STABLE ISOTOPE-DETERMINED DIETS OF BLACK OYSTERCATCHERS *HAEMATOPUS BACHMANI* IN THE NORTHERN GULF OF ALASKA

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Received 15 July 2022, accepted 28 December 2022

ABSTRACT

CARNEY, B., TESSLER, D., COLETTI, H., WELKER, J.M., & CAUSEY, D. 2023. Stable isotope-determined diets of Black Oystercatchers *Haematopus bachmani* in the Northern Gulf of Alaska. *Marine Ornithology* 51: 125–135.

Black Oystercatchers *Haematopus bachmani* (BLOY) feed on intertidal invertebrates along coasts of the northern Gulf of Alaska and elsewhere. Details of their feeding ecology have only been marginally delineated, however, and as population sizes are small and limited geographically, rapid ecological changes may alter their prey base, placing BLOY resiliency in jeopardy. We examined the diets of BLOYs occupying the coast at three sites in Southeast Alaska using stable isotope analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) to answer the following three questions: (1) what are the diet proportions of prey groups consumed at different locations along the northern Gulf of Alaska; (2) how do individual diets vary; and (3) how do current diets compare to those of the past? Results indicate that: (a) the diet of individual BLOYs was approximately ~52% mussels *Mytilus trossulus* or other filter feeders, ~41% limpets *Lottia* spp. or other kelp and algal grazers, and ~5% dogwinkles *Nucella* spp. or other secondary consumers; (b) little variation in diet existed between seasons or locality; and (c) diets of adults during summer have varied little over the last 100 years. These findings indicate that BLOYs have a very specialized feeding niche that has not changed substantially over time. We discuss the possibility that changing ocean processes may alter the abundance of filter feeders and ultimately have effects on BLOY success in the study region.

Key words: Black Oystercatcher, *Haematopus bachmani*, stable isotopes, diet, Gulf of Alaska

INTRODUCTION

Understanding the dietary ecology of migratory and free-ranging animals is important in the face of a changing climate as well as anthropogenic land and sea-use, especially in the sub-Arctic and Arctic (Causey *et al*. 2014, Rogers *et al*. 2015, 2021). Quantifying diets of individual organisms is critical to characterizing the nature of food webs at various spatial scales, which are subject to modification by natural processes such as cyclical and directional climate alterations (e.g., Pacific Decadal Oscillation). Food webs can also be altered by the management of natural resources, such as fish harvesting practices (Becker & Bessinger 2006). While there are multiple means by which animal diets can be estimated (e.g., direct observation, fecal analysis, stomach contents, or midden analyses), the analysis of stable isotopes in animal tissues, particularly carbon and nitrogen (δ^{13}C and δ^{15}N), provides a robust means of examining diet through multiple time and spatial scales (Inger & Bearhop 2008, Stanek *et al*. 2017, Rogers *et al*. 2015, 2021).

Black Oystercatchers *Haematopus bachmani* (BLOY) breed, migrate, and winter along the western coast of North America (Tessler *et al*. 2014, Andres & Falxa 2020). They forage in the intertidal zone and nest on adjacent higher ground. BLOY feed exclusively on intertidal invertebrates, species that may be vulnerable to ocean acidification, ocean warming (Harley *et al*. 2006, Johnson *et al*. 2010), and/or harvest by humans, all of which in turn may affect the dietary ecology, fecundity, and sustainability of the species (Johnson *et al*. 2010, Hipfner & Elner 2013, Robinson *et al*. 2019). Thus, understanding species' diet is a cornerstone of intertidal food web ecology. In the end, such knowledge may be important in determining conservation practices (i.e., warm blob; Yang *et al*. 2019), and in understanding trajectories of change in subarctic coastal habitats (Rogers *et al*. 2021), including impacts on their intertidal invertebrates (Manriquez *et al*. 2022).

The large majority (80%) of BLOY breeding sites are located in Alaska and British Columbia (Tessler *et al*. 2014, Andres & Falxa 2020). Previous studies conducted in Alaska form much of our current collective understanding of BLOY life history (Coletti *et al*. 2011). Additionally, the southern coast of Alaska is located along the global gradient for the subarctic region, a particularly vulnerable region for the effects of changing ocean climate (Guo *et al*. 2022). Considering the highly specialized nature of BLOY feeding ecology and the vulnerability of tidal organisms (Manriquez *et al*. 2022), increasing our basic understanding of their life history will be valuable in informing future conservation measures and management decisions.

The limited BLOY life history information has been summarized by Andres & Falxa 2020). Most notably lacking is information on long-term diet patterns, the level of variation in diet among individuals and groups over space and time, and seasonal movements of BLOY. Previous studies on the diet of BLOYs investigated adult and chick diet through visual observation (Frank 1982), stomach content analysis (Hazlitt *et al*. 2002), shell fragment collection (Poe *et al*. 2009), or some combination of these methods. While previous work on diet forms the foundation of our collective knowledge of BLOY prey preferences, the traditional methods used in the aforementioned studies each have limitations (Robinson *et al.* 2018). For example, stomach content analyses reflect only the undigested portions of recently ingested food and provide only an instantaneous snapshot of an individual's diet (Robinson *et al*. 2018. Ibanez *et al*. 2021). Data from shell collection are constrained by how representative they are of overall diet (Robinson *et al*. 2019). Observational studies are limited by the observer's ability to visually discern and correctly identify prey before it is ingested, and these limitations are compounded by the difficulty associated with conducting effective foraging observations throughout daily and seasonal time periods (LaRoche *et al*. 2021). Nevertheless, we know that BLOYs in Alaska consume mussels *Mytilus trossulus* and limpets *Lottia* spp. in large quantities, as well as trace amounts of dogwinkles *Nucella* spp. (Tessler *et al*. 2014, Robinson *et al*. 2019).

Because BLOYs feed on prey species from several distinct trophic groups (Lindberg *et al*. 1987), including grazers, filter feeders, and carnivores, determining the contributions of each group to the overall diet is possible with stable isotopes, providing a more temporally integrative record of diet patterns (Post 2002, LaRoche *et al*. 2021). Of particular value toward understanding of overall foraging ecology of BLOY, the information garnered from traditional studies can help to qualitatively guide the interpretation of stable isotope data. That is, isotope mixing models provide information in more detail than just the trophic level of a diet, as long as the isotope signatures of prey are available for the models (see below).

Carbon isotopes (^{13}C) are indicative of primary production sources (benthic versus pelagic, for example, at the largest scale), while nitrogen isotopes (^{15}N) change with trophic levels (Jennings & van der Molen 2015). Different time scales can offer different perspectives on diet. Isotopic values are incorporated into blood within 17–21 days, and blood is representative of diet integrated over at least three weeks prior to collecting samples (Hobson & Clark 1992). Values of feathers, however, represent the diet during the time of feather growth (Bearhop *et al*. 2002). Thus, differences in adult vs chick diet conceivably could be investigated.

Alaska populations of BLOYs undergo a partial molt that includes head, body, and covert feathers in the spring (March to May) and another partial molt of flight feathers from July to August (Andres & Falxa 2020). Based on recorded observations of BLOYs in the breeding grounds in spring and late summer, we expected isotopic values of body and covert feathers to represent diet at the study sites in spring, just before the start of the breeding season. Since BLOYs exhibit high site fidelity and often return to the same nest area year after year, we expected flight feathers to be representative of diet on the breeding grounds from the previous summer (July, August). We also expected feather values to be slightly more enriched in both ^{13}C and ^{15}N relative to BLOY blood (Caut *et al*. 2009).

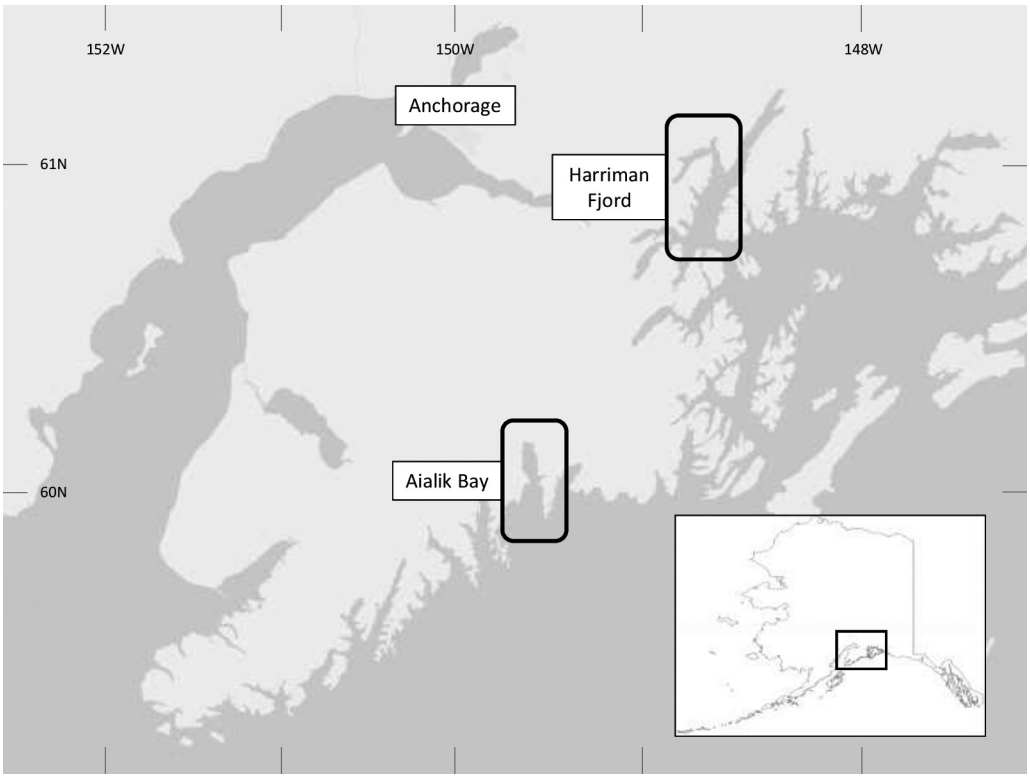

Fig 1. The northern coast of the Gulf of Alaska showing field study sites, Aialik Bay and Harriman Fjord, USA. Aialik Bay is approximately 161 km to the southwest of Harriman Fjord. Protected, estuarine waters and shorelines of cobblestone/rocky beaches and sheer cliffs characterize both sites. Map is from USGS Map Viewer (http://viewer.nationalmap.gov/viewer).

Mixing models assess the relative importance of prey groups to a consumer's diet when isotopic values for both consumer and prey are known and after values of either the consumer or prey are adjusted to account for isotopic discrimination associated with digestion, metabolism, and assimilation (Miller *et al*. 2022). Using isotopic values in a simple or complex mixing model to estimate the consumption of different prey resources requires an accurate estimation of isotope discrimination from prey to consumer. Diet-to-tissue discrimination factors (DTDF) for ^{15}N and ^{13}C are published for several species of birds (Caut *et al*. 2009). However, these published values vary widely depending on diet, sample processing, and tissue types. Large discrepancies in DTDFs (± 4‰) coupled with the importance of these values to any mixing model used to infer diet illustrate the need for accurate, species-specific information. Few studies exist on DTDFs of shorebirds, and there has been only one previous study on DTDFs of birds in the *Haematopus* genus (Caut *et al*. 2009). While Dunlin *Calidris alpina* and African Oystercatchers *Haematopus moquini* are the two species most similar to BLOYs in their available DTDF published values, the values may still be quite different across species due to differences in diet, environment, and species-specific physiology (Lindberg *et al*. 1987, Robinson 2019). Given the wide variation in values across species, species-specific values for DTDFs are ideal for use in any mixing model. Additionally, different metabolic processes are involved in the fractionation of whole blood and feathers, and numerous studies have demonstrated different DTDFs for each of these tissues (Caut *et al*. 2009).

To assess the assimilated diet of adult BLOYs breeding along the coast in the northern Gulf of Alaska (i.e., Southeast Alaska), we conducted field and captive studies addressing the following questions: (1) What are the proportions of prey groups to assimilated diet of adult breeding BLOYs along the northern Gulf of Alaska coast? (2) How do the diets vary among individual BLOYs? (3) How do current BLOY diets compare to those of the past? (4) What are the DTDFs for feathers and blood using captive BLOYs?

METHODS

Study sites

We conducted fieldwork May–June in 2012 and 2013 to coincide with annual nesting phenology of BLOY. Adult BLOY pairs are territorial during breeding and are more easily captured during this time (Andres & Falxa 2020). We focused field efforts in two locations in the northern Gulf of Alaska and selected specific study sites based on three criteria: (1) previous documentation of concentrated BLOY nesting activity, (2) logistical feasibility, and (3) relevance to related studies by partnering agencies. Study sites were located in Aialik Bay, an area of focus for the National Park Service's Nearshore Marine Monitoring Program, as well as in Harriman Fjord, a focus area for the USDA Forest Service and the State of Alaska's Wildlife Diversity Program (Fig. 1). Aialik Bay and Harriman Fjord support roughly 28 consistently occupied BLOY breeding territories (McFarland & Konar 2010, Tessler *et al*. 2014, Robinson 2019).

Aialik Bay is a glacial fjord located within Kenai Fjords National Park on the Kenai Peninsula of Alaska at approximately 59°47′N, 149°42′W, 75 km from Seward, Alaska. It is long, deep (up to 270 m in depth), and narrow, with numerous coves and inlets. Shorelines are diverse and range from steep cliffs to boulder-rich beaches, to both steep and shallow-sloping cobblestone and gravel beaches. During summer months, waters are cool (7 °C to 10 °C) and are often heavy with ice deposits from Aialik Glacier, located at the head of the bay. Holgate Arm is a smaller fjord located on the west side of Aialik Bay. It is narrow with shorelines consisting of steep cliffs and shallow-sloping cobblestone beaches. Holgate Glacier forms the head of the arm. Survey and capture efforts were focused on shorelines in the northern 12 miles of the bay from Aialik Glacier to just to the south of Holgate Arm. Harriman Fjord is a glacial fjord located within Prince William Sound at approximately 61°01′N, 148°18′W and roughly 55 km northeast from Whittier, Alaska. Harriman is narrow and deep (up to 148 m), with cool summertime waters influenced by two tidewater glaciers, Harriman and Surprise, and outflow from several hanging glaciers. Like Aialik Bay, the shoreline consists of steep cliffs and scattered boulder, cobblestone, or gravel beaches, but there are fewer deeply incised coves.

Prey sampling

We collected whole intertidal invertebrates of taxa known to be constituents of BLOY diets at various locations in each study area where oystercatchers were either observed feeding and/or in nearby mussel beds in which the species of interest were abundant. We collected prey items during low tide from the middle and upper tidal zones, which previous observation-based studies have determined is the primary BLOY feeding area (Tessler 2014, Robinson 2019). In 2012, we opportunistically collected a minimum of 15 specimens each of mussels, limpets, and dogwinkles. We used results from 2012 to inform the total minimum sample size needed in 2013 for specimens in each prey group. We based minimum sample sizes (n = 15) on the number of samples needed to attain ≤ 1‰ of standard error for each of the three groups. We did not attempt to collect the full suite of potential prey items consumed by BLOYs. Rather, we focused on three taxa that have been documented in their diet in previous studies and which we expected would have distinct stable isotope values. We also surmised that the isotopic values of these taxa—mussels, limpets, and dogwinkles—would be representative of other intertidal invertebrates within their trophic groups (i.e., filter feeders, grazers, and carnivores respectively; Lindberge *et al*. 1987, Poe *et al*. 2009). We sorted prey items by species, then placed them in plastic bags and froze them until further processing. Additionally we also collected potential prey species (e.g., littorine snails, barnacles, and worms) to test assumptions regarding the similarity of isotopic values among and within some trophic groups (e.g., littorine snails and limpets).

Oystercatcher sampling

At each study site, we surveyed the shoreline via boat to locate active BLOY breeding territories. We located pairs visually or by playing a territorial call over a loudspeaker, which often provoked a vocal response by birds occupying the site. We searched occupied territories on foot to locate nests and recorded nest coordinates using a handheld GPS. We observed nesting pair members to identify likely foraging areas for invertebrate sampling. We attempted to capture breeding pair members only after clutch completion and the onset of active incubation to reduce the risk of nest abandonment. We captured nesting adults using several methods developed for other species, adapted for BLOYs, including nest nooses and noose mats (Benson & Suryan 1999, McGowan & Simons 2005). We banded each captured adult with a stainless-steel federal band

on the left leg and with an alphanumeric coded band on each leg. We removed any pre-existing metal bands and retained them for ongoing demography studies.

We drew 0.5 mL of blood from the medial metatarsal vein using a 26-gauge sterile needle following American Ornithologist Union approved guidelines (Oring *et al*. 1998, Owen 2011). We froze whole blood samples immediately after collection following Bugoni *et al*. (2008), who demonstrated this method of field-based storage, as compared to other methods of storing blood in alcohol or salt-based solutions. Our method resulted in the lowest amount of variation in isotopic values. We collected body and covert feathers from each captured bird and clipped one primary tip from a subset of captured birds. We placed feathers in a dry envelope and stored them with blood samples. We also collected head feathers from captured individuals in 2012 but omitted this from the methods in 2013 given the similar values between head and body feathers and the difficulty of processing the smaller feathers.

Collection of historical feather samples

In addition to the field work we conducted for this study, we also collaborated with several museums to obtain BLOY feather samples from specimens collected in southcentral Alaska up to 100 years ago. We explored this path of collection and analysis to determine if there is evidence that oystercatchers have diets today that are similar to those in earlier years. Stable isotope analysis methods were the same for both newly collected and museum collection feathers.

Controlled feeding trial

During the period of this study, the Alaska SeaLife Center (ASLC; https://www.alaskasealife.org/; accessed 14 September 2022) cared for the only two captive BLOYs in the world, both females, at their facility in Seward, Alaska. During winter months, the two healthy individuals were removed from the open-air aviary and kept in a warmer, secluded area under stable conditions. This location is secluded from other birds and food choices, making it an ideal setting to conduct a controlled diet trial for the purpose of establishing tissue- and species-specific DTDFs.

Published half-lives of carbon and nitrogen in whole blood in birds range from 10 to 16 d (Bearhop *et al*. 2002), which translates to reaching 80% turnover completion in these elements in whole blood in 24 to 54 d. Because the process of turnover is asymptotic, reaching 100% turnover is unrealistic. To reach the target of 80% turnover of ^{13}C and ^{15}N in blood, we kept captured individuals on a constant diet for six weeks, or 42 d. The duration of the study was limited by the need to return the birds to the main outdoor aviary for the summer season. Periods of growth or nutritional stress can result in abnormally high $\delta^{13}N$ values in animals (Bearhop *et al*. 2002). To minimize nutritional stress, the controlled feeding trial diet closely resembled the captive birds' normal diet, although it differed somewhat from that of BLOY in the wild. We weighed individuals on the first day of the trial, each subsequent week, and at the conclusion of the trial to monitor whether they maintained a consistent weight.

The birds were kept on a constant diet of 60% oysters *Crassostrea gigas* and mussels and 40% forage fish mixture for approximately four months prior to the feeding trial. At the start of the feeding trial, we altered dietary proportions so that 60% consisted of razor clams *Siliqua patula*, which are primary consumers with a benthic isotopic signature. The remaining 40% of the diet consisted of items from the pre-trial diet. Initially, each bird received 600 g of food per day. We noted the daily consumption during the first few days of the trial and reduced the daily ration from 600 g to 440 g (while maintaining the same ratios of food items) for the remainder of the trial (40 d) to ensure each bird consumed the entire daily allotment. The amounts of food given to each bird daily were 270 g razor clams (61%), 80 to 90 g oysters (18%), and 22.5 g each of eulachon *Thaleichthys pacificus*, silversides (Atherinidae), capelin *Mallotus villosus*, and herring *Clupea pallasii* (a total of 21%).

ASLC veterinary staff collected whole blood samples (0.5mL) from the jugular vein on days 1, 36, and 42 of the trial. Samples were immediately frozen at -80 °F until further processing. Staff opportunistically removed emerging body feathers on days 36 and 42 of the trial, placed them in a dry envelope, and stored them at room temperature for further processing. We ensured that diet items came from the same shipment and package of food for the duration of the trial. We collected one daily portion of diet items for stable isotope analysis and kept it frozen until processing. A sub-sample of the daily portion was homogenized and analyzed *en masse*. Additionally, a sub-sample of the individual diet items were homogenized and analyzed individually. We present the results for DTDF values as the change in isotopic values between diet and tissue ($\delta^{13}C$, $\delta^{15}N$).

Stable isotope analysis

We conducted all sample preparation and stable isotope analysis in the Environment and Natural Resources Institute STable Isotope Lab at the University of Alaska Anchorage, using standard protocols (Hobson & Clark 1992). We removed mollusk prey from shells and cleaned the soft tissue with distilled water. We cut a cross-section consisting primarily of muscle from fish prey and cleaned with distilled water. We dried prey specimens in a freeze dryer for 48 h and then ground them to a homogenous powder using a bead mill. We freeze-dried whole blood samples for 24–48 h and subsequently ground those to a homogenous powder using mortar and pestle. We cleaned feathers using a 2:1 chloroform:methanol solution, after which they were air dried (Hobson & Clark 1992). A 1 mg (± 0.2 mg) subsample of each prey and blood sample was weighed for processing, as was a clipping of the distal tip (1 mg ± 0.2 mg) of each feather. We transferred the weighed samples into tin capsules and analyzed for ^{13}C and ^{15}N ratios via a Costec EA front peripheral connected in series to a Finnigan Delta Stable Isotope Mass Spectrometer operated in continuous flow.

We present the results as the ratio of heavy to light isotope abundance in a sample relative to that of international standards (traceability to the Vienna PeeDee Belemnite scale for carbon, atmospheric air for nitrogen) and reported in parts per thousand (‰) according to the equation:

$$X = ([Rsample/Rstandard]–1) \times 1000 \quad (1)$$

where X is either $\delta^{13}C$ or $\delta^{15}N$, and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Hobson & Clark 1992). All results are presented in ‰ ± standard error (SE) unless otherwise noted. We adjusted $\delta^{13}C$ values of archival specimens to correct for anthropogenic increases in atmospheric carbon since the Industrial Age—also known as the

"Suess effect" (Gruber et al. 1999)—using equation 2 in Farmer & Leonard (2011) and values for the North Pacific (Watanabe *et al*. 2011). Adjustments to measured values were accordingly 0.036‰ (1899), 0.312‰ (1920), and 0.158‰ (1981); no adjustments were made to contemporary samples.

Statistical analysis

We used R Statistical Software and Microsoft Excel for data analysis. We found the data to be normally distributed using the Shapiro-Wilk test, $P < 0.1$. We tested for initial differences between study sites and years for isotopic values of prey items, BLOY blood, and feathers using a two-tailed Welch's *t*-test. Isotopic values of the three feather types (head, body, covert) were compared using ANOVA. We analyzed diet using the mixing model program STable Isotope Analysis in R (SIAR, now MixSIAR; Parnell *et al*. 2010). We chose to use SIAR to produce mixing models rather than previously developed programs because SIAR follows a Bayesian approach to determine the most likely proportions of various prey groups rather than only providing a range of possible values. In addition, the model provides probability densities associated with the posterior distributions of results.

Turnover rates were determined from the controlled study using the non-linear regression equation (Hobson & Clark 1992)

(2) $y = a + be^{-rt}$

where y = δ^{13}C or δ^{15}N, and are parameters determined by initial and asymptotic isotopic values of whole blood, r is turnover rate, and t is time. We utilized the standard approach that isotopic equilibrium was reached at 80 % turnover (Li *et al*. 2018). We calculated the half-life of each stable isotope using the equation

(3) $-ln(0.5)/h = r$

where h is half-life.

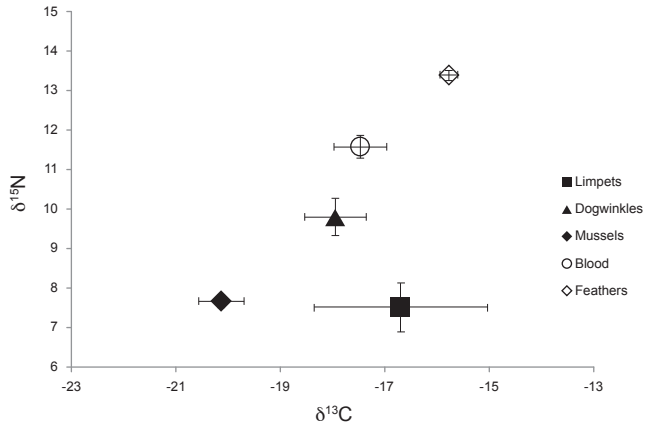

Fig 2. Mean values of δ^{13}N and δ^{13}C (± 1 standard error) for all invertebrate groups and Black Oystercatcher *Haematopus bachmani* (BLOY) tissues analyzed. Values of δ^{13}N increase with trophic level, and δ^{13}C values are indicative of primary production pathways. BLOY tissues are enriched in ^{15}N and ^{13}C relative to all prey groups, and feathers are enriched in both ^{15}N and ^{13}C compared to blood.

RESULTS

Diet-to-tissue discrimination factors

Both captive birds in the controlled feeding trial maintained constant weight (Bird 006: mean = 526.4 g with < 1% [2.8 g] variation; Bird 007: mean = 529.8 g with < 2% [10.07g] variation). The mean value of the daily diet when homogenized and analyzed as a whole was 9.34‰ δ^{15}N and -17.27‰ δ^{13}C. Values of individual diet items (n = 20 each item) were: razor clams (7.97‰ δ^{15}N and -15.71‰ δ^{13}C), oysters (8.95‰ δ^{15}N and -19.69‰ δ^{13}C), silversides (13.09‰ δ^{15}N and -18.52‰ δ^{13}C), capelin (13.09‰ δ^{15}N and -19.66‰ δ^{13}C), eulachon (15.08‰ δ^{15}N and-21.65‰ δ^{13}C), and herring (14.24‰ δ^{15}N and -18.2‰ δ^{13}C). Mean values for whole blood on day 1 of the trial were 15.85‰ δ^{15}N and -19.12‰ δ^{13}C. At the close of the trial on day 42 they were 13.35‰ δ^{15}N and -16.73‰ δ^{13}C. Mean values for emerging feathers collected at the end of the trial were 14.08‰ δ^{15}N and -15.46‰ δ^{13}C.

Half-lives for whole blood were 8.6 d for ^{13}C and 9.3 d for ^{15}N, which fall within the expected values based on published values of shorebirds (Ogden *et al*. 2004). Using non-linear regression, we calculated discrimination factors for whole blood to be 0.62‰ (± 0.40‰, r^2 = 0.99) δ^{13}C and 4.05‰ (± 0.60‰, r^2 = 0.99) δ^{15}N (Fig. 3). We obtained the discrimination values for feathers by calculating the difference between the known, weighted diet sum value and mean feather values, which were as follows: 1.80‰ (± 0.27‰) δ^{13}C and 4.74‰ (± 0.71 ‰) δ^{15}N. Discrimination values for feathers were higher than for blood for both carbon and nitrogen.

Prey items

We collected and processed a total of 71 mussels, 45 limpets, and 42 dogwinkles. As hypothesized, the mean isotope values for each prey group differed (Table 1). Mean δ^{15}N values for prey items were: mussels 7.66‰ (± 0.41‰), limpets 7.5‰ (± 0.79‰), and dogwinkles 9.8‰ (± 0.47‰). Mean δ^{13}C values for mussels, limpets, and dogwinkles were -20.13‰ (± 0.65‰), -16.69‰ (± 1.29 ‰), and -17.95‰ (± 0.77 ‰) δ^{13}C, respectively. Mean values of δ^{15}N and δ^{13}C (mean ± 1 SE) and the number of individuals sampled (n) are shown for all groups.

Values for mussels ranged from 6.49‰ to 8.77‰ δ^{15}N and -22.18‰ to -18.53‰ δ^{13}C across both years and locations. Limpets had the widest range of values among the sampled groups from 6.11‰ to 9.45‰ δ^{15}N and -20.20‰ to -13.37‰ δ^{13}C. Dogwinkle values ranged from 8.71‰ to 11.1‰ δ^{15}N and -19.88‰ to -16.34‰ δ^{13}C.

TABLE 1
Stable isotope values for Black Oystercatchers *Haematopus bachmani* (BLOY) tissues and invertebrate prey specimens sampled in two study sites in South Central Alaska (Fig. 1)

	δ^{13}N	δ^{13}C
Blood (n = 13)	11.58 ± 0.53	-17.47 ± 0.71
Feathers (n = 15)	13.39 ± 0.37	-15.77 ± 0.42
Mussels (n = 71)	7.66 ± 0.41	-20.13 ± 0.65
Limpets (n = 45)	7.50 ± 0.79	-16.69 ± 1.29
Dogwinkles (n = 42)	9.8 ± 0.47	-17.95 ± 0.77

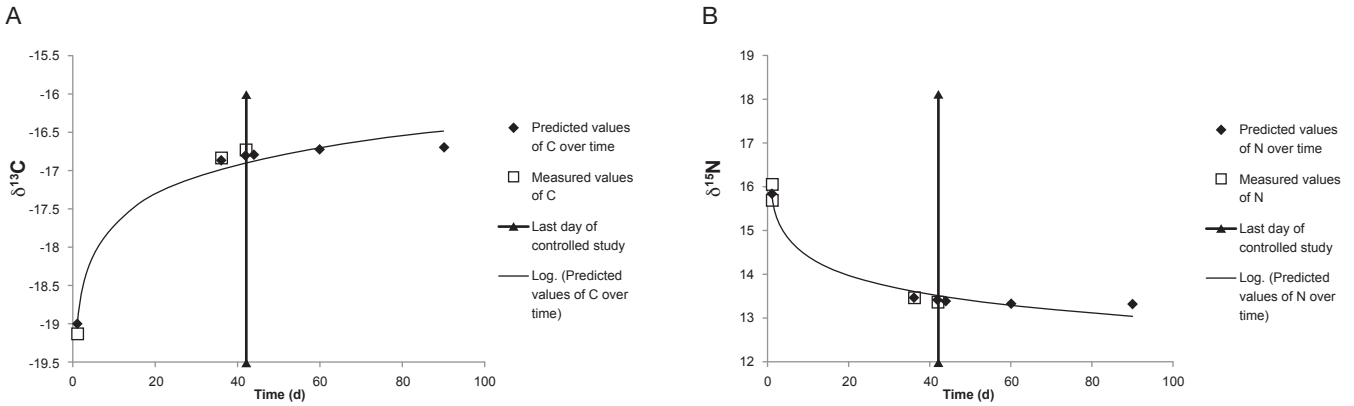

Fig 3. Exponential models of (A) δ^{13}C and (B) δ^{15}N for Black Oystercatcher *Haematopus bachmani* (BLOY) whole blood. Open squares are measured values (n = 2 for each point), closed diamonds are predicted values, and closed triangles represent the end of the study.

Statistically significant differences ($P < 0.1$) were found for δ^{15}N and δ^{13}C values for all three prey groups between locations and years. However, compared across prey groups, there was no overlap in SE. All differences within each prey group (Fig. 2) fell within the natural expected variation (1‰ to 2 ‰). For these reasons, and because the focus of our study is on diet patterns rather than on minute differences with a given prey group over space and time, prey items were categorized by trophic group for diet analysis.

Oystercatchers

We captured 15 BLOY. We collected feathers from all of them, but two escaped before obtaining blood (below). Captures occurred during two field seasons; the majority of this sampling effort was in Aialik Bay (n = 13), with lesser effort in Harriman Fjord (n = 2). Logistical constraints limited total sample size. Mean values for blood (n = 13) for both study years and locations combined were 11.58‰ (± 0.53 ‰) for δ^{13}N and -17.4‰ (± 0.71 ‰) for δ^{13}C (Table 1); we found no significant locality effects (Dixon's Q test for Outliers, $P > 0.05$).

Blood values fell within the expected range based on the known values of δ^{13}C for marine organisms as well as a stepwise increase in δ^{13}N values at higher trophic levels. The range of isotopic values for whole blood among sampled individuals was minimal (10.62‰ to 12.20‰ δ^{13}N and -18.85‰ to -16.13‰ δ^{13}C), based on comparable studies (Cherel *et al*. 2005). While there was some variation in δ^{13}C and δ^{13}N values among individuals, there was little variation in diet proportions among individuals when each was placed in the mixing model, indicating little variation in summer breeding season diet among individuals. Welch's t-tests for all year and location combinations showed only a significant difference between the blood values obtained from Aialik Bay in 2012 and in 2013 for ^{13}C (P = 0.001). Despite this difference and because of the accepted variation of < 2‰ in natural settings (Cherel *et al*. 2005), we analyzed the blood values as one group.

Mean values for feather types from the 13 captured oystercatchers were: body (n = 22, including multiples from the same individuals, 13.34‰ (± 0.77‰) δ^{13}N and -15.55‰ (± 0.93‰) δ^{13}C), covert (n = 11, 13.21‰ (± 0.65‰) δ^{13}N and -15.55‰ (± 0.68‰) δ^{13}C), head (n = 3, 13.37‰ (± 0.57‰) δ^{13}N and -15.55‰ (± 0.62‰) δ^{13}C), and primary (n = 5, 13.34‰ (± 0.69‰) δ^{13}N and -16.12‰ (± 0.72‰) δ^{13}C). Mean values for all feathers were 13.39‰ (± 0.37‰) δ^{13}N and -15.77‰ (± 0.42‰) δ^{13}C (Table 1, Fig. 2). Based on published information on their molting cycles (Andres & Falxa 2020), we expected values for body and covert feathers to represent the diet in spring, while primaries to represent summer diet. There were no significant differences in values between feather types (ANOVA: $F_{3,12}$ = 0.257, P = 0.86 for δ^{13}N; $F_{3,12}$ = 0.194, P = 0.90 for δ^{13}C), and the total range of isotopic values for feathers among sampled individuals (12.2‰ to 14.7‰ δ^{13}N and -14.5‰ to -16.9‰ δ^{13}C) indicated a relatively consistent isotopic diet throughout the molting periods of spring and late summer.

Diet inferred from mixing models

To determine the early summer diet of the sampled wild BLOYs, we used mean values and standard deviation (SD) of prey groups and whole blood values as well as the DTDF for whole blood determined from the controlled feeding trial as inputs into SIAR. SIAR applies DTDFs and standard deviations for both prey and

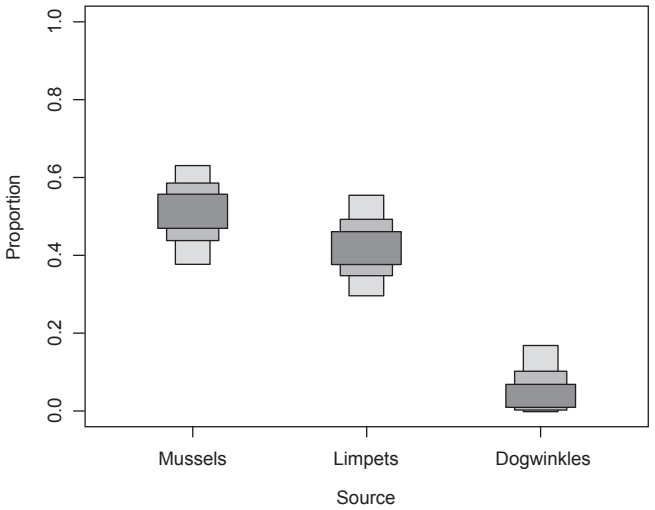

Fig 4. Box plot of diet proportions. Results were determined by the SIAR package in R using whole blood values, mean prey values (± 1 standard deviation [SD]), and the diet-to-tissue discrimination factor (± 1 SD) from the controlled study. Outer boxes represent 95% confidence intervals and inner boxes represent 50% confidence intervals.

consumer to prey means. Early summer diet based on whole blood (n = 13) was estimated at 52% mussels (95% confidence interval [CI]: 37%–63%), 41% limpets (95% CI: 29%–55%), and 4% dogwinkles (95% CI: 0%–8%) as shown in Fig. 4. These findings provide further evidence of the largely limpet-mussel diet of BLOYs described previously. There were no significant differences among individual Oystercatchers or between study sites.

Because there were no significant differences based on feather type, we pooled feather types together for diet analysis (n = 40). The limited variation in feather values suggests that diet is consistent through spring and late summer, given the known molt sequence (Andres & Falxa 2020). Therefore, we pooled all feathers to analyze diet across spring and late summer periods. We used mean isotopic values and standard deviations for feathers and prey groups, as well as DTDFs determined in the controlled feeding trial as inputs to the SIAR model. Using these inputs, the mixing model determined the diet included: 10% mussels (95% CI: 3%–18 %), 43% limpets (95% CI: 37%–50%), and 46% dogwinkles (95% CI: 39%–53 %).

Analysis of feathers from museum collections indicates that BLOY diets have remained similar for over a century (Fig. 5). Values of

TABLE 2
Mean diet-to-tissue discrimination factors for whole blood and feathers of selected avian species

Study	Species	Half-life of fractional turnover: whole blood (days)		Diet-to-tissue discrimination value: whole blood		Diet-to-tissue discrimination value: feathers	
		^{13}C	^{15}N	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Bearhop *et al*. 2002	Great Skua *Stercorarius skua*	15.7 ± 2.1	14 ± 4	4.3	2.6	5.3	4.4
Cherel *et al*. 2005	King Penguin *Aptenodytes patagonica*			-0.81	2.07	0.07	3.49
	Southern Rockhopper Penguin *Eudyptes chrysocome*			0.02	2.72	0.11	4.40
Hobson & Clark 1992	Domestic chicken *Gallus gallus*					-0.4 ± 0.2	1.1 ± 0.1
	Japanese Quail *Coturnix japonica*			1.2 ± 0.6	2.2 ± 0.2	1.4 ± 0.6	1.6 ± 0.1
	Peregrine Falcon *Falco peregrinus*			0.2 ± 0.1	3.3 ± 0.4	2.1 ± 0.08	2.7 ± 0.5
Ogden *et al*. 2004	Dunlin *Calidris alpina pacifica*	11.2 ± 0.8	10.0 ± 0.6	1.10	3.2	-1.6 ± 1.3	-2.8 ± 2.1
Pearson *et al.* 2003	American Yellow Warbler *Setophaga aestiva*	3.9 to 6.1	7.5 to 27.7	-1.2 to 2.2	1.7 to 2.7		
Mizutani *et al*. 1992	Black-tailed Gull *Larus crassirostris*					3.6 ± 0.5	50.3 ± 0.8
	Nankeen Night Heron *Nycticorax caledonicus*					30.2 ± 0.4	40.2 ± 0.3
	Great White Egret *Egretta alba*					3.1 ± 0.4	30.9 ± 0.2
	Grey Heron *Ardea cinerea*					3.4 ± 0.6	40.3 ± 0.4
	Humboldt's Penguin *Spheniscus humboldti*					2.9 ± 0.2	40.8 ± 0.5
	Great Cormorant *Phalacrocorax carbo*					3.8 ± 0.5	30.7 ± 0.6
	Scarlet Ibis *Eudocimus ruber*					3.8 ±0.3	40.5 ± 0.4
	White Ibis *Eudocimus albus*					2.5 ± 0.5	40.3 ± 0.5
	Flamingo *Phoeniconaias* spp.					3.6 ± 0.6	50.6 ± 0.3
Kohler *et al.* 2011	African Black Oystercatcher *Haematopus moquini*					0.2 ± 0.4	2.7 ± 0.4

δ^{13}N varied by only about 2‰ (e.g., 12.5‰–14.5 ‰), representing less than one trophic level. Values of δ^{13}C were more variable, ranging from about -12‰ to -17 ‰. Given the limited sample size of this effort, we hesitate to draw too many conclusions about this data, but nonetheless, we believe that our findings raise interesting possibilities that warrant further study.

DISCUSSION

Our dietary findings indicate that limpets and mussels are the primary BLOY food sources throughout the breeding season (spring through late summer) along the northern Gulf of Alaska coast. In addition, unlike other dietary studies, we found tremendous consistency between BLOY individuals and between two distinct breeding populations separated by 80 km and over multiple years. This consistency in diets speaks to the reliability of prey at this trophic level and throughout the breeding season.

Results for prey values showed some variation, especially for limpets, and this variation potentially weakened our ability to interpret results from the mixing models. Limpets and mussels occupy the same trophic level, represented by δ^{13}N values, but have different δ^{13}C values, which are indicative of their different primary production pathways (Fig. 2). Dogwinkles occupy a higher trophic level and thus have enriched δ^{13}N values compared to the other two prey groups. Additional sampling of limpets across years and within each of the study sites, as well as classification of this genus of invertebrates to the species level, may reduce this variation by revealing patterns that account for the variation (i.e., based on species, location, year, or some combination of these factors). Supplementary sampling of other species in each of the trophic groups (i.e., chitons [*Mollusca: Polyplacophora*] in addition to limpets) could also result in finer interpretation of mixing model results.

We note that many species can be isotopically indistinguishable (e.g., limpets, littorine snails, and potentially chitons), and thus, our results are not meant to indicate that BLOYs feed exclusively on the taxa represented here. Rather, our results demonstrate that the diet of oystercatchers is composed of predictable ratios of invertebrate grazers, filter feeders, and carnivores. BLOY may well consume a variety of prey sharing the isotopic profiles of the trophic groups that we have identified. For example, oystercatchers may consume chitons and other grazers in addition to limpets, predatory worms, and dogwinkles, but the overall proportions of grazers, filter feeders, and carnivores in their diet still applies.

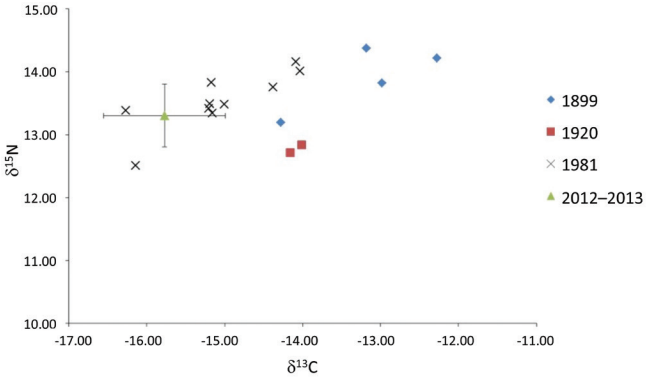

Fig 5. Historical values of δ^{13}N and δ^{13}C obtained from breast feathers collected in this study and museum specimens. Values from 2012–2013 are displayed as mean and standard error of specimens sampled in this study (see also Fig. 2). All other data points represent single individuals.

Our study design closely aligns with methods used by others to determine discrimination values via controlled diet trial (Bearhop *et al*. 2002, Cherel *et al*. 2005). Given our small sample size for the controlled study, we also considered published DTDFs for whole blood and feathers for other avian species for use in our mixing models (Table 2). Initial field results of BLOY whole blood and at least one known diet item (mussels) showed an approximate δ^{15}N of 4‰, which is approximately 1.5‰ higher than the only other published DTDF values for shorebirds (Dunlin and African BLOYs; see Table 2), which confirmed that species-specific DTDFs are needed for BLOY.

The DTDF values we calculated are higher than many avian species but fall within the range of published values for avian whole blood and feathers (Table 2). Diet items were processed without removing lipids, which likely resulted in higher discrimination values for both blood and feathers than if lipids had been removed (Bearhop *et al*. 2002, Cherel *et al*. 2005). Values were determined by controlled studies or, in the case of Kohler *et al*. (2011), a field study where only one prey type was available. Lead authors, species, turnover rates, and diet-to-tissue discrimination factors for ^{15}N and ^{13}C (± 1 SE) are listed for whole blood and/or feathers where applicable. Discrimination factors are positive unless noted as negative.

Mixing models are sensitive to discrimination factors and the broad range of values for avian whole blood (Table 2), as well as the differences in published DTDFs; those we calculated from the controlled study illustrate the importance of using species-specific discrimination factors. Application of our applied DTDFs for blood translated well to field studies. On the other hand, using our calculated DTDFs for feathers in wild birds gave results that deviated from expected values. Prior knowledge of BLOY diets, most notably that mussels make up the largest portion of mass in their diet, led us to question the results of the feather mixing model.

Additionally, the consistent δ^{13}N values for both feathers and blood provide evidence that the mixing model likely does not show a true shift in diet. Feathers are grown over a broad time period, including March through the beginning of our sampling period in May. Some feathers collected from wild birds in this study were in development at the time of sampling, which led us to believe that they represent the same diet as the blood, a tissue with a signature integrated over the previous three weeks or more. Rather than representing a true shift in diet, our prediction is that the discrepancy between the two sets of results stems from the DTDF used in the mixing model. Mixing models are especially sensitive to DTDFs when prey values are only separated by two to three per mil, which is true for BLOYs.

Differences in the blood:feather enrichment between birds in the field-based and controlled studies indicate that differences in diet or other variables may be affecting DTDF in each situation. Wild birds sampled had blood:feather enrichment factors of 1.8‰ δ^{13}N

and 1.7‰ δ^{13}C, and birds used in the controlled study had factors of 0.8‰ δ^{13}N and 1.2‰ δ^{13}C. Pearson *et al*. (2004) hypothesized that differences in the mean isotopic signature, as well as the elemental concentration of diet, can have a significant effect on DTDFs and suggested that DTDFs increase with decreasing C:N ratios. The latter may be the case in this study (mean C:N ratios are 4.3 for wild prey and 5.1 for the controlled study prey). Alternatively, testing of this hypothesis and others found that protein quality has an effect on DTDF but the C:N ratio does not. Conducting a controlled study with prey items consumed by wild birds would result in a study-specific discrimination factor and may resolve this discrepancy, leading to more accurate DTDFs for feathers.

Other factors may also have affected the DTDF for feathers. While Caut *et al.* (2009) found no effect of lipid extraction from prey samples on δ^{13}N or δ^{13}C values, they did find a significant effect of environment on DTDFs for carbon for multiple species and tissues. Specifically, they found DTDFs to be highest in freshwater systems (1.33‰) and lower in marine systems (0.96‰). The high freshwater input to the study area may facilitate higher DTDFs than the specifically marine diet fed to BLOY in the controlled study. Additionally, Hobson & Clark (1992) hypothesized that, because metabolic rates are higher in wild populations than in captive populations due to the higher energy demands on wild populations, the turnover rates associated with signature integration are likely different for wild populations than captive animals. This could also contribute to the differences between the two populations.

CONCLUSIONS

BLOYs are considered an indicator of intertidal ecosystem change and monitored by various government agencies and organizations. The consistent values of both whole blood and feathers indicate that, in addition to having a highly specialized habitat, BLOY have a specialized diet that varies little throughout the breeding season and between breeding seasons. Measurements of isotopic values in archived BLOY feathers indicate little variation in diet over the last 100 years. Our results provide evidence of the potential susceptibility of BLOYs to shifts in the abundance and species composition of intertidal invertebrates. Because our results for nitrogen show that wild BLOYs consistently feed at the trophic level of primary intertidal consumers (e.g., mussels and limpets), changes to the abundance and distribution of invertebrates, such as mussels and limpets, may cause some level of nutritional stress to the birds.

Responses of intertidal invertebrates to effects of climate change, such as increases in sea surface temperature and ocean acidification, demonstrate that shifts are and will be numerous and complex (Manriquez *et al*. 2022, Martel *et al*. 2022). It is beyond the scope of this study to make predictions about how intertidal invertebrate communities in the Gulf of Alaska may respond to such circumstances.

ACKNOWLEDGMENTS

This work was made possible by a collaborative effort between the Alaska Department of Fish and Game, the US National Park Service, and the University of Alaska Anchorage. We thank the curators of the ornithology collections of the American Museum of Natural History, Cornell University Museum of Vertebrates, and the Royal Ontario Museum for feather samples used in this analysis. We appreciate the efforts of reviewers whose comments helped to improve our paper.

IACUC protocols R13-01-01 (issued by the Alaska SeaLife Center), and UAA #344640 and UAA #333194 (issued by the University of Alaska Anchorage) governed all aspects of this study. Birds were captured and handled under the authority of scientific collecting permits USFWS 795841 and ADFG 12-085.

We appreciate the hard work in the field and lab by N. Bargmann, W. Carney, M. Harrington, M. Kansteiner, K. Mueller, V. Padula, L. Phillips, J. Paszalek, M. Snively, S. Wesser, and N. Wolf. Thanks also to T. DiMarzio and T. Hollmen at the Alaska SeaLife Center for their assistance in planning and carrying out the controlled feeding experiment.

This publication is dedicated to Dr. David Tessler, USFWS scientist, whose untimely passing diminishes us all. Dave was a dedicated, enthusiastic, and superb non-game biologist and ecologist in Alaska and Hawai‘i. Dave’s contributions include establishing highly interdisciplinary teams comprising Federal and State researchers, university students and faculty, and the public. He was committed to providing relevant ecological data and information to inform resource managers and conservation programs. He is missed.

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