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Exploring the biotic resistance of the invasive green crab (*Carcinus maenas*) by examining the diet of North American river otters (*Lontra canadensis*)

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Abstract—We examined the potential of North American river otters (*Lontra canadensis*) to buffer the expansion of the invasion by green crab (*Carcinus maenas*) on the West Coast of the United States, documenting the diet of otters from scat remains on the Wa'atch and Tsoo-Yess Rivers, in Washington State, in 2018 and 2019. We tallied hard remains of prey and calculated frequency of occurrence, and we compared predation of the green crab to monthly values of catch per unit of effort for this crab species. North American river otters did not consume green crab in the Tsoo-Yess River and infrequently consumed green crab in the Wa'atch River (1.66% frequency of occurrence), likely because of the lower abundance of the green crab compared to the abundance of other prey in these rivers. Although our results indicate that North American river otters were not a biotic control of green crab, future studies on the population status of the green crab and North American river otter in both rivers and the long-term predator–prey dynamics could help to better gauge the potential for biotic resistance in populations of the green crab.

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The green crab (*Carcinus maenas*) is an invasive species known for its effects on eelgrass beds and juvenile bivalves (Cohen et al., 1995; Curtis et al., 2012; Howard et al., 2019). Green crab have been documented in the waters of Makah Bay on the Makah Indian Reservation in northwest Washington through removal trapping efforts, specifically efforts in the estuaries of the Wa'atch and Tsoo-Yess Rivers (Yamada[1]) (Fig. 1). The absence of green crab in nearby Neah Bay might be a result of competition and predation by larger cancrid crab species, such as the red rock crab (*Cancer productus*) and adult Dungeness crab (*Metacarcinus magister*), both of which are more prevalent in Neah Bay than in the channels of the 2 coastal rivers that enter Makah Bay (Jensen et al., 2007). On the western coast of Vancouver Island, in Canada, increasing abundances of Dungeness crab, red rock crab, or graceful crab (*Metacarcinus gracilis*) have resulted in reduced densities of green crab (Howard, 2019). Hence, biological resistance might be a principal factor in mitigating the expansion of the invasion by green crab on the West Coast of the United States.

The North American river otter (*Lontra Canadensis*) often forages in coastal environments in Washington State and is known to predate several marine crab species (Guertin et al., 2010; Buzzell et al., 2014; Russell, 2015). Little attention has been given to North American river otters and their potential to act as a biotic control for invasive species (Feltrop et al., 2016). Latrines (sites of marking

[1] Yamada, S. B., C. Royer, S. Schooler, J. Fisher, A. Randall, C. Buffington, A. Stote, and A. Akmajian. 2022. Status of the European green crab, *Carcinus maenas*, in Oregon and Washington coastal estuaries: report for 2020 and 2021, 18 p. Report prepared for Aquatic Nuissance Species Project, Pacific State Marine Fisheries Commission. [Available from Aquat. Nuissance Species Proj., Pac. State Mar. Fish. Comm., 205 SE Spokane St., Ste. 100, Portland, OR 97202.]

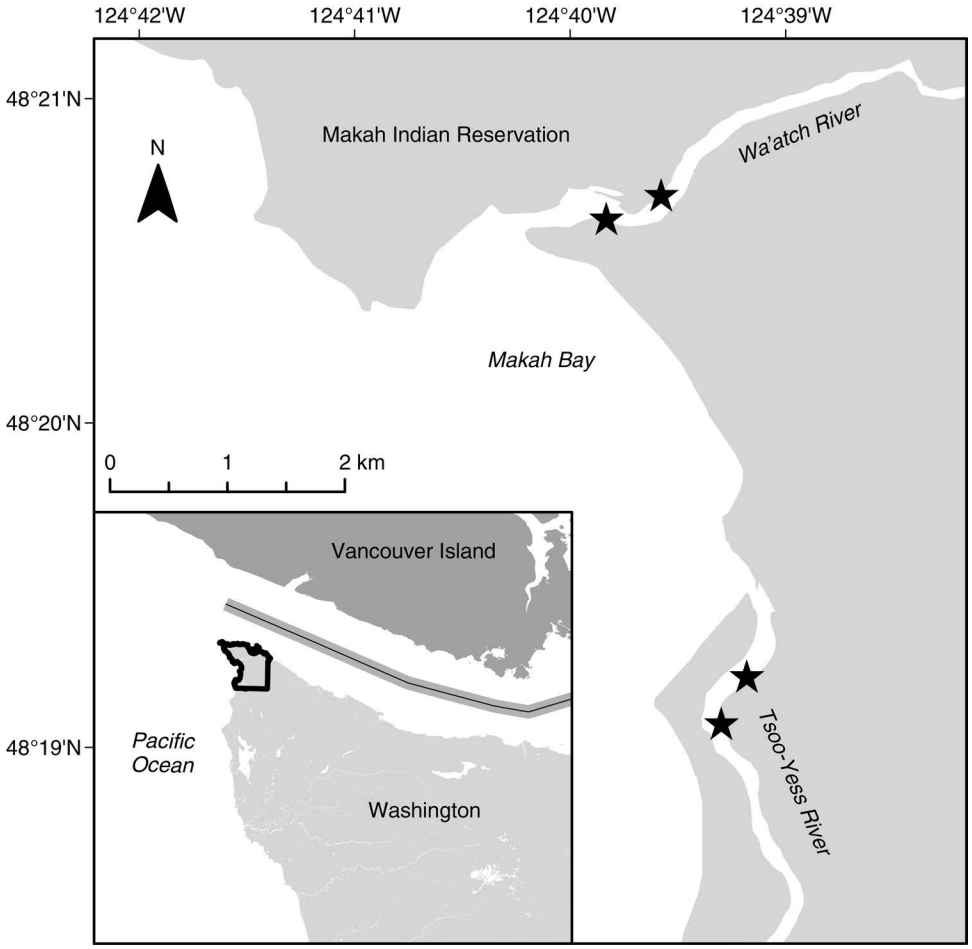

Figure 1

Map of the sites (stars) where samples of scat from North American river otters (*Lontra canadensis*) were collected during the summer of 2018 in the Wa'atch River and during the spring and summer of 2019 in the Wa'atch and Tsoo-Yess Rivers. Collection sites were latrines, areas of marking and defecation by otters, located within the boundaries of the Makah Indian Reservation in Washington State. Scat samples were used to examine the diet of North American river otters and the potential for predation by otters to control populations of the invasive green crab (*Carcinus maenas*). 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, NP.

and defecation) of North American river otters have been observed along the lower Wa'atch and Tsoo-Yess Rivers during removal efforts targeting green crab (A. Akmajian, personal observ.). Because of this apparent overlap of habitats of North American river otters and green crab and the known predation of North American river otters on green crab in other regions (Mason and Macdonald, 1980), we hypothesized that North American river otters are consuming green crab in both rivers and may act as a natural control for green crab in these estuaries.

The first step in assessing the potential of North American river otters to serve as a biotic control of green crab was to determine 1) if North American river otters consume green crab and 2) if such consumption varies relative to time or abundance of green crab. We analyzed the hard remains found in scat from North American river otters to describe their diet and the relative importance of prey items, focusing on consumption of green crab. We investigated differences in consumption of green crab between rivers, seasons (spring and summer of 2019), and years (summers of 2018 and 2019). Finally, to explore possible mitigation of the invasive green crab through their consumption by otters, we examined the consumption of green crabs by North American river otters in relation to the availability of green crab

based on average catch rates during removal trapping efforts in 2019.

Materials and methods

The estuaries of the Wa'atch River and Tsoo-Yess River of the Makah Indian Reservation are located on the northwest coast of the Olympic Peninsula in Washington State (Fig. 1). The 2 rivers extend inland more than 16 km and up to 600 m in elevation, with the 4 river kilometers at the lowest elevations classified as brackish emergent tidal marsh (Heady et al., 2014). Active latrine sites used by North American river otters were identified along both the Wa'atch and Tsoo-Yess Rivers (Fig. 1). On the Wa'atch River, 1 latrine site was located on each of the north and south banks less than 1.5 km upstream from the river mouth. On the lower Tsoo-Yess River, 2 latrine sites were found on the east bank, approximately 0.8 and 1.2 km upstream from the river mouth. The locations of the latrines in relation to the coast, bays, and one another are depicted in Figure 1.

Prey identification was conducted by using analysis of undigested remains (bones and shells) found in scat samples, a widely used method for documenting diet (Stenson et al., 1984; Day et al., 2015). Scat collection was completed every other week alongside green crab trapping efforts on the Wa'atch River in August and September 2018 and for a longer period in 2019 from April through September, but scat samples were collected on the Tsoo-Yess River only during May–September 2019. Samples of scat collected in the summer (July–September) from the latrines along the Wa'atch River were used to compare diet between years, but only samples collected in 2019 were used to compare diet between rivers and seasons (between spring, April–June, and summer). If latrines contained fewer than 15 scat samples, collections were made on additional days in the following week. Protocols for the collection and cleaning of scat were based on methods described for pinnipeds in Lance et al.[2]

Prey items were identified to the lowest possible taxon but for brevity are reported herein only to the family level, apart from green crab and Dungeness crab. Color, claw, texture, and carapace morphology were all factors used to identify remains of crab. Fish remains were identified by using reference bones and otoliths housed at the NOAA Marine Mammal Laboratory in Seattle, Washington. We used frequency of occurrence (Trites and Joy, 2005) to examine and describe spatial and temporal variations in the diet of North American river otters, meaning differences between the Tsoo-Yess and Wa'atch Rivers, between seasons (spring and summer), and between years. Minimum number of individuals was determined for crustaceans by using protocols adapted from Lance et al.[2] With the exception of green crab, frequency of occurrence (FO) is reported for all prey groups with FO of at least 2% and was calculated as follows:

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

where O_i = 0 if taxon i is absent in fecal sample k and 1 if taxon i is present in fecal sample k; and
s = total number of scat samples.

We used catch per unit of effort (CPUE), defined as the number of green crab caught per trap set per day, as a proxy for abundance because no other information was available on populations of green crab in the study area. Trapping catch data from Makah Fisheries Management, Makah Tribe, were used in calculations of CPUE. Trap descriptions and protocols can be found in the summary report on trapping efforts in 2019 (Akmajian[3]). Average monthly values for CPUE of green crab and Dungeness crab were generated for each river to explore relative densities of prey. Although fish were also caught in traps, CPUE for other species in bycatch were not included in this study.

Results and discussion

In this study, 722 scat samples were collected in both rivers combined (Table 1). Green crab were present in samples from the Wa'atch River (with FO of 1.66%) but absent in samples from the Tsoo-Yess River. Although green crab were scarce in the diet of North American river otters, green crab were observed in scat samples collected from both latrine sites along the Wa'atch River and on 7 separate dates, indicating that otters recognized green crab as prey (Suppl. Figure). Even so, green crab are elusive and aggressive, possibly making them more difficult to capture and a less-favored prey type overall (Cohen et al., 1995).

Fish composed the most frequently found and numerous group consumed by North American river otters in both rivers, a result that is consistent with those from other otter diet studies in coastal areas (Table 1) (Buzzell et al., 2014; Russell, 2015). Among fish taxa, sculpins (Cottidae) made up the most frequently consumed prey group overall (65.37% FO), followed by gunnels (Pholidae) (57.20% FO) and righteye flounders (Pleuronectidae) (49.45% FO). Cancrid crabs (mostly Dungeness crab) composed the most consumed crustacean prey group (28.54% FO), but FO of cancrid crabs has varied in other studies (Table 1) (Guertin et al., 2010; Russell, 2015).

The relative importance of prey groups in the diet of North American river otters was similar between 2018 and 2019; however, most prey taxa and groups, including the green crab, had increased occurrence in scat samples

[2] 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. Alsk. Fish. Sci. Cent. Proc. Rep. 2001-04, 29 p. [Available from website, accessed November 2022.]

[3] Akmajian, A. 2020. European green crab trapping summary for the 2019 season, 30 p. [Available from Makah Fish. Manag., Makah Tribe, P.O. Box 115, Neah Bay, WA 98357.]

Table 1

Frequency of occurrence (FO) for prey items found in samples of scat from North American river otters (*Lontra canadensis*) collected during the summer of 2018 in the Wa'atch River and during the spring and summer of 2019 in the Wa'atch and Tsoo-Yess Rivers. Frequency of occurrence is reported for all prey groups that had FO >2%. The number of scat samples (*n*) is given for each collection period.

		Wa'atch River			Tsoo-Yess River	
		2018	2019		2019	
Prey	Overall FO (%) *n*=722	Summer FO (%) *n*=139	Spring FO (%) *n*=135	Summer FO (%) *n*=179	Spring FO (%) *n*=125	Summer FO (%) *n*=144
Teleostei						
Cottidae (sculpins)	65.37	66.91	73.33	79.89	44.00	56.94
Pholidae (gunnels)	57.20	48.20	62.96	65.92	44.00	61.11
Pleuronectidae (Righteye flounders)	49.45	42.45	45.93	66.48	31.20	54.17
Embiotocidae (surfperches)	24.79	21.58	25.19	44.13	8.80	17.36
Gasterosteidae (sticklebacks)	22.02	23.74	27.41	31.84	13.60	10.42
Syngnathidae (pipefishes and seahorses)	17.04	3.60	45.93	10.61	16.00	11.81
Salmonidae (salmons and trouts)	12.05	0.72	20.00	6.15	25.60	11.11
Stichaeidae (pricklebacks)	5.96	14.39	2.96	7.26	0.80	3.47
Teleostei (unidentified fish)	4.29	7.19	0.74	7.82	3.20	1.39
Liparidae (snailfishes)	3.46	4.32	–	8.94	2.40	–
Scorpaenidae (rockfishes)	2.91	0.72	13.33	1.12	–	–
Decapoda						
Cancridae (rock crabs)	28.53	36.69	37.78	40.78	7.20	15.28
Astacidae (crayfishes)	11.50	2.16	5.19	5.03	24.00	23.61
Varunidae (shore crabs)	3.05	1.44	1.48	8.94	1.60	–
Carcinus maenas (Portunidae)	1.66	0.72	5.19	2.23	–	–
Miscellaneous						
Ranidae (true frogs)	2.91	1.44	2.96	2.79	3.20	4.17

collected in 2019 (Table 1). With the exception of sticklebacks (Gasterosteidae) consumed by otters on the Tsoo-Yess River, the other 5 most frequently occurring prey groups increased in FO to some degree from spring to summer on both rivers. Seasonal change in the FO of green crab in the scat samples collected on the Wa'atch River was not apparent because of low consumption, where only 7 and 4 individuals occurred in scat samples collected in spring and summer, respectively (Suppl. Figure).

Dungeness crab had greater CPUE overall in trapping efforts in both rivers (1.40 individuals·set^{-1}·d^{-1}) than green crab (0.63 individuals·set^{-1}·d^{-1}). Such a difference coincides with the consumption of crabs by North American river otters, where both overall FO and the FO of Dungeness crab were higher than the FO of green crab (Table 1, Suppl. Figure). The CPUE of green crab was higher on the Tsoo-Yess River (0.84 individuals·set^{-1}·d^{-1}) than on the Wa'atch River (0.39 individuals·set^{-1}·d^{-1}), but this difference was marginal compared to the greater overall CPUE of Dungeness crab on both rivers during most of the trapping season. Although we used CPUE only as a proxy of prey abundance and availability, the difference between crab species in both CPUE and FO in the diet of North American river otters supports the hypothesis posited by others that this otter species consumes prey species in proportion to their relative abundance and availability (Ryder, 1955; Day et al., 2015). Therefore, low consumption of green crab was likely a result of the overall lower abundance of green crab in both rivers compared with the abundance of other prey items.

Several studies have documented the limitations of diet studies that use FO and minimum number of individuals (Crimmins et al., 2009; Tsukada et al., 2020). Scat collection is subjective and can lead to pseudoreplication, where there is a strong likelihood that multiple scat samples 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). Estimating species abundance by using CPUE has limitations because of the high variability in trapping efficacy; in future studies, an aim should be to use methods, such as mark-recapture techniques, that are more accurate (Munch-Petersen et al., 1982, Bergshoeff et al., 2018; Bernier et al., 2020). Although it is important to consider these biases, the objective of this study was to detect green crab in the diet of North American river otters and to describe important prey types, which was possible because of the timeframe of our study.

On the basis of our results, it is unlikely that North American river otters currently serve as a natural control of green crab populations that are at low densities. However, in recent years, population densities of green crab have continued to increase in Makah Bay and elsewhere along the coastline of Washington. Predation of green crab by North American river otters will likely increase as green crab become more abundant and available, but gauging potential effects will require estimating population densities for both North American river otters and green crab. As such, future studies should focus on understanding predator–prey interactions involving green crab and other likely predators, such as adult Dungeness crab, that might cumulatively buffer a higher density of green crab and further mitigate effects of green crab invasions on sensitive coastal habitats along the West Coast.

Resumen

Examinamos el potencial de las nutrias de río norteamericanas (*Lontra canadensis*) para amortiguar la expansión de la invasión del cangrejo verde (*Carcinus maenas*) en la costa oeste de Estados Unidos, documentando la dieta de las nutrias a partir de restos de excrementos en los ríos Wa'atch y Tsoo-Yess, en el estado de Washington, en 2018 y 2019. Contamos los restos duros de presas, calculamos la frecuencia porcentual de ocurrencia, y comparamos la depredación del cangrejo verde con los valores mensuales de captura por unidad de esfuerzo para esta especie de cangrejo. Las nutrias de río norteamericanas no consumieron cangrejos verdes en el río Tsoo-Yess y consumieron con poca frecuencia cangrejos verdes en el río Wa'atch (1.66% de frecuencia de ocurrencia), probablemente debido a la menor abundancia del cangrejo verde en comparación con la abundancia de otras presas en dichos ríos. No obstante que nuestros resultados indican que las nutrias de río norteamericanas no constituyen un control biologico del cangrejo verde, futuros estudios sobre el estado de las poblaciones del cangrejo verde y nutria de río norteamericana en ambos ríos y la dinámica depredador-presa a largo plazo podrían ayudar a calibrar mejor el potencial de resistencia biótica de las poblaciones del cangrejo verde.

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