Ecosystem-based management affecting Brandt's Cormorant resources and populations in the central California Current region

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ABSTRACT

The Brandt's Cormorant of the California Current is a "boom-or-bust" species like its congeners in other eastern boundary, upwelling driven ecosystems, and like many of the prey upon which they depend. These birds produce many recruits when fish availability is high, leading to rapidly increasing populations, but few recruits, and may even exhibit die-offs, when the opposite is true. Unlike cormorants in the Peru and Benguela currents, however, Brandt's Cormorant population changes have yet to be correlated with those of its prey. Herein, using multi-decadal time series of cormorant colony size, diet, prey availability and mortality, in the context of changes in breeding site and fishery management, we provide insight into why central California colonies near San Francisco — a major portion of this species' global population — expanded from principally one offshore island in the 1960–70s to include a large mainland component by the 1990s. Involved were increases and decreases, respectively, of northern anchovy, a coastal forage species, and young-of-the year rockfish, more prevalent offshore. With protection of breeding sites and a shift towards ecosystem-based fisheries management by the 1990s, variations of the central California Brandt's Cormorant population are now driven naturally by forage fish availability, and perhaps inter- and intraspecific competition for prey and space when population sizes are high. This species, owing to its "boom-or-bust" natural history and the relative ease of assessing breeding population size and diet, may be ideal for monitoring the state of the central California Current food web.

1. Introduction

The Brandt's Cormorant (*Phalacrocorax penicillatus*) shares major aspects of the morphology, life history traits and behavior of an avian species group that pre-eminently characterizes Earth's upwelling-driven boundary currents: Benguela, California, Peru and Somali — Cape (*P. capensis*), Brandt's, Guanay (*P. bougainvillii*) and Socotra (*P. nigrogularis*) cormorants, respectively. The Canary Current, perhaps due to lack of breeding islands, is the only such current system that lacks an abundant, endemic, large-bodied, "boom-or-bust," densely colonial, mid-water diving, and flock foraging cormorant. The "boom-or-bust" breeding strategy, made possible by large brood sizes (4-egg clutch) along with young age of recruitment (2 years) when forage is plentiful (older when not plentiful), leads to the rapid response of these cormorants to variation in prey availability. During periods of low prey availability, cormorant populations may exhibit reduced reproductive effort and performance, but mass mortality may also occur (i.e., "bust"; Murphy, 1925, 1936, 1981). In the California Current, the Brandt's

Cormorant clearly fits this general model (Boekelheide et al., 1990; Wallace and Wallace, 1998). These attributes render these species' populations perfectly suited to the high productivity of upwelling boundary currents, but also the high level of interannual and decadal variability in the availability of schooling, forage fish characteristic of these ecosystems (e.g. Glantz and Thompson, 1981; Lluch-Belda et al., 1992).

Decadal time series of population size and distribution exist for most of the cormorant species inhabiting upwelling ecosystems (e.g. Tovar et al., 1987; Capitolo et al., 2014; Crawford et al., 2016). In the case of the Benguela and Peru currents, long time series of Cape and Guanay cormorants indicate changes in population size and distribution closely linked to availability of their main prey, clupeoid fishes. These time series are a function of protection for guano production and monitoring of ecosystem effects of major fisheries for anchovy (*Engraulis* spp.) and sardine (*Sardinops* spp.) (e.g. Murphy, 1981; Pauly and Tsukayama, 1987; Crawford et al., 2015). In accord, cormorant populations have exhibited extraordinary, interannual and decadal fluctuations in size and location depending on where the fish are most available, along with long term decline over recent decades as fishery take increased (Murphy, 1981; Tovar et al., 1987; Jahncke et al., 2004; Crawford et al., 2016). Tovar et al. (1987) deemed that the Guanay Cormorant was more specialized and far more sensitive to changes of forage availability than the other guano birds of the Peru Current.

It has been hypothesized that changes in the numbers and distribution of Brandt's Cormorants along the central California coast, the species' center of distribution (Wallace and Wallace, 1998), are linked to prey quantity and quality, as deduced from changes in diet or indirect correlations to interannual environmental and climate variability indices (Capitolo et al., 2014; Schmidt et al., 2014; Elliott et al., 2015). According to Wallace and Wallace (1998), nearly 40% of the world population of this species nests in central California from Point Reyes to Point Conception, and recent colony shifting of breeding birds within that region has been evident (Capitolo et al., 2004, 2014). Other than investigations of Brandt's Cormorant productivity linked to prey availability, either measured (Ainley et al., 1995a, 1995b) or inferred (Schmidt et al., 2014, 2015), there are no analyses in which Brandt's Cormorant population size changes have been directly correlated to measures of prey availability, unlike the cormorants in other upwelling systems. For one thing, the food web sustaining upper level predators of the California Current may be more complex, e.g. eastern boundary currents share the importance of anchovies and sardines but the others seem to lack the rockfish (*Sebastes* spp.) analog, which is hugely important to the California Current food web (Lenarz, 1980; Ainley et al., 2014, 2015). Herein, we present an assessment of the various drivers and changes for most of a presumed meta-population of Brandt's Cormorant off central California (Fig. 1), perhaps being a well-studied proxy for factors affecting the species elsewhere in its range. We connect Brandt's Cormorant population changes at seven colonies in the Gulf of the Farallones, including the South Farallon Islands, where the species' largest single breeding assemblage has occurred, to multiple-decade time series of: 1) forage fish availability, the result of annual sampling in adjacent waters; 2) diet change at offshore and mainland sites, sampled from items in regurgitated pellets; 3) mortality as indexed at 29 adjacent mainland beaches; and 4) changes in competition for space between the cormorants and humans, pinnipeds and other seabird species. We also present results of 20 years of at-sea censuses to depict the areas where this metapopulation forages. The role of climate variability is reserved to citing the literature on how climate variation affects forage fish abundance in the study area (MacCall, 1996; Rykaczewski and Checkley, 2008; Ralston et al., 2013, 2015; McClatchie et al., 2017). We address the prospects that the central California Current Brandt's Cormorant population may be limited and structured spatially both by food availability, primarily, but also breeding space, and that regulated exploitation of fishery resources and protection of mainland breeding sites is proving to be a success in the institution of effective ecosystem-based management.

1.1. History of management

During most of the last two hundred years, intense disturbance of colonies by human activities was the norm for the offshore South Farallon Islands as well as for rocks/headlands along the adjacent mainland coast (Ainley and Lewis, 1974; White, 1995; Carter et al., 2001; Appendix 1). Intense human activity at the Farallones became sharply curtailed in the late 1960s, was further reduced into the early 1970s, and the colonies have since been fully protected. Paramount in this history was establishment of the Farallon Islands National Wildlife Refuge in 1909, and its expansion in 1969. A similar scenario of wildlife management had begun for colonies along the mainland coast in the early 1960s, extending into the 1970s–early 1980s. Año Nuevo Island in the late 1980s was the last colony in the Gulf of the Farallones where human activity was reduced sufficiently to allow cormorant breeding.

Similarly, fishery management was inadequate through the 1950s and 1960s, with the crash of the Pacific sardine (*Sardinops sagax caerulea*) stock in Monterey Bay as a prime example of the failure to recognize shifts in productivity of fish populations in response to climate shifts (Clark and Marr, 1955; Fréon et al., 2005; Lindegren et al., 2013). As the northern anchovy (*Engraulis mordax*), a species with a somewhat similar life history and ecological role, increased following the sardine's decline, fisheries biologists at the time presumed that intensively fishing anchovy would help in sardine recovery (McEvoy, 1990; MacCall, 2009). This came just as researchers in Peru proposed to "replace" (i.e. outcompete) the guano birds of the Peru Current (including *P. bougainvillii*) with human fisheries for the Peruvian anchoveta (*E. ringens*), which was both then and now the world's largest (by volume) fishery (Schaefer, 1967). Ironically, the development of the Peruvian anchoveta fishery was based to a large extent on the transfer of both industrial capacity and technical expertise from the collapsed California sardine fishery and industry (Radovich, 1982; MacCall, 2009). Both of these ideas were examples of the "command and control" nature of marine resource managers of the time, reflecting the desire to dampen and control variability in ecosystem structure and productivity, rather than accommodating the natural variation of various fish or predator stocks inherent in these ecosystems (Holling and Meffe, 1996).

Subsequently, a first step in ecosystem-based fisheries management came with passage of the Magnuson-Stevens Fishery Conservation and Management Act in 1976, which established the framework for managing fisheries at a sustainable level. For example, the Act enabled the development of a fishery management plan for northern anchovy, which in turn explicitly recognized that "benefit to the nation occurs by leaving fish in the ocean," with respect to the needs of dependent predators and game fish (PFMC, 1978). On the basis of rules in the anchovy management plan, the anchovy reduction fishery was closed in 1983 owing to stock size decreasing below cut-off levels (Appendix 1). Similarly, the requirements to rebuild overfished populations that came with the Sustainable Fisheries Act of 1996 led to a reversal of long-running declines in rockfish and many other groundfish populations in the California Current, such that overfishing was largely eliminated, most populations were increasing, and many were above target levels by the early 2000s (Worm et al., 2009; Bjorkstedt et al., 2016).

Other fishery management measures with ecosystem implications have followed, such as precautionary reductions in catch limits of shortbelly rockfish (*S. jordani*) in recognition of their role as forage, a ban on krill fishing in recognition of their central role as forage, and most recently a ban on new fisheries for currently unexploited forage species (PFMC, 2013, 2015). Ecosystem models and ecosystem-based management principles increasingly guide fisheries and marine resource management decisions in the California Current System, although such models tend to suffer from a lack of both adequate data and a mechanistic understanding of ecosystem function and energy
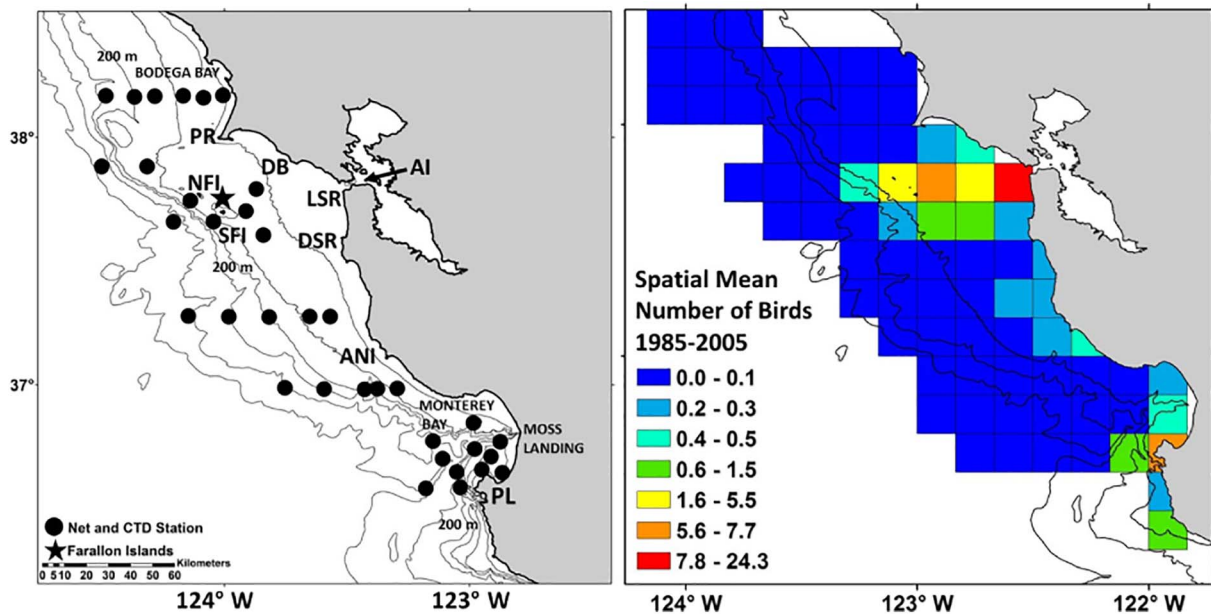
Fig. 1. Left panel: Study area showing locations of Brandt's Cormorant colonies in the Gulf of the Farallones and Monterey Bay, as well as trawl stations in the Rockfish Recruitment and Ecosystem Assessment Survey. Beach carcass surveys occurred from Bodega to Moss Landing, 1971–1983; from Bodega to Año Nuevo Island, 1993–2015; and from Año Nuevo to Monterey, 1997–2015. ANI – Año Nuevo Island, DSR —Devil's Slide Rock and mainland, LSR — Lobos/Seal Rocks, AI — Alcatraz Island, DB — Drakes Bay rocks, PR — Point Reyes Headlands, SFI — South Farallon Islands, NFI — North Farallon Islands, PL — Point Lobos (Monterey). Depth contour lines are 50, 100, 200, 500, 1000, and 2000 m isobaths. Right panel: Mean number of cormorants seen on strip surveys per cell block, spring/summer 1985–2005; data collected on RREAS cruises, along trawl lines and elsewhere as time allowed.

flow. The result is a current greater movement towards more simplistic and highly focused models rather than all-encompassing models of every component of the ecosystem (Collie et al., 2016; Punt et al., 2016). Although fisheries management does not yet have a clear mandate to manage principally from an ecosystem perspective, there is a mandate to consider ecosystem needs in making management decisions. Therefore, management of fisheries resources at both state and federal levels has become more precautionary and cognizant of the trade-offs between ecological and economic objectives (PFMC, 2013, 2015).

2. Methods

2.1. Study area

The Gulf of the Farallones encompasses the waters stretching along the California coast from Point Reyes south to Año Nuevo Island and offshore to the edge of the continental shelf at the Farallon Ridge, including the Farallon Islands (Fig. 1). Within this region, Brandt's Cormorant colonies exist at Point Reyes Headlands, Drakes Bay rocks (three colonies combined), Alcatraz Island (in central San Francisco Bay), Lobos/Seal Rocks, Devils Slide Rock and mainland, Año Nuevo Island and the South Farallon Islands. Few Brandt's Cormorant nest at the North Farallon Islands annually (never > 100 pairs), and are not included in our analyses (Capitolo et al., 2014). The only other concentration of Brandt's Cormorants comparable in size to the Gulf of the Farallones population at its peak is in the California Channel Islands, 300 km south, although other smaller Brandt's Cormorant colonies are distributed along the mainland coast immediately to the north and south of the Gulf, where suitable habitat is available, e.g. Point Lobos. The Gulf also includes ample habitat for cormorant foraging (Fig. 1). Among some of their major prey, rockfish spawning habitat abounds along the Farallon Ridge and Escarpment, Cordell Bank (seaward from Point Reyes) and various banks elsewhere in the Gulf; northern anchovy spawn in the San Francisco Bay, spreading outward from the Golden Gate (McGowan, 1986); and other fish, such as sanddabs (*Citharichthyes* spp.), frequent the sand and other soft bottom habitats elsewhere in the

Gulf. Pelagic young-of-the-year (YOY) rockfish and sanddabs are broadly distributed in waters throughout the Gulf of the Farallones, while northern anchovy tend to have a more coastal distribution (Ralston et al., 2015; Santora et al., 2014).

Also included in the fisheries study area is Monterey Bay immediately to the south of the Gulf of the Farallones. Some Gulf-breeding cormorants almost certainly forage there, especially those from the large Año Nuevo colony, and it is also a major wintering area for Gulf-breeding cormorants (Wallace and Wallace, 1998; Webb and Harvey, 2015). As noted above, a sizeable colony exists at Point Lobos at southern end of Monterey Bay (2000–5000 pairs; Sowls et al., 1980; Bechaver et al., 2013; Fig. 1), but we have not included it because the time series of annual counts is far less complete than for Gulf colonies.

2.2. Colony size

Two procedures were used to assess Brandt's Cormorant colony size (Fig. 2): 1) direct counts of nests from elevated vantage points, along with estimates of inaccessible areas taken from a small boat, in early June, for the Farallones during 1971–1985, 1991–92, 1996, and 2008–2015 (details in Boekelheide et al., 1990; Warzybok et al., 2015); and for Lobos/Seal Rocks along the mainland coast during 1979–1980 (Sowls et al., 1980); and 2) counts of nests from aerial photographs of mainland coast colonies during 1979–2015 and for the Farallones during 1986–1990, 1993–1995, and 1997–2007 (Capitolo et al., 2014; P. Capitolo, G. McChesney, unpubl. data).

2.3. At-sea distribution

Seabirds were counted during the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) cruises using 300 m wide strip transects, whenever the ship was underway during daylight during late spring-early summer, 1985–2005 (see Ainley and Hyrenbach, 2010 for description of survey effort and sampling details). Survey effort was conducted along and between tracklines where trawl and hydrographic sampling stations were located (Fig. 1), resulting in a comprehensive census of seabirds in coastal and pelagic habitats (Ford et al., 2004). We
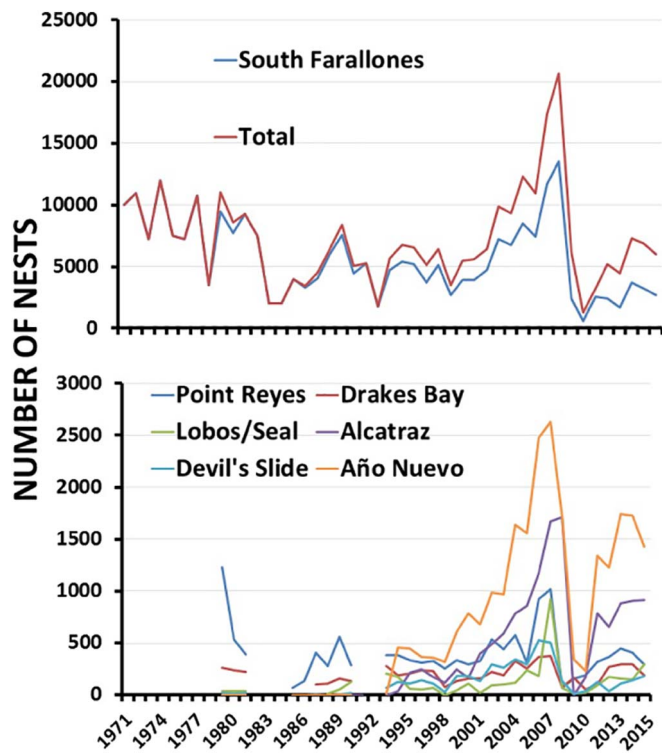
Fig. 2. Number of Brandt's Cormorant nests in the Gulf of the Farallones 1971–2015. Top, offshore South Farallon Islands colony and Gulf of the Farallones total (including mainland coast colonies); bottom, mainland coast colonies only (n = 6).
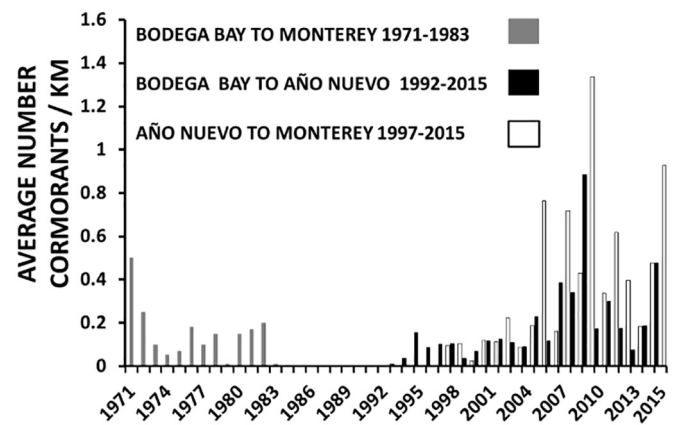

Fig. 3. Rate of Brandt's Cormorant carcass deposition on beaches from three time series: a) Gulf of the Farallones and Monterey Bay, 1971–1983 (41 beaches, Bodega to Monterey); b) Gulf of the Farallones 1993–2015 (29 beaches, Bodega to Año Nuevo Island); and c) Monterey Bay 1997–2015 (11 beaches, Año Nuevo to Monterey). Data from 1997 to 2015 for Año Nuevo to Monterey Bay were divided by 10 to make values more compatible to those from other areas/time periods.

integrated all survey data derived from Ainley and Hyrenbach (2010) in a Geographic Information System in order to quantify a spatial climatology that is representative of the general foraging distribution of Brandt's Cormorant, and to resolve key foraging areas adjacent to offshore and mainland colonies (Fig. 1). Following Santora et al. (2012), all seabird survey data were spatially joined to grid cells (n = 79, each ∼250 km²) overlaid on the RREAS core area, in order to derive a spatial mean and standard deviation of Brandt's Cormorant abundance.

2.4. Cormorant mortality

As a counter to population size in order to understand better the major swings in population, and as a complement to what has been described for Guanay Cormorants in the Peru Current (Murphy, 1925, 1936), we also include an assessment of year-to-year levels of cormorant mortality (Fig. 3). Volunteers organized by the Greater Farallones Association on contract with Greater Farallones National Marine Sanctuary, in an effort known as "Beach Watch," surveyed 29 beaches monthly, 1993–2015, stretching from Bodega Bay (Sonoma County), through Marin and San Francisco counties, to Año Nuevo Point (San Mateo – Santa Cruz County border). Similarly, volunteers organized by the Monterey Bay National Marine Sanctuary and Moss Landing Marine Laboratories, in an effort known as "BeachCOMBERS —Coastal Ocean Mammal/Bird Education and Research Surveys," surveyed 11 beaches monthly, 1997–2015, from Año Nuevo Point to Monterey (Santa Cruz and Monterey counties). When a new Brandt's Cormorant carcass was encountered, it was marked so as not to be tallied as new deposition on subsequent surveys. Information is reported as cumulative number of Brandt's Cormorants found per kilometer by year; carcasses not identified to species were not included. A complete review of methods for the survey programs can be found in Roletto et al. (2003) and Nevins et al. (2011). Results from an earlier effort, Bodega to mid-Monterey 1971–83 (41 beaches including all those of Beach Watch and Beach-COMBERS), were extracted from

Stenzel et al. (1988, their Fig. 28). In that survey, Brandt's Cormorant carcasses were not marked, but rather thrown well above the highest high tide line. As there was some chance that a few of those carcasses would be counted on the next month's survey, those results may be slightly elevated compared to those from the more recent surveys, but provide important historical context.

2.5. Diet

Fish otoliths and other prey hard parts were extracted from the boluses or regurgitated pellets that Brandt's Cormorant produce approximately daily to identify prey species and quantify relative importance by number (for further detail see Ainley et al., 1981; Elliott et al., 2015; Webb and Harvey, 2015; Fig. 4). Pellets were collected at the Farallones, the offshore site, during 1973–77, 1994, 1999 and 2003–2015; and at Año Nuevo Island, a mainland coastal site, during 2000–2015. With rare exception, specifically 2003 (n = 22), pellet sample sizes were 50–100 per year at the Farallones, leading to at least 1000 otoliths obtained per year (see Ainley et al., 1981; Elliott et al., 2016); likewise, at Año Nuevo pellet counts were 45–75 (except for n = 23 in 2000, = 10 in 2007, = 27 in 2012; J. Beck, M. Elliott, unpubl. data). Otolith shape is typically taxonomically distinct, but levels of what we report ranged from species to family, depending on the degree to which prey identification could be resolved (e.g. YOY rockfish cannot reliably be distinguished to the species level; J Fields, pers. obs.). Fresh pellets were picked up after cormorants had departed colonies, usually in or after August, to avoid disturbance, and, therefore, indicate diet throughout the breeding period (April–July), though mainly diet of chicks and adults in the later portion (June–July). In the lab, otoliths were compared with voucher specimens for species identification. We report results only for the 8 most frequently encountered prey taxa, and in most cases, except for anchovy and midshipman (*Porichthys notatus*), species were lumped by family. Cephalopod beaks also were found in the pellets but, since squid or octopus were minor prey, results are reported in the category "other," which included remaining fish species.

There was an important gap in Farallon cormorant diet between 1977 and 2003. To fill in the gap, especially for the two major prey (YOY rockfish, anchovy), knowing already that diet of these two avian species during summer at the Farallones is very similar (Ainley et al., 1990), we used as a proxy for the missing cormorant values the diet of Common Murre (*Uria aalge*) nestlings, for which we had a continuous series covering the entire time period. Diet variation in the two seabird species was particularly close in the prevalence of anchovy and YOY
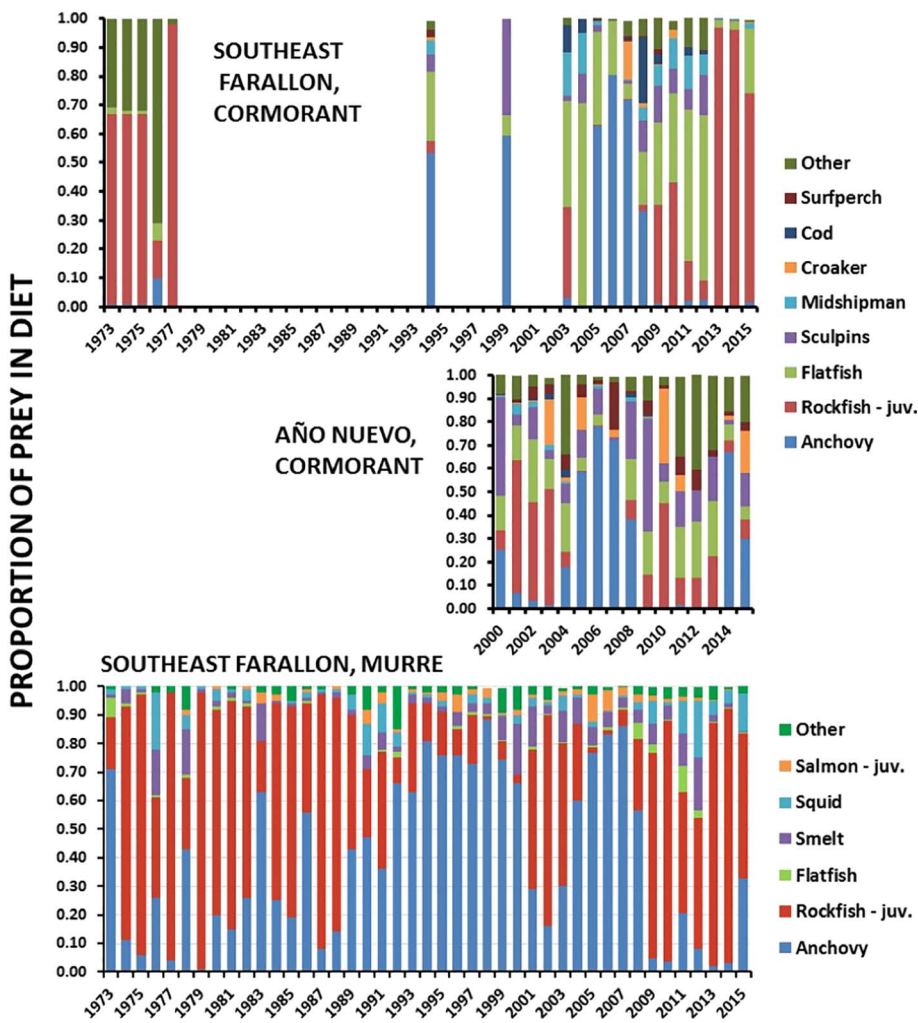
Fig. 4. Top panels: proportion of prey species, by number, in the diet of Brandt's Cormorants nesting on offshore Farallon Islands, 1973–2015 (with gaps), and on mainland Año Nuevo Island, 2000–2015. Data based on > 50 and > 45 pellets analyzed each year at Farallones and Año Nuevo, respectively, providing > 1000 otoliths (see text). Bottom panel: for comparison and as a proxy for missing years of Farallon cormorant data, the diet of co-foraging Common Murres nesting on the Farallon Islands, 1973–2015 (data based on > 1000 prey observations per year) — for correlation between Farallon murre and cormorant diet, anchovy $r = 0.82$, rockfish $r = 0.80$, both $p < 0.001$.

Data from Warzybok et al., 2015, their Fig. 8; see also Wells et al., 2017.

rockfish during the 20 years of temporal overlap (Fig. 4). We used Pearson correlation on the proportion of the diet, by number, for the comparison. Murre diet was determined by observing in an annual series of all-day watches the prey fed to chicks, the parents carrying the fish in full view in their bills; prey items observed exceeded 1500 per year (Ainley et al., 1990; Warzybok et al., 2015).

2.6. Prey availability

The RREAS acquired data on prey availability, was conducted annually 1983–2015 by National Marine Fisheries Service, and is described in Ralston et al. (2013, 2015). Briefly, during May–mid June, thus coinciding closely with the cormorant/murre diet data, a modified mid-water Cobb trawl was used to enumerate pelagic YOY (also referred to as juvenile) rockfishes at 35 stations along transects spanning the area from Point Reyes through Monterey Bay (Fig. 1). A total of 2534 trawl samples were used to determine average number of YOY rockfishes, as well as other well-represented fish species, e.g. adult northern anchovy and flatfish (mostly juvenile Pacific sanddabs *C. sordidus*), collected per trawl in each year (i.e., catch per-unit-effort, CPUE; Fig. 5). These are the three prey species most frequent in the Brandt's Cormorant diet (see Results). The trawls were made at night, targeted fishing at 30–40 m depth and at each station water-column properties were assessed using a conductivity-temperature-depth profiling instrument (CTD), deployed from the surface to just above the bottom.

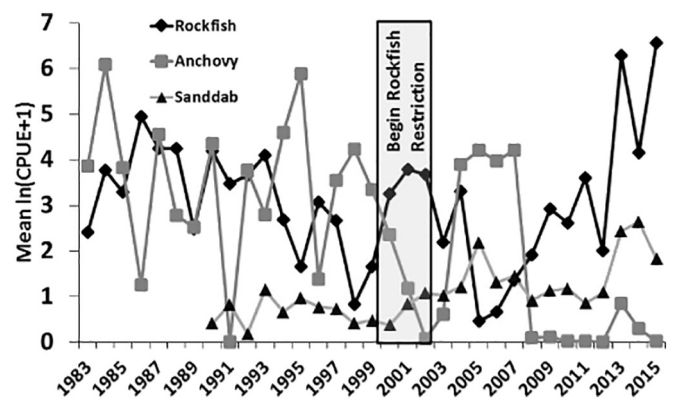Using correlation analyses, we compared breeding population size

Fig. 5. An index to the prevalence of YOY rockfish, YOY sanddabs and northern anchovy in the Gulf of the Farallones and Monterey Bay as determined by mid-water research trawls, 1983–2015 (see Fig. 1 for sampling grid).

of cormorant colony to RREAS fish time series (mean ln CPUE + 1) covering 1983–2015 for the South Farallon Islands, and for 1993–2015 (consistent population counts) for all other mainland cormorant colonies.

All prey abundance and cormorant population time series were examined for the presence of long-term trends. Series with significant trends were detrended prior to correlation analysis to reduce spurious relationships. We did not use rate of change in cormorant numbers, deeming it unnecessary given the rapid response by the cormorants

owing to changes in recruitment and movement to changes in forage.

3. Results

3.1. Changes in Brandt's Cormorant colony size and location

The total number of Brandt's Cormorants breeding at sites in the Gulf of the Farallones over the past 50 years reached a peak twice: 8000–12,000 breeding pairs during much of the late 1960s–early 1980s (see also Ainley and Lewis, 1974; Boekelheide et al., 1990) and ~17,000–20,000 pairs in the mid-2000s (2006–2007; Fig. 2). Before the first peak, likely there were very few Brandt's Cormorants nesting in the Gulf owing to intense disturbance at most sites (Appendix 1; Ainley and Lewis, 1974). During the first peak, almost all Brandt's Cormorants were at the Farallones. At that time there were none breeding at Alcatraz or Año Nuevo islands, and indications were that only hundreds in total bred at other mainland sites (cf Osborne and Reynolds, 1971; Ainley and Whitt, 1973; Sowls et al., 1980). Numbers declined after the first peak, reaching a low point in the mid-1980s, a level maintained for several years. Breeding at Año Nuevo and Alcatraz islands began in the late 1980s – early 1990s and increased substantially in the mid-1990s (Fig. 2; Saenz et al., 2006; Capitolo et al., 2014). Numbers then surged in the 2000s at all Gulf of the Farallones colonies to reach the second peak of > 20,000 pairs in 2007. Numbers then plummeted to reach a low point in 2009–10 at all sites. Later, colonies began to recover, but mainland sites more so than the Farallones, resulting in a sub-peak in 2013–15 of ~7000 pairs, with slightly more at mainland sites (3300–3600) than at the Farallones (2700–3300).

The dramatic decrease in numbers of Brandt's Cormorants after 2007 coincided with unusual mortality events as detected by beach-cast specimens tallied along Gulf of the Farallones and Monterey Bay mainland beaches (especially in 2009; Fig. 3); a smaller but noticeable decrease in Brandt's Cormorants total numbers in 2015 also coincided with elevated carcass deposition, although El Niño conditions may have prevented many birds from breeding to thus contribute (i.e. fledglings/juveniles) to this decrease (see Schmidt et al., 2015). In contrast, a peak in beach-cast carcasses in 1971, when few Brandt's Cormorants were breeding at sites along the mainland, did not correspond with any noticeable decrease in Brandt's Cormorant colony numbers (Figs. 2, 3). Carcass deposition rates were higher in the latter part of the study period consistent with a much larger cormorant population then; and also were higher along Monterey Bay beaches compared to the Gulf of the Farallones.

3.2. Colony foraging areas

The colony distribution of Brandt's Cormorants is the result of both coastal physiography (availability of suitable habitat) and distribution of suitable prey; in large part, especially for the mainland sites, the cormorants forage near to the colony. Cormorants from most Gulf of the Farallones colonies mainly forage between Point Reyes and Pillar Point, particularly in what is the San Francisco Bay Plume (brackish water emanating tidally through the Golden Gate (Fig. 1; see also maps in Ainley et al., 1990)). Cormorants from Año Nuevo Island forage in a "halo" around that island adjacent to the foraging area of the other Gulf colonies. Cormorants from Alcatraz Island apparently forage mainly within the San Francisco Bay, adjacent to the main cormorant foraging area just outside the Golden Gate (Yakich, 2005; Saenz et al., 2006).

3.3. Changes in diet and prey availability

Annual variation in the numerical proportion of anchovy and YOY rockfish in the diet of Common Murre nestlings on the Farallones (n = 17 years) was significantly correlated with proportions in the diet of Brandt's Cormorants on the Farallones (Fig. 4; for anchovy — Pearson $r = 0.82$, $r^2 = 0.67$, $p < 0.0001$; for rockfish — $r = 0.80$,

$r^2 = 0.65$, $p = 0.0002$); proportion of flatfish (mostly sanddab) was not correlated (Pearson $r = 0.18$, $r^2 = 0.03$, $p = 0.44$). Therefore, we were able to use murre diet, at least in regard to anchovy and rockfish, as a proxy for Farallon cormorant diet in the years when no cormorant diet data were available. Though a shorter time series was available for comparison (n = 10–12 years), Farallon Brandt's Cormorant diet correlated with that at Año Nuevo Island for anchovy (Pearson $r = 0.78$, $r^2 = 0.62$, $p = 0.004$), but not for rockfish (Pearson $r = 0.07$, $r^2 = 0.005$, $p = 0.84$) nor flatfish (Pearson $r = 0.43$, $r^2 = 0.18$, $p = 0.16$). Flatfish were far more prevalent in the diet of Farallon compared to Año Nuevo cormorants, which generally had a more diverse diet than Farallon cormorants (compare, for instance, the prevalence of "other" species of prey in the diets; Fig. 4). At Alcatraz Island, in 2000–2002, anchovy was the most abundant prey taken (25%), with the remainder of the diet mostly being composed of flatfish, sculpins and midshipmen (Yakich, 2005).

During the first peak in Brandt's Cormorant numbers (early 1970s), cormorant diet was mainly juvenile rockfish, a few other fish species, and virtually no anchovy (Fig. 4). There were no diet data from Brandt's Cormorants breeding at mainland sites (e.g., Año Nuevo Island) at that time (in fact there were no nesting Brandt's Cormorants then at Año Nuevo; Appendix 1, Fig. 2). The prevalence of rockfish slowly decreased in the Farallon diet and by the 1990s, a period of unusually low YOY rockfish abundance in this region, rockfish were replaced by anchovy. During that period the population of cormorants on the Farallon Islands decreased. During the second Gulf-wide peak, at both the Farallon Islands and the mainland colonies, cormorants preyed principally on anchovy, and the cormorant populations both offshore and nearshore increased dramatically (Figs. 2, 4). Before and after a 2004–2007 anchovy surge, cormorants preyed heavily on flatfish at the Farallones, giving way to rockfish by the end of the study period. Curiously, despite high anchovy prevalence in trawls during 2004, only murres but not cormorants at either the Farallones or Año Nuevo Island fed on anchovy to an appreciable degree. This may have been related to prey size (juveniles vs adults), or trawls vs seabirds sampling methods. That appears to be the only obvious anomaly in the patterns being described; sanddabs appeared to be the prey choice in 2004. The most recent recovery of cormorant numbers, after 2010, was likely fueled by YOY rockfish, which have been at high levels in the 2009–2015 period, including three of the highest observed abundance levels in trawls (2013–2015) in the 34-year time series. At Año Nuevo Island, after the anchovy surge, the diet was diverse with no fish species dominant, until the last two years when anchovy became prevalent again.

The trawl time series started in 1983, after the first Brandt's Cormorant population peak, but the decrease in cormorant numbers thereafter corresponded to a progressive, though statistically insignificant decrease in prevalence of YOY rockfish in the trawls (Fig. 5). Recovery of cormorant numbers beginning around 2000 corresponded to a resurgence in YOY rockfish prevalence. This coincided with both high constraints on commercial and recreational catches (Appendix 1) as well as with an extraordinarily strong 1999 year class that propelled central California rockfish populations to considerably greater abundance levels (Field et al., 2010; Ralston et al., 2013; Thorson et al., 2013). YOY rockfish then largely disappeared in the research catch between 2004 and 2007, when a surge in anchovy prevalence occurred. That surge in anchovy corresponded to the high prevalence of that prey species in the diet of both Farallon Islands and mainland cormorants, as noted. In 2007, YOY rockfish reappeared in trawls and in subsequent years progressively increased in prevalence to reach levels exceeding that of the 1980s, at the beginning of the trawl record.

During the period 1983–2015, in the RREAS catch there was a significant decrease in anchovy abundance, an increase in sanddabs ($r^2 = 0.33$, $r = -0.57$, $p = 0.0005$; $r^2 = 0.48$, $r = 0.68$, $p < 0.0001$, respectively) and no trend in YOY rockfish ($r^2 = 0.0009$, $r = -0.03$, $p = 0.86$). These trends were removed prior to comparison with cormorant time series. Among cormorant colonies, only populations at Año

Nuevo and Alcatraz islands displayed significant temporal trends ($r^2 = 0.36$, $r = 0.60$, $p = 0.002$; $r^2 = 0.34$, $r = 0.58$, $p = 0.003$, respectively), and these trends were also removed prior to relating them to forage fish abundance.

Relationships between Brandt's Cormorant breeding colony size and fish abundances in research trawls indicated the importance of prey species availability in affecting cormorant population size. During 1983–2015, there was a significant relationship between South Farallon Island colony size with either YOY rockfish (negative) and anchovy (positive) ($r = -0.36$, $p = 0.04$, and $r = 0.38$, $p = 0.02$, respectively). Total cormorant population size was significantly related to anchovy abundance ($r = 0.41$, $p = 0.02$). After 2008, cormorants mostly consumed YOY anchovy (Elliott et al., 2016), not delineated in our availability data, which fits with a large increase in that age group close to shore (Sakuma et al., 2016; Davison et al., 2017). In regard to sanddabs, they became enumerated in the research catch after 1987, but there was no relationship between sanddab abundance and either South Farallon colony size nor total cormorant population size ($r = 0.32$, $p = 0.11$; $r = 0.31$, $p = 0.12$). It is possible that some portion of the sanddabs being taken by cormorants are in areas or depths (i.e. settled to the bottom) not sampled by the trawls.

During 1993–2015, when all colony counts were consistent through time and thus comparable to fish abundance time series, sizes of all colonies except Alcatraz were significantly correlated with anchovy abundance; none were correlated with YOY rockfish (Table 1). Drakes Bay colony size was also positively related to sanddabs ($r = 0.59$, $p = 0.003$).

4. Discussion

4.1. Population changes

Brandt's Cormorant distribution is centered in the central portion of the California Current, and specifically the Gulf of the Farallones, where the species' largest single breeding assemblage has occurred at the South Farallon Islands (Wallace and Wallace, 1998). To the north and south, the species is more spread out at typically smaller-sized colonies, except for a large concentration at the California Channel Islands (Carter et al., 1992; P. Capitolo, unpubl. data). During the period of the present study, 1971–2015, two Brandt's Cormorant breeding population peaks were exhibited in the Gulf of the Farallones, the second about 60% larger than the first. Peaks at the Farallon Islands were about the same, while the second Gulf-wide peak reflected substantial mainland population growth. The first peak lasted about a decade, while the second peak was much shorter. Both peaks were followed by population crashes, possibly indicating that a ceiling to Brandt's Cormorant

Table 1
Correlation coefficients, with statistical significance, between Brandt's Cormorant colony size and fish abundance, 1993–2015 (significant values in bold type).

	YOY rockfish	Sanddabs	Anchovy
Point Reyes	− 0.17	0.25	**0.51**
	$p = 0.432$	$p = 0.245$	**$p = 0.013$**
Drakes Bay	0.03	**0.59**	**0.46**
	$p = 0.877$	**$p = 0.003$**	**$p = 0.029$**
Lobos/Seal	− 0.06	0.26	**0.47**
	$p = 0.778$	$p = 0.232$	**$p = 0.024$**
Devil's Slide	− 0.29	0.20	**0.49**
	$p = 0.186$	$p = 0.370$	**$p = 0.018$**
Alcatraz	− 0.31	0.16	0.38
	$p = 0.146$	$p = 0.476$	$p = 0.072$
Año Nuevo	− 0.31	0.27	**0.59**
	$p = 0.155$	$p = 0.211$	**$p = 0.003$**
South Farallon	− 0.36	0.31	**0.56**
	$p = 0.092$	$p = 0.151$	**$p = 0.005$**
Total	− 0.29	0.31	**0.58**
	$p = 0.184$	$p = 0.149$	**$p = 0.004$**

population size in the Gulf of the Farallones exists. If so, is it a limitation related to foraging, one related to nest site availability, or both?

In regard to the first peak and mortality event, it appears that Brandt's Cormorant numbers had increased dramatically at the Farallones in late 1960s–early 1970s with a lessening of disturbance there (cf Ainley and Lewis, 1974; White, 1995). Thus, a large number of pre-recruits in the population could have contributed to a great degree to the 1971 mortality event without affecting the breeding population, unlike what happened in the later major mortality event. Carcasses during that first mortality peak might have been remnants from the 1971 San Francisco oil spill, precipitated by two tankers colliding underneath the Golden Gate Bridge in January of that year (Stenzel et al., 1988). The slightly higher "background" deposition rates apparent in the late 1970-early 1980s could have been the result of incidental catches of cormorants in coastal gill net fisheries (Wild, 1990; Julian and Beeson, 1998; Appendix 1). In general, higher carcass deposition during the second population peak was consistent with the larger cormorant population by then. The large mortality event after the second population peak occurred in conjunction with three other phenomena: 1) a severe drop in availability of anchovy coinciding with a strong El Niño (Santora et al., 2014); 2) a decrease in abundance and body condition of adult Chinook salmon (*Oncorhynchus tshawytscha*; a possible cormorant competitor) that precipitated the so-called Salmon Emergency Closure (California Department of Fish and Game, 2010; Adams et al., 2017 ms), thus indicating a general diminution of the preyscape; and 3) a series of harmful algae bloom generating toxic domoic acid and die-offs of several vertebrate species, with such blooms being more frequent in warmer Monterey Bay (and farther south) than in the Gulf of the Farallones (Bargu et al., 2010; Nevins et al., 2011).

During the first peak in the late 1960s–early 1970s, almost all Brandt's Cormorants nested on the Farallones with only 100 s at mainland sites. This pattern with little doubt was largely the result of greater levels of disturbance by human activities along the coast than at the Farallon Islands. Since the 1970s–late 1980s, however, it appears that Brandt's Cormorants have been free enough from human disturbance at other Gulf of the Farallones habitats for the whole population to be responding principally to prey distribution and availability. The rapid swings in populations among sites, akin to the pattern seen in Guanay and Cape cormorants (Murphy, 1981; Tovar et al., 1987; Jahncke et al., 2004; Crawford et al., 2016), indicate that more than reproductive success is important in determining a colony's future size, and that the entire Gulf population may be one or part of a larger metapopulation, with individuals somewhat free to move among sites in accord with seeking the best breeding conditions.

Structuring the spread of the metapopulation, energetic demands of foraging are reduced when breeding closer to foraging areas, a hypothesis put forth by our analysis, and further supported by observations of Farallon-banded cormorants nesting at mainland colonies at least from Point Reyes to Año Nuevo (Saenz et al., 2006; Capitolo et al., 2014). Among the several thousand Farallon cormorants banded through 1982, recoveries of pre-breeders on mainland beaches extended even farther, mostly from Cape Mendocino (~300 km north of San Francisco) to Point Sur (~220 km south of San Francisco; Boekelheide et al., 1990). Over the past 15 years, with a larger total Gulf population, recoveries of banded pre-breeders have continued to be found primarily in these same areas, but with an additional few percent ranging north as far as Oregon, Washington, and British Columbia, and south to the Channel Islands and northwest Baja California (R. Bradley, pers. comm.).

During the second peak, only two-thirds of the Gulf population bred at the Farallon Islands (vs. ~90% in the 1970s peak), indicating a spreading of the population to coastal sites and perhaps facilitating the slightly higher incidence of juvenile band recoveries farther afield. More recent Brandt's Cormorant breeding population growth farther south in the California Channel Islands (Carter et al., 1992) and along the central California coast (e.g., 15,000 pairs from Monterey Bay to

Point Conception in 2006, only slightly less than the Gulf population that year; P. Capitolo, G. McChesney, unpubl. data) could also be due in part to Gulf of the Farallones emigrants. Similarly, Brandt's Cormorants in southern California appear to have decreased at the outermost of the northern Channel Islands relative to increases on islands closer to the mainland and farther south (P. Capitolo, unpubl. data). Our observation of a Gulf of the Farallones (or beyond) metapopulation, thus, may be indicative of a larger-scale phenomenon.

The similar peaks at the Farallon Islands (~ 12,000 vs 13,500 pairs) may indicate a possible limit to the Brandt's Cormorant population there. Following the first peak, low-lying portions of the islands not far above the high tide line were taken over by pinnipeds recovering from former persecution, but that habitat was never extensively used by the cormorants (Ainley and Boekelheide, 1990). On the other hand, the population of Common Murres at the Farallones has increased 5 × from 50,000 to 250,000 breeding birds during the study period and they have taken over areas used extensively in the past by the cormorants (Warzybok et al., 2015). The murres occupy their nesting sites, shoulder to shoulder, months before the cormorants arrive for breeding, thus increasing the murres' advantage in competition for space. However, it does appear that space still exists for further cormorant expansion (as well as murres; G. McChesney, R. Bradley, pers. obs.). At mainland sites in the Gulf of the Farallones, room for growth over 2007 peaks is more limited, given the smaller sizes of the islands, sea stacks, and headlands (P. Capitolo, G. McChesney, pers. obs.). Similarly, Cape Cormorants in the Benguela Current must compete for space with other seabirds (sulids) as well as with recovering pinnipeds (Crawford et al., 1991; Kirkman, 2009); and Guanay Cormorants of the Peru Current must compete for space with sulids and pelicans (Murphy, 1925, 1936), with cormorant and sulid peaks being negatively associated (Tovar et al., 1987). That the murres have been steadily increasing in the Gulf of the Farallones, while cormorant numbers have been dramatically fluctuating is likely related to the murres' advantage in trophic competition as well — the murres take their 3-week old flightless chicks to where food is abundant and complete rearing there, unlike the cormorants that have to continue their more energetically costly mode of being central place foragers for multiple chicks for another month or more.

4.2. Relationship of population changes to prey

It is possible that competition for prey is a factor for limiting the size of the Brandt's Cormorant metapopulation inhabiting the Gulf of the Farallones, most likely in the form of interference competition. In the latter, the flock foraging exercised by cormorants would negatively affect prey patch quality (prey school driven deeper, more diffuse, smaller etc.), reducing the effectiveness by which additional cormorants can readily find food at a given location. Furness and Birkhead (1984) proposed that large colonies of seabirds, not specifying whether by consumptive or interference competition, can limit the size of other colonies within foraging range of the large colony, and this has been shown empirically in a number of cases, e.g. for penguins (*Pygoscelis* spp.; Ainley et al., 1995a, 1995b, 2004) and Black-legged Kittiwakes (*Rissa tridactyla*; Ainley et al., 2003).

All Gulf of the Farallones Brandt's Cormorant colony sites are within foraging range of one another (with possible exception of Pt. Reyes and Año Nuevo, the two extremes), the means by which this foraging pressure by larger numbers of cormorants would be applied. Consistent with the pattern seen in the penguin and kittiwake studies, in which birds from large colonies by the density of their foraging can exclude those of nearby smaller colonies from foraging in the same area, cormorants from the Año Nuevo Island colony forage adjacent to but not within the dense concentration of foraging cormorants just to its north. Similarly, cormorants from the Alcatraz Island colony, for which we found no significant correlation in size to Gulf of the Farallones prey availability, appear to forage in central San Francisco Bay, adjacent to the dense foraging among individuals from other colonies just outside

the Bay. There, the Alcatraz cormorants, while consuming a lot of anchovy, take mostly benthic prey (Yakich, 2005; Saenz et al., 2006; B.L. Saenz, pers. comm.). Additionally, the trophic competition need not necessarily be limited to intraspecific interaction but could have interspecific aspects as well. This principally would involve murres, which have undergone large recent population increases, as noted, and essentially prey on the same main forage species as the cormorants (Fig. 4) and exercise the same deep diving for prey in flocks in the same foraging areas (Ainley and Boekelheide, 1990; Ainley et al., 2014, 2015). It has been suggested that murres, by virtue of their numbers and density, can exclude other abundant diving seabird predators, e.g. Sooty Shearwaters (*Ardenna grisea*), from coastal California Current foraging areas (Ainley et al., 1990, 2009). Most murres nesting in the Gulf of the Farallones typically forage within the Gulf and southward not quite as far as Año Nuevo, and rarely within the Golden Gate (Ainley et al., 1990; Wells et al., 2017). Their abundance in the main cormorant foraging area in the Gulf would further encourage development of the adjunct foraging areas among cormorants nesting at Año Nuevo and Alcatraz islands.

In responding to ocean conditions, the Brandt's Cormorants in the Gulf of the Farallones most directly are affected by prey availability, and principally that of YOY rockfish, anchovy and sanddabs. Our analysis found a stronger correlation with anchovy than YOY rockfish, but the research trawl time series did not overlap the early part of the cormorant population or diet time series. If it had, a greater importance of the rockfish might well have been evident. During the early 1970s, Brandt's Cormorant reproduction was closely linked to prevalence of YOY rockfish in the cormorant diet (Ainley et al., 1990, 1995b). While anchovy and YOY rockfish are particularly important in the cormorant diet, notable but lesser importance of sanddabs may be a proxy for the more diverse prey selection that occurs when and where rockfish and anchovy are not available (Ainley and Boekelheide, 1990; Elliott et al., 2015, 2016).

The California Current rockfish and anchovy variability frequently coincides with regional upwelling indices of warm-water vs cold-water conditions, the data coming largely from the RREAS (Santora et al., 2014; Ralston et al., 2015). Warmer years with weaker upwelling coincide with more anchovy in the diet, and years of colder water and stronger upwelling coincide with rockfish (see also Wells et al., 2017). These regional aspects of ocean climate are in part tied to broader, ocean basin-scale signals. For instance, Schmidt et al. (2014, 2015) found that Brandt's Cormorant demographic parameters were correlated with El Niño Southern Oscillation indices, hypothesizing that it was the preyscape that was being affected by ocean-climate variability, which in turn influenced cormorant breeding. However, basin-scale ocean-climate indices are proxy variables that do not provide a mechanistic understanding of regional marine ecosystem dynamics. While, as noted, cormorant breeding population size and success in the early part of the study was highest in years of high abundance of YOY rockfish (which were decreasing in prevalence), by the 1990s, when the diet was switching to anchovy, cormorant breeding success became high again (Sydeman et al., 2001). The latter was also the period when mainland breeding sites became more important. Our study indicates that the diet of Brandt's Cormorants reflects the availability of prey, which in turn affects the degree to which cormorants in this metapopulation occupy the Farallon Islands vs mainland breeding sites. It would be interesting to have information on the cormorant diet during the non-breeding season, when the cormorants may be assessing spatial aspects of prey availability to 'decide' where to nest. During the mid-2000 anchovy surge, both the winter and summer diet of the cormorants at Año Nuevo Island was dominated by anchovy (cf Webb and Harvey, 2015 and our Fig. 4), a period when the Año Nuevo cormorants were increasing dramatically.

4.3. Summary and conclusions

In summary, the pattern observed in this study was that, as the availability of rockfish decreased during the 1970–90s, the numbers of Brandt's Cormorants on the offshore Farallon Islands decreased as well. At the same time, the cormorants began to feed more and more on anchovy, which occur closer to the coast (Santora et al., 2012; Ralston et al., 2015; Wells et al., 2017). The size of the central California Current anchovy stock was low during the mid-1980s to early 2000s (Davison et al., 2017), and in lower abundance they were confined even closer to the coast (MacCall et al., 2016). With human disturbance becoming severely reduced at mainland sites, cormorants began to breed in larger numbers there and at more sites in the 1990s. A large but ephemeral spike in anchovy biomass in the mid-2000s (Ralston et al., 2015; Davison et al., 2017) brought a dramatic increase in cormorants at all sites, with anchovy spreading farther off the coast (cf MacCall et al., 2016). As rockfish populations recovered and YOY abundance levels increased during the 2000s (see Fig. 5), a return to foraging heavily on rockfish, at least by Farallon Islands cormorants, resulted (Fig. 4). In accord, the cormorant metapopulation remains spread out among the various nesting sites.

Thus, it appears that management of fish stocks to allow more forage fish, as well as land use management that reduced disturbance to cormorant breeding sites, are major indirect factors explaining changes in the populations of Brandt's Cormorants in the central portion of their breeding range, the Gulf of the Farallones. Free to use a number of breeding sites in the Gulf, the cormorants now appear to be responding principally to prey availability, which itself has been highly volatile, though they are also limited by the amount of available breeding space adjacent to foraging areas. Now breeding at more sites, the population also is more resilient to other potential impacts such as oil spills. On the other hand, the more coastal prevalence of the cormorants makes them more susceptible to coastal harmful algal blooms and local mortality episodes, as evidenced by much higher carcass deposition rates in Monterey Bay than in the Gulf. In general, though, the situation for Brandt's Cormorant in the California Current has become the opposite of that of the Cape Cormorant in the Benguela Current, for which fishery and colony management have reduced populations to the point of being labeled as "endangered" under IUCN Red List criteria (Crawford et al., 2017). In comparison, Guanay Cormorant is listed as "near threatened" and Brandt's Cormorant as a species of "least concern" (IUCN, 2017). Given the boom-or-bust aspect of their breeding, their propensity to move in response to prey availability, as well as the ease by which their breeding numbers can be assessed, Brandt's Cormorants represent an ideal species for ecosystem monitoring, thus to understand dynamics of coastal California ocean and food web conditions. In that regard, Schmidt et al. (2014, 2015) noted a shift in the degree to which the demography of Farallon Island cormorants correlated to ocean climate, a shift that coincided with the second population peak and crash. Clearly, more work is needed to disentangle the various factors driving variation in the cormorant response to the environment. Building on the effort by Schmidt et al. (2014, 2015), as well as the energetics of prey switching (Warzybok et al., 2017 ms), development of a robust metapopulation dynamics model should account for boom-or-bust cycles and would further assess the relationship between forage fish availability and Brandt's Cormorant populations.

Appendix 1 Important milestones in the management of biotic resources relevant to cormorant population dynamics in the Gulf of the Farallones region. Many of the federal milestones listed can be found in the Federal Register; otherwise see text for references

Farallon Islands

1809–1838 Seal hunting, for most of the period by the Russian American Fur Company. Much disturbance, subsidence hunting of seabirds.

1855–1972 South Farallon a lighthouse station; WWII military outpost.

1851–1896 Commercial egg collecting (mostly murre eggs but much disturbance).

1909 Presidential proclamation declared all islands as Farallon Islands Reserve (subsequently National Wildlife Refuge) except for South Farallon Islands

1962 Families (4) of U.S. Coast Guard (USCG) lightkeepers removed; rotating contingent of 4 persons thereafter.

1969 South Farallon Islands added to Refuge.

1970 Point Reyes Bird Observatory (PRBO, now Point Blue Conservation Science) establishes year round research station, occupying one of the two family houses.

1971 PRBO, with agreement of USCG, institutes rules restricting access to much of the outer portions of the South Islands; subsequently (ca 1974) made official by U.S. Fish and Wildlife Service.

1972 U.S. Navy photoflash bombing of Middle and North Farallones terminated. USCG automates all aids-to-navigation and vacates Southeast Farallon. Islands remain closed to the public, with only limited numbers of researchers, wildlife managers, and contractors permitted.

1974 All islands except Southeast Farallon designated Federal Wilderness Areas (Farallon Wilderness); PRBO restrictions formalized by Wilderness Plan for West End and other islets.

Año Nuevo Island

1872 to 1948 USCG light station with personnel living on island.

1948–1967 Unrestricted public access.

1967 California Department of Parks and Recreation closes the island to the public.

1989 Researcher access restricted on south terrace of island during cormorant breeding season.

1992 Monterey Bay National Marine Sanctuary designated; establishes zones that restrict. motorized aircraft (including drones) from flying below 1000 ft.

2010 Sea lion exclusion fence built, creating visual barrier from researcher activity, bringing less disturbance to cormorants breeding on the south terrace.

Mainland rocks, Marin and San Francisco County coast

1870–1975 Point Reyes Headlands occupied by a lighthouse and keepers quarters. Much disturbance present, e.g. dynamiting cliffs for construction etc.

1962 Point Reyes National Seashore designated, management/protection of mainland rocks instituted (Headlands and Drakes Bay colony complex).

1972 Alcatraz Island and Lobos/Seal rocks made part of Golden Gate National Recreation Area; portions of Alcatraz closed to public access.

1975 Point Reyes Coastal Reserve prohibits boats to within 1000 ft (305 m) of PR Headlands lighthouse automated.

1976 Point Reyes National Seashore congressionally designated Federal Wilderness along coastline including waters within ¼ mile of shore including Point Reyes Headland and Drakes Bay rocks.

1981 Greater Farallones National Marine Sanctuary designated; establishes zones that restrict motorized aircraft (including drones) from flying below 1000 ft.

1995 Point Reyes Headland and Drakes Bay complex seabird colonies were selected as control sites for monitoring recovery of seabirds from oil spills. Daily observations during the nesting season yielded increased observations and reporting of disturbances to law enforcement.

2000 Bureau of Land Management California Coastal National Monument designated, protects all coastal rocks, including Devil's Slide Rock 2001 – Personal Motorized Watercraft were banned from all national parks, including Point Reyes National Seashore and Golden Gate National Recreation Area.

2007 California Central Coast Marine Protected Areas (MPAs), including Año Nuevo State Marine Reserve (No Take) went into effect; prohibits all boat traffic nearshore of colonies.

2010 California North Central Coast MPAs went into effect. These included SMRs at Point Reyes, NFI, and SFI, State Marine Conservation Areas at Point Reyes and SFI, and Special Closures to prohibit boat traffic near colonies at a distance of either 300 or 1000 ft seaward of Point Reyes, Point Resistance, Stormy Stack, North Farallones, South Farallones, and Devils Slide; reduces boat traffic nearshore of colonies.

2015 Drones banned from all national parks without a permit, including Point Reyes National Seashore and Golden Gate National Recreation Area.

Fishery regulations

1974 Marine Mammal Protection Act restricts control of pinniped populations, whose numbers began to increase dramatically thereafter; allows recovery of cetaceans.

1976 Passage of Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA).

1978 Northern Anchovy Management Plan adopted (first ecosystem-based regulation).

1980–1987 Intense near-shore gill-netting Gulf of the Farallones region/Monterey Bay with high bird bycatch although cormorants apparently little affected (5% of take).

1983 Northern anchovy biomass declines below the 300,000 mt threshold, reduction fishery is closed; total landings fall from the 50,000–150,000 mt range to the 1000–5000 mt annual take thereafter (only for bait used in other fisheries).

1990s Ground fish take begins to be restricted; extensively curtailed since 2000.

1992 PFMC establishes low acceptable biological catch of shortbelly rockfish; reduced 50% in 2001.

1996 Sustainable Fisheries Act — Amendments to MSFCMA.

2003 Implementation of the Rockfish Conservation Areas closes most of continental shelf to both commercial and recreational rockfish fishing (nearshore fisheries remain open).

2013 Pacific Coast Fishery Ecosystem Plan adopted.

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