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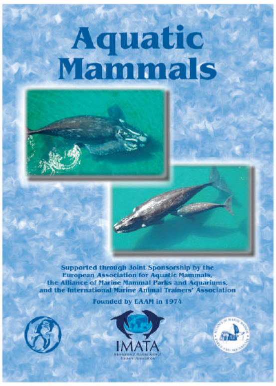

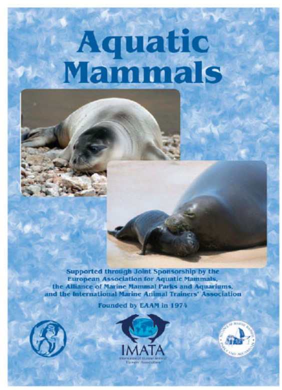

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Spatial and Temporal Variation in River Otter (*Lontra canadensis*) Diet and Predation on Rockfish (Genus *Sebastes*) in the San Juan Islands, Washington

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Abstract

The effectiveness of marine protected areas (MPAs) and their effects on the predators of target species have been a matter of discussion for some time. In the Salish Sea, a number of MPAs protect several species of rockfish (*Sebastes* spp.), three of which are currently listed under the Endangered Species Act (ESA); however, the role of coastal river otter (*Lontra canadensis*) predation on rockfish populations is poorly understood. This study describes the scarcely studied diet of river otters in the San Juan Islands, Washington, as a first step in assessing the potential effect of these predators on rockfish. Using frequency of occurrence (% FO), we described coastal river otter diet for San Juan, Orcas, and Fidalgo Islands during the summer of 2008. River otters consumed a variety of both fish and invertebrate species. Fish occurred most frequently in their diet at all three islands, including gunnels (Pholidae) (present in 83.6 to 97.3% of scats), sculpins (Cottidae) (79.5 to 97.3%), and pricklebacks (Stichaeidae) (58.9 to 78.1%). Rockfish were present in 2.7 to 21.9% of river otter scat with the highest occurrence at San Juan Island (21.9%). Scat also contained a higher occurrence of juvenile rockfish vs adult specimens. Although rockfish consumption by river otters at San Juan Island has increased since the summer of 1999, consistent with the establishment of MPAs, we cannot attribute the establishment of MPAs as the cause or address the positive or negative potential effects of river otter predation on rockfish recovery. However, this information may assist future studies that use more modern techniques in assessing these effects on rockfish populations.

Key Words: river otters, *Lontra canadensis*, diet analysis, marine protected areas, rockfish, *Sebastes* spp., San Juan Islands, spatial variation, temporal variation

Introduction

Overfishing has led to the decline in abundance and size of rockfish (*Sebastes* spp.) and other economically valuable fish stocks over the last several decades (Palsson, 1998; Safford, 2011). In the Salish Sea, overfishing led to the creation of marine protected areas (MPAs) in 1990 (Washington State Legislature [WSL], 1990; Weispfenning, 2006). The Salish Sea includes the inland waters of three main basins: (1) the Strait of Juan de Fuca; (2) the Strait of Georgia; and (3) the Puget Sound, which includes the San Juan Islands. Five of the seven MPAs currently located within the San Juan Islands are listed as limited no-take reserves, protecting several species of rockfish. San Juan County has in addition created eight voluntary no-take zones for bottomfish recovery (Kaill, 2001). The San Juan Islands provide habitat for more than a dozen distinct species of rockfish, several of which are in critical condition, including Endangered Species Act-listed yelloweye (*S. ruberrimus*) and canary (*S. pinniger*) rockfish (Palsson et al., 2009; U.S. Federal Register, 2010).

MPAs are a valuable tool in the recovery of overexploited fish stocks because they reduce human sources of mortality (Murray et al., 1999; Palsson et al., 2009). There are many examples of the ecological and economic benefits of MPAs when fishing restrictions are appropriately enforced (Tuya et al., 2000; Fanshawe et al., 2003; Greenstreet et al., 2009; Lester et al., 2009; Palsson et al., 2009; Hargreaves-Allen et al., 2011). However, there is growing concern that MPAs may generate a top-down trophic cascade through increased predator abundance in response to increased prey (Salomon et al., 2002; Shears & Babcock, 2003; Baskett et al., 2006; Beaudreau & Essington, 2009; Ward et al., 2012). Birds, lingcod (*Ophiodon elongates*), harbor seals (*Phoca vitulina*), and other marine mammals and fish are some of the better-known predators of rockfish (Palsson et al., 2009). River otters (*Lontra canadensis*) are one of many potential predators of rockfish in the San Juan Islands (Jones, 2000), yet very little is known about their diet in the area. River otters are commonly and widely distributed along the shorelines of Washington State, and they have been observed moving among the islands (Speich & Pitman, 1984; Jones, 2000). It was estimated that between 208 and 590 river otters lived at San Juan Island in 2000 (Jones, 2000). There are no more recent estimates for the species on San Juan Island, adjacent islands, or the remaining Washington coast.

River otters are opportunistic feeders whose diet generally reflects prey availability (Jones, 2000; Kruuk, 2006). They are able to dive up to 20 m and can remain under water for up to 4 min, but their diet is likely limited by their swimming ability as they consume slow-moving, easily captured fish and crustaceans (Larivière & Walton, 1998; Jones, 2000; Kruuk, 2006; Franco et al., 2013). Scat samples collected at San Juan Island in 1999 and 2000 indicated rockfish occurred in 6.7% of scats (Jones, 2000). Although no other diet studies of river otters have been conducted within the San Juan Islands, studies from other coastal areas along the North Pacific indicate that the occurrence of rockfish and other prey types varies with location. For instance, rockfish were observed in 17% of scat samples at Prince of Wales Island, Alaska (Larsen, 1984). Off the Gulf of Georgia in coastal British Columbia, Canada, rockfish occurred in up to 30% of scats sampled (Stenson et al., 1984). Consequently, to understand the potential impact of river otters on threatened fish stocks in the San Juan Islands, it is important to describe their diet among several sites within the archipelago.

In general, rockfish abundance has apparently increased in the San Juan Islands since the 1990s, presumably due to protection provided by MPAs (Palsson et al., 2009; Williams et al., 2010). Rockfish consumption by lingcod in the San Juan Channel was reportedly higher within MPAs compared to non-reserves (Beaudreau & Essington, 2009). Copper (*S. caurinus*) and black (*S. melanops*) rockfishes were recorded in higher densities within San Juan MPAs compared to fished areas (Eisenhardt, 2001, 2002; Palsson & Pacunski, 2005). The majority of rockfish stocks that reside near the San Juan Islands are still in precautionary status, but this is most likely due to the lack of recent data on population trends (Palsson et al., 2009). Since river otter diet was last described for San Juan Island when MPAs were first being established (Jones, 2000), it is possible that rockfish occurrence in river otter diet has also increased as a result of MPAs.

As a first step in assessing the potential impact of river otters on rockfish in the San Juan Islands, we compared the spatial variation in the diet of river otters among San Juan, Orcas, and Fidalgo Islands. We also compared the temporal variation in diet of river otters in San Juan Island since the establishment of MPAs in the archipelago. Given the lack of adequate information regarding spatial variation in river otter diet in the Salish Sea, we also include a comparison of river otter diet between San Juan Island and southern Vancouver Island.

Methods

The San Juan Islands (48° 33' N, 123° 00' W; Figure 1), Washington, consist of hundreds of islands carved out by glacial movements (Kenady et al., 2002). The uneven and rocky coastline is comprised of exposed bedrock, boulder fields, and coarse sediments (Palsson et al., 2009). Pairs and larger groups of river otters are most often observed in exposed, more diverse, rocky intertidal communities, while individuals are frequently sighted in soft-bottom intertidal communities (Jones, 2000). To choose collection sites on San Juan, Orcas, and Fidalgo Islands, we selected latrine sites from Jones (2000) and local sources (Figure 1; Table 1). Collection dates occurred every 2 wks and were dependent on good weather conditions. Scat was collected from May to September, and we accessed latrine sites by boat and foot. Scats estimated to be 0 to 5 d old, determined by moisture content and cohesion, were collected and transported on ice back to the processing lab at Western Washington University in Bellingham. Scats were kept frozen and then thawed when ready to process.

To separate prey parts from scat, samples were rinsed through nested mesh sieves and strainers, and all hard parts were recovered with forceps (Lance et al., 2001). Prey parts were stored in glass vials with 70% isopropyl alcohol until further processing could begin. After 2 wks, the alcohol was poured off and samples dried in a drying oven. Prey were identified to the lowest possible taxon using a dissecting microscope, reference fish bone collections from Washington and Oregon, invertebrate dichotomous keys, and published fish bone and otolith keys (Morrow, 1979; Cannon, 1987; Kozloff, 1996; Sept, 1999; Harvey et al., 2000). Rockfish were further identified to juvenile and adult remains, which were determined through visually clear differences in otolith and bone size. By separating occurrences of juvenile and adult rockfish, we can better analyze potential foraging habitat (Morris, 2005).

Statistically detecting differences in prey via > 5% frequency of occurrence (% FO) of scat among sites and times requires over 59 scat samples (Trites & Joy, 2005). Due to time and budgeting constraints, we randomly subsampled our

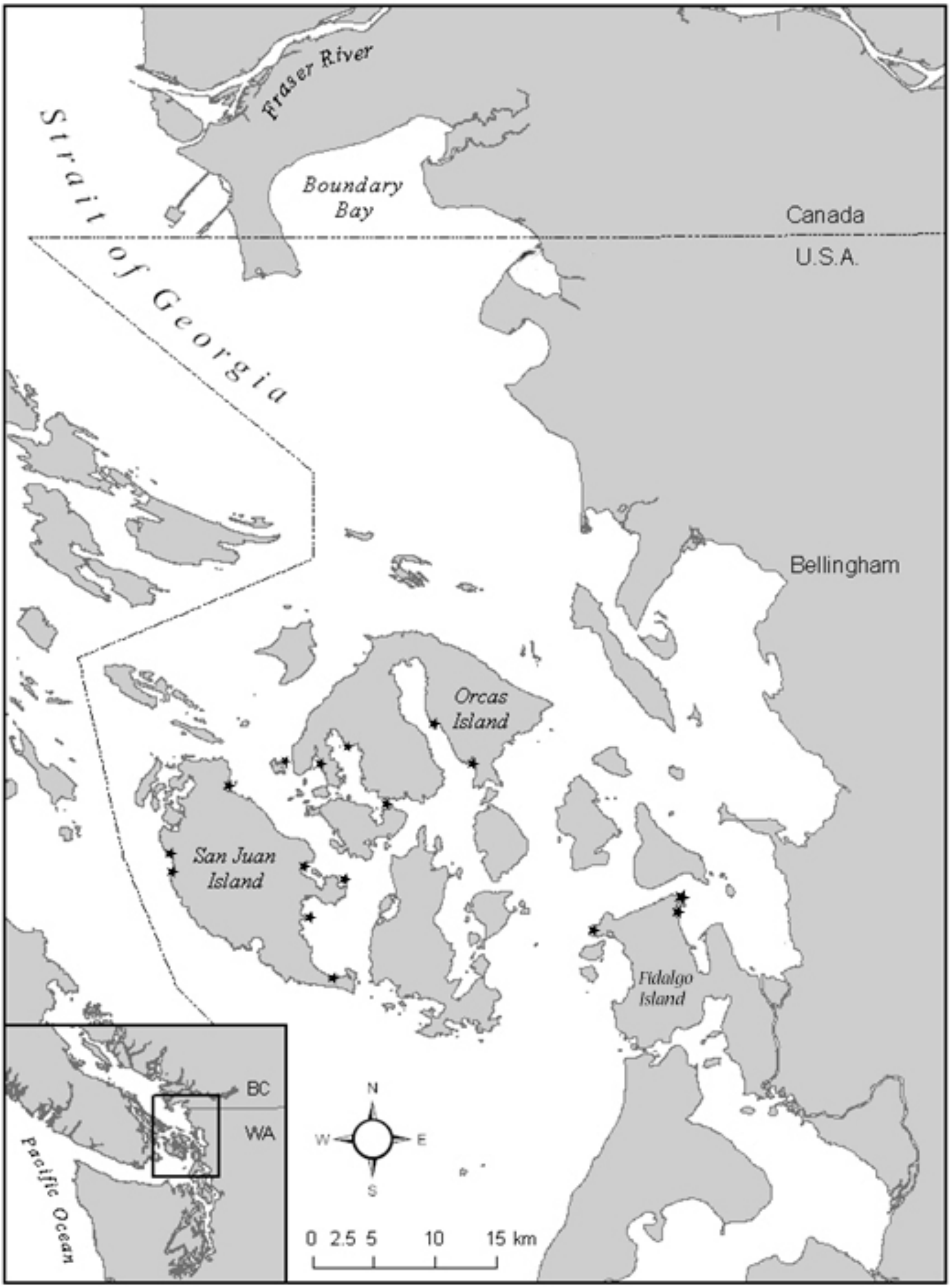

Figure 1. River otter scat collection sites in the San Juan Islands Archipelago, Washington, USA; stars denote a unique collection site.

Table 1. Coordinates of river otter collection sites for the summer of 2008; the asterisks denote sites used in 1999 (Jones, 2000).

San Juan latrine sites	Coordinates
Andrews Bay*	N 48.5470°, W 123.1616°
Smallpox Bay*	N 48.5406°, W 123.1624°
Turn Island*	N 48.5330°, W 122.9735°
Friday Harbor*	N 48.5566°, W 123.0121°
San Juan Historic Park	N 48.4560°, W 123.0227°
Rocky Bay*	N 48.5993°, W 123.1024°
Dinner Island*	N 48.5072°, W 123.0083°
Orcas latrine sites	**Coordinates**
Deer Harbor	N 48.6200°, W 123.0100°
Shaw Island	N 48.5732°, W 122.9573°
Jones Island	N 48.6145°, W 123.0464°
Rosario	N 48.6467°, W 122.8737°
Leiber Haven	N 48.6053°, W 122.8166°
West Sound	N 48.6319°, W 122.9614°
Unknown site 1	(Unknown coordinates)
Unknown site 2	(Unknown coordinates)
Fidalgo latrine sites	**Coordinates**
Washington Park	N 48.5000°, W 122.6952°
Anacortes Marina	N 48.5041°, W 122.6021°
Anacortes Marina Site 2	N 48.5146°, W 122.6032°

dataset to generate 73 scat samples for each study island during the summer season (June-August) of 2008. The composition of the river otter diet was described using % FO (Trites & Joy, 2005):

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

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

To be conservative in our analyses, we defined primary prey taxa as that with ≥ 10% FO. Spatial comparisons of primary prey among San Juan, Orcas, and Fidalgo Islands were analyzed with Pearson's chi-square contingency tables (Patterson et al., 1998; Bull, 2000; Jones, 2000; Malo et al., 2004). Given the relatively short food transit time of rivers otters (average of about 3 h) (Davis, et al., 1992), we can accurately observe each study island as a unique population; however, we cannot confidently compare among latrine sites due to the probability of scats being excreted by the same individual, and also that prey items observed at one site may not have been ingested within the immediate proximity of the collection site.

Temporal comparisons of San Juan Island's primary prey between the summer seasons of 1999 and 2008 were conducted in a similar manner to the spatial comparisons. A second spatial comparison was carried out between San Juan Island and non-harbor sites in southern Vancouver Island, Canada, where a similar river otter diet study was conducted in the summer of 2008 (Guertin et al., 2010). Non-harbor scat collection sites for southern Vancouver Island were similar in habitat (i.e., less urbanization, presence of rocky shores) to those we employed in the San Juan Islands. For all tests, we used the Bonferonni correction to adjust α and compensate for multiple comparisons (Zar, 1996). Differences in diet diversity among San Juan, Orcas, and Fidalgo Islands were examined with a Kruskal-Wallis rank sum test and *post hoc* tests (Zar, 1996) after we developed species accumulation curves to verify that each island reached an asymptote and, thus, that we had enough samples to compare diversities (Colwell & Coddington, 1994). We used the statistical software program *R* (Version 2.14.1) to run all analyses.

Results

Diet Composition and Spatial Variation: San Juan, Orcas, and Fidalgo Islands, Summer 2008

Fish comprised the majority of the river otter diet in the San Juan, Orcas, and Fidalgo Islands (Table 2). Although a large variety of fish taxa were identified, there was a similar occurrence of most prey items among the three study islands. Gunnels (Pholidae) occurred at the highest frequency for all three islands (83.6 to 97.3%), followed by sculpins (Cottidae) (79.5 to 97.3%), pricklebacks (Stichaeidae) (58.9 to 78.1%), righteye flounders (Pleuronectidae) (42.5 to 58.9%), northern clingfish (*Gobiesox maeandricus*) (6.9 to 27.4%), and several species of codfishes (Gadidae or Merluccidae). Although primary fish prey taxa were similar across the study islands, some differences were evident (Table 3). Among the fish taxa defined as primary prey, consumption of gunnel, sculpin, Pacific staghorn sculpin (*Leptocottus armatus*), high cockscomb (*Anoplarchus purpurescens*), northern clingfish, and rockfish varied among the study islands. In contrast, Irish lord (*Hemilepidotus* spp.), prickleback, righteye flounder, starry flounder (*Platichthys stellatus*), snailfish, and codfish prey occurrences did not vary among study islands.

Rockfish consumption varied among the three study islands (Table 3). Rockfish (either occurrences of adult or juveniles) were collectively consumed most often at San Juan Island, with a frequency of occurrence of 21.9%. They were observed in 12.3 and 2.7% of scat at Orcas and Fidalgo Islands, respectively. Rockfish occurrence varied significantly with island ($p = 0.0020$).

Table 2. Prey items found in river otter scat from San Juan, Orcas, and Fidalgo Islands for the summer of 2008; results are reported as percentage frequency of occurrence (% FO).

	San Juan		Orcas		Fidalgo	
Prey item	*n* = 73	% FO	*n* = 73	% FO	*n* = 73	% FO
Fish	73	100.0	73	100.0	73	100.0
Unidentified fish species	1	1.4	--	--	1	1.4
Unknown fish species	--	--	6	8.2	3	4.1
Gunnel (Pholidae)–unidentified	71	97.3	70	95.9	61	83.6
Sculpin (Cottidae)	71	97.3	68	93.2	58	79.5
Irish lord (*Hemilepidotus* spp.)	14	19.2	11	15.1	6	8.2
Pacific staghorn sculpin (*Leptocottus armatus*)	3	4.1	25	34.2	13	17.8
Great sculpin (*Myoxocephalus polyacanthacephalus)*	--	--	2	2.7	--	--
Rosylip sculpin (*Ascelichthys rhodorus*)	5	6.8	1	1.4	--	--
Unidentified sculpins	53	72.6	52	71.2	--	--
Prickleback (Stichaeidae)	43	58.9	50	68.5	57	78.1
High cockscomb (*Anoplarchus purpurescens*)	6	8.2	13	17.8	3	4.1
Unidentified pricklebacks	37	50.7	44	60.3	57	78.1
Righteye flounder (Pleuronectidae)	39	53.4	43	58.9	31	42.5
Starry flounder (*Platichthys stellatus*)	11	15.1	25	34.2	18	24.7
English sole (*Pleuronectes vetulus*)	2	2.7	3	4.1	1	1.4
Unidentified flatfish	27	37.0	23	31.5	15	20.6
Northern clingfish (*Gobiesox maeandricus*)	20	27.4	10	13.7	5	6.8
Codfishes (Gadidae or Merluccidae)	11	15.1	18	24.7	9	12.3
Walleye pollock (*Theragra chalcogramma*)	4	5.5	4	5.5	7	9.6
Pacific cod (*Gadus macrocephalus*)	1	1.4	1	1.4	--	--
Pacific tomcod (*Microgadus proximus*)	1	1.4	2	2.7	--	--
Pacific hake (*Merluccius productus*)	5	6.8	--	--	1	1.4
Unidentified codfishes	9	12.3	11	15.1	1	1.4
Rockfish (*Sebastes* spp.)	16	21.9	9	12.3	2	2.7
Rockfish–juvenile	10	13.7	7	9.6	2	2.7
Rockfish–adult	6	8.2	2	2.7	--	--
Snailfish (Liparidae)	10	13.7	4	5.5	2	2.7
Pacific herring (*Clupea pallasi*)	6	8.2	5	6.8	5	6.8
Shiner perch (*Cymatogaster aggregata*)	--	--	6	8.2	1	1.4
Plainfin midshipman (*Porichthys notatus*)	--	--	4	5.5	--	--
Eelpouts (Zoarchidae)	--	--	4	5.5	--	--
Pacific sand lance (*Ammodytes hexapertas*)	2	2.7	--	--	--	--
Threespine stickleback (*Gasteroseus aculeatus*)	1	1.4	2	2.7	--	--
Smelt (Osmeridae)	1	1.4	--	--	--	--
Crustaceans	66	90.4	63	86.3	54	74.0
Unidentified crustaceans	--	--	11	15.1	9	12.3
Decapods	46	63.0	40	54.8	31	42.5
Unidentified decapods	6	8.2	9	12.3	1	1.4
Caridean shrimp	18	24.7	9	12.3	13	17.8
Pandalid shrimp	17	23.3	17	23.4	12	16.4
Stout shrimp (*Heptacarpus brevirostris*)	1	1.4	--	--	--	--
Unidentified caridean shrimp	--	--	2	2.7	1	1.4
Hermit crabs (*Pagurus* spp.)	5	6.9	1	1.4	--	--
Armed hermit crab (*Pagurus armatus*)	2	2.7	1	1.4	--	--
Hairy hermit crab (*Pagurus hirsutiusculus*)	1	1.4	--	--	--	--
Unidentified hermit crabs	4	5.5	--	--	--	--
True crabs (*Brachyura*)	42	57.3	31	42.5	31	42.5
Unidentified true crabs	2	2.7	--	--	1	1.4
Rock crabs (*Cancer* spp.)	23	31.5	21	28.8	20	27.4
Graceful crab (*Cancer gracilis*)	--	--	--	--	3	4.1
Rock crabs (cont.)						

	San Juan		Orcas		Fidalgo	
Prey item	n = 73	% FO	n = 73	% FO	n = 73	% FO
Red rock crab (*Cancer productus*)	1	1.4	3	4.1	1	1.4
Dungeness crab (*Cancer magister*)	7	9.6	5	6.9	14	19.2
Unidentified rock crabs	16	21.9	14	19.2	7	9.6
Pea crabs (*Pinnixa* spp.)	7	9.6	9	12.3	5	6.9
Western pea crab (*Pinnixa occidentalis*)	1	1.4	4	5.5	3	4.1
Gaper pea crab (*Pinnixa littoralis*)	2	2.7	3	4.1	--	--
Burrowing pea crab (*Scleroplax granulata*)	--	--	2	2.7	--	--
Unidentified pea crabs	5	6.9	4	5.5	5	6.9
Helmet crab (*Telmessus cheiragonus*)	7	9.6	2	2.7	2	2.7
Shore crab (*Hemigrapsus oregonensis*)	6	8.2	4	5.5	3	4.1
Kelp crab (*Pugettia gracilis*)	3	4.1	--	--	--	--
Snails (Gastropoda)	44	60.3	51	69.9	33	45.2
Bivalves (Bivalvia)	20	27.4	46	63.0	24	32.9
Plant or algae	17	23.3	10	13.7	22	30.1
Foraminifera *(Elphidium incertum)*	14	19.2	19	26.0	11	15.1
Acorn barnacle (*Balanus crenatus*)	9	12.3	21	28.8	8	11.0
Chitons (Polypacophora)	8	11.0	2	2.7	1	1.4
Isopods	13	17.8	12	16.4	11	15.1
Sphaeromatidae isopod (*Dynamenella benedicti*)	6	8.2	4	5.5	5	6.9
Oregon pill bug (*Gnorimosphaeroma oregonense*)	4	5.5	8	11.0	6	8.2
Valviferan isopods (*Idotea* spp.)	4	5.5	2	2.7	2	2.7
Flabellifera isopods–unidentified	3	4.1	--	--	--	--
Unidentified isopods	--	--	2	2.7	1	1.4
Seed shrimp (Ostracoda)	3	4.1	8	11.0	4	5.5
Amphipods–unidentified	2	2.7	--	--	--	--
Gammaridea	4	5.5	--	--	4	5.5
Skeleton shrimps (Caprellidae)	--	--	--	--	--	--
Marine annelid worm (Polychaeta)	1	1.4	--	--	2	2.7
Spirorbidae	2	2.7	--	--	--	--
Oligochaeta	--	--	1	1.4	2	2.7
Unknown inorganic material	--	--	1	1.4	1	1.4

River otters consumed juvenile rockfish somewhat frequently (~3 to 14%) at all three islands, while adult rockfish occurred only at San Juan and Orcas Islands (8.2 and 2.7%, respectively). However, the consumption of juvenile rockfish was not significantly different among the islands (p = 0.0594). Adult rockfish alone were not considered primary prey at any of the study islands and were therefore not included in the spatial analyses.

Crustaceans and other invertebrates occurred frequently in the diet of river otters (Table 2). River otters chew their food well, which made it difficult to identify most of the invertebrate specimens to the species level. Taxa of true crabs (Brachyura) and other decapods occurred in more than 40% of prey remains at all study islands, including nine distinguishable species. Rock crabs (*Cancer* spp.) occurred the most (27.4 to 31.5%) of all crustacean prey items for all three islands. Dungeness crab (*C. magister*) was the most frequently occurring crab species and was observed the most in Fidalgo Island scat (19.2%). Caridean shrimp, especially the pandalid variety, were observed in 12.3 to 24.7% of scats for all study islands. Small fragments and whole specimens (< 2 cm in length) of bivalves and snails also occurred frequently in prey remains (> 80%). Plant and algae collectively occurred in 13.7 to 30.1% of remains. Plant and algae were not identified to a lower taxa level from a lack of distinguishing characteristics but were grouped together in order to roughly quantify how much of the river otter diet was vegetative. Few invertebrate specimens varied by island (Table 3). Occurrences of crustaceans and more specifically decapod crabs, along with bivalves (Bivalvia) and snails (Gastropoda), was significantly varied among study islands. Occurrence of shrimps, seed shrimp (Ostracoda), true crabs, rock crabs (and dungeness crab), isopods, foraminifera, and plant/algae did not vary among study islands.

Table 3. Spatial comparisons among primary river otter prey taxa in San Juan, Orcas, and Fidalgo Islands for the summer of 2008; bold *p* values indicate significance after the Bonferonni correction was applied. Taxa with ≥ 10% FO in any island were included in the analyses. (Refer to Table 2 for sample size and respective % FO.)

Taxon	$\chi^2_{(df=2)}$	*p*
Gunnel	11.61	**0.0030**
Sculpin	14.05	**0.0009**
Irish lord	3.68	0.1586
Pacific staghorn sculpin	21.85	**<0.0001**
Prickleback	6.22	0.0446
High cockscomb	7.98	**0.0185**
Righteye flounder	4.10	0.1290
Starry flounder	7.23	0.0270
Northern clingfish	11.90	**0.0026**
Rockfish (adult & juvenile)	12.42	**0.0020**
Juvenile rockfish	5.65	0.0594
Snailfish	7.23	0.2697
Codfishes	4.27	0.1184
Crustaceans	7.78	**0.0205**
Caridean shrimp	3.73	0.1548
Pandalid shrimp	1.27	0.5309
Seed shrimp	3.01	0.2225
True crabs	4.43	0.1091
Decapods	6.28	**0.0434**
Rock crabs	0.31	0.8568
Dungeness crab	5.92	0.0519
Isopods	0.42	0.8118
Oregon pill bug	1.45	0.4837
Barnacles	10.00	**0.0067**
Foraminifera	2.79	0.2482
Snails	9.29	**0.0096**
Bivalves	22.18	**0.0001**
Plant/algae	5.73	0.0570

Temporal Variation: San Juan Island, Summers of 1999 and 2008

Almost all river otter prey taxa in San Juan Island changed during the past decade (Table 4). The exceptions were Pacific sand lance (*Ammodytes hexapertas*) and helmet crab (*Telmessus cheiragonus*); both decreased in occurrence and were statistically similar. Most prey species included in the analyses increased in occurrence: gunnel, sculpin, prickleback, righteye flounder, bivalve, pandalid shrimp, plant/algae, rockfish, isopod, codfish, and chiton. Sculpin was the most frequently observed prey in both time periods, occurring in over 72% of scats during the summer of 1999 but significantly increasing to 97.3% in the summer of 2008 ($p \leq 0.0001$). Gunnel occurred in only 20.1% of scats in 1999 but significantly increased to 97.3% in 2008 ($p \leq 0.0001$). The consumption of rockfish (adult or juvenile rockfish occurrence in a scat) significantly increased from 7.2% in 1999 to 21.9% in 2008 ($p = 0.0019$), representing a tripling of rockfish frequency of occurrence during the past decade.

Spatial Variation: San Juan Island and Southern Vancouver Island, Summer 2008

There were several differences in the diet of river otters between San Juan Island and southern Vancouver Island (Table 5). Rockfish were not observed in the river otter diet at southern Vancouver Island (Guertin et al., 2010). Sculpin, Irish lord, righteye flounder, and crustaceans all occurred at greater frequencies around San Juan Island compared to occurrences at Vancouver Island (Table 5). In contrast, Pacific staghorn sculpin, rosylip sculpin (*Ascelichthys rhodorus*), prickleback, high cockscomb, northern clingfish, and snailfish prey taxa were observed more frequently at southern Vancouver Island than at San Juan Island. Gunnel and starry flounder prey taxa occurred at similar frequencies for both study islands.

Diet Diversity: San Juan, Orcas, and Fidalgo Islands, Summer 2008

Each island reached an asymptote respective to its species accumulation curve; thus, we had an adequate number of samples from each island to confidently compare diversity. Diet diversity varied among San Juan, Orcas, and Fidalgo Islands (Kruskal-Wallis $\chi^2 = 20.589$, $p \leq 0.0001$). *Post hoc* analyses indicated that the diet diversity of Fidalgo Island was significantly less diverse compared to both San Juan and Orcas Islands (Kruskal-Wallis $\chi^2 = 7.4556$, $p = 0.0063$ and Kruskal-Wallis $\chi^2 = 19.97$, $p \leq 0.0001$, respectively). Statistically, the diet in San Juan and Orcas Islands was similarly diverse (Kruskal-Wallis $\chi^2 = 3.3893$, $p = 0.0656$).

Discussion

Coastal, marine river otter diet observed in this study was consistent with diet previously reported using scat analysis (Larsen, 1984; Stenson et al., 1984; Jones, 2000; Guertin et al., 2010). Gunnel, sculpin, righteye flounder, and prickleback were the most frequently observed prey items in the river otters' diet throughout the North Pacific coast. These fishes are abundant in the tide pools and rocky shores of Washington State (Simenstad et al., 1977; Jones, 2000). Crustaceans were a more consistent prey item in the San Juan Islands (74 to 90.4% FO), compared to that of the studies in Alaska (10 to 15% FO) and British Columbia, Canada (50% FO) (Larsen, 1984; Stenson et al., 1984; Guertin et al., 2010; Table 5). Generally, river otters at both San Juan Island and southern Vancouver Island primarily consumed small,

Table 4. Temporal comparisons between river otter prey taxa from summer 1999 (Jones, 2000 data) and summer 2008 in San Juan Island; bold p values indicate significance after the Bonferonni correction. Taxa with ≥ 0% FO in either year were included in the analyses.

	San Juan Island 1999		San Juan Island 2008			
Taxon	n = 139	% FO	n = 73	% FO	$\chi^2_{(df=1)}$	p
Gunnel	28	20.1	71	97.3	114.3545	**<0.0001**
Sculpin	101	72.7	71	97.3	18.919	**<0.0001**
Prickleback	44	31.7	43	58.9	14.6879	**0.0001**
Righteye flounder	28	20.1	39	53.4	24.5255	**<0.0001**
Bivalves	6	4.3	20	27.4	23.6966	**<0.0001**
Pandalid shrimp	7	5.0	18	24.7	17.7157	**<0.0001**
Plant/algae	6	4.3	17	23.3	17.8103	**<0.0001**
Adult & juvenile rockfish	10	7.2	16	21.9	9.643	**0.0019**
Isopods	2	1.4	13	17.8	19.5065	**<0.0001**
Codfishes	7	5.0	11	15.1	6.2004	**0.0128**
Helmet crab	15	10.8	7	9.6	0.0744	0.7850
Pacific sand lance	32	23.0	2	2.7	14.6214	**0.0001**

Table 5. Spatial comparisons between river otter prey taxa from San Juan Island and southern Vancouver Island (non-harbor) for the summer of 2008; bold p values indicate significance after the Bonferonni correction. Taxa with ≥ 10% FO for either island were included in the analyses.

	San Juan Island		S. Vancouver Island			
Taxon	n = 73	% FO	n = 62	% FO	$\chi^2_{(df=1)}$	p
Gunnel	71	97.3	55	88.7	3.94	0.0472
Sculpin	71	97.3	39	62.9	26.23	**<0.0001**
Irish lord	14	19.2	1	1.6	96.44	**<0.0001**
Pacific staghorn sculpin	3	4.1	9	14.5	91.18	**<0.0001**
Rosylip sculpin	5	6.8	9	14.5	6.92	**0.0085**
Prickleback	43	58.9	52	83.9	10.02	**0.0015**
High cockscomb	6	8.2	42	67.7	51.84	**<0.0001**
Righteye flounder	39	53.4	20	32.3	6.11	**0.0135**
Starry flounder	11	15.1	4	6.5	2.52	0.1124
Northern clingfish	20	27.4	40	64.5	18.71	**<0.0001**
Snailfish	10	13.7	19	30.6	5.71	**0.0169**
Crustaceans	66	90.4	5	8.1	91.18	**<0.0001**

intertidal and subtidal fish species, but most prey items were consumed at different frequencies (Table 5). This difference most likely may be a result of discrepancies between the compositions of the communities around each island.

Most of the small invertebrates (e.g., gastropods, bivalves, foraminifera, chitons) observed in this study co-occurred with fish and larger crab remains, suggesting these prey items may have been consumed via secondary ingestion (Pierce et al., 2004). Rock crabs (*Cancer* spp.) and several species of bottomfish consume several varieties of demersal crustaceans and other small marine invertebrates observed in the scat of this study (Stevens et al., 1982; Asson-Batres, 1986; Murie, 1995; Yamada & Boulding, 1996; Sulkin et al., 1998; Sept, 1999; Smith et al., 1999; Reum & Essington, 2008; Bourdeau, 2009; Lee & Sampson, 2009). Similar diet items observed in past river otter diet studies were also reported as secondary ingestion (Larsen, 1984; Guertin et al., 2010). Thus, it is possible that some prey species observed in this study were actually secondary prey rather than primary or target prey species.

Birds have been a common category of prey for river otters in other regions across the Pacific Coast, including San Juan Island (Larsen, 1984; Stenson et al., 1984; Jones, 2000; Guertin et al., 2010); however, they were not consumed in this study. Plants and algae were prevalent in river otters' diet; however, past river otter diet studies have had contrary results on the consumption of plant material. While Jones (2000) previously observed fruit and algae remains in river otter scat, Guertin et al. (2010)

did not find any evidence of vegetation in the river otters' diet. Plant material can be more easily broken down and degraded in digestive processes than hard remains and is one of the several potential biases of examining fecal remains (Pierce et al., 2004). Bivalve innards could be similarly ingested without remnants, but past studies have only found fragments of bivalves and other molluscs, again suggesting secondary ingestion (Larsen, 1984; Stenson et al., 1984; Jones, 2000).

This study was limited to the summer season, and it is important to note that river otters can alter their diet seasonally based on availability of prey in San Juan Island. Jones (2000) found that sculpins, rockfish, and greenling prey species collectively varied by season at San Juan Island during 1999 and 2000. Consumption of rockfish alone occurred more frequently during the spring than in any other season. In contrast, collective consumption of fish, crabs, and birds did not vary by season and were stable sources of food year-round (Jones, 2000). Multiyear and year-round studies of river otter diet among the San Juan Islands will aid in understanding interannual and seasonal changes in diet.

San Juan Island river otter diet significantly changed in the past decade (Table 4), increasing the consumption of rockfish from 7.2% in 1999 to 21.9% in 2008 (Table 2). Since there is no previous diet information for Orcas or Fidalgo Islands, no conclusions can be reached on potential diet changes over time in these islands. MPAs are more prevalent throughout the coastline of San Juan Island, San Juan Channel, and Haro Strait (WSL, 1990), which we speculate may account for the higher observed consumption of rockfish around the San Juan study island. Most collection sites for San Juan Island were located near MPAs, but the Friday Harbor collection site was the only latrine site within the boundaries of an MPA (a site that had zero occurrences of rockfish in scat). Clearly, without knowledge of river otter spatial movements (foraging location and latrine site), the effects of rockfish-based MPAs on river otter diet are unknown.

Juvenile rockfish occurred more frequently than adult rockfish in the diet of river otters and may be explained in part by their preferred habitat. Adult rockfish tend to inhabit deeper depths than their younger counterparts and are also larger in size and more difficult prey to handle (Love et al., 1991), thus making it more difficult to capture them. Adults may also occur with juveniles in the water column and may be consumed opportunistically when river otters come across large schools of juveniles. Alternatively, diet tends to reflect the general abundance of prey species within the seasonal range of river otters (Mills et al., 2007). The more frequent consumption of juvenile rockfish simply may represent a greater abundance of juvenile rockfish compared to that of adult rockfish, but the impact by river otter consumption of more juveniles than adult rockfish could result in fewer reproducing adults in the future.

Although species of rockfish could not be identified, given the large number of species that are either threatened, endangered, or species of concern (Palsson et al., 2009; U.S. Federal Register, 2010), there is a possibility of river otters consuming one or more of these categories of rockfishes. Bocaccio (*Sebastes paucispinis*), yelloweye, and canary rockfish inhabit depths that surpass the diving capacity of river otters, but juveniles of these threatened species tend to inhabit nearshore, shallower depths (Palsson et al., 2009). However, other stable populations of rockfish, including Puget Sound (*S. emphaeus*), black, and yellowtail (*S. flavidus*) rockfishes, are also found at shallower, more accessible depths. River otter consumption may have different implications dependent on species and its status. Overfishing has left some species of rockfish vulnerable to even the slightest increase in mortality rates (Ruckelshaus et al., 2009), which is why further investigations are needed on river otters' diet and their direct impact on rockfish populations.

River otters are a common predator of intertidal and subtidal fish and crustaceans in the San Juan Islands marine ecosystem. Although coastal river otters are not legally considered a marine mammal (Marine Mammal Commission [MMC] & National Marine Fisheries Service [NMFS], 2007), they are a common predator along the shores of marine habitats, including the San Juan Islands, and need to be included in ecological models used in fisheries management. Understanding river otters' diet and their place in the coastal food web is essential in determining their role in Salish Sea ecology (Emerson, 2012). A significant increase in the frequency of rockfish in river otters' diet since the creation of MPAs suggests a direct response to protection by rockfish and an indirect response by a rockfish predator. The potential effects of river otter predation on rockfish recovery require further attention. One approach could be to estimate the abundance and energetic requirements of river otters and their diet to calculate the consumption of rockfish by river otters in the region as recently carried out for harbor seals (Howard et al., 2013). A complementary approach could be to integrate the river otters' diet with their spatial movements to identify concentrations of rockfish consumption (e.g., Ward et al., 2012). The two approaches together will provide information to fish managers and ecosystem modelers to evaluate the response of rockfish to river otter consumption and to determine the role of this predator species in the San Juan Islands ecosystem.

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