Holistic approaches for invasive species management: Exploring biotic resistance of European green crab (*Carcinus maenas*) via river otter (*Lontra canadensis*) diet

By

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ABSTRACT

Establishment of the European green crab (*Carcinus maenas*) on the west coast United States has led to concerns regarding loss of eelgrass beds and influence on marine communities. To begin examining whether predators can potentially buffer green crab expansion, I studied river otter (*Lontra canadensis*) diet from scat remains and estimated green crab abundance from removal trapping efforts. River otter scats on the Wa'atch and Tsoo-Yess rivers, Washington, USA, were collected during August-September 2018 and April-September 2019. Hard remains of prey were reported as percent frequency of occurrence, and green crab prey were compared to monthly catch-per-unit-effort (CPUE). Scats collected from the Tsoo-Yess River contained no green crab, perhaps due to the relatively low abundance of green crab compared to other crustacean and fish prey. River otters consumed green crab in the Wa'atch River, but its low occurrence in their diet (0.7-5.2%) suggests that they were not an important prey source. However, I hypothesize that if green crab numbers increase there will be a subsequent increase in consumption by river otters and, as such, suggest documenting the population status of green crabs in both rivers, and conducting additional predator-prey diet studies to gauge the potential for long-term biotic resistance of green crab populations.

ACKNOWLEDGMENTS

Scientific studies are rarely the product of a single individual, and I would like to take a moment to acknowledge the many that contributed to my thesis work. First, I would like to thank the Makah Tribe for allowing me to conduct this study on their land and the lands of their ancestors. Adrianne Akmajian took me in on faith as the lead for this project prior to my acceptance into graduate school. Adrianne's support and mentorship has been critical to the implementation and development of this study. My thesis committee chair Alejandro Gutiérrez-Acevedo has been a long-time mentor for me since I was an undergraduate and has shaped me into the scientist I am today. Alejandro's constructive criticism, guidance, and patience with manuscript edits and revisions have been instrumental for the progression of my thesis. Benjamin Miner served as a thesis committee member, providing as-needed guidance on the focus of thesis writing. Lora Halttunen and Angelina Woods helped with scat collections and cleaning. William Walker provided training in prey identification and hard parts analysis and conducted all fish prey identification, otolith counts and measurements. Chaya Gaberria, Jeffrey Jasper, and Maren Stratton helped sort hard remains, and Orly Lindner helped with cleaning scats. Peter Thut helped me establish a scat-cleaning room and acquired/supplied miscellaneous equipment to facilitate scat processing. Tracey Finch and Theresa Barnhart guided my efforts in attaining grant funding and navigating Western Washington University's Research and Sponsored Programs. This work was funded by the North Pacific Coast Marine Resource Committee of Jefferson County, Conservation Research and Education Opportunities International, and Western Washington University's Research and Sponsored Programs.

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INTRODUCTION

Successful establishment and propagation of non-indigenous species can greatly alter ecosystems and adversely impact cultural and economic resources (Pimentel et al. 2005). Consequently, mitigation of invasive species, especially those of known negative socioeconomic effects, is one of the principal environmental concerns for present-day conservation efforts (Meffe, 2006). Establishment and persistence of invasive species is often dependent on the vulnerability of the native community, but the response of native species can help buffer the impact of invasions (Henriksson et al. 2016). For example, the hemlock wooly adelgid (*Adelges tsugae*) is an invasive insect linked to the death and decline of hemlock trees in eastern North America (Rose et al. 2020). In western Washington and Oregon, a lineage of the hemlock wooly adelgid is also present, but there is no evidence of impact on native hemlocks such as that in eastern North America. Several species of aphid flies (*Leucopis argenticollis, L. piniperda*, *Laricobius nigrinus*) prey upon the western lineage of adelgid, suggesting that these predators could be used as a biological control in eastern North America. Similarly, the wooly apple aphid (*Eriosoma lanigerum*) is a pest of apple orchards in eastern Washington, but the cumulative effects of a parasite and two natural predators have suggested that the potential for suppression of this aphid is best accomplished by supporting native predator communities (Gontijo et al., 2015). Understanding predatory-prey interactions after the introduction of invasive species can be helpful in creating a holistic approach to invasive species control (Ehler, 1998; Zavaleta et al., 2001; Van Driesche et al., 2010). However, the first step in understanding such interactions is to document the diet of potential predators of the invasive species in question.

The European green crab, *Carcinus maenas* (Linnaeus, 1758; hereafter “green crab”), is listed as one of the 100 worst invasive species by the International Union for Conservation of

Nature (GISD, 2009). The green crab is a shore crab with broad temperature and salinity tolerances that inhabits both rocky and soft-bottomed estuaries and marshes, making it highly adaptable and quick to colonize new habitats (Grosholz and Ruiz, 2002; Hidalgo et al., 2005). Green crab were first introduced mainly through shipping activity on the U.S. east coast in the 1800's, then propagated northward and established in the Canadian Atlantic (Williams, 1984; Grosholz and Ruiz, 1996). Eventually, green crab abundance led to a significant decline of the softshell clam (*Maya arenaria*) fishery in the mid-1900's and is still a well-known threat to east coast aquaculture (Glude 1955, Tan and Beal 2015). Green crab were not detected on the U.S. west coast until 1989 in San Francisco Bay, but rapidly spread northward to Oregon, Washington, and British Columbia over the next 10 years (Cohen et al. 1995, Grosholz and Ruiz 1996). Rapid migration has been attributed to larval dispersal during El Niño events, such as the recent El Niño event of 2014-15 which introduced green crab into the Salish Sea (Jamieson et al. 2002, Yamada et al. 2005, 2017). Persistence of these warming events due to climate change suggests green crab will continue to propagate along the west coast and potentially establish as far as the northeast Pacific (Hines et al. 2004; Yamada et al. 2008).

Green crab affects coastal flora and fauna communities through predation and the uprooting of eelgrass beds (Davis et al., 1998; Grosholz et al., 2000; Jackson et al., 2001). Eelgrass disturbance is of particular concern along the west coast of Washington State, USA, due to the potential to destroy habitat for juvenile fish such as ESA-listed Pacific salmon (*Onchorhynchus* spp.), and plant dwelling invertebrates such as juvenile and sub-adult Dungeness crab *(Metacarcinus magister*) (Murphy et al. 2000, Jackson et al. 2001, Polte et al. 2005, Morris et al. 2011). In addition, these invasive crabs successfully prey upon and outcompete juvenile Dungeness crabs in a manipulated artificial setting (Dare et al., 1983;

McDonald et al., 2001; de Rivera et al., 2011). Consequently, the possible ecological and economic impact of their propagation has become a priority concern for natural resource managers in Washington State (Grosholz and Ruiz 1996, Colnar and Landis 2007, Drinkwin et al. 2019).

Green crabs were recently documented in the waters of the Makah Indian Reservation in northwest Washington State (Akmajian, 2017). From 2018 through 2020, the Makah Tribe trapped green crabs for removal within the lower estuaries of the Wa'atch and Tsoo-Yess rivers, catching more than 3,500 green crabs. By contrast, no green crab have been captured inside Neah Bay on the Strait of Juan de Fuca side of the Reservation (Grason, 2018). This absence might be due to competition and predation by larger cancrid crab species, such as red rock crab (*Cancer productus*) and adult Dungeness crab, which are prevalent in the bay compared to the channels and sloughs of the two coastal rivers (Jensen et al. 2007). Hunt and Yamada (2003) observed little overlap of the red rock crab and green crab in Yaquina, Oregon, which was attributed to the aggressiveness of the red rock crab. Hence, biological resistance might be a principal factor in mitigating the expansion of green crab on the US west coast.

The North American river otter, *Lontra canadensis* (Shreber, 1777; hereafter otter), is an aquatic mustelid that frequently inhabits coastal environments in Washington State (Jones, 2000; Buzzell et al., 2014; Russell, 2015). Otter diet affects multiple trophic levels, influencing ecosystems through both direct predation and indirect nutrient transfer between terrestrial and marine habitats (Ben-David et al. 1998, Roe et al. 2010). As such, much attention has been given to otters and their potential influence on fisheries, particularly salmon and hatcheries (Serfass et al. 1990, Dolloff 1993, Scordino et al. 2016), but less so on their potential to act as a buffer for invasive species management (Feltrop et al., 2016). In this regard, a study in Illinois documented invasive Asian carp (*Hypophthalmichthys molitrix* and *H. nobilis*) in the diet of otters (Feltrop et al., 2016). Although the occurrence of the invasive was low (2.6% of scats), two scats revealed the presence of Asian carp where the species had not previously been found. Consequently, otter diet provided information on the spatial range of the Asian carp, and thus can be used as an indicator of invasive species presence.

With few exceptions, otters most often consume fish in both marine and freshwater habitats, but crustaceans also play an important role in their diet (Larsen 1984, Bowyer et al. 1994, Ben-David et al. 1998, Jones 2000, Cote et al. 2008). Specific prey items are most often dictated by habitat, relative prey abundance, and ease of capture (Cote et al., 2008; Day et al., 2015). Seasonality also influences river otter diet, as it dictates fluxes in prey availability (Crowley et al., 2013). For example, otters tend to consume more crustaceans from early spring to summer in coastal habitats and more fish in fall and winter (Larsen, 1984; Jones, 2000; Day et al. 2015; Oates et al., 2019). It has been suggested that this compensatory relationship in coastal-marine otter diets is due to summer low tides that restrict the movement of water and thus water volume used by potential prey species (Larsen 1984, Jones 2000). Consequently, documenting otter diet in the spring and summer allows for a greater diversity of crab prey to be observed compared to fall and winter.

The green crab was previously reported as a predominant prey type for European river otters (*Lutra lutra*) in a Scottish sea loch, and as a potential prey item of river otters in Massachusetts (Mason and Macdonald 1979, Conkerton et al. 2017). In Washington State, potential predation of green crabs by otters was suspected in south Padilla Bay due to the remains of one green crab found during exploratory trapping (Grason, 2017). In 2018, otter latrines, or commonly used areas for defecation and marking, were observed along the lower

Wa'atch River within the same vicinity of green crab removal efforts. This observation prompted the question of whether otters consume green crab at these sites. In May of 2019, additional otter latrines were discovered along the banks of the Tsoo-Yess River, also in the same vicinity as green crab removal trapping. Due to this apparent overlap in habitat, there is reason to believe otters are consuming green crab in both rivers and could act as a natural control for green crab in these estuaries.

The response of green crab populations to otter predation would determine the potential of the latter as a natural control. However, the first step is to determine (1) if river otters consume green crab and (2) if such consumption varies relative to time and/or green crab abundance. I used scat analysis of hard remains to thoroughly describe otter diet for estuaries of the Wa'atch and Tsoo-Yess rivers from August to September 2018 and April to September of 2019, with a particular focus on green crab consumption. I hypothesized that green crab would occur more frequently in scats found at Tsoo-Yess River latrines than at Wa'atch River latrines because greater numbers of green crab are captured in removal trapping on the Tsoo-Yess River than in the Wa'atch River (Akmajian 2020). I investigated differences in consumption of green crab between seasons (spring and summer of 2019) and years (summers of 2018 and 2019). Finally, to explore possible green crab mitigation via otter consumption. I also examined the association between green crab consumption by otters and green crab abundance based on average catch rates during the 2019 trapping season.

METHODS

Study Sites

The present study was conducted within 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, USA (Figure 1). The Wa'atch River and the Tsoo-Yess River originate in the lower foothills of the Olympic Mountain range and empty into the Pacific Ocean at Makah Bay. The two rivers are several miles long with the last two miles heavily influenced by tidal mixing. The habitat of the Wa'atch and Tsoo-Yess riverine estuaries is mainly composed of brackish emergent tidal marsh (West Coast Estuaries Explorer[1]). The mixed semidiurnal tides and increased freshwater output during periods of heavy rain dictate erosion of the banks and tide pools within both rivers.

A variety of fish and crab inhabit both rivers, including economically important species like salmon and juvenile Dungeness crab. The Makah National Fish Hatchery raises and releases steelhead (*O. mykiss*), Chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*) into both rivers (Zajac 2002). Releases are based on factors including fish size and physiological condition, tides, time of day, river conditions (low and high tides), hatchery conditions, and operational logistics[2]. The two rivers also serve as refuge for chum salmon (*O. keta*), cutthroat trout (*O. clarkia*), pink salmon (*O. gorbuscha*), subadult Dungeness crab, hairy and purple shore crabs (*Hemigrapsus oregonensis* and *H. nudus*, respectively), bay pipe fish (*Syngnathus leptorhynchus*), gunnels (*Pholis* sp.), three-spine stickleback (*Gasterosteus aculeatus*), Pacific

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[1] https://estuaries.pacificfishhabitat.org/
[2] Cross, B. 2019. Personal commun. Supervisory Fish Biologist, U.S. Fish and Wildlife Service, Western Washington Fish and Wildlife Conservation Office 510 Desmond Drive SE, Ste. 102 Lacey, WA 98503, Benjamin_cross@fws.gov.

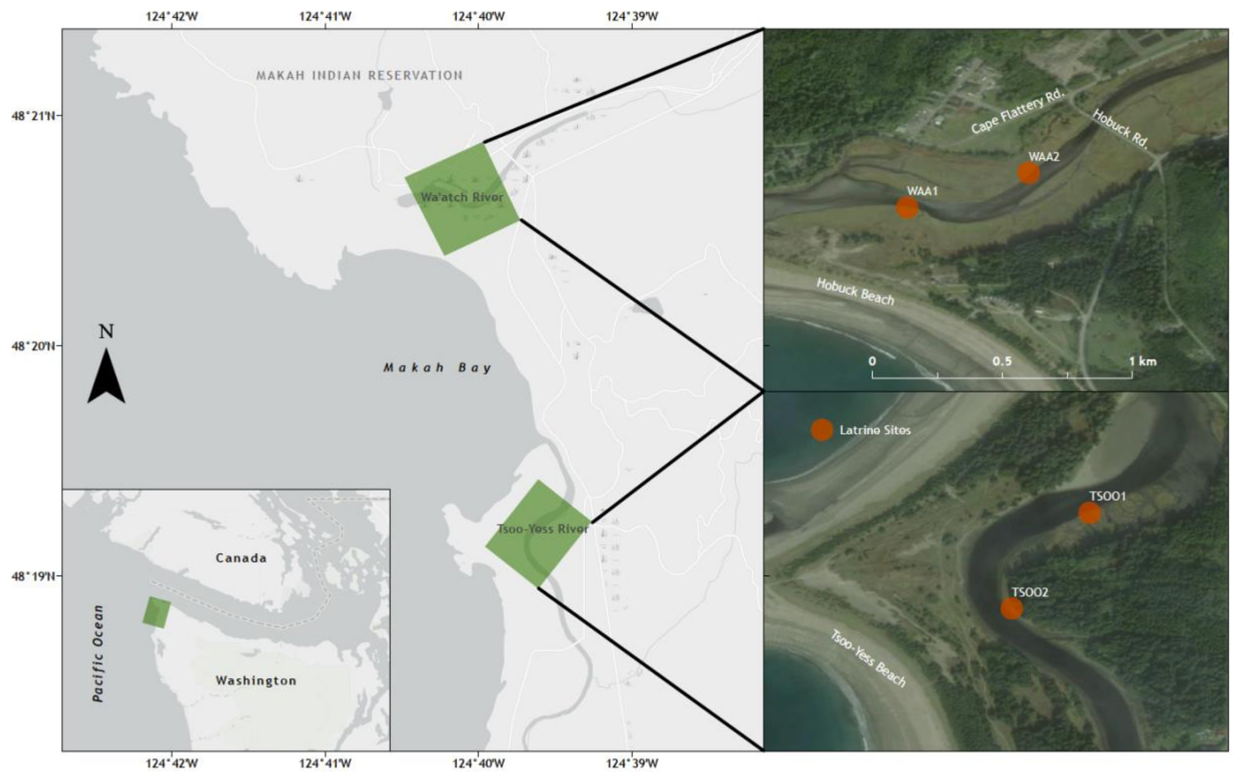

Figure 1

River otter (*Lontra canadensis*) scat collection sites (latrines) for the lower Wa'atch and Tsoo-Yess rivers, located within the boundaries of the Makah Indian Reservation in Washington State[3].

[3] Map layer sources: WA State Parks GIS, ESRI, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, USDA, NRCan, Parks Canada, GeoEye, Maxar, FAO, NOAA, Bureau of Land Management, NPS

staghorn sculpin (*Leptocottus armatus*), prickly sculpin (*Cottus asper*), tidepool sculpin (*Oligocottus maculosus*), shiner perch (*Cymatogaster aggregata*), and more (Zajac 2002, Akmajian 2020).

Four active river otter latrine sites were identified along the Wa'atch and Tsoo-Yess rivers during the spring and summer of 2019 (Figure 1). On the Wa'atch River, latrine sites were located on each of the north (WAA1) and south (WAA2) banks less than 1.5 km upstream of the river mouth. On the lower Tsoo-Yess River two latrine sites were found on the east bank (TSOO1 and TSOO2), approximately 0.8 and 1.2 km upstream of the river mouth. There are currently no population estimates for otters on the Makah Reservation, hence it is unknown how many otters use each latrine. Otters consistently return to the same latrines to defecate and leave behind scent to increase avoidance among groups and individuals (Lariviere et al. 1998). Such behavior suggests a strong likelihood that the same individuals returned to the same latrine sites over the course of sample collections.

Diet Analysis

Prey identification via scat analysis of undigested remains (bones and shells) is a widely used method for documenting diet (Larsen 1984, Stenson et al. 1984, Manning 1990, Day et al. 2015). Despite inherent biases caused by the likeliness of over and underestimating prey consumption, identifying prey through scat remains is non-invasive and can still reveal information about prey taxon, size, count, and diet preferences when analyzed conservatively (Lance et al., 2001; Crimmins et al., 2009). Transit time of food by otters has been documented at an average time of roughly 3 hours, which can provide a snapshot of current diet (Davis et al., 1992; White et al., 2007). Thus, this method allows for perspective on recently consumed prey items.

Scat Collection

Rarefaction curves were used to determine a sampling goal prior to the start of sampling (Trites and Joy 2005). Using scat samples and prey data from previously documented coastal otter diet, 50 otter scats per river and per month would be adequate for describing otter diet (Buzzell et al. 2014). Rarefaction curves with hypothetical asymptotes were then used *a posteriori* to visually assess if enough scats were collected for describing diet by river and season with the given number of identified prey species. All rarefaction curves were conducted in R (vers. 1.2.5; R Core Team 2019).

Collection of otter scat began in April 2019 on the Wa'atch River and in May for the Tsoo-Yess River. Otter scats were collected bi-weekly during low tide to ensure accessibility of the latrine sites and to coincide with scheduled green crab trapping efforts. However, if latrines were scarce of scats during those weeks, additional collection days occurred the next week to maintain the minimum collection goal for each month. While I completed most 2019 collections on my own, Makah Fisheries technicians and volunteers also collected scat samples. Scats in 2018 were collected by Makah Fisheries staff and technicians.

I followed collection and scat cleaning protocols based on methods described for pinnipeds in Lance et al. (2001), which have been used for otters in multiple studies (Buzzell et al., 2014; Russell, 2015; Scordino et al., 2016). Briefly, individual scats were collected in Ziploc® bags with labels stating the date, location, and a unique identifier, then stored in a lab freezer at the Makah Tribal Center until further processing could take place. I prioritized the collection of fresher scats, which could be distinguished from older scats by color, smell, and moisture content. Drier scats that appeared dark in color and with no evidence of erosion, or visually undisturbed, were still collected due to the happenstance that they were exposed to more intense heat in the last few days prior to collection. Uncollected, old scats were destroyed via disposal in the river to prevent confusion during subsequent collections. To clean scats, each bag of scat was removed from the freezer and thawed in warm water mixed with liquid dish soap for one hour or more. Individual scats were then agitated in the bag before rinsing them through 1 mm and 500 µm stacked test mesh sieves (Gilson company, INC). All hard parts were removed with forceps and placed in 20 ml glass scintillation vials. After filling vials with 70% isopropyl alcohol (Mountain Falls™), the vials were stored for at least 2 weeks before being placed in a drying oven set at 90° C for 3 days or until all liquid was evaporated.

Prey Identification and Reporting

Prey items were identified to the lowest possible taxon which specificity was dependent on the condition of remains and available reference specimens. Reference invertebrate prey specimens of various lengths and sizes were collected during green crab trapping and beach seines (courtesy of the Makah Tribe; collection housed at WWU). Color, claw, texture, and carapace morphology were all factors used to identify remains of crabs. Green crabs have unique identifying characteristics compared to other native crabs within Washington State (e.g., Dungeness crab, hairy shore crab), which greatly aided in classification (Leignel et al., 2014). Fish remains were identified similarly by an experienced food habits specialist, William Walker at the NOAA Marine Mammal Lab, using reference bones and otoliths housed at the NOAA

Marine Mammal Lab in Seattle, Washington. Several fish prey taxa with “cf.” indicate confidence with the identification of genus and strong likelihood with species when either reference specimens were not available or samples lacked distinguishable features (e.g., otoliths). Prey with cf. are reported separately from prey taxa with confident species identification.

Based on Trites and Joy (2005), I used frequency of occurrence to examine and describe spatial (Tsoo-Yess and Wa’atch rivers) and temporal (spring and summer seasons, months, years) variations in otter diet of green crab. Percent frequency of occurrence (%FO) is expressed as:

$$(1) \quad \%\mathrm{FO}_i = \frac{\sum_{k=1}^{s} \mathrm{O}_{ik}}{s} \times 100$$

where $O_i = 0$ if taxon *i* is absent in fecal *k*

1 if taxon *i* is present in fecal *k*

s = total number of scat samples

Supplementary information was collected to determine minimum number of individuals (MNI) consumed in individual scats and fish prey size for prey taxa when possible (Harvey et al. 2000, Lance et al. 2001). Mr. Walker enumerated and graded otoliths according to condition (“poor”, “fair”, and “good”) following Tollit et al. (2004), and measured otolith lengths (mm) to the nearest 0.1mm using digital calipers under 10x magnification. For salmonids, he also measured vertebrae width (mm) to classify salmonids into life-stage category (i.e., smolt, juvenile, adult). For fish, a true MNI using all possible prey structures was not calculated (Browne et al. 2002), however *a posteriori* I used the greater count of right and left otoliths to discuss MNI relative to season and individual scats. Length regressions from Harvey et al. (2000) and Nelson et al. (in press) were applied to fish otolith lengths (mm) to estimate standard length (cm) of fish prey when possible. Salmonid release information and dates for 2019 were acquired from the Makah National Fish Hatchery to compare with river otter consumption and MNI. For crustaceans, MNI was determined using protocols adapted from Lance et al. (2001) to enumerate crustacean rostrums, legs and claws when these types of remains were present.

Green Crab Trapping and CPUE

To better understand the potential for green crab mitigation by otters in Makah Bay, I used catch-per-unit-effort (CPUE) of green crab for the 2019 trapping season as an estimate of green crab abundance for both rivers. For this study, CPUE was defined as number of crabs per trap per day. CPUE has been previously used to estimate green crab abundance but is limited in that it cannot account for behavioral and environmental influences on abundance estimates (Murray and Seed 2010, Duncombe and Therriault 2017). Despite these limitations, I used CPUE as a proxy for abundance given that there is no population information on green crabs in the rivers.

Green crab trapping protocols were adapted from Washington Sea Grant Green Crab Team (Grason et al., 2018). The Makah Tribe Fisheries Department conducted green crab trapping biweekly from April to September of 2018 and 2019 during the height of green crab activity (McDonald et al., 2006; Akmajian and Halttunen, 2019; Akmajian, 2020). On both rivers, four different baited trap types were used of varying brands: Collapsible crayfish traps (Promar® Model TR-101, Gardena, CA), minnow (Gee®, Tackle Factory, Fillmore, NY), Russell shrimp trap (custom made McKay Shrimp and Crab Gear, Brinnon, WA; and Makah Fisheries Management (MFM), Neah Bay, WA), and 16-gauge recreational shrimp traps

(Willapa Marine, Raymond, WA). Crayfish traps had mesh made with polyethylene thread mesh and were collapsible, measuring approximately 24 inches by 18 inches by 8 inches. The 18-inch opening on either side of the trap was zip tied in two places to reduce the effective size of the opening to three, 6-inch openings. Minnow traps were cylindrical made with galvanized steel and modified to have 1.5-2-inch openings. Russell shrimp traps measured 24.5 inches by 24.5 inches by 14 inches (McKay) and 16.25 inches by 16.25 inches by 8.25 inches (MFM), and recreational shrimp traps measured 24 inches by 24 inches by 13 inches. Both Russell and recreational shrimp traps had a 1-inch mesh. Minnow, crayfish, and Russell traps used bait jars (Scotty, Sidney, BC), while shrimp traps have a built-in bait tunnel in the center of the traps made of 1-inch mesh.

Exact placement of traps was dependent on tides, but smaller traps (crayfish and minnow) were generally placed in the narrow channels and sloughs and larger Russell and shrimp traps were placed in the main channels of each river. Pacific herring (*Clupea pallasii*) was used to bait each trap due to its regional effectiveness and economic feasibility (Favaro et al. 2020). Traps were set during low tide and soaked for 24 hours, then redeployed and retrieved after another 24 hours. Shrimp traps were rebaited after the first 24 hours. At each of the 24-hour intervals, traps were emptied into a 5-gallon bucket and all captures were counted and identified to species. Other biological data (e.g., carapace width, color, sex, condition, etc.) was also collected on green crab, but are not relevant for the purposes of this study.

An average monthly CPUE of green crab was generated for each river (number of crabs per trap set). Damaged or malfunctioning traps were excluded from the summary. CPUE was graphed and plotted together with the minimum number of green crab documented during prey identification. CPUE of other important prey species was also generated where appropriate to examine a possible relationship between prey abundance and otter prey consumption.

RESULTS

Sampling Effort

A total of 540 otter scats were collected on the Wa'atch and Tsoo-Yess rivers between April and September of 2019 at the four latrine sites, and 134 otter scats were collected from WAA1 in 2018 (Table 1). Using all encountered prey taxa, rarefaction curves were conducted for each river by season and approached hypothetical asymptotes (Figure 2). Wa'atch spring and summer seasons approached hypothetical asymptotes at approximately 125 and 150 scats, respectively; Tsoo-Yess spring and summer seasons approached hypothetical asymptotes at approximately 75 and 105 scats, respectively. No rarefaction curve was completed for 2018 prey taxa because only crustacean prey results were available at the time of writing.

Prey Composition

Table 2 reports prey species with overall > 2 %FO to include green crab and Appendix Table 1 reports all other prey items with < 2 %FO. However, all salmon taxa were included in Table 2 regardless of %FO to not separate this prey group. Marine and freshwater fish and crustacean species were documented in otter diet at both rivers for scats collected in 2019. Fish were the most important and diverse prey source consumed by otters in the Wa'atch and Tsoo-Yess rivers, composed of 30 prey species and an additional 10 prey items identified to family or genus (Table 2, Appendix Table 1). However, only 3 fish prey taxa occurred at more than 50 %FO overall, and relative importance of these taxa were also reflected in MNI (Appendix Table 2). Based on the greater count of left or right otoliths present, the minimum number of fish

Table 1

Number of river otter (*Lontra canadensis*) scat collections by month for each river by latrine sites on the Wa'atch (WAA1 and WAA2) and Tsoo-Yess (TSOO1 and TSOO2) rivers in 2019 (2018 not included in Wa'atch subtotal or overall total).

River and Latrine Site	April	May	June	July	August	September	TOTAL by River/Site
Tsoo-Yess	-	44	58	79	31	15	227
TSOO1	-	30	18	51	10	12	121
TSOO2	-	14	40	28	21	3	106
Wa'atch	30	63	41	51	79	49	313
WAA1	30	47	25	19	75	49	245
WAA2	-	16	16	32	4	-	68
WAA1 (2018)	-	-	-	-	59	75	134
TOTAL by Month (2019)	30	107	99	130	110	64	540

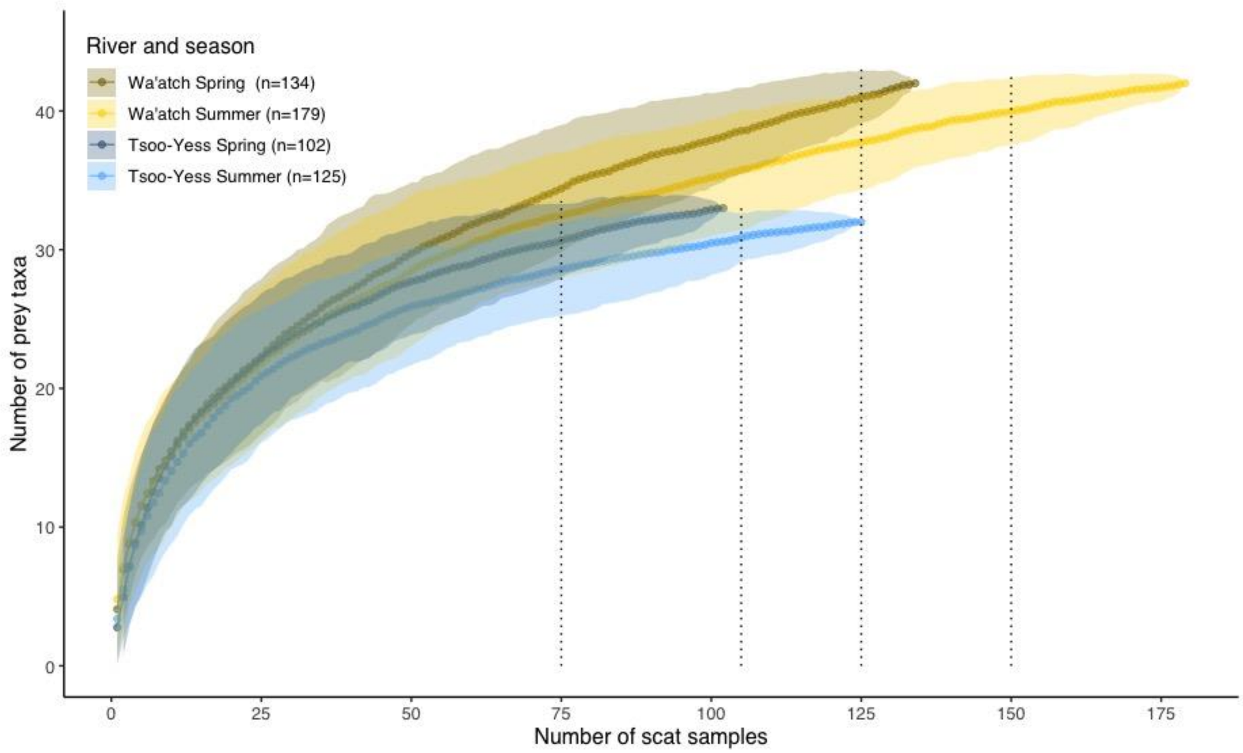

Figure 2

Rarefaction curves and variance of prey taxa by river and season observed in river otter (*Lontra candensis*) scats collected from latrines in spring (April-June) and summer (July-September) of 2019 on the Wa'atch and Tsoo-Yess river estuaries in Neah Bay, Washington; dotted vertical lines represent approximate number of samples at hypothetical asymptotes of 42 prey taxa (Wa'atch spring and summer) and 33 and 32 prey taxa (Tsoo-Yess spring and summer respectively) (permutations=100).

Table 2

Prey items found in > 2 % of river otter (*Lontra canadensis*) scats collected from the estuarine zones of the Wa'atch and Tsoo-Yess rivers for the spring and summer of 2019 (salmon kept together for brevity); results are reported as percentage frequency of occurrence (%FO) and total samples (n) are given for each collection period (* indicates possible scavenging event).

		Tsoo-Yess			Wa'atch		
Prey	Overall (n=540)	Spring (n= 102)	Summer (n=125)	Overall (n=227)	Spring (n=134)	Summer (n=179)	Overall (n=313)
GUNNEL							
Saddleback gunnel, likely (*Pholis* sp. cf. *P. ornata*)	63.9	53.9	70.4	63.6	63.4	65.4	64.5
FLATFISH							
Starry flounder (*Platichthys stellatus)*	53.0	36.3	61.6	50.7	41.8	64.8	55.0
SCULPIN							
Pacific staghorn sculpin (*Leptacottus armatus*)	51.5	19.6	45.6	34.2	56.7	69.8	64.2
Prickly sculpin (*Cottus asper*)	28.3	15.7	16.0	16.0	39.6	35.8	37.4
Padded sculpin, likely (*Artedius* sp. cf. *A. fenestralis*)	15.7	3.9	8.8	6.7	10.4	31.3	22.4
Slim sculpin (*Radulinus asprellus*)	5.6	16.7	8.0	12.0	1.5	0.6	1.0
Sculpin, unidentified (Family: Cottidae)	4.1	7.8	5.6	6.7	3.0	1.7	2.2
Irish lord, unidentified (*Hemilepidotus* sp.)	3.1	3.9	2.4	3.1	0.7	5.0	3.2
Red Irish lord (*Hemilepidotus hemilepidotus*)	2.6	2.0	5.6	4.0	3.7	-	1.6
Buffalo sculpin (*Enophrys bison*)	2.4	-	1.6	0.9	3.7	3.4	3.5
Sharpnose sculpin (*Clinocottus acuticeps*)	2.4	2.0	0.8	1.3	3.7	2.8	3.2
CRAB							
Dungeness crab (*Metacarcinus magister*)	28.1	8.8	16.8	13.3	36.6	40.8	39.0
Hairy shore crab (*Hemigrapsis oregonensis*)	3.3	1.0	-	0.4	0.7	8.9	5.4
European green crab (*Carcinus maenas*)	2.0	-	-	-	5.2	2.2	3.5
SURFPERCH							
Shiner perch (*Cymatogaster aggregata*)	27.2	10.8	19.2	15.6	25.4	43.6	35.8
STICKLEBACK							
Threespine stickleback (*Gasterosteus aculeatus*)	23.3	16.7	12.0	14.2	27.6	31.8	30.0
PIPEFISH							
Bay pipefish (*Sygnathus leptorhynchus*)	21.9	19.6	13.6	16.4	46.3	10.6	25.9
CRAYFISH							
Signal crayfish (*Pacifastacus leniusculus*)	11.1	23.5	20.8	22.2	2.2	3.9	3.2
Crayfish, unidentified (Family: Astacidae)	3.7	5.9	6.4	6.2	3.0	1.1	1.9
SALMON							
Salmon, unidentified (*Oncorhynchus* sp.)	8.0	7.8	6.4	7.1	14.9	3.9	8.6
Steelhead (*Oncorhynchus mykiss*)	2.8	12.7	1.6	6.7	-	-	-
Chinook salmon (*Oncorhynchus tshawytscha*)	2.2	4.9	4.8	4.9	0.7	-	0.3
Steelhead, likely (*Oncorhynchus* sp. cf. *O. mykiss*)	2.0	4.9	-	2.2	3.7	0.6	1.9
Coho salmon, likely (*Oncorhynchus* sp. cf. *O. kisutch*)	0.7	2.9	-	1.3	0.7	-	0.3
Coho salmon (*Oncorhynchus kisutch*)	0.6	-	0.8	0.4	0.7	0.6	0.6
Chinook salmon, likely (*Oncorhynchus* sp. cf. *O. tshawytscha*	0.4	-	-	-	-	1.1	0.6
Cutthroat trout (*Oncorhynchus clarkii*)	0.2	-	-	-	0.7	-	0.3
PRICKLEBACK							
Prickleback, unidentified (Family: Stichaeidae)	5.0	2.9	4	3.5	0.7	10.1	5.7
ROCKFISH							
Rockfish, unidentified (*Sebastes* sp.)*	3.7	-	-	-	13.4	1.1	6.4
MISCELLANEOUS							
Frog, unidentified (*Rana* sp.)	3.5	3.9	4.8	4.4	3.0	2.8	2.9
SNAILFISH							
Slipskin snailfish, likely (*Liparis* sp. cf. L. *fucensis*)	3.1	2.9	-	1.3	-	7.8	4.5
WRYMOUTH							
Giant wrymouth (*Cryptacanthodes giganteus*)	2.8	3.9	1.6	2.6	0.7	4.5	2.7

recovered in individual scat varied widely (Appendix Table 2). Estimated standard fish lengths were consistently estimated under 90 cm, with the exception of one coho salmon estimated at 183.4 cm (Appendix Table 3).

Among fish prey taxa, saddleback gunnel (*Pholis* sp. cf. *P. ornata*) was the most frequently observed fish prey on the Wa'atch and Tsoo-Yess rivers (64.5 %FO and 63.6 %FO, respectively). Starry flounder (*Platichthys stellatus*; 50.2 %FO in the Tsoo-Yess and 55.0 %FO in the Wa'atch) and Pacific staghorn sculpin (*Leptacottus armatus*; 34.2 %FO in the Tsoo-Yess and 64.2 %FO in the Wa'atch) followed saddleback gunnel (Table 2). Prickly sculpin, shiner perch, threespine stickleback, bay pipefish, and padded sculpin (*Artedius* sp. cf. *fenestralis*) occurred relatively less frequent overall (ranging from 15.7-28.3 %FO); however, %FO range of these prey items was higher on the Wa'atch than on the Tsoo-Yess River (22.4-35.4 %FO on the Wa'atch and 6.7 -16.4 %FO on the Tsoo-Yess). Steelhead, Chinook salmon, coho salmon, cutthroat trout (*Oncorhynchus clarkia*), and unidentified salmon (*Oncorhynchus* sp.) occurred overall in 0.2-8.0 %FO of scats. Unidentified salmon was the most predominant followed by steelhead on the Wa'atch River (8.6 %FO and 1.9 %FO, respectively) and Tsoo-Yess River (7.1 %FO and 6.7 %FO, respectively). Slim sculpin (*Radulinus asprellus*), unidentified sculpin (Family: Cottidae), unidentified prickleback (Family: Stichaidae), giant wrymouth (*Cryptacanthodes giganteus*), rockfish (*Sebastes* sp.), Irish lords (*Hemilepidotus* spp.), and slipskin snailfish (*Liparis fucensis*) occurred the least of all fish taxa reported overall in Table 2 (2.6-5.6 %FO). Otter consumption of slim sculpin was higher on the Tsoo-Yess River (12 %FO) than on the Wa'atch River (1.0 %FO). Unidentified flatfish (Family: Pleuronectidae), Pacific halibut (*Hippoglossus stenolepis*), English sole (*Parophyrys vetulus*), arrowtooth flounder (*Atherestes stomias*), sanddab (*Citharichthys* sp.), rock sole (*Lepidopsetta bilieneata*), and speckled sanddab (*Citharichthys stigmaeus*) occurred in <2 %FO of scats in both the Tsoo-Yess and Wa'atch rivers (Appendix Table 1).

Marine and freshwater crustaceans were also a diverse prey group in otter diet, with 8 identified species and an additional 7 whose identification was limited due to a lack of distinguishable characteristics (Table 2, Appendix Table 1). On the Wa'atch River, Dungeness crab occurred the most frequently (39.0 %FO) among crustacean prey, followed by hairy shore crab (5.4 %FO), green crab (3.5 %FO), and signal crayfish (*Pacifistacus leniusculus;* 3.2 %FO). Unidentified crayfish (Family: Astacidae) occurred in 1.9 %FO of Wa'atch scats, respectively; however, it is likely these remnants are signal crayfish but lacked key features to accurately identify to species (e.g., rostrum). Prey composition was similar for scats collected from Tsoo-Yess River latrines, but signal crayfish occurred in greater frequency than Dungeness crab overall (22.2 %FO and 13.3 %FO, respectively). Hairy shore crab occurred the least of crustacean prey and no green crab were observed in Tsoo-Yess River scats. Ghost shrimp (*Neotrypaea* sp.), Caridean shrimp (Infraorder: Caridea), bird (Class: Aves), squid (Class: Cephalopoda), and minnow (Family: Crypinidae) occurred in <2 % of scat in both rivers (Appendix Table 1). Polychaete worm jaws, sparse bivalve fragments, and whole-bodied isopods and amphipods occurred frequently in scats, but these remains were small (<1 cm) and most likely the result of incidental ingestion. For brevity, these items are not listed here as actively consumed prey. Frogs (*Rana* sp.) were also observed in low frequency (3.5 %FO; Table 2).

Fish prey results from 2018 were not ready at the time of thesis completion and are therefore not included. However, crustacean results from 2018 are available. Similar to Wa'atch prey data from 2019, Dungeness crab was the most frequently observed crustacean prey (17.8 %FO). An unidentified species of *Metacarcinus* (most likely Dungeness or graceful crab

(*Metacarcinus gracilis*)) was documented at 10.6 %FO. All other observed crustaceans, including green crab, hairy shore crab, signal crayfish, northern kelp crab (*Pugettia producta*) occurred in less than 2 %FO of otter scats.

Seasonal Prey Composition

Otter diet on the Wa'atch and Tsoo-Yess rivers show some evidence of seasonal variation between the spring and summer for several fish and crustacean prey species. In the Tsoo-Yess River, otters increased their consumption of saddleback gunnel, starry flounder, Pacific staghorn sculpin, dungeness crab, and shiner perch from spring to summer as shown in both %FO and MNI (Table 2; Appendix Table 2). Otter consumption of slim sculpin decreased from spring (16.7 %FO, MNI 85) to summer (8.0 %FO, MNI 18) and consumption of steelhead decreased from spring (12.7 %FO, MNI 18) to summer (1.6 %FO, MNI 1) in the Tsoo-Yess. Although the %FO of Chinook salmon shows marginal change from spring to summer (4.9 to 4.8 %FO), a minimum number of 58 individual Chinook smolts ranging from 61.7-88.6 mm were consumed in the spring on the Tsoo-Yess, specifically from a single collection day in May (Appendix Table 2, Appendix Table 3). In the Wa'atch River, otter consumption of starry flounder, Pacific staghorn sculpin, padded sculpin, and shiner perch increased from spring (41.8 %FO, 56.7 %FO, 10.4 %FO, 25.4 %FO, respectively) to summer (64.8%FO, 69.8 %FO, 31.3 %FO, 43.6 %FO, respectively), which is also reflected in MNI. Change in consumption of Dungeness crab was marginal from spring to summer on the Wa'atch River (36.6 to 40.8 %FO); however, MNI increased from 76 to 130 from spring to summer. Similarly, consumption of saddleback gunnel had a marginal increase from spring to summer in the Wa'atch River (63.4 to 65.4 %FO) but the MNI tripled from spring to summer (MNI 32 to 97). Otter consumption of giant wrymouth also increased from spring (0.7 %FO) to summer (4.5 %FO) on the Wa'atch River. Prey decreases for Wa'atch scats were observed for bay pipefish, and unidentified salmon, and rockfish from spring (46.3 %FO, 14.9 %FO, and 13.4 %FO, respectively) to summer (10.6 %FO, 3.9 %FO, and 1.1 %FO respectively). Green crab %FO change was marginal from spring to summer (5.4 %FO to 2.2 %FO, respectively) as is also reflected in MNI (MNI 7 to 4, respectively).

Green Crab Consumption and CPUE

Green crab consumption by otters was low in contrast to other fish (e.g., gunnels, flatfish, and sculpins) and crustaceans (Dungeness crab and crayfish) (Table 2). No green crab were observed in scats collected from the Tsoo-Yess River latrine sites, but green crabs were found in 11 scats collected in 2019 and in 1 scat collected in 2018 from the Wa'atch River latrine sites (Figure 3A; Table 2). Including all trap types (shrimp, Russell, crayfish, and minnow), CPUE of green crab averaged 0.39 crabs per trap on the Wa'atch River and 0.84 crabs per trap on the Tsoo-Yess River over the course of 6 months of trapping (Figure 3B). Shrimp traps were most successful in catching green crab on both rivers (1.5-11.25 CPUE), followed by Russell (0.33-1.63 CPUE), crayfish (0.09-0.84 CPUE), and then minnow (0.03-0.33 CPUE). Dungeness crab was selected as an appropriate prey species to report with green crab because it was also commonly caught during trapping efforts and was frequently consumed by otters (Table 2). CPUE of Dungeness crab averaged 1.95 crabs per trap on the Wa'atch River and 0.94 crabs per trap on the Tsoo-Yess River over the course of 6 months of trapping (Figure 3B). Shrimp traps were also most successful for catching Dungeness crab (13-90.5 CPUE), followed by Russell (0.33-10.00 CPUE), crayfish (0.13-4.34 CPUE), and minnow (0-0.10 CPUE). Overall, Dungeness crab was consistently trapped and consumed more frequently than green crab.

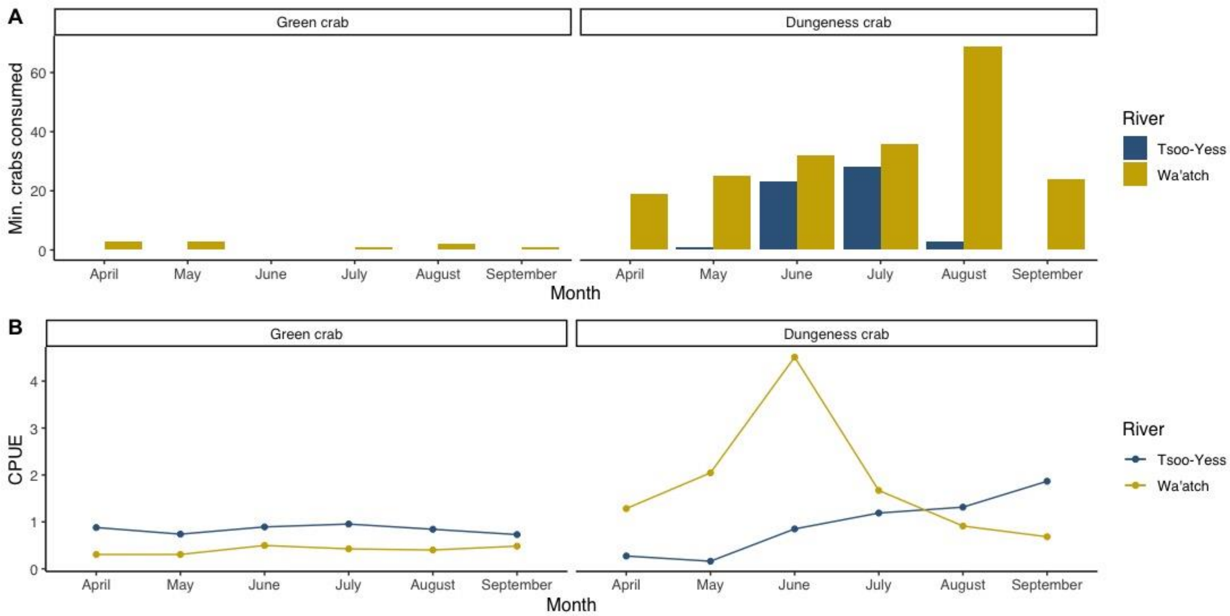

Figure 3

(A) Minimum number of European green crab (*Carcinus maenas*) and Dungeness crab (*Metacarcinus maenas*) consumed by otters based on leg, claw, and rostrum counts; and (B) average monthly catch-per-unit-effort (CPUE; CPUE = number of crabs per trap per day) of green and Dungeness crab on the Wa'atch and Tsoo-Yess rivers in Neah Bay, Washington, during 2019.

DISCUSSION

My results document one of the most diverse river otter diets for Washington State, with 38 distinct species identified among 18 prey groups separated by family and/or class (Table 2; Appendix Table 1). Although the occurrence of green crab in otter diet was low for the Wa'atch River and non-existent for the Tsoo-Yess River, I confirmed for the first time the presence of green crab in otter diet within Washington State. While consumed less than fish prey, green crab was consistently observed in scats across the sampling period, indicating otters recognized green crab as a prey item. Otters most commonly consume abundant, slow-moving fish and crustacean species, whose proportions are driven by habitat type and prey availability (Day et al. 2015). Green crab are elusive and aggressive, which might make them more difficult to capture and thus a less-favored prey type (Cohen et al. 1995).

Coastal otters regularly consume crustaceans in soft-bottomed intertidal and subtidal zones, however %FO varies among studies (Guertin et al. 2010, Buzzell et al. 2014, Jensen 2014, Russell 2015). For this study area, crustaceans were the fourth most commonly consumed prey group overall, particularly Dungeness crab on the Wa'atch River (Table 2). Dungeness crab overall had greater CPUE in both rivers relative to green crab and such difference was reflected in otter consumption (Figure 3). Multiple trap types with varying levels of effectiveness were used to calculate average CPUE; however, here I only used CPUE as a proxy for abundance and future studies should aim to more accurately assess green crab population status using alternative methods such as mark-recapture studies (Munch-Petersen et al. 1982, Bernier et al. 2020). Green crab CPUE was higher on the Tsoo-Yess River compared to the Wa'atch River, but this difference was marginal compared to the overall greater CPUE of dungeness crab on both rivers.

Thus, low consumption of green crab was likely due to overall lower abundance of green crab in both study areas compared to other prey items such as what was observed with Dungeness crab.

No temporal or spatial statistical comparisons were conducted because green crab consumption was infrequent, but overall spatial and seasonal trends of prey were described to document patterns in relative prey abundance and availability and help understand the lack of green crab consumption (Cote et al. 2008, Day et al. 2015). As previously noted, Dungeness crab and signal crayfish were the most important crustacean prey types for otters on the Wa'atch and Tsoo-Yess rivers, respectively (Table 2). In the Lake Ozette watershed on the Olympic Peninsula, signal crayfish were the most frequently consumed prey at 83.5 %FO (Scordino et al. 2016). The moderate frequency of crayfish on the Tsoo-Yess River (21.8 %FO) in otter diet was a surprise given the majority of prey were estuarine and marine species; however, signal crayfish can inhabit brackish waters and are able to withstand gradual exposure to environments that contained 28% seawater over 2 weeks (Holdich et al. 1997). Signal crayfish were not trapped in either river, but their presence in scats might suggest otters are foraging in freshwater systems nearby or further upriver prior to moving downstream to forage. The majority of crayfish could be identified as signal crayfish, but several occurrences were reported conservatively at the family level (Astacidae) due to a lack of identifying features (Table 2). I suspect these unknown crayfish were signal crayfish, but the possibility remains that invasive crayfish, such as the red swamp crayfish (*Procambarus clarkia*), could be observed in future otter studies as was recently reported in San Francisco Bay, California (Oates et al. 2019).

Dungeness crab and other cancrid crabs have been previously reported in coastal otter diet in British Columbia, Canada, and Puget Sound, Washington, but identification to species level is not always complete (Stenson et al. 1984, Guertin et al. 2010, Buzzell et al. 2014, Russell

2015). Importance of crabs varies by study in coastal otter diet, and only in the Snohomish River estuary within Puget Sound were crustaceans the most frequently consumed prey type (Russell 2015). In this study, Dungeness crab are considered an important prey item, occurring in nearly one-third of scats overall. Greater consumption of Dungeness crab on the Wa'atch River is most likely explained by the prey's relatively higher abundance on the Wa'atch River compared to the Tsoo-Yess River as noted earlier (Figure 3). Sub-adult Dungeness crab typically prefer estuaries with higher salinity, and less structured habitat (Holsman et al. 2006, Lewis et al. 2020). Based on these criteria, the Wa'atch River most likely consists of more suitable habitat for sub-adult Dungeness crab in contrast to the Tsoo-Yess River which can have higher freshwater output, but detailed habitat characterization has not been completed for these rivers.

Otters do not always exhibit a seasonal pattern in diet, and variation is usually more prevalent in comparing winter and summer diets due to shifts in prey abundance (Larsen 1984, Jones 2000, Cote et al. 2008, Day et al. 2015). When otter predation of crustaceans increases, it often reflects a compensatory relationship with decreases in fish presence (Day et al. 2015); however, this relationship was not clear in this study since most species with observable variation increased in %FO with the exception of salmon and bay pipefish (Table 2). Based on %FO, Dungeness crab consumption by otters increased two-fold from spring to summer on the Tsoo-Yess and had a marginal increase from spring to summer on the Wa'atch River; however, MNI more strongly reflected an increase from spring to summer in consumption of Dungeness crab on the Wa'atch River (Table 2, Appendix Table 2). Hence, consumption of Dungeness crab was consistent on the Wa'atch but summer MNI suggests more Dungeness crab were consumed in each feeding. Interestingly, CPUE of Dungeness crab on the Wa'atch River decreased in the same month otter consumption of Dungeness crab increased, which might indicate a lack of overlap between trapping locations and otter foraging habitat during the summer.

Otters also had observable increases in consumption of several fish prey species in both rivers from spring to summer (saddleback gunnel, Pacific staghorn sculpin, starry flounder, shiner perch), and the relative importance of these fish prey have been documented in other west coast otter diet studies (Buzzell et al. 2014, Russell 2015, Oates et al. 2019). Consumption of saddleback gunnel increased from spring to summer on the Tsoo-Yess River based on %FO, but similar to Dungeness crab, this increase was better observed in MNI for the Wa'atch River (Table 2; Appendix Table 2). For both rivers, MNI increased three-fold from spring to summer for saddleback gunnel. Bay pipefish, unidentified salmon, and unidentified rockfish decreased in otter diet on the Wa'atch, while only the consumption of steelhead had a decrease from spring to summer on the Tsoo-Yess River. Since changes in prey consumption by otters often reflect changes in prey abundance, it is thus likely that prey taxa that exhibited seasonal changes were most likely driven by variable freshwater output from the rivers, tidal fluctuations, hypoxic conditions, presence of eelgrass, or prey life histories (e.g., movement into deeper or shallower water) (Sobocinski et al. 2018, Schwartzkopf et al. 2020).

MNI derived from otolith counts is used conservatively for inferences due to its gross underestimate of actual consumed fish, however MNI provides insight into foraging strategies of otters (Tollit et al. 1997). Pacific staghorn, prickly, padded, and slim sculpins were observed with as many as 10-16 individuals in a single scat, and shiner perch ranged from 1-26 individuals in a single scat. Several samples consisted of remains with as many as 200-300 saddleback gunnels in a single scat[4]. Bay pipefish were also observed with high counts but lacked otoliths to report. Hence, otters consumed numerous individual fish in a single feeding. This observation suggest that otters are either employing techniques to consume hundreds of these intertidal and demersal fish in a single feeding or these fish unknowingly exist in aggregations.

Smaller (<80 cm) fish from sculpin, gunnel, surfperch, stickleback, pipefish and flatfish prey groups represented the majority of prey consumed and are often the most abundant of fish within intertidal to subtidal kelp and eelgrass beds (Johnson et al. 2003). Coastal otter diet on Vancouver Island in British Columbia and in the San Juan Islands of Washington State reflected similar importance of these prey groups, with exception to pipefish, surfperch and sticklebacks, which were relatively unimportant prey species in those study areas (<2.2 %FO; Guertin et al. 2010, Buzzell et al. 2014). Pricklebacks were the third most frequently consumed prey item on both Vancouver Island and in the San Juan Islands (>50 %FO), but were one of the least frequently consumed prey in both the Wa'atch and Tsoo-Yess rivers (5 %FO overall). Prickly and Pacific staghorn sculpin were the most frequently consumed sculpins overall (28.3 %FO and 51.5 %FO overall, respectively) and both commonly inhabit brackish waters (Tabor et al. 2015; Schwartzkopf et al. 2020). Prickly sculpin was the most frequently consumed fish species for otters foraging in the Lake Ozette watershed (Scordino et al. 2016). Pacific staghorn has been frequently observed in coastal otter diet, but only in this study were Pacific Staghorn sculpin observed in > 50 %FO (Guertin et al. 2010, Buzzell et al. 2014). In summary, while otter diet in the lower Tsoo-Yess and Wa'atch rivers reflect similarities among other west coast studies (both freshwater and marine), generalizations across regions are somewhat limited when the

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complexity of surrounding habitats increases (e.g., access to river, wetland, estuaries, intertidal, etc.).

Although the focus of this study was green crab consumption, having the ability to examine all diet items, allowed for unexpected findings. One such finding is evidence of increased predation on salmon and steelhead smolts following releases from the Makah National Fish Hatchery[5] located on the Tsoo-Yess River (Table 2; Appendix Table 3). Steelhead smolts released on April 26th, 2019 were followed by heightened occurrences of steelhead in Tsoo-Yess river otter scats collected on May 8th. Similarly, Chinook salmon smolts released on May 29th were followed by heightened occurrences of Chinook salmon in river otter scats collected on May 31st. A total of 104 otoliths were recovered in five scats from that date, comprising a minimum of 58 Chinook salmon smolts. Given that not all otoliths are recovered, this is likely an underestimate of the total number of Chinook smolts eaten as seen in work with pinniped scat studies (Tollit et al. 1997). However, not all hatchery releases coincided with greater occurrences in scats and the trend should be given greater attention in future studies.

In line with unexpected findings, giant wrymouth was observed in otter diet on both rivers, which species' life history has been little studied (Beal et al. 2016). Giant wrymouth can grow in length of 123 cm and inhabit depths from 6 to 128 m but are most often found in depths less than 20 m (Schnell and Hilton 2015). The presence of giant wrymouth and other subtidal species (e.g., red Irish lord, greenlings) might indicate otters are foraging further into Makah Bay, these species are brought into the rivers during high tides, or juveniles of these species are using estuaries. On one occasion I observed an otter foraging on Tatoosh Island in August 2019,

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an approximate 0.8 km swim from the most northwest tip of Cape Flattery and 8.5 km to circumnavigate the coastline of Cape Flattery to the lower Wa'atch River. In Prince William Sound, Alaska, home ranges of coastal river otters can vary greatly up to approximately 160 km of shoreline and can cross >6 km of open water (Blundell 2001; Blundell et al. 2002). Thus, mainland-bound otters might deposit feces at Wa'atch and/or Tsoo-Yess River latrines that reflect species consumed in Makah Bay rather than in the river estuaries. Otters are also known scavengers where fish carcasses have washed up after spawning events or have been discarded by fishers[6], and might explain the infrequent consumption of deep water, marine prey such as rockfish and Pacific halibut (Hewson 1995). These findings further support otters as opportunistic foragers and provide information on niche predator-prey dynamics that otherwise would go unobserved.

Otter foraging behavior is also dictated by social groups, or in the case of female otters separation from male cohorts; however, population demographics for otters on the Makah Indian Reservation are not available, but this information might provide more context for why green crab are consumed less frequently (Albeke et al. 2015). Male cohorts of otters tend to have increased consumption of pelagic fishes in contrast to lone female otters since they utilize cooperative feeding strategies (Blundell 2002). Additionally, juvenile otters are less skilled in catching fast-swimming fishes and tend to consume crustaceans more frequently than adults (Watt 1993). Hence, juvenile and female otters might be more likely predators of green crab compared to males.

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For future studies, I suggest using noninvasive genetic methods (e.g., fecal genotyping) to document otter populations, but also remove bias when collecting multiple scats from a single latrine (Brzeski et al. 2013, Tsukada et al. 2020). Several studies have documented the limitations of diet studies using %FO and MNI (Van Dijk et al. 2007, Crimmins et al. 2009, Tsukada et al. 2020). Scat collection is subjective and can lead to pseudoreplication, where there's a strong likelihood multiple scats from a single collection are from the same individual, leading to an overestimate of frequently consumed species and an underestimate of infrequently consumed species (Tsukada et al. 2020). Over-representation of larger prey items is also an issue with %FO when exclusively using hard parts to identify prey (Crimmins et al. 2009). As previously stated, MNI can severely underrepresent counts of prey taxa, however MNI in this study is supplemental evidence and not primary evidence for understanding shifts in predominant prey types. While these biases are important considerations, the objective of this study was not obstructed since the goal was first and foremost detecting green crab in otter diet. Additionally, scats were consistently collected over a prolonged time frame, which allows for a relative understanding of important prey types and shifts in prey availability.

Estimating species abundance using CPUE also has limitations due to the high variability in trapping efficacy (Taggart et al. 2004, Maunder et al. 2006, Bergshoeff et al. 2018). Green crab in the Tsoo-Yess and Wa'atch rivers averaged < 1 CPUE but there was considerable variation in CPUE based on trap type, ranging from 0.03-11.25 CPUE (Figure 3). Relative to the Wa'atch and Tsoo-Yess rivers, east coast green crab is consistently more abundant, where densities have ranged from 27.4-122.15 CPUE (Abt Associates Inc. 2008). Despite these variations, CPUE derived from consistent trapping over a period of time provides reliable information on green crab presence and densities; however, comparisons should be limited within the same geographical regions utilizing the same trapping effort (Poirier et al. 2017). Relative densities derived from CPUE in this study provide insight into the reason why green crab are not consumed as frequently as Dungeness crab, and supports the hypothesis that otters consume prey species in proportion to prey abundance and availability (Ryder 1955; Day et al. 2015).

If green crab populations continue to rise in Makah Bay and elsewhere along Washington's coastline, I hypothesize otter predation of green crab will increase as this prey species becomes more abundant and available. As such, it is essential to continue monitoring green crab populations to provide a better understanding of their long-term impact on local ecosystems. Although it is unlikely otters currently serve as a natural control of green crab populations on their own, documenting their interaction is a first step in understanding the potential influence of green crabs within food webs of Washington coasts. In addition, otters compose of only a fraction of predation pressure on green crab. Other predators of green crab include shore birds, intertidal and subtidal fish, mink, harbor seal, and also other crab (including green crab) (Klassen and Locke 2007). Supporting these predator populations will maximize the potential for a community-wide mitigation response to the establishment of green crab. As such, future studies should be directed at understanding predator-prey interactions involving green crab and potential predators which might cumulatively buffer green crab overabundance, and furthermore mitigate green crab impacts on sensitive coastal habitats along the west coast.

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APPENDIX

Appendix Table 1

Prey items found in <2% of river otter (*Lontra canadensis*) scats collected from the estuarine zones of the Wa'atch and Tsoo-Yess rivers for the spring and summers of 2019; results are reported as percentage frequency of occurrence (% FO) and total samples (n) are given for each collection period (* indicates possible scavenging event).

Prey	Overall (n=540)	Tsoo-Yess Spring (n= 102)	Tsoo-Yess Summer (n=125)	Tsoo-Yess Overall (n=227)	Wa'atch Spring (n=134)	Wa'atch Summer (n=179)	Wa'atch Overall (n=313)
FLATFISH							
Flatfish, unidentified (Family: Pleuronectidae)	1.9	1.0	0.8	0.9	3.7	1.7	2.6
Pacific halibut (*Hippoglossus stenolepis*)*	0.9	-	0.8	0.4	3.0	-	1.3
English sole (*Parophyrys vetulus*)	0.6	-	2.4	1.3	-	-	-
Arrowtooth flounder (*Atheresthes stomias*)	0.2	1.0	-	0.4	-	-	-
Sanddab, whiff, or flounder, unidentified (*Citharichthys* sp.)	0.2	-	-	-	-	0.6	0.3
Rock sole (*Lepidopsetta bilineata*)	0.2	-	-	-	0.7	-	0.3
Speckled sanddab (*Citharichthys stigmaeus*)	0.2	1.0	-	0.4	-	-	-
SCULPIN							
Northern sculpin, likely (*Icelinus* sp. cf. *I. borealis*)	1.3	-	0.8	0.4	-	3.4	1.9
Red Irish lord, likely (*Hemilepidotus* sp. cf. *H. hemilepidotus*	0.2	1.0	-	0.4	-	-	-
CRAB							
Purple shore crab (*Hemigrapsus nudus*)	0.7	2.0	-	0.9	-	1.1	0.6
Northern kelp crab (*Pugettia producta*)	0.7	-	-	-	1.5	1.1	1.3
Decapod crab, unidentified (Order: Decapoda)	0.6	-	-	-	1.5	0.6	1.0
Dungeness or graceful crab (*Metacarcinus* sp.)	0.4	-	0.8	0.4	0.7	-	0.3
Spider crab, unidentified (Family: Inachidae)	0.4	-	-	-	-	1.1	0.6
Shore crab, unidentified (*Hemigrapsus* sp.)	0.2	-	-	-	0.7	-	0.3
Striped shore crab (*Pachygrapsus crassipes*)	0.2	-	-	-	-	0.6	0.3
Red rock crab (*Cancer productus*)	0.2	-	-	-	0.7	-	0.3
SURFPERCH							
Pile perch (*Damalichthys vacca*)	0.6	-	0.8	0.4	-	1.1	0.6
MISCELLANEOUS							
Bird, unidentified (Class: Aves)	0.7	-	3.2	1.8	-	-	-
Insect, unidentified (Class: Insecta)	0.2	1.0	-	0.4	-	-	-
Plastic fragment	0.6	1.0	-	0.4	-	1.1	0.6
Fish, unidentified (Infraclass: Teleostei)	0.2	-	-	-	0.7	-	0.3
Minnow, unidentified (Family: Cyprinidae)	0.2	1.0	-	0.4	-	-	-
Squid, unidentified (Class: Cephalopoda)	0.2	-	-	-	0.7	-	0.3
SNAILFISH							
Snailfish, unidentified (Family: Liparidae)	0.2	-	-	-	-	0.6	0.3
GREENLING							
Greenling, unidentified (*Hexagrammos* sp.)	1.7	2.0	1.6	1.8	-	2.8	1.6
Kelp greenling (*Hexagrammos decagrammus*)	0.2	-	-	-	-	0.6	0.3
PRICKLEBACK							
Rock prickleback (*Xiphister mucosus*)	1.1	1.0	2.4	1.8	-	1.1	0.6
Snake prickleback (*Lumpenus saggita*)	0.4	-	-	-	1.5	-	0.6
SMELT							
Smelt, unidentified (Family: Osmeridae)	0.6	-	-	-	2.2	-	1.0
Longfin smelt (*Spirinchus thaleichthys*)	0.4	2.0	-	0.9	-	-	-
SHRIMP							
Caridean shrimp, unidentified (Infraorder: Caridea)	0.6	-	-	-	1.5	0.6	1.0
Ghost shrimp, unidentified (*Neotrypaea* sp.)	0.2	-	-	-	0.7	-	0.3
HERRING							
American shad (*Alosa sapidissima*)	0.2	-	-	-	0.7	-	0.3

Appendix Table 2

Total, average, and range of minimum number of individuals (MNI) for select river otter (*Lontra canadensis*) prey taxa (MNI ≥ 10) documented in scats collected in April through September of 2019 on the Wa'atch and Tsoo-Yess rivers, Washington state (n=number of scats with identified prey taxa); MNI for fish is based on the greater count of right and left otoliths recovered and not all prey structures, and MNI of crustaceans based on counts of claws, legs, and rostrums.

			Tsoo-Yess				Wa'atch			
Prey	n	Total	Spring	Summer	Average	Range	Spring	Summer	Average	Range
Pacific staghorn sculpin (*Leptacottus armatus*)	190	566	22	54	1.7	1-6	156	334	3.4	1-15
Shiner perch (*Cymatogaster aggregata*)	113	430	16	57	2.7	1-7	140	217	4.2	1-26
Saddleback gunnel, likely (*Pholis* sp. cf. *P. ornata*)	138	364	67	168	3.1	1-13	32	97	2.0	1-8
Starry flounder (*Platichthys stellatus*)	183	319	24	102	1.8	1-5	55	138	1.7	1-7
Dungeness crab (*Metacarcinus magister*)	139	240	24	31	1.8	1-5	76	109	1.7	1-5
Prickly sculpin (*Cottus asper*)	100	197	8	25	1.6	1-4	100	64	2.1	1-10
Padded sculpin, likely (*Artedius* sp. cf. *A. fenestralis*	52	167	-	-	-	-	50	117	3.2	1-16
Signal crayfish (*Pacifastacus leniusculus*)	54	163	87	66	3.3	1-12	3	7	1.4	1-3
Slim sculpin (*Radulinus asprellus*)	26	121	85	18	4.3	1-15	18	-	9.0	4-14
Chinook salmon (*Oncorhynchus tshawytscha*)	7	60	58	1	9.8	1-21	1	-	1.0	-
Padded sculpin (*Artedius* sp. cf. *A. fenestralis*)	11	40	3	37	3.6	1-23	-	-	-	-
Giant wrymouth (*Cryptacanthodes giganteus*)	15	27	5	2	1.2	1-2	1	19	2.2	1-9
Hairy shore crab (*Hemigrapsis oregonensis*)	13	24	6	-	6.0	1-6	1	17	1.5	1-4
Red Irish lord (*Hemilepidotus hemilepidotus*)	10	23	4	6	1.3	1-2	13	-	6.5	6-7
Crayfish, unidentified (Family: Astacidae)	19	21	7	10	1.2	1-3	4	0	1.0	1
Steelhead (*Oncorhynchus mykiss*)	13	20	18	1	1.6	1-5	1	-	1.0	1
Irish lord, unidentified (*Hemilepidotus* sp.)	8	16	4	7	2.8	1-6	-	5	1.3	1-2
Rock prickleback (*Xiphister mucosus*)	6	10	1	7	2.0	1-3	-	2	1.0	-
European green crab (*Carcinus maenas*)	10	10	-	-	-	-	7	3	1.0	-

Appendix Table 3

River otter (*Lontra canadensis*) fish prey otolith lengths (mm) and standard lengths (cm) from scats collected in April through September of 2019 from the Wa'atch and Tsoo-Yess rivers, Washington State.

	Tsoo-Yess		Wa'atch	
Prey (n=Tsoo-Yess, Wa'atch)	Otolith size range (mm)	Standard Length (cm)	Otolith size range (mm)	Standard Length (cm)
Artedius sp. cf. *A. fenestralis* (n=32, 142)	1.7-3.0	-	1.2-4.2	-
Citharichthys sp. (n= , 1)	-	-	1.5	-
Citharichthys stigmaeus (n=1,)	1.8	-	-	-
Cottus asper (n=18, 60)	1.9-5.4	-	1.7-6.7	-
Clinocottus acuticeps (n= , 5)	-	-	2.3-3.8	-
Cryptacanthodes giganteus (n=5, 13)	1.0-2.1	-	1.0-3.5	-
Cymatogaster aggregata (n=55, 268)	1.3-4.5	≤7.3	1.1-6.8	≤11.3
Damalichthys vacca (n= , 2)	-	-	4.2-4.4	-
Enophrys bison (n=1, 3)	2.3	-	2.2-2.8	-
Gasterosteus aculeatus (n=1,)	0.8	-	-	-
Hemilepidotus hemilepidotus (n=7, 9)	2.4-6.5	-	1.4-4.4	-
Hemilepidotus sp. (n=10, 5)	1.3-4.2	-	1.5-3.8	-
Hexagrammos decagrammus (n= , 1)	-	-	3.8	-
Hexagrammos sp. (n=1, 4)	2.0	-	2.2-2.5	-
Icelinus sp. cf. *I. borealis* (n=1, 3)	2.5	-	2.1-2.4	-
Leptacottus armatus (n=24, 220)	1.9-7.4	≤16.8	1.4-8.5	≤19.6
Liparis sp. cf *L. fucensis* (n=2, 5)	1.5-1.6	-	1.4-8.5	-
Lumpenus saggita (n= , 1)	-	-	1.5	-
Oncorhynchus clarkii (n= , 1)	-	-	2.6	-
Oncorhynchus kisutch (n=4, 2)	2.5-3.3	≤18.3	2.1-4.4	≤3.1
Oncorhynchus mykiss (n=17, 0)	2.5-3.5	≤18.8	-	-
Oncorhynchus sp. (n=1, 5)	-	-	1.0-1.5	-
Oncorhynchus sp. cf. *O. kisutch* (n=6, 1)	1.2-2.8	-	17.2-125.0	-
Oncorhynchus sp. cf. *O. mykiss* (n=4, 10)	-	-	1.5-1.8	-
Oncorhynchus tshawytscha (n=46, 1)	1.9-2.5	6.2-8.9	61.7	-
Parophyrys vetulus (n=4,)	1.7-1.9	-	-	-
Pholis sp. cf. *P. ornata* (n=191, 107)	1.2-2.1	-	1.2-2.2	-
Platichthys stellatus (n=41, 70)	2.1-5.0	≤16.9	1.3-5.1	≤17.3
Radulinus asprellus (n=73, 10)	0.9-4.0	-	2.2-3.5	-
Xiphister mucosus (n=6, 2)	2.1-3.5	-	3.0-3.1	-