



Abstract—The North American river otter (*Lontra canadensis*) is mainly an opportunistic forager inhabiting coastal areas throughout the Pacific Northwest of the United States. Using parts from scat samples, collected along the estuaries of the Wa'atch and Tsoo-Yess Rivers in Washington State during the summer of 2018 and the spring and summer of 2019, we analyzed the diet of this species in estuaries of Makah Bay. We documented one of the most diverse diets of North American river otters in Washington: 45 prey species were identified among 17 fish families and 10 decapod taxa. Pacific staghorn sculpin (*Leptocottus armatus*), saddle-back gunnel (*Pholis* sp. cf. *ornata*), and starry flounder (*Platichthys stellatus*) were the 3 most prevalent species in the diet of North American river otters (>47% frequency of occurrence for each of the 3 species). We suggest that the variation among prey species in the diet was driven primarily by habitat, followed by prey abundance and availability. Limited incidences of subtidal prey species, instances of high-volume predation on dense aggregations of fish prey, and the presence of commercially important species open interesting insights into foraging behavior or prey species distribution. Our study resulted in the first description of the diet of North American river otters in the area.

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Estuarine diet of North American river otters (*Lontra canadensis*) in Makah Bay on the Makah Indian Reservation in Washington

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North American river otters (*Lontra canadensis*) are typically opportunistic feeders and frequently forage in coastal environments, leading to highly diverse diets of teleost fish species and crustacean species (Guertin et al., 2010; Buzzell et al., 2014). The diet of North American river otters affects multiple trophic levels, influencing ecosystems through direct predation (Ben-David et al., 1998). Consequently, much attention has been paid to documenting the diet of this species and to examining its potential effect on species of conservation or management concern (Buzzell et al., 2014; Scordino et al., 2016; Buzzell et al., 2023).

North American river otters eat fish in both marine and freshwater habitats, but specific prey items are most often dictated by habitat, ease of capture and handling, and optimal metabolic benefit (Cote et al., 2008; Thompson and Stelle, 2014; Cosby and Szykman Gunther, 2021). Seasonality also influences their diet, as it dictates changes in prey availability (Crowley

et al., 2013; Day et al., 2015). For example, North American river otters in coastal habitats tend to consume more crustaceans from early spring to summer and more fish in fall and winter (Larsen, 1984; Day et al., 2015). Therefore, they may have an effect on species of conservation concern, such as rockfishes (*Sebastes* spp.) (Buzzell et al., 2014), Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) (Scordino et al., 2016) but also on detrimental species of management concern, such as the invasive European green crab (*Carcinus maenas*) (Buzzell et al., 2023).

The Wa'atch River and Tsoo-Yess River estuaries of the Makah Indian Reservation, on the northwest coast of the Olympic Peninsula in Washington State, are 2 sites for which describing the diet of North American river otters is important. The 2 rivers host economically important species like Pacific salmon and steelhead (hereafter, when referring to these taxa together, we will use the term *salmonids*) and

juvenile Dungeness crab (*Metacarcinus magister*). The Makah National Fish Hatchery raises and releases steelhead, Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) into both rivers, which empty into Makah Bay (USFWS¹). The 2 rivers also serve as refuges for chum salmon (*O. keta*), coastal cutthroat trout (*O. clarkii*), and a variety of other estuarine and nearshore fishes and crustaceans (Bizzarro et al.²).

In a previous study, we examined the potential of North American river otters to serve as a biotic control of green crab in the Wa'atch and Tsoo-Yess Rivers (Buzzell et al., 2023). Herein, we provide a detailed description of the diet of the North American river otter to assess consumption of species of concern and to document dietary patterns.

Materials and methods

We followed routine methods of collecting scat samples and analyzing parts found in them that are described in Buzzell et al. (2023). Briefly, 4 active latrines (sites of marking and defecation) used by North American river otters were studied along both the Wa'atch and Tsoo-Yess Rivers. Prey identification was conducted by analyzing undigested remains (bones and shells) found in scat samples. Samples of scat were collected every other week on the Wa'atch River during August–September 2018 and April–September 2019 and on the Tsoo-Yess River during May–September 2019. All scat samples were collectively pooled to describe the diet of this species in Makah Bay.

Prey items were identified to the lowest possible taxon. Crustacean prey items were identified by the senior author by using reference specimens of various lengths and sizes (courtesy of the Makah Tribe; collection housed at Western Washington University [WWU]). Other invertebrates (e.g., insects and mollusks) and miscellaneous prey taxa were diagnosed by using morphological characteristics and reference collections, with identifications made to the lowest reliable taxonomic level on a case-by-case basis. Color, claw type, texture, and carapace morphology were all diagnostic characteristics used to identify the remains of crabs. Fish remains were identified by an experienced food habits specialist, William Walker of the NOAA Marine Mammal Laboratory, who used reference bones and otoliths housed at that laboratory in Seattle, Washington. For a fish taxon mentioned in this text and for several fish taxa listed as prey items in [Supplementary Tables 1 and 2](#), the use of the abbreviation *cf.* indicates confidence with the identification of genus and strong likelihood with species when either reference specimens were not available or

when samples lacked distinguishable features (e.g., otolith samples). Prey items with *cf.* in their names are considered to be in a separate category from prey taxa with confident species identification.

We used frequency of occurrence (FO) (Trites and Joy, 2005) to examine and describe spatial (Tsoo-Yess and Wa'atch Rivers) and temporal (spring and summer seasons) variations in the diet of North American river otters. Values of FO are expressed in percentages and were calculated as follows:

$$FO_i = \frac{\sum_{k=1}^s O_{ik}}{s} \times 100,$$

where $O_{ik} = 0$ if taxon i is absent in scat sample k and 1 if taxon i is present in scat sample k ; and s = the total number of scat samples.

For relatively small FO values (<10%), we also report the number of scat samples containing the prey item to describe notable observations in changes between scat collection dates and periods.

Counts of fish otoliths were recorded to determine the minimum number of individuals (MNI) consumed in individual scat samples, and size of fish taxa found in samples were recorded when possible (Harvey et al., 2000; Lance et al.³). For crustaceans, MNI was determined by using protocols adapted from Lance et al.³ to enumerate crustacean rostrums, legs, and claws when these types of remains were present. Several studies have revealed the limitations of diet studies in which FO and MNI, which can both underestimate and overestimate prey taxa, are used (Van Dijk et al., 2007; Crimmins et al., 2009; Tsukada et al., 2020). However, we offer these metrics as descriptive indices rather than standalone measures of prey importance. Additionally, scat samples were consistently collected over several months, improving knowledge of relative shifts in prey availability and important prey types.

Otoliths were enumerated and graded according to condition (*poor*, *fair*, and *good*), following Tollit et al. (2004), and otolith lengths were measured to the nearest 0.1 mm by using digital calipers under 10× magnification. For salmonids, widths of vertebrae were measured (in millimeters) in the absence of otoliths to classify them into a life stage (i.e., smolt, juvenile, or adult). For all fish, a true MNI from the use of all possible prey structures was not calculated (Browne et al., 2002); however, we a posteriori used the count of right or left otoliths, whichever was greater, to discuss MNI. Length regression formulas from various sources were applied to fish otolith lengths (in millimeters) to estimate standard lengths (in centimeters) of fish prey when possible. Formulas were derived from Harvey et al. (2000) to estimate lengths of Pacific staghorn sculpin (*Leptocottus armatus*), starry flounder (*Platichthys stellatus*), and shiner perch (*Cymatogaster aggregata*). The

¹ USFWS (U.S. Fish and Wildlife Service). 2009. Quilcene, Quinalt, and Makah National Fish Hatcheries: assessments and recommendations. Final report, 259 p. Hatch. Review Team, Pac. Region, USFWS, Portland, OR. [Available from [website](#).]

² Bizzarro, J. J., J. Selleck, K. Sherman, J. Drinkwin, V. C. Hare, and D.S. Fox. 2022. State of the knowledge: U.S. West Coast nearshore habitat use by fish assemblages and select invertebrates, 182 p. Pac. Mar. Estuar. Fish Habitat Partnersh., Portland, OR. [Available from [website](#).]

³ Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. NOAA, Natl. Mar. Fish. Serv., Alsk. Fish. Sci. Cent., AFSC Process. Rep. 2001-04, 29 p. [Available from [website](#).]

formula for steelhead was derived from Sweeney and Harvey (2011), and the formula for coho salmon was derived from Nelson et al. (2021).

Information on the release of salmonids was acquired from the Makah National Fish Hatchery, located approximately 5.5 km up the Tsoo-Yess River, and was compared with the prey consumption (FO and MNI values) by North American river otters estimated from scat samples.

Results and discussion

We recorded one of the most diverse diets of North American river otters for Washington State. In 453 scat samples collected on the Wa'atch River and 269 scat samples collected on the Tsoo-Yess River, a total of 45 teleost and crustacean species were identified among 27 prey groups separated by family or a broader taxon (Suppl. Table 1). Diet composition was dominated by brackish-water species, reflecting the estuarine nature of both river systems, although freshwater and marine taxa were commonly consumed as well. The number of prey species exceeds those of other diet studies in coastal habitats of the Pacific Northwest, including southern Vancouver Island, in Canada, and the San Juan Islands, in Washington, by 15 and 17 species, respectively (Guertin et al., 2010; Buzzell et al., 2014). Still, a key finding was similar between these studies and our study: teleost fishes were the most frequently consumed taxonomic group, followed by decapod crustaceans.

In this study, 3 fish taxa, including Pacific staghorn sculpin, saddleback gunnel (*Pholis* sp. cf. *ornata*), and starry flounder, occurred in scat samples as prey items at FO >47%. Dungeness crab and shiner perch were the fourth and fifth most frequently observed prey species overall (FO: 25.5% and 24.4%, respectively). With few exceptions, the most frequently consumed taxa were the same whether FO or MNI was used. One of the exceptions was salmonids, which had a relatively low FO (<6%), but a minimum of 60 individual Chinook salmon were observed in scat samples. Although the relative importance of fish species found in the diet of North American river otters varies along the west coast of North America, our findings are similar to those from other studies in which marine and estuarine diets were documented for North American river otters in the Pacific Northwest (Guertin et al., 2010; Buzzell et al., 2014; Russell, 2015).

North American river otters appeared to eat small fish (Suppl. Table 2). Standard lengths (SL) of identified fish that could be calculated from otoliths were consistently estimated at <20 cm, and all precaudal and abdominal vertebrae measurements for salmonids were those typical of juveniles (under 3.0 mm; Thomas et al., 2017). Pacific staghorn sculpin measured ≤19.7 cm SL, starry flounder measured between 4.6 and 18.7 cm SL, and shiner perch measured ≤11.3 cm SL. Salmonids measured ≤18.3 cm SL, except for one coho salmon estimated at 35.9 cm SL. Using measurements of vertebrae in addition to otoliths for salmonids, we found that 32 scat samples contained bones

from fish estimated to be the size of adults (≥37.5 cm SL), 26 scat samples had parts from fish estimated to the size of smolts (≤20 cm SL), and 25 scat samples contained vertebrae for which size was classified as unknown (Nelson et al., 2021). Notably, 58 smolts of Chinook salmon ranging in size from 61.7 to 88.6 mm SL were encountered in 12 scat samples collected on a single day (31 May 2019) from the Tsoo-Yess River. Given that otoliths from all eaten fish are not recovered, this number is likely an underestimate of the total consumption of Chinook salmon smolts (Crimmins et al., 2009). Our results are typical of those of other studies in which North American river otters generally ate fish of small sizes, typically less than 25 cm SL, with few exceptions (e.g., Cote et al., 2008).

Increased predation on salmonid smolts followed releases from the Makah National Fish Hatchery on the Tsoo-Yess River. The release of steelhead smolts on 26 April 2019 coincided with higher occurrences of steelhead in scat samples collected on 8 May (7 samples), and release of Chinook salmon smolts on 29 May 2019 coincided with higher occurrences (and MNI values) in scat samples collected on 31 May (5 samples). Few scat samples collected from the Tsoo-Yess River in May contained adult salmonids (3 samples), whereas scat remains collected in May from the Wa'atch River had more adults (7 samples) and fewer smolts (3 samples). In both rivers, occurrences of smolts declined after June (April–June: 23 scat samples; July–September: 4 samples), and occurrences of adults slightly increased (April–June: 15 samples; July–September: 19 samples). Adult Chinook and coho salmon and hatchery-reared steelhead return to the Tsoo-Yess River starting in September–October, and steelhead of natural origin return from mid-March through June (USFWS¹). Scat samples collected in spring (April–June) may reflect consumption of natural-origin adult steelhead, whereas scat samples collected in late summer likely capture the consumption of other salmonids at the start of fall returns. Similar trends have been observed in other studies of the diet of river otters for sockeye salmon (*O. nerka*) and Atlantic salmon (*Salmo salar*) (Scordino et al., 2016; Sortland et al., 2023). Yet, not all hatchery releases and adult migrations coincided with higher scat occurrences, warranting further investigation.

North American river otters are also known to scavenge fish carcasses that have washed up after spawning events or that have been discarded by fishermen (Hewson, 1995), possibly explaining the occasional presence of adult salmonids or deepwater marine prey, such as rockfishes and Pacific halibut (*Hippoglossus stenolepis*) (Suppl. Table 1). Parts of Pacific halibut were present in 4 scat samples collected from the Wa'atch River on 28 May 2019, and the collection of those samples coincided with known discards of fish carcasses into the river following a recreational fishery opening (A. Akmajian, unpubl. data). Although diagnostic parts were absent in samples and, therefore, not available to document the size of these prey species, these results support the idea that North American river otters are opportunistic foragers and highlight predator–prey interactions that might otherwise go unnoticed.

Identifications through the use of other remains (e.g., vertebrae) indicate that some species were eaten in greater quantities than could be discerned from identifications with otoliths alone. For example, parts of >150 individuals identified as gunnels (Pholidae) were found in a single scat sample, an observation never seen before in the diet of North American river otters (Walker⁴). Apart from analysis of remains of gunnels, counts of otoliths and vertebrae of several sculpin species (Cottidae), shiner perch, and bay pipefish (*Syngnathus leptorhynchus*) found in individual scat samples indicate that North American river otters were consuming >10 individuals of these species in a single feeding (Suppl. Table 1); hundreds of scutes from bay pipefish were also collected. North American river otters are known to use cooperative foraging strategies to corral schooling pelagic fishes (e.g., salmonids; Blundell et al., 2002a). Except for shiner perch, the other intertidal species (gunnels, sculpins, and bay pipefish) are not schooling species, and the presence of multiple individuals in a single scat sample likely reflects high local prey density, although similar cooperative foraging behavior cannot be ruled out. Specific species varied in numerical dominance, but this finding was consistent throughout the study period and mirrors the opportunistic diet strategy reported in previous studies (Day et al., 2015; Scordino et al., 2016). However, to our knowledge, this estimate is the first for prey quantity in samples of scat of North American river otters collected on the west coast of North America (Cote et al., 2008).

One unexpected finding was the observation of giant wrymouth (*Cryptacanthodes giganteus*) in scat samples from both rivers. The life history of giant wrymouth has been little studied (Beal et al., 2016). The species can grow to a total length of 123 cm, and it inhabits depths from 6 to 128 m but is most often found in depths <20 m (Schnell and Hilton, 2015). The presence of giant wrymouth and other subtidal species in scat samples indicates that North American river otters are foraging in marine waters (such as those in Makah Bay), encountering these species during high tides, or targeting juveniles that are using estuaries as nurseries (Schwartzkopf et al., 2020). In Prince William Sound, in Alaska, home ranges of coastal North American river otters can vary up to approximately 60 km and individuals can cross more than 6 km of open water (Blundell et al., 2002b). Although the depths at which this species dives have not been studied, Eurasian otters (*Lutra lutra*) have been reported to strongly prefer diving in waters <3 m deep (Nolet et al., 1993). Therefore, it is plausible that North American river otters deposit feces at latrines along the Wa'atch River or Tsoo-Yess River, the remains in which reflect prey captured in nearshore waters of Makah Bay, rather than those captured within the estuaries themselves.

The Dungeness crab was the most frequently occurring crustacean (FO: 25.5%), followed by signal crayfish

(*Pacifastacus leniusculus*) (FO: 8.6%) (Suppl. Table 1). Notably, MNI estimates indicate a seasonal increase between spring and summer in consumption of Dungeness crab from 76 to 130 individuals in scat samples collected on the Wa'atch River. This pattern likely reflects reduced opportunities for fish foraging caused by low river flows in summer. Signal crayfish occurred more frequently in scat samples from the Tsoo-Yess River (FO: 18.6%) than in those from the Wa'atch River (FO: 2.7%). In the Lake Ozette watershed on the Olympic Peninsula, signal crayfish have been found to be the most frequently consumed prey at an FO of 83.5% (Scordino et al., 2016). The moderate frequency of signal crayfish on the Tsoo-Yess River (FO: 21.8%) observed in this study indicates that North American river otters have a broad foraging range, given that most prey were either estuarine or marine species. Signal crayfish occur in the main channel of the Tsoo-Yess River and in tidal marshes of both rivers in areas that are typically above or outside of saltwater influence (Moss and Scordino⁵). This finding indicates that North American river otters forage upriver prior to moving downstream.

Because the diet of North American river otters often reflects changes in prey abundance and distribution, observed spatial differences in prey composition (e.g., consumption at the Wa'atch River versus that at the Tsoo-Yess River) likely mirror habitat variation, and temporal differences are driven by environmental factors. These factors include variable freshwater discharge, tidal dynamics, water temperature and salinity, hypoxia, presence of eelgrass, and prey life history traits (e.g., seasonal movements between deepwater and shallow water) (Sobocinski et al., 2018; Schwartzkopf et al., 2020). In addition, although latrines were located along the Wa'atch and Tsoo-Yess Rivers, the detection of deepwater species like the giant wrymouth indicates that some foraging likely occurred outside the estuaries, possibly in Makah Bay, or during high tides. This notion highlights the need for further research into the movement patterns of North American river otters, given that scat analysis alone may not fully capture the spatial scale of foraging behavior.

Anthropogenic activities also significantly shape the presence and abundance of managed prey species (Scordino et al., 2016; Moore et al., 2024). In our study, mass hatchery releases and discarded fish carcasses likely contributed to incidental predation and scavenging events. However, these occurrences should not be interpreted as evidence of a single-source diet but rather as evidence of opportunistic foraging behavior shaped by human-influenced food sources. Such behavior may also result in short-term, localized top-down pressure on vulnerable prey populations, particularly during predictable pulses like smolt releases in constrained systems (Crowley et al., 2013; Moore et al., 2024). This heightened predation

⁴ Walker, W. 2021. Personal commun. Mar. Mamm. Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sandy Point Way NE, Bldg. 1, Seattle, WA 98115-6349.

⁵ Moss, R., and J. Scordino. 2021. Where are the crayfish? [Poster presented as part of the Makah Fisheries Management Summer Internship Program run by the Makah Tribe.] [Available from [website](#).]

underscores the importance of considering predator–prey dynamics in the timing and management of hatchery operations.

Findings from this study emphasize the ecological importance of North American river otters as both predators and scavengers, influencing multiple trophic levels in estuarine and nearshore systems. Although the results of our study further support the notion of opportunistic and optimal foraging behavior for this species, with individuals selecting the most available prey (e.g., sculpins, gunnels, and Dungeness crab), North American river otters likely have prey preferences (e.g., salmonids and scavenged fish carcasses) to maximize caloric benefits when provided the opportunity. Future research should integrate movement studies to clarify foraging ranges, assess the effects on species of conservation concern, and inform adaptive management strategies that account for both natural and human-influenced food sources.

Resumen

La nutria de río norteamericana (*Lontra canadensis*) es principalmente un animal oportunista que habita las zonas costeras del noroeste de los Estados Unidos. Utilizando restos de excrementos, recogidos a lo largo de los estuarios de los ríos Wa'atch y Tsoo-Yess en el estado de Washington durante el verano de 2018 y en la primavera y el verano de 2019, analizamos la dieta de esta especie en los estuarios de la bahía de Makah. Documentamos una de las dietas más diversas de las nutrias de río norteamericanas en Washington: se identificaron 45 especies de presas entre 17 familias de peces y 10 taxones de decápodos. El charrasco de astas (*Leptocottus armatus*), el pez silla (*Pholis* sp. cf. *ornata*) y el lenguado estrellado (*Platichthys stellatus*) fueron las tres especies más frecuentes en la dieta de las nutrias de río norteamericanas (con una frecuencia de aparición superior al 47% para cada una de las tres especies). Sugerimos que la variación entre las especies de presas en la dieta se debió principalmente al hábitat, seguido de su abundancia y la disponibilidad. La incidencia limitada de especies de presas intermareal, los casos de depredación de gran volumen en densas agregaciones de presas piscícolas y la presencia de especies de importancia comercial ofrecen interesantes perspectivas sobre el comportamiento de búsqueda de alimento o la distribución de las especies de presas. Nuestro estudio dio como resultado la primera descripción de la dieta de las nutrias de río norteamericanas en la zona.

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