands, all-island censuses for Brandt's cormorants on South Farallon Islands (SFI) have been conducted each year in late May or early June, depending on the timing of peak incubation (Capitolo et al., 2014). Census begins at 0930, and all well-built nests on SFI (which includes SEFI, West End Island, and the Islets) that can be viewed from land are counted, usually in a single day. Nests that are counted are established sites (i.e., well-built nests) occupied by a breeding pair of birds. Poorly-built nests or nests that have been abandoned are not counted. When weather conditions permit, areas not viewable by land but visible from boat are also counted. Multiplying the number of well-built nests by two provides an annual estimate for breeding population size.

For VAN, censuses were conducted of all potential breeding habitat along Point Arguello at least once per week from 1 April through the end of July of each year. All nest sites with evidence of breeding behavior (i.e., birds observed in incubation posture for >2 weeks; presence of eggs, chicks, and/or fledglings) are mapped. The maximum number of nests observed for the year is then multiplied by two to obtain an estimate of breeding population size.

2.3. Brandt's Cormorant productivity

Brandt's cormorants were monitored for chick productivity from a subset of at least 60 nests per year on SEFI from 1971 to 2012. At VAN, all nests viewable from land were monitored from 2000 to 2012. Nest contents were recorded every five days (SEFI) or seven days (VAN) from observation blinds using 10 × 42 binoculars and 20–60× spotting scopes from late March through August/September. During each

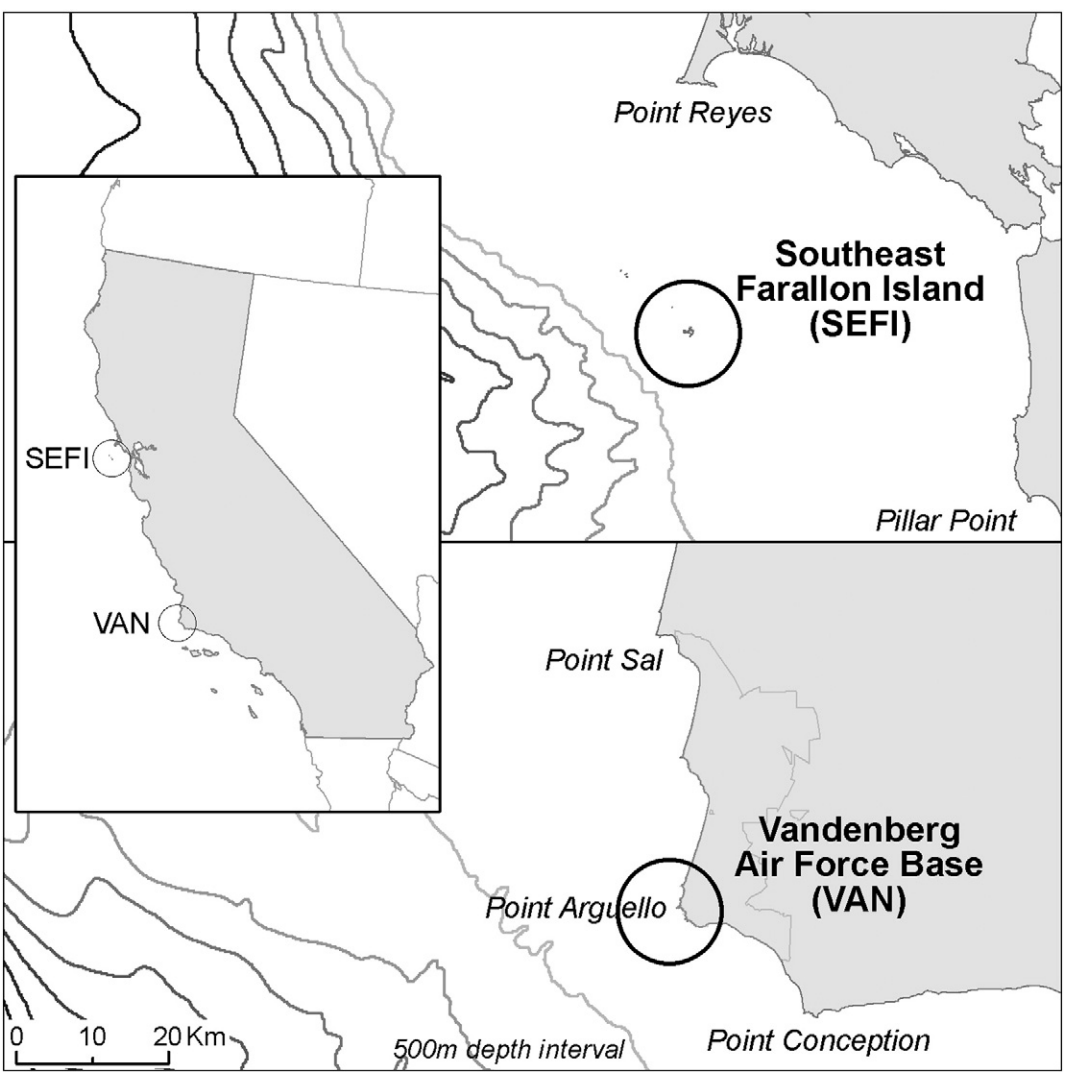

Fig. 1. Locations of the Southeast Farallon Island and Vandenberg Air Force Base Brandt's cormorant colonies.

monitoring visit, we recorded the following: nest condition, number of adults attending (and whether one was in incubating posture), number of eggs, number of chicks, feather condition of chicks (used to estimate chick age), number of fledglings (defined as mostly feathered and wandering chicks), and the reason of a failed nest (e.g., abandoned eggs, dead chicks, evidence of predation). The incubation period for Brandt's cormorants lasts 29–30 days and fledging occurs approximately 30–40 days after hatching, though chicks become independent of the nest and start wandering at 25–30 days old. We consider chicks fledged when they wander from the nest, usually to join groups of other fledglings near the water. Nest checks end once chicks from followed nests begin to wander on a regular basis.

For this study, we estimated breeding productivity as the number of fledglings produced per breeding pair. Productivity was based on nests in which at least one egg was produced and included all nesting attempts (including first attempts and relays). We used only nests for which we successfully determined the number of fledglings produced. We calculated productivity by dividing the total number of fledglings produced by the number of nests with known fledgling numbers.

At VAN, all nests viewable from land were monitored from 2000 to 2012 once every seven days. A nest suitable for productivity monitoring is one in which eggs, chicks, and fledglings can be clearly viewed and enumerated without disturbing the nesting adults. In some cases, only chicks and fledglings were viewable.

2.4. Brandt's Cormorant diet

We collected regurgitated pellets from three main Brandt's cormorant breeding areas on SEFI after each breeding season, whereas pellets from VAN were collected from three different roost sites throughout the breeding season when cormorants were not present (in order to not disturb the birds). Each pellet was stored in a plastic bag, and each bag was labeled with the date and location of collection. All pellets were stored in a freezer and analyzed at the Point Blue Laboratory in Petaluma, California.

For analysis, we soaked each pellet in water with detergent (to suppress further enzyme action and further erosion of contents). We poured the contents over a 0.5 mm sieve and rinsed the contents to remove dirt and other small debris. We transferred the remaining contents to a 14.5 cm plastic dish to examine contents under a dissecting microscope. We removed all sagittal otoliths, preopercle spines, and cephalopod beaks and used these to identify fish and cephalopod prey. All otoliths and beaks were identified to the lowest taxonomic level possible. We enumerated the number of prey in each taxonomic group by using the higher number of left and right otoliths, or upper and lower beaks for cephalopods.

To estimate the size of prey, lengths of otoliths that were not eroded were measured with an ocular micrometer to the nearest 0.1 mm; otolith sizes were then applied to species-specific regression equations from the literature or created from our otolith reference collection relating otolith size to fish length, as well as relating fish length to wet weight (Harvey et al., 2000; Love et al., 2002; Wyllie Echeverria, 1987; Yakich, 2005).

We calculated annual proportions of the most common prey species/groups by adding the number of each prey group and dividing by the number of identifiable prey. For SEFI, we used data from years 1994, 2003, 2005, and 2007–2012, as these years had sufficient sample sizes to characterize diet. Other years of diet data shown are published (1973–77: Ainley and Boekelheide, 1990) or unpublished data (1993: Point Blue, unpublished data). All years of diet collections from VAN (2006–2012) were used in analysis.

To compare the diets of the two colonies, we conducted a chi-square goodness-of-fit test to compare frequency of occurrence of the different prey groups (Archie and Bray, 1999). We used the six years where diet data existed for both colonies (2007–12) for this test, and rarer prey families were combined in order to meet the assumptions of the test.

2.5. Species composition of fish assemblages

While fish otoliths provide accurate information about diet composition, it is difficult to verify species within some genera (e.g., rockfishes, *Sebastes* spp.). Therefore, we investigated the diet of the rhinoceros auklet (*Cerorhinca monocerata*), another seabird breeding on SEFI to better understand the species composition of certain fish families/genera. In the case of rhinoceros auklets, diet data have been shown to reflect prey availability as whole diet items can be collected without undue disturbance and identified (Thayer and Sydeman, 2007).

Diet samples for rhinoceros auklets were collected during annual efforts to capture and mark breeding birds. Auklets were captured beginning at the peak hatching period (when approximately 50% of occupied sites have hatched) and continuing through the chick-rearing period. We captured auklets using mistnets as they returned from foraging trips to provision their chicks. These auklets provision their chicks with multiple whole fish, which they carry in their bills. When netted, they drop the fish. We collected all fish from netted birds, and we identified (to species), weighed and measured the fish. Identifications of most species of juvenile rockfish are conducted after the field season with the assistance of persons in the National Marine Fisheries Service lab, Santa Cruz, California. For the most frequently observed rockfish species in the auklet diet, we calculated annual proportions of those species in relation to all the rockfish in the diet. We tested for trends in the annual proportions of these rockfish species through linear regression analysis.

3. Results

3.1. Population change

Overall, the number of breeding adults at SFI has declined through the 1970s and 1980s, fluctuated at low numbers through the 1990s, increased in the early 2000s, and declined dramatically after 2007 (Fig. 2; see also Capitolo et al. (2014)). The highest count of 23,800 adults was recorded in 1974, while the lowest count of 1248 adults was noted in 2009. The population has remained near or below 5000 since 2008. Conversely, the number of breeding Brandt's cormorants at VAN has increased through time (Fig. 3), even beyond the decline observed at SFI in 2008. The VAN colony has increased from 36 adults in 2000 to 372 adults in 2012.

3.2. Productivity

The annual productivity estimates on SEFI have varied through time, with a long-term mean productivity of 1.39 fledglings produced per breeding pair (Fig. 4). Historically, years of anomalously low productivity have been isolated (e.g. 1978, 1983, 1992) and correspond to years with El Niño or other warm-water events (Ainley et al., 1995). More recently, four of the last five years of this time series (2008–12) lie below the 80% confidence interval around the long-term mean.

Productivity of cormorants at VAN has remained relatively stable (Fig. 5). Overall, the long-term productivity at VAN (2.19 fledglings/pair) is greater than the productivity on SEFI for the same time period (1.30 fledglings/pair for 2000–2012). Most years fell within the 80% confidence intervals, with one year (2003) of anomalously high productivity.

3.3. Diet

SEFI Brandt's cormorants ate a variety of fish species, with most consumed species falling into three groups: northern anchovy (*Engraulis mordax*, family Engraulidae), rockfish species (genus *Sebastes*, family Scorpaenidae), and flatfish species (order Pleuronectiformes; Fig. 6). Other common prey items included plainfin midshipman (*Porichthys notatus*), sculpin species (family Cottidae), cod species (family Gadidae),

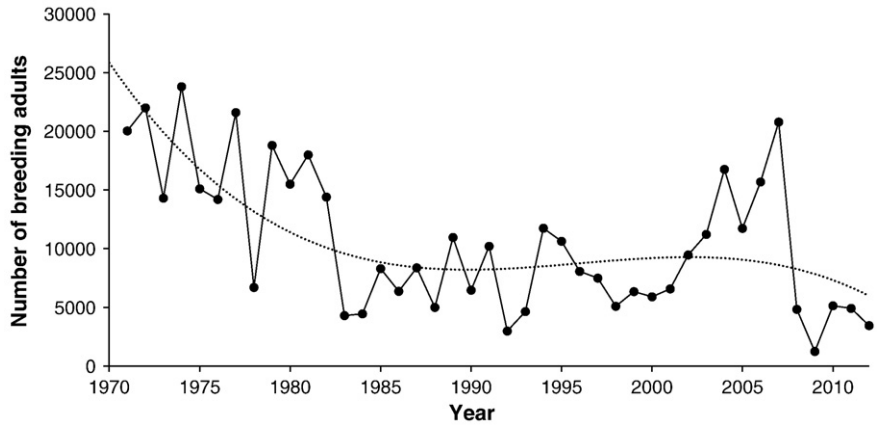

Fig. 2. Number of breeding Brandt's cormorants on South Farallon Islands, 1971–2012. (Trendline represents a third-order polynomial.).

and spotted cusk-eel (*Chilara taylori*). Diet in the 1970s (e.g., 1974, 1975, 1977) and 1993 was largely dominated by rockfish. However, in 1994, northern anchovy became the more frequently consumed prey; by 2008, anchovy was decreasing in the diet, and was replaced by rockfish. In 2011, rockfish decreased in the diet, and flatfish became the main prey in the final years of this time series.

VAN cormorants also consumed mostly anchovy, rockfish and flatfish (Fig. 7). Other important prey at this location included surfperch species (family Embiotocidae), sculpin species, greenling species (family Hexagrammidae), and cephalopods (class Cephalopoda). Northern anchovy was the main diet item in 2007, but was then replaced by flatfish and rockfish. Rockfish began to decline in the diet in 2011; in 2011–12, the diet was mostly flatfish species.

A chi-square goodness-of-fit showed significant differences in diet between the two colonies ($\chi^2 = 232.95$, df = 11, $p < 0.001$). The prey groups contributing the most to the chi-square value were surfperch, greenling, and plainfin midshipman, with these first two groups occurring frequently in VAN samples and the last prey occurring frequently in the SEFI diet. Flatfish was the next prey group contributing to the significant differences between the colonies, as the occurrence of flatfish in the SEFI cormorant diet was higher than expected while flatfish in the VAN cormorant diet was lower than expected.

Estimated sizes of prey were <150 mm in length; in general, the flatfish consumed (e.g., Pacific sanddab (*Citharichthys sordidus*), speckled sanddab (*Citharichthys stigmaeus*), and English sole (*Parophrys vetulus*)) were larger than anchovy and rockfish (Table 1). Most northern anchovy consumed by cormorants at both colonies were <100 mm and most rockfish consumed were <150 mm.

Estimated sizes of consumed prey at VAN were smaller than the same species consumed at SEFI, with the exception of rockfish (Table 1). Similar to SEFI cormorants, flatfish consumed at VAN were larger than anchovy and rockfish.

3.3.1. Species composition of fish assemblages

Rhinoceros auklet diet data showed large amounts of rockfish being consumed in the late 1980s and again in the early 2000s (Fig. 8). Similar to Brandt's cormorants, northern anchovy became the dominant prey item in 2005–07, and then rockfish became a larger portion of the diet in subsequent years. Auklets consumed many other species that cormorants do not eat, such as Pacific saury (*Cololabis saira*), juvenile salmon species (family Salmonidae), and sablefish (*Anoplopoma fimbria*).

To better understand the rockfish species composition available to Brandt's cormorants, we examined the rockfish species in the rhinoceros auklet diet. There are four species that comprise the majority of the rockfish portion of the auklet diet: shortbelly rockfish (*Sebastes jordani*), yellowtail rockfish (*S. flavidus*), blue rockfish (*S. mystinus*), and widow rockfish (*S. entomelas*). Significant declines in shortbelly rockfish were observed through time (Fig. 9a). Combined proportions of yellowtail and blue rockfish increased significantly through time (Fig. 9b), and widow rockfish also increased with time, although this was marginally significant (Fig. 9c).

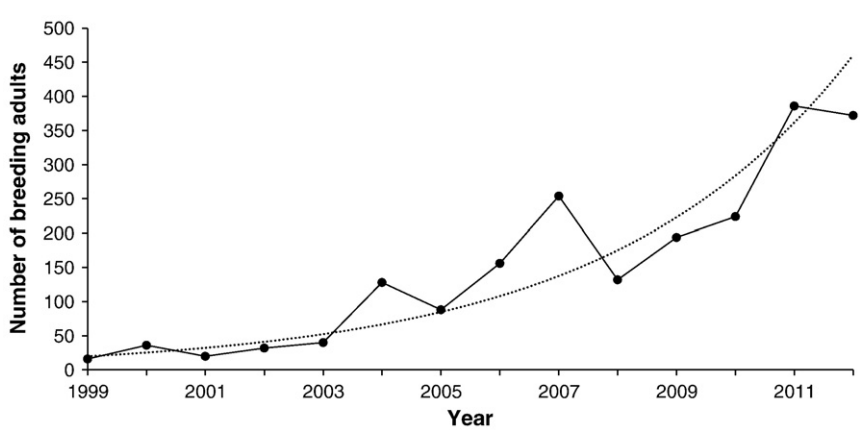

Fig. 3. Number of breeding Brandt's cormorants at Vandenberg Air Force Base, 2000–12. (Trendline represents an exponential line.).

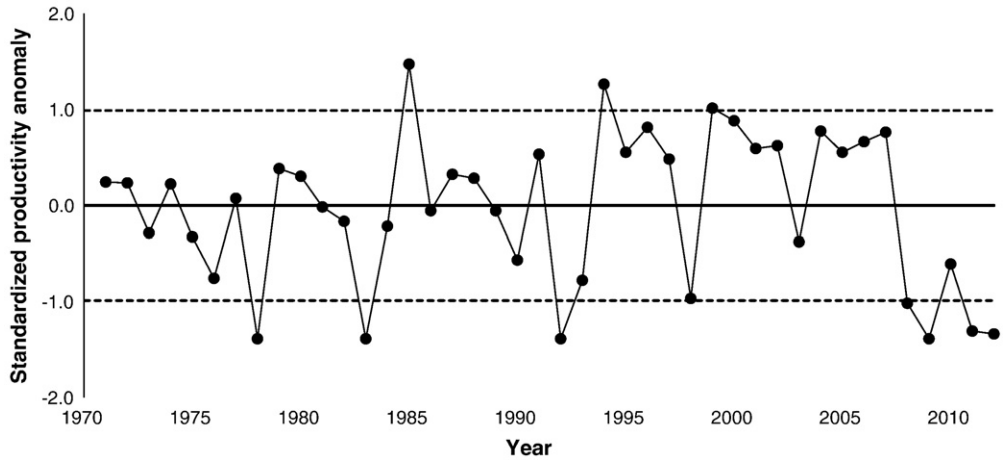

Fig. 4. Standardized productivity anomaly for Brandt's cormorants on Southeast Farallon Island, 1971–2012. (The zero-line represents the long-term mean productivity of 1.39 fledglings per breeding pair. The dotted lines represent the 80% confidence interval around the long-term mean.).

4. Discussion

Our results suggest a shift in prey community structure since the 1970s from a community dominated by offshore rockfish species to one dominated by more nearshore-settling rockfish species and neritic flatfish. Shortbelly rockfish are an offshore species that as adults occur above the bottom over the continental slope, while blue and yellowtail rockfish are nearshore species that settle to kelp beds associated with shallow reefs (Love et al., 2002). Juvenile widow rockfish have a similar offshore distribution as shortbelly rockfish, but settle to reefs on the deep shelf (100–200 m; Love et al., 2002). Once settled, these species are likely too large and too deep for Brandt's cormorants to access (Wallace and Wallace, 1998). Changes in oceanographic conditions could be favoring this shift in rockfish species abundance and distribution (Miller and Sydeman, 2004; Ralston and Stewart, 2013; Ralston et al., 2013; Thayer et al., 2008), and these conditions are also favorable to other neritic species such as flatfish (Cloern and Jassby, 2012). The establishment and rapid growth of the VAN Brandt's cormorant colony, as well as other Brandt's cormorant colonies throughout central California, are likely the result of the decline in offshore rockfish and an increase in the abundance of neritic fishes. Since 1995, several central California mainland Brandt's cormorant breeding colonies have been founded and others have increased in size (Capitolo et al., 2014; Saenz et al., 2006). This apparent increase in neritic fish species has also benefitted other seabird species breeding at VAN. The diet of the California least tern (*Sternula antillarum brownii*) nesting at VAN has shown trends similar to the VAN cormorant diet. Least terns have previously been shown to forage mostly within 1 mile (1.6 km) of shore (Atwood and Minsky, 1983), making them more dependent on nearshore prey (Thompson et al., 1997). This is a more limited foraging range than Brandt's cormorants, who can forage up to 80 km from their breeding site on SEFI (Ainley and Boekelheide, 1990). Northern anchovy dominated the diet of the VAN least terns in 2006, but decreased in occurrence through 2008; occurrence of young-of-the-year (YOY) rockfish began increasing in 2007 and have been the dominant prey for least terns since 2008. Furthermore, the occurrence of rockfish in the tern diet is positively correlated with breeding productivity (Robinette et al., 2013). The pelagic cormorant (*Phalacrocorax pelagicus*) population at VAN has shown an increase similar to Brandt's cormorants since 1999, and breeding productivity has been stable throughout the time series (Robinette and Howar, 2013). Though we lack diet data for pelagic cormorants, past studies at mainland colonies have shown this species to be highly dependent on nearshore demersal fishes like rockfish and flatfish (Hobson, 2013), and they utilize the same foraging habitats as Brandt's cormorants at VAN (Robinette et al., 2012). Finally, the pigeon guillemot (*Cepphus columba*) population breeding at VAN has been increasing steadily since 1999. The diet of this population is dominated by nearshore-settling sanddabs (*Citharichthys* sp.), and the proportion of sanddabs in the diet is positively correlated with upwelling conditions that promote sanddab recruitment (Robinette et al., 2007).

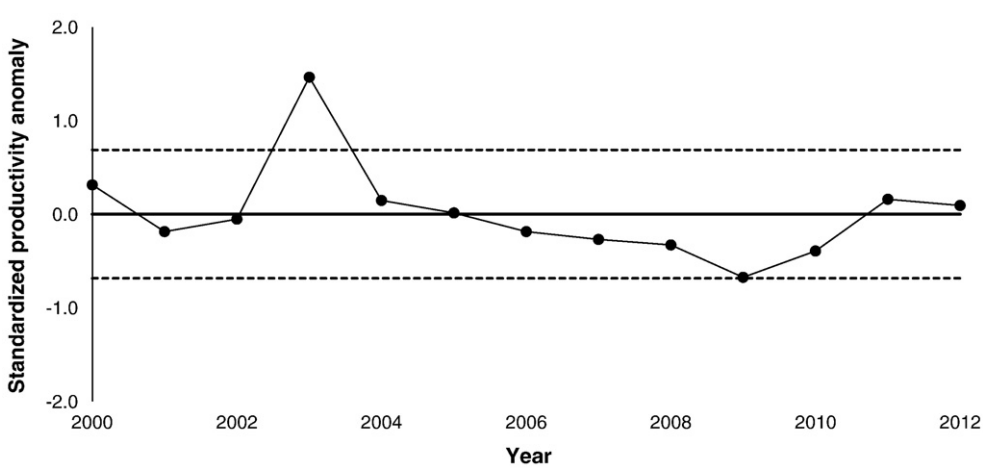

Fig. 5. Standardized productivity anomaly for Brandt's cormorants on Vandenberg Air Force Base, 2000–12. (The zero-line represents the long-term mean productivity of 2.19 fledglings per breeding pair. The dotted lines represent the 80% confidence interval around the long-term mean.).

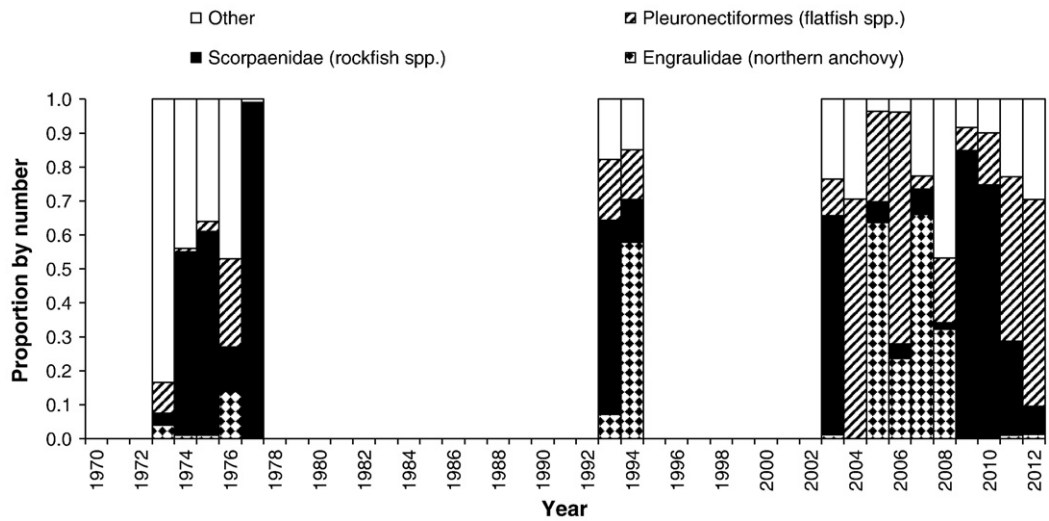

Fig. 6. Brandt's cormorant diet results from Southeast Farallon Island, 1973–2012. Note: years 1973–77 from Ainley and Boekelheide (1990).

The decrease in availability of offshore rockfish species is the likely explanation for the decreased breeding productivity and declining population of Brandt's cormorants at SEFI. This decline in offshore rockfish did not affect the nearshore VAN Brandt's cormorants, as they were able to subsist on fish species found in nearshore habitats. Comparable to VAN cormorants, Brandt's cormorant diet data collected from inshore roosts in the Monterey Bay region during the non-breeding season also confirmed their reliance on nearshore anchovy and flatfish (Webb and Harvey, 2015-in this volume). The estuarine Brandt's cormorants colony at Alcatraz in San Francisco Bay was established in the early 1990s and grew rapidly; diet data from this colony revealed northern anchovy and benthic fishes as their main prey in the early 2000s (Yakich, 2005). While breeding success at SEFI is significantly lower during El Niño and other warm-water periods (e.g., 1983, 1992, 1998; Ainley et al., 1995; Ainley and Boekelheide, 1990), the low breeding success on SEFI since 2008 cannot be explained by ENSO, with the exception of 2010 (NOAA/NWS, 2013). It is worth noting that the Brandt's cormorant population at SFI is currently 5–10 times larger than the VAN cormorant colony; the size of this SFI colony, in addition to the thousands of seabirds and other piscivorous predators also present, creates significant competitive pressure for food in the waters near SEFI and may have interspecies impacts on the local foraging dynamics. The decline in offshore fish species likely left the cormorants at SEFI with less available prey, and these birds spent more time traveling to nearshore areas in search of anchovies, other rockfish species and flatfish, and their productivity suffered. In support of this hypothesis, Brandt's cormorants were observed more frequently in nearshore habitats, particularly near the mouth of San Francisco Bay, during at-sea surveys in the Gulf of the Farallones beginning in 2010 (Elliott and Jahncke, 2014). In addition, the Brandt's cormorant breeding population and productivity on the Farallones increased in 2013 in an apparent response to increases in juvenile shortbelly rockfish abundance (Point Blue, unpubl. data). While diet samples collected in 2013 have not yet been analyzed, surveys of juvenile rockfish abundance off central California found a high abundance of shortbelly rockfish in 2013 (Keith Sakuma, NOAA/NMFS, personal communication). The rhinoceros auklet diet results also support our hypothesis, with decreases in shortbelly rockfish since 1987, but increases in nearshore-settling species. Rhinoceros auklets breeding at SEFI tend to forage more offshore along the continental slope (Ainley and Boekelheide, 1990). The increased occurrence of blue and yellowtail rockfish in their diet could indicate a behavioral response to decreased shortbelly rockfish abundance. Rhinoceros auklets also appeared to supplement their diet with the offshore widow rockfish, although the positive trend in the widow rockfish's proportion in the auklet diet was weak and marginally significant (Fig. 9c).

The cormorant diets at SEFI and VAN were similar in that both colonies saw a drastic decline in the amount of northern anchovy consumption (around 2007–08) to increased consumption of rockfish and

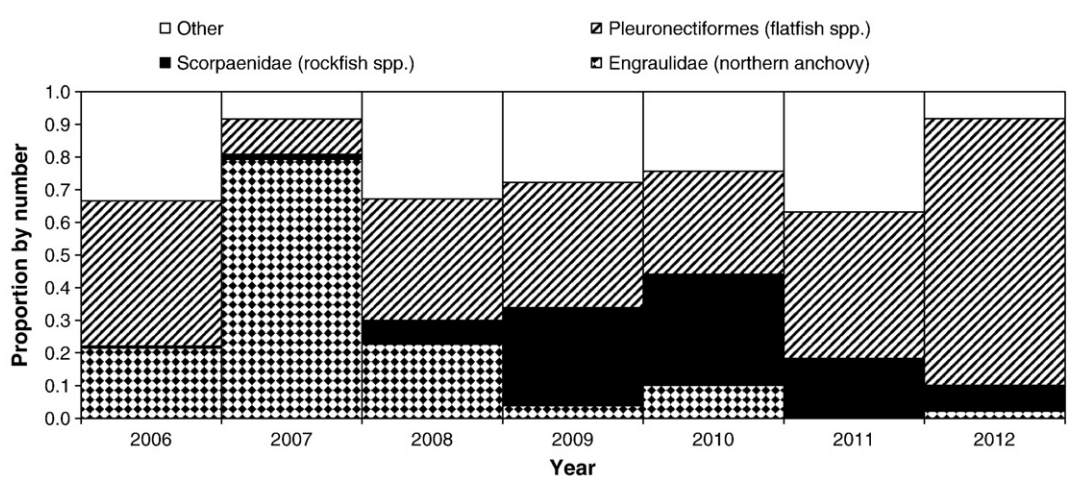

Fig. 7. Brandt's cormorant diet results from Vandenberg Air Force Base, 2006–12.

Table 1
Estimated size ranges (in mm) of frequently consumed fish species found in Brandt's cormorant diet, Southeast Farallon Island and Vandenberg Air Force Base.

Colony	Species	Average	Range (min–max)	N
SEFI*	northern anchovy[a]	79	40–102	154
	rockfish spp.[b]	51	20–223	386
	Pacific sanddab[a]	141	76–234	451
	speckled sanddab[b]	78	33–167	219
	English sole[a]	100	11–183	201
VAN	northern anchovy[a]	67	25–107	317
	rockfish spp.[b]	68	18–239	498
	Pacific sanddab[a]	118	76–225	463
	speckled sanddab[b]	72	16–139	508
	English sole[a]	90	8–167	102

[a] Standard length estimated.
[b] Total length estimated.
* Size estimates from years 1994, 2003, 2005, and 2007–12.

flatfish species. However, the two diets were significantly different, as cormorants at SEFI consumed more rockfish than VAN cormorants. The significant chi-square results denoted a greater occurrence of flatfish in the SEFI cormorant diet than expected, signifying a switch to flatfish from other types of prey. Flatfish consumed by cormorants at both colonies are a combination of fish that are still in their pelagic phase and those who have settled to the benthic environment, based on the estimated sizes of consumed flatfish (Table 1) and the sizes at which these species are known to settle. Pacific sanddab can settle at >50 mm length (Sakuma and Larson, 1995); settled adults of this species are known to be pelagic feeders (Pearcy and Hancock, 1978). Speckled sanddab can settle as small as 25 mm length and a mean settled size of 35 mm length (Ahlstrom et al., 1984, as referenced in Rackowski and Pikitch, 1989; Sakuma and Larson, 1995). English sole also settle to the benthos at a small size (20–25 mm; Krygier and Pearcy, 1986). VAN cormorants have access to more sheltered, nearshore environments that flatfish are known to inhabit and settle (Krygier and Pearcy, 1986; Rackowski and Pikitch, 1989; Sakuma and Larson, 1995), and which might explain why flatfish are a larger portion of their diet than the offshore SEFI cormorants.

In general, the fish eaten by SEFI cormorants were larger, with the exception of rockfish. Most northern anchovy consumed by cormorants at both colonies are <100 mm and are likely YOY (Parrish et al., 1985). Most rockfish consumed at both colonies are also YOY and still in their pelagic stage. Juvenile rockfish of species common to the California Current are born in the winter and early spring, and they remain in the water column (available to cormorants and other seabirds) until June or July when they become large and settle to deeper waters (Ainley and Boekelheide, 1990; Love et al., 2002). While it depends on the conditions of the year, most nearshore rockfish species settle at a small size (~30–40 mm; Tom Laidig, NOAA/NMFS, personal communication). The fact that VAN cormorants are consuming larger rockfish than SEFI cormorants suggests that they could be exploiting rockfish that have settled to kelp and other nearshore habitats that are not available to SEFI cormorants. Also, some rockfish consumed at VAN (particularly in 2008) were >100 mm; most rockfish of this size have settled (Tom Laidig, NOAA/NMFS, personal communication). Rockfish are also known to release larvae earlier in more southern latitudes (Love et al., 2002), so it is possible that the larger rockfish consumed by VAN cormorants may simply reflect the earlier parturition season for this region relative to SEFI.

Though time intensive, analyzing regurgitated pellets is a relatively easy, cost-effective method to investigate the diet of seabirds, and it provides a way to compare diets from multiple sites (see also Webb and Harvey (2015-in this volume). The collection of pellets at these two colonies differed. The increased pellet collection frequency at VAN may produce a more comprehensive picture of cormorant diet than the once-a-year collections at SEFI, where pellets cast towards the beginning of the breeding season may have disintegrated and not be well-represented in collections. While we could not address the bias in this paper, we assume that the pellets collected from SEFI represent diet throughout the breeding season. Cormorant pellets are encased in mucous, which dries and stores otoliths and other contents inside; only when we soaked pellets in detergent water could the pellet be loosened and unraveled to separate out the diet remains. Results from this study clearly show how seabird population size, productivity and diet can be used to indicate changes in forage fish populations in the central California Current, which has had noticeably different effects on these two cormorant colonies.

Chavez et al. (2003) demonstrated how basin-level changes in ocean climate can impact community structure over multiple decades. Though we lack diet data for the "warm sardine regime" that occurred between the mid-1970s and mid-1990s, our diet results are consistent with Chavez et al. (2003) in that anchovies and rockfish dominated cormorant diet during "cold anchovy regime" years prior to the mid-1970s and after the mid-1990s. Like anchovies, rockfish are considered cold water species that benefit during cold water regimes. However, our results suggest that species-specific shifts in community structure within these ocean climate regimes can have major implications for upper trophic level predators like cormorants. Schmidt et al. (2014) showed how the relationships between reproductive success of Farallon Brandt's cormorants and basin scale climate variables have shifted in recent years. While cold water regimes are favorable for multiple rockfish species, our results suggest that not all cold water regimes are the same and that more specific differences in oceanographic conditions may

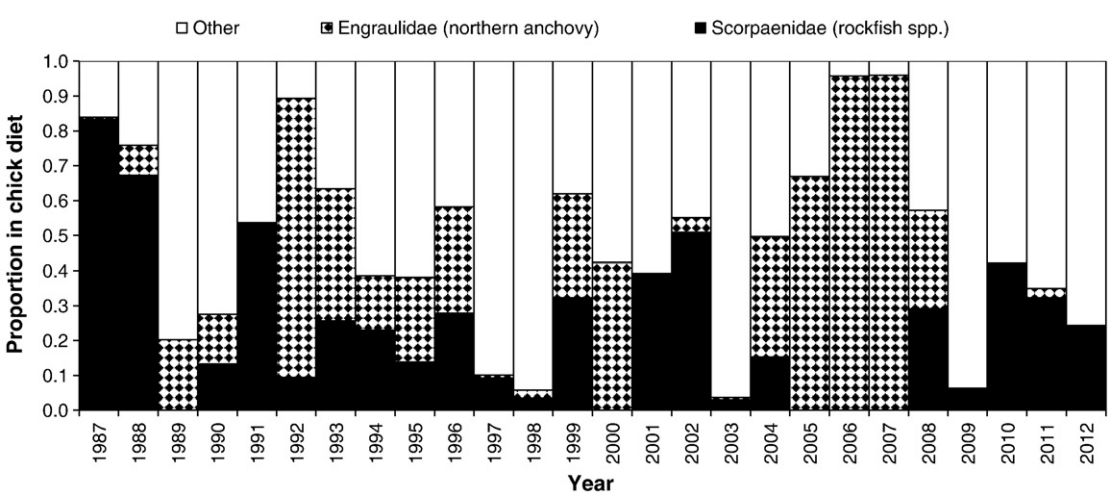

Fig. 8. Rhinoceros auklet chick diet on Southeast Farallon Island, 1994–2012.

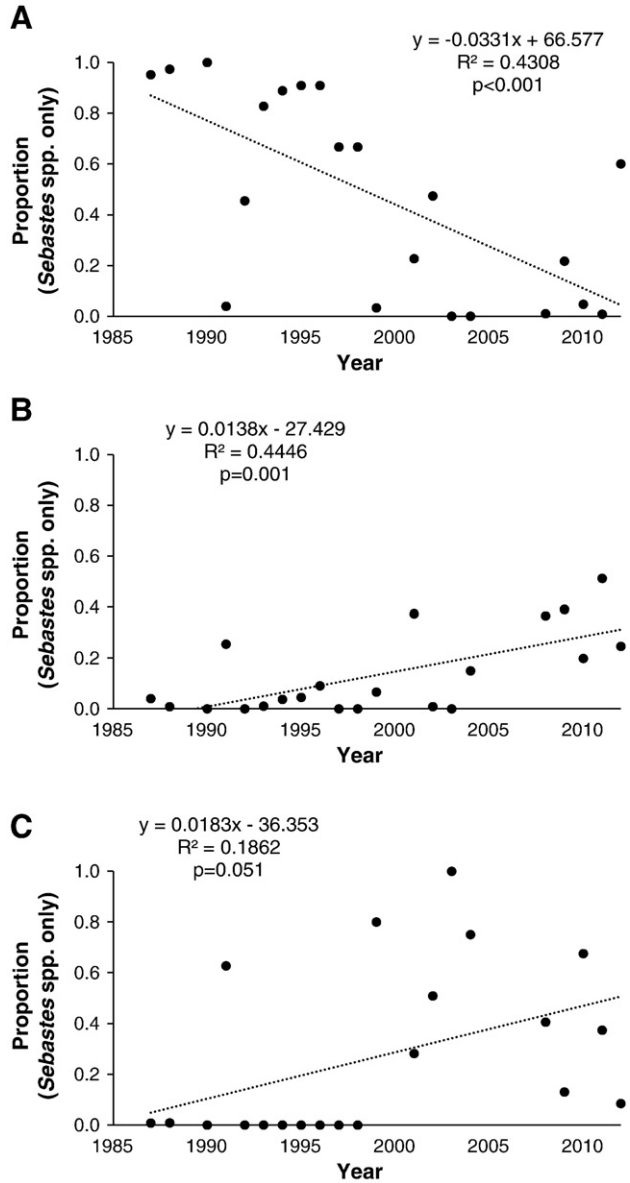

Fig. 9. Proportions of four different rockfish species in the rockfish portion of rhinoceros auklet diet on Southeast Farallon Island, 1987–2012. a) Shortbelly rockfish (*Sebastes jordani*); b) combined yellowtail (*S. flavidus*) and blue (*S. mystinus*) rockfish; and c) widow rockfish (*S. entomelas*).

differentially promote spawning among cold water species. In our study, the ocean climate prior to the mid-1970s appears to have favored spawning in shortbelly rockfish while conditions after the mid-1990s favored species like yellowtail, blue, and widow rockfish. Field et al. (2007) also confirm a decline shortbelly rockfish abundance during the 1990s to the early 2000s. Understanding which oceanographic parameters are promoting spawning for different species within a given regime will be necessary for the success of any ecosystem-based fisheries management program.

In addition to ocean and climate impacts, rockfish species were severely overfished off central and southern California from the mid-1970s to the early 1980s, beginning with species inhabiting shallow-water reefs and followed by deepwater species (Love et al., 2002). While all the repercussions of overfishing the rockfish community are not well understood, overexploitation has led to clear changes in fish assemblages in this region over the last few decades, including declines in fish size, declines in several rockfish species, and increases in flatfish species (Levin et al., 2006). Other predators may have also impacted certain rockfish species. The Humboldt squid (*Dosidicus gigas*) has greatly expanded its range to the central California coast since the 1997 El Niño, and shortbelly rockfish are known prey of this voracious predator (Litz et al., 2011; Zeidberg and Robison, 2007). Changing ocean conditions coupled with high predation rates may have long-term negative impacts on offshore rockfish species and the cormorants that depend on them.

Our results illustrate the value of including the predator perspective in understanding community-level responses to ocean climate shifts. Changes in forage fish populations within the central California Current had noticeably different effects on the diet, breeding productivity and breeding population size of our two study colonies. Further investigations of mainland and offshore seabird breeding colonies will help tease out specific oceanographic parameters that define community structure within a given ocean climate regime. Analyzing regurgitated pellets is a relatively easy, cost-effective method to investigate the diet of seabirds, and it provides a way to compare diets from multiple sites.

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