CHARACTERIZING THE DIET OF A THREATENED SEABIRD, THE MARBLED MURRELET *BRACHYRAMPHUS MARMORATUS*, USING HIGH-THROUGHPUT SEQUENCING

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ABSTRACT

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Understanding prey consumption patterns is critical to understanding the ways in which seabirds cope with a changing ocean. However, characterizing the dietary habitats of seabirds can be challenging. In this study, we investigated the diet of the Marbled Murrelet *Brachyramphus marmoratus* population that lives in waters off California, Oregon, and Washington, USA, using fecal DNA, custom metabarcoding, and high-throughput sequencing. Murrelets were captured at sea by dip-netting at night. Across this region, murrelets consumed highly diverse prey types including 17 fish species and 10 invertebrate species, in accord with previous work indicating the species' forage on a wide range of prey. Pacific Herring *Clupea pallasii* was the most common prey in Washington and Oregon (frequency of occurrence = 0.84 and 0.69, respectively), replaced by Northern Anchovy *Engraulis mordax* in California (frequency of occurrence = 0.77). In Oregon, where our sample size was sufficient, diet composition differed between the 2017 and 2018 breeding seasons, with an apparent decline in the proportional consumption of energy-dense prey. Common and energy-dense prey were consumed in equal proportions by males and females, perhaps because of foraging in the same habitat. Diet did not vary between breeders and non-breeders. Our study offers the first detailed report on the diet of adult Marbled Murrelets in waters where they are listed as Threatened by the US federal government. This indicates that managing fisheries and conserving spawning habitat for high-occurrence prey species could benefit murrelet populations.

Key words: metabarcoding, fecal DNA, Illumina MiSeq, climate change, prey

INTRODUCTION

Ocean productivity shapes the population structure and dynamics of marine predators via bottom-up processes and, conversely, marine predators can influence the structure of prey communities via top-down effects (Frederiksen *et al.* 2006, Horswill *et al.* 2016, Lynam *et al.* 2017). Detailing these contrary interactions is increasingly important for understanding seabird population change in the era of ocean warming, overfishing, habitat degradation, pollution, and other factors (Halpern *et al.* 2015, O'Hara *et al.* 2021). A critical step in the process involves characterizing food consumption patterns within the available food web. Seabirds, however, can pose special challenges to the study of food habits because they are difficult to sample and they reside in an environment 'foreign' to human researchers (Barrett *et al.* 2007). Visual observation can provide some insights into prey consumed at sea, but prey species can be difficult to identify from a distance and seabirds are known to consume some prey underwater (Barrett *et al.* 2007).

The recent development and refinement of high-throughput sequencing ("metabarcoding") approaches for screening prey DNA contained within fecal or stomach samples have substantially enhanced the ability to characterize seabird diet (Alonso *et al.* 2014, McInnes *et al.* 2017, Young *et al.* 2020). Diet metabarcoding relies on obtaining prey DNA extracted from fecal material, from nest fecal sacs, or through regurgitation of stomach contents. Metabarcoding involves the development and optimization of both a series of taxa-specific primers (e.g., fish or invertebrates) as well as libraries of prey DNA through polymerase chain reaction (PCR) amplification and individual barcoding, followed by high-throughput sequencing and comparison of sequences to reference databases. Accordingly, metabarcoding can yield information regarding what prey are in the diet of marine predators when other approaches are impractical, provided that fecal material can be obtained. However, substantial investments are typically needed to develop new or optimize existing primers to ensure that the specific prey species consumed have a high likelihood of being detected.

Here, we characterize the diet of a seabird designated as Threatened by the US federal government (Stein & Miller 1992), the Marbled Murrelet *Brachyramphus marmoratus* (hereafter, "murrelets"), by analyzing fecal samples from individuals captured at sea in the California Current portion of its range (Washington, Oregon, and California, USA) using a custom metabarcoding approach. Murrelets are unique among seabirds in that they typically nest at low densities on treetops in coastal-mature and old-growth forests. Therefore, they are somewhat unavailable for the direct observation that is possible for many other alcids. During the breeding season, murrelets often commute tens of kilometers inland from nearshore waters (*ca*. April to July; Peery *et al.* 2007) to incubate a single egg and deliver prey, carried in its bill, to its nestling (Hamer & Nelson 1995). Declines in murrelet populations over the past century are mostly due to loss of old-growth forest nesting habitat (Raphael *et al.* 2006). On the other hand, murrelet populations are known to fluctuate in response to ocean conditions and prey availability (Peery *et al.* 2004, Becker & Beissinger 2006, Becker *et al.* 2007). Therefore, the species' interaction with ocean resources also deserves attention towards devising management options. More comprehensive information on diet and foraging would greatly facilitate the development of marine protected areas, fisheries management strategies, and other conservation measures for this imperiled seabird (USFWS 2012).

As noted, assessing prey consumption is challenging even for nestlings, given that this species nests secretively high in tall trees. Indeed, food consumption studies for murrelets are largely anecdotal (Burkett 1995, Henkel & Harvey 2006) or based on stable isotopes (Becker & Beissinger 2006, Becker *et al.* 2007), with little information on the specific prey species consumed, the proportion consumed, or how prey consumption varies over time and space. In this study, we provide the first detailed diet analyses of adult Marbled Murrelets in Oregon, comparing results with prey consumption of adults in the non-breeding seasons in California and Washington. We also assessed variation in murrelet diet across years, between sexes, and between breeders and non-breeders, as allowed by sampling constraints.

METHODS

Sample collection

We captured Marbled Murrelets for fecal sampling at sea overnight between 20h00 and 05h00 from small vessels using the night-lighting/dip-netting technique (Whitworth *et al.* 1997). Sampling was conducted in Año Nuevo Bay in central California (hereafter "California"); near Newport, Oregon ("Oregon"); and in the Strait of Juan de Fuca, Washington ("Washington"). All murrelets in Oregon were sampled during the 2017 and 2018 breeding seasons as part of ongoing radio-telemetry studies seeking to locate nest sites (Northrup *et al.* 2018). However, permitting restrictions precluded sampling murrelets during the breeding season in the small California population (Peery *et al.* 2006) and the rapidly declining Washington populations (McIver *et al.* 2021). Accordingly, we limited sampling in these areas to pre- and post-breeding seasons in California (2016 and 2017) and Washington (2018 and 2019); during these periods, murrelets can be more dispersed and even more challenging to capture (Peery *et al.* 2008). Sampling occurred in different years and seasons among the three locations for logistical reasons. These constraints resulted in smaller sample sizes in Washington and California compared to Oregon. The more robust

sampling in Oregon provided a valuable opportunity to leverage novel metabarcoding approaches to better understand how murrelet diets vary among years, by breeding status, and by sex.

Upon capture, murrelets often defecate while being handled. When they did so, we collected fecal material using a sterile disposable transfer pipette then transferred the sample to a sterile 50-mL conical tube containing ~25 mL of 100% ethanol. We also swabbed the cloaca of some individuals that did not defecate during handling. In total, we collected 196 samples: 171 from Oregon in May 2016 (*n* = 11), May 2017 (*n* = 72, including 13 cloacal swabs), and May 2018 (*n* = 88, including 11 cloacal swabs) during the breeding season; 18 from California in September 2016 (*n* = 7) and August 2017 (*n* = 11) during the post-breeding season; and seven from Washington in March 2018 (*n* = 2), November 2018 (*n* = 3), and October 2019 (*n* = 2) during the pre- and post-breeding seasons combined. Samples were stored at −20 °C until preparation for DNA extraction.

DNA extraction, primer optimization, and library building

To prevent ethanol carry-over during DNA extraction, we removed the fecal samples from cold storage and centrifuged them at 12 000 rpm for five minutes. We then removed most of the ethanol from the tubes via pipette and inserted filter-paper containing silica beads into the tube to finish drying the sample. The samples were then transferred back to −20°C to ensure preservation of the DNA sample prior to extraction. After drying, we extracted DNA from the fecal material using QIAamp DNA Stool Mini Kits (51504, Qiagen) for all 2016 and 2017 fecal samples, as well as 35 of the 2018 fecal samples from Oregon, all following the manufacturer's protocol. Due to discontinuation of the QIAamp DNA Stool Mini Kit, we extracted 42 of the 2018 fecal samples from Oregon using the Qiagen Fast DNA Stool Mini Kit (51604, Qiagen) with the following change to the manufacturer's protocol: after adding the InhibitEX buffer, we incubated the samples at 30 °C with rocking for one hour. For all cloacal swabs, we extracted genomic DNA using a QIAamp DNA Investigator Kit (56504, Qiagen) following the manufacturer's protocol for a buccal swab extraction. We quantified DNA concentration for all extractions using a qubit fluorometer and high-sensitivity assay.

The mitochondrial genes, the large subunit ribosomal rRNA (16S), and the cytochrome *c* oxidase I (COI) have been successfully used in several previous genetic-based dietary analyses of marine predators, including seabirds (Deagle *et al.* 2009, Bowser *et al.* 2013). Similarly, universal 16S and COI primers have already been developed for the fish species that likely constitute murrelet prey in California (Deagle *et al.* 2007, Bowser *et al.* 2013). To optimize and develop primers, we first PCR-amplified four fecal DNA extractions using universal primers designed to amplify multiple prey species and short amplicon fragments (~130–300 base pairs) from Tollit *et al.* (2009) and Deagle *et al.* (2007). After PCR amplification, we cloned all positively amplified PCR products (*n* = 4 and *n* = 3 for 16S and COI, respectively). We then selected eight colonies from each plate and PCR-amplified them using standard vector primers. For pair-end sequencing, we chose six positive PCR reactions that contained a single amplified band for each gene per individual genomic DNA sample. We visualized the sequence chromatograms for 96 sequences, and we manually aligned the forward and reverse sequences in MEGA 7.0.26 (Kumar *et al.* 2016). After alignment, we used BLAST (Altschul *et al.* 1990) to search the sequences to

determine identity. Since the Deagle *et al.* (2007) 16S primer for fish was the only primer to successfully amplify prey, we created new primers to amplify cephalopods, malacostracans (shrimp, krill, prawn, crab), and copepods. See Table A1 (in the Appendix, available online) for primer creation details.

Details of prey amplification and library building can be found in the Appendix. Briefly, we amplified a fragment of the 16S gene in prey DNA using single-primer PCR reactions for four primer sets: 16S (fish, Deagle *et al.* 2007), SQ16S (cephalopods), Cala16S (copepods and amphipods), and Mala16S (malacostracans). To determine if fecal DNA extractions were contaminated by ocean water from birds being captured at sea, we extracted DNA from ocean water samples collected from California and Oregon by scooping 50 mL of surface water into a sterile 50-mL conical tube. Ocean water samples were stored at −20 °C until DNA extraction (see Appendix). After cleaning and barcoding all amplified PCR products, three libraries each containing 79 samples, three ocean water controls, three duplicates, two positive controls, and one negative control (*n* = 88) per library were then sequenced on Illumina MiSeq 2 × 250 nano runs with one library per lane by the University of Wisconsin-Madison Biotechnology Center.

Data analysis

We used the QIIME2 microbiome bioinformatics platform (Bolyen *et al.* 2019) for all filtering and processing of raw sequence data— see Appendix for detailed methods on data filtering. To determine if we had adequate sampling units for estimating diversity statistics and species richness for our sampling locations, we used the "iNext" package (Hsieh *et al.* 2020) implemented in R, version 3.6.2, on a presence-absence dataset. We estimated diversity for Oregon as a single population in addition to estimating for Oregon 2017 samples and Oregon 2018 samples separately, as these were the only sampling locations and times in which we had sufficient sample units for estimating diversity indices (see Fig. A1 in Appendix). Species richness was not included in the analysis because the sample accumulation curve did not flatten (Figs. A1 and A2). We then used the R package "vegan" (Oksanen *et al.* 2020) for all downstream analyses. We estimated α (Shannon and Simpson diversity indices) for Oregon combining 2017 and 2018 as well as keeping the years separate.

We calculated frequency of occurrence (FOO, the percentage of murrelets in which each prey type was present) and percent of occurrence (POO, the percentage of murrelets in which each prey was present, calculated by number of samples that contained a prey item in the total of the diet). This was done for all samples, pooled across locations at the family and species levels, as well as for each location at the species level. To visualize the differences in prey consumption by sampling location and by year (2017 and 2018) for the Oregon samples, we built a plot-web using the presence-absence dataset. We conducted PERMANOVA using the *adonis2* function on a Raup-Crick dissimilarity matrix with 999 permutations to test for differences in diet composition for the Oregon 2017 and 2018 samples, brood patch score (presence-absence), and sex. Brood patch was considered to be absent if given a score of 0, 1, or 2, and present if given a score of 2A, 2.5, or 3 (Sealy 1974). We removed two samples from the sex and brood patch PERMANOVA, as we had no metadata for these two metrics. To ascertain if sampling bias was impacting our PERMANOVA results when using the complete dataset, we also conducted all analyses on a rarified dataset,

where rarefaction was conducted using the R package "phyloseq" (McMurdie & Holmes 2013).

The influence of diet composition on seabird reproduction and survival is ultimately influenced by the abundance/availability of prey consumed, the energy expended to acquire prey, and the quality/condition of the prey; these are all variable (Bertram & Kaiser 1993, Therriault *et al.* 2009). Because our diet assessment method provides FOO data, we cannot assess individual prey quality, number consumed, or size. We can, however, examine the relative energy density of species consumed between years; in other words, whether there are more energy-dense species in some years relative to other years. To investigate changes in energy density between 2017 and 2018 in Oregon, we calculated an average energy density (kJ g⁻¹) for each prey species or prey group, depending upon available published data (Fig. A1). Energy density values for prey items were obtained by searching the literature for wet-weight energy density values and taking the average of the reported values (Fig. A1). We designated a prey item as having a high energy density based on two criteria: (1) published resources that determined a prey item to be energetically important for Marbled Murrelets based on measurements of fish obtained from nests and from adult surveys (Gutowsky *et al.* 2009, Janssen *et al.* 2011), and (2) published resources that indicated certain species maintained a high energy density regardless of size (Schrimpf *et al.* 2012). We then used the average energy density calculated for these species (i.e., Pacific Herring *Clupea pallasii*, Pacific Sand Lance *Ammodytes personatus*, Northern Anchovy *Engraulis mordax*, and Pacific Sardine *Sardinops sagax*) as a cut-off for high energy density (> 5.00 kJ g⁻¹). We classified a fish as having a medium energy density when values were between 4.00 kJ g⁻¹ and 5.00 kJ g⁻¹ and a low energy density when values were 4.00 kJ g⁻¹ or lower. We grouped all invertebrate species together because of their similar energy densities (e.g., average energy density of crustaceans = 2.71 kJ g⁻¹ [Haynes & Wigley 1969, Hunt *et al.* 2005, Glaser 2010] and of squid = 2.90 kJ g⁻¹ [van Pelt *et al.* 1997, Schrimpf *et al.* 2012]). See Table A2 for average energy density values used for consumed prey species.

Data depository

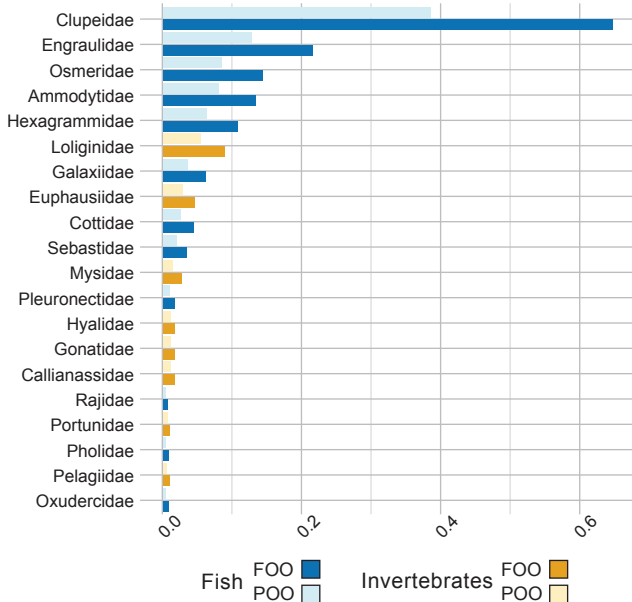Read count tables, sample metadata, and R code are available on Dryad (Fountain 2023).

RESULTS

We successfully extracted DNA from all fecal material and swabs except for one fecal sample collected from Oregon in 2018. The mean number of raw sequences per sample was 9 726 reads (min = 5 251 and max = 18 789), with a mean quality score of 27. After trimming low-quality base pairs to decrease the probability of genotyping error, the quality scores of all reads were ≥ 30 (Ewing & Green 1998). After trimming and filtering, taxonomic assignments were made for six fecal samples from California 2016, eight from California 2017, eight from Oregon 2016, 61 from Oregon 2017, 55 from Oregon 2018, and all seven samples from Washington, for a total of 145 samples. After filtering these assignments for the minimum number of read counts (15 for fish and 30 for invertebrates), four samples from California 2016, five from California 2017, six from Oregon 2016, 44 from Oregon 2017, 45 from Oregon 2018, and all seven samples from Washington remained, for a total of 111 samples for downstream analyses. The ocean water samples

were filtered from additional analyses because either they had too few reads or they lacked hits to our database. The loss of the ocean water reads from filtering indicates that contamination from an environmental source did not affect our results.

In total, we detected 17 fish species and 10 invertebrate types. When all samples across California, Oregon, and Washington were pooled, fish from the family Clupeidae had the highest FOO and POO, followed by Engraulidae (Fig. 1), with Pacific Herring and Northern Anchovy being the most frequent species detected (Fig. 2) in these two families, respectively. Fish families constituted the top five highest FOO and POO values, with squid in the family Loliginidae (Market Squid *Doryteuthis opalescens* and *Loligo* spp.) having the highest FOO and POO for invertebrates (Figs. 1, 2). Invertebrates occurred at lower FOO and POO values, with squid and krill (Euphausiidae) having the highest occurrence of the group (Fig. 1).

Fish were the major taxonomic group consumed by murrelets in each of the three locations (Fig. 3). Pacific Herring had the highest FOO and POO in Oregon and Washington; however, Northern Anchovy had the highest FOO and POO in California, followed by Pacific Sardine and Pacific Herring (Fig. 3). Pacific Sea Nettle *Chrysaora fuscescens* and Night Smelt *Spirinchus starksi* were unique to the California population, and 15 other taxa were unique to Oregon (Fig. 4). Although sample sizes were too small in California and Washington to sufficiently estimate diversity based on sample accumulation curves (Fig. A1), the sample size in Oregon was adequate (Figs. A1, A2). This indicates that any unique species in California and Washington either did not or very rarely occurred in the diet of the Oregon population. In Oregon, the Shannon and Simpson diversity indices were higher in 2018 than in 2017 (2.224 Shannon and 0.823 Simpson for 2018, 1.917 Shannon and 0.766 Simpson for 2017), with unique taxon appearing in their diet in each year (Fig. 4). However, the frequency of commonly consumed prey was similar between years in Oregon.

PERMANOVA suggested the diet composition differed significantly between 2017 and 2018 in Oregon ($P = 0.002$, Table 1). This difference apparently reflected a shift towards less energy-dense prey, with a higher proportion of invertebrates and low-energy-density fish in 2018 (Fig. 5). Based on PERMANOVA, males and females in Oregon did not consume significantly different prey ($P = 0.055$; Table 1). The presence of rare prey (i.e., prey species occurring in only one fecal sample) drove the differences between males and females. Individuals with and without brood patches did not consume significantly different prey ($P = 0.153$) based on PERMANOVA (Table 1).

DISCUSSION

Our study provides the first detailed examination of the prey consumed by Marbled Murrelets in Oregon during the breeding season, as well as similar information in California and Washington during the non-breeding season. Murrelets consumed a range of prey, with 17 fish and 10 invertebrate types detected, which more than likely reflects availability within the species' capability (long, thin bill favoring similarly shaped prey). Such prey lend themselves to be carried by parents, in their bill, to their offspring. Pacific Herring had the highest FOO in Oregon, in Washington, and for all samples combined. In California, Northern Anchovy and Pacific Sardine had the highest FOO, which supports stable isotope results (Becker *et al.* 2007). Collectively, these results indicate that species in the order Clupeiformes serve as an important food resource for murrelets in all three sampling locations. Given the sensitivity of PCR and high-throughput sequencing, some invertebrates that we detected in murrelet fecal material could have been the result of secondary predation (e.g., Bowser *et al.* 2013). However, previous observational studies and morphological analyses of
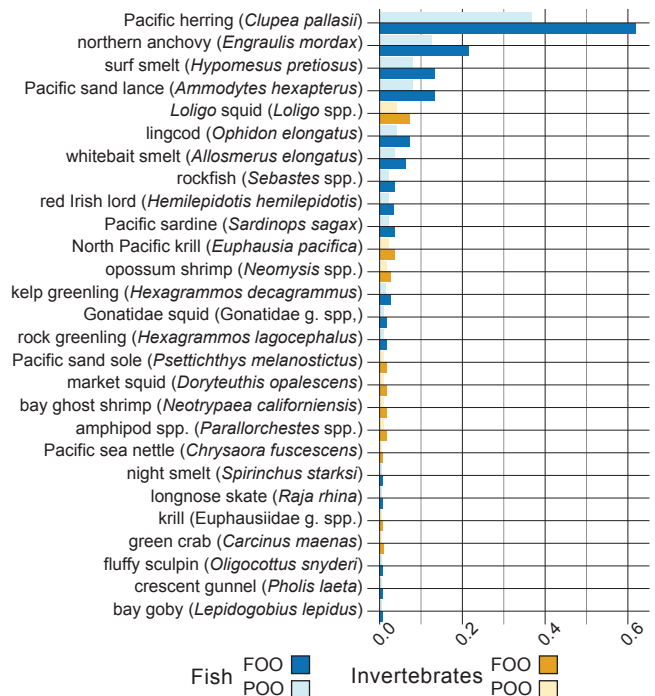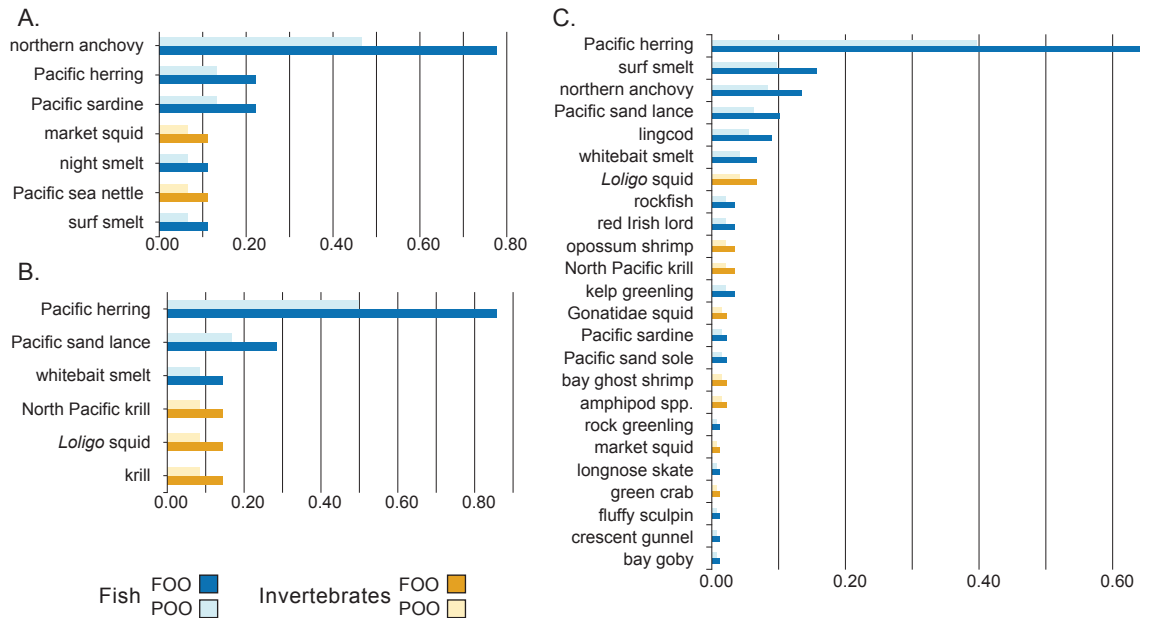

Fig. 1. Calculated frequency of occurrence (FOO) and percent of occurrence (POO) at the family level for prey items of Marbled Murrelet *Brachyramphus marmoratus* in the western USA for all sampling areas combined (California, Oregon, Washington).


Fig. 2. Calculated frequency of occurrence (FOO) and percent of occurrence (POO) at the species level for prey items of Marbled Murrelet *Brachyramphus marmoratus* in the western USA for all sampling areas combined (California, Oregon, Washington).

Fig. 3. Calculated frequency of occurrence (FOO) and percent of occurrence (POO) at the species level for prey items of Marbled Murrelet *Brachyramphus marmoratus* in the western USA off (A) California (post-breeding), (B) Washington (post-breeding), and (C) Oregon (breeding season).
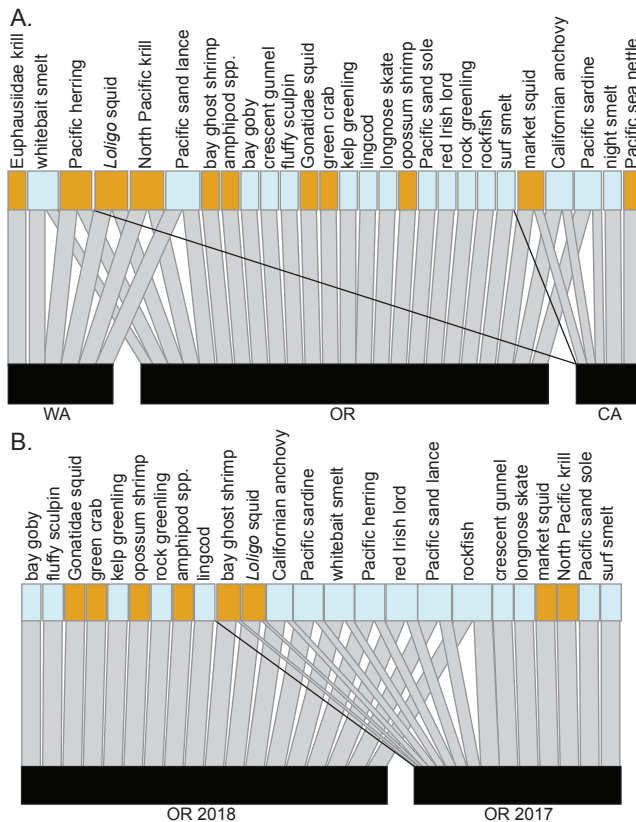
Fig. 4. Plot-webs showing the species consumed (top boxes) by Marbled Murrelet *Brachyramphus marmoratus* off the west coast of the USA for (A) each sampling location across all years (bottom boxes; WA is Washington, CA is California) and (B) the Oregon (OR) sampling location in 2017 and 2018. The line and box width represent the frequency of occurrence for a consumed species, with wider boxes or lines representing a higher frequency of occurrence. Blue boxes denote fish and orange boxes are invertebrates.

stomach contents have found murrelets capturing and consuming euphausiids, mysids, and amphipods (Sealy 1975a, 1975b; Sanger 1987; Vermeer 1992; Burkett 1995), indicating that invertebrates can constitute important murrelet prey.

While we did not directly compare Marbled Murrelet diets among the three sampling regions because of differences in the seasonality and years of sampling, the qualitative geographic differences in diet we observed are not surprising, given that our sampling areas were separated by approximately 1 250 km. Potential clinal changes in diet indicated by our data (i.e., species composition was most similar between California and Oregon and between Oregon and Washington, with almost no dietary overlap between California and Washington) are supported by previous ecological studies (e.g., Sealy 1975a, Burkett 1995, Becker *et al.* 2007, Pontius & Kirchhoff 2009). Although all sampling sites were located within the coastal California Current region, the most northerly area in Washington occurs at the southern edge of the Eastern Coastal Transition Zone, which shares physical characteristics with both the Gulf of Alaska and the California Current (McGowan *et al.* 1998). The increase in FOO that we observed for Pacific Sand Lance from south to north has been described for another alcid, the Rhinoceros Auklet *Cerorhinca monocerata* (Thayer *et al.* 2008). In accord, Marbled Murrelet diet studies further north in British Columbia and Alaska have found Pacific Sand Lance to be an important, if not dominant, prey item during the breeding season (e.g., Sealy 1975a, Carter 1984, Pontius & Kirchhoff 2009). Apparent differences in diet across space may also be driven by changes in the seasonal availability of important prey species. Again, using the Pacific Sand Lance as an example, this prey species is largely unavailable during winter when they are inactive or in hibernation while buried in substrates (Robards *et al.* 1999). As a result, we would expect them to be a more important murrelet food source during the breeding season. This single fish prey example illustrates the importance of considering changes in prey availability across their range and between seasons when developing range-wide conservation actions that consider marine issues.

TABLE 1

PERMANOVA using Raup-Crick dissimilarity matrix and 999 permutations comparing Marbled Murrelet *Brachyramphus marmoratus* diet composition for Oregon, USA across years (2017 and 2018), between sexes, and between brood patch scores

Variable (*n*)	Sum Sqs	*F* statistic	R^2	*P* value
Year: 2017 (44) versus 2018 (45)	1.425	4.871	0.051	0.002*
Sex: male (43) versus female (44)	1.152	1.987	0.046	0.055
Brood patch: present (57) versus absent (30)	0.580	1.968	0.023	0.085

* significant *P* value based on $\alpha = 0.05$

Marbled Murrelet diets observed in this study may have been shaped by an unprecedented heat wave ("the Blob"), which was followed by a strong El Niño off the North Pacific coast of the USA from 2014 to 2016. These events caused strong shifts in both prey abundance and size (Bond *et al.* 2015, di Lorenzo & Mantua 2016, Jacox *et al.* 2016), and water temperatures (as an indicator of ocean climate) were still above normal off the coasts of Oregon and Washington in 2017 (Morgan *et al.* 2019). An increase in Market Squid (Sakuma *et al.* 2016) and North Pacific Krill *Euphausia pacifica* populations (Morgan *et al.* 2019) relative to long-term averages were in accord with periods marked by above-average oceanic temperatures. Seemingly, these conditions led to the unexpectedly high occurrence of squid and krill in the diet of murrelets during 2017 and an even higher occurrence in 2018. We

Fig. 5. The proportions of invertebrates and energy-dense fish consumed by Marbled Murrelets *Brachyramphus marmoratus* in Oregon, USA by year (2017 *n* = 44 and 2018 *n* = 45), based on energy density (ED) values from published studies. A dietary shift to sources considered less energy-dense, such as invertebrates (i.e., squid and krill), increases by year.

also found evidence for differences in breeding season diet between years in Oregon: 85% of the diet consisted of fish classified as having high or medium energy density in 2017 (i.e., Pacific Herring, Northern Anchovy, and Pacific Sand Lance), but this declined to 75% in 2018. This shift occurred largely because of a reduction in fish classified as medium energy density and a more diverse diet consisting of low-energy-density fish, invertebrate taxa, and rare prey items in 2018. Moreover, the decline in energy-rich foods in 2018 corresponds with the low post-larval biomass of forage fish in the spring of 2018 in the California Current (Thompson *et al.* 2018).

Changes in murrelet diet quality and quantity can have reproductive and potential survival consequences (Becker & Beissinger 2006, Becker *et al.* 2007, Betts *et al.* 2020), which, in turn, can have significant population level impacts (e.g., Jones *et al.* 2018, 2019; Piatt *et al.* 2020). In Oregon, however, murrelet nest occupancy was higher in 2018 than in 2017 (Betts *et al.* 2020) despite the shift towards medium- and low-energy-density fish and invertebrates, indicating that murrelet breeding is impacted by more than diet diversity. Perhaps the relatively consistent presence of high-energy-density fish found in the diet of murrelets in 2017 and 2018 buffered their breeding in 2018. Without direct measures of prey biomass consumed by murrelets, we could not assess the energetic consequences of this diet to Marbled Murrelets between the two years. For example, they may have consumed fish of higher energy density and of larger size in 2018 than in 2017, resulting in no net change in total calories consumed. More years of sampling would reveal the importance of these patterns.

Our sampling period within Oregon occurred over a relatively short time period, and the narrow sampling window may have resulted in the low FOO of other important prey items such as osmerid smelt. Smelt are a dominant prey item for Common Murres *Uria aalge* in central Oregon and are abundant in the nearshore habitat that is often foraged by Marbled Murrelets (Gladics *et al.* 2015, Suryan *et al.* 2017, Strong 2019); they have also been found to be an important prey item for murrelets in Alaska (Sanger 1987). However, the lack of smelt may be due to a spatial difference of where we sampled Marbled Murrelets versus other studies on species such as Common Murre.

Dietary differences between males and females during the breeding season in Oregon were not statistically significant. Previous studies of some other seabirds (e.g., Bearhop *et al.* 2006, Owen *et al.* 2013, Thalinger *et al.* 2018) found that differences between male and female diets may be explained by the fact that females producing eggs have different nutritional and energetic demands during the approximately two-week egg-producing window. However, the FOO of the primary prey (Pacific Herring) in the murrelet diet was nearly identical in Oregon breeding season males and females.
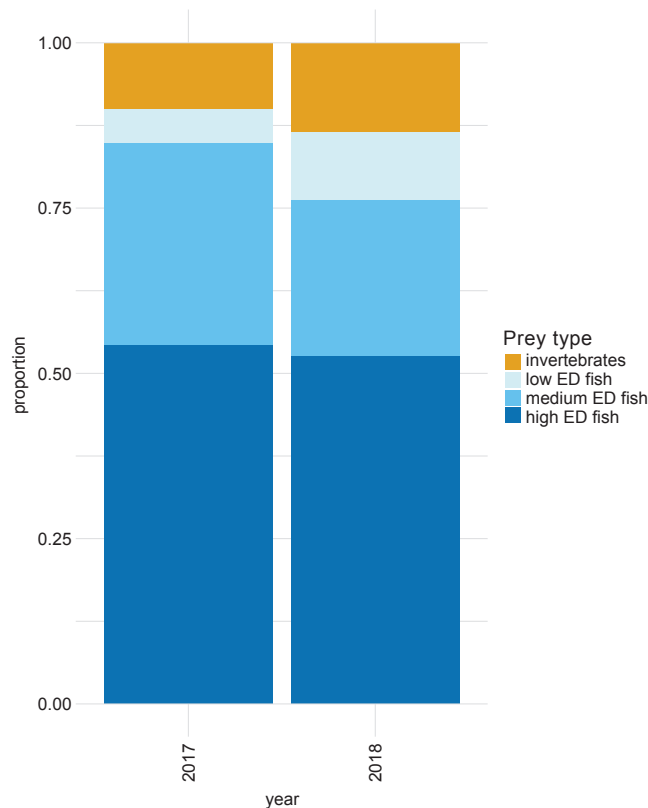
These commonalities in our study may be attributed to similar energetic demands throughout the breeding season; both males and females fly considerable distances inland (up to 70 km) to incubate eggs in 24-hour shifts and provision young during the 8- to 10-week nesting cycle. Both male and female murrelets usually carry larger, higher-quality fish to their nestlings and consume lesser-quality prey themselves (Nelson 2020). Sealy (1975a) found no difference between the diets of males and females in British Columbia, likely attributed to male and female pairs occurring together year-round—generally within a few meters of each other (Nelson 2020). Likewise, sampling a larger number of males and females may result in a statistically significant difference in prey composition, but our sample sizes were limited.

We found little difference in the diet of breeders and non-breeders in Oregon despite the very high energetic demands of nesting in murrelets (Hull *et al.* 2001). This is attributable to several non-exclusive reasons. First, even non-breeders fly inland to prospect for nests and engage in other behaviors, thus, like breeders, incurring the energetic demands of inland flights (Peery *et al.* 2004). Second, nest habitat (along with nest predators) rather than prey availability or food consumption may limit reproduction in some areas, and such factors could lead to similar diets between breeders and non-breeders (Raphael 2006). Third, brood patches may not be the best indicator of breeding status, given that individuals without well-developed brood patches at the time of sampling could develop brood patches and initiate breeding at a later date (McFarlane Tranquilla *et al.* 2003). Finally, while breeders and non-breeders may consume similar prey, breeders may capture more prey biomass overall leading to better body condition and promoting nest initiation. Indeed, prey availability has been implicated as a possible cause for episodic and chronically low reproduction in murrelets in some regions (Peery *et al.* 2004, Becker & Beissinger 2006, Becker *et al.* 2007, Beissinger & Peery 2007). Improved understanding of the mechanisms by which prey availability promotes breeding propensity in murrelets will likely be important for increasing reproductive success, given that this species appears to suffer from chronically low reproductive output in some regions (e.g., Peery *et al.* 2004, 2006, 2007).

Our results have implications for fisheries management measures intended to maintain adequate abundance of important forage fish biomass (Cury *et al.* 2011), reduce their bycatch (e.g., Hannah *et al.* 2015), and prioritize efforts to identify and protect their spawning habitat (e.g., Ostrand *et al.* 2005, Ronconi & Burger 2008, Weber & McClatchie 2010, Tomlin *et al.* 2021). For example, several murrelet prey species consumed in central California constitute important commercial fisheries in the region. Becker & Beissinger (2006) noted that the trophic level at which Marbled Murrelet exists in California waters appears to have decreased during the last several decades. The causes for this shift may be related to the forage fish in nearshore waters; however, the exact mechanisms driving the change remains obscure. California fisheries already maintain ecosystem-based managed fisheries (Ainley 2019), and we encourage continued research and monitoring of these important fish species as well as the contemporary impacts of their fisheries on murrelet populations.

Our study identified the Pacific Herring as having a high occurrence in murrelet diet. Because forage fish like the Pacific Herring act as energy conduits from lower trophic level to piscivorous predators like the Marbled Murrelet, preserving their ecosystem function is critical. Pacific Herring adult survival (Siple *et al.* 2018) and spawning biomass (Siple & Francis 2016, Thompson *et al.* 2017) has declined over the past three decades and population fluctuations are increasing, particularly in Oregon and California (Thompson *et al.* 2017). This may be related to climate variability (Sydeman *et al.* 2013), overfishing, and loss of suitable spawning habitat (Gaeckle *et al.* 2011, Simenstad *et al.* 2011, SSPHAMST 2018). Consequently, protection of water and vegetation quality in nearshore environments should benefit both herring and murrelets. Indeed, the conservation of marine predators would be strengthened with a better understanding of the distribution and abundance of forage fish, the factors influencing their populations, and the status of predator populations.

CONCLUSIONS

In summary, our genetics-based approach to screening murrelet diets provided a good picture of the food habits of Marbled Murrelets in the California Current portion of its range. Our results may provide insights that could help justify the continuation and even improvement of ecosystem-based fishery management in this system (e.g., Ainley 2019).

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