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Spatiotemporal Variability in the Diet of Nonbreeding Brandt's Cormorant (*Phalacrocorax penicillatus*) in the Monterey Bay Region

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SPATIOTEMPORAL VARIABILITY IN THE DIET OF
NONBREEDING BRANDT'S CORMORANT (*PHALACROCORAX PENICILLATUS*)
IN THE MONTEREY BAY REGION

A Thesis

Presented to

The Faculty of the Department of Marine Science

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Lisa Annette Webb

December 2013

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The Designated Thesis Committee Approves the Thesis Titled

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December 2013

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ABSTRACT

SPATIOTEMPORAL VARIABILITY IN THE DIET OF NONBREEDING BRANDT'S CORMORANT (*PHALACROCORAX PENICILLATUS*) IN THE MONTEREY BAY REGION

by Lisa Annette Webb

Brandt's Cormorant (*Phalacrocorax penicillatus*) diet composition was investigated using pellets (n = 285) collected on 19 sampling days at 3 locations during the 2006-07 and 2007-08 nonbreeding seasons in the Monterey Bay region. The conventional diet method was used, and the efficacy of the all-structure technique was evaluated. Although 29 species were consumed, Northern Anchovy (*Engraulis mordax*) dominated the diet and Speckled Sanddab (*Citharichthys stigmaeus*) also was important. Few rockfishes (*Sebastes* spp.) and Market Squid (*Doryteuthis opalescens*) were consumed compared with the number consumed in previous studies in the region during the 1970s. El Niño and La Niña conditions during the study provided a unique opportunity to examine predator response. Greatest prey number and diversity occurred at locations within Monterey Bay during cooler ocean conditions, whereas the outer coast location remained unchanged. Short-term specialization was observed, but mean prey diversity indicated a generalist feeding mode. Patterns of prey number and diversity within a nonbreeding season were not consistent among locations. This study demonstrated the importance of periodic sampling at multiple locations within a region to detect spatiotemporal variability in the diet of this opportunistic generalist.

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INTRODUCTION

The Brandt's Cormorant (*Phalacrocorax penicillatus*) is the most abundant locally nesting seabird in the Monterey Bay region of central California. Four new colonies formed and grew rapidly from 1989 to the mid-2000s (Carter et al. 1992, Bechaver et al. 2013). As a generalist predator (Cutler 1983) occupying a middle-to-upper trophic position in the nearshore marine food web (Ainley et al. 1995), the species consumes young-of-the-year and juvenile-age classes of fishes and, to a lesser extent, squid (Sydeman et al. 2001). Given their reliance on the nearshore environment (Wallace and Wallace 1998), year-round occurrence, restricted foraging range within 10 km of the shore (Briggs et al. 1987), and consumption of approximately 20% of their body mass per day (Ancel et al. 1997), there is potential for Brandt's Cormorants to extract large numbers of prey from the nearshore environment in the Monterey Bay region, yet little is known about their diet there.

Brandt's Cormorants are medium-sized, foot-propelled pursuit divers with a stiff, rudder like tail, an elongated neck, and a long, hooked bill (Boekelheide et al. 1990). They are visual predators (Hubbs et al. 1970) and Henkel (2006) reported they occurred more often in the clearest water available in Monterey Bay despite greater productivity in more turbid waters. The wettable plumage of cormorants appears to reduce buoyancy (Owre 1967), possibly allowing them to descend faster and remain at depth with less effort compared with other diving seabirds; however, no time-depth recorders have been placed on this species. They counter buoyancy at shallow depths by controlling body tilt

with their tail (Ribak et al. 2004). These characteristics promote maneuverability while foraging underwater and allow them to feed from the surface to the bottom.

A review of Brandt's Cormorant diet throughout their range indicated nearly equal proportion of schooling and non-schooling prey (Ainley et al. 1981). Foraging depths inferred from habitat of prey consumed were 12% taken from surface to mid-depth, 47% from mid-depth to the bottom, 29% on the bottom, and 12% cryptic species on the bottom. When foraging in Monterey Bay during winter, prey were taken in a variety of substrates with 36% in flat sand or mud, 32% in rocky reef, 28% in the water column from surface to mid-depth, and 4% in flat area near rocks.

From 1979 to 2011, there were 18 Brandt's Cormorant colonies in the Monterey Bay region with maximum abundance of approximately 20,500 breeding birds in 2006 (Bechaver et al. 2013; USFWS, unpublished data). Three colonies were located north of the bay on the outer coast and 5 colonies were within Monterey Bay. The remaining 10 colonies were located south of the bay on the Monterey Peninsula outer coast, the largest of which is Bird Island, averaging approximately 1,900 breeding birds (Bechaver et al. 2013).

Recent Brandt's Cormorant population growth and expansion may be related to changing prey resources in the region and warrants investigation. Año Nuevo Island is located north of Monterey Bay on the outer coast and has been identified as important seabird habitat in California (Briggs et al. 1987). Brandt's Cormorants began nesting on Año Nuevo Island in 1989 (Carter et al. 1992) and increased to nearly 5,000 breeding birds by 2006 (USFWS, unpublished data). Nesting began just outside the northern

opening to Monterey Bay between Terrace Pt. and Pt. Santa Cruz in 1996 (Hebshi 1998) and averaged 80 breeding birds from 2003 to 2006 (Bechaver et al. 2013). Nesting within Monterey Bay was first recorded in the mid-1990s and increased to nearly 2,500 breeding birds at 5 colonies by 2006 (Bechaver et al. 2013). Three of the 5 colonies were located at or near Monterey Harbor, where diverse habitat may provide abundant prey resources. Nesting began in the central bay in 2004 (personal observation) at Moss Landing Harbor (< 200 breeding birds) and in northern Monterey Bay in 2005 at Seaciff Cement Ship (< 500 breeding birds; Bechaver et al. 2013). It is unknown if Brandt's Cormorants in the Monterey Bay region forage in Elkhorn Slough, situated just east of the Moss Landing Harbor, where fish spawning and nursery habitat are located and abundant and diverse fishes occur seasonally (Yoklavich et al. 1991).

The two previous Brandt's Cormorant diet studies in Monterey Bay were both during the 1970s and sampled the nonbreeding season (Baltz and Morejohn 1977, Talent 1984; Fig. 1). Results differed somewhat, potentially because each study had small sample size ($n \leq 11$) and collected birds in different habitats (inshore versus offshore) during different years. Rockfishes (*Sebastes* spp.) and Pacific Sanddab (*Citharichthys sordidus*) were the two main prey during the 1970-71 nonbreeding season and also occurred during the 1974-75 nonbreeding season; however, Northern Anchovy (*Engraulis mordax*) and Market Squid (*Doryteuthis opalescens*) also were important in 1974-75. Since then, a substantial decrease in abundance of juvenile rockfishes occurred during the 1990s in the central California Current with only partial recovery as of the early 2000s (Mills et al. 2007). Commercial Market Squid landings in Monterey Bay

decreased substantially beginning in 2005 (CDFG 2009) indicating decreased abundance. The change in dominant ichthyofauna correlate to cyclical changes in sea surface temperature that are the result of either the Pacific Decadal Oscillation on a longer time scale or the El Niño Southern Oscillation on a shorter time scale (Chavez et al. 2003). Determining present diet composition will aid in our understanding of how a major avian predator in the region responds to a decrease of multiple important prey resources and will provide important information about Monterey Bay food web dynamics.

Figure 1. Brandt's Cormorant diet composition by percent number (%N) for past studies in central California. Prey species comprising less than 5.0% were combined into category "Other". Shannon-Wiener diversity index (H) is provided above each bar and time, location, region, and breeding status below each bar. Data are from 1) Talent 1984, 2) Baltz and Morejohn 1977, 3) Ainley et al. 1990, 4) Sydeman et al. 1997, 5) Cutler 1983, and 6) Yakich 2005.

Brandt's Cormorants are capable of short-term specialization on abundant prey but also may diversify their diet with changing ocean conditions (Baltz and Morejohn 1977, Cutler 1983, Talent 1984, Ainley et al. 1990, Sydeman et al. 1997, Yakich 2005; Fig. 1). For example, at Southeast Farallon Island where diet was investigated for many breeding seasons during the 1970s, rockfishes made up 99% of the diet by number late in the 1977 breeding season, yet during the 1976 breeding season when ocean conditions were anomalously warm, rockfishes were only 13% of the diet by number with the remaining 87% split among 12 fish species and Market Squid (Ainley et al. 1990).

There also is some evidence that Brandt's Cormorant foraging behavior and diet vary as a function of habitat available near the colony or roost, likely because of their limited foraging range (Briggs et al. 1987, Hebshi 1998). Hebshi (1998) observed Brandt's Cormorants foraging in northern Monterey Bay from Soquel Pt. to Davenport Pt. in shallow kelp forest and sandy substrate habitat. The most important factors determining where cormorants foraged were 1) proximity to colony or roost, 2) amount of kelp canopy cover, 3) presence of rocky substrate, and 4) less long-term exposure to wind and heavy seas. Diet at Alcatraz Island in San Francisco Bay included appreciable numbers of Bay Goby (*Lepidogobius lepidus*) (Yakich 2005; Fig. 1) when Bay Goby was abundant (Fish et al. 2011). Similarly, appreciable numbers of Market Squid were reported only in the diet of birds collected offshore in Monterey Bay (Baltz and Morejohn 1977; Fig. 1), and Monterey Bay has an important Market Squid spawning ground (McInnis and Broenkow 1978). Overall, these findings are consistent with localized foraging and opportunistic predation.

Variability in seasonal distribution of Brandt's Cormorants in the Monterey Bay region may be important when interpreting diet variation. Brandt's Cormorants occur in Monterey Bay throughout the year (Baltz and Morejohn 1977, Briggs et al. 1987), but they do not use the area homogeneously. During breeding, April through August, nesting cormorants act as central place foragers because they must return to their colonies to maintain nests, incubate eggs, and provision young (Boekelheide et al. 1990). During the nonbreeding season, September through March, individuals remain within 25 km of any acceptable roosting location (Briggs et al. 1987) because they must return to shore to rest, thermoregulate, and dry their feathers. At-sea strip transect survey data in Monterey Bay from 1997 to 2005 indicated a clumped distribution during breeding with more dense concentrations of Brandt's Cormorants near colonies at Monterey Harbor and Moss Landing Harbor than elsewhere in the bay. During winter the observed distribution in the bay was more uniform (D. Croll, unpublished data). Thus, movements are less constrained during the nonbreeding season and may be regional (> 50 km) during the course of a few days.

Intraseasonal forcing on Brandt's Cormorant behavior and diet are linked to seasonal oceanographic influences that affect prey availability and should be accounted for when sampling cormorant diet. Greater marine productivity occurs in Monterey Bay during summer after northwest winds generate coastal upwelling north of the bay at Point Año Nuevo. Cold, nutrient rich waters are advected into the bay via cyclonic surface circulation (Breaker and Broenkow 1994, Rosenfeld et al. 1994, Paduan and Rosenfeld 1996). Pulses of primary productivity also occur during spring, and occasionally fall,

making the region productive for much of the year but less so during winter (November through January; Pennington and Chavez 2000). The timing of the Brandt's Cormorant breeding season is aligned with peak ocean productivity and abundant prey (Boekelheide and Ainley 1989) that occur during the upwelling season (spring and summer). The nonbreeding season corresponds to the non-upwelling season which includes postbreeding (September and October), winter (November to January), and prebreeding (February and March). Dominant fishes in Monterey Bay vary seasonally (Cailliet et al. 1979). Rockfishes and Market Squid occurred in moderate numbers and greater frequency in summer. During winter Northern Anchovy occurred in greater numbers and frequency and Pacific Sanddab and Speckled Sanddab (*Citharichthys stigmaeus*) occurred frequently but in lesser numbers.

Brandt's Cormorant diet also may differ by location according to diversity in the nearshore habitats of the Monterey Bay region. Areas with greater habitat diversity are more likely to have a greater diversity of fishes because fish species generally occur in one or a few habitat types. Habitat used by various families and species of fish can be characterized by depth, distance from shore, marine zones (estuarine, subtidal, neritic, pelagic), distance from the bottom, and substrate type (Miller and Lea 1972). Año Nuevo Island is 1 km from shore, exposed on the outer coast, and 11 km from a canyon that extends in from the shelf break. Año Nuevo Bay has shallow depths of less than 25 m and primarily sandy substrate with a few rocky outcrops and some beds of giant kelp (*Macrocystis pyrifera*) (Henkel and Harvey 2006). Within Monterey Bay, the opening at the north and south has exposed, rocky coast with abundant kelp forests. In central

Monterey Bay there are large areas with sand or mud substrate. Elkhorn Slough, the third largest estuary in California, is located just inland of the Moss Landing Harbor.

Monterey Bay is bisected by the vast Monterey Submarine Canyon (Shepard 1973). Several other canyons extend in from the shelf break in the region. Pelagic water is closest to Moss Landing Harbor and nearly equidistant from Año Nuevo Island and Monterey Harbor.

Collecting diet samples at multiple locations is necessary for examining spatial variation in the region. Three of four colonies that were more recently colonized were accessible to sample and provided representation of northern (Año Nuevo Island), central (Moss Landing Harbor), and southern (Monterey Harbor) portions of the Monterey Bay region. Año Nuevo Island is approximately 60 km from Moss Landing Harbor and 70 km from Monterey Harbor. Moss Landing Harbor and Monterey Harbor are approximately 25 km apart. The diverse habitats of the Monterey Bay region are represented by these three locations.

Many methods are available to study seabird diet (Barrett et al. 2007).

Cormorants produce one pellet per day containing prey remains from the prior 24 h (Duffy and Laurenson 1983, Jobling and Breiby 1986, Zijlstra and Van Eerden 1995). Some considered cormorant pellets equivalent to stomach samples (Jordán 1959, Ainley et al. 1981), and the daily consumption derived from pellets matched energetic demands in a few studies (Voslamber 1988, Dirksen et al. 1995). Most fish otoliths, cephalopod beaks, and other prey hard parts contained in cormorant pellets have enough structure to determine species (Duffy and Laurenson 1983).

Collecting pellets at colony or roost locations is well suited for a study with the aim of addressing fine-scale spatiotemporal variation because birds do not have to be killed to obtain the larger sample sizes required, the diet sample is not biased by the habitat the bird is collected in (Hubbs et al. 1970), and the diet is not time-averaged over months like many other dietary methods (Barrett et al. 2007). Increased sampling frequency is important because at a regional scale Brandt's Cormorants may alter their foraging habitat on the order of days (Hubbs et al. 1970), especially during the nonbreeding season when they are less constrained. Prey remains in pellets can be identified and enumerated with unparalleled taxonomic resolution at minimal cost.

Some have criticized using pellets to reconstruct the diet because otoliths from small size classes of fishes, and otoliths of certain fish species with fragile otoliths may be disproportionately digested, thereby leading to their underestimation (Duffy and Laurenson 1983, Duffy and Jackson 1986, Jobling and Breiby 1986, Johnstone et al. 1990, Casaux et al. 1995, Zijlstra and Van Eerden 1995). These potential biases are consistent through time; therefore, pellets do provide an index of diet. Overall, pellets are useful for answering broad spatiotemporal questions such as comparing diet between seasons or years (Ainley et al. 1981, Duffy and Laurenson 1983, Duffy and Jackson 1986, Barrett et al. 1990, Harris and Wanless 1993, Sapoznikow et al. 2009). In pinniped diet studies, using the all-structure technique rather than just otoliths has improved prey detection (Tollit et al. 2003), but this technique has not yet been evaluated for seabird pellets.

The objectives of this study were to 1) evaluate the efficacy of nested sieves and the all-structure technique for increasing prey detection, 2) quantify the 2006-07 and 2007-08 nonbreeding season diet, 3) estimate prey size, 4) examine fine-scale spatiotemporal differences in diet composition within and between nonbreeding seasons, and 5) examine temporal differences in diet composition between the present diet and historical diet and the possible influence of relative abundance of prey and oceanographic conditions.

I expected that using nested sieves and the all-structure technique would increase prey detection for a few species compared with using a single sieve and identifying only fish otoliths and cephalopod beaks. I hypothesized that prey number and diversity would be greater in the nonbreeding season with cooler, more productive oceanographic conditions. I predicted that prey number would be lesser and prey diversity greater during winter (November through January) compared with postbreeding (September and October) and prebreeding (February and March) because oceanographic conditions would be less productive in Monterey Bay during winter (Pennington and Chavez 2000) and Brandt's Cormorants have less constrained movements at that time (Briggs et al. 1987). I expected prey number and prey diversity would be greater at locations within the bay (Moss Landing Harbor and Monterey Harbor) compared with the location outside the bay (Año Nuevo Island) because in a single day Brandt's Cormorants foraging within Monterey Bay would encounter more habitat types. I expected that regardless of nonbreeding season, prey diversity would be in accordance with habitat diversity near each location: greatest at Monterey Harbor, intermediate at Moss Landing Harbor, and

least at Año Nuevo Island. I expected diet composition to primarily be explained by location because of general differences in nearby habitat and secondarily explained by time period within the nonbreeding season because of differential availability of abundant prey. I expected the present diet to be different from historical diet because of major changes in dominant ichthyofauna, particularly that there would be lesser numbers of rockfishes and Market Squid.

METHODS

2.1 Study area and sampling scheme

The study was conducted in central California and included Monterey Bay and surrounding coastal areas (36°50'N, 122° 05'W; Fig. 2). Regurgitated pellets were collected once or twice per month at roosting locations at Año Nuevo Island, Moss Landing Harbor, and Monterey Harbor on 19 randomly selected days from approximately mid-September through March during the 2006-07 and 2007-08 nonbreeding seasons. Monterey Harbor was sampled only during 2007-08 (Table 1 and Fig. 3). Breeding activities were monitored so that disturbance was minimized. Sampling began in the fall when all chicks had fledged, and sampling was ceased in the spring once courtship behaviors were observed.

Figure 2. The Monterey Bay region study area and 3 sampling locations. Depth contours are shown every 10 m to 600 m depth, depicting the continental shelf and canyon features. Map inset indicates the location of the Monterey Bay region in central California.

Table 1. Sample size by time and location.

Time	Location	n
09/21/06	Moss Landing Harbor	10
09/26/06	Año Nuevo Island	12
12/18/06	Moss Landing Harbor	11
12/19/06	Año Nuevo Island	9
02/22/07	Moss Landing Harbor	13
03/02/07	Año Nuevo Island	12
09/25/07	Año Nuevo Island	12
09/28/07	Moss Landing Harbor	15
10/19/07	Monterey Harbor	13
11/09/07	Moss Landing Harbor	14
11/15/07	Año Nuevo Island	12
11/29/07	Monterey Harbor	14
12/21/07	Moss Landing Harbor	8
12/26/07	Monterey Harbor	13
01/17/08	Año Nuevo Island	11
02/20/08	Moss Landing Harbor	13
03/10/08	Monterey Harbor	15
03/24/08	Año Nuevo Island	14
03/26/08	Moss Landing Harbor	8
2006-07	Año Nuevo Island	33
2006-07	Moss Landing Harbor	34
2007-08	Año Nuevo Island	49
2007-08	Moss Landing Harbor	58
2007-08	Monterey Harbor	55
All	Año Nuevo Island	82
All	Moss Landing Harbor	92
All	Monterey Harbor	55
2006-07	All	67
2007-08	All	162
All	All	229

Figure 3. Sampling scheme with 19 sampling days during 2006-07 and 2007-08 nonbreeding seasons at 3 locations: Año Nuevo Island (ANI, triangles), Moss Landing Harbor (MLH, squares), and Monterey Harbor (MOH, circles).

2.2 Sample collection and processing

Locations were observed before sample collection to determine where Brandt's Cormorants roosted. On sampling days pellets were collected shortly after sunrise because cormorants cast pellets at daybreak (Ainley et al. 1981, Zijlstra and Van Eerden 1995), bird abundance decreases after sunrise as birds leave to forage (Ainley et al. 1981), and gulls may scavenge cormorant pellets (Spear 1993). Fresh pellets are clear to yellow and mucilaginous. Older pellets can be distinguished because they harden and become darker (Ainley et al. 1981). Only fresh, intact pellets with no tears in the outer covering were collected. Gull pellets were avoided because they have no outer covering

and are primarily composed of fish bones. Pellets were not collected in areas where Double-crested Cormorants (*P. auritus*) or Pelagic Cormorants (*P. pelagicus*) roost. All seabirds were counted before flushing, and counts were evaluated throughout the study period for rapid decreases that may have been attributed to disturbance from collecting pellets. Up to 50 pellets were collected per sampling day. Each pellet was placed in an individual storage bag, labeled, and frozen until later processing.

In the laboratory, each pellet was thawed in a separate jar with water and a small amount of detergent to slow digestive enzyme activity and limit further erosion of prey remains. After an initial 30-min soak the pellet was carefully opened using forceps. The jar was gently agitated to ensure thorough mixing of the detergent solution with the prey remains and then left to soak overnight. A 500 μm sieve was used to sort all samples. For each sampling day, approximately 20% of samples were sorted with nested 500 μm and 250 μm sieves to assess if identifiable prey remains were missed. Each sieve was examined for prey remains first with the naked eye and then again at 6.7X to 40X magnification with a zoom stereo microscope. Prey remains were stored for later identification, enumeration, and measurement. Hard parts such as fish otoliths, fish bones, and invertebrate carapace fragments were stored dry in petri dishes (Lance et al. 2001). Other tissues such as fish and cephalopod eye lenses, cephalopod beaks, and other chitinous invertebrate parts were stored in vials containing 40% isopropyl alcohol (Baltz and Morejohn 1977, Lance et al. 2001).

During identification and enumeration, all prey remains were examined at 6.7X to 40X magnification with a zoom stereo microscope. Images were taken as needed to

provide documentation of characteristics of the prey remains using a custom-mounted, digital color microscope camera with 12-bit color depth and $1,600 \times 1,200$ pixel resolution (Scion CFW-1612C digital color camera, Scion Corporation, Frederick, MD, USA). Prey remains were identified using guides (Schmitt 1921, Cannon 1987), scientific literature (Allis 1909, Chapman 1944a, Chapman 1944b, Iverson and Pinkas 1971, Liem 1986, Hansel 1988, Hayashi and Kim 1999, Harvey et al. 2000, Gobalet et al. 2004), reference collections (Moss Landing Marine Laboratories, Point Blue Conservation Science [formerly Point Reyes Bird Observatory], University of California at Santa Cruz, and NOAA Fisheries Service Fisheries Ecology Division), and consultation with taxonomic experts (Joe Bizzarro at Moss Landing Marine Laboratories and Cristie Boone at University of California at Santa Cruz).

Some prey remains could be resolved only to family or genus because of erosion or lack of unique morphological characteristics, and they were combined into prey categories (e.g., rockfishes, sculpins, perches). However, in most instances prey remains could be resolved to species (e.g., Black Rockfish [*Sebastes melanops*], Pacific Staghorn Sculpin [*Leptocottus armatus*], Pile Surfperch [*Rhacochilus vacca*]). Thus, an effort was made to identify all prey remains to the lowest taxonomic level and prey categories were used only in cases of uncertainty. Because prey remains were not all identified to species, the term prey category will be used hereafter.

2.3 Pellet content analysis

Prey remains were enumerated using the food habits protocol outlined by Lance et al. (2001). The number and size of single and paired structures (e.g., atlas vertebra, right and left sagittal fish otoliths, upper and lower cephalopod beaks, small and large sculpin preopercles) were used to conservatively estimate the minimum number of individuals (MNI). Prey that could not be enumerated were noted as present or absent and conservatively contributed to prey number (e.g., presence of perch teeth or pieces of perch pharyngeal plate indicated 1 perch). The all-structure technique was evaluated by noting other fish remains such as eye lenses, premaxilla, dentary, preopercle, pharyngeal plate, teeth, atlas, axis, hypural vertebra, and other vertebrae (Tollit et al. 2003). This was extended to invertebrates by using cephalopod eye lenses or chitinous exoskeleton fragments that indicated their number or presence. Other materials such as parasites, sediment, plant material, and small rocks were noted.

Fish otolith erosion was graded following Tollit et al. (1997): Grade 1 (least erosion), Grade 2 (moderate erosion), and Grade 3 (heavy erosion). Grade 1 otoliths have a distinct sulcus and features such as clear lobations. They were measured to the nearest 0.01 mm using a digital caliper. Fish length was estimated only for Grade 1 otoliths using published regression equations that relate otolith length to fish length (Harvey et al. 2000), and the mean fish length was determined by species. Cephalopod beaks were too worn to be measured for size estimation.

2.4 Diet description

The prey number was standardized to a percentage on a per pellet basis. Then mean prey-specific number (Amundsen et al. 1996), frequency of occurrence, and mean percent number (Hyslop 1980) metrics were calculated as follows:

(1) mean percent prey-specific number:
$$\%PN_i = \frac{\sum_{j=1}^n \%N_{ij}}{n_i} \times 100$$

(2) percent frequency of occurrence:
$$\%FO_i = \frac{n_i}{n} \times 100$$

(3) mean percent number:
$$\%N_i = \frac{\sum_{j=1}^n \%N_{ij}}{n} \times 100$$

where N_{ij} is the proportion of prey i in an individual sample j , n_i is the number of samples containing prey i , and n is the total number of samples. These metrics were calculated for each nonbreeding season, sampling location, and each combination of nonbreeding season and location. The mean prey-specific number refers to the average proportion consumed of each prey i , but only when prey i was consumed. When mean prey-specific number is multiplied by percent frequency of occurrence, or the proportion of samples containing prey i , the result is mean percent number. Mean percent number is a compound index that summarizes overall importance of prey i in the diet (Brown et al. 2012).

Differences in the diet for a location and nonbreeding season were deciphered and visualized using a feeding strategy diagram that incorporates %PN and %FO metrics to indicate if, as a group of individuals, the feeding strategy of the predator was a specialist (%PN > 50%) or generalist (%PN < 50%; Costello 1990). Taking this concept a step further, Amundsen et al. (1996) defined the inter- and intra-individual components of niche width. When a prey was consumed frequently in great number, the prey was defined as dominant in the diet (%FO > 50 and %PN > 50%). Conversely, when a prey was infrequently consumed in lesser numbers the prey was defined as rare in the diet (%FO < 50% and %PN < 50%). Infrequently consumed prey eaten in great number (%FO < 50% and %PN > 50%) indicated only some individuals were specialists. Frequently consumed prey eaten in lesser number (%FO > 50% and %PN < 50%) indicated many individuals were generalists.

Lastly, diet diversity was calculated using Shannon's entropy, H , also known as Shannon-Wiener diversity index (Shannon 1948):

(4) Shannon-Wiener diversity index:
$$H = -\sum_{i=1}^q p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the i^{th} species in the dataset and q is the total number of prey species.

2.5 Sample size sufficiency

To determine if there were sufficient samples to precisely estimate the %PN metric for the top five prey species, a custom program (R-Project Organization) was written to randomly resample %PN values and calculate mean %PN and standard error (SE) for increasing sample size (J. Harvey, personal communication). Adequate sample size for a precise %PN estimate was deemed to be where the variability (SE of %PN) stabilized.

To determine if enough pellets had been sampled to sufficiently characterize the number of prey categories in the diet, a cumulative prey curve (Ferry and Cailliet 1996) was generated for each nonbreeding season (EstimateS, Version 8.2., R. K. Colwell, <http://viceroy.eeb.uconn.edu/estimates>). The estimated number of unique prey categories and associated 95% confidence intervals were plotted against the cumulative number of pellets examined. Sufficient sample size was determined to be where the linear regression of the ultimate four samples became asymptotic ($b \leq 0.05$) (Bizzarro et al. 2007).

2.6 Statistical analysis of diet variation

Analysis of variance (ANOVA) was used to test for the effect of three fixed factors on prey number and prey diversity: nonbreeding season (2006-07 and 2007-08), time period within a nonbreeding season (postbreeding, winter, and prebreeding), and location (Año Nuevo Island, Moss Landing Harbor, and Monterey Harbor). Interdependence among factors was assessed with ANOVA interaction terms. Only two

nonbreeding seasons were selected for examination so this was considered a fixed factor. Postbreeding, winter, and prebreeding periods are biologically meaningful times during the nonbreeding season and all of those times were examined, so time period was considered a fixed factor. Location was considered a fixed factor because the three locations examined were of interest because of recent colonizations and habitat differences that were hypothesized to affect the diet.

The study design was not orthogonal because Monterey Harbor was sampled only during 2007-08; therefore, a separate two-way ANOVA was used to test location and time period for each nonbreeding season. A three-way ANOVA was used to test season, time period, and location, but only for Año Nuevo Island and Moss Landing Harbor that were sampled during both nonbreeding seasons. Samples containing no prey were excluded from the analysis and random samples were dropped until sample size per cell was equal. Before testing, the data were log transformed by $\ln(x + 1)$ to meet assumptions of normality and equal variance and then the data were backtransformed to report means.

The assemblage of species consumed by a predator form a multivariate data matrix containing columns of univariate prey variables with interdependencies and rows that are independent observation vectors, in this case, pellet samples (Legendre and Legendre 1998). When one prey occurs in great number because it is abundant in the environment and it is readily encountered and consumed, other prey numbers are lesser in the diet because the predator has a limit to the amount of food it can consume at any one time. Similarly, prey species encountered in a particular habitat type are more likely to

be similar to one another (e.g., consuming several species of benthic fishes in an area with rocky substrate). Thus, prey variables often contain a large number of zeros making them greatly skewed. These data properties do not conform to parametric statistics with underlying assumptions of normality and equal variance and simple transformations cannot solve all of the underlying problems.

Ordination techniques project multivariate data into a smaller number of dimensions with limited loss of information by using a dissimilarity measure to make pairwise comparisons of the samples, producing a sample-by-sample data matrix (Legendre and Legendre 1998). The interpretation of absence of two prey species, or double-zeros, is ambiguous because multiple scenarios could lead to that result. Data sets with many double-zeros are not well suited for the metric dissimilarity measures that are required in many ordination methods because they are attributed as similarities when this may not be the case. This interpretation can result in an illogical conclusion known as the species abundance paradox: two sites without any species in common may be represented in ordination space with less distance between them than another pair of sites with species in common. Nonmetric multidimensional scaling (NMDS) is an unconstrained ordination technique that allows the use of dissimilarity measures appropriate for ecological data sets. The Bray-Curtis dissimilarity measure was used with NMDS ordination to compare fine-scale spatiotemporal diet variation among the 19 sampling days in this study and to compare historical Brandt's Cormorant diet data to season and location data subsets in this study.

RESULTS

3.1 Nested sieves and efficacy of all-structure technique

Fish remains were mostly otoliths, lenses, and degraded vertebrae, but perch (*Embiotocidae*) pharyngeal plate pieces and teeth, and sculpin preopercles also were found. Fish otoliths provided the greatest MNI estimate with the best taxonomic resolution. Within samples, perch pharyngeal teeth or pharyngeal plate pieces were always accompanied by perch otoliths. Similarly, even when various sizes of sculpin preopercles were considered to produce the greatest possible MNI by sculpin preopercles, it rarely produced a greater MNI than sculpin otoliths.

Invertebrate remains included squid and octopus beaks, crab carapace and claws, mollusk shells, polychaete jaws, and shrimp and isopod exoskeleton and appendage parts, all of which are composed of chitinous material that resist digestion. Thus, invertebrate remains potentially were from secondary prey, consumed first by a fish that was then eaten by a cormorant. Cephalopod beaks were too eroded for measurement and subsequent accurate size estimation, but they generally were of the size class that would be consumed by a seabird and cephalopods have been reported previously in Brandt's Cormorant diet (Hubbs et al. 1970, Baltz and Morejohn 1977, Ainley et al. 1981); therefore, squid and octopus were considered primary prey. Other invertebrates occurred with the following frequency: crabs (3.9%), mollusks (2.8%), polychaetes (5.6%), and shrimps (31.2%). These invertebrates were unlikely consumed directly by the cormorant because Brandt's Cormorants are visual predators that feed on fishes in motion (Hubbs et al. 1970), they do not have bill morphology conducive to eating invertebrates (Cutler

1983), and stable isotope analysis performed on diet samples from Southeast Farallon Island in central California did not indicate invertebrate consumption (Sydeman et al. 1997). Samples containing these prey items also contained fishes that eat these invertebrates (Barry et al. 1996). Therefore, crabs, mollusks, polychaetes, and shrimps were considered secondary prey and excluded from the analyses. Isopods were small and likely present from eating fish infected with these parasites.

Overall, neither the nested 250 μm sieve nor the all-structure technique increased prey detection. These additional steps in sample processing greatly reduced efficiency and yielded little benefit. The 250 μm sieve contained prey remains 56.0% of the time, but they were almost exclusively secondary prey remains with the remainder being indecipherable parts from fishes. Fish otoliths and cephalopod beaks yielded the greatest counts and taxonomic resolution. Fish bones were too eroded to go beyond family or genus taxonomic level. Other fish parts such as eye lenses, sculpin preopercles, perch teeth, and perch pharyngeal plates occurred frequently, but generally did not contribute more to the fish count than fish otoliths. Cephalopod lenses also did not contribute more to the cephalopod count.

3.2 Sampling results

Fifteen pellets were processed from each of 19 sampling days for a total of 285 samples. Of these, 229 (80.4%) had identifiable and enumerable primary prey remains. The remaining 56 samples (19.6%) either only contained prey likely to have been consumed secondarily (49 samples, or 17.1%) or were empty (7 samples, 2.5%). Of the

229 samples containing primary prey, 208 (90.8%) contained only fish remains, 20 (8.7%) contained fish and cephalopod remains, and 1 (0.4%) contained only cephalopod remains. Occurrence of non-prey items included sediment (27.7%), plant material (17.9%), parasitic worms (53.3%), ticks (1.8%), and rocks of less than 1 cm diameter (3.2%). No man-made materials (e.g. plastics) were found.

3.3 Diet description

Brandt's Cormorants fed almost exclusively on fishes (98%N, 18 families and 27 species represented) compared with few invertebrates (2%N, 2 families and 2 species represented; Table 2). Fish taxonomic nomenclature follows Page et al. (2013). Only five fish species each comprised greater than 2.0% of the diet by mean percent number (Table 3). In both nonbreeding seasons, Northern Anchovy dominated the diet by mean prey-specific number and frequency, although more so during 2006-07 (2006-07: 80.1%PN and 89.6%FO, 2007-08: 73.9%PN and 60.5%FO). Speckled Sanddab was the second most important prey in the diet with substantial numbers consumed much of the time (2006-07: 34.2%PN and 29.9%FO, 2007-08: 45.4%PN and 44.4%FO). Moderate numbers of Pacific Sanddab also were consumed with some frequency (2006-07: 16.1%PN and 17.9%FO, 2007-08: 19.9%PN and 24.7%FO). Topsmelt (*Atherinopsis affinis*) and Pacific Sardine (*Sardinops sagax*) were consumed less frequently, but when consumed, were consumed in great number (Topsmelt, 2006-07: 25.0%PN and 1.5%FO, 2007-08: 58.4%PN and 15.4%FO and Pacific Sardine, 2006-07: 53.7%PN and 3.0%FO, 2007-08: 42.7%PN and 11.1%FO).

Table 2. Taxonomic classification, common name, and code for prey species in Brandt's Cormorant diet.

Order	Family	Species	Common name	Code
Fishes				
Atheriniiformes	Atherinidae	<i>Atherinopsis affinis</i>	Topsmelt	Aaf
Batrachoidiiformes	Batrachoididae	<i>Porichthys notatus</i>	Plainfin Midshipman	Pno
Clupeiformes	Clupeidae	<i>Sardinops sagax</i>	Pacific Sardine	Ssa
	Engraulididae	<i>Engraulis mordax</i>	Northern Anchovy	Emo
Gadiformes	Merlucciidae	<i>Merluccius productus</i>	Pacific Hake	Mpr
Ophidiiformes	Ophidiidae	<i>Chilara taylori</i>	Spotted Cusk-eel	Cta
Perciformes	Ammodytidae	<i>Ammodytes hexapterus</i>	Pacific Sandlance	Ahe
	Carangidae	<i>Trachurus symmetricus</i>	Jack Mackerel	Tsy
	Embiotocidae	<i>Embiotoca lateralis</i>	Striped Seaperch	Ela
		<i>Hypsurus caryi</i>	Rainbow Seaperch	Hca
		<i>Rhacochilus vacca</i>	Pile Surfperch	Rva
		Unidentified perches	Perches	Per
	Gobiidae	<i>Rhinogobiops nicholsii</i>	Blackeye Goby	Rni
	Sciaenidae	<i>Genyonemus lineatus</i>	White Croaker	Gli
	Scombridae	<i>Scomber japonicus</i>	Pacific Mackerel	Sjo
	Pleuronectiformes	<i>Citharichthys sordidus</i>	Pacific Sanddab	Cso
		<i>Citharichthys stigmaeus</i>	Speckled Sanddab	Cst
	Cynoglossidae	<i>Symphurus atricauda</i>	California Tonguefish	Sat
	Pleuronectidae	<i>Eopsetta jordani</i>	Petrale Sole	Ejo
		<i>Lepidopsetta bilineata</i>	Rock Sole	Lbi
		<i>Microstomus pacificus</i>	Dover Sole	Mpa
		<i>Parophrys vetulus</i>	English Sole	Pve
Scorpaeniformes	Cottidae	<i>Artedius lateralis</i>	Smoothhead Sculpin	Ala
		<i>Chitonotus pugetensis</i>	Roughback Sculpin	Cpu
		<i>Leptocottus armatus</i>	Pacific Staghorn Sculpin	Lar
		<i>Scorpaenichthys marmoratus</i>	Cabazon	Sma
		Unidentified sculpins	Sculpins	Scu
	Hexagrammidae	<i>Ophiodon elongatus</i>	Lingcod	Oel
	Scorpaenidae	<i>Sebastes melanops</i>	Black Rockfish	Sme
		<i>Sebastes</i> spp.	Rockfishes	Seb
Unid. Teleostei	Unidentified	Unidentified fishes	Unidentified fishes	Uni
Cephalopods				
Octopoda	Octopodidae	<i>Octopus rubescens</i>	East Pacific Red Octopus	Oru
Teuthida	Loliginidae	<i>Doryteuthis opalescens</i>	Market Squid	Dop

Table 3. Brandt's Cormorant diet composition by mean percent number (%N), mean percent prey-specific number (%PN), and frequency of occurrence (%FO) for combined sampling locations during the 2006-07 nonbreeding season (n = 67), 2007-08 nonbreeding season (n = 162), and 2006-07 and 2007-08 nonbreeding seasons combined (n = 229).

Species	2006-07			2007-08			2006-07 and 2007-08		
	%N	%PN	%FO	%N	%PN	%FO	%N	%PN	%FO
<i>Engraulis mordax</i>	71.7	80.1	89.6	44.7	73.9	60.5	52.6	76.3	69.0
<i>Citharichthys stigmaeus</i>	10.2	34.2	29.9	20.2	45.4	44.4	17.3	43.0	40.2
<i>Atherinopsis affinis</i>	0.4	25.0	1.5	9.0	58.4	15.4	6.5	57.1	11.4
<i>Citharichthys sordidus</i>	2.9	16.1	17.9	4.9	19.9	24.7	4.3	19.1	22.7
<i>Sardinops sagax</i>	1.6	53.7	3.0	4.7	42.7	11.1	3.8	43.8	8.7
Unidentified perches	1.9	25.8	7.5	2.0	20.1	9.9	2.0	21.5	9.2
Unidentified sculpins	2.4	23.2	10.4	1.3	10.4	12.3	1.6	13.7	11.8
Unidentified fishes	2.5	10.0	25.4	0.8	11.4	7.4	1.3	10.6	12.7
<i>Octopus rubescens</i>	0.1	7.1	1.5	1.7	19.2	8.6	1.2	18.4	6.6
<i>Parophrys vetulus</i>	0.0	0.0	0.0	1.6	12.9	12.3	1.1	12.9	8.7
<i>Sebastes</i> spp.	0.2	13.3	1.5	1.5	48.4	3.1	1.1	42.6	2.6
<i>Porichthys notatus</i>	1.1	18.0	6.0	1.0	12.7	8.0	1.0	13.9	7.4
<i>Leptocottus armatus</i>	1.0	10.8	9.0	0.9	7.0	13.0	0.9	7.8	11.8
<i>Doryteuthis opalescens</i>	1.5	100.0	1.5	0.5	21.0	2.5	0.8	36.8	2.2
<i>Ammodytes hexapterus</i>	< 0.1	2.1	1.5	0.7	18.8	3.7	0.5	16.4	3.1
<i>Microstomus pacificus</i>	0.0	0.0	0.0	0.7	18.7	3.7	0.5	18.7	2.6
<i>Rhacochilus vacca</i>	0.5	33.3	1.5	0.3	26.7	1.2	0.4	28.9	1.3
<i>Embiotoca lateralis</i>	0.2	6.3	3.0	0.4	14.4	3.1	0.4	12.1	3.1
<i>Trachurus symmetricus</i>	0.0	0.0	0.0	0.5	41.7	1.2	0.4	41.7	0.9
<i>Sebastes melanops</i>	1.1	72.7	1.5	0.1	10.0	0.6	0.4	41.4	0.9
<i>Scorpaenichthys marmoratus</i>	0.0	0.0	0.0	0.5	41.1	1.2	0.4	41.1	0.9
<i>Merluccius productus</i>	0.0	0.0	0.0	0.5	75.0	0.6	0.3	75.0	0.4
<i>Genyonemus lineatus</i>	0.2	6.1	3.0	0.2	13.1	1.9	0.2	10.3	2.2
<i>Chilara taylori</i>	0.2	5.2	3.0	0.2	12.6	1.9	0.2	9.6	2.2
<i>Scomber japonicus</i>	0.1	7.1	1.5	0.2	9.6	2.5	0.2	9.1	2.2
<i>Rhinogobiops nicholsii</i>	0.0	0.0	0.0	0.2	33.3	0.6	0.1	33.3	0.4
<i>Symphurus atricauda</i>	0.1	4.6	3.0	0.1	5.8	2.5	0.1	5.4	2.6
<i>Artedius lateralis</i>	0.0	0.0	0.0	0.1	20.0	0.6	0.1	20.0	0.4
<i>Ophiodon elongatus</i>	< 0.1	0.4	1.5	0.1	14.7	0.6	0.1	7.5	0.9
<i>Chitonotus pugetensis</i>	0.0	0.0	0.0	0.1	3.5	2.5	0.1	3.5	1.7
<i>Hypsurus caryi</i>	0.1	6.3	1.5	0.0	0.0	0.0	< 0.1	6.3	0.4
<i>Eopsetta jordani</i>	0.0	0.0	0.0	< 0.1	2.0	1.2	< 0.1	2.0	0.9
<i>Lepidopsetta bilineata</i>	0.0	0.0	0.0	< 0.1	2.6	0.6	< 0.1	2.6	0.4

Precision (SE) of %PN was calculated using resampled means for the top five species consumed (Fig. 4). Variation stabilized for all 5 species indicating sufficient samples had been examined. The sample size required ranged from 12 to 50 samples. Fewer samples were required for prey consumed in smaller numbers and less frequently (Pacific Sanddab, Topsmelt, and Pacific Sardine) than for prey consumed in larger numbers more frequently (Northern Anchovy and Speckled Sanddab).

Figure 4. Precision (SE) of resampled means for percent prey-specific number (%PN) for the top five prey species. Sufficient sample size was obtained where precision stabilized and is denoted by an arrow.

Cumulative prey curves generated from samples reached an asymptote at $n = 84$ samples for the 2006-07 nonbreeding season and $n = 100$ samples for the 2007-08 nonbreeding season indicating adequate sample size had been obtained to characterize the overall number of prey categories consumed in those years (Fig. 5). The estimated number of prey categories was 22 for the 2006-07 nonbreeding season and 29 for the 2007-08 nonbreeding season.

Figure 5. Cumulative number of prey categories (solid line) and 95% confidence intervals (dashed lines) for the diet of Brandt's Cormorant during the 2006-07 and 2007-08 nonbreeding seasons. Sufficient sample size was obtained where the slope is statistically equivalent to zero and is denoted by an arrow at $n = 84$ (22 prey categories) for 2006-07 and $n = 100$ (29 prey categories) for 2007-08.

Northern Anchovy dominated the diet, especially at the outer coast (Año Nuevo Island 69.8%N, Moss Landing Harbor 45.0%N, and Monterey Harbor 39.7%N; Table 4). Other important prey (>5%N) were Pacific Sardine (6.5%N) at Año Nuevo Island, Speckled Sanddab (28.6%N), Pacific Sanddab (7.3%N), and Topsmelt (5.9%N) at Moss Landing Harbor, and Speckled Sanddab (19.1%N) and Topsmelt (15.8%) at Monterey Harbor.

Table 4. Brandt's Cormorant diet composition by mean percent number (%N), mean percent prey-specific number (%PN), and frequency of occurrence (%FO) at Año Nuevo Island (n = 82), Moss Landing Harbor (n = 92), and Monterey Harbor (n = 55).

Species	Año Nuevo Island 2006-07 and 2007-08			Moss Landing Harbor 2006-07 and 2007-08			Monterey Harbor 2007-08		
	%N	%PN	%FO	%N	%PN	%FO	%N	%PN	%FO
<i>Engraulis mordax</i>	69.8	88.1	79.3	45.0	64.7	69.6	39.7	75.3	52.7
<i>Sardinops sagax</i>	6.5	58.9	11.0	1.2	28.3	4.3	4.2	33.3	12.7
Unidentified perches	4.3	39.5	11.0	1.0	9.3	10.9	< 0.1	1.2	3.6
<i>Citharichthys stigmaeus</i>	3.3	33.7	9.8	28.6	46.2	62.0	19.1	39.0	49.1
Unidentified sculpins	2.3	48.0	4.9	0.9	5.6	16.3	1.7	12.0	14.5
<i>Octopus rubescens</i>	1.7	46.4	3.7	0.3	5.5	5.4	2.0	15.6	12.7
<i>Sebastes</i> spp.	1.7	46.1	3.7	0.3	25.0	1.1	1.7	46.0	3.6
Unidentified fishes	1.5	14.1	11.0	1.2	8.2	15.2	1.2	10.8	10.9
<i>Parophrys vetulus</i>	1.2	47.7	2.4	1.5	10.1	15.2	0.4	5.3	7.3
<i>Citharichthys sordidus</i>	1.0	16.8	6.1	7.3	19.2	38.0	4.3	19.6	21.8
<i>Leptocottus armatus</i>	1.0	16.8	6.1	0.8	4.4	18.5	1.0	10.5	9.1
<i>Porichthys notatus</i>	1.0	20.4	4.9	1.2	10.8	10.9	0.9	15.7	5.5
<i>Scorpaenichthys marmoratus</i>	1.0	80.0	1.2	< 0.1	2.2	1.1	0.0	0.0	0.0
<i>Atherinopsis affinis</i>	0.9	37.5	2.4	5.9	49.3	12.0	15.8	66.7	23.6
<i>Sebastes melanops</i>	0.9	72.7	1.2	0.0	0.0	0.0	0.2	10.0	1.8
<i>Rhacochilus vacca</i>	0.7	26.7	2.4	0.0	0.0	0.0	0.6	33.3	1.8
<i>Rhinogobiops nicholsii</i>	0.4	33.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Artedius lateralis</i>	0.2	20.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Embiotoca lateralis</i>	0.2	6.6	3.7	0.1	6.8	2.2	0.9	25.6	3.6
<i>Genyonemus lineatus</i>	0.1	6.1	2.4	0.4	13.1	3.3	0.0	0.0	0.0
<i>Hypsurus caryi</i>	0.1	6.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Chilara taylori</i>	< 0.1	3.7	1.2	0.4	13.4	3.3	0.1	4.2	1.8
<i>Lepidopsetta bilineata</i>	< 0.1	2.6	1.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Microstomus pacificus</i>	0.0	0.0	0.0	0.1	2.5	3.3	1.9	34.9	5.5
<i>Trachurus symmetricus</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.5	41.7	3.6
<i>Doryteuthis opalescens</i>	0.0	0.0	0.0	1.2	27.3	4.3	1.4	75.0	1.8
<i>Scomber japonicus</i>	0.0	0.0	0.0	0.1	3.7	3.3	0.6	17.3	3.6
<i>Symphurus atricauda</i>	0.0	0.0	0.0	0.1	3.3	3.3	0.4	7.5	5.5
<i>Ammodytes hexapterus</i>	0.0	0.0	0.0	1.1	19.8	5.4	0.3	7.9	3.6
<i>Chitonotus pugetensis</i>	0.0	0.0	0.0	0.1	3.7	2.2	0.1	3.4	3.6
<i>Eopsetta jordani</i>	0.0	0.0	0.0	< 0.1	2.9	1.1	< 0.1	1.1	1.8
<i>Merluccius productus</i>	0.0	0.0	0.0	0.8	75.0	1.1	0.0	0.0	0.0
<i>Ophiodon elongatus</i>	0.0	0.0	0.0	0.2	7.5	2.2	0.0	0.0	0.0

Spatiotemporal differences in diet by location and nonbreeding season were compared using feeding strategy diagrams (Fig. 6). Diet composition was similar at Año Nuevo Island during both nonbreeding seasons. Northern Anchovy was the dominant prey, occurring frequently (2006-07: 87.9%FO; 2007-08: 73.5%FO), and when consumed, it was consumed in great number (2006-07: 84.8%PN; 2007-08: 90.7%PN; Table 5 and Table 6). Ancillary prey ($< 50\%$ FO and $\geq 50\%$ PN), included a similar mix of benthic and pelagic fishes with Black Rockfish, sculpins, and Pacific Sardine during 2006-07 compared with Cabezon (*Scorpaenichthys marmoratus*), rockfishes, Pacific Sardine, and Topsmelt during 2007-08.

Figure 6. Feeding strategy diagrams for Brandt's Cormorant diet by location and nonbreeding season.

Table 5. Brandt's Cormorant diet composition by mean percent number (%N), cumulative mean percent number (Cumulative %N), mean percent prey-specific number (%PN), and frequency of occurrence (%FO) during 2006-07 nonbreeding season at Año Nuevo Island (n = 33) and Moss Landing Harbor (n = 34).

Año Nuevo Island 2006-07				
Species	%N	Cumulative %N	%PN	%FO
<i>Engraulis mordax</i>	74.5	74.5	84.8	87.9
Unidentified sculpins	4.2	78.7	69.4	6.1
Unidentified perches	3.7	82.4	41.2	9.1
<i>Sardinops sagax</i>	3.3	85.7	53.7	6.1
Unidentified fishes	2.9	88.6	13.5	21.2
<i>Sebastes melanops</i>	2.2	90.8	72.7	3.0
<i>Porichthys notatus</i>	1.8	92.6	29.5	6.1
<i>Citharichthys stigmaeus</i>	1.7	94.3	18.9	9.1
<i>Leptocottus armatus</i>	1.6	95.9	26.7	6.1
<i>Rhacochilus vacca</i>	1.0	96.9	33.3	3.0
Moss Landing Harbor 2006-07				
Species	%N	Cumulative %N	%PN	%FO
<i>Engraulis mordax</i>	69.0	69.0	75.7	91.2
<i>Citharichthys stigmaeus</i>	18.5	87.5	36.9	50.0
<i>Citharichthys sordidus</i>	4.8	92.3	16.5	29.4
<i>Doryteuthis opalescens</i>	2.9	95.3	100.0	2.9
Unidentified fishes	2.2	97.5	7.5	29.4

Table 6. Brandt's Cormorant diet composition by mean percent number (%N), cumulative mean percent number (Cumulative %N), mean percent prey-specific number (%PN), and frequency of occurrence (%FO) during 2007-08 nonbreeding season at Año Nuevo Island (n = 49), Moss Landing Harbor (n = 58), and Monterey Harbor (n = 55).

Año Nuevo Island 2007-08				
Species	%N	Cumulative %N	%PN	%FO
<i>Engraulis mordax</i>	66.7	66.7	90.7	73.5
<i>Sardinops sagax</i>	8.6	75.3	60.4	14.3
Unidentified perches	4.7	80.0	38.6	12.2
<i>Citharichthys stigmaeus</i>	4.3	84.4	42.6	10.2
<i>Octopus rubescens</i>	2.8	87.2	46.4	6.1
<i>Sebastes</i> spp.	2.6	89.7	62.5	4.1
<i>Parophrys vetulus</i>	1.9	91.7	47.7	4.1
<i>Scorpaenichthys marmoratus</i>	1.6	93.3	80.0	2.0
<i>Citharichthys sordidus</i>	1.1	94.5	18.4	6.1
Unidentified sculpins	1.1	95.5	26.5	4.1
<i>Atherinopsis affinis</i>	1.0	96.6	50.0	2.0

Moss Landing Harbor 2007-08				
Species	%N	Cumulative %N	%PN	%FO
<i>Citharichthys stigmaeus</i>	34.6	34.6	50.1	69.0
<i>Engraulis mordax</i>	30.9	65.5	54.3	56.9
<i>Atherinopsis affinis</i>	9.4	74.8	49.3	19.0
<i>Citharichthys sordidus</i>	8.7	83.6	20.3	43.1
<i>Parophrys vetulus</i>	2.4	86.0	10.1	24.1
<i>Sardinops sagax</i>	1.9	88.0	28.3	6.9
<i>Ammodytes hexapterus</i>	1.7	89.6	24.2	6.9
<i>Porichthys notatus</i>	1.6	91.3	11.9	13.8
Unidentified perches	1.5	92.8	11.0	13.8
<i>Merluccius productus</i>	1.3	94.1	75.0	1.7
<i>Leptocottus armatus</i>	1.1	95.2	4.9	22.4
Unidentified sculpins	1.0	96.2	6.0	17.2

Monterey Harbor 2007-08				
Species	%N	Cumulative %N	%PN	%FO
<i>Engraulis mordax</i>	39.7	39.7	75.3	52.7
<i>Citharichthys stigmaeus</i>	19.1	58.8	39.0	49.1
<i>Atherinopsis affinis</i>	15.8	74.6	66.7	23.6
<i>Citharichthys sordidus</i>	4.3	78.9	19.6	21.8
<i>Sardinops sagax</i>	4.2	83.1	33.3	12.7
<i>Octopus rubescens</i>	2.0	85.1	15.6	12.7
<i>Microstomus pacificus</i>	1.9	87.0	34.9	5.5
Unidentified sculpins	1.7	88.8	12.0	14.5
<i>Sebastes</i> spp.	1.7	90.4	46.0	3.6
<i>Trachurus symmetricus</i>	1.5	92.0	41.7	3.6
<i>Doryteuthis opalescens</i>	1.4	93.3	75.0	1.8
Unidentified fishes	1.2	94.5	10.8	10.9
<i>Leptocottus armatus</i>	1.0	95.5	10.5	9.1

In contrast, at Moss Landing Harbor the feeding strategy differed between nonbreeding seasons (Fig. 6). Northern Anchovy dominated during 2006-07 (75.7%PN, 91.2%FO) and although infrequent, Market Squid was consumed (100.0%PN, 2.9%FO; Table 5 and Table 6). Speckled Sanddab was moderately consumed (36.9%PN, 50.0%FO) and Pacific Sanddab was rarely consumed (16.5%PN, 29.4%FO). During 2007-08, Northern Anchovy decreased in number and frequency and Speckled Sanddab increased in number and frequency so that they were equally important (Northern Anchovy: 30.9%N, Speckled Sanddab: 34.6%N). Topsmelt, which was not present during 2006-07, was moderately consumed (49.3%PN, 19.0%FO). Pacific Hake was consumed infrequently (75.0%PN, 1.7%FO).

Monterey Harbor was sampled only during 2007-08. Northern Anchovy was dominant (75.3%PN, 52.7%FO; Table 6; Fig. 6). Speckled Sanddab and Topsmelt were consumed in appreciable numbers (39.0%PN and 66.7%PN, respectively) and frequency (49.1%FO and 23.6%, respectively). Market Squid was consumed infrequently (75.0%PN, 1.8%FO).

Overall, Northern Anchovy was the primary prey at all locations and Speckled Sanddab was important at locations inside Monterey Bay, Moss Landing Harbor and Monterey Harbor. In addition, all locations except Moss Landing Harbor during 2006-07 included a unique and diverse set of benthic and pelagic prey that were consumed in smaller numbers and infrequently (< 50%FO and < 50%PN).

3.4 Prey number and diversity

For analysis of variance tests of prey number and diversity, normality (KS test) and equal variance (Levene's test) assumptions were met unless otherwise stated and all statistical tests were performed at $\alpha = 0.05$ (SYSTAT 12.0). Least squares plots and boxplots with median, first and third quartiles, and 95% confidence intervals were examined to aid interpretation.

When comparing mean prey number during the 2006-07 nonbreeding season among time periods and between locations, there was no significant interaction between the main effects (two-way ANOVA, Model I, $F_{2,48} = 1.011$, $p = 0.371$; Table 7); therefore, the main effect hypotheses were investigated. Mean prey number ranged from 5.9 during winter to 13.3 during postbreeding, but did not significantly differ among time periods ($F_{2,48} = 2.267$, $p = 0.115$). Mean prey number was not significantly different between locations (9.2 at Año Nuevo Island and 10.6 at Moss Landing Harbor; $F_{1,48} = 0.171$, $p = 0.681$). Median prey number at Año Nuevo Island and Moss Landing Harbor were similar and prey number was less during winter at both locations (Fig. 7). Prey number was greatest during prebreeding at Año Nuevo Island with a mean of 17.4 prey.

Table 7. Two-way ANOVA results comparing prey number among time periods and between locations during the 2006-07 nonbreeding season.

Time period	LS mean	SE	n	ANOVA
Postbreeding	13.3	0.3	18	$F_{1,48} = 2.267, p = 0.115$
Winter	5.9	0.3	18	
Prebreeding	12.0	0.3	18	
Location	LS mean	SE	n	ANOVA
ANI	10.6	0.2	27	$F_{1,48} = 0.171, p = 0.681$
MLH	9.2	0.2	27	
Time period*Location	LS mean	SE	n	ANOVA
Postbreeding ANI	13.5	0.4	9	$F_{2,48} = 1.011, p = 0.371$
Winter ANI	4.8	0.4	9	
Prebreeding ANI	17.4	0.4	9	
Postbreeding MLH	13.0	0.4	9	
Winter MLH	7.3	0.4	9	
Prebreeding MLH	8.3	0.4	9

Figure 7. Number of prey consumed in Brandt's Cormorant diet by time period (postbreeding, winter, and prebreeding) and location (A = Año Nuevo Island, ML = Moss Landing Harbor, MO = Monterey Harbor) during the 2006-07 (n = 9, N = 54) and 2007-08 (n = 8, N = 72) nonbreeding seasons. Boxplots indicate medians (line), first and third quartiles (bottom and top of box), 95% confidence intervals (whiskers), and outliers (points).

When comparing mean prey number among time periods and among locations during the 2007-08 nonbreeding season there was a significant interaction (two-way ANOVA, Model I, $F_{4,63} = 4.122$, $p = 0.005$; Table 8); therefore, main effects could not be interpreted. The pattern over time was different for all three locations. At Año Nuevo Island, mean prey number was least during postbreeding and winter and increased to 12.7 during prebreeding. Moss Landing Harbor had the greatest mean prey number during postbreeding, 62.6 prey per bird per day, the greatest of any time during the study, followed by a decrease to 8.8 during winter, and then a decrease to 5.8 during prebreeding. Monterey Harbor also had greater mean prey number during postbreeding

at 31.4 prey, was least during winter at 7.0 prey, and then increased to 21.3 prey during prebreeding (Fig. 7). Tukey's HSD test for time periods indicated that overall in the region, birds consumed significantly greater number of prey during postbreeding than winter ($p = 0.001$) and prebreeding ($p = 0.051$), but winter and prebreeding were not significantly different ($p = 0.345$). Mean prey number was variable during the 2007-08 nonbreeding season and overall location differences were not significantly different (Tukey's HSD). The ANOVA least squares means plot for location indicated that birds using Año Nuevo Island ate less prey than at Moss Landing Harbor and Monterey Harbor.

Table 8. Two-way ANOVA and multiple comparison test results comparing prey number among time periods and locations during the 2007-08 nonbreeding season.

Time period	LS mean	SE	n	Tukey's HSD
Postbreeding	24.9	0.2	24	Post, Winter: $p = 0.001$
Winter	7.4	0.2	24	Winter, Pre: $p = 0.345$
Prebreeding	11.7	0.2	24	Pre, Post: $p = 0.051$
Location	LS mean	SE	n	Tukey's HSD
ANI	8.6	0.2	24	ANI, MLH: $p = 0.189$
MLH	15.2	0.2	24	MLH, MOH: $p = 0.931$
MOH	17.0	0.2	24	MOH, ANI: $p = 0.092$
Time period*Location	LS mean	SE	n	ANOVA
Postbreeding ANI	7.5	0.4	8	$F_{4,63} = 4.122, p = 0.005$
Winter ANI	6.5	0.4	8	
Prebreeding ANI	12.7	0.4	8	
Postbreeding MLH	62.6	0.4	8	
Winter MLH	8.8	0.4	8	
Prebreeding MLH	5.8	0.4	8	
Postbreeding MOH	31.4	0.4	8	
Winter MOH	7.0	0.4	8	
Prebreeding MOH	21.3	0.4	8	

When comparing mean prey number during 2006-07 and 2007-08 nonbreeding seasons there was a significant interaction between nonbreeding season, time period, and location (multifactorial ANOVA, Model I, $F_{2,84} = 3.362$, $p = 0.039$; Table 9); therefore, main effects could not be interpreted. Mean prey number was not significantly different during 2006-07 compared with 2007-08 (Tukey's HSD, $p = 0.671$). Within nonbreeding season, the only significant difference was that prey number was greater during postbreeding compared with winter (Tukey's HSD, $p = 0.007$). Overall, prey number was not significantly different between Año Nuevo Island and Moss Landing Harbor (Tukey's HSD, $p = 0.373$), the only two locations sampled during both nonbreeding seasons. The overall pattern for mean prey number was consistent between nonbreeding seasons: greater during postbreeding, especially at Moss Landing Harbor, lesser during winter at both locations, and greater during prebreeding at only Año Nuevo Island (Fig. 7).

Table 9. Three-way ANOVA and multiple comparison test results comparing prey number between 2006-07 and 2007-08 nonbreeding seasons, among time periods within nonbreeding seasons, and between locations.

Season	LS mean	SE	n	Tukey's HSD
2006-07	10.2	0.2	48	2006-07, 2007-08: p = 0.671
2007-08	11.3	0.2	48	
Time period	LS mean	SE	n	Tukey's HSD
Postbreeding	17.7	0.2	32	Post, Winter: p = 0.007 Winter, Pre: p = 0.467
Winter	6.9	0.2	32	
Prebreeding	10.0	0.2	32	Pre, Post: p = 0.141
Location	LS mean	SE	n	Tukey's HSD
ANI	9.6	0.2	48	ANI, MLH: p = 0.373
MLH	12.0	0.2	48	
Season*Time period	LS mean	SE	n	ANOVA
2006-07 Postbreeding	14.3	0.3	16	$F_{2,84} = 0.744, p = 0.478$
2006-07 Winter	6.3	0.3	16	
2006-07 Prebreeding	11.6	0.3	16	
2007-08 Postbreeding	21.8	0.3	16	
2007-08 Winter	7.6	0.3	16	
2007-08 Prebreeding	8.6	0.3	16	
Season*Location	LS mean	SE	n	ANOVA
2006-07 ANI	10.8	0.3	24	$F_{1,84} = 1.901, p = 0.172$
2006-07 MLH	9.6	0.3	24	
2007-08 ANI	8.6	0.3	24	
2007-08 MLH	14.9	0.3	24	
Time period*Location	LS mean	SE	n	ANOVA
Postbreeding ANI	11.2	0.3	16	$F_{2,84} = 4.021, p = 0.021$
Postbreeding MLH	27.4	0.3	16	
Winter ANI	5.4	0.3	16	
Winter MLH	8.8	0.3	16	
Prebreeding ANI	14.4	0.3	16	
Prebreeding MLH	6.9	0.3	16	
Season*Time period*Location	LS mean	SE	n	ANOVA
2006-07 Postbreeding ANI	16.7	0.5	8	$F_{2,84} = 3.362, p = 0.039$
2006-07 Postbreeding MLH	12.2	0.5	8	
2006-07 Winter ANI	4.4	0.5	8	
2006-07 Winter MLH	8.9	0.5	8	
2006-07 Prebreeding ANI	16.2	0.5	8	
2006-07 Prebreeding MLH	8.2	0.5	8	
2007-08 Postbreeding ANI	7.5	0.5	8	
2007-08 Postbreeding MLH	60.2	0.5	8	
2007-08 Winter ANI	6.5	0.5	8	
2007-08 Winter MLH	8.8	0.5	8	
2007-08 Prebreeding ANI	12.7	0.5	8	
2007-08 Prebreeding MLH	5.8	0.5	8	

Shannon-Wiener diversity values and mean number of prey categories consumed by each bird were calculated for combinations of time and space (Table 10). For both nonbreeding seasons combined individual Brandt's Cormorants consumed 2.5 ($s = 1.9$) prey categories per day ($H = 1.67$). Prey diversity was greater during the 2007-08 nonbreeding season ($H = 1.77$) compared with the 2006-07 nonbreeding season ($H = 1.21$). For location, overall prey diversity was greatest at Monterey Harbor ($H = 1.66$), followed closely by Moss Landing Harbor ($H = 1.59$) and least at Año Nuevo Island ($H = 0.93$). On 2 March 2007 during prebreeding at Año Nuevo Island, Brandt's Cormorants specialized on a single prey item, Northern Anchovy. A maximum of 10 prey categories was observed on 10 March 2008 during prebreeding at Monterey Harbor.

Table 10. Mean ($\pm$ SD) and range for number of prey categories consumed by Brandt's Cormorants and Shannon-Wiener diversity index (H) by time period and location.

Time	Location	Mean $\pm$ SD	Range	H
09/21/06	Moss Landing Harbor	3.5 $\pm$ 2.1	1 - 7	1.21
09/26/06	Año Nuevo Island	2.4 $\pm$ 1.2	1 - 5	0.61
12/18/06	Moss Landing Harbor	2.0 $\pm$ 1.2	1 - 4	1.22
12/19/06	Año Nuevo Island	2.3 $\pm$ 1.7	1 - 6	2.09
02/22/07	Moss Landing Harbor	2.5 $\pm$ 1.8	1 - 6	1.19
03/02/07	Año Nuevo Island	1.0 $\pm$ 0.0	1 - 1	0.00
09/25/07	Año Nuevo Island	2.6 $\pm$ 1.4	1 - 5	1.88
09/28/07	Moss Landing Harbor	5.6 $\pm$ 2.0	2 - 9	1.45
10/19/07	Monterey Harbor	3.3 $\pm$ 1.7	2 - 7	0.96
11/09/07	Moss Landing Harbor	3.1 $\pm$ 2.4	1 - 9	1.59
11/15/07	Año Nuevo Island	1.5 $\pm$ 0.7	1 - 3	1.48
11/29/07	Monterey Harbor	3.1 $\pm$ 2.3	1 - 9	1.35
12/21/07	Moss Landing Harbor	2.9 $\pm$ 2.0	1 - 7	1.02
12/26/07	Monterey Harbor	2.2 $\pm$ 1.7	1 - 7	1.19
01/17/08	Año Nuevo Island	1.4 $\pm$ 0.7	1 - 3	0.39
02/20/08	Moss Landing Harbor	2.3 $\pm$ 1.8	1 - 6	0.89
03/10/08	Monterey Harbor	2.1 $\pm$ 2.3	1 - 10	0.84
03/24/08	Año Nuevo Island	1.1 $\pm$ 0.4	1 - 2	0.05
03/26/08	Moss Landing Harbor	2.5 $\pm$ 1.4	1 - 5	1.60
2006-07	Año Nuevo Island	1.9 $\pm$ 1.3	1 - 6	0.68
2006-07	Moss Landing Harbor	2.6 $\pm$ 1.8	1 - 7	1.25
2007-08	Año Nuevo Island	1.6 $\pm$ 1.0	1 - 5	1.06
2007-08	Moss Landing Harbor	3.5 $\pm$ 2.3	1 - 9	1.66
2007-08	Monterey Harbor	2.7 $\pm$ 2.0	1 - 10	1.66
All	Año Nuevo Island	1.7 $\pm$ 1.1	1 - 6	0.93
All	Moss Landing Harbor	3.2 $\pm$ 2.2	1 - 9	1.59
All	Monterey Harbor	2.7 $\pm$ 2.0	1 - 10	1.66
2006-07	All	2.3 $\pm$ 1.6	1 - 7	1.21
2007-08	All	2.6 $\pm$ 2.0	1 - 10	1.77
All	All	2.5 $\pm$ 1.9	1 - 10	1.67

When comparing mean prey diversity among time periods and locations during the 2006-07 nonbreeding season there was not a significant interaction (two-way ANOVA, Model I, $F_{2,48} = 2.104$, $p = 0.133$; Table 11); therefore, the main effect hypotheses were examined. The data were normally distributed; however, variances were not equal despite several transformations (Levene's = 9.222, $p < 0.001$). Only

anchovy were consumed during prebreeding at Año Nuevo Island, thus mean prey diversity and variance were zero. Even though the assumption of equal variance was not met the patterns in the data were reflected in the ANOVA results, so they were interpreted with caution. Prey diversity among time periods was nearly significant ($F_{2,48} = 3.111$, $p = 0.054$) with greatest mean prey diversity during winter ($H = 0.384$) and least during prebreeding ($H = 0.122$). Mean prey diversity was significantly greater at Moss Landing Harbor compared with Año Nuevo Island ($F_{1,48} = 4.195$, $p = 0.046$). Mean prey diversity was greatest at Moss Landing Harbor during postbreeding ($H = 0.461$; Fig. 8).

Table 11. Two-way ANOVA results comparing prey diversity among time periods and between locations during the 2006-07 nonbreeding season.

Time period	LS mean	SE	n	ANOVA
Postbreeding	0.285	0.1	18	$F_{2,48} = 3.111$, $p = 0.054$
Winter	0.384	0.1	18	
Prebreeding	0.122	0.1	18	
Location	LS mean	SE	n	ANOVA
ANI	0.172	0.1	27	$F_{1,48} = 4.195$, $p = 0.046$
MLH	0.353	0.1	27	
Time period*Location	LS mean	SE	n	ANOVA
Postbreeding ANI	0.130	0.1	9	$F_{2,48} = 2.104$, $p = 0.133$
Winter ANI	0.425	0.1	9	
Prebreeding ANI	0.000	0.1	9	
Postbreeding MLH	0.461	0.1	9	
Winter MLH	0.344	0.1	9	
Prebreeding MLH	0.259	0.1	9

Figure 8. Prey diversity in Brandt's Cormorant diet by time period (postbreeding, winter, and prebreeding) and location (A = Año Nuevo Island, ML = Moss Landing Harbor, MO = Monterey Harbor) during the 2006-07 (n = 9, N = 54) and 2007-08 (n = 8, N = 72) nonbreeding seasons. Boxplots indicate medians (line), first and third quartiles (bottom and top of box), 95% confidence intervals (whiskers), and outliers (points).

When comparing mean prey diversity among time periods and locations during the 2007-08 nonbreeding season there was no significant interaction (two-way ANOVA, Model I, $F_{4,63} = 0.252$, $p = 0.907$; Table 12); therefore, main effect hypotheses were examined. Once again the data were normally distributed, but variances were not equal (Levene's $s = 5.437$, $p < 0.001$). Like in 2006-07, only anchovy were consumed during prebreeding at Año Nuevo Island in 2007-08, thus mean prey diversity and variance were zero. The ANOVA results reflected the data well, so they were interpreted with caution. There was a significant difference among time periods ($F_{2,63} = 6.275$, $p = 0.003$) and locations ($F_{2,63} = 9.723$, $p < 0.001$). Tukey's HSD multiple comparison tests indicated

that mean prey diversity was significantly greater during postbreeding compared with winter and prebreeding, and prey diversity was significantly less at Año Nuevo Island compared with Moss Landing Harbor and Monterey Harbor (Table 12; Fig. 8).

Table 12. Two-way ANOVA and multiple comparison test results comparing prey diversity among time periods and locations during the 2007-08 nonbreeding season.

Time period	LS mean	SE	n	Tukey's HSD $F_{2,63} = 6.275, p = 0.003$
Postbreeding	0.664	0.1	24	Post, Winter: $p = 0.049$
Winter	0.366	0.1	24	Winter, Pre: $p = 0.554$
Prebreeding	0.254	0.1	24	Pre, Post: $p = 0.003$
Location	LS mean	SE	n	Tukey's HSD $F_{2,63} = 9.723, p < 0.001$
ANI	0.177	0.1	24	ANI, MLH: $p < 0.001$
MLH	0.689	0.1	24	MLH, MOH: $p = 0.125$
MOH	0.435	0.1	24	MOH, ANI: $p = 0.048$
Time period*Location	LS mean	SE	n	ANOVA
Postbreeding ANI	0.465	0.1	8	$F_{4,63} = 0.252, p = 0.907$
Winter ANI	0.943	0.1	8	
Prebreeding ANI	0.619	0.1	8	
Postbreeding MLH	0.112	0.1	8	
Winter MLH	0.602	0.1	8	
Prebreeding MLH	0.430	0.1	8	
Postbreeding MOH	0.000	0.1	8	
Winter MOH	0.548	0.1	8	
Prebreeding MOH	0.275	0.1	8	

When comparing mean prey diversity during 2006-07 and 2007-08 nonbreeding seasons there was a significant interaction between season and time period (multifactorial ANOVA, Model I, $F_{2,84} = 4.145, p = 0.019$; Table 13) and season and location ($F_{1,84} = 4.932, p = 0.029$); therefore, main effects could not be interpreted. The assumption of

equal variance was not met. Neither location had a consistent pattern in mean prey diversity between nonbreeding seasons (Fig. 8). Tukey's HSD multiple comparison tests indicated that 2007-08 had significantly greater mean prey diversity compared with 2006-07 ($p = 0.034$; Fig. 8). In addition, prebreeding mean prey diversity was significantly less than postbreeding ($p = 0.003$) and moderately less than winter ($p = 0.068$). Mean prey diversity at Año Nuevo Island was significantly less compared with Moss Landing Harbor ($p < 0.001$).

Table 13. Three-way ANOVA and multiple comparison test results comparing prey diversity between 2006-07 and 2007-08 nonbreeding seasons, among time periods within nonbreeding seasons, and between locations.

Season	LS mean	SE	n	Tukey's HSD $F_{1,84} = 4.663, p = 0.034$
2006-07	0.267	0.0	48	2006-07, 2007-08: $p = 0.034$
2007-08	0.419	0.0	48	
Time period	LS mean	SE	n	Tukey's HSD $F_{2,84} = 5.888, p = 0.004$
Postbreeding	0.474	0.0	32	Post, Winter: $p = 0.511$
Winter	0.374	0.0	32	Winter, Pre: $p = 0.068$
Prebreeding	0.190	0.0	32	Pre, Post: $p = 0.003$
Location	LS mean	SE	n	Tukey's HSD $F_{1,84} = 24.518, p < 0.001$
ANI	0.179	0.0	48	ANI, MLH: $p < 0.001$
MLH	0.525	0.0	48	
Season*Time period	LS mean	SE	n	Tukey's HSD
2006-07 Postbreeding	0.265	0.1	16	$F_{2,84} = 4.145, p = 0.019$
2006-07 Winter	0.415	0.1	16	
2006-07 Prebreeding	0.138	0.1	16	
2007-08 Postbreeding	0.719	0.1	16	
2007-08 Winter	0.335	0.1	16	
2007-08 Prebreeding	0.244	0.1	16	
Season*Location	LS mean	SE	n	Tukey's HSD
2006-07 ANI	0.181	0.1	24	$F_{1,84} = 4.932, p = 0.029$
2006-07 MLH	0.361	0.1	24	
2007-08 ANI	0.177	0.1	24	
2007-08 MLH	0.709	0.1	24	
Time*Location	LS mean	SE	n	Tukey's HSD
Postbreeding ANI	0.297	0.1	16	$F_{2,84} = 0.998, p = 0.373$
Postbreeding MLH	0.677	0.1	16	
Winter ANI	0.264	0.1	16	
Winter MLH	0.495	0.1	16	
Prebreeding ANI	0.000	0.1	16	
Prebreeding MLH	0.416	0.1	16	
Season*Time period*Location	LS mean	SE	n	ANOVA
2006-07 Postbreeding ANI	0.147	0.1	8	$F_{2,84} = 0.628, p = 0.536$
2006-07 Postbreeding MLH	0.395	0.1	8	
2006-07 Winter ANI	0.435	0.1	8	
2006-07 Winter MLH	0.395	0.1	8	
2006-07 Prebreeding ANI	0.000	0.1	8	
2006-07 Prebreeding MLH	0.296	0.1	8	
2007-08 Postbreeding ANI	0.465	0.1	8	
2007-08 Postbreeding MLH	1.016	0.1	8	
2007-08 Winter ANI	0.112	0.1	8	
2007-08 Winter MLH	0.602	0.1	8	
2007-08 Prebreeding ANI	0.000	0.1	8	
2007-08 Prebreeding MLH	0.548	0.1	8	

3.5 Prey size

Few fish otoliths were classified as Grade 1 and suitable for otolith length measurements to estimate fish length. The average size of the dominant prey, Northern Anchovy, was 8.6 cm ($s = 0.6$ cm, $n = 49$). Prey size was estimated for 12 species (Table 14). Speckled Sanddab was the smallest prey (6.4 to 8.0 cm) and White Croaker (*Genyonemus lineatus*) the largest (13.8 to 16.2 cm).

Table 14. Sample size of otoliths with minimal erosion, mean ($\pm$ SD) of otolith lengths (mm), and range of estimated standard lengths (cm) of fishes consumed by Brandt's Cormorants.

Species	n	Otolith length (mm)	
		Mean $\pm$ SD	Range of estimated standard lengths (cm)
<i>Ammodytes hexapterus</i>	2	2.91 $\pm$ 0.05	13.6 - 14.0
<i>Atherinopsis affinis</i>	4	1.97 $\pm$ 0.14	7.4 - 8.4
<i>Chilara taylori</i>	2	3.27 $\pm$ 0.09	10.1 - 10.6
<i>Citharichthys sordidus</i>	1	3.05	12.0
<i>Citharichthys stigmaeus</i>	7	2.47 $\pm$ 0.39	6.4 - 8.0
<i>Embiotoca lateralis</i>	4	4.85 $\pm$ 0.08	8.2 - 8.6
<i>Engraulis mordax</i>	49	3.40 $\pm$ 0.28	8.0 - 9.2
<i>Genyonemus lineatus</i>	5	6.79 $\pm$ 0.80	13.8 - 16.2
<i>Leptocottus armatus</i>	5	5.07 $\pm$ 0.87	8.6 - 13.0
<i>Parophrys vetulus</i>	3	2.83 $\pm$ 0.19	7.4 - 8.8
<i>Porichthys notatus</i>	2	4.26 $\pm$ 0.02	9.3 - 9.4
<i>Trachurus symmetricus</i>	1	5.97	na

3.6 Fine-scale spatiotemporal variation

Spatiotemporal variation in the multivariate diet composition data (%N) for the 19 sampling days (Fig. 9) was examined using nonmetric multidimensional scaling (NMDS, nonmetric fit, $R^2 = 0.991$, Stress = 0.10; Fig. 10). The outer coast location, Año Nuevo Island, was distinct from locations within the bay, Moss Landing Harbor and Monterey Harbor. Sampling days were interspersed within the ordination space occupied by each of those locations indicating that differences in diet composition were better determined

by location than nonbreeding season. Northern Anchovy and perches were associated with diet at Año Nuevo Island. Three flatfishes, Speckled Sanddab, Pacific Sanddab, and English Sole (*Parophrys vetulus*), were associated with diet at Moss Landing Harbor and Monterey Harbor. Topsmelt was most strongly associated with 19 October 2007 at Monterey Harbor, and to a lesser degree, sampling dates at Moss Landing Harbor. Pacific Sandlance (*Ammodytes hexapterus*) was associated with 26 March 2008 at Moss Landing Harbor. The prey category for sculpins was centrally located in the ordination indicating similar proportion in the diet throughout the region.

Figure 9. Fine-scale spatiotemporal variation in Brandt's Cormorant diet by mean percent number (%N) among 6 sampling days during 2006-07 nonbreeding season and 13 sampling days during 2007-08 nonbreeding season ($n = 15$, $N = 285$). Sampling locations were Año Nuevo Island (ANI), Moss Landing Harbor (MLH), and Monterey Harbor (MOH). Prey species comprising less than 5% of the diet were combined into category "Other".

Figure 10. Nonmetric multidimensional scaling ordination comparing spatiotemporal variation in diet composition by percent number (%N) among 19 sampling days. Locations sampled were Año Nuevo Island (triangles), Moss Landing Harbor (squares), and Monterey Harbor (circles). Polygons group locations by nonbreeding season (2006-07 dashed and 2007-08 solid). Proximity to the three letter species codes indicates importance in the diet. The last sampling day of each season at each location is marked by an arrow with the month and year.

3.7 Comparing historical and present diet composition

When the results of this study are placed in context with all available diet data sets for central California a clear pattern of major changes in the diet composition emerges (Fig. 11). During the 1970s and early 1990s the dominant prey in the diet of Brandt's Cormorants was rockfishes at the locations examined, Monterey Bay and Southeast Farallon Island. When the diet was examined again in the early 2000s at Alcatraz Island and in Monterey Bay during this study from 2005 (pilot study) to 2007-08, Northern Anchovy was a substantial portion of the diet by number and consumption of rockfishes was rare. Throughout the time series there was a decrease in consumption of Pacific Sanddab and increase in Speckled Sanddab.

Figure 11. Brandt's Cormorant diet composition by percent number (%N) for past studies in central California and this study. Prey species comprising less than 5.0% were combined into category "Other". Shannon-Wiener diversity index (H) is provided above each bar and time, location, region, and breeding status below each bar. Data are from 1) Talent 1984, 2) Baltz and Morejohn 1977, 3) Ainley et al. 1990, 4) Sydeman et al. 1997, 5) Cutler 1983, 6) Yakich 2005 and 7) this study (including a pilot study in 2005).

The overall multivariate diet composition data (%N) for the two historical nonbreeding season diet data sets in Monterey Bay during the 1970s (Baltz and Morejohn 1977, Talent 1984) and the five location and nonbreeding season combinations sampled in this study were compared using nonmetric multidimensional scaling (NMDS, nonmetric fit, $R^2 = 0.999$, Stress 0.04; Fig. 12). The first NMDS axis separates the historic data from this study by differences in dominant prey: rockfishes were prevalent in the historical data compared with Northern Anchovy in this study. The second NMDS axis further separates by ancillary prey that were consumed in particular nonbreeding seasons and locations. Pacific Sanddab was consumed during both studies during the 1970s whereas Market Squid was only in the diet of birds collected offshore in Monterey

Bay during the 1974-75 nonbreeding season. During this study, perches occurred in the diet at Año Nuevo Island, Speckled Sanddab was prevalent in the diet at both locations inside Monterey Bay, whereas Topsmelt was mainly observed in the diet at Monterey Harbor. For the two locations sampled during both nonbreeding seasons during this study, Año Nuevo Island and Moss Landing Harbor, diet composition was more similar during the 2007-08 nonbreeding season than the 2006-07 nonbreeding season.

Figure 12. Nonmetric multidimensional scaling ordination comparing overall Brandt's Cormorant diet composition by percent number (%N) among studies in the Monterey Bay region. Each study is represented by a number and studies with the same location are circled. Prey species comprising less than 5% of the diet were combined into category "Other fishes". Proximity to three letter prey species codes indicates importance in the diet. Historic data are from 1) Talent 1984 and 2) Baltz and Morejohn 1977 while the remaining data are from this study.

DISCUSSION

In a review of Brandt's Cormorant diet throughout their range Ainley et al. (1981) reported that 59% of the prey consumed occurred in the water column and 41% on the bottom. Comparatively, in this study approximately 69% of prey were taken in the water column. Northern Anchovy, a schooling, coastal pelagic species was 52.6% of the overall diet by number. During fall and winter Northern Anchovy form large schools from the surface to 55 m (Love 1996). The size of Northern Anchovy consumed was small, 8.0 to 9.2 cm, indicating they were young-of-the-year or age 1 fishes (Love 1996). The second and fourth most abundant species in the diet were Speckled and Pacific Sanddab, together comprising 21.6% of the diet by number. Sanddabs consumed were 6 to 12 cm in length which is between 1 and 2 years of age (Rackowski and Pikitch 1989). Sanddabs occur on the bottom mostly in sandy or sandy mud substrate (Fitch and Lavenberg 1971). The third most abundant prey was Topsmelt, a schooling species that occurs in the upper 9 m (Love 1996), and they represented 6.5% of the diet by number. Topsmelt consumed were approximately 8 cm; therefore, they were young-of-the-year (Love 1996). Pacific Sardine, another schooling coastal pelagic species, was the fifth most abundant species with 3.8% of the overall diet by number. No Pacific Sardine otoliths were suitable for length measurement and subsequent fish length estimation.

Changes in dominant ichthyofauna correlate to changes in sea surface temperature (SST) and the oceanography of Monterey Bay is influenced by interannual and multidecadal forcing in the California Current System (CCS). The CCS is one of the most productive current systems in the world, although annual productivity is variable

because it is generated by periodic, wind-driven coastal upwelling and influenced by the El Niño Southern Oscillation (ENSO; Glantz and Thompson 1981). The ENSO cycle is rather frequent, approximately every 3 to 7 years, while the Pacific Decadal Oscillation (PDO) operates at a much longer cycle of approximately 50 years (Chavez et al. 2003). The PDO is correlated with a shift between two abundant species in the CCS, occurring approximately every 25 years with basin-scale changes in SST: a warmer regime is associated with Pacific Sardine and a cooler regime is associated with Northern Anchovy. The warmer “sardine regime” is characterized by less nutrients, less primary productivity, more sardines, fewer anchovy, and fewer rockfishes compared with more nutrients, more primary production, fewer sardines, more anchovy, and more rockfishes during the cooler “anchovy regime” (Chavez et al. 2003).

Evaluating historical Brandt’s Cormorant diet in the context of PDO regimes explains only some of the prey relative abundances observed. The PDO indicates a cooler water anchovy regime from 1947 to 1976-77, a warmer sardine regime until 1998, and then a regime shift back to cooler water conditions (Chavez et al. 2003; Peterson and Schwing 2003). Studies on Brandt’s Cormorant diet during the early-to-mid 1970s were during an anchovy dominated cooler regime, and accordingly, their diet contained appreciable numbers of rockfishes and Northern Anchovy. Two studies were conducted within the warmer regime from 1976-77 to 1998. In 1979 only a small number of birds were sampled near Half Moon Bay, but a rockfish dominated diet was indicated (Cutler 1983) which is in conflict with expectations. Similarly, in 1993 rockfishes dominated the diet at Southeast Farallon Island (Sydeman et al. 1997) despite warmer water conditions.

More work is needed to understand if there is a relationship between PDO influenced changes in ichthyofauna and the diet of the Brandt's Cormorant, a nearshore predator.

Annual midwater trawl surveys have been conducted by NOAA Fisheries Service (Fisheries Ecology Division, SWFSC) in late spring along central California since 1983 and provide data on the relative abundance of pelagic juvenile rockfishes and other juvenile fishes (PaCOOS 2013). The abundance is reported as the standardized anomalies from the log of mean catch rates. There was a positive anomaly for abundance of juvenile rockfishes in the 1993 survey when great numbers of juvenile rockfishes were observed in Brandt's Cormorant diet at Southeast Farallon Island (Sydeman et al. 1997). Brandt's Cormorant diet data collected during this study from 2005 to 2008 was well correlated with the positive anomalies for Northern Anchovy, the negative anomalies for rockfishes and Market Squid, but was not well correlated with the positive anomalies for Pacific Sardine. This indicates that Brandt's Cormorants are consuming prey that is relatively abundant in their environment.

The much shorter time scale of the ENSO may more directly influence Brandt's Cormorant diet because of annual influences on prey recruitment success, especially given the young age classes consumed. Different oceanographic conditions described in CalCOFI (2008) were present before this study, during the two nonbreeding seasons examined in this study, and after the study. Before the pilot study in fall 2005, there was late onset of spring upwelling and a warm sea surface temperature anomaly. Although this was not an El Niño the anomaly had similar effects. In spring 2006, late onset of upwelling occurred again and a moderate El Niño ensued, but rapidly decayed in early

2007 when upwelling began early and continued longer than usual. By summer 2007 a moderate-to-strong La Niña had developed with a cooler than average sea surface temperature anomaly of -2°C . La Niña conditions peaked during January and February 2008 and then weakened substantially by March 2008. These contrasting oceanographic conditions affected Brandt's Cormorant diet.

When cooler oceanographic conditions occurred during the summer 2007 La Niña prey number was expected to increase. Although this was not observed at a regional scale it was observed within Monterey Bay. The greatest number of prey recorded was during the 2007 postbreeding period at Moss Landing Harbor followed by a continuous decline through prebreeding 2008. Prey number also was great at Monterey Harbor during postbreeding 2007, lesser in winter 2007, but then increased by prebreeding 2008. Prey number did not increase at Año Nuevo Island until prebreeding 2008. Thus, the overall effect of the 2007 La Niña was greater prey number in Brandt's Cormorant diet within the bay during the 2007-08 nonbreeding season (Moss Landing Harbor, mean = 15.2; Monterey Harbor, mean = 17.0) than on the outer coast (Año Nuevo Island, mean = 8.6).

These changes in prey number from 2005-06 to 2007-08 were accompanied by changes in diet composition. Overall, Northern Anchovy waned in the diet during 2007-08. Although diet composition at Año Nuevo Island was dominated by Northern Anchovy during both years, it was less so during 2007-08. Prey diversity did not increase at Año Nuevo Island because the slight decrease of Northern Anchovy was replaced with English Sole and perches, the same prey consumed in 2006-07. At Moss

Landing Harbor, the loss of Northern Anchovy during 2007-08 was largely replaced with Speckled Sanddab. Other species that increased in the Brandt's Cormorant diet included Pacific Sanddab, and to a lesser degree, a combination of Topsmelt, English Sole, and sculpins. Therefore, prey diversity increased as expected during cooler oceanographic conditions but only at Moss Landing Harbor. Monterey Harbor was sampled only during the colder-water year and overall diet composition was approximately equal amounts of Northern Anchovy, Speckled Sanddab, and Topsmelt.

The expectation that diversity would increase during winter relative to postbreeding or prebreeding was observed only in part of this study. The expected pattern was observed during the 2006-07 nonbreeding season with greater diversity during winter at Año Nuevo Island and Moss Landing Harbor. However, during the 2007-08 nonbreeding season prey diversity did not increase during winter at any location, but it did increase earlier during postbreeding 2007, likely reflecting the more productive conditions during the La Niña. The mean winter diversity values were similar for 2006-07 ($H = 0.384$) and 2007-08 ($H = 0.366$). The anomalous La Niña event seems to have altered typical timing. During normal oceanographic conditions the pattern of greater diversity during winter likely prevails.

There is some evidence that another major fluctuation in the dominant prey of Brandt's Cormorants began at the end of this study. Northern Anchovy were common in the diet of Brandt's Cormorants at Southeast Farallon Island from 2002 to 2008 but were less frequently observed from 2009 to 2011 (Warzybok and Bradley 2011). A large die-off event of Brandt's Cormorants occurred during the 2009 breeding season in central

California, and because disease tests were negative, starvation was considered the most likely cause (H. Nevins, unpublished data). This is consistent with the loss of Northern Anchovy as a prey resource. That Brandt's Cormorants did not respond to the loss of Northern Anchovy by consuming other prey species possibly represents time required to transition from foraging mostly as a specialist back to foraging mostly as a generalist.

Increased abundance of juvenile rockfishes was observed in the 2012 and 2013 midwater trawl surveys in central California (PaCOOS 2013); therefore, it is likely that abundance of juvenile rockfishes also increased in Brandt's Cormorant diet in the Monterey Bay region. Another possible indication of diet composition returning to cold-water affiliated species came with opportunistic samples collected at Moss Landing Harbor in March 2010 that contained numerous juvenile Market Squid, far in excess of anything observed from 2005 to 2008.

This study is the first to examine fine-scale spatiotemporal diet variation in Brandt's Cormorants. The sampling scheme detected different location responses to the same oceanographic stimulus. This study demonstrated the importance of periodic sampling at multiple locations within a region to detect changes in the diet of this opportunistic generalist.

Seabirds have increasingly been studied as indicators of the marine ecosystem (Piatt et al. 2007). Northern Anchovy, rockfishes, and Market Squid that are common in Brandt's Cormorant diet are important to many other predators in the CCS (Morejohn et al. 1978, Ainley et al. 1990). As a piscivorous generalist, the Brandt's Cormorant is a good candidate for a nearshore indicator species because their distribution includes the

full extent of the CCS. This would allow large areas to concurrently be examined thereby providing insight into the geographic extent of prey fluctuations.

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