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Novel vs. Traditional Approaches to Sampling Seabird Diet: Nest and Pellet Analysis of Brandt's Cormorants (*Phalacrocorax penicillatus*)

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Abstract.—Diet of the Brandt's Cormorant (*Phalacrocorax penicillatus*) breeding population on Alcatraz Island, California, USA was determined for 2014-2016 using two sampling methods. Regurgitated pellets and complete nests were collected, once all chicks had left colonies, to reduce disturbance to nesting birds. Results identified 25 prey taxa including 23 teleost fishes and two cephalopods. Diet was dominated by northern anchovy (*Engraulis mordax*) and speckled sanddab (*Citharichthys stigmaeus*), with plainfin midshipman (*Porichthys notatus*), sole *spp.* (Pleuronectidae), and sculpin *spp.* (Cottidae) rounding out the top five abundant species. Comparison of diet by sample type yielded similar results in terms of prey species composition, but total diet differed between the two samples due to rare prey items being more prevalent in nest samples. Determining cormorant diet using a combination of pellet and nest samples is a novel approach with the potential to provide a better representation of prey consumed during the full breeding period (up to 6 months for cormorants), and similar methods may be informative for other seabirds that produce pellets. In contrast, diet determined from pellets alone may only represent a short time period just prior to collection, as pellets are often blown away by strong winds or disintegrate through trampling and/or exposure to the elements in open seabird breeding colonies. Received 6 November 2018, accepted 20 May 2019.

Key words.—Alcatraz Island, California, cormorant, diet analysis, nest sample, regurgitated pellet, San Francisco Bay, seabird diet

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Seabirds are important members of marine ecosystems and food webs and investigating their biology and ecology can help understand these complex systems. For almost a century, it has been well known that seabird diet and reproductive success can provide insights into the health of fish stocks (Cairns 1987; Montevecchi 1993; Piatt *et al.* 2007) and can herald changes in oceanographic conditions (Murphy 1936; Ashmole 1971; Furness and Camphuysen 1997). Diet is only known for roughly half of the world's seabird species (Karpouzi *et al.* 2007), and thus we are limited in understanding the dynamics of many of the habitats they utilize. Seabirds are one of the most accessible links in marine food chains because they are surface-dwelling, produce large and easily monitored colonies, and are easily captured and sampled. As such, researchers have been investigating their feeding habits and diet for many decades.

There have been many methods developed to determine seabird diets directly, ranging from opportunistic collections to targeted observations (Barrett *et al.* 2007).

For many species that bring whole prey items back to the breeding colony (e.g., auks and guillemots), diet estimation can be done with simple binocular or spotting scope observations or by setting up cameras to record fish deliveries (Larson and Craig 2006; Robertson *et al.* 2016), however, this method can have high prey identification error and is not available for species that fully ingest prey. For the latter, there are other options for collecting samples of consumed prey. Upper gastrointestinal tract and stomach samples can provide accurate estimates of prey enumeration and measurements (Collis *et al.* 2002), yet this method either involves killing the bird or using a non-lethal water offloading technique (lavage) that is invasive and labor intensive (Ito *et al.* 2009). Stomach content analysis has also been done with beached carcasses (Petry *et al.* 2009; Donnelly-Greenan *et al.* 2014), which likely does not represent accurate diet as these birds have often died from starvation or illnesses that may alter normal feeding habits. Many seabird species readily regurgitate stomach contents

when frightened (Barrett *et al.* 2007), and while this can provide easily identifiable prey remains, it requires a high level of disturbance to colonies and is entirely opportunistic in its nature.

A widely used diet research method requiring little to no disturbance to seabird species that fully ingest prey is the collection of pellets (Harris 1965; Grémillet *et al.* 1998; Naves and Vooren 2006). These regurgitated packets of indigestible hard parts of prey, produced daily by many species (e.g. cormorants/shags, Ainley *et al.* 1981; gulls, Harris 1965; skimmers, Naves and Vooren 2006; skuas and terns, reviewed in Barrett *et al.* 2007), can theoretically be obtained throughout the year. Unlike other methods in which data can only be collected during the breeding season, regurgitated pellets provide an easy way to measure temporal variability in diet. While some winter diets have been examined (e.g., Webb and Harvey 2015), breeding season diet is often desired to investigate mechanisms of reproductive performance. To avoid disturbance, pellets are typically only collected in nesting colonies at the end of the breeding season when all birds have left the colony site (Carney and Sydeman 1999). Certain colony configurations may promote accumulation of pellets (e.g., rocks and/or high nest density for pellets to lodge between, nests further from cliff edges so pellets are not expelled, and nests in less windy areas). However, pellets in open seabird breeding colonies are often blown away by strong winds or disintegrate through trampling and/or exposure to the elements, such as in some Brandt's Cormorant colonies (H. J. Robinson, pers. obs.). Since each individual pellet only represents approximately one 24-hour period of foraging, it follows that diet composition reconstructed from these samples corresponds to a short time period (Duffy and Laurenson 1983; Zijlstra and Van Eerden 1995), unless one assumes that pellets from throughout the breeding season accumulate and can be collected with relatively equal representation in a seasonal sample. However, if pellets are typically destroyed quickly due to colony conditions,

pellets collected at the end of the breeding season may only represent diet from after the time during which the greater part of reproductive success has been determined. For diet to provide insight into factors that possibly affect reproductive success, samples must also be collected during the earlier months of the breeding season. Collecting pellets during this time, however, would create large amounts of disturbance, adversely affecting reproduction and thus is typically not feasible (Carney and Sydeman 1999).

An alternative approach to sampling diet is collecting whole-nest samples. A pair of cormorants builds a large nest out of vegetation and spends the next four to five months constantly protecting it, along with eggs and chicks, until the time when chicks are large, in creches, and rarely return to the nest site. Considering that cormorants each produce one pellet per day (Ainley *et al.* 1981; Barrett *et al.* 2007) and commonly regurgitate food (Barrett *et al.* 2007; H. J. Robinson pers. obs.), each nest has the potential to accumulate a great deal of prey hard parts over the course of the breeding season. Collecting nests can be done at the end of breeding season, so no disturbance occurs, and could provide diet information from a much longer time period during which breeding success is determined.

In this study, we developed a new method of sampling cormorant diet using whole-nest samples of Brandt's Cormorants (*Phalacrocorax penicillatus*) from Alcatraz Island in San Francisco Bay (SFB), California, USA in order to determine diet during the breeding season. Our primary objective was to compare methods for sampling the diet of Brandt's Cormorants obtained from the conventional pellet method to that obtained from the new whole-nest method. We hypothesized that diet determined from the two sample types would be similar, but given the length of time cormorants inhabit nests, that whole-nest samples would contain more dietary information than pellets, in both the number of prey hard parts and species diversity.

METHODS

Study Area and Species

Alcatraz Island (37° 49' 32.00" N, 122° 25' 16.00" W) lies in the mouth of San Francisco Bay, California, USA (Fig. 1). Besides being a popular tourist attraction, it is home to several species of breeding seabirds. With almost 1,900 nesting pairs in recent years, Alcatraz is the site of one of the largest colonies of Brandt's Cormorants in California (Robinson *et al.* 2018a unpubl. report; see also Capitolo *et al.* 2014 and Ainley *et al.* 2018) and constitutes one of only two places this pelagic species breeds in an estuarine environment. The colony breeding season usually begins in March when cormorants arrive at Alcatraz, form mating pairs, and build nests. Eggs are typically laid in April and are incubated for roughly 30 days, then chicks take six to eight weeks to fledge, and typically by the end of September cormorants have left breeding colonies (Saenz *et al.* 2006, Robinson *et al.* 2018a unpubl. report).

Field Sample Collection

Diet samples were collected at the end of Brandt's Cormorant breeding seasons on one or two days in September of each year, 2014-2016. Specific days were chosen to ensure all cormorant chicks had fledged and left breeding colonies, thereby causing little to no disturbance to the population. Samples were obtained from all breeding areas on Alcatraz to get representation from the whole population. Naturally dried and intact pellets were randomly chosen while ensuring that no prey hard parts were lost or that pellets were

not incomplete. Whole cormorant nests were collected by carefully scoring the ground around each nest with a shovel and gently lifting, making sure to not dig into the sediment below the nest. This was to ensure that the sample contained only nest material and contents from the current breeding season and that no actual "digging" was performed on a National Historic Landmark. Once removed from the underlying sediment, nests were placed in individually labeled polypropylene sandbags.

Pellet Sample Processing

To remove all otoliths and cephalopod beaks from pellets, we placed pellets in individual petri dishes, rehydrated them with water and detergent to prevent further digestive enzyme activity, and gently pulled pellets apart with forceps under a dissecting microscope to reveal all contents. We identified all otoliths and cephalopod beaks to the lowest possible taxonomic level using pertinent literature (Harvey *et al.* 2000; Lowry 2011). Otoliths from some related species (rockfishes, surfperches, and sculpins) have very similar morphologies that are difficult to distinguish, particularly after erosion, and therefore we only identified these groups to family level. For each otolith, we determined side (left/right) and grade of erosion (1-3) following methods outlined in Lance *et al.* (2001), and we measured length with digital calipers. Cephalopod beaks were classified as upper or lower, but due to the brittle nature and morphological deformation of dried beaks, no measurements were made.

We ran cumulative species curves with Matlab (v. R2015a) to determine if enough pellets had been collected in each year to properly describe diet. These curves were produced with repetitive random sampling of diet data and plotting cumulative number of samples versus cumulative numbers of prey taxa. We determined adequate sample size (number of pellets) from the points at which curves reached asymptotes, indicating that new prey items are introduced only rarely (Ferry and Cailliet 1996; Cortéz 1997).

Nest Sample Processing

Before removal of prey hard parts could occur, nests required preliminary processing, in which all large nesting material was removed. Each nest was placed in a separate five-gallon bucket that was filled with water to gently break apart nesting material. Contents of buckets were poured incrementally through a sieving complex that consisted of a piece of 0.5-inch wire mesh placed over a 500- μ m sieve, and gently washed. All material retained in the sieve was then dried using a food dehydrator. We completed secondary processing of nests by rehydrating material with water, one petri dish at a time, and using forceps under a dissecting microscope to remove all otoliths and cephalopod beaks.

After two full nests were sorted, we determined that due to the large amount of material still present after sieving and time/budget constraints, all other nests would be sub-sampled. We ran a cumulative species curve in Matlab (v. R2015a), similar to that described

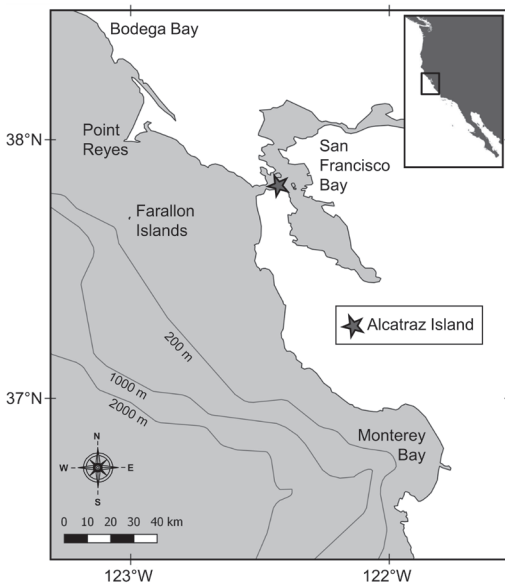


Figure 1. Location of Alcatraz Island in San Francisco Bay, California, USA where all Brandt's Cormorant (*Phalacrocorax penicillatus*) pellet and nest samples were collected from 2014-2016.

above for pellets but using individual petri dishes from the two fully analyzed nests as “samples”, to determine the amount (fraction) of sieved nest that was needed to accurately describe diet. The result was one quarter of a nest. We weighed all subsequent nests, systematically divided them into quarters which were each weighed to ensure their evenness, and placed quarters into separate sample bags. We randomly selected one quarter of each of the remaining nests and removed hard parts as described above for secondary processing of nests. Otoliths and cephalopod beaks were identified, recorded and measured as described above for pellet samples.

Diet Description

Cormorant diet was described using two Relative Measures of Prey Quantity (RMPQs), number and mass. Traditional methods for calculating the number of fish consumed employ a simple technique where otoliths are assigned orientations (left/right), the total number of each side is counted, and the highest value is used as the Minimum Number of Individuals (MNI) for each species. While this method is simple, it has the potential to underestimate how many individuals were consumed. To provide a more realistic estimate of the number of individuals, we developed a “pairing” method in which all lengths were used to match up pairs of left and right otoliths, resulting in a Modified Minimum Number of Individuals (MMNI; Robinson *et al.* 2018b). Mille *et al.* (2015) found no significant differences in the lengths of left and right otoliths for several fishes, and only one species had a difference of 0.2 mm that was determined to be biologically inconsequential. For this study, as we were dealing with partially eroded otoliths, we considered 0.5 mm to be a more conservative level of difference, so left and right otoliths were paired if their lengths fell within that range of each other. If any otoliths did not have opposite-side length matches less than the designated 0.5 mm threshold, they were left unpaired. Thus, our MMNI became the total number of pairs plus any unpaired otoliths within each sample.

Because we did not measure cephalopod beaks, we could not use our pairing method for these structures, therefore cephalopods were enumerated using the greatest number of upper or lower beaks to calculate a traditional MNI. Within each sample, we determined % Number that each species made up of the total MNI of all species, and then averaged across all samples to calculate the mean % Number for each species in the diet, keeping nests separate from pellets. For further analysis, prey that contributed to the top 95% of diet (% Number) in any year were retained as individual categories, all right-eyed flatfish were combined into “Sole spp.”, and any remaining species were combined into two additional categories, “other fishes” and “cephalopods”.

Lengths of otoliths with low levels of erosion (grade 1 and 2) were used in regression equations from publications and personal communications (Table 1) to determine the biomass of prey species consumed by cormorants. Resulting masses were averaged within samples and multiplied by MMNI to determine the

Minimum Biomass of Individuals (MBI) for each species. We added grade 3 otoliths to calculations when determining MBI for samples in which no grade 1 or 2 otoliths were present, or where grade 3 otoliths were > 1 mm in length from the largest or smallest grade 1 or 2 otolith in a sample (thus representing a wider size range of prey). While we recognize using eroded otoliths likely underestimated prey masses, this was preferable to having truncated size ranges or no estimates at all. We determined the percent by mass (% Mass) that each species made up of total MBI within each sample and then averaged across all samples to calculate a mean % Mass for all fish species in cormorant diet. No mass estimates were possible for cephalopod species because no beak measurements were made. As cephalopod contribution to the diet was negligible and gelatinous cephalopod mass is generally less than bony fish mass, this made little overall difference to mass estimates.

Statistical Analysis

All diet data were logit-transformed to adjust for non-normality (Collett 2002; Warton and Hui 2011) and statistical differences in diet composition among variables were analyzed using PRIMER-E (v. 6.1.5, 2006). We used % Number data to compare between the nest and pellet methods. Due to the difference in sample sizes between methods we created groups of pellets, based on date and location of collection (sub-colony areas of Alcatraz), in which % Number values were averaged. Similarity matrices were constructed for each dataset using the Bray-Curtis similarity coefficient, and ANOSIM tests were performed to determine significance of similarity between sampling methods (Daly *et al.* 2009; Thayer *et al.* 2014). Similarity percentages (SIMPER) were used to identify which taxonomic categories made the greatest contributions to any dissimilarity (Thayer *et al.* 2014) between nest samples and pellet samples. All resulting relationships were visualized using non-metric multidimensional scaling plots and resulting stress values less than 0.10 suggested that sufficient dimensionality was used to depict spread of data points (Clarke and Warwick 2001).

RESULTS

Diet Description

A total of 614 cormorant pellets were collected for this study ($n_{2014} = 198$; $n_{2015} = 200$; $n_{2016} = 216$) of which 97 (16%) contained no otoliths or beaks ($n_{2014} = 17$; $n_{2015} = 44$; $n_{2016} = 36$) and were removed from further analysis. Cumulative species curves revealed that to accurately determine Brandt’s Cormorant diet, roughly 40-70 pellet samples containing prey items were needed (Fig. 2) and that all years had more than enough samples (n_{2014}

Table 1. Regression equations used to estimate Minimum Biomass of Individuals (MBI) for all identified fish taxa in diet samples found in pellets and nests of breeding Brandt's Cormorants (*Phalacrocorax penicillatus*) on Alcatraz Island, California, USA from 2014-2016. These equations either required a two-step calculation in which otolith length (OL) was converted to fish standard length (SL) and then converted into weight (W), or otolith length was converted directly to weight when relationships were available. Species habitats are denoted as follows: E = epipelagic; M = mesopelagic; D = demersal.

Prey Fishes		Length (mm)/Weight (g) Regression Equations	
Scientific Name	Common Name	OL to SL	SL (or OL) to W
<i>Ammodytes hexapterus</i> (D)	Pacific sand lance	SL = 4.06 (OL) + 2.01 ^a	W = 0.0063 SL ^{2.790a}
Atherinopsidae (E)	Silversides	SL = 3.72 (OL) + 0.55 ^a	W = 0.1698 SL ^{1.733a}
<i>Chilara taylori</i> (D)	Spotted cusk eel	SL = 2.51 (OL) + 2.15 ^a	W = 0.0004 SL ^{3.761a}
<i>Citharichthys sordidus</i> (D)	Pacific sanddab	SL = 2.87 (OL) + 3.29 ^a	W = 0.0352 SL ^{2.710a}
<i>Citharichthys spp.</i> (D)	Sanddab spp.	SL = 3.178 (OL) - 0.186 ^b	W = 1.000 OL ^{2.263b}
<i>Citharichthys stigmaeus</i> (D)	Speckled sanddab	SL = 3.178 (OL) - 0.186 ^b	W = 1.000 OL ^{2.263b}
<i>Clupea pallasii</i> (E)	Pacific herring	SL = 5.24 (OL) - 1.85 ^a	W = 0.0044 SL ^{3.398a}
Cottidae (D)	Sculpins	SL = 2.58 (OL) - 2.26 ^a	W = 0.0111 SL ^{3.229a}
Embiotocidae (E)	Surfperches	SL = 1.74 (OL) - 0.52 ^a	W = 0.0100 SL ^{3.515a}
<i>Engraulis mordax</i> (E)	Northern anchovy	SL = 2.28 (OL) + 0.85 ^a	W = 0.0485 SL ^{2.413a}
<i>Genyonemus lineatus</i> (D)	White croaker	SL = 1.52 (OL) + 4.66 ^a	W = 0.0550 SL ^{2.700a}
<i>Glyptocephalus zachirus</i> (D)	Rex sole	SL = 4.80 (OL) - 2.50 ^a	W = 0.0238 SL ^{2.692a}
<i>Lepidogobius lepidus</i> (D)	Bay Goby	SL = 3.64 (OL) - 0.96 ^c	W = 0.0454 SL ^{2.113c}
<i>Lyopsetta exilis</i> (D)	Slender sole	SL = 3.37 (OL) + 1.08 ^a	W = 0.0058 SL ^{3.293a}
<i>Microstomas pacificus</i> (D)	Dover sole	SL = 3.72 (OL) + 6.97 ^a	W = 0.0094 SL ^{3.092a}
<i>Parophrys vetulus</i> (D)	English sole	SL = 3.82 (OL) - 2.76 ^a	W = 0.0163 SL ^{2.939a}
<i>Pepirus simillimus</i> (E)	Pacific pompano	SL = 3.629 (OL) - 5.334 ^b	W = 0.017 OL ^{5.023b}
Pleuronectidae (D)	Flatfishes	SL = 3.72 (OL) + 6.97 ^a	W = 0.0094 SL ^{3.092a}
<i>Porichthys notatus</i> (D)	Plainfin midshipman	SL = 2.80 (OL) - 2.59 ^a	W = 0.0207 SL ^{2.916a}
<i>Sardinops sagax</i> (E)	Pacific sardine	SL = 6.108 (OL) - 1.618 ^d	W = 2.064 SL ^{1.180c}
<i>Sebastes spp.</i> (E)	Rockfishes	SL = 1.689 (OL) + 1.095 ^c	W = 2.136 SL ^{1.219c}
<i>Synodus lucioceps</i> (D)	California lizardfish	SL = 5.827 (OL) - 2.515 ^f	W = 0.009 SL ^{2.907g}
<i>Trachurus symmetricus</i> (E)	Jack mackerel	SL = 3.317 (OL) + 0.567 ^d	W = 0.0635 SL ^{2.556d}

Regression sources: ^aHarvey et al. 2000; ^bM. Lowry/National Marine Fisheries Service, pers. comm.; ^cPhillips 2005; ^dSweeney 2008, ^eYakick 2005, ^fGamboa 1991, ^gRodriguez-Romero et al. 2009.

= 181; $n_{2015} = 156$; $n_{2016} = 180$). In each of the three years we collected ten whole-nest samples, all of which contained prey hard parts.

From the 517 pellets with hard parts and the 30 nests, we identified 25 different prey taxa in Brandt's Cormorant diet, including 23 fishes (Table 1) and two cephalopods (Table 2). Despite the different sample sizes between the two methods, we found similar total fish MMNI values in pellets and nests (10,295 and 7,238, respectively). Fishes included epipelagic (8) and demersal species (15), and cephalopods included one pelagic squid (Market squid, *Doryteuthis opalescens*) and one octopus species (Red octopus, *Octopus rubescens*). Of the 25 prey identified, there were 4 species (California lizardfish, *Synodus lucioceps*; Pacific herring, *Clupea pallasii*; Pacific sardine, *Sardinops sagax*; Slender

sole, *Lyopsetta exilis*) that were found only in nest samples. For further analysis, prey taxa were reduced to eleven categories: northern anchovy (*Engraulis mordax*), speckled sanddab (*Citharichthys stigmaeus*), plainfin midshipman (*Porichthys notatus*), sculpin *spp.* (Cottidae), sole *spp.* (Pleuronectidae, that was 92-100% English sole, *Parophrys vetulus*), white croaker (*Genyonemus lineatus*), surfperch *spp.* (Embiotocidae), Pacific sanddab (*Citharichthys sordidus*), bay goby (*Lepidogobius lepidus*), other fishes, and cephalopods (Table 2).

Sampling Method Comparison

Examination of diet using % Number revealed similar results for both sample types (nests and pellets) in each year, where the

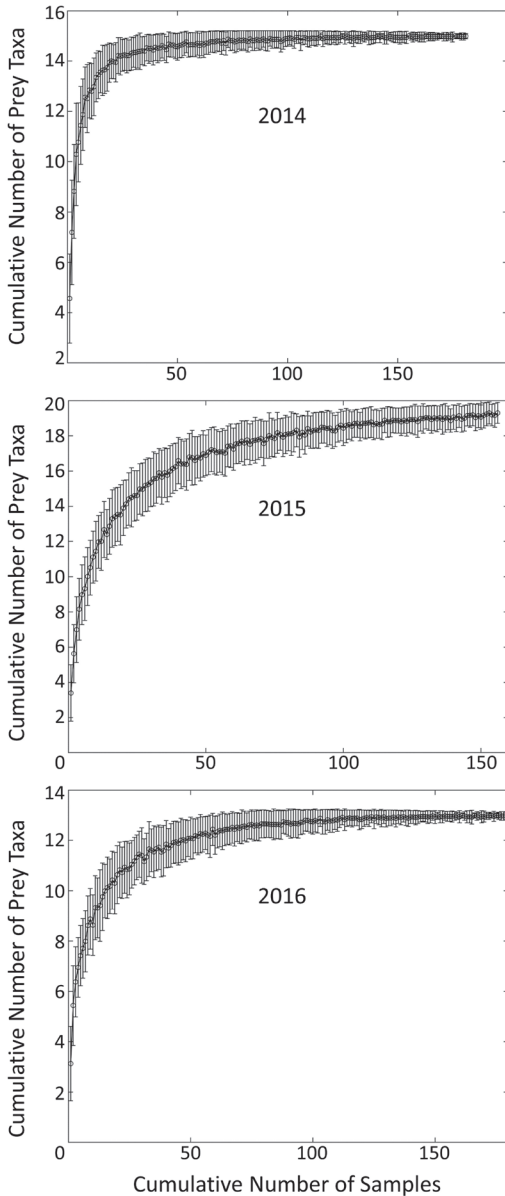


Figure 2. Yearly cumulative species curves for all Brandt's Cormorant (*Phalacrocorax penicillatus*) pellets processed from 2014–2016. Curve asymptote indicates point at which there are enough pellets to accurately characterize predator diet, as new prey taxa are rarely encountered.

most abundant prey species were northern anchovy, speckled sanddab, and plainfin midshipman (Fig. 3, Table 2). However, in 2014 when consumption of northern anchovy was lowest, the most abundant prey species also included sculpin and sole. In gener-

al, more anchovy were found in nest samples (*post hoc* t-test: $t = 4.03$; $P < 0.001$) whereas more speckled sanddab and plainfin midshipman were found in pellet samples.

Overall diet for all years combined was significantly different between the two sampling methods ($R^2 = 0.26$, $P = 0.001$). SIMPER tests revealed 20% dissimilarity between nest and pellet diets due mostly to minor prey items (bay goby, white croaker, cephalopods) being present in higher numbers in nest samples (Fig. 4A). Even when a subsequent analysis was run examining only the most abundant five prey items (northern anchovy, speckled sanddab, plainfin midshipman, sculpin, sole) diets were still significantly different between nest and pellet samples ($R = 0.13$, $P = 0.001$) although the dissimilarity dropped to 9%. Within each separate year, diets remained significantly different between the sampling methods ($R^2_{2014} = 0.26$, $P = 0.006$; $R^2_{2015} = 0.37$, $P = 0.001$; $R^2_{2016} = 0.40$, $P = 0.022$), however, levels of dissimilarity varied as did the species contributing most to the differences. In 2014, diet was 19% dissimilar between nests and pellets due to greater amounts of midshipman and bay goby in nests and more white croaker in pellets (Fig. 4B). The 2015 diet had the greatest dissimilarity between sample types (22%), which was due to higher numbers of bay goby and surfperch in nests and more cephalopods in pellets (Fig. 4C). Finally, in 2016, diet was 16% dissimilar between nests and pellets mainly due to more Pacific sanddab and bay goby in nests and more surfperch in pellets (Fig. 4D).

DISCUSSION

Brandt's Cormorants breeding on Alcatraz Island in central California have a diverse diet of 25 identified fish and cephalopod taxa, however only three species dominate: northern anchovy, speckled sanddab, and plainfin midshipman. The only other study of Brandt's Cormorant diet at Alcatraz Island reported a composition similar to our study, yet with greater amounts of staghorn sculpin (*Leptocottus armatus*) and English sole (Yakich 2005). Other studies of Brandt's

Table 2. Composition of Brandt's cormorant (*Phalacrocorax penicillatus*) diet from Alcatraz Island, California, USA based on percent by number (% Number) and percent by mass (% Mass). Number of samples containing prey items within each year are in parentheses. Prey groups are ordered greatest to least based on a mean % Number across all years.

Prey Group	Percent by Mass											
	Percent by Number						Percent by Mass					
	2014		2015		2016		2014		2015		2016	
	Pellets (181)	Nests (10)	Pellets (156)	Nests (10)	Pellets (172)	Nests (10)	Pellets (181)	Nests (10)	Pellets (155)	Nests (10)	Pellets (171)	Nests (10)
Northern anchovy	25.2	29.7	38.9	62.9	37.0	49.5	19.1	13.7	36.0	44.2	34.4	27.4
Speckled sanddab	27.8	21.9	28.0	13.7	23.8	23.4	19.0	9.6	25.4	8.8	17.2	11.0
Plainfin midshipman	5.6	10.7	12.7	5.5	18.4	6.3	10.5	36.9	18.1	18.7	28.2	35.0
Sculpin <i>spp.</i>	12.8	14.6	3.6	5.5	7.1	7.4	15.2	17.0	3.6	9.8	7.2	8.1
Sole <i>spp.</i>	7.4	7.8	5.7	3.7	6.8	6.2	8.1	5.9	2.6	2.9	6.4	4.6
White croaker	10.2	3.2	1.5	1.5	1.4	1.5	15.0	6.1	3.6	4.9	2.2	4.7
Surfperch <i>spp.</i>	1.8	2.0	1.8	3.0	3.0	1.7	1.8	1.3	1.8	3.6	2.5	3.9
Pacific sanddab	3.7	2.9	2.5	0.9	0.2	1.1	9.2	8.0	6.0	5.4	0.7	3.6
Cephalopods	2.2	0.7	3.6	0.5	0.6	0.1	<i>na</i>	<i>na</i>	<i>na</i>	<i>na</i>	<i>na</i>	<i>na</i>
Bay goby	1.9	5.3	0.2	1.9	1.7	2.4	1.2	0.8	0.1	0.5	1.2	0.5
Other fishes	1.5	1.1	1.6	1.1	0.0	0.5	0.8	0.8	2.9	1.2	0.0	1.1

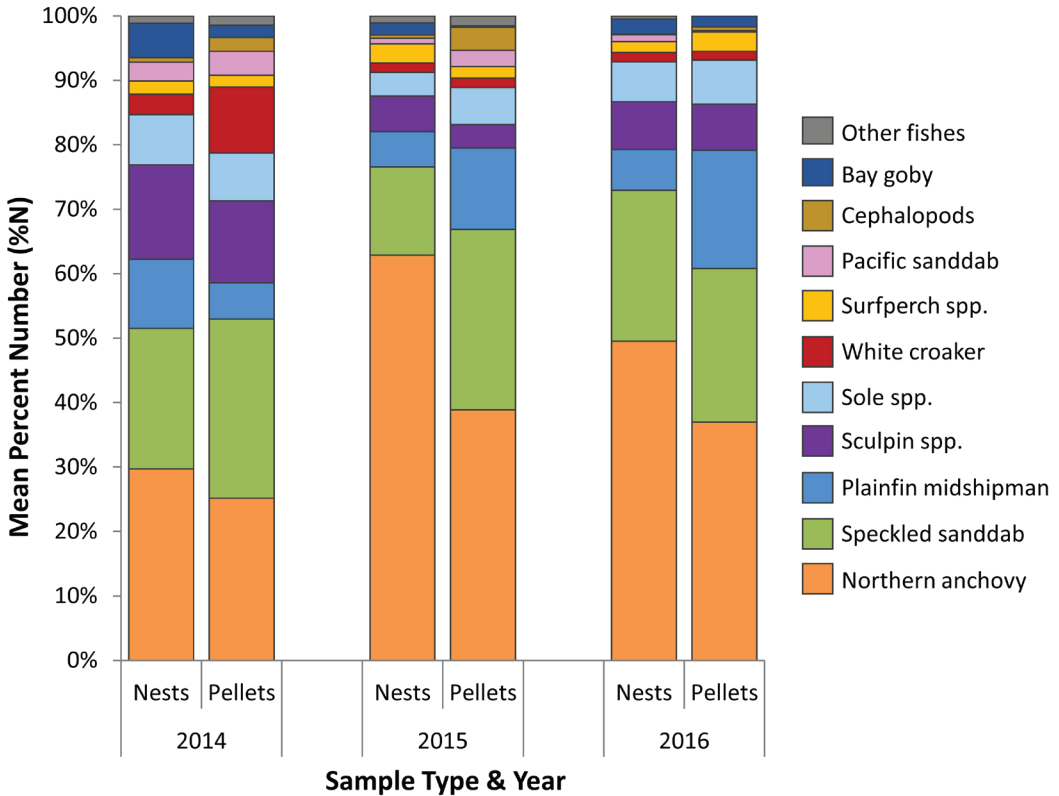


Figure 3. Breeding Brandt's Cormorant (*Phalacrocorax penicillatus*) diet composition from pellets and nests on Alcatraz Island in San Francisco Bay, California, USA from 2014-2016, expressed as percent by number (% Number) in nest samples and pellet samples.

Cormorant diet, from the nearby but off-shore Farallon Islands, reported summer diet of Brandt's Cormorant was composed of a high proportion of juvenile rockfishes interspersed with years of dominance by anchovy and Pleuronectid flatfishes (Ainley *et al.* 1981; Elliott *et al.* 2015; Ainley *et al.* 2018). Our data revealed almost no rockfish was consumed by the Alcatraz population. Juvenile rockfish are typically found along the continental shelf edge and schooling above deep sea canyons (Chess *et al.* 1988; Santora *et al.* 2012), and so are less available near-shore.

Northern anchovy was a consistent top prey item for Brandt's Cormorants across all central California studies. At the Farallon Islands, Elliott *et al.* (2015) reported a drastic decline in anchovy consumption in the late 2010s, likely in response to the crash in the central stock of northern anchovy (Mac-

Call *et al.* 2016; Thayer *et al.* 2017). The Department of Fish and Wildlife's San Francisco Bay Study and the Interagency Ecological Program for the San Francisco Estuary (SF Bay Study) has conducted monthly bottom and midwater trawl surveys at 52 stations throughout San Francisco Bay to sample fish and invertebrate populations since 1980, which revealed higher annual mean values of anchovy abundance in the 2010s (California Department of Fish and Wildlife [CDFW] 2018). This finding, along with high proportion of anchovy we observed in Alcatraz cormorant diet, suggests that despite the coastal stock crash, anchovy populations within San Francisco Bay remained intact.

Cormorant nests in our study had both a greater diversity of prey and different amounts of individual prey species than did pellet samples. Significant differences in the proportions of major prey taxa between di-

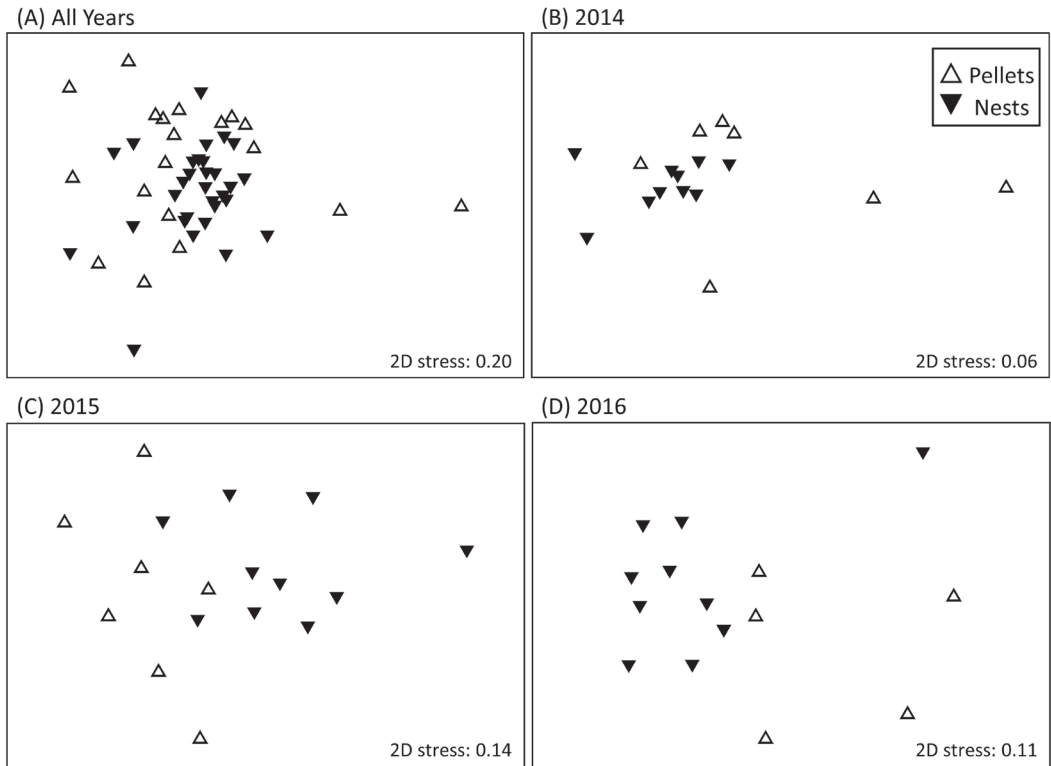


Figure 4. Multidimensional Scaling plots of Brandt's Cormorant (*Phalacrocorax penicillatus*) diet on Alcatraz Island, San Francisco Bay, California, USA. Panel (A) depicts nest samples (filled triangles) relative to pellet samples (empty triangles) in all years (2014-2016). Panels (B-D) depict nest samples and pellet samples within each separate year. Stress values less than 0.10 were regarded as being unlikely to result in misinterpretation of the data (Clarke & Warwick 2001) so the stress in these plots suggests that additional dimensionality may better represent the spread of data points.

ets constructed from nests and pellets may indicate shifts in foraging behavior over the course of a breeding season, as also suggested by a study of Alcatraz cormorant foraging behavior in the early 2000s (Saenz and Thayer, unpubl. data). We found higher amounts of northern anchovy in nest samples than in pellet samples and the opposite trend for speckled sanddab and plainfin midshipman.

Through the SF Bay Study time series, seasonal trends of fishes are apparent (CDFW 2018). Anchovy move into San Francisco Bay in late spring and then return to the Pacific Ocean in fall. Brandt's Cormorants arriving to Alcatraz and incubating clutches in spring/summer can thus take advantage of the incoming anchovy when they are able to remain away from the colony for longer periods, to seek out scattered patches of this epipelagic, schooling species. During summer, plainfin midshipman, speckled sanddab,

and English sole all migrate into the San Francisco Bay to spawn, and the SF Bay Study has found that abundances of these species have been higher in the central Bay in the recent decade than in the previous three decades (CDFW 2018). These demersal species are spatio-temporally more predictable on a local scale than schooling anchovy, and available in mid to late cormorant breeding season when cormorants need to provision not only themselves but also a brood of chicks. Our samples indicate that while anchovy are still consumed throughout breeding season, cormorants are consuming more midshipman and speckled sanddab later in the season as they become abundant.

In terms of minor prey items, nest samples yielded a more diverse diet with greater amounts of rarely consumed fishes than did pellet samples. Supplemental prey species may serve to fill gaps in diet when primary

prey species are not available and thus provide stability, similar to the idea of the portfolio effect (Schindler *et al.* 2010). Such information may provide insight into cormorant resilience as climate changes, in the face of shifting diet and foraging strategies.

Characterization of diet throughout the entire breeding period is important to understand changes in reproductive performance (Harding *et al.* 2007), particularly failures during the incubation and early chick-rearing stages. Traditional methods of examining cormorant diet using regurgitated pellets collected at the end of breeding season has been widely used (Ainley *et al.* 1981; Sydeman *et al.* 1997; Elliott *et al.* 2015). Given that individual pellets only represent one 24-hour feeding period (Duffy and Laurenson 1983), where pellets do not accumulate this method likely provides information from a short time span, yet researchers have assumed it represents diet of the entire six-seven month breeding season. This may explain why connections between cormorant diet and reproductive success that have been suggested to date have not been strong (Elliott *et al.* 2015). Until now there has been no method developed in which diet on a longer temporal scale can be sampled during the summer without causing great disturbance to nesting colonies. Cormorant nests, however, are structures that two adults inhabit for the first four-five months of breeding season (Boekelheide *et al.* 1990) and thus could act as repositories for a large number of pellets and prey regurgitations. We have demonstrated that not only do cormorant nests indeed contain large amounts of prey hard parts and reveal a greater diversity of prey, but they can also provide information that can be significantly different from that obtained using pellet samples. Therefore, we believe nest samples are a viable method for determining cormorant diet during breeding season which can either be used in conjunction with pellet samples or can be used instead of traditional methods.

For almost a century, scientists have been investigating the diet of seabirds and using the findings to indicate health of marine ecosystems. We have provided evidence

that nest sampling is a viable new method for determining cormorant diet. And while regular production of regurgitated pellets is limited to only a few seabird groups, many seabirds bring back whole prey or regurgitate prey items that may leave hard parts within nests, thus this method could be investigated for other species. Not only is nest collection a non-invasive sampling approach that contains a large amount of prey material, but nests also provide researchers with information pertaining to the early phases of breeding season, a time period that may not always be easy to sample. Furthermore, when nest samples are combined with other conventional methods (e.g., pellets, chick regurgitations, stable isotopes, etc.) results could lead to a more accurate and complete understanding of breeding season diet and its role in influencing reproductive success.

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LITERATURE CITED

- Ainley, D. G., D. W. Anderson and P. R. Kelly. 1981. Feeding ecology of marine cormorants in southwestern North America. *Condor* 83: 120-131.
- Ainley, D. G., J. A. Santora, P. J. Capitolo, J. C. Field, J. N. Beck, R. D. Carle, E. Donnelly-Grennan, G. J. McChesney, M. Elliot, R. W. Bradley, K. Lindquist, P. Nelson, J. Roletto, R. Warzybok, M. Hester and J. Jahncke. 2018. Ecosystem-based management affecting Brandt's Cormorant resources and populations in the central California Current region. *Biological Conservation* 217: 407-418.
- Ashmole, N. P. 1971. Sea Bird Ecology and the Marine Environment. Pages 224-271 *in* Avian Biology Volume I (D. S. Farner and J. R. King, Eds.) Academic Press, New York, New York.
- Barrett, R. T., K. C. J. Camphuysen, T. Anker-Nilssen, J. W. Chardine, R. W. Furness, S. Garthe, O. Hüppop,

- M. F. Leopold, W. A. Montevecchi and R. R. Veit. 2007. Diet studies of seabird: a review and recommendations. *ICES Journal of Marine Science* 64: 1675-1691.
- Boekelheide, R. J., D. G. Ainley, S. H. Morrel and T. J. Lewis. 1990. Brandt's Cormorant. Pages 163-195 in *Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling system community* (D. G. Ainley and R. J. Boekelheide, Eds.) Stanford University Press, Palo Alto, California.
- Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261-271.
- California Department of Fish and Wildlife (CDFW). 2018. San Francisco Bay Study. <http://www.dfg.ca.gov/delta/projects.asp?ProjectID=BAYSTUDY>, accessed 1 November 2018.
- Capitolo, P. J., G. J. McChesney, H. R. Carter, M. W. Parker, L. E. Eigner and R. T. Golightly. 2014. Changes in breeding population sizes of Brandt's Cormorants *Phalacrocorax penicillatus* in the Gulf of the Farallones, California 1979-2006. *Marine Ornithology* 42: 35-48.
- Carney, K. M. and W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68-79.
- Chess, J. R., S. E. Smith and P. C. Fischer. 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. *CalCOFI Report* 39: 129-136.
- Clarke, K. R. and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, Second edition. PRIMER-E, Plymouth.
- Collett, D. 2002. Modelling binary data. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131: 537-550.
- Cortez, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 726-738.
- Daly, E. A., R. D. Brodeur and L. A. Weitkamp. 2009. Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? *Transactions of the American Fisheries Society* 138: 1420-1438.
- Donnelly-Greenan, E. L., J. T. Harvey, H. M. Nevins, M. M. Hester and W. A. Walker. 2014. Prey and plastic ingestion of Pacific Northern Fulmars (*Fulmarus glacialis rogersii*) from Monterey Bay, California. *Marine Pollution Bulletin* 85: 214-224.
- Duffy, D. C. and L. J. B. Laursen. 1983. Pellets of Cape Cormorants as indicators of diet. *Condor* 85: 305-307.
- Elliot, M. L., R. W. Bradley, D. P. Robinette and J. Jahncke. 2015. Changes in forage fish community indicated by the diet of the Brandt's cormorant (*Phalacrocorax penicillatus*) in the central California Current. *Journal of Marine Systems* 146: 50-58.
- Ferry, L. A. and G. M. Cailliet. 1996. Sample size and data analysis: are we characterizing and comparing diet properly? Pages 71-80 in *Gutshop '96* (D. MacKinlay and K. Shearer, Eds.). Feeding ecology and nutrition on fish symposium proceedings. San Francisco State University, San Francisco, California.
- Furness, R. W. and C. J. Camphuysen. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* 54: 726-737.
- Gamboa, D. A. 1991. Otolith Size versus Weight and Body-length Relationships for Eleven Fish Species of Baja California, Mexico. *Fisheries Bulletin* 89: 701-706.
- Grémillet, D., G. Argentin, B. Schulte and B. M. Culik. 1998. Flexible foraging techniques in breeding cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? *Ibis* 140: 113-119.
- Harding, A. M. A., J. F. Piatt and J. A. Schmutz. 2007. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269-274.
- Harris, M. P. 1965. The food of some *Larus* gulls. *Ibis* 107: 43-53.
- Harvey, J. T., T. R. Loughlin, M. A. Perez and D. S. Oxman. 2000. Relationship between fish size and otolith length for 63 species of fishes from the eastern North Pacific Ocean. NOAA Technical Report NMFS 150.
- Ito, M., H. Minami, Y. Tanaka and Y. Watanuki. 2009. Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird. *Marine Ecology Progress Series* 393: 273-284.
- Karpouzi, W., R. Watson and D. Pauly. 2007. Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series* 343: 87-99.
- Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. Alaska Fisheries Science Center /National Marine Fisheries Service Report.
- Larson, K. and D. Craig. 2006. Digiscoping vouchers for diet studies in bill-load holding birds. *Waterbirds* 29: 198-202.
- Lowry, M. S. 2011. Photographic catalog of California marine fish otoliths: Prey of California sea lions (*Zalophus californianus*). NOAA-TM-NMFS-SWFSC-483.
- MacCall, A. D., W. J. Sydeman, P. C. Davison and J. A. Thayer. 2016. Recent collapse of northern anchovy biomass off California. *Fisheries Research* 175: 87-94.
- Mille, T., K. Mahe, M. C. Villanueva, H. De Pontual and B. Ernande. 2015. Sagittal otolith morphogenesis asymmetry in marine fishes. *Journal of Fish Biology* 87: 646-663.
- Montevecchi, W. A. 1993. Birds as indicators of change in marine prey stocks. Pages 217-266 in *Birds as*

- monitors of environmental change (R. W. Furness and D. J. Greenwood, Eds.). Chapman and Hall, London.
- Murphy, R. C. 1936. *Oceanic Birds of South America* Volumes I and II. Macmillan and American Museum of Natural History, New York, New York.
- Naves, L. C. and C. M. Vooren. 2006. Diet of Black Skimmers in Southern Brazil. *Waterbirds* 29: 335-344.
- Petry, M. V., L. Krüger, W. S. de Silva Fronseca, J. Brummelhaus and R. de Cruz Piuco. 2009. Diet and ingestion of synthetics by Cory's Shearwater *Calonectris diomedea* off southern Brazil. *Journal of Ornithology* 150: 601-606.
- Phillips, E. M. 2005. Results of a captive feeding study with the Pacific harbor seal (*Phoca vitulina richardii*): Implications for scat analysis. M. S. Thesis. San Francisco State University, San Francisco, California.
- Piatt, J. F., W. J. Sydeman and F. Wiese. 2007. Introduction: a modern role for seabirds as indicators. *Marine Ecology Progress Series* 352: 199-204.
- Robertson, G. S., M. Bolton and P. Monaghan. 2016. Influence of diet and foraging strategy on reproductive success in two morphologically similar sympatric seabirds. *Bird Study* 63: 319-329.
- Robinson, H., J. Thayer, W. Merkle and V. Seher. 2018a. Breeding Ecology of Brandt's Cormorant and Western Gulls on Alcatraz Island, 2018. Unpublished report, U. S. Department of the Interior, National Park Service, Golden Gate National Recreation Area, San Francisco, California.
- Robinson, H., J. Thayer, W. J. Sydeman and M. Weise. 2018b. Changes in California sea lion diet during a period of substantial climate variability. *Marine Biology* 165: 169.
- Rodriguez-Romero, J., D. S. Palacios-Salgado, J. Lopez-Martinez, S. Hernandez Vazquez, and J. I. Velazquez-Abunader. 2009. The length-weight relationship parameters of demersal fish species off the western coast of Baja California Sur, Mexico. *Journal of Applied Ichthyology* 25: 114-116.
- Saenz, B. L., J. A. Thayer, W. J. Sydeman and D. A. Hatch. 2006. An urban success story: breeding seabirds on Alcatraz Island, California, 1990-2002. *Marine Ornithology* 34: 43-49.
- Santora, J. A., J. C. Field, I. D. Schroeder, K. M. Sakuma, B. K. Wells and W. J. Sydeman. 2012. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Progress in Oceanography* 106: 154-174.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465: 609-612.
- Sweeny, J. M. 2008. Variables affecting hard part recovery from scats and spew of California sea lions (*Zalophus californianus*). M. S. Thesis, San Francisco State University, San Francisco, California.
- Sydeman, W. J., K. A. Hobson, P. Pyle and E. B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. *Condor* 99: 327-336.
- Thayer, J. A., J. C. Field and W. Sydeman. 2014. Changes in California Chinook salmon diet over the past 50 years in relation to marine climate: Relevance to the recent population crash. *Marine Ecology Progress Series* 498: 249-261.
- Thayer, J. A., A. D. MacCall, W. J. Sydeman and P. C. Davidson. 2017. California anchovy population remains low, 2012-16. *CalCOFI Report* 58: 69-76.
- Warton, D. I. and F. K. C. Hui. 2011. The arcsine and asinine: the analysis of proportions in ecology. *Ecology* 92: 3-10.
- Webb, L. A. and J. T. Harvey. 2015. Diet of a piscivorous seabird reveals spatiotemporal variation in abundance of forage fishes in the Monterey Bay region. *Journal of Marine Systems* 146: 59-71.
- Yakich, J. D. 2005. A dietary analysis of Brandt's Cormorants (*Phalacrocorax penicillatus*) breeding in central San Francisco Bay. M.S. thesis, San Francisco State University, San Francisco, California.
- Zijlstra, M. and M. R. Van Eerden. 1995. Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: trials with captive birds. *Ardea* 83: 123-131.