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Diet of a piscivorous seabird reveals spatiotemporal variation in abundance of forage fishes in the Monterey Bay region

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ABSTRACT

Brandt's Cormorant (*Phalacrocorax penicillatus*) diet was investigated using regurgitated pellets (n = 285) collected on 19 sampling days at three locations during the 2006–07 and 2007–08 nonbreeding seasons in the Monterey Bay region. The efficacy of using nested sieves and the all-structure technique to facilitate prey detection in the pellets was evaluated, but this method did not increase prey enumeration and greatly decreased efficiency. Although 29 prey species were consumed, northern anchovy (*Engraulis mordax*) dominated and speckled sanddab (*Citharichthys stigmaeus*) also was important in the diet. Few rockfishes (*Sebastes* spp.) and market squid (*Doryteuthis opalescens*) were consumed compared with great prevalence in previous studies during the 1970s. El Niño and La Niña during the study provided a unique opportunity to examine predator response to variation in prey availability. Patterns of prey number and diversity were not consistent among locations. Greatest number and diversity of prey occurred at locations within Monterey Bay during La Niña, results not evident at the outer coast location. Short-term specialization occurred but mean prey diversity indicated a generalist feeding mode. This study demonstrated the importance of periodic sampling at multiple locations within a region to detect spatiotemporal variability in the diet of opportunistic generalists.

1. Introduction

The Brandt's Cormorant (*Phalacrocorax penicillatus*) is the most abundant locally nesting seabird in the Monterey Bay region of central California. From 1989 to the mid-2000s many new colonies formed, some with rapid growth, including the first report of nesting within Monterey Bay (Bechaver et al., 2013; Capitolo et al., 2014; Carter et al., 1992). 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, juvenile, and small adult fishes and, to a lesser extent, squid (Elliott et al., 2015-in this issue; Sydeman et al., 2001; this study). Given their reliance on the inner continental shelf habitat, year-round occurrence (Briggs et al., 1987; Wallace and Wallace, 1998), and consumption of approximately 20% of their body mass per day (Ancel et al., 1997), Brandt's Cormorants can potentially extract large numbers of prey from the Monterey Bay region. However, little is known about their diet there. Two previous diet studies in Monterey Bay were conducted more than 30 years earlier and had small sample sizes (n ≤ 11) from a variety of locations (Baltz and Morejohn, 1977; Talent, 1984).

A review of diet studies throughout their range indicated that Brandt's Cormorants forage locally and are opportunistic (Ainley et al., 1981). One or two prey generally dominate the diet in a given location with the remainder being a diverse set of fishes consumed in smaller numbers. Consecutive years of diet samples in the 1970s during the breeding season at Southeast Farallon Island in central California indicated that Brandt's Cormorants not only specialized on abundant prey, mainly rockfishes, but also diversified their diet when prey were less available during El Niño and other anomalous conditions (Ainley et al., 1990). We reviewed published diet studies for central California and found that prey representing at least 15% of the diet included rockfishes (*Sebastes* spp.), northern anchovy (*Engraulis mordax*), Pacific and speckled sanddabs (*Citharichthys sordidus* and *Citharichthys stigmaeus*), market squid (*Doryteuthis opalescens*), Pacific tomcod (*Microgadus proximus*), and spotted cusk-eel (*Chilara taylori*) (Ainley et al., 1990; Baltz and Morejohn, 1977; Cutler, 1983; Sydeman et al., 1997; Talent, 1984; Yakich, 2005). Although at a larger spatial scale (entire range) diet can vary greatly (Ainley et al., 1981), none of these studies in central California reported diet concurrently at more than one location; thus, the variation in diet is unknown at smaller scales. Overfishing and an unfavorable warm water period caused a substantial decrease in abundance of juvenile rockfishes 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. Our goal was to determine present diet composition to aid our understanding of how a major avian predator

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responds to a decrease of multiple important prey resources, thereby providing important information about central California food web dynamics.

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). Sampling during the breeding season is not possible because of the potential for disturbance and subsequent nest abandonment. Most diet sampling, using pellets, has been conducted at the end of the breeding season with inference made to the entire five-month season (e.g., Ainley et al., 1981), but such sampling precludes understanding diet variability through time. During the nonbreeding season, September through March, movements are less constrained and birds may forage regionally (>50 km) during the course of a few days. A modeling study by Wiens and Scott (1975) reported greatest energy demands during the nonbreeding season, approximately 500 kcal per bird per day. Three of four more recently colonized locations that also were used during the nonbreeding season 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 approximately 88 km from the Farallon Islands to the northwest) and 70 km from Monterey Harbor. Moss Landing Harbor and Monterey Harbor are approximately 25 km apart. The diverse habitats in which Brandt's Cormorants forage in coastal central California seemingly were represented by these three locations.

Intra-seasonal forcing on Brandt's Cormorant behavior and diet are linked to oceanographic influences that affect prey availability and should be considered when sampling predator diet in central California waters. Greater marine productivity occurs in Monterey Bay during spring and summer when northwest winds generate an upwelling plume extending southward from Point Año Nuevo. Cold, nutrient rich waters are advected into Monterey Bay via cyclonic surface circulation (Breaker and Broenkow, 1994; Paduan and Rosenfeld, 1996; Rosenfeld et al., 1994). Pulses of upwelling also occur occasionally during 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 that includes postbreeding (September and October), winter (November to January), and prebreeding phases of the cormorant's annual cycle (February and March; Wallace and Wallace, 1998). During the year, dominant fishes in Monterey Bay vary seasonally (Cailliet et al., 1979), thus cormorant diet should vary accordingly.

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) and may be equivalent to stomach samples (Ainley et al., 1981; Jordán, 1959). Indeed, the daily consumption derived from pellets matched energetic demands in a few studies (Dirksen et al., 1995; Voslamber et al., 1995).

Most fish otoliths, cephalopod beaks, and other prey hard parts contained in cormorant pellets have enough structure to determine species ingested (Duffy and Laurenson, 1983). Collecting pellets at colony or roost locations on a frequent schedule (e.g., daily) is well suited for a study with the aim of addressing fine-scale spatiotemporal variation. Birds do not have to be killed to obtain the larger sample sizes required, the diet is not biased by the habitat that the bird is collected in (Hubbs et al., 1970) because pellets represent fishes consumed in foraging habitats used over the course of a day, 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). 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 an underestimate of representation in the diet (Casaux et al., 1995; Duffy and Jackson, 1986; Duffy and Laurenson, 1983; Jobling and Breiby, 1986; Johnstone et al., 1990; 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 among seasons, years, or regions (Ainley et al., 1981; Barrett et al., 1990; Duffy and Jackson, 1986; Duffy and Laurenson, 1983; 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) examine fine-scale spatiotemporal differences in diet composition within and between nonbreeding seasons, 4) estimate prey size, 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.

2. 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. 1). 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. Breeding activities were monitored so that disturbance was minimized. Sampling began in the fall when all chicks had fledged, and sampling ceased in spring once courtship behaviors were observed.

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 distinguished because they lack an outer covering and are primarily composed of fish bones. Pellets were not collected in areas where Double-crested Cormorants (*Phalacrocorax auritus*) or Pelagic Cormorants (*Phalacrocorax pelagicus*) roosted. 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 activities. 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 softened and broken up 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