VARIATION IN DIET AND ACTIVITY OF RIVER OTTERS (*LONTRA*
CANADENSIS) BY SEASON AND AQUATIC COMMUNITY

by

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ABSTRACT

Variation in Diet and Activity of River Otters (*Lontra canadensis*) by Season and Aquatic Community

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Keystone predators can impact many prey species, including those that are endangered. In order to assess the impact predators have on different prey populations, it is essential to identify the species being consumed in different types of aquatic communities, while accounting for possible seasonal variation in consumption. Here I use analysis of river otter (*Lontra canadensis*) scat to assess the impact otters have on prey populations, particularly endangered salmonids and migrating birds. I analyzed the prey composition of 1,411 river otter scats collected from 10 sites in Humboldt County, California, between 2011 and 2012. Analysis of prey items in scat divided study sites into four distinct clusters based on diet. Fish, particularly from the families Gasterosteidae (sticklebacks), Cottidae (sculpins), and Pholidae (gunnels), formed the main prey component, but crustaceans, birds (*Anas* sp. and *Fulica* sp.), amphibians, and insects were also main components of otter diet. Salmonids formed less than 5% of overall diet, but otters consumed the largest percentage of salmon during salmon spawning season at the inland cluster where salmonids spawn. Scat marking intensity varied between latrine sites, clusters, and seasons, with the most scats collected in the fall and the fewest in the winter/spring, except at the inland cluster where marking activity was reversed. Otters may be responding to seasonal migrations of endangered and threatened salmonids. Birds comprised 21% of diet and were eaten most frequently during the winter migration

season, and no endangered bird species were found. Diet surveys of this type are useful for monitoring resource use by top predators in wetlands and other aquatic ecosystems.

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INTRODUCTION

North American river otters (*Lontra canadensis*, hereafter otters) are carnivores in the family Mustelidae, subfamily Lutrinae. Otters are keystone species in the ecosystems in which they occur, affecting a wide variety of prey species and distributing aquatic nutrients into terrestrial environments (Ben-David et al. 1998*a, b*). Otters can potentially impact prey species during critical times, such as during large migrations of certain bird and fish species. This is a particularly significant factor in Humboldt County of northern California, a major flyway for many migrating bird species and home to many anadromous salmonids (Barnhart et al. 1992, Colwell 1994, NRS 2005). Knowing what species otters consume is important for recreational fishing, salmonid and crab fisheries, bird management, and river otter management, particularly if otters are eating endangered or threatened salmonids (*Oncorhynchus spp.*) or birds (e.g., snowy plovers, *Charadrius alexandrinus*). For management of otters and coexisting endangered and threatened salmonids, it is also critical to know if otters are “following” spawning salmonids and moving between marine and freshwater ecosystems throughout the year.

Depending on the region and the season, otters eat a combination of fish, birds, crustaceans, amphibians, large insects, mollusks, reptiles, and small mammals (Toweill 1974, Melquist and Hornocker 1983, Kruuk 1995, Cote et al. 2008, Penland and Black 2009). Otters tend to take fish in proportion to their relative availability and in inverse proportion to their swimming speed (Ryder 1955, Erlinge 1968, Larsen 1984, Carss 1995, Polednik et al. 2004). Many studies of otters across the continent have recorded a diet of mainly slow, mid-sized fish species from the families Cottidae (sculpins), Cyprinidae

(carps and minnows), Catostomidae (suckers), Gasterosteidae (sticklebacks), Ictaluridae (catfish), Pleuronectidae (flounders), and Centrarchidae (bass and sunfishes), and some swifter fish from Salmonidae (salmon and trout) (Appendix A) (Toweill 1974, Modaferrri and Yocum 1980, Melquist and Hornocker 1983, Larsen 1984, Crait and Ben-David 2006). Diets vary seasonally in some areas, with otters switching major prey components depending on prey abundance (Larsen 1984, Beja 1991, Crait and Ben-David 2006, Penland and Black 2009), but diets do not vary seasonally in other locations (Stenson et al. 1984, Cote 2008).

Otters are opportunistic carnivores, whether they are foraging in inland freshwater environments or in coastal intertidal regions (Stenson et al. 1984, Cote 2008). In Portugal, Beja (1991) studied Eurasian otter (*Lutra lutra*) diet differences between marine, brackish, and freshwater habitats that were spatially in close association with one another. Contrary to what he expected, he observed that Eurasian otters hunted inland rather than on the coast, especially in the spring and summer. It was thought that otters preferred to hunt inland because freshwater inland prey is more profitable than marine prey, which tend to have lower caloric content per item (Conroy and Jenkins 1986, Beja 1991). However, other studies have found that marine systems can serve as the best environment for river otters due to a more diverse prey base (Kruuk and Hewson 1978, Conroy and Jenkins 1986).

River otters in Humboldt County, California eat a diet comprised mostly of fish, with a large percentage of invertebrates and a smaller percentage of birds (Reeves 1988,

Penland and Black 2009). One recent year-long study found that otter scats from around Humboldt Bay had frequencies of occurrence for fish ranging from 48 - 82%, but this study did not examine the variety of species consumed (Penland and Black 2009). A study completed at a freshwater site on Redwood Creek in Humboldt County found that over three summers, sculpins, salmonids, sticklebacks, and suckers comprised 65-83% of otter diet, and composition varied between freshwater and estuarine environments (Reeves 1988). However, no studies have examined otter diet differences or species of fish or birds consumed between freshwater, brackish, and marine communities while accounting for seasonal variation and animal movements. The Humboldt Bay system is unique in that it contains many areas of these three systems with otters resident in each of them (Oldham and Black 2009, Penland and Black 2009, Brzeski 2010).

Humboldt Bay contains 110 species of marine and estuarine fish (Barnhart et al. 1992). In the freshwater watersheds that surround Humboldt Bay, including Jacoby Creek, Freshwater Creek, Salmon Creek, and Elk River, there are three threatened anadromous salmonids: coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*) and steelhead trout (*O. mykiss*), as well as the cutthroat trout (*O. clarki clarki*) which is not currently listed under the Endangered Species Act (NRS 2005).

True salmon (chinook and coho) die directly after spawning in the winter season; thus their population status and life cycles are extremely vulnerable (NRS 2005). Otters are known to eat salmonids up to 80 cm in length, particularly in spawning season, but the extent of predation is unknown in Humboldt County (Toweill 1974, Larsen 1984, Carss et al. 1990). Dolloff (1993) found a group of four otters in Alaska that consumed at

least 3,300 juvenile salmonids over a six-week period; this level of consumption can potentially have a large effect on the fish population. Melquist and Hornocker (1983) discovered that during fall and winter, salmonids occurred more frequently in otter scat than most other types of fish, and in the fall, otters would congregate at spawning beds to take advantage of the rich prey source. Crait and Ben-David (2006) found a distinct increase in otter fecal deposition rates on spawning streams but a decrease in deposition rates on Yellowstone Lake during trout spawning, with a reversal of activity after spawning.

Birds also form a relatively large percentage of Humboldt otter diets, ranging from 1-21% occurrence in scats (Penland and Black 2009). The area around Humboldt Bay has many shorebird and waterfowl species and serves as a crucial stopover location (usually in winter and spring) for many migratory water-bird species on the Pacific flyway (Colwell 1994, Harris 2005). Studies along the Pacific Northwest have found that otters eat American coot (*Fulica americana*), American wigeon (*Anas americana*), canvasback duck (*Aythya valisineria*), common merganser (*Merque merganser*), double-crested cormorant (*Phalacrocorax auritus*), glaucous-winged gull (*Larus glaucescens*), and ruddy duck (*Oxyura jamaicensis*) (Toweill 1974, Hayward et al. 1975, Reeves 1988, Price and Aries 2007). It is unknown whether otters are actively hunting birds, coming across carcasses incidentally, or both. However, as with fish, no studies have examined which species of birds otters are eating around Humboldt Bay and what type of impact otters might have on bird populations.

Otters are elusive, primarily nocturnal, opportunistic predators, making them difficult to study in the wild. However, otter scats, collected non-invasively, can be used in diet analysis and demographic studies. Otters deposit scats, urine, and gelatinous “scat-jellies” at specific sites on land called latrines. The scats deposited at latrines are very distinctive from those of other species in terms of shape, smell, and content (Greer 1955, Webb 1976).

With careful analyses of hard parts observed in otter scats, like fish otoliths, scales, vertebrae, shells, feathers, and other bones, classification of otter prey (often to species) can be determined (Webb 1976, Wise 1980, Harvey et al. 2000). However, scat analysis does not describe the proportions of prey consumed; it overestimates minor prey items, and it underestimates major prey items and prey with large proportions of soft material (Carss 1995).

In order to assess the impact of otters on different prey populations in northern California and to help inform future management policies regarding otters, managers first need to know what species otters are consuming in marine, brackish (estuarine and marsh), and freshwater sites, and approximately how much they may take. I determined the species of fish and birds that otters are eating. I tested the hypotheses that (1) otter diet is influenced by aquatic community (marine, brackish, or freshwater) and season, and (2) otters respond to migratory fish movements. I tested the predictions that a) otters display a more varied diet at marine and brackish sites than at freshwater sites due to a greater number of species found there (Kruuk and Hewson 1978, Conroy and Jenkins 1986), b) more birds would be consumed in winter (during migration) than in the rest of

the year and c) more scats would be found at inland freshwater latrine sites during the time of salmon spawning (winter/rainy season) than during the other seasons.

STUDY AREA

Otter scats were collected across central Humboldt County (40° 44' 50" N, 123° 59' 17" W) in northern coastal California. The county is characterized by redwood (*Sequoia sempervirens*) forest, agricultural tracts, marshes (Arcata Marsh and Wildlife Sanctuary and Humboldt Bay National Wildlife Refuge), Humboldt Bay and its watershed, and residential areas including the towns of Eureka and Arcata. The total county population is about 130,000, with approximately 50,000 in Eureka and Arcata combined (U.S. Census Bureau 2010).

Due to the marine influence, temperatures are fairly constant year-round, with winter lows at 5-6 °C and summer highs at 16-18 °C. The mean yearly precipitation is 97 cm, most of which falls from November to February (Barnhart et al. 1992). Winters tend to be mild and rainy, and summers dry and relatively cool. County elevation ranges between sea level and 2100 m to the east (Barnhart et al. 1992).

Humboldt Bay is 22.5 km long and 7.2 km wide at its widest point, the second largest enclosed bay in California (Barnhart et al. 1992). Wetlands surrounding the bay are dominated by saltgrass (*Distichlis spicata*), pickleweed (*Salicornia virginica*), and cordgrass (*Spartina densiflora*) (Barnhart et al. 1992).

I visited previously identified and recently discovered latrine sites from 10 distinct locations, including from north to south: the mouth of Mad River, Mad River Inland, Mad River Slough, Arcata Marsh and Wildlife Sanctuary, Bracut, Freshwater Creek, Elk River, Gill's dock, Humboldt Bay National Wildlife Refuge, and Hookton Slough (Figure 1).

Figure 1. Study area of river otter latrine sites for otter scat collection in Humboldt County in northern California (shown in inset), 2011 – 2012.

These locations included marine sites (Gill's dock and Bracut), estuarine sites less than 3 km from the coast (Hookton Slough, Elk River mouth, Mad River Slough, and the mouth of Mad River), brackish marsh sites (Arcata Marsh and Humboldt Bay NWR), and freshwater sites at least 3 km from the coast (Freshwater Creek, and Mad River Inland). There were 1 to 5 latrines at each site. All latrines at a site were less than 1 km apart, except for Mad River Inland, which had two latrines that were spaced about 5.5 km apart. One of these latrines (near the Mad River Fish Hatchery) located along the Mad River did not have enough scats for independent analysis, so for all analyses it was combined with the Mad River Inland site, which was most similar in diet composition and the closest site geographically.

METHODS

Scat Collection

I collected otter scats from each known latrine at the 10 sites every 2 weeks from May 2011 through May 2012. I divided the year into three equal-length seasons based on the mild Pacific Northwest climate and rainfall amounts: low-rainfall or summer (May 1-August 31), medium-rainfall or fall (September 1-December 20), and high-rainfall or winter/spring (December 21-April 30). Over the year of my study, low-rainfall months had a cumulative total of 9.5 cm of rain, medium-rainfall months had 24.4 cm of rain, and high-rainfall months had 78.5 cm of rain (Weather Underground Almanac 2012). I collected scats in individual quart-size plastic bags (ZiplocTM, S. C. Johnson, Racine, WI), recorded the date and location of each sample, and stored the samples in a freezer at -15°C until analysis. At each latrine, I collected three quarters of every scat present, smashing the remaining portions of scat into the substrate with a clean glove or bag. This allowed otter scent to remain at the latrine in order to minimize any potential change in marking behavior, as well as prevent recounting of old scats in the future. To reduce pseudoreplication, if more than 10 scats were collected at one site on a single day, I used a random number generator to choose 10 scats for analysis. I also determined scat marking intensity, which was the total number of scats counted per time unit at each site. Marking intensity was used as an indicator of otter activity and compared across sites and seasons.

Scat Processing

I placed each scat in a separate nylon knee-high stocking with a unique scat ID label (Golightly et al. 1994) written on waterproof paper (Rite in the RainTM, J. L. Darling Corporation, Tacoma, WA). I then knotted the stockings, placed them in a mesh bag, and washed them on a gentle cycle in a washing machine (Model LWA50AW, AmanaTM, Newton, IA) with liquid laundry detergent (SunTM Products Corporation, Salt Lake City, UT) and a tablespoon of bleach for 15 min. Afterwards, I emptied each scat from the stockings into individual aluminum trays. I dried the scats in the trays for 24 hours at 90° C, and stored them in desiccators until analysis.

Undigested prey remains were coarsely classified under a dissecting scope; then items were more carefully examined using a compound microscope to identify them to family, genus or species. To identify fish, bird, amphibian, and invertebrate taxa, I examined sagittal otoliths (fish ear bones), vertebrae (fish and amphibian), jaws (fish and amphibian), scales, feathers, and shells and compared them to general identification keys (Casteel 1974, Webb 1976, Morrow 1979, Harvey et al. 2000). Bird feathers were identified by comparing to specimens in the Humboldt State University Wildlife Museum Collection. I used the Humboldt State University fish otolith reference collection of some local species. For each scat sample, I recorded the occurrence of each prey item detected. I sent nine samples that were good representatives of fish otoliths to Pacific Identifications Incorporated (Vancouver, BC) for species/genus/family confirmations.

Otolith Measurements

I measured the length of otoliths with digital calipers to the nearest 0.01 mm of species that had known regression equations relating otolith length to fish length and weight (Harvey et al. 2000, Browne et al. 2002). I measured only otoliths that were in good condition (not broken or worn). However, otoliths were probably at least partially degraded (smaller) than fresh otoliths due to otter digestion and the washing process; therefore all fish length estimates are conservative. Because each fish has two otoliths, I measured otoliths randomly within each scat and assumed (used) every second measurement represented the length of a fish consumed (Cote et al. 2008).

Fish and Bird Abundance Indices

I compared diet results with concurrent fish collection data from the California Department of Fish and Wildlife (CDFW). Multiple times a year, CDFW seines for fish along some sloughs in Humboldt County, counting and measuring salmonids while making general abundance estimates of non-salmonids (J. Garwood and M. Wallace, CDFW, pers. comm.). Three scat sampling locations overlapped with creeks that CDFW sampled: Elk River (Martin Slough), Freshwater (Freshwater Creek, Ryan Slough, Wood Creek), and the Humboldt Bay National Wildlife Refuge (Salmon and Cattail Creeks). I used CDFW salmonid and non-salmonid count data that occurred during my 12-month study at the overlapping sites to see how general percentages of particular species otters were eating compared to the relative amount available reflected by fish collections, and to see if otters appeared to follow migrating fish in certain areas. To create a conservative estimate, I calculated indices for each of the three sites by summing the minimum

possible number (CDFW lowest estimate) of individual fish per species available (caught) over the course of the study.

To examine whether otters were consuming birds (waterfowl, coots, and shorebirds) in proportion to their general availability across sites and seasons, I conducted an index count of all water-birds seen (instantaneous) within 50 m of each latrine upon arrival for scat collection and tallied all shorebirds and waterfowl/rallids. I averaged the numbers from each latrine for each site and accounted for the number of sampling weeks in each season. I compared these general index counts to the number of otter scats that contained bird feathers from the associated sites and seasons.

Statistical Analyses

To evaluate importance of different prey items, I calculated relative frequency of occurrence of all the prey found in scat. Relative frequency of occurrence is the proportion of the total number of scats collected that contained a specific prey (Larsen 1984, Carss 1995). In order to examine possible prey differences between different sites and seasons, I used a combination of Principal Components Analysis (PCA), Ward's Cluster Analysis, chi-square tests, and Fisher's exact tests (Sinclair and Zeppelin 2002). Based on the results of the PCA and cluster analysis, I created cluster groups of latrine sites containing similar diets.

I used chi-square goodness-of-fit tests to assess whether relative frequency of occurrence of prey items differed among latrine sites, clusters, and seasons, respectively. The null hypothesis for each of these tests was that distribution of prey item frequency of occurrence in scats across categories was in proportion to the distribution across

categories of all scats used in the prey item analysis. For example, the seasonal distribution of the 1411 scats analyzed was 37% summer, 35% fall, and 28% winter/spring, so under the null hypothesis, the expected distribution of the 1027 observed fish in these scats was 380 in summer, 359 in fall, and 288 in winter/spring. Rejection of the null hypothesis would indicate seasonal differences in occurrence of fish in the diet. In all chi-square tests involving multiple tests (e.g., one test for each prey category), Bonferroni's correction was used to adjust individual-test P values for the total number of categories tested in order to keep the family error rate at or below $\alpha = 0.05$. Where expected counts were too small to meet the conditions of the chi-square goodness-of-fit test, I used Fisher's exact test.

Frequency of occurrence was analyzed in three different categorizations of prey: 1) broad taxonomic level (fish, bird, crustacean, amphibian, insect, other), 2) five orders, genera, or species that each had frequency of occurrence across all scats exceeding 5%, and 3) 20 additional orders or genera that each had frequency of occurrence across all scats of less than 5%. Categorizations 1 and 2 defined 11 "primary" prey groups, and the third categorization defined 20 "secondary" prey groups. The 11 primary prey groups were included in all analyses of frequency of occurrence; the secondary groups were included in analyses of frequency of occurrence across clusters and seasons.

Chi-square tests for independence were used to test whether distribution of otter activity (as measured by total number of scats) across seasons was independent of that across locations (considered both by site and by cluster). For the purposes of seasonal comparisons, marking intensity was defined as number of scats counted per sampling

week, and analysis of variance (ANOVA) was used to test for differences in mean marking intensity among the three seasons. Significant results from ANOVA were followed by Tukey post-hoc comparisons.

I measured otoliths and compared the lengths to regression equations in order to estimate the length of fish that were eaten by otters at each site (Harvey 2000, Browne 2002). For fish taxa that I had at least 20 otolith measurements, I used ANOVA to test for differences in average fish length among the clusters. Significant results were followed by Tukey post-hoc comparisons. A chi-square goodness of fit test was used to assess whether distribution of fish species in otter scats differed from species distribution observed in CDFW fish seine hauls. Only the four most common species observed in seining were used in this analysis. A chi-square goodness of fit test was also used to assess whether distribution across clusters of birds (waterfowl, coots, and shorebirds) in otter scats differed from the observed (null) distribution of birds across clusters, as estimated from my counts. A similar test was used to assess whether distribution of birds in the diet across seasons differed from observed distribution based on my counts. All hypothesis tests were performed at $\alpha = 0.05$.

To ensure I had a sufficient number of scats for diet analyses across cluster groups, I used Microsoft Excel to make random successive draws of groups of 10 processed scats (no replacement) for each site, cluster, and season. The cumulative relative frequency of occurrence for every prey category was calculated after each successive draw (Trites and Joy 2005, Trejo 2012). A sufficient sample size was established when the cumulative frequency of occurrence of each prey item no longer

changed (i.e., became less variable) with additional sampling (usually leveled off between 40-90 scats). When the cumulative relative frequency did not level off, I either did not include that site, cluster, or season in analysis, or in one case, combined the data with another similar grouping for analysis.

RESULTS

Prey Identification and Site Comparisons

A total of 2,276 river otter scats were counted and collected for all sites from May 2011-May 2012; 1,411 were analyzed for prey content. The frequency of occurrence for all prey items was determined for the 1,411 river otter scats across 10 sites (Table 1). The number of prey items ranged from 1 to 5 items per scat. Fifty-two percent of scats had 1 prey item only, 38% had 2 items, and about 10% of scats contained 3 or more items. Based on the primary prey groups, fish were the most common prey item at all sites (Appendix A), followed by crustaceans (crab [e.g., *Cancer* and other genera] and crayfish [e.g., *Pacifastacus* and other genera]), birds (Appendix B), amphibians (e.g., *Rana* and other genera), other items (Appendix C), and insects. The “Other” category was created for all trace, incidental, and unidentifiable prey items.

For fish taxa identified in scat, three-spined sticklebacks (*Gasterosteus aculeatus*, Family Gasterosteidae), sculpins (Cottidae), and gunnels (Pholidae) were all in the secondary prey category (Appendix D). Other fish families that were in the third prey category were gobies (Gobiidae), surfperches (Embiotocidae), salmonids (Salmonidae), flatfish (Pleuronectiformes), smelt (Osmeridae), toadfish (Batrachoididae), and eelpouts (Zoarcidae). Bird genera that fell into prey category 2 included ducks of the genus *Anas*, and American coots (*Fulica sp.*). Tests of significance in diet analyses only used prey items that composed at least 5% frequency of occurrence (Sinclair and Zeppelin 2002). Out of the 11 prey items in prey categories 1 and 2, there was a significant difference in prey composition among all 10 sites in all 11 prey groupings (Table 2).

Table 1. Summary of number of primary prey item occurrences and percent frequency of occurrence (freq. of occ.) of prey items in river otter scats in Humboldt County, California, 2011-2012.

Site (from N to S)	n	Fish		Crustacean		Bird		Amphibian		Other		Insects	
		Freq. of occ.	Count of prey	Freq. of occ.	Count of prey	Freq. of occ.	Count of prey	Freq. of occ.	Count of prey	Freq. of occ.	Count of prey	Freq. of occ.	Count of prey
Mad River Coast	72	87.5	63	19.4	14	12.5	9	2.8	2	16.7	12	4.2	3
Mad River Inland	119	94.1	112	35.3	42	0.8	1	2.5	3	4.2	5	6.7	8
Mad River Slough	110	64.5	71	41.8	46	19.1	21	14.5	16	10.0	11	11.8	13
Arcata Marsh	188	53.2	100	16.5	31	45.2	85	29.8	56	3.7	7	19.7	37
Bracut	73	56	41	21	15	33	24	36	26	5	4	10	7
Freshwater	82	84.1	69	34.1	28	7.3	6	9.8	8	6.1	5	2.4	2
Elk River	225	80.9	182	44.0	99	9.8	22	2.2	5	13.8	31	4.0	9
Gill's Dock	174	81.0	141	35.1	61	17.8	31	2.9	5	27.6	48	5.2	9
Humboldt Bay NWR	202	70.3	142	39.6	80	31.2	63	7.4	15	3.5	7	7.9	16
Hookton Slough	166	63.9	106	54.8	91	22.9	38	9.0	15	4.8	8	5.4	9
Total	1411	72.8	1027	35.9	507	21.3	300	10.7	151	9.8	138	8.0	113

Table 2. Tests for differences in relative frequency of primary prey items among river otter latrine sites in Humboldt County, California, 2011-2012. All chi-square tests have 9 degrees of freedom.

Prey Item	n	Chi-square statistic	P-value
Fish	1027	30.2	< 0.001*
Gasterosteidae	371	78.8	< 0.001*
Cottidae	244	161.8	< 0.001*
Pholidae	74	128.9	< 0.001*
Bird	300	113.5	< 0.001*
<i>Anas sp.</i>	68	72.8	< 0.001*
<i>Fulica sp.</i>	66	70.3	< 0.001*
Crustacean	507	52.5	< 0.001*
Amphibian	151	147.1	< 0.001*
Insects	113	46.6	< 0.001*
Other	138	89.4	< 0.001*

*Indicates significant differences at Bonferroni-adjusted level of significance

Cluster Formation and Principal Components Analysis

The top six general classes of prey items and the top three fish families were included in the cluster formation and the Principal Components Analysis. The cluster analysis formed four groupings: Cluster 1 (Arcata Marsh, Humboldt Bay NWR, Hookton Slough), Cluster 2 (Bracut, Freshwater Creek, Mad River Coast, Mad River Slough), Cluster 3 (Elk River, Gill's dock), and Cluster 4 (Mad River Inland; Figure 2). Cluster 1 was characterized by a diet high in sticklebacks, birds, amphibians, and insects with fewer sculpins and gunnels represented (Table 3). The otters in Cluster 2 ate a wide variety of prey including more sculpins and amphibians, but fewer fish, crustaceans, gunnels, and other. Cluster 3 was characterized by an otter diet with many fish, crustaceans, gunnels, and other. Cluster 4 was characterized by a great proportion of fish, including sculpins, a relatively large percentage of salmonids, and few birds.

Using Principal Components Analysis, for the 1,411 scats analyzed, 43.6% of the diet variation could be explained by the first component, 35.2% was explained by the second component, and 12.2% was explained by the third component (Figure 3). The remaining components comprised a total of 9% of the overall variation, and were not useful for describing the clusters based on prey type. This analysis corresponded to the same four clusters formed by cluster analysis.

Figure 2. Similar latrine sites based on river otter diet differences determined by Principal Components Analysis in Humboldt County, California, 2011 – 2012. Cluster 1 (solid line) corresponds to Humboldt Bay NWR and the Arcata Marsh. Cluster 2 (dashed line) is split into two sections (Mad River Coast and Mad River Slough in the north, and Bracut and Freshwater Creek further south). Cluster 3 (dotted line) surrounds Elk River and Gill's Dock. Cluster 4 (dash-dot line) is located on the inland portion of Mad River.

Table 3. Prey variable loadings that were highly correlated (+ positively or – negatively) with principal components. Variables with loading values greater than 0.3 were included in the interpretation of the principal component. Data collected in Humboldt County, California, 2011-2012.

Principal Component No.	Variables	Loadings (+/-)
1	Amphibians	-0.468
	Birds	-0.412
	Cottidae	+0.374
	Gasterosteidae	-0.330
	Insects	-0.418
2	Birds	-0.301
	Crustacean	-0.460
	Fish	-0.524
	Gasterosteidae	-0.325
	Other	-0.344
	Pholidae	-0.375
3	Cottidae	-0.380
	Crustacean	-0.322
	Gasterosteidae	-0.417
	Other	+0.528
	Pholidae	+0.422

Figure 3. Principal Components Analysis diagram of latrine cluster formations based on prey proportions found in river otter scats in Humboldt County, California 2011-2012 (AM= Arcata Marsh, BR= Bracut, ER= Elk River, FW= Freshwater, GD= Gill's dock, HR= Humboldt Bay National Wildlife Refuge, HS= Hookton Slough, MC= Mad River Coast, MI= Mad River Inland, MS= Mad River Slough). Diagram on left shows the main two components of diet variation, Principal Component (PC) 1 on the x-axis versus PC2 on the y-axis. Diagram on the right shows PC2 on the x-axis versus PC3 on the y-axis.

Regional and Seasonal Comparisons based on Clusters

Relative frequency of occurrence of all primary prey items except for crustaceans differed across the four clusters (Table 4, Figure 4). Relative frequency of occurrence differed across the four clusters in six of the secondary prey items (Pholidae, *Anas sp.*, *Fulica sp.*, Embiotocidae, Salmonidae, and Osmeridae).

Relative frequency of occurrence of all primary prey items except for Cottidae differed across the three seasons (Figure 5, Table 5, Appendix E). Fish were generally eaten more often in summer and birds more often in winter (Table 6). Secondary prey items that differed in relative frequency across seasons were Batrachoididae, *Bucephala sp.*, *Oxyura sp.*, and Salmonidae. Salmonids were the only fish eaten more often in winter/spring than in other seasons.

Scat Marking Intensity

I collected 797 scats in the summer, with a mean of 88.5 collected per sampling period ($n = 9$, $SE = 13.35$), 917 scats in the fall with a mean of 114.6 per sampling period ($n = 8$, $SE = 8.39$), and 562 scats in winter/spring with a mean of 62.4 per sampling period ($n = 9$, $SE = 10.20$). There was a significant difference in marking intensity between seasons ($F_{2,23} = 5.47$, $P = 0.011$). A post-hoc Tukey test (Lowry 1998) indicated that marking activity was significantly greater in fall than in winter/spring ($Q_{2,23} = 4.848$, $P < 0.01$), but that there was no significance difference in marking activity between fall and summer ($Q_{2,23} = 2.31$, $P > 0.05$) or between summer and winter/spring ($Q_{2,23} = 2.47$, $P > 0.05$).

Figure 4. Prey frequency of occurrence (for prey items in categories 1 and 2) for each of the four clusters for river otter scats collected in Humboldt County, California, 2011-2012.

Table 4. Tests for differences in relative frequency of primary and secondary prey items among the four diet clusters in Humboldt County, California, 2011-2012. All chi-square tests have 3 degrees of freedom

Prey Item	Test	Chi-square statistic	P-value
Fish	Chi-square	19.0	< 0.001*
Gasterosteidae	Chi-square	58.9	< 0.001*
Cottidae	Chi-square	93.0	< 0.001*
Pholidae	Fisher's Exact		< 0.001*
Gobiidae	Fisher's Exact		0.130
Embiotocidae	Fisher's Exact		< 0.001*
Salmonidae	Fisher's Exact		< 0.001*
Pleuronectiformes	Fisher's Exact		0.0643
Osmeridae	Fisher's Exact		< 0.001*
Batrachoididae	Fisher's Exact		0.182
Zoarcidae	Fisher's Exact		0.164
Agonidae	Fisher's Exact		0.418
Atherinidae	Fisher's Exact		0.394
Catostomidae	Fisher's Exact		0.481
Hexagrammidae	Fisher's Exact		0.365
Scorpaenidae	Fisher's Exact		1
Bird	Chi-square	76.1	< 0.001*
<i>Anas sp.</i>	Fisher's Exact		0.002
<i>Fulica sp.</i>	Fisher's Exact		< 0.001*
<i>Oxyura sp.</i>	Fisher's Exact		0.490
Podicipedidae	Fisher's Exact		0.761
<i>Aythya sp.</i>	Fisher's Exact		0.625
<i>Phalacrocorax sp.</i>	Fisher's Exact		1
<i>Bucephala sp.</i>	Fisher's Exact		0.714
<i>Melanitta sp.</i>	Fisher's Exact		0.714
<i>Gavia sp.</i>	Fisher's Exact		1
<i>Mergus sp.</i>	Fisher's Exact		1
Crustacean	Chi-square	4.7	0.198
Amphibian	Chi-square	51.3	< 0.001*
Insects	Chi-square	13.3	0.004
Other	Chi-square	64.1	< 0.001*

*Indicates significant differences at Bonferroni-adjusted level of significance.

Figure 5. Primary and secondary prey frequencies of occurrence across seasons from river otter scats collected in Humboldt County, California, 2011-2012. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 - April 30).

Table 5. Tests for differences in relative frequency of primary and secondary prey items among the three seasons in Humboldt County, California, 2011-2012. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 - April 30).

Prey Item	Test	Chi-square statistic	P-value
Fish	Chi-square	9.6	0.008
Gasterosteidae	Chi-square	10.6	0.005
Cottidae	Chi-square	2.3	0.312
Pholidae	Chi-square	27.6	< 0.001*
Gobiidae	Chi-square	6.6	0.037
Embiotocidae	Chi-square	13.7	0.001*
Salmonidae	Chi-square	13.4	0.001*
Pleuronectiformes	Fisher's Exact		0.669
Osmeridae	Fisher's Exact		0.065
Batrachoididae	Fisher's Exact		< 0.001*
Zoarcidae	Fisher's Exact		0.134
Agonidae	Fisher's Exact		1
Atherinidae	Fisher's Exact		0.061
Catostomidae	Fisher's Exact		1
Hexagrammidae	Fisher's Exact		1
Scorpaenidae	Fisher's Exact		1
Bird	Chi-square	59.1	< 0.001*
<i>Anas sp.</i>	Chi-square	7.8	0.020
<i>Fulica sp.</i>	Chi-square	45.4	< 0.001*
<i>Oxyura sp.</i>	Fisher's Exact		0.030
Podicipedidae	Fisher's Exact		0.183
<i>Aythya sp.</i>	Fisher's Exact		0.090
<i>Phalacrocorax sp.</i>	Fisher's Exact		1
<i>Bucephala sp.</i>	Fisher's Exact		0.048
<i>Melanitta sp.</i>	Fisher's Exact		1
<i>Gavia sp.</i>	Fisher's Exact		1
<i>Mergus sp.</i>	Fisher's Exact		1
Crustacean	Chi-square	6.1	0.048
Amphibian	Chi-square	26.2	< 0.001*
Insects	Chi-square	12.7	0.002
Other	Chi-square	18.4	< 0.001*

*Indicates significant differences at Bonferroni-adjusted level of significance.

Table 6. Percent differences in prey in river otter scats (in decreasing order of importance in diet) between observed and expected frequencies by season in Humboldt County, California, 2011-2012. Only differences exceeding 5% are listed. The null hypothesis for each of these tests was that distribution of prey item proportion to the distribution across categories of all scats used in the prey item analysis. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 – December 20), and winter/spring had high rainfall (December 21 – April 30).

Prey Taxa	Summer	Fall	Winter/Spring
Fish	+7		-15
Gasterosteidae	+18	-12	-14
Pholidae	+9	+39	-90
Gobiidae	+18	+16	-53
Embiotocidae	+34	+13	-84
Salmonidae	-47	-28	+49
Batrachoididae	+57	-63	-100
Bird	-49		+38
<i>Anas sp.</i>	-36	+30	
<i>Fulica sp.</i>	-100	+18	+51
<i>Oxyura sp.</i>	-100		+60
<i>Bucephala sp.</i>	-100	-100	+72
Crustacean	+12	-5	-11
Amphibian	+31	-52	
Insects	+29	-24	-22
Other	+15	+24	-62

Distribution of otter activity across seasons was not independent of distribution across locations ($\chi^2_{18} = 393.41$, $P < 0.001$) or clusters ($\chi^2_6 = 174.20$, $P < 0.001$; Table 7, Figure 6). The expected marking intensities at each of the clusters during each season often varied from the observed marking intensities (Figure 7). Otters tended to use Clusters 1 and 2 more during summer than expected and Cluster 3 less during summer. Otters tended to use Cluster 3 more than expected in the fall, and Clusters 1, 2 and 4 less than expected in the fall. Otters used Cluster 4 more than expected in the winter/spring, and among the clusters displayed the largest percent differences between observed and expected marking activity between seasons (Appendix F). This was the opposite seasonal trend of marking activity when all clusters were combined.

Fish Lengths Based on Otoliths

Length was measured for 117 otoliths across eight fish families: Atherinidae ($n = 9$, mean fish length = 7.49 cm, SE = 0.46), Batrachoididae ($n = 1$), Clupeidae ($n = 2$, mean = 9.1 cm, SE = 2.62), Cottidae ($n = 11$, mean = 8.67 cm, SE = 0.72), Embiotocidae ($n = 43$, mean = 5.09 cm, SE = 0.29), Osmeridae ($n = 23$, mean = 8.99 cm, SE = 0.54), Pleuronectidae ($n = 15$, mean = 8.04 cm, SE = 0.60), and Salmonidae ($n = 13$, mean = 4.82 cm, SE = 0.92; Appendix G).

For the Osmerid *Hypomesus pretiosus*, lengths were significantly longer from otoliths found in scats at Cluster 2 as compared to Cluster 3 ($t_{20} = 3.7364$, $P = 0.001$). Lengths of the Embiotocid *Cymatogaster aggregata* were significantly different between Clusters 1, 2, and 3 ($F_{2,40} = 5.75$, $P = 0.006$). Embiotocid otoliths measured from Cluster 2 were significantly larger than those in both Cluster 1 ($Q_{2,40} = 5.036$, $P < 0.01$) and Cluster 3

Table 7. Percent differences between observed and expected river otter scat marking intensity counts (more +, or fewer -) at latrine sites by season around Humboldt Bay, California, 2011-2012. Only differences exceeding 10% are listed. Expected counts were obtained under the assumption that seasonal distribution of use was independent of location. Seasons were established by rainfall amounts: summer had low rainfall (May 1 – August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 - April 30).

Latrine	Summer	Fall	Winter/Spring
Cluster 1	+22	-14	-16
Arcata Marsh and Wildlife Sanctuary	+17	-23	
Humboldt Bay National Wildlife Refuge	+24	-16	-19
Hookton Slough	+24		-44
Cluster 2	+12	-19	
Bracut	-69	-65	+67
Freshwater Creek			
Mad River Coast	+31		-80
Mad River Slough	+42	-31	-52
Cluster 3	-28	+22	
Elk River	-38	+22	
Gill's Dock		+25	-45
Cluster 4		-70	+54
Mad River Inland		-70	+54

Figure 6. Scat marking intensity as proportions of the totals collected for each of the four clusters over the scat collection period in Humboldt County, California, 2011-2012. Vertical lines represent season breaks. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 - April 30).

Figure 7. River otter scat marking intensity expected values (dashed lines) versus actual values (bars) for each cluster by season in Humboldt County, California, 2011-2012. Expected counts were obtained under the assumption that seasonal distribution of use is independent of cluster. Seasons were established by rainfall amounts: summer had low rainfall (May 1 – August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 - April 30).

($Q_{2,40} = 8.676$, $P < 0.01$), but lengths did not differ between Clusters 1 and 3 ($Q_{2,40} = 1.325$, $P > 0.05$).

Comparison with Fish and Bird Abundances

Based on the general abundance counts of fish from CDFW, otters in this study ate fish from 10 out of 13 families that were caught by CDFW throughout the year, including Atherinidae, Clupeidae, Cottidae, Embiotocidae, Gasterosteidae, Gobiidae, Osmeridae, Pleuronectidae, Salmonidae and Syngnathidae. Fish families that were seined but not seen in the otter diet include Cyprinidae, Engraulidae, and Poecilidae. At the sites where scat sampling overlapped with CDFW fish sampling, Atherinids were caught but not observed in scat. The most frequently seined fish (in order of abundance) were sticklebacks, salmonids, sculpins, and gobies (all over 5% relative frequency of occurrence). A comparison of the relative percent frequencies of occurrence (the number of a particular fish type observed divided by the total number of all fish observed) for seined fish families as compared to those recorded in otter scat suggested that otters consumed fish in different proportions to what is caught by CDFW seine nets ($\chi^2_3 = 45.28$, $P < 0.0001$). During my study otters ate fewer salmon and sticklebacks than expected but ate more sculpins. All of the other families were seen in low abundances both in otter diet and in the seine nets, except for Embiotocidae, which were seen more frequently in scat. Scat analysis is also influenced by the differential digestion of prey items based on species and size consumed which can have an effect on frequency of occurrence (Floyd et al. 1978; Sheffield and Grebmeier 2009).

Distribution of birds (waterfowl, coots, and shorebirds) in the diet across clusters did not differ from the observed distribution ($\chi^2_3 = 3.41$, $P = 0.33$). Distribution of birds

in the diet across seasons differed significantly from the observed seasonal distribution ($\chi^2_2 = 13.09$, $P = 0.001$). A larger percentage of birds was consumed during winter/spring than the distribution observed, and a smaller percentage of birds was consumed in the fall.

DISCUSSION

Seasonal and regional diet variations in Humboldt Bay river otters are very distinct. Using Principal Components Analysis, I was able to configure a pattern of otter diets into four clusters. Similarly, Sinclair and Zeppelin (2002) applied PCA to prey in scats from Steller sea lions (*Eumetopias jubatus*) to group their collection sites such that diet patterns could be described by location and season, and determined that Steller sea lions in their study also had four different geographic foraging regions, with each region represented by a distinct diet and its own seasonal variation.

These four clusters based on diet can be characterized by location. Even though they are located on opposite sides of the Bay, the Arcata Marsh and the Humboldt Bay National Wildlife Refuge and Hookton Slough grouped together as Cluster 1. All three of these locations contain marsh environments. These marsh areas serve as habitats for native birds and stop-over locations for migrating birds, which was reflected in the large intake of birds by otters at these sites. Additionally, these marsh areas serve as habitats for amphibians and freshwater aquatic insects, which is also reflected by the otter diet in this cluster (Fish and Wildlife Service 1999, Friends of the Arcata Marsh 2012).

Cluster 2 was comprised of Bracut, Freshwater Creek, Mad River Coast, and Mad River Slough. All of these sites are either tidally influenced sloughs or estuaries except Bracut, which is directly on Humboldt Bay near the mouth of an estuary (Jacoby Creek). The otter diet in Cluster 2 contained greater amounts of sculpins and amphibians. While sculpins tend to be marine and brackish organisms, amphibians tend to be more

associated with freshwater and occasionally brackish environments (Eschmeyer and Herald 1983, Mestre and Tejado 2003). The intermediate salinities of the estuarine environments of Cluster 2 are areas where both prey types can successfully live.

Cluster 3 included Elk River and Gill's dock. These two sites are spatially close to one another, with the Elk River site located on a tidal estuary near Humboldt Bay, and the Gill's Dock site situated directly on the Bay. Both sites have a strong marine influence, which was shown in the otter diet. Otters in this cluster ate more crustaceans and gunnels (as well as the greatest levels of surfperch). Elk River and Gill's dock are the closest sites to the entrance of Humboldt Bay, perhaps allowing for greater accessibility of more marine prey, like gunnels and surfperch. The otters' diet reflected the marine-orientation of these fish; almost all instances of surfperch intake were from Cluster 3, with fewer instances in Clusters 1 and 2, and no instances in Cluster 4. Surfperch (Embiotocidae), particularly shiner surfperch (*Cymatogaster aggregata*), are one of the most abundant fish in Humboldt Bay and tend to be inshore marine species (Eschmeyer and Herald 1983, Barnhart et al. 1992). Gunnels are eel-like, dwell on the bottom of intertidal areas, and are almost exclusively marine-oriented (Eschmeyer and Herald 1983).

Cluster 4 contained only the Mad River Inland site. This site was a freshwater environment. Otters at this cluster ate mostly fish such as sculpins and salmonids, and very few birds. Salmonids spawn in freshwater creeks, and otters at this cluster ate a relatively large percentage of salmonids compared to the other clusters.

I found the greatest overall marking intensity at Elk River. This may be due to the situation of Elk River as a connection point for the north and south portions of Humboldt

Bay, as well as it being an area that is utilized by the greatest number of river otters (Brzeski 2010). The most intense levels of marking activity over my sampling period and sites occurred at Elk River from mid-August through October in 2011, with each sampling week having between 20 and 71 scats. The intense marking activity during this time frame was confirmed in 2012 (Torgerson, unpublished data). There could also be more cooperative foraging occurring during this time of year, with males forming foraging groups (Blundell et al. 2002), perhaps to take advantage of schools of spawning shiner surfperch.

River otters often alter their spatial distribution according to the availability of certain key seasonal resources (Mason and Macdonald 1986, Reid et al. 1994, Crait and Ben-David 2006). Beja (1991) determined that when otters occur in closely associated habitats, they forage in non-marine environments because either prey availability or prey quality is better in freshwater and brackish environments than in the ocean. Conroy and Jenkins (1986) found that otters foraging in marine environments captured more prey per dive and ate more fish per hunt than otters in freshwater environments, which could be due to the smaller sizes and lower caloric value of marine prey in their study area. I found that river otters around Humboldt Bay had similar tendencies; based on the ingested otolith regression lengths of surf smelt and surfperch, larger fish tended to be taken from the estuarine locations of Cluster 2 than from the marine sites of Cluster 3. Another possible explanation for the size discrepancy could involve a separate aspect of otter foraging behavior: male otters tend to take larger fish than females (Kruuk and Moorhouse 1990). Since coastal river otters tend to temporarily form social male groups while females are more solitary (Shannon 1989, Blundell et al. 2002, Brzeski 2010),

perhaps the size differences of fish eaten at different sites reflect gender-biased regional resource exploitation. Groups of males may be exploiting the larger fish at the estuarine sites, while females take the smaller fish at the other sites.

My results are comparable to the general findings of Humboldt Bay otter diet examined by Penland and Black (2009), with a large intake of fish and crustaceans overall, a large bird intake at the Arcata Marsh, and fewer accounts of insects. However, with a larger sampling effort, I found more seasonal variation with fish and insects, while bird and crustacean variation between seasons were similar in both studies. Reeves (1988) studied river otter diet along Redwood Creek in Humboldt County at freshwater and estuarine sites with similar findings, except he found greater frequencies of Catostomidae, Cottidae, Salmonidae, and insects. Inconsistencies between my data and these studies could be attributed to variation in prey availability, differences in scat sampling location, annual differences in otter social groupings, variation in otter sex and age class, or a combination of these factors.

Three-spined sticklebacks were found more often in scats during the summer season, perhaps becoming more accessible to otters as they move into shallower areas to breed, or perhaps because otters might focus on shallower water areas to hunt. Sticklebacks are tolerant of a wide range of salinities (euryhaline), and breed from April through July in shallow brackish or freshwater areas, where males guard the nest (Veniers 1953, Eschmeyer and Herald 1983). Male sticklebacks would be particularly easy targets for otters during this time of year because they are restricted to the nest while guarding their eggs.

Many fish that otters consumed, including sculpins, gunnels, flounders, toadfish, eelpouts, and sucker fish, tend to be slow-moving fish that stay near the bottom of the water column, supporting the finding that otters tend to take slower fish (Erlinge 1968, Eschmeyer and Herald 1983). Other studies have noted the importance of sculpins (Cottidae) to North American otter diet (Toweill 1974, Melquist and Hornocker 1983, Larsen 1984, Stenson et al. 1984, Cote et al. 2008) and Eurasian otter diet (Heggberget and Moseid 1994, Polednik et al. 2004, Brzezinski et al. 2006). Sculpins are sluggish, demersal (bottom-dwelling), bottom-feeders (Eschmeyer and Herald 1983). Though most sculpin species are marine-oriented, some sculpins (*Cottus sp.*) live in freshwater (Eschmeyer and Herald 1983, Barnhart et al. 1992). The steady level of sculpin consumption over the course of the year indicates a constant, reliable, and accessible food source for otters. More details on the ecology of fish taxa consumed by otters in smaller numbers can be found in Appendix H.

Salmon were observed in otter scat more frequently during the winter/spring spawning season than in other seasons, comprising 17.2% of Cluster 4 (Mad River Inland) otters' diet during that time. Similarly, the increase in marking intensity at Mad River Inland during the winter/spring season was twice what was expected, the largest percent increase in marking intensity across all clusters throughout the entire year, possibly due to otters following spawning salmon inland from the coast. The only latrines to show marking intensity at least 10% greater than expected in winter/spring were Bracut and Mad River Inland, with many sites showing marking intensity at least 10% less than expected (Table 6). While overall marking intensity at all surveyed sites was very close to expected in the summer season, there was much greater than expected

marking activity in the fall and much less than expected activity in the winter/spring.

These findings could indicate that otters use latrine sites in other (not surveyed) locations during the salmon spawning season. Alternatively, changes in marking intensity over the year may have occurred due to weather (affecting scat collection and/or otter behavior), or otter scent communication about prey, reproductive, or social status (Rostain et al. 2004, Oldham and Black 2009).

Based on marking intensity, it also seems that otters may not utilize salmon spawning runs at the inland sites (Cluster 4) during the traditional December-January spawning. However, while coho and Chinook salmon run between October and January, steelhead and cutthroat trout spawn a few months later, from late winter through the spring (NRS 2005). Since Mad River Inland was the only Cluster 4 site in my study, it is possible that there are other inland latrines not surveyed that are being used seasonally. Overall, salmonids did not appear to be a main source of prey for river otters in Humboldt Bay as compared to other prey items. However, this could be due to otters not consuming as many bones (especially otoliths) because spawning salmon can reach up to a meter in length (NRS 2005), and therefore might be under-represented in the scats.

By examining otter digestive tracts, Toweill (1974) found that otters in coastal habitats across western Oregon ate a majority of fish (mostly salmonids and sculpins). He concluded that the predation effects of otters on salmon numbers were not important to the salmon population due to the low density of otters and because some salmon were probably carrion (Toweill 1974). While otters may be consuming spawning salmonids as they move inland from Humboldt Bay, it appears as if they are taking relatively small

proportions of salmon as compared to other prey items such as birds and other fish species around the Bay.

Despite the proportions of fish consumed by otters differing from the abundances estimated by the California Department of Fish and Wildlife, otters are still taking many of the same fish, overlapping 10 out of 13 families sampled. Sticklebacks and sculpins were both most common in otter diet and were seined in the greatest numbers. The inconsistency of salmon numbers collected by CDFW versus observed in otter diet could simply reflect the selectivity of the sampling method, or perhaps fewer salmon bones consumed by the otters. The presence of some fish families (Cyprinidae, Engraulidae, Poecilidae) captured by CDFW but not observed in otter diet could be due to otters not eating these small, quick fish, or tiny otoliths going unnoticed in scats. CDFW did not seine any gunnels (Pholids) even though they comprised an important percentage of otter diet. This could have been due to an inefficiency of the seining methods at capturing gunnels, gunnels not occurring in the CDFW estuarine sampling areas, otters actively selecting gunnels over availability, or a combination of these factors.

Crustaceans formed a large part of otter diet around Humboldt Bay (range 16.5 – 54.8% frequency of occurrence per site, mean = 35.9%, SE = 0.66). Though I did not identify crustaceans to genus in this study, some crabs they ate could have come from a commercially important species such as Dungeness crab (*Metacarcinus magister*). Future research should focus on whether or not river otters impact this industry.

Birds formed a greater percentage (range 0.8 - 45.2% frequency of occurrence per site, mean = 21.3%, SE = 0.95) of yearly otter diet in Humboldt County than almost any other area where they have been studied in North America (Greer 1955, Toweill 1974,

Modaferri and Yocum 1980, Melquist and Hornocker 1983, Reid et al. 1994) with the exception of a marsh in central California (38%; Grenfell 1974) and near a storm-petrel colony in Alaska (86%; Quinlan 1983). There was a dramatic increase in bird consumption during the fall and winter seasons, which is the time of year many birds are stopping over in Humboldt Bay during migration (Colwell 1994). Otters consumed the most birds in the Cluster 1, reaching 61% of winter diet there. The marsh areas were also where bird index counts were highest. The ponds at the Arcata Marsh and Humboldt Bay NWR serve as stop-over havens for many migrating waterfowl and other bird species, and otters are taking advantage of the large numbers of birds (particularly *Fulica sp.*) during the fall and winter migration season. Many of the birds that appeared in otter scats during the summer (non-migration period) were *Anas sp.*, like mallards (*Anas platyrhynchos*), which are resident year-round (Barnhart et al. 1992). They may take more mallard in summer and fall when there are ducklings around and when they cannot fly.

Limitations of Study

With scat analysis, soft-bodied prey, large fish (where the otoliths were either not consumed or broken before analysis), and major prey items were probably underestimated, while minor items were probably overestimated (Carss 1995). Identification of prey items was likely biased towards easily recognizable bones and feathers; stickleback spines and coot feathers, in particular, became very obvious to identify. There were also many otoliths that were small, incomplete or difficult to identify, and some might have been mislabeled, unlabeled, or not found at all. It should also be noted that frequency of occurrence is an index; it does not reflect the number of

individual prey animals eaten. As for comparisons of otter diet and local fish counts, due to the way CDFW catches the fish with seine nets, many fish families may be over- or under-represented, and the abundance data I used here are conservative and may not be most appropriate for comparison to otter diet. The bird index count was also a rough, general index of how many birds were at each location. However, birds are very mobile, and the birds most vulnerable to predation may have been birds roosting at night when surveys did not occur.

Finally, there is a chance that prey found in scats deposited at a particular site could have been consumed closer to another site. River otters frequently move between sites, and can move up to 42 km over the course of a day (Melquist and Hornocker 1983; Brzeski 2010). However, White et al. (2007) found that captive river otters had a digestive passage rate of 167-188 minutes, a relatively short period of time to travel between the latrine sites, though wild otters may have longer passage rates than captive otters. Despite potential spatial diet discrepancies, I thought it reasonable to assume that the marking intensity at a site reflected the relative resource usage of the associated water body closest to it.

CONCLUSIONS

Coastal river otters in northern California eat a wide variety of prey, with an emphasis on fish (sticklebacks, sculpins, gunnels, gobies, surfperch, salmon), crustaceans (crab, crayfish), birds (ducks, coots), amphibians, and insects. They switch their eating patterns depending on location, season, and resource availability, taking advantage of natural processes like spawning and migration of a variety of prey.

Otters are aquatic keystone predators, thus managing for an adequate prey base is critical for maintaining a healthy ecosystem. Though not a major contributor to otter diet around the bay, salmon may form a more important part of otter diet further inland during spawning seasons. Birds form a large part of otter diet around Humboldt Bay, and good quality bird habitat should continue to be managed for, especially during migration periods at marsh sites like the Arcata Marsh and Wildlife Sanctuary and the Humboldt Bay National Wildlife Refuge.

Though time consuming, scat analysis using otoliths and other bones is a good and relatively inexpensive way of describing otter diet. Future diet studies should focus on diet across a larger area with a greater number of inland sites, and be compared to concurrent fish availability surveys conducted at all latrine sites. Stable isotope analysis may also be conducted for scat collected across latrine sites to demonstrate how otters are distributing nutrients from marine, brackish, and freshwater prey to their terrestrial latrines, connecting otherwise distinct ecosystems (Ben-David et al. 2005).

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Appendix A. Primary fish taxa present in Humboldt Bay (H; according to Barnhart et al. 1992) and/or eaten by river otters in other studies (O), and found in otter scats in this study (#). Parentheses indicate most likely taxa, but not definitive.

Family	Genus	Species	Common Name	Humboldt &/or Other Studies	# Found in my study
Agonidae			poachers	H, O	10
Ammodytidae	<i>Ammodytes</i>	<i>hexapterus</i>	sandlance	H	1
Atherinidae	(<i>Atherinops</i>)	(<i>affinis</i>)	silversides	H	6
Batrachoididae	<i>Porichthys</i>	<i>notatus</i>	Plainfin midshipman	O	27
Catostomidae	<i>Catostomus</i>	<i>occidentalis</i>	Sacramento sucker	H, O	6
	<i>Catostomus</i>	<i>rimiculus</i>	Klamath smallscale sucker	O	
Centrarchidae			sunfishes	O	0
Clupeidae			herrings	H, O	3
Cottidae	<i>Blepsias</i>	<i>cirrhosus</i>	silverspotted sculpin	H	5
	<i>Cottus</i>	<i>sp.</i>	coastrange/prickly sculpin	H, O	32
	<i>Enophrys</i>	<i>bison</i>	buffalo sculpin	H	4
	<i>Hemilepidotus</i>	<i>sp.</i>	Irish lords	H	3
	<i>Leptocottus</i>	<i>armatus</i>	Pacific staghorn sculpin	H, O	19
	<i>Scorpaenichthys</i>	<i>marmoratus</i>	cabezon	H	13
	Other/unknown sculpin				168
Cyprinidae			carps and minnows	O	0
Embiotocidae	(<i>Cymatogaster</i>)	(<i>aggregata</i>)	surfperches	H, O	46
Engraulidae			anchovies	H	0

Appendix A. Primary fish taxa present in Humboldt Bay (H; according to Barnhart et al. 1992) and/or eaten by river otters in other studies (O), and found in otter scats in this study (#). Parentheses indicate most likely taxa, but not definitive. (Continued)

Family	Genus	Species	Common Name	Other Studies &/or Humboldt	# Found in my study
Gasterosteidae	<i>Gasterosteus</i>	<i>aculeatus</i>	threespine stickleback	H, O	371
Gobiidae	<i>Lepidogobius</i>	<i>lepidus</i>	bay goby	H	22
	Unknown goby				38
Hexagrammidae			greenlings	H, O	5
Ictaluridae			catfish	O	0
Osmeridae	(<i>Hypomesus</i>)	(<i>pretiosus</i>)	smelts	H, O	24
Percidae			perch	O	0
Pholidae	(<i>Pholis</i>)	(<i>ornata</i>)	gunnels	H	78
Pleuronectiformes	<i>Parophrys</i>	<i>vetulus</i>	English sole	H, O	2
	<i>Platichthys</i>	<i>stellatus</i>	starry flounder	H, O	13
	Other/unknown flatfish				10
Salmonidae	<i>Oncorhynchus</i>	<i>tshawytscha</i>	chinook salmon	H	2
	<i>Oncorhynchus</i>	<i>clarki</i>	cutthroat trout	H, O	0
	<i>Oncorhynchus</i>	<i>mykiss</i>	steelhead	H	1
	<i>Oncorhynchus</i>	<i>kisutch</i>	coho	H, O	12
	Other/unknown salmonid				20
Scorpaenidae			rockfish	H, O	4
Syngnathidae	<i>Syngnathus</i>	<i>leptorhynchus</i>	pipefishes	H	1
Zoarcidae	<i>Bothrocara</i>	<i>sp.</i>	eelpouts		15

Appendix B. Bird taxa found in otter scats in Humboldt County, California, 2011-2012.

Family	Genus	Species	Common Name	# Found in my study
Anatidae	<i>Anas</i>	<i>acuta</i>	pintail	3
	<i>Anas</i>	<i>americana</i>	American wigeon	2
	<i>Anas</i>	<i>carolinensis</i>	green winged teal	5
	<i>Anas</i>	<i>clypeata</i>	shoveler	4
	<i>Anas</i>	<i>cyanoptera</i>	cinnamon teal	3
	<i>Anas</i>	<i>platyrhynchos</i>	mallard	11
	Other/unknown	<i>Anas sp.</i>		40
	<i>Aythya</i>	<i>sp.</i>	scaup	11
	<i>Bucephala</i>	<i>sp.</i>	bufflehead and goldeneye	5
	<i>Oxyura</i>	<i>jamaicensis</i>	ruddy duck	14
	<i>Melanitta</i>	<i>sp.</i>	scoters	5
	<i>Mergus</i>	<i>sp.</i>	mergansers	1
Gaviidae	<i>Gavia</i>	<i>sp.</i>	loons	2
Phalacrocoracidae	<i>Phalacrocorax</i>	<i>pelagicus</i>	cormorants	1
Podicipedidae	<i>Aechmophorus</i>	<i>sp.</i>	Western and Clark's grebes	3
	<i>Podilymbus</i>	<i>podiceps</i>	pied-billed grebe	1
	Other/unknown Podiciped			8
Rallidae	<i>Fulica</i>	<i>americana</i>	American coot	66

Appendix C. All diet items aside from fish and birds found in river otter scats in Humboldt County, California, 2011-2012.

Type	Description	# Found in my study
Amphibians	Frogs (<i>Rana</i> sp., etc.) and (possibly) salamanders	151
Bivalve shells ^{a, b}	Tiny shells	14
Crab	<i>Cancer</i> sp., etc.	468
Crayfish	<i>Pacifastacus</i> sp., etc.	39
Insects	Beetles, caddis flies, dragonfly larva, etc.	113
Mammals ^a	Mice (Muridae)	2
Shrimp/amphipods ^{a, b}		88
Snail shells ^{a, b}		26
Trash ^{a, b}	Small pieces of fishing line or blue plastic	2

^a Included in the “Other” category in my study

^b Most likely incidental; occurred in small amounts and never occurred alone.

Appendix D. Number of prey taxa occurrences and frequency of occurrence (%) of prey taxa in river otter scats by site in Humboldt County, California, 2011-2012. (Table continued on next page)

Prey Taxa	<u>Arcata</u>		<u>Bracut</u>		<u>Elk River</u>		<u>Freshwater</u>		<u>Gill's Dock</u>		<u>Humboldt Bay NWR</u>	
	<u>Marsh</u>											
	<u><i>n</i>^a = 188</u>		<u><i>n</i> = 73</u>		<u><i>n</i> = 225</u>		<u><i>n</i> = 82</u>		<u><i>n</i> = 174</u>		<u><i>n</i> = 202</u>	
	# ^b	%	#	%	#	%	#	%	#	%	#	%
Fish	100	53.2	41	56.2	182	80.9	69	84.1	141	81	142	70.3
Gasterosteidae	71	37.8	19	26	36	16	21	25.6	20	11.5	96	47.5
Cottidae	5	2.7	8	11	45	20	23	28	27	15.5	21	10.4
Pholidae	0	0	0	0	30	13.3	5	6.1	33	19	2	1
Gobiidae	4	2.1	2	2.7	6	2.7	4	4.9	9	5.2	15	7.4
Embiotocidae	1	0.5	2	2.7	26	11.6	4	4.9	5	2.9	1	0.5
Salmonidae	0	0	3	4.1	6	2.7	5	6.1	2	1.1	1	0.5
Pleuronectiformes	0	0	0	0	4	1.8	1	1.2	4	2.3	1	0.5
Osmeridae	0	0	17	23.3	5	2.2	1	1.2	0	0	1	0.5
Batrachoididae	0	0	0	0	2	0.9	0	0	1	0.6	2	1
Zoarcidae	5	2.7	3	4.1	0	0	3	3.7	0	0	1	0.5
Crustacean	31	16.5	15	20.5	99	44	28	34.1	61	35.1	80	39.6
Bird	85	45.2	24	32.9	22	9.8	6	7.3	31	17.8	64	31.7
<i>Anas sp.</i>	32	17	2	2.7	5	2.2	3	3.7	8	4.6	9	4.5
<i>Fulica sp.</i>	29	15.4	6	8.2	3	1.3	1	1.2	2	1.1	12	5.9
<i>Oxyura sp.</i>	3	1.6	1	1.4	0	0	0	0	2	1.1	3	1.5
Amphibian	56	29.8	25	34.2	5	2.2	8	9.8	5	2.9	15	7.4
Insects	37	19.7	7	9.6	9	4	2	2.4	9	5.2	16	7.9
Other	7	3.7	4	5.5	31	13.8	5	6.1	48	27.6	7	3.5

^a The # of scats analyzed per site

^b The # of scats containing a specified prey item

Appendix D. Number of prey taxa occurrences and frequency of occurrence (%) of prey taxa in river otter scats by site in Humboldt County, California, 2011-2012. (Continued)

Prey Taxa	<u>Hookton</u> <u>Slough</u> <u>n^a = 166</u>		<u>Mad River</u> <u>Coast</u> <u>n = 72</u>		<u>Mad River</u> <u>Inland</u> <u>n = 119</u>		<u>Mad River</u> <u>Slough</u> <u>n = 110</u>		<u>Total</u> <u>n = 1411</u>	
	# ^b	%	#	%	#	%	#	%	#	%
Fish	106	63.9	63	87.5	112	94.1	71	64.5	1027	72.8
Gasterosteidae	48	28.9	5	6.9	29	24.4	26	23.6	371	26.3
Cottidae	16	9.6	38	52.8	55	46.2	6	5.5	244	17.3
Pholidae	2	1.2	0	0	0	0	2	1.8	74	5.2
Gobiidae	7	4.2	2	2.8	0	0	10	9.1	59	4.2
Embiotocidae	0	0	1	1.4	0	0	5	4.5	45	3.2
Salmonidae	2	1.2	0	0	16	13.4	0	0	35	2.5
Pleuronectiformes	2	1.2	11	15.3	1	0.8	1	0.9	25	1.8
Osmeridae	0	0	0	0	0	0	0	0	24	1.7
Batrachoididae	8	4.8	0	0	0	0	10	9.1	23	1.6
Zoarcidae	0	0	0	0	0	0	2	1.8	15	1.1
Crustacean	91	54.8	14	19.4	42	35.3	46	41.8	507	35.9
Bird	38	22.9	9	12.5	1	0.8	21	19.1	301	21.3
<i>Anas sp.</i>	5	3	0	0	0	0	4	3.6	68	4.8
<i>Fulica sp.</i>	9	5.4	3	4.2	0	0	1	0.9	66	4.7
<i>Oxyura sp.</i>	4	2.4	0	0	0	0	1	0.9	14	1
Amphibian	15	9	2	2.8	3	2.5	16	14.5	150	10.6
Insects	9	5.4	3	4.2	8	6.7	13	11.8	113	8
Other	8	4.8	12	16.7	5	4.2	11	10	138	9.8

^a The # of scats analyzed per site

^b The # of scats containing a specified prey item

Appendix E. Number of prey item occurrences and relative frequency of occurrence of prey items in river otter scats for each cluster in Humboldt County, California, during each season in 2011-2012. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 – December 20), and winter/spring had high rainfall (December 21 - April 30). (Table continued on next page)

Prey	Summer (<i>n</i> = 520)								Fall (<i>n</i> = 492)							
	Cluster 1		Cluster 2		Cluster 3		Cluster 4		Cluster 1		Cluster 2		Cluster 3		Cluster 4	
	<i>n</i> ^a = 223		<i>n</i> = 121		<i>n</i> = 137		<i>n</i> = 39		<i>n</i> = 196		<i>n</i> = 125		<i>n</i> = 155		<i>n</i> = 16	
	# ^b	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
Fish	165	74.0	86	71.1	119	86.9	36	92.3	125	63.8	104	83.2	133	85.8	13	81.3
Gasterosteidae	110	49.3	21	17.4	18	13.1	18	46.2	72	36.7	24	19.2	14	9.0	4	25.0
Cottidae	16	7.2	27	22.3	26	19.0	23	59.0	15	7.7	31	24.8	26	16.8	6	37.5
Pholidae	1	0.4	1	0.8	28	20.4	0	0	3	1.5	4	3.2	35	22.6	0	0
Gobiidae	13	5.8	8	6.6	6	4.4	0	0	10	5.1	7	5.6	8	5.2	0	0
Embiotocidae	0	0.0	6	5.0	19	13.9	0	0	1	0.5	6	4.8	11	7.1	0	0
Salmonidae	1	0.4	3	2.5	1	0.7	2	5.1	0	0.0	4	3.2	2	1.3	3	18.8
Osmeridae	0	0.0	0	0.0	3	2.2	0	0	0	0.0	8	6.4	0	0.0	0	0
Bird	41	18.4	9	7.4	6	4.4	0	0	61	31.1	23	18.4	23	14.8	0	0
<i>Anas sp.</i>	12	5.4	3	2.5	1	0.7	0	0	21	10.7	5	4.0	8	5.2	0	0
<i>Fulica sp.</i>	0	0.0	0	0.0	0	0.0	0	0	21	10.7	4	3.2	3	1.9	0	0
Crustacean	84	37.7	46	38.0	62	45.3	21	53.8	77	39.3	32	25.6	49	31.6	9	56.3
Amphibian	50	22.4	23	19.0	6	4.4	2	5.1	17	8.7	6	4.8	2	1.3	0	0
Other	11	4.9	14	11.6	31	22.6	4	10.3	8	4.1	15	12.0	39	25.2	1	6.3
Insects	30	13.5	17	14.0	9	6.6	3	7.7	15	7.7	3	2.4	8	5.2	3	18.8

^a The # of scats analyzed per cluster within each season

^b The # of scats containing a specified prey item

Appendix E. Number of prey item occurrences and relative frequency of occurrence of prey items in river otter scats for each cluster in Humboldt County, California, during each season in 2011-2012. Seasons were established by rainfall amounts: summer had low rainfall (May 1 - August 31), fall had medium rainfall (September 1 - December 20), and winter/spring had high rainfall (December 21 – April 30). (Continued)

Prey	Winter/Spring (<i>n</i> = 492)							
	Cluster 1		Cluster 2		Cluster 3		Cluster 4	
	<i>n</i> ^a = 137		<i>n</i> = 91		<i>n</i> = 107		<i>n</i> = 64	
	# ^b	%	#	%	#	%	#	%
Fish	58	42.3	54	59.3	71	66.4	63	98.4
Gasterosteidae	33	24.1	26	28.6	24	22.4	7	10.9
Cottidae	11	8.0	17	18.7	20	18.7	26	40.6
Pholidae	0	0.0	2	2.2	0	0.0	0	0
Gobiidae	4	2.9	3	3.3	1	0.9	0	0
Embiotocidae	1	0.7	0	0.0	1	0.9	0	0
Salmonidae	2	1.5	2	2.2	5	4.7	11	17.2
Osmeridae	1	0.7	11	12.1	2	1.9	0	0
Bird	84	61.3	28	30.8	24	22.4	1	1.6
<i>Anas sp.</i>	13	9.5	1	1.1	4	3.7	0	0
<i>Fulica sp.</i>	29	21.2	7	7.7	2	1.9	0	0
Crustacean	41	29.9	25	27.5	49	45.8	12	18.8
Amphibian	19	13.9	23	25.3	2	1.9	1	1.6
Other	3	2.2	3	3.3	9	8.4	2	3.1
Insects	17	12.4	5	5.5	1	0.9	0	0

^a The # of scats analyzed per cluster within each season

^b The # of scats containing a specified prey item

Appendix F. Scat marking intensity observed values (Obs. *n*) and expected values (Exp. *n*) by latrine site and cluster, in Humboldt County, California, 2011-2012.

Sites		Summer	Fall	Winter/Spring	Totals
Cluster 1	Obs. <i>n</i>	352	271	162	785
	Exp. <i>n</i>	274.9	316.3	193.8	
Arcata Marsh	Obs. <i>n</i>	116	85	74	275
	Exp. <i>n</i>	96.30	110.80	67.90	
HBNWR	Obs. <i>n</i>	135	98	58	291
	Exp. <i>n</i>	101.90	117.24	71.86	
Hookton Slough	Obs. <i>n</i>	101	88	30	219
	Exp. <i>n</i>	76.69	88.24	54.08	
Cluster 2	Obs. <i>n</i>	162	133	111	406
	Exp. <i>n</i>	142.2	163.6	100.3	
Bracut	Obs. <i>n</i>	10	13	70	93
	Exp. <i>n</i>	32.57	37.47	22.96	
Freshwater Creek	Obs. <i>n</i>	22	43	20	85
	Exp. <i>n</i>	29.76	34.25	20.99	
Mad River Coast	Obs. <i>n</i>	42	37	4	83
	Exp. <i>n</i>	29.06	33.44	20.49	
Mad River Slough	Obs. <i>n</i>	88	40	17	145
	Exp. <i>n</i>	50.78	58.42	35.80	
Cluster 3	Obs. <i>n</i>	239	497	219	955
	Exp. <i>n</i>	334.4	384.8	235.8	
Elk River	Obs. <i>n</i>	146	346	181	673
	Exp. <i>n</i>	235.67	271.15	166.18	
Gill's Dock	Obs. <i>n</i>	93	151	38	282
	Exp. <i>n</i>	98.75	113.62	69.63	
Cluster 4	Obs. <i>n</i>	44	16	70	130
	Exp. <i>n</i>	45.52	52.38	32.10	
Season totals		797	917	562	2276

Appendix G. Averages of fish length based on otolith measurements from river otter scats in Humboldt County, California, 2011-2012. Regression equations for estimating fish standard lengths from Harvey et al. (2000) and Browne et al. (2002).

Family	Species	n (=117)	Seasons found	Cluster(s) found in	Average Length (cm)	Standard Error	Regression Equation using Otolith Lengths (OL)
Atherinidae	<i>Atherinops affinis</i>	9	Fall	1	7.49	0.46	=3.72(OL) + 0.55
Batrachoididae	<i>Porichthys notatus</i>	1	Fall	2	17.01	-	=2.80(OL) – 2.59
Clupeidae	<i>Clupea pallasii</i>	2	Fall	3	9.15	2.62	=5.24(OL) – 1.85
Cottidae	<i>Leptocottus armatus</i>	11	Fall, Summer	1, 2, 3	8.67	0.72	=2.58(OL) – 2.26
Embiotocidae	<i>Cymatogaster aggregata</i>	43	Fall, Summer	1, 2, 3	5.09	0.29	=1.74(OL) – 0.52
Osmeridae	<i>Hypomesus pretiosus</i>	22	All	2, 3	8.99	0.54	=3.61(OL) – 0.63
	<i>Spirinchus thaleichthys</i>	1	Fall	2	6.66	-	=2.64(OL) – 0.20
Pleuronectidae	<i>Platichthys stellatus</i>	13	All	1, 2, 3	8.04	0.60	=3.35(OL) + 0.23
	<i>Parophrys vetulus</i>	2	Fall	2	6.98	2.10	=3.82(OL) – 2.76
Salmonidae	<i>Oncorhynchus kisutch</i>	13	All	1, 2, 3	4.82	0.92	=6.73(OL) – 10.4

Appendix H. Details on the ecology of other fish species that river otters prey upon in Humboldt County, California, 2011-2012.

As reflected in the otters' diet, gunnells (Pholidae) are marine fish that tend to live in shallow intertidal areas (Eschmeyer and Herald 1983). They are long (up to 46 cm), eel-like, and hide under rocks or among eelgrass and seaweed where they feed on small mollusks and crustaceans (Eschmeyer and Herald 1983). The large incidence of small copepod crustaceans in the Other category (which was highest in Cluster 3) could have been ingested incidentally via the stomachs of gunnells.

Gobies (Gobiidae) are small demersal fish (most under 10 cm) that live at shallow depths in salt water, brackish water, or sometimes freshwater (Eschmeyer and Herald 1983, Nelson 1994). Bay gobies (*Lepidogobius lepidus*) are strongly euryhaline and one of the most abundant fish in Humboldt Bay (Barnhart et al. 1992). There are three other species of gobies in Humboldt Bay, including the endangered tidewater goby (*Eucyclogobius newberryi*) which is found in coastal lagoons and brackish areas near stream mouths (Eschmeyer and Herald 1983). Though I could identify bay gobies in otter scats, I could not distinguish between the other goby species, so it is possible that otters are consuming tidewater gobies, but in very small amounts (maximum of unknown gobies frequency of occurrence = 2.7%).

Surf smelt were most abundant in otter diet in Cluster 2, particularly Bracut, which is directly on the bay. Smelt (Osmeridae), such as surf smelt (*Hypomesus pretiosus*), are marine/brackish species and sometimes anadromous (Eschmeyer and Herald 1983). They bury their eggs on beaches in the surf zone (Eschmeyer and Herald 1983). Otters took more Osmerids (though not significant) during the winter season.

Perhaps otters were taking advantage of spawning Osmerids in the surf zone near the estuaries.

Though not comprising a large percentage of otter diet, toadfish (Batrachoididae) were seasonal in otter diet, with most occurrences in summer. These fish are sluggish bottom-dwellers, and common in bays especially during spawning season (Eschmeyer and Herald 1983). Otters may take advantage of the seasonal spawning behavior of these fish as well.