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Seasonal Food Habits of the North American River Otter (*Lontra canadensis*) in Point Reyes National Seashore and Peyton Slough Wetlands Complex, California

Stori Oates, Terence Carroll, and Megan Isadore

THE RIVER OTTER ECOLOGY PROJECT

PO Box 103
Forest Knolls, CA 94933
megan@riverotterecology.org

Background

The North American river otter (*Lontra canadensis*) is a semi-aquatic mustelid endemic to North America, an apex predator, and a sentinel for environmental contamination (Kruuk, 2006; Larivière and Walton, 1998). However, very little is known about the current status, distribution, and ecology of river otters in the San Francisco Bay Area (SFBA). Historically documented, but shortly thereafter extirpated from much of their range in the early twentieth century (Grinnell et al, 1937), the recovery and range expansion of the species in the SFBA only recently has been documented (Bouley et al., 2015).

Although the species is highly dependent on freshwater, river otters utilize a variety of habitats, including terrestrial, marine, estuarine, and freshwater ecosystems (Toweill and Tabor 1982). River otters are known to prey on an array of species such as insects, crustaceans, freshwater, anadromous, and marine fishes, amphibians, reptiles, waterbirds, and small mammals (Melquist et al., 2003). The diet of river otters also can vary seasonally and is assumed to reflect seasonal changes in availability of prey communities, particularly slow-moving, midsize prey (Greer 1955; Larsen 1984; Melquist and Hornocker 1983; Reid et al. 1994; Stenson et al. 1984; Toweill and Tabor 1982). Previous studies also have shown that river otters can have a significant influence on the structure of local ecosystems through trophic effects (Garwood et al., 2013) and by transferring aquatic nutrients to terrestrial environments (Ben-David et al., 2005).

Understanding spatial and temporal relationships between these predators and their prey is critical for recognizing factors that might limit the recovery and success of this top carnivore and impact local ecosystems (Kruuk and Conroy, 1987). Additionally, diet has direct implications for protecting other aquatic resources (e.g., threatened and endangered salmonids, migrating waterbirds). Recent publications on river otter diet in California, however, are limited (Cosby, 2013; Grenfell, 1974; Manning, 1990; Modafferi and Yocom, 1980; Morejohn, 1969; Penland and Black, 2009; Reeves, 1988; Salman, 2007); and until now, there have been no baseline prey species studies for river otters in the greater SFBA with the exception of Suisun Marsh (Grenfell, 1974).

River otters are a potential keystone species in SFBA aquatic habitats (Bouley et al., 2015); and this study has allowed us to gain a better understanding of the ecological role river otters play in coastal (Point Reyes National Seashore) and inland areas (Peyton Slough Wetlands Complex) of central California. We hypothesized that relative importance of prey types consumed by river otters would vary considerably among our focal study sites. We also predicted that river otters would feed opportunistically on seasonally available prey, with fish and crustaceans being consumed year round (Penland and Black, 2009) and aquatic birds more often during winter and early spring (Accurso, 1992).

Study Sites

Point Reyes National Seashore, Marin County, CA

The four focal study sites within Point Reyes National Seashore included, from north to south, Northern Tomales Bay/Walker Creek, Abbotts Lagoon, Southern Tomales Bay/Giacomini Wetlands, and Drakes Bay (Fig. 1). These focal study sites reflect a diversity of habitat types (e.g., coastal lagoons, streams, intertidal marshes, wetlands) and are host to numerous groups of

river otters (Table 1).

Peyton Slough Wetlands Complex, Contra Costa County, CA
Moorhen and McNabney Marshes comprise River Otter Ecology Project's only focal study site outside Marin County (Fig. 2). This site is an interesting contrast to the Point Reyes National Seashore sites because river otters were never extirpated from the Martinez area and both marshes are heavily managed (Table 1). Moorhen Marsh is a 0.8 km^2, constructed wetland dependent solely on treated effluent as its primary water source. The Shell Martinez Refinery surrounds it on two sides, and Interstate 680 borders the north side. McNabney Marsh is a restored, muted tidal wetland located northeast of I-680 in Martinez, California. Mt. View Sanitary District (MVSD) and the East Bay Regional Park District jointly own the 0.56 km^2 wetland, with an agreement that gives MVSD responsibility for its management. In 2009, as part of remediation for an oil spill, tidal flows were re-introduced to McNabney Marsh through a tide gate structure, resulting in shifts in plant and wildlife species, abundance and distribution.

Methods
Studies of river otter diet have utilized fecal (scat) analysis as a non-invasive means of determining prey consumption (Larsen, 1984; Kruuk and Conroy, 1987). Most prey species are comprised of hard parts such as bones, scales, feathers, hair, or exoskeletons that are indigestible and pass out of the digestive system. During 2014 to 2016, we collected 84 river otter scats from Abbotts Lagoon, 37 scats from Drakes Bay, 84 scats from Northern Tomales Bay, and 81 scats from Southern Tomales Bay (Table 2). During 2017 to 2018, we collected 75 river otter scats from Abbotts Lagoon, 53 scats from Drakes Bay, 53 scats from North Tomales Bay, and 77 river otter scats from South Tomales Bay (Table 3). A total of 49 scat samples also were collected from the Peyton Slough Wetlands Complex to compare diet of coastal and inland river otter populations in the San Francisco Bay Area (Table 3).

Diet analysis was performed by trained River Otter Ecology Project volunteers, interns, and students from Marin Academy and Tomales High School (Fig. 3-4), and was based on methods described by Crait and Ben-David (2006). Briefly, individual otter scats were soaked for >30 minutes in a mixture of denture cleaner (Efferdent, Pfizer Consumer Healthcare, Morris Plains, New Jersey) and water and then agitated to separate mucilaginous material from undigested prey remains (Berg, 1999; Conroy et al., 1993; Jenkins et al., 1979). Samples were then washed through a series of fine-meshed sieves (2.0mm, 0.5mm, 0.25mm openings). Recovered fish otoliths, scales, and skeletal material were sorted and stored dry, and invertebrates (e.g., crustaceans, insects) were preserved in 70% isopropyl alcohol (Lance et al., 2001). Samples were identified to lowest possible taxon by comparing remains with keys of freshwater invertebrates (Hobbs, 1972; Hobbs, 1989; Hobbs, 1991; Usinger, 1968), fish scales, bones, and otoliths (Cannon, 1987; Casteel, 1972, 1973, 1976; Conroy et al., 1993; Daniels 1996; Harvey et al., 2000; Lagler 1947; Morrow, 1979; Oates et al., 1993; Wheeler and Jones, 1989), amphibians (Duellman, 1994), reptiles (Romer, 1997), bird feathers (Day, 1966), and mammal hair (Day, 1966; Moore et al., 1974).

Students recorded the frequency of occurrence of prey types for each focal study site (calculated as number of occurrences of a prey item divided by total number of fecal

samples; Erlinge, 1968). Frequency of occurrence was then expressed as a percentage by multiplying that number by 100 (Fedriani et al., 1998; Melquist and Hornocker, 1983). This method provided an index of the presence-absence of prey in the diet. Contingency tables (X^2) were used to compare frequency of prey types among sites and seasons for each time period (Penland and Black, 2009). Seasons in coastal northern California are not clearly defined by severe climate variables; therefore data were organized into periods of low and high rainfall, and were based on water flow levels in local streams (Josselyn, 1983). Periods of low rainfall occurred during May through October and periods of high rainfall occurred during November through April.

Results

River otters foraging in Point Reyes National Seashore appeared to be opportunistic carnivores that fed on a wide variety of prey species. Of the 548 fecal samples collected, 543 (99%) contained at least one prey item. Of these 732 individual prey occurrences, 439 (60%) were fishes, 131 (18%) were crustaceans, 85 (12%) were waterbirds, 56 (8%) were insects, 10 (1%) were mammals, and 11 (2%) were unknown vertebrates (Table 4-5). Additionally, one plastic fragment (approximately 9x4x1mm) was recovered from a single scat sample collected from the Drakes Bay focal study site.

During the 2014-16 sampling period, frequency of prey type differed significantly among sites ($X^2 = 66.603$, $df = 6$, $p < 0.0001$; Table 6). Fishes occurred most frequently in the diet of river otters foraging in Point Reyes National Seashore across all sites; however, waterbirds varied in frequency among sites with most occurring at Abbotts Lagoon, followed by Drakes Bay, Southern Tomales Bay, and Northern Tomales Bay. Invertebrates (e.g., crayfish, insects) also varied in occurrence among sites with most occurring at Southern Tomales Bay, followed by Northern Tomales Bay, Drakes Bay, and Abbotts Lagoon (Fig. 5). Frequency of prey type also differed significantly between seasons ($X^2 = 10.581$, $df = 2$, $p = 0.005$; Table 7) with waterbirds occurring most frequently during the wet season. There were no significant differences between seasons for fish or invertebrates (Fig. 6).

Similarly, during the 2017-18 sampling period, frequency of prey type differed significantly among sites ($X^2 = 60.972$, $df = 8$, $p < 0.0001$; Table 8). Fishes occurred most frequently in the diet of river otters foraging at Abbott's Lagoon followed by Southern Tomales, Drakes Bay, Northern Tomales, and Peyton Slough Wetlands Complex. Waterbirds varied in frequency among sites with most occurring at Drakes Bay, followed by Abbotts Lagoon, Southern Tomales Bay, and Northern Tomales Bay. Invertebrates also varied in occurrence among sites with most occurring at Peyton Slough Wetlands complex followed by Southern Tomales Bay, Northern Tomales Bay, Drakes Bay, and Abbotts Lagoon (Fig. 7). Frequency of prey type also differed significantly between seasons ($X^2 = 7.672$, $df = 2$, $p = 0.0216$; Table 9) with waterbirds occurring most frequently during the wet season. There were no significant differences between seasons for fish or invertebrates (Fig. 8).

Fish species identified thus far include sand sole (*Psettichthys melanostictus*), carps and minnows (Cyprinidae), staghorn sculpin (*Leptocottus armatus*), plainfin midshipman (*Porichthys notatus*) and surfperches (Embiotocidae). Crustaceans include signal crayfish (*Pacifastacus leniusculus*), red swamp crayfish (*Procambarus clarkia*), and European green crab (*Carcinus*

maenas). Insects include weevil (Curculionidae), grasshopper (Acrididae), ladybug (Coccinellidae), caddisfly larva (Trichoptera), and Darner dragonfly nymph (Aeshnidae), waterbirds include Pied-billed grebe (*Podilymbus podiceps*).

River otters foraging in or near Moorhen and McNabney Marshes also appeared to be opportunistic carnivores that consumed fishes, crustaceans, and aquatic insects. Of the 49 fecal samples collected from river otters in Moorhen and McNabney Marshes, California during 2017-18, all contained at least one prey item. Of these 193 individual prey occurrences, 165 (85.5%) were crayfish, 23 (11.9%) were fishes, and 5 (2.6%) were insects. Red swamp crayfish (*Procambarus clarkia*) was the predominant crayfish prey species, sand sole (*Psettichthys melanostictus*), carps and minnows (Cyprinidae), sculpins (Cottidae), and toothcarps (Cyprinodontiformes) were the predominant prey fish species that could be identified below class, and darner dragonfly nymph (Aeshnidae) was the predominant insect species consumed by river otters. No birds, mammals, amphibians, or reptiles were recovered from fecal samples. The most important prey species consumed by river otters during the 2017-18 sampling period was the red swamp crayfish, an invasive species that is abundant in the San Francisco Bay Area (USFW, 2015). Fishes were the second most important prey species and included sculpins, flatfishes, carp/goldfish, toothcarps, perch-like fishes, and a juvenile sturgeon (*Acipenser* spp.). The juvenile sturgeon was identified tentatively from two dorsal scutes, but needs further validation to confirm species.

Summary

Our study is the first to describe the feeding ecology of river otters in coastal and inland areas of the SFBA since Grenfell (1974). The general patterns documented during this study support our hypotheses and as with previous studies of river otters in California (Cosby, 2013; Penland and Black, 2009), indicate river otters are opportunistic predators that most likely take prey in relation to their availability. For example, fish were available in all focal study sites year-round; however, the greater frequency of bird remains in coastal river otter scat during the wet season corresponds to the peak influx of migratory birds in winter and early spring (Accurso, 1992). Diet data from inland otters also supports idea that otters take abundant, slow-moving prey as their diet was dominated by the slow-moving and easily captured red swamp crayfish.

Further identification and validation of otoliths, scales, bones, and feathers are needed to determine if otters truly switch their eating patterns based on resource availability and are able to take advantage of natural processes such as spawning and migration of a variety of prey. 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.

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Table 1. North American river otter (*Lontra canadensis*) latrine site characteristics in Point Reyes National Seashore and Peyton Slough Wetland Complex, California.

Site	Habitat Type	Social Group Size	Latrines	Months in Use
Abbotts Lagoon				
Abbotts Lagoon	Coastal Lagoon	4-6	1-5: Sandy shore/rocky shore/vegetated	12
Drakes Bay				
Drakes Beach	Ocean Intertidal Wetland	4-7	1: Vegetated	12
Drakes Pond	Coastal Wetland/Man-made pond	4-7	1: Vegetated	12
Elephant Seal Overlook Rocks	Ocean/Coastal Stream	4-7	1: Rocky shore	12
Northern Tomales Bay				
Walker Creek	Intertidal Stream		1-3: Sandy shore	12
Cave Beach	Intertidal Bay	5-9	1: Sandy shore	12
White Gulch	Intertidal Bay	5-9	2: Rocky shore	12
Southern Tomales Bay				
Giacomini Wetland	Intertidal marsh and stream	7-9	1-4: Vegetated	12
Tomales Bay Trail	Intertidal marsh and stream	7-9	1: Vegetated	12
Peyton Slough				
Moorhen Marsh	Man-made wetland	1-8	1-6: Vegetated	12
McNabney Marsh	Man-made wetland	1-8	1-2: Vegetated	12

Table 2. Number of North American river otter (*Lontra canadensis*) fecal samples collected from locations in Abbotts Lagoon, Drakes Bay, Northern Tomales Bay, and Southern Tomales Bay, California during 2014 to 2016.

	Location				
Season[a]	Abbotts Lagoon	Drakes Bay	Northern Tomales Bay	Southern Tomales Bay	Season Totals
Wet	11	2	10	32	55
Dry	74	35	75	49	233
Location Totals	85	37	85	81	288

[a]Seasons in coastal northern California are not clearly defined by severe climate variables; therefore data were organized into periods of low and high rainfall, and were based on water flow levels in local streams (Josselyn, 1983). Periods of low rainfall occurred during May through October and periods of high rainfall occurred during November through April.

Table 3. Number of North American river otter (*Lontra canadensis*) fecal samples collected from locations in Abbotts Lagoon, Drakes Bay, Northern Tomales Bay, Southern Tomales Bay, and Peyton Slough Wetlands Complex, California during 2017 to 2018.

	Location					
Season[a]	Abbotts Lagoon	Drakes Bay	Northern Tomales Bay	Southern Tomales Bay	Peyton Slough	Season Totals
Wet	24	10	11	35	14	94
Dry	53	43	42	42	35	215
Location Totals	77	53	53	77	49	309

[a]Seasons in coastal northern California are not clearly defined by severe climate variables; therefore data were organized into periods of low and high rainfall, and were based on water flow levels in local streams (Josselyn, 1983). Periods of low rainfall occurred during May through October and periods of high rainfall occurred during November through April.

Table 4. Frequency of occurrence of prey remains recovered from river otter fecal samples at focal study sites in Point Reyes National Seashore, California collected during 2014 to 2016. The total for each category was divided by the total sample size at each focal study site to determine frequency of occurence.

	Abbotts Lagoon				Drakes Bay				Northern Tomales Bay				Southern Tomales Bay			
	Wet n=11		Dry n=73		Wet n=2		Dry n=34		Wet n=10		Dry n=74		Wet n=32		Dry n=49	
Taxa	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Fish	5	45.5	54	74.0	1	50.0	28	82.4	9	90.0	69	93.2	18	56.3	34	69.4
Bird	6	54.5	24	32.9	2	100.0	5	14.7	2	20.0	0	0.0	7	21.9	2	4.1
Crustacean	0	0.0	0	0.0	0	0.0	5	14.7	0	0.0	16	21.6	14	43.8	30	61.2
Insect	1	9.1	8	11.0	0	0.0	2	5.9	0	0.0	1	1.4	0	0.0	2	4.1
Mammal	0	0.0	1	1.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Unknown Vertebrate	0	0.0	2	2.7	0	0.0	3	8.8	0	0.0	3	4.1	0	0.0	2	4.1

Table 5. Frequency of occurrence of prey remains recovered from river otter fecal samples at focal study sites in Point Reyes National Seashore and Peyton Slough Wetlands Complex, California collected during 2017 to 2018. The total for each category was divided by the total sample size at each focal study site to determine frequency of occurence.

	Abbotts Lagoon				Drakes Bay				Northern Tomales Bay				Southern Tomales Bay				Peyton Slough			
	Wet n=23		Dry n=52		Wet n=10		Dry n=43		Wet n=11		Dry n=42		Wet n=35		Dry n=42		Wet n=14		Dry n=35	
Taxa	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Fish	16	69.6	48	92.3	10	100.0	41	95.3	7	63.6	38	90.5	29	82.9	32	76.2	11	78.6	14	40.0
Bird	8	34.8	1	1.9	1	10.0	16	37.2	1	9.1	1	2.4	7	20.0	2	4.8	0	0.0	0	0.0
Crustacean	1	4.3	1	1.9	3	30.0	8	18.6	4	36.4	21	50.0	7	20.0	21	50.0	14	100.0	35	100.0
Insect	0	0.0	13	25.0	3	30.0	16	37.2	2	18.2	3	7.1	4	11.4	1	2.4	1	7.1	3	8.6
Mammal	1	4.3	2	3.8	0	0.0	1	2.3	0	0.0	1	2.4	2	5.7	2	4.8	0	0.0	0	0.0
Unknown Vertebrate	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.4	0	0.0	0	0.0	0	0.0	0	0.0

Table 6. Chi-square contingency table values comparing river otter prey remains recovered from fecal samples at focal study sites in Point Reyes National Seashore, California collected during 2014 to 2016 when seasons were pooled (*df*=6).

	Fish				Bird				Invertebrate			
	Observed		Expected		Observed		Expected		Observed		Expected	
Sites	With	Without	With	Without	With	Without	With	Without	With	Without	With	Without
Abbotts Lagoon	59	25	62.29	20.33	30	54	13.71	71.17	9	75	22.00	62.50
Drakes Bay	29	8	27.33	8.98	7	30	6.02	31.43	7	30	9.65	27.60
Northern Tomales Bay	78	6	61.65	20.47	2	82	13.57	71.63	17	67	21.78	62.90
Southern Tomales Bay	52	29	66.73	18.22	9	72	14.46	63.77	44	37	23.57	56.00
X^2	7.9				31.4				27.2			
P	0.049				<0.0001				<0.0001			

Table 7. Chi-square contingency table values comparing river otter prey remains recovered from fecal samples during the wet and dry seasons in Point Reyes National Seashore, California collected during 2014 to 2016 when sites were pooled (*df*=2).

	Wet				Dry					
	Observed		Expected		Observed		Expected			
Prey Taxa	With	Without	With	Without	With	Without	With	Without	X^2	*P*
Fish	33	22	41.07	13.14	185	45	176.9	53.86	1.72	0.1897
Bird	17	38	9.04	46.47	31	199	38.96	190.53	7.59	0.0059
Invertebrate	15	40	14.88	40.39	64	166	64.12	165.61	1.00	1.00

Table 8. Chi-square contingency table values comparing river otter prey remains recovered from fecal samples at focal study sites in Point Reyes National Seashore and Peyton Slough Wetlands Complex, California collected during 2017 to 2018 when seasons were pooled (*df*=8).

	Fish				Bird				Invertebrate			
	Observed		Expected		Observed		Expected		Observed		Expected	
Sites	With	Without	With	Without	With	Without	With	Without	With	Without	With	Without
Abbotts Lagoon	64	11	49.77	17.20	9	66	7.49	76.11	15	60	30.75	43.69
Drakes Bay	51	2	54.86	7.78	17	36	8.25	34.44	29	24	33.89	19.77
Northern Tomales Bay	45	8	42.98	10.42	2	51	6.46	46.11	29	24	26.56	26.47
Southern Tomales Bay	61	16	56.55	16.44	9	68	8.51	72.78	30	47	34.94	41.78
Peyton Slough	25	24	41.85	9.16	0	49	6.29	40.56	49	0	25.86	23.28
X^2	11.563				18.982				30.401			
P	0.0209				0.0008				0.0001			

Table 9. Chi-square contingency table values comparing river otter prey remains recovered from fecal samples during the wet and dry seasons in Point Reyes National Seashore, California collected during 2017 to 2018 when sites were pooled (*df*=2).

	Wet				Dry					
	Observed		Expected		Observed		Expected			
Prey Taxa	With	Without	With	Without	With	Without	With	Without	X^2	*P*
Fish	62	17	62.19	12.15	159	20	158.8	24.85	1.00	1.00
Bird	17	62	10.41	72.58	20	159	26.59	148.42	4.95	0.0261
Invertebrate	24	55	30.39	49.26	84	95	77.61	100.74	1.59	0.2073

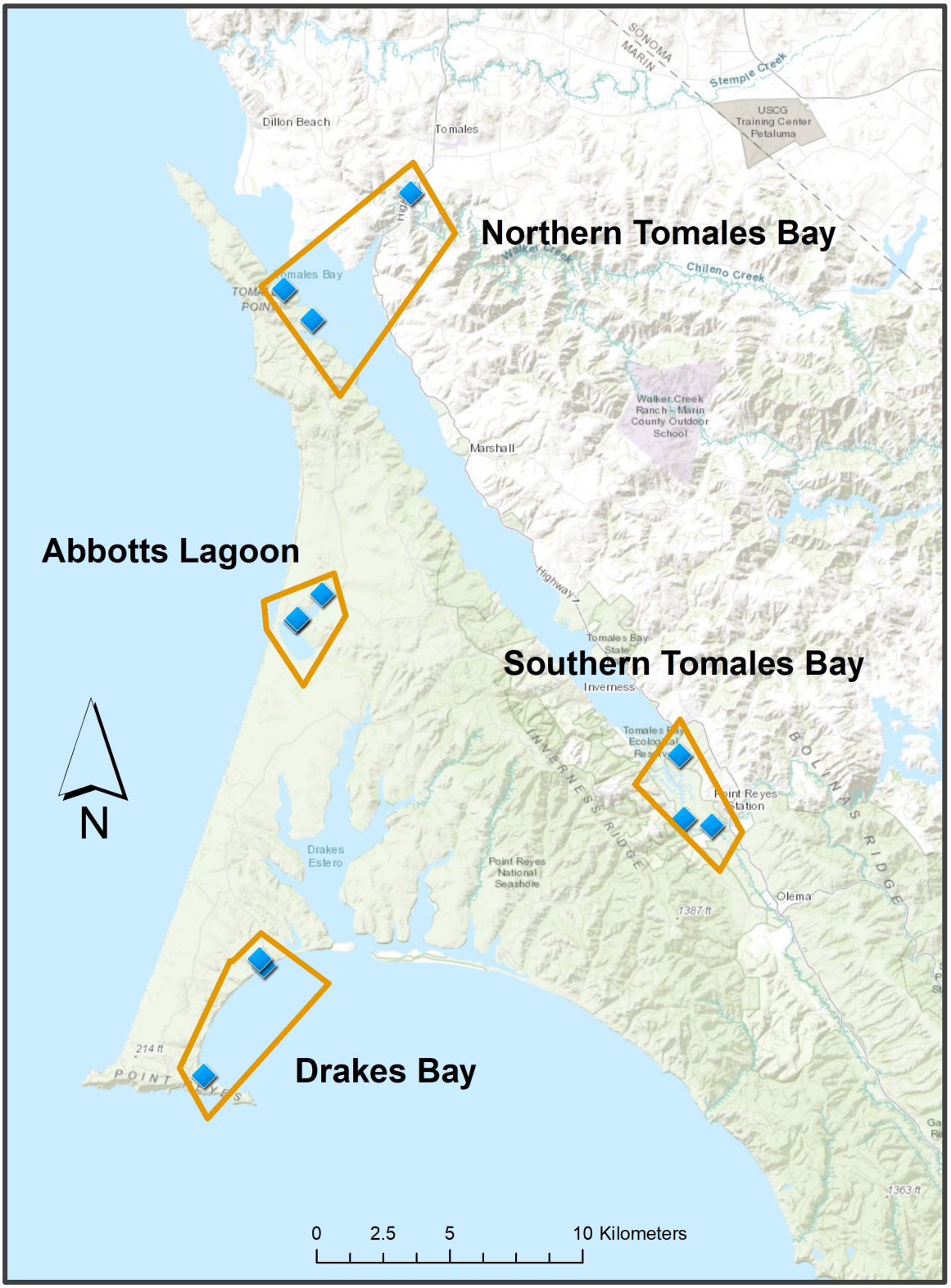

Figure 1. Map of focal study sites (orange boxes) and river otter latrine (blue squares) in Point Reyes National Seashore, California.

Figure 2. Map of Mt. View Sanitary District study area with camera and latrine sites represented by multi-colored symbols.

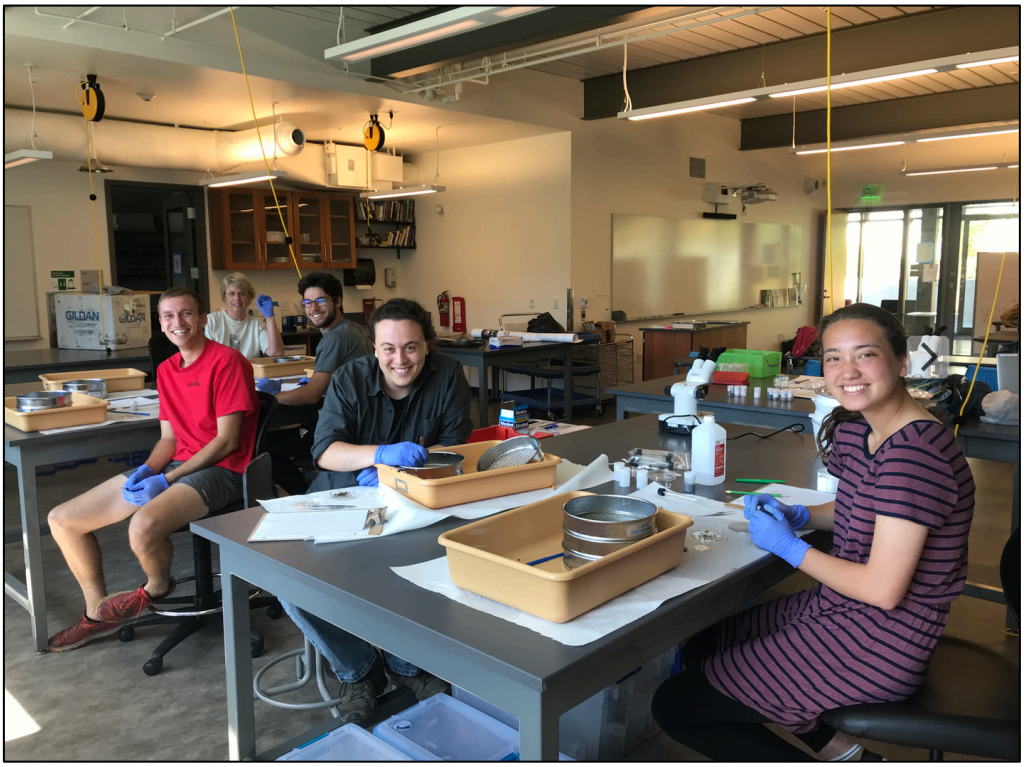

Figure 3. River Otter Ecology Project volunteers and interns sorting river otter scat samples at the Marin Academy lab facility.

Figure 4. Tomales High School students participating in Hands on Science program sort and identify prey remains recovered from river otter scat samples.

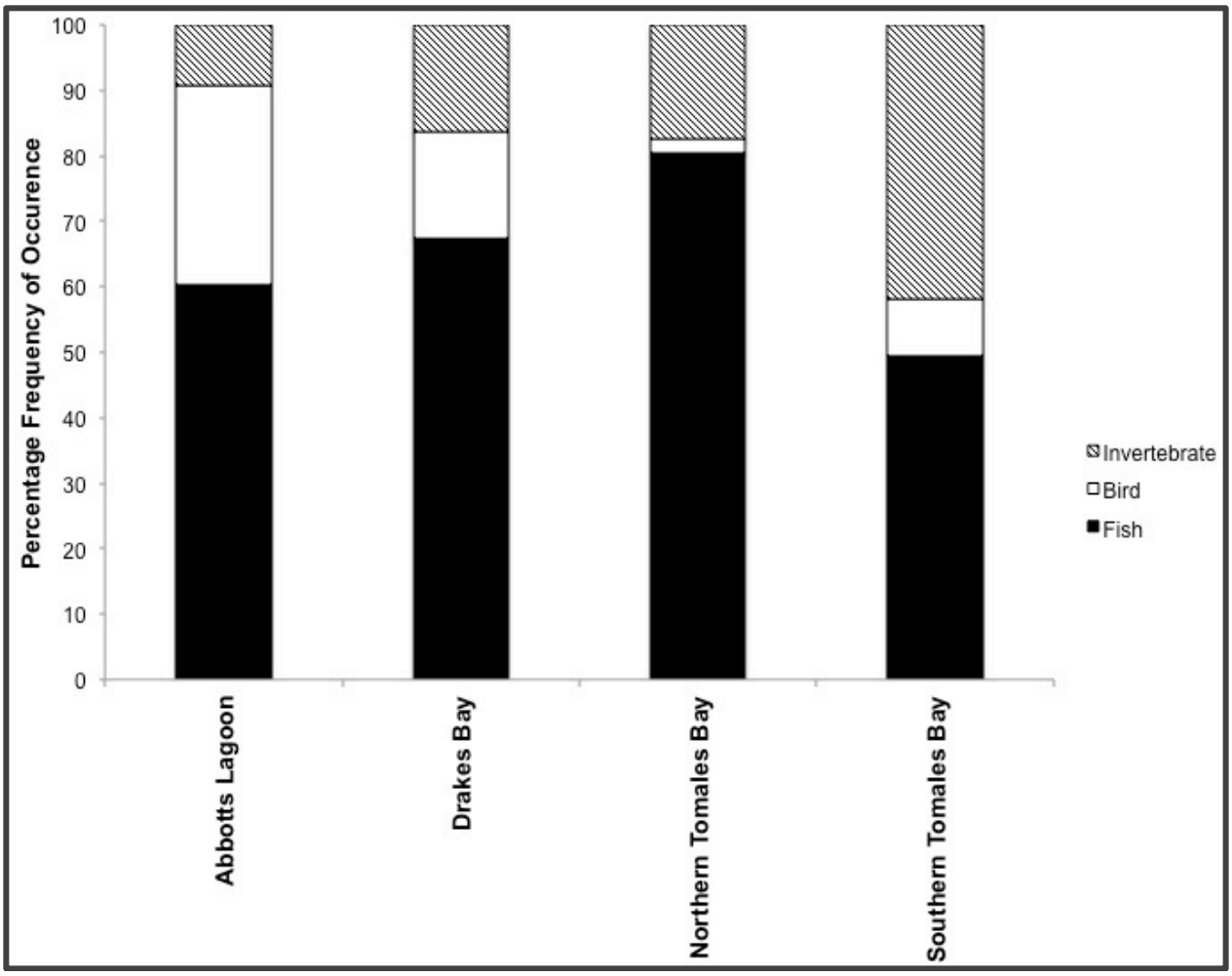

Figure 5. Percentage frequency of occurrence of river otter prey remains recovered from fecal samples at focal study sites in Point Reyes National Seashore during 2014-16 when seasons were pooled.

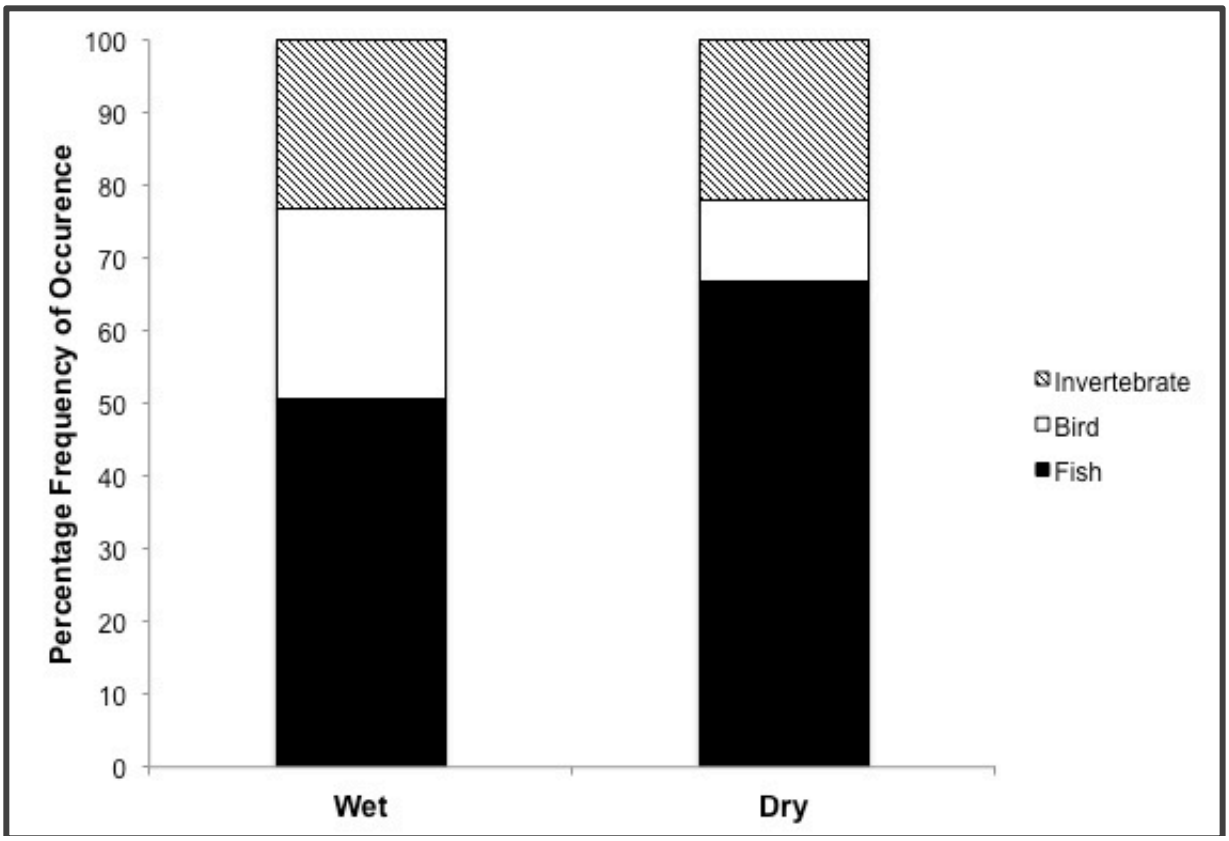

Figure 6. Percentage frequency of occurrence river otter prey remains recovered from fecal samples during the wet and dry seasons in Point Reyes National Seashore, California collected during 2014 to 2016 when sites were pooled.

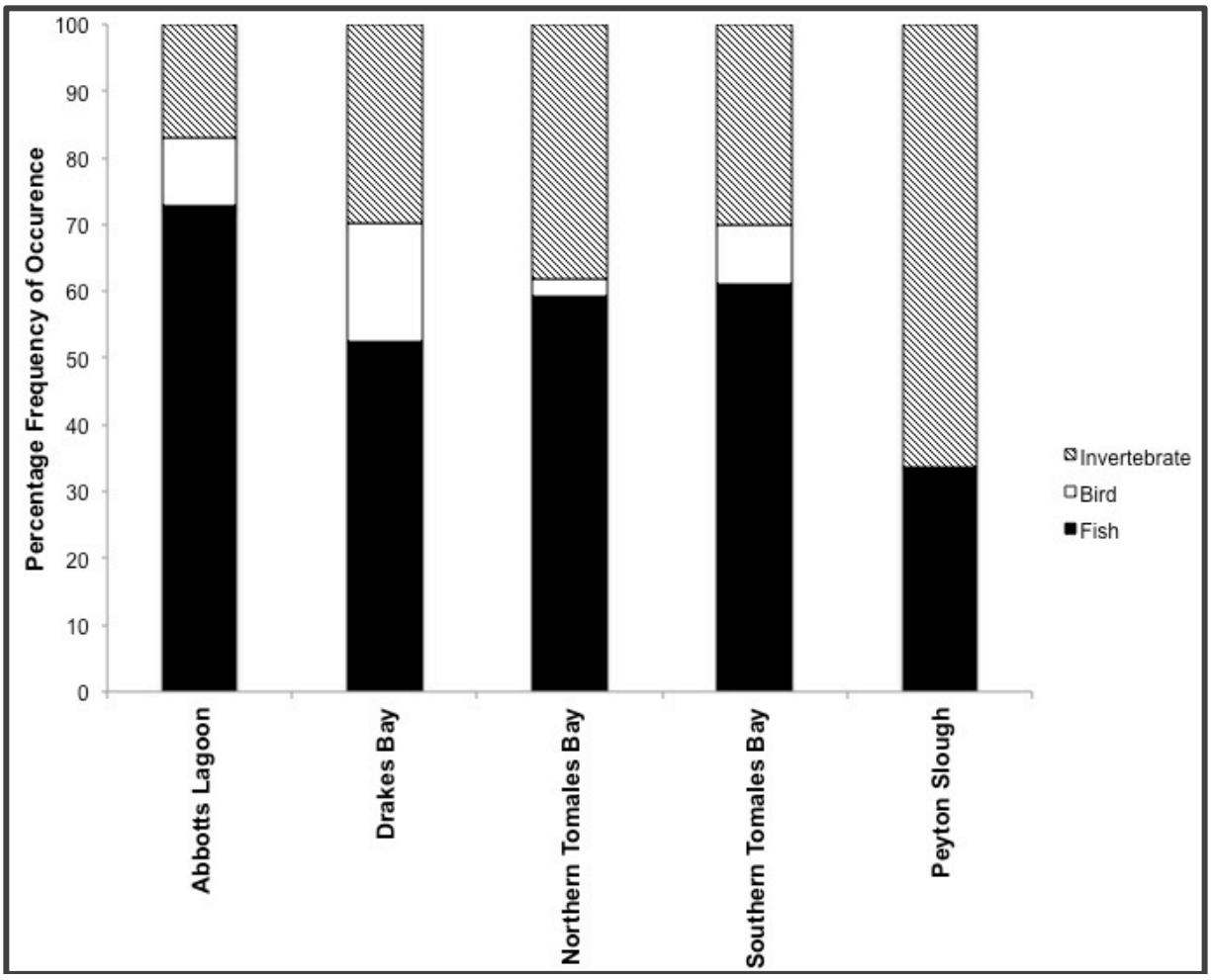

Figure 7. Percentage frequency of occurrence of river otter prey remains recovered from fecal samples at focal study sites in Point Reyes National Seashore and Peyton Slough Wetlands Complex, California collected during 2017 to 2018 when seasons were pooled.

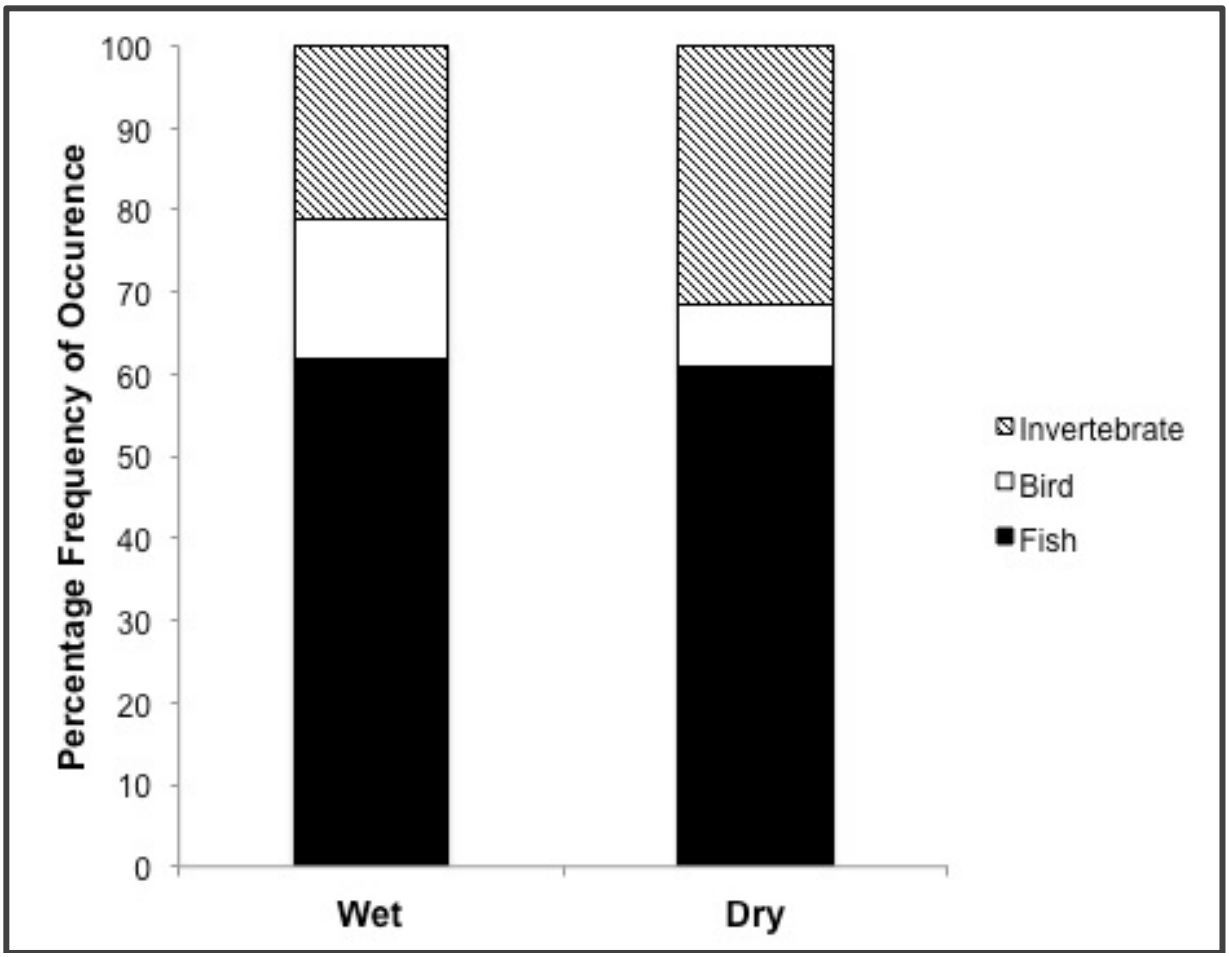

Figure 8. Percentage frequency of occurrence river otter prey remains recovered from fecal samples during the wet and dry seasons in Point Reyes National Seashore, California collected during 2017 to 2018 when sites were pooled.