IDENTIFYING DIETARY PREFERENCES IN BREEDING PIGEON GUILLEMOT (*CEPPHUS COLUMBA*) USING DIFFERENT METHODS

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ABSTRACT—We investigated dietary preferences in Pigeon Guillemot (*Cepphus columba*) across different breeding stages in Puget Sound, WA. Observations of prey delivered to chicks were conducted during the breeding season (June–September) at 28 colonies on Whidbey Island over a 12-y period (2008–2019). We conducted stable isotope analysis on discarded eggshells collected below active Pigeon Guillemot burrows distributed across 9 colonies on Whidbey Island during the 2019 breeding season. We estimated the relative percent contribution of fish and invertebrates to the diet of pre-laying adult Pigeon Guillemot using the $\delta^{15}N$ and $\delta^{13}C$ in eggshell membrane tissue. Results of our mixing model showed that adults derive nearly 75% of their energy and nutrients from demersal fish species (rockfish, gunnel, and sculpin) during the pre-laying period, and prey-delivery observations showed that Pigeon Guillemot preferentially deliver gunnel (Pholidae) to chicks. These results demonstrate a consistent foraging pattern and dietary preference in this population over the course of 2 different stages during the breeding season.

Key words: community science, foraging, Pigeon Guillemot, Puget Sound, stable isotopes

Applying multiple tools to address ecological questions in nearshore systems has become common as researchers seek to understand the spatial and temporal complexity inherent within them (Sydeman and others 1997; Davies and others 2009). To study food webs and trophic relationships, traditional methods such as direct observations of individuals can be paired with techniques such as stable isotope analysis (Sydeman and others 1997; Davies and others 2009), which uses chemical tracers extracted from an organism's tissues as an indicator of their diet and the environment from which their nutrients were obtained. Stable isotope analysis is a complementary approach that can integrate information on prey consumed across days to years (depending on the tissue type analyzed, Pethybridge 2018), and is thus less susceptible to rare foraging events. Further, nitrogen and carbon signatures can indicate trophic position and the flow of energy, respectively (Hobson and others 1994; Fredriksen 2003; Quillfeldt and others 2008), and therefore can augment information from direct observations to provide a better understanding of the system in which individuals forage, and the nature of their interactions within that system.

Seabirds, particularly alcid (Alcidae) species, are known to exhibit flexible feeding strategies, shifting their foraging preferences and trophic position according to breeding stage (Sydeman and others 1997; Davies and others 2009). Here,

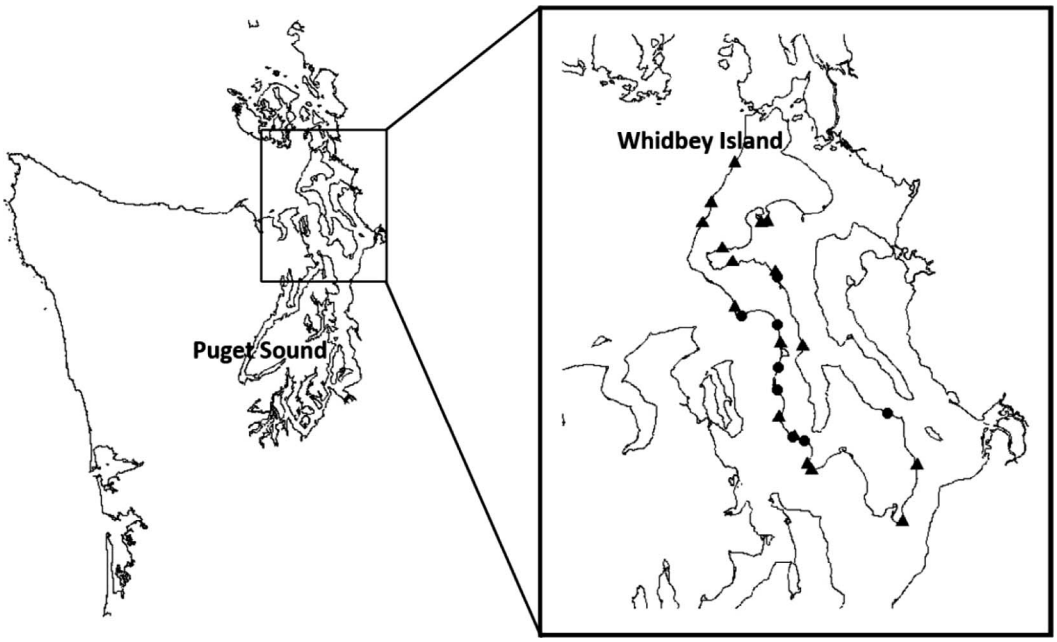

FIGURE 1. Pigeon Guillemot monitoring sites ($n = 25$) on Whidbey Island in Puget Sound, WA. Triangles denote sites where observation data was collected, circles mark sites where isotopic data were also collected (12 June and 1 September 2019).

we asked whether Pigeon Guillemot (*Cepphus columba*) in Puget Sound, Washington, demonstrated seasonal shifts in foraging related to breeding stage. Year-round residents of Puget Sound, Pigeon Guillemot are known, across their breeding range, to be both pelagic and epibenthic foragers that prey on a wide range of fish species within several kilometers of their nest sites (Ewins 1993; Litzow and others 2000; Pearson and Hamel 2013). Previous studies have shown that Pigeon Guillemot feed at a consistent trophic level throughout successive breeding stages (Davies and others 2009), whereas individual birds or entire colonies can specialize in their selection of prey or foraging sites, often in response to prey abundance (Kuletz 1983; Golet and others 2000; Litzow and others 2000; Owen and others 2019). Consequently, foraging patterns may differ among regions, and these differences can reflect local prey availability and other factors.

We used 2 approaches to investigate foraging of Pigeon Guillemot in Puget Sound across 2 breeding stages. Foraging observations by community scientists were made during the breeding season and provided information about the types of prey selected by adult Pigeon Guillemot for delivery to their chicks. Analysis of the stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) of discarded egg tissues provided information about the adult female's diet during a short period prior to breeding (Polito and others 2009; Kowalczyk and others 2014). Eggs are typically laid between mid-May and mid-June (Ewins 1993), and isotopes found in egg tissues likely reflect Pigeon Guillemot foraging near their colony sites during April to June. Chicks or adults often expel egg fragments from the burrows after hatching, which can then be found below the breeding colony, often on the beach (Frances Wood, Guillemot Research Group, pers comms). Collecting this tissue offers a non-invasive method for obtaining isotope data (Oppel and others 2009) and provides an opportunity for researchers to collaborate with community scientists and naturalists.

METHODS

Study Location

We conducted this study on Whidbey Island in Puget Sound, WA (Fig. 1) where long-term monitoring of Pigeon Guillemot colonies is

performed by a community science group, the Guillemot Research Group (GRG). The GRG has surveyed breeding colonies on Whidbey Island every summer since 2008 (see Bishop and others 2016 for full survey methods), and in 2019 they surveyed 28 breeding-colony sites, 9 of which also had eggshell tissue samples collected for stable isotope analysis (described below). All survey sites were selected based on bird activity in prior years and were located in bluffs and occasionally human-made structures around the island.

Pigeon Guillemot Prey-Delivery Observations

We used observations made over an 11-y period to characterize diet and relative prey selection among breeding Pigeon Guillemots. Observers from the GRG recorded prey delivery for 1 h wk^{-1} during the breeding seasons of 2008–2019, with 10–12 observation periods per season. Prey were classified as 1 of 3 fish taxa (gunnel, sculpin, and other) delivered by adult birds to burrows with chicks. For each site, we averaged prey taxa across all observation periods within each year. After accounting for effort (not all sites reported observations in all years), we combined the averages from all sites over the years 2008–2019 and in 2019 alone (so as to compare prey observations with the stable isotope analysis, conducted only in 2019) to represent Pigeon Guillemot diet on Whidbey Island as a whole.

Pigeon Guillemot Isotopes

Eggshell Tissue Sample Collection.—From 12 June to 1 September 2019, researchers and GRG volunteers collected 16 egg tissue samples from a total of 9 sites (Fig. 1). Volunteers collected discarded egg tissue at the base of bluffs and outside of burrows (Fig. 2) while performing their weekly surveys and placed them in whirl packs labeled with the colony site name and GPS coordinates. At the end of the breeding season, once birds had fully abandoned their colonies, researchers returned to several sites where burrows were within arm's reach to check for additional egg tissue samples. Most samples were collected from below burrows dug into sandy cliffs; however, some were collected from within the burrows themselves. Following the collection of egg tissue, samples were kept in a cool and dark environment for 2–8 wk until they could be transported to NOAA's Northwest Fisheries Science Center (NWFSC) where the specimens were held in a freezer.

FIGURE 2. Pigeon Guillemot nesting habitat: volunteer observing an adult delivering prey to a burrow.

Laboratory Analysis.—We focused our stable isotope analyses on egg membranes (exclusive of the calcareous shell tissue) and followed procedures described by Oppel and others (2009). For each egg tissue sample, we separated the membrane from the shell and recorded an initial weight. After weighing, we cleaned the membrane by spraying it with deionized water and gently wiping/scraping with a laboratory-grade cotton swab until the sample tissue was devoid of other visible material. We then placed cleaned membrane tissue into glass vials and placed those vials, cap-less, in a drying oven at 60°C for 24 h. We ground the samples into a fine powder by loading dried tissue into grinding vials with ball bearings and then placing them into a SPEX Sample Prep 5100 Mixer Mill for 3 minutes each. Fully homogenized tissue was then returned to glass vials. We weighed 0.25–0.35 mg of each membrane sample into 6 mm x 4 mm tin capsules and analyzed samples for carbon and nitrogen isotopes using a Thermo Scientific Delta V Advantage continuous-flow stable isotope-ratio mass spectrometer (IRMS).

Stable isotope abundance ratios are expressed in δ notation in parts per thousand (‰), according to the equation $\delta X = [(R_{sample}/$

$R_{standard}$) – 1], where X is ^{15}N or ^{13}C and R is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. These values were based on the V-PeeDee Belemnite standard for ^{13}C and atmospheric N_2 for ^{15}N.

As part of the NWFSC's laboratory quality-assurance plan, a method blank and a National Institute of Standards and Technology (NIST) Standard Reference Material (lipid-extracted Lake Trout muscle SRM 1946, used as an in-house interim reference material) were processed with every set of samples to monitor for instrumental analytical accuracy. All quality-assurance measures associated with isotope analyses met established laboratory criteria (Sloan and others 2019). Specifically, sample precision, as indicated by within-run standard deviation of $\delta^{15}N$ and $\delta^{13}C$ reference materials, was less than or equal to 0.17‰. In addition, 12% (2 out of 16) of our samples were analyzed in triplicate to check for consistency and measurements from the same membrane were averaged for inclusion in statistical analyses.

Statistical Analyses.—We estimated the relative percent contribution of fish and invertebrates to the diet of Pigeon Guillemot using MixSIAR, a package in R statistical software (RStudio version 1.2.5033) (R Core Team 2018). MixSIAR is a Bayesian mixing model that incorporates source variability to estimate probability distributions describing the percent contribution of each primary producer's contribution to a consumers' diet (Stock and Semmens 2016; Stock and others 2018). Data from a concurrent study analyzing stable isotopes of fish and invertebrates from around Whidbey Island were used as input to the model (full methods described in Chittaro 2020). Specifically, during the summers of 2018 and 2019 (June–October and July–August, respectively), we collected invertebrates and fish throughout Puget Sound. Specimens were placed on ice and transported to the NWFSC where they were processed for stable isotope analysis using aforementioned procedures (Gates and others 2020).

We used MixSIAR to estimate the relative proportions of rockfish (*Sebastes* spp.), sculpin (*Leptocottus* spp.), gunnel (*Apodichthys* spp., *Pholis* spp.), salmon (*Oncorhynchus tshawytscha*), shiner perch (*Cymatogaster* aggregate), shrimp (*Hippolyte* spp., *Pandalus* spp.), and crab (*Pugettia* spp., *Telmessus* spp.) in the diets of adult Pigeon Guillemot that were transferred to egg membrane. Because mixing models are sensitive to isotopic separation of sources (e.g., fish versus invertebrates), we evaluated, *a priori*, whether sources should be aggregated based on overlapping isotope values (Phillips and others 2014). To evaluate isotopic similarity among sources we used a multivariate analysis of variance (MANOVA) with $\delta^{15}N$ and $\delta^{13}C$ values as dependent variables and sources as the independent variable. If significant differences were found among sources, we then used a Tukeys post-hoc test to evaluate pairwise comparisons. Sources were pooled for MixSIAR analysis if their $\delta^{15}N$ and $\delta^{13}C$ values did not differ significantly.

For all mixing models we used an uninformative prior to give an equal probability of consumption among sources. To retrieve the posterior density estimates of source contribution, each mixing model was run with a 1,000,000 chain length, 500,000 burn-in, and a residual-error structure. Our inputs into MixSIAR included $\delta^{15}N$ and $\delta^{13}C$ values for each of our sources and consumers (Pigeon Guillemot), as well as trophic discrimination factors to correct isotope enrichment in consumer tissues. The trophic discrimination factors account for the process by which the heavy isotope (^{15}N of $^{15}N/^{14}N$ and ^{13}C of $^{13}C/^{12}C$) from the sources are preferentially incorporated into consumer tissue resulting in a bias in consumer isotopic signatures (Zanden and Rasmussen 2001). Because there are no trophic discrimination factors specific to Pigeon Guillemot egg membrane tissues in the published literature, we applied the best available factors from the literature to our consumers to correct this shift in isotope values. Specifically, we used discrimination factors derived from Common Murre (*Uria aalge)* (cellular) blood, 2.91 for $\delta^{15}N$ and 1.09 for $\delta^{13}C$ (Jenkins and others 2020), and adjusted for the fractionation difference between blood and egg albumen, –0.4 for $\delta^{15}N$ and –0.3 for $\delta^{13}C$ (Bond and Diamond 2010) to give fractionation factors of 2.51 $\delta^{15}N$ and 0.79 for $\delta^{13}C$. Estimates of the contributions of each prey to consumer diets are sensitive to trophic discrimination factors (Phillips et al. 2014). To investigate this sensitivity, we varied our trophic discrimination factors by +/- 0.5‰ for δ15N and δ13C following procedures reported by Resano-Mayor and others (2014).

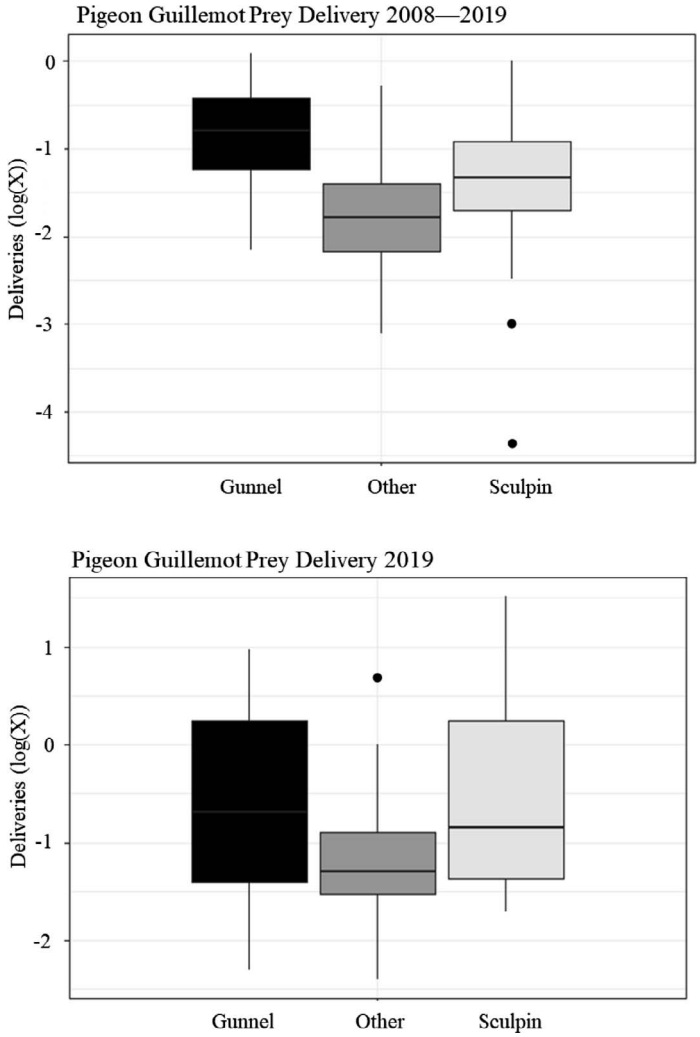

FIGURE 3. Average numbers of prey (grouped into gunnel, sculpin, or other taxa) delivered by adult Pigeon Guillemot to their chicks, across all survey years from 2008 to 2019 (top, $n = 7034$ observations) and during 2019 (bottom, $n = 285$ observations) at sites located on Whidbey Island.

Results

Visual Observations

Visual observations made by the GRG of fish delivered to burrows by adult birds suggest that Pigeon Guillemots are selective in the prey species they choose for their chicks. Specifically, birds at sites across Whidbey Island, on average, were observed delivering gunnel with greater frequency than sculpin or other taxa (Fig. 3). This pattern is clear in the combined observations made between 2008–2019. The pattern shows more variance, but similar proportions of use, among fish categories from observations made in 2019 alone. Both the period 2008–2019 and 2019 alone are consistent in that fish other than gunnel and sculpin were delivered with low frequency.

Stable Isotopes

Analyses comparing isotope values of sources (from 2018 and 2019) revealed δ15N and δ13C values did not differ significantly for 3 fish taxa: rockfish ($n = 60$; *Sebastes* spp., *S. caurinus*, *S. maliger*, and *S. emphaeus*), Pacific Staghorn

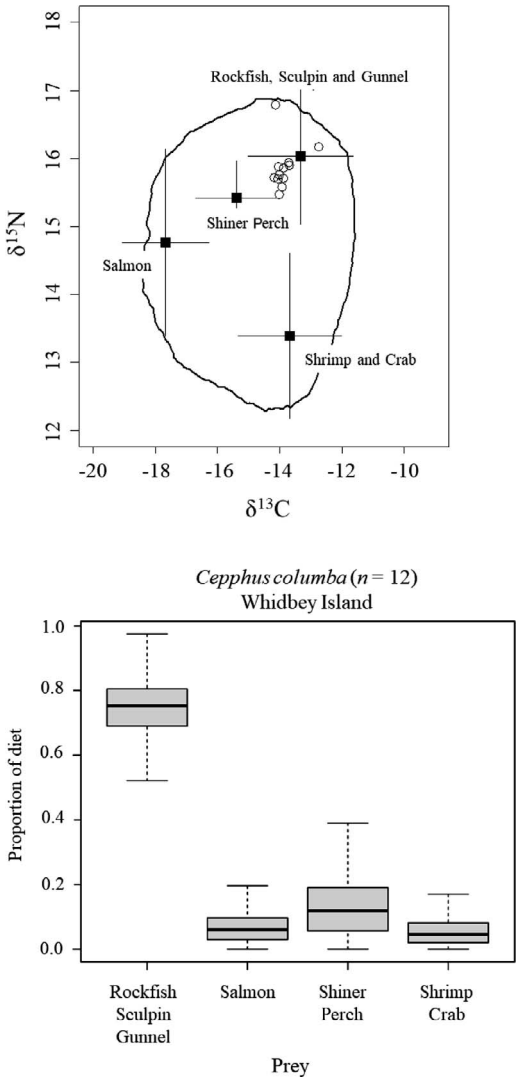

FIGURE 4. Isospace plot (top) and boxplot (bottom) showing MixSIAR results of Pigeon Guillemot eggshell stable isotopes and potential prey stable isotopes (Rockfish/Sculpin/Gunnel, Salmon, Shiner Perch, Shrimp/Crab). Circles in top plot correspond to the stable isotope ratios for Pigeon Guillemot of which four of the 16 samples were removed because they fell outside the isospace (oval). Box plots show median, 25th and 75th percentile, and range are represented by thick horizontal line, top and bottom of box, and whiskers, respectively.

Sculpin ($n = 22$; *Leptocottus armatus*), and gunnels ($n = 21$; *Pholis ornate*, *P. laeta*, and *Apodichthys flavidus*). In addition, δ15N and δ13C values did not differ significantly for 7 invertebrate taxa: shrimp ($n = 39$; *Hippolyte californiensis*, *Pandalus danae*, and *P. hypsinotus*), crab ($n = 19$; *Cancer productus*, *Telmessus cheiragonus*, and *Pugettia producta*), and *Idotea* spp. ($n = 11$). Therefore, these fish taxa were pooled, as were the invertebrate data for the purpose of our mixing model analysis.

Results from the mixing model analysis (Fig. 4) showed that across sites on Whidbey Island, in 2019, rockfish, sculpin, and gunnel were the greatest contributors to the diet of adult female Pigeon Guillemot (74% ± 8%, mean and standard deviation, respectively), followed by shiner perch (13% ± 9%), salmon (6% ± 4%), and shrimp and crab (5% ± 4%). Sensitivity analysis found that the rank order of dietary composition remained unchanged: rockfish, sculpin, and gunnel represented 58–82% of Pigeon Guillemot's diet, shiner perch 8–21% , salmon 4–10%, and shrimp and crabs 5–10%.

DISCUSSION

Stable isotopes derived from discarded Pigeon Guillemot egg tissues and community-science observations of prey delivery by adults to chicks provide dietary information for two periods of time during the breeding season. Isotopes reflect the diet of females during the pre-laying period (May–June), whereas visual observations record chick diet or adult prey preference when feeding chicks (June–August). We can combine this information for evidence of dietary preferences across breeding stages. For Pigeon Guillemot on Whidbey Island, isotopic evidence suggests that adults primarily feed on rockfish, gunnel, and sculpin during the early breeding season, prior to egg-laying, with visual observations also reporting that adults preferentially deliver gunnel and sculpin to their chicks once hatched.

Two previous studies similarly used a combination of stable isotope analysis and visual observations to describe foraging during different stages of breeding in Pigeon Guillemot. Using visual observations, Sydeman and others (1997) reported that Pigeon Guillemot chicks in a central California population had a diet composed of nearly 90% rockfish and sculpin, whereas isotopic evidence identified the diet of adults simply as piscivorous. Davies and others (2009) observed a slight increase in average $\delta^{13}C$ and $\delta^{15}N$ signatures in Pigeon Guillemot chick blood compared to pre-laying adult blood,

which could suggest a possible difference in diet between adults and chicks. Both Sydeman and others (1997) and Davies and others (2009) were able to identify distinct dietary shifts in other alcid species (e.g., Rhinoceros Auklet [*Cerorhinca monocerata*] and Tufted Puffin [*Fratercula cirrhata*]) across breeding stages by looking for changes in trophic position. However, this method is limited in that it is only informative for species that exhibit these distinct shifts and cannot discern more subtle dietary patterns that seabird species such as Pigeon Guillemot may display. Our use of a mixing model with isotopic information from potential prey species allowed us to infer prey preferences via diet composition.

The consistency in Whidbey Island Pigeon Guillemot foraging preferences for gunnel and sculpin demonstrates the importance of this prey source to their reproductive success. Other studies found that breeding pairs that specialize in prey selection for feeding chicks show greater reproductive success than those that generalize in prey selection. Moreover, those that choose high-fat, schooling fish (e.g., Pacific Sand Lance [*Ammodytes personatus*] and Pacific Herring [*Clupea pallasii*]) tend to show greater reproductive success than those that specialize on lower-fat demersal fish (e.g., sculpin and gunnel), and chicks that are preferentially fed high-lipid content fish have a higher growth rate (Golet and others 2000; Litzow and others 2002). Despite this, we found that Pigeon Guillemot adults on Whidbey Island appear to specialize on demersal fish, such as gunnel and sculpin, throughout the breeding season, including the period before chicks hatch when adults are less spatially constrained for foraging. Golet and others (2000) also observed this preference by some breeding pairs for prey delivery to chicks. This somewhat paradoxical pattern could be due to the possible advantage of specializing on a prey source that is more consistently available, particularly in nearshore areas close to colonies, although of a lower quality (the 'quality-variability tradeoff' hypothesis; Kuletz 1983; Litzow and others 2004). However, 'quality' itself is also prone to variability, as 'high-quality' forage fish can lose their nutritional value under extreme ocean conditions, like the North Pacific marine heat wave of 2014–2016 (von Biela and others 2019). The clear prey preference demonstrated by this population of Pigeon Guillemot adults demonstrates the importance of nearshore demersal fish for their reproductive success. In addition, the stable isotope analysis validates the long-term observations made by community-science volunteers on this population of Pigeon Guillemots.

Challenges, Limitations, and Conclusions

Several sources of uncertainty are associated with using the stable isotope analysis to infer diet. The lack of discrimination factors for Pigeon Guillemot egg membrane required the use of discrimination factors from other species and tissues. Although Common Murre are closely related Pigeon Guillemot and the differences in discrimination factors between tissues across seabird species are relatively consistent (Quillfeldt and others 2008), the inappropriate use of isotopic values of tissues can lead to inaccurate estimations about diet (Polito others 2009). Mixing model results are also influenced by the source data, in this case fish and invertebrates, and thus the inclusion of additional potential prey items would shift the estimated diet contribution. The fish and invertebrates used as source information in our mixing model were from a study whose sampling differed in the extent to which it overlapped, in space and time, with that of this study. It is unclear what the influence of this imperfect overlap in our sampling has on our conclusions.

We found that stable isotope analysis of discarded egg tissues is a feasible approach for conducting research on Pigeon Guillemot foraging dynamics. Moreover, we note the value of community scientists as partners in field research. Although previous studies have combined field observations with stable isotope analysis, this study, to our knowledge, is the first to couple non-disruptive tissue collection with community-science observations. Combining isotopic information with observational data taken at the same sites improved confidence in the results. This study offers a starting point for future studies using similar techniques to advance our understanding of how this seabird utilizes its environment for foraging, to help identify future changes to its prey base.

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LITERATURE CITED

BISHOP E, ROSLING G, KIND P, WOOD F. 2016. Pigeon Guillemots on Whidbey Island, Washington: A six-year monitoring study. Northwestern Naturalist 97:237–245.

BOND AL, DIAMOND AW. 2010. Nutrient allocation for egg production in six Atlantic seabirds. Canadian Journal of Zoology 88:1095–1102.

*CHITTARO P. 2020. Investigating the Contribution of Kelp-and Eelgrass-Derived Carbon and Nitrogen to Marine Herbivores and Carnivores in Puget Sound. Proceedings of a symposium 22 April 2020. The Salish Sea Ecosystem Conference.

DAVIES WE, HIPFNER JM, HOBSON KA, YDENBERG RC. 2009. Seabird seasonal trophodynamics: Isotopic patterns in a community of Pacific alcids. Marine Ecology Progress Series 382:211–19.

EWINS PJ. 1993. Pigeon Gillemot (*Cepphus columba*). In: Poole A, Gill F, editors. The birds of North America Online, version 2.0. Ithaca, NY: The Cornell Lab of Ornithology.

FREDRIKSEN S. 2003. Food web studies in a Norwegian kelp forest based on stable isotope (Δ13C and Δ15N) analysis. Marine Ecology Progress Series 260:71–81.

GATES JB, CHITTARO PM, VEGGERBY KB. 2020. Standard operating procedures for measuring bulk stable isotope values of nitrogen and carbon in marine biota by isotope ratio mass spectrometry (IRMS). Seattle, WA: US Department of Commerce, NOAA. Processed Report NMFS-NWFSC-PR-2020-04. 37 p.

GOLET GH, KULETZ KJ, ROBY DD, IRONS DB. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. The Auk 117:82–91.

HOBSON KA, PIATT JF, PITOCCHELLI J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786–98.

JENKINS E, GULKA J, YURKOWSKI DJ, WONG E, DAVOREN GK. 2020. Isotopic discrimination ($\delta^{15}N$, $\delta^{13}C$) in captive and wild Common Murres (*Uria aalge*) and Atlantic Puffins (*Fratercula arctica*). Physiological and Biochemical Zoology 93:296–309.

KOWALCZYK ND, CHIARADIA A, PRESTON TJ, REINA RD. 2014. Linking dietary shifts and reproductive failure in seabirds: A stable isotope approach. Functional Ecology 28:755–765.

KULETZ KJ. 1983. Mechanisms and consequences of foraging behavior in a population of breeding Pigeon Guillemots [thesis]. Irvine, CA: University of California. 79 p.

LITZOW MA, PIATT JF, ABOOKIRE AA, PRICHARD AK, ROBARDS MD. 2000. Monitoring temporal and spatial variability in Sandeel (*Ammodytes hexapterus*) abundance with Pigeon Guillemot (*Cepphus columba*) diets. ICES Journal of Marine Science 57:976–986.

LITZOW MA, PIATT JF, PRICHARD AK, ROBY DD. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286–295.

LITZOW MA, PIATT JF, ABOOKIRE AA, PRICHARD AK, ROBARDS MD. 2004. Energy density and variability in abundance of Pigeon Guillemot prey: Support for the quality-variability trade-off hypothesis. Journal of Animal Ecology 73:1149–1156.

OPPEL S, POWELL AN, O'BRIEN DM. 2009. Using eggshell membranes as a non-invasive tool to investigate the source of nutrients in avian eggs. Journal of Ornithology 150:109–115.

OWEN E, WAKEFIELD E, HOLLINRAKE P, LEITCH A, STEEL L, BOLTON M. 2019. Breeding together, feeding apart: Sympatrically breeding seabirds forage in individually distinct locations. Marine Ecology Progress Series 620:173–183.

PEARSON SF, HAMEL NJ. 2013. Marine and terrestrial bird indicators for Puget Sound. Olympia, WA: Washington Department of Fish and Wildlife and Puget Sound Partnership. 55 p.

PETHYBRIDGE HR, CHOY CA, POLOVINA JJ, FULTON EA. 2018. Improving marine ecosystem models with biochemical tracers. Annual Review of Marine Science 10:199–228.

PHILLIPS DL, INGER R, BEARHOP S, JACKSON AL, MOORE JW, PARNELL AC, SEMMENS BX, WARD EJ. 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92:823–835.

POLITO MJ, FISHER S, TOBIAS CR, EMSLIE SD. 2009. Tissue-specific isotopic discrimination factors in Gentoo Penguin (*Pygoscelis papua*) egg components: Implications for dietary reconstruction using stable isotopes. Journal of Experimental Marine Biology and Ecology 372:106–112.

QUILLFELDT P, BUGONI L, MCGILL RAR, MASELLO JF, FURNESS RW. 2008. Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: Implications for food web studies. Marine Biology 155:593–598.

* Unpublished

Resano-Mayor J, Hernández-Matías A, Real J, Moleón M, Parés F, Inger R, Bearhop S. 2014. Multi-scale effects of nestling diet on breeding performance in a terrestrial top predator inferred from stable isotope analysis. PLoS ONE 9(4):e95320.

Sloan CA, Anulacion BF, Baugh KA, Bolton JL, Boyd D, Chittaro PM, da Silva DAM, Gates JB, Sanderson BL, Veggerby K, Ylitalo GM. 2019. Quality assurance plan for analyses of environmental samples for polycyclic aromatic hydrocarbons, persistent organic pollutants, dioctyl sulfosuccinate, estrogenic compounds, steroids, hydroxylated polycyclic aromatic hydrocarbons, stable isotope ratios, and lipid classes. Seattle, WA: US Department of Commerce, NOAA. Technical Memorandum NMFSNWFSC-147. 40 p.

Stock BC, Semmens BX. 2016. MixSIAR GUI User Manual. Version 3.1. https://github.com/brianstock/MixSIAR.

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096.

Sydeman WJ, Hobson KA, Pyle P, McLaren EB. 1997. Trophic relationships among seabirds in central California: Combined stable isotope and conventional dietary approach. The Condor 99:327–336.

Zanden JV, Rasmussen JB. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46:2061–2066.

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