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Food Habits of Harbor Seals (*Phoca vitulina*) in Two Estuaries in the Central Salish Sea

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Abstract

This study describes the seasonal diet composition of the Pacific harbor seal (*Phoca vitulina*) in two estuaries, Padilla Bay and Drayton Harbor, in the central Salish Sea. Prey remains were recovered from harbor seal fecal samples (scats) collected at haul-out sites during spring and summer/fall in 2006. Top prey taxa (≥ 25% frequency of occurrence) were compared between seasons, estuaries, and between estuarine and non-estuarine haul-out sites. Overall, prey from at least 26 taxonomic families were identified in 198 harbor seal scats. In Padilla Bay, the most common prey were gunnel (family Pholidae; 88.6%), snake prickleback (*Lumpenus sagitta*; 59.1%), Pacific staghorn sculpin (*Leptocottus armatus*; 50.0%), and shiner perch (*Cymatogaster aggregata*; 47.7%). Threespine stickleback (*Gasterosteus aculeatus*; 95.5%) and Pacific herring (*Clupea pallasi*; 83.1%) were the most frequently consumed species in Drayton Harbor; shiner perch, snake prickleback, mammal, and Pacific staghorn sculpin also each occurred in ≥ 50% of samples from at least one season. Occurrences of top prey taxa varied by season, estuary, and habitat type. Diet composition suggests that harbor seals in Padilla Bay and Drayton Harbor foraged primarily within estuarine habitats such as those found near the haul-out sites. Temporal and spatial variations in diet appeared to reflect differences in the availability of prey taxa. This study also identifies mammals as a potentially novel prey item for harbor seals in Drayton Harbor.

Key Words: harbor seal, *Phoca vitulina*, scat analysis, diet composition, estuaries, temporal variation, spatial variation

Introduction

The Salish Sea, which encompasses the inland marine waters of Washington State and British Columbia, is one of the most richly diverse ecosystems in North America. It is home to thousands of species, including more than 200 fish and 20 marine mammal species (Gaydos & Brown, 2009). The Pacific harbor seal (*Phoca vitulina*) is the most abundant and widely distributed pinniped species in the Salish Sea, as well as the only pinniped that is present year-round (Jeffries et al., 2000). Historically, harbor seals were blamed for declines in commercial salmon fisheries, prompting the State of Washington to finance a bounty program from 1943 to 1960 (Scheffer & Sperry, 1931; Newby, 1973). Since the program's termination and the establishment of the Marine Mammal Protection Act in 1972, the harbor seal population in Washington has increased seven to ten times (Jeffries et al., 2003). There are now more than 50,000 harbor seals in the Salish Sea (Olesiuk et al., 1990; Jeffries et al., 2003). Over the last two decades, harbor seal predation was identified as a potential major stressor in the declines of Pacific herring (*Clupea pallasi*), Pacific hake (*Merluccius productus*), and walleye pollock (*Theragra chalcogramma*) fisheries in Puget Sound (West, 1997). In addition, harbor seals may impose significant predation on out-migrating juvenile and returning adult salmonids (National Marine Fisheries Service [NMFS], 1997; Yurk & Trites, 2000). Given their potential to impact prey populations, several recent studies have examined the diet and foraging behavior of harbor seals in the central Salish Sea, focusing on rocky haul-out sites in non-estuarine habitats (Thomas et al., 2011; Lance et al., 2012; Peterson et al., 2012). However, knowledge of the diet of harbor seals in soft-bottomed, estuarine habitats in this region is still quite limited.

Harbor seals are central place foragers that return to a centralized location (a haul-out site) between foraging bouts to rest, socialize, and nurture their young. Individuals generally exhibit fidelity to haul-out sites, particularly during breeding and molting seasons (Pitcher & McAllister, 1981; Yochem et al., 1987; Suryan & Harvey, 1998; Härkönen & Harding, 2001). It is believed that most adult harbor seals forage within 50 km of haul-out sites (Thompson et al., 1998; Tollit et al., 1998; Wright et al., 2007), with the majority of foraging activity within 20 km (Stewart et al., 1989; Tollit et al., 1998; Cordes et al., 2011). Throughout the Salish Sea, harbor seals use two general types of haul-out sites: (1) estuarine, which are found in shallow, soft-bottomed bays, and (2) non-estuarine, which include rocky reefs, islands, and beaches that are surrounded by hard substrata and deep water (Olesiuk et al., 1990; Jeffries et al., 2000). Recent studies suggest that foraging trip distance and duration, haul-out site fidelity, and home range size of harbor seals are related to these haul-out site types: seals at non-estuarine sites tend to travel farther, forage for longer periods of time, use multiple haul-out sites over a greater area, and have more segmented home ranges than harbor seals at estuarine haul-out sites (Reuland, 2008; Peterson et al., 2012). These observations suggest that there may also be differences in harbor seal diet between estuarine and non-estuarine habitats.

Harbor seals are opportunistic predators that feed on a variety of fish and cephalopods, with locally abundant species comprising the majority of the diet. In this way, diet composition tends to reflect differences in prey communities in distinct habitats (Härkönen, 1987; Payne & Selzer, 1989; Tollit et al., 1998), as well as temporal changes in the abundance and availability of prey (Olesiuk et al., 1990; Pierce et al., 1991; Tollit & Thompson, 1996; Brown & Pierce, 1998; Hall et al., 1998). For instance, variation in harbor seal diet between different habitats in eastern Canada is due in part to differences in the distribution of alewife (*Alosa pseudoharengus*), winter flounder (*Pseudopleuronectes americanus*), hake (*Urophycis* spp.), and capelin (*Mallotus villosus*; Bowen & Harrison, 1996). In the Strait of Georgia, salmonids are more important prey inside estuaries than outside estuaries (Olesiuk et al., 1990). Short-term, or seasonal, changes in diet composition are often related to migrations of prey species such as the return of anadromous fish to estuaries and rivers (Olesiuk et al., 1990; Middlemas et al., 2006). In the San Juan Islands, harbor seal predation on salmonids increases in the summer and fall, when large numbers of these fish pass through the region on the way to their natal streams (Lance et al., 2012). Long-term, or interannual, differences in diet may be a reflection of variability in fish stock abundance (Bowen & Harrison, 1996; Thompson et al., 1996) or may indicate large-scale changes in ecosystem health (e.g., increased abundance of prey in marine reserves). As a first step to understanding harbor seal predation on fish populations in the central Salish Sea, diet must be examined over multiple spatial (estuarine and non-estuarine) and temporal (seasonal and interannual) scales.

Within the last 5 y, the diet of harbor seals at predominantly rocky haul-out sites in the central Salish Sea has been studied extensively (Lance et al., 2012), yet there has been no comparable description of diet in nearby estuaries. Previous investigations have included data from estuaries in other parts of the Salish Sea, including the Strait of Georgia, the southern Puget Sound, and the Hood Canal (e.g., Scheffer & Sperry, 1931; Calambokidis et al., 1978; Olesiuk et al., 1990; London et al., 2001); however, these studies are over 10 y old and, thus, are unlikely to reflect recent trends in prey abundance and availability. In this study, we use fecal samples (scats) to describe the diet of harbor seals in two estuaries in this region: Padilla Bay and Drayton Harbor (Figure 1). To examine temporal and spatial variation in diet, we compared harbor seal prey between (1) seasons, (2) similar haul-out site habitats (estuarine), and (3) different haul-out site habitats (estuarine vs non-estuarine).

Methods

Study Area

Padilla Bay is an extremely shallow bay located in Skagit County, Washington (Figure 1). It is characterized by sandy or muddy substrates and extensive seagrass (e.g., eelgrass [*Zostera marina*]) meadows that cover more than 70% of the sea-bed (Bulthuis, 1995). Harbor seals haul out along the edges of tidal channels that are exposed during low tide. Scat samples were collected from two haul-out sites: East Swinomish (48° 28.93' N, 122° 30.97' W) and West Swinomish (48° 29.09' N, 122° 32.22' W). Each haul-out site is used by approximately 100 to 200 harbor seals (Jeffries et al., 2000; K. Luxa, unpub. data). Drayton Harbor is a 6.5-km^2 estuary located just south of the United States-Canada border (Figure 1). Like Padilla Bay, Drayton Harbor is a shallow, intertidal estuary that includes large eelgrass meadows. Here, samples were collected from the floating breakwater that surrounds Semiahmoo Marina at the east end of Semiahmoo Spit (48° 59.11' N, 122° 46.42' W). This haulout is available independent of low tide, and is utilized by over 200 harbor seals, with average values around 100 harbor seals

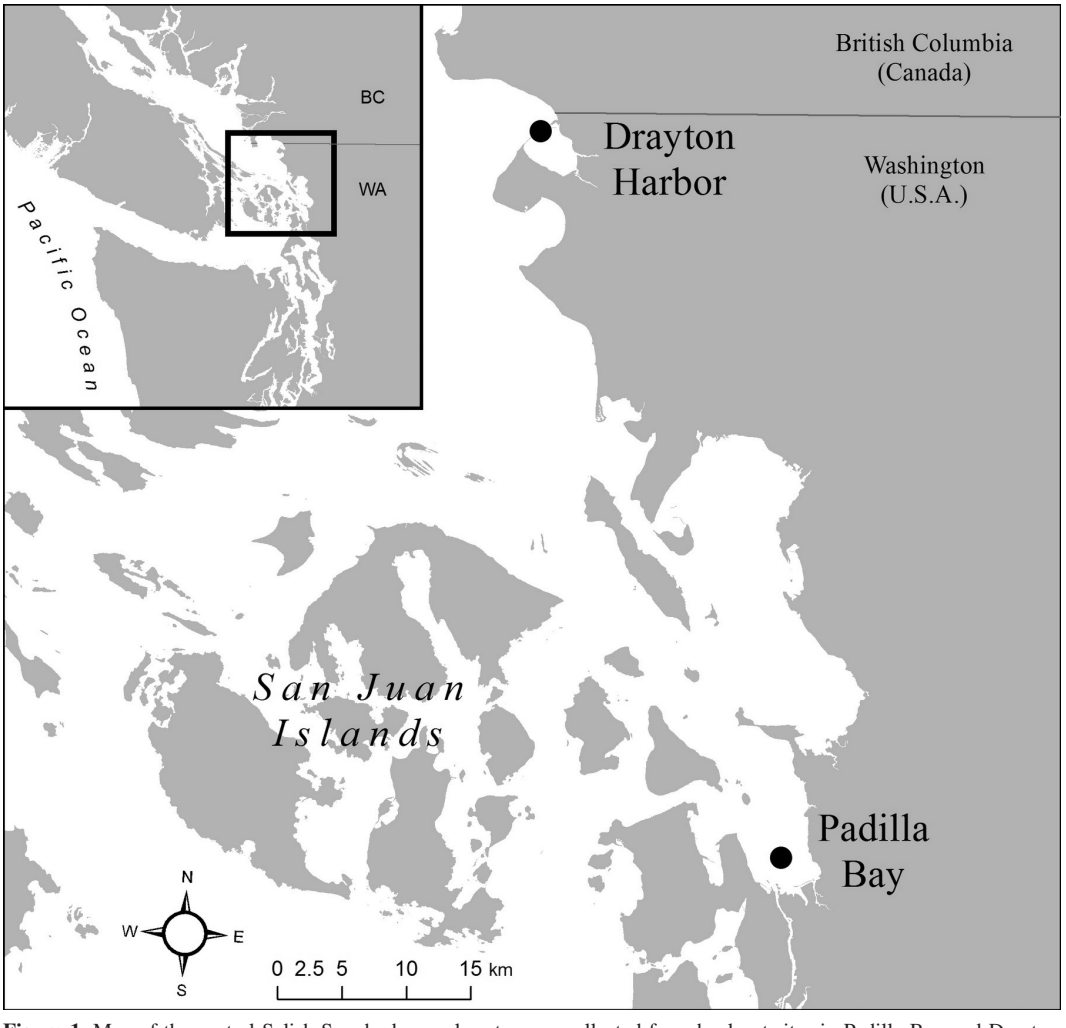

Figure 1. Map of the central Salish Sea; harbor seal scats were collected from haul-out sites in Padilla Bay and Drayton Harbor (indicated by dots).

(Patterson & Acevedo-Gutiérrez, 2008). These estuaries were selected, in part, for their proximity to rocky, non-estuarine habitats where seal diet has been studied by the Washington Department of Fish and Wildlife (Lance et al., 2012), as well as for harbor seal abundance (to maximize the potential for scat deposition) and the relative ease with which the haul-out sites could be reached for scat collection.

Sample Collection and Analysis

Scats were collected in Padilla Bay and Drayton Harbor during two seasons in 2006: spring (late March through June) and summer/fall (July through September) after Lance et al. (2012). In Padilla Bay, samples were collected every 10 to 14 d during daytime low tides from 30 March to 7 September. Samples from the two haul-out sites were pooled for diet analyses because the sites are relatively close to one another (within 2.2 km) and surrounded by similar habitats (e.g., sandy/muddy substrate, eelgrass). On some collection trips, very small quantities of fecal matter were found scattered across the beach. To avoid overestimating sample size, "mini scats" that were within 1 m of one another and had similar color and texture were collected as a single sample. In Drayton Harbor, samples were collected up to four times per month (one trip per week) between 2 May and 30 September. We collected all scats that appeared to have been recently deposited (i.e., were still moist); on occasion, drier scats were collected, but only if they were still intact (i.e., not fractured into separate pieces) and were not covered in debris

(e.g., bird feathers and droppings, broken shells, seal fur). All scats were placed in individual bags, returned to the lab, and stored frozen. Samples were later thawed and rinsed through a series of nested mesh sieves: 2.0 mm, 1.0 mm, and 0.71 mm (Riemer & Mikus, 2006). As an additional means of removing organic matter, some samples were first processed in a washing machine on a "gentle" cycle (Orr et al., 2003). Hard parts were dried and stored in glass vials, whereas cephalopod structures were stored in 70% isopropyl alcohol to prevent distortion (Browne et al., 2002).

Prey remains, including fish otoliths and skeletal bones, cartilaginous parts of elasmobranchs and lampreys (family Petromyzontidae), and cephalopod beaks, were identified to the lowest possible taxonomic level using bone and otolith identification keys (Cannon, 1987; Harvey et al., 2000), and the comparative reference collection at the National Marine Mammal Laboratory (Seattle, Washington). K. Luxa attended fish skeletal anatomy and bone identification training with Dr. Susan Crockford (Pacific Identifications, Inc., Victoria, BC), who also verified the identification of remains in 55 complete samples and approximately 120 additional structures. Fish remains that could not be confidently identified to family but that were clearly distinct from other taxa within a sample were reported as "unidentified fish" (Olesiuk et al., 1990; Browne et al., 2002). Mammal bone fragments were identified by comparing their texture to mammal structures confirmed by Pacific Identifications, Inc.

To describe the relative importance of prey taxa, we calculated the percent frequency of occurrence (% FO), which expresses the percentage of samples that contain a particular taxon. Harbor seal diet richness, relative to season and site, was determined by calculating the mean number of taxa per scat sample (Lance & Jeffries, 2007; Lance et al., 2012). To examine temporal and spatial variation in diet composition, we plotted frequencies of occurrence with exact 95% binomial confidence intervals (Wright, 2010). Species accumulation curves for Padilla Bay (summer/fall) and Drayton Harbor (spring and summer/fall) samples did not reach prolonged asymptotes, suggesting that we may not have collected enough samples to identify all prey species consumed by harbor seals at these sites (Lance et al., 2001). For this reason, comparisons were limited to the most frequently occurring (i.e., ≥ 25% FO) prey taxa from a given season or site. Top prey taxa were compared in time between (1) spring and summer/fall in Drayton Harbor, and in space between (2) estuarine haul-out sites (Padilla Bay vs Drayton Harbor) during summer/fall, and (3) estuarine (Padilla Bay and Drayton Harbor) and non-estuarine (San Juan Islands; Lance & Jeffries, 2007) haul-out sites during July and August 2006.

Results

Diet Composition

A total of 44 scats were found at Padilla Bay haul-out sites during summer/fall; no samples were found during spring. All scats contained identifiable remains of ray-finned fishes (Table 1). Overall, prey from at least 15 taxonomic families were identified. Samples contained 4.0 ± 1.7 prey taxa (mean ± SD), and no samples had more than eight taxa. Taxa that were most frequently consumed by harbor seals were gunnel (family Pholidae; 88.6%), snake prickleback (*Lumpenus sagitta*; 59.1%), Pacific staghorn sculpin (*Leptocottus armatus*; 50.0%), and shiner perch (*Cymatogaster aggregata*; 47.7%).

In Drayton Harbor, all scats collected during spring (n = 35) and summer/fall (n = 119) contained identifiable remains (Table 1). Ray-finned fishes were found in all samples; mammal (56.5%), nereid worm (18.8%), lamprey (7.8%), cephalopod (6.5%), elasmobranch (4.5%), and bird (0.6%) remains were also present. Prey from at least 26 taxonomic families were identified in samples from this site. On average, spring samples contained 6.1 ± 2.8 prey taxa, although some had as many as 13 taxa. Threespine stickleback (88.6%), Pacific herring (68.6%), and goby (family Gobiidae; 45.7%) were the most frequently consumed prey taxa. Mammal remains were found in 42.9% of summer/fall samples. One structure was tentatively identified as American mink (*Neovison vison*), but most of the remains were too fragmented and eroded to be identified to species; even so, their size and texture were consistent with juvenile small mammals (S. Campbell, pers. comm., March 2008). Flatfish (order Pleuronectiformes), plainfin midshipman (*Porichthys notatus*), shiner perch, gunnel, adult salmonid, and smelt (family Osmeridae) were also top (i.e., ≥ 25% FO) prey in this season.

Summer/fall samples contained 9.2 ± 3.0 prey taxa. No samples had fewer than two taxa, and one sample contained 18 taxa. Threespine stickleback, Pacific herring, shiner perch, snake prickleback, Pacific staghorn sculpin, and mammal were the most frequently consumed prey, all occurring in ≥ 60% of samples (Table 1). Other top prey included Pacific sand lance (*Ammodytes hexapterus*; 49.6%), flatfish (48.7%), adult salmonid (42.9%), smelt (42.9%), juvenile salmonid (35.3%), northern anchovy (*Engraulis mordax*; 35.3%), goby (29.4%), and plainfin midshipman (26.1%).

Table 1. Percent frequency of occurrence (FO) of species in harbor seal scats collected from Padilla Bay and Drayton Harbor during spring and summer/fall in 2006

		% FO		
		Padilla Bay	Drayton Harbor	
		summer/ fall	spring	summer/ fall
Class/family	Species	*n* = 44	*n* = 35	*n* = 119
Actinopterygii (Ray-finned fishes)				
Agonidae	Unidentified poacher	2.3	0.0	0.8
Ammodytidae	Pacific sand lance (*Ammodytes hexapterus*)	22.7	22.9	49.6
Batrachoididae	Plainfin midshipman (*Porichthys notatus*)	2.3	31.4	26.1
Clupeidae	Unidentified clupeid	2.3	0.0	5.0
	American shad (*Alosa sapidissima*)	0.0	0.0	1.7
	Pacific herring (*Clupea pallasi*)	11.4	68.6	87.4
	Pacific sardine (*Sardinops sagax*)	2.3	0.0	0.0
Cottidae	Unidentified sculpin	11.4	2.9	19.3
	Pacific staghorn sculpin (*Leptocottus armatus*)	50.0	8.6	69.7
Cyprinidae	Northern pikeminnow (*Ptychocheilus oregonensis*)	0.0	0.0	5.0
Embiotocidae	Unidentified surfperch	4.5	2.9	4.2
	Pile perch (*Rhacochilus vacca*)	0.0	0.0	3.4
	Shiner perch (*Cymatogaster aggregata*)	47.7	28.6	85.7
Engraulidae	Northern anchovy (*Engraulis mordax*)	0.0	8.6	35.3
Gadidae	Unidentified gadid	0.0	0.0	4.2
	Pacific cod (*Gadus macrocephalus*)	0.0	2.9	0.0
	Walleye pollock (*Theragra chalcogramma*)	2.3	5.7	0.8
Gasterosteidae	Threespine stickleback (*Gasterosteus aculaeatus*)	18.2	88.6	97.5
Gobiidae	Unidentified goby	0.0	45.7	29.4
Hexagrammidae	Unidentified greenling	4.5	0.0	6.7
Osmeridae	Unidentified smelt	18.2	25.7	42.9
Pholidae	Unidentified gunnel	88.6	28.6	21.0
Pleuronectiformes[1]	Unidentified flatfish	15.9	34.3	48.7
Salmonidae	Unidentified salmonid	0.0	2.9	16.0
	Unidentified salmonid – adult	0.0	28.6	42.9
	Unidentified salmonid – juvenile	4.5	17.1	35.3
Scorpaenidae	Unidentified rockfish	0.0	22.9	8.4
Stichaeidae	Unidentified prickleback	2.3	0.0	0.8
	Snake prickleback (*Lumpenus sagitta*)	59.1	17.1	73.9
Syngnathidae	Bay pipefish (*Syngnathus leptorhynchus*)	4.5	0.0	2.5
Trichodontidae	Pacific sandfish (*Trichodon trichodon*)	0.0	0.0	2.5
(Unknown)	Unidentified fish	22.7	20.0	20.2
Aves (Birds)				
(Unknown)	Unidentified bird	0.0	0.0	0.8
Cephalaspidomorphi (Lampreys)				
Petromyzontidae	Unidentified lamprey	0.0	0.0	2.5
	River lamprey (*Lampetra ayresii*)	0.0	8.6	5.0
Cephalopoda (Squid and octopus)				
(Unknown)	Unidentified cephalopod	0.0	5.7	0.0
Teuthida[1]	Unidentified squid	0.0	17.1	1.7
Chondrichthyes (Cartilaginous fishes)				
Elasmobranchii[2]	Unidentified elasmobranch	0.0	2.9	0.0
Rajidae	Unidentified skate	0.0	5.7	3.4
Mammalia (Mammals)				
(Unknown)	Unidentified mammal	0.0	42.9	60.5
Polychaeta (Polychaete worms)				
Nereididae	Unidentified nereid worms	0.0	11.4	21.0

[1]Order; [2]Subclass

Temporal Variation in Harbor Seal Diet
Fifteen prey taxa occurred in ≥ 25% of samples from at least one season in Drayton Harbor (Figure 2). The % FO for top taxa was typically higher during summer/fall than spring. Shiner perch, northern anchovy, and snake prickleback increased by approximately three to four times, while Pacific staghorn sculpin increased by eight times. Diet richness was also higher during summer/fall than spring.

Spatial Variation in Harbor Seal Diet
Fifteen prey taxa occurred in ≥ 25% of samples from at least one estuary during summer/fall (Figure 3). Only three of these taxa (Pacific staghorn sculpin, shiner perch, and snake prickleback) were top prey in both estuaries. All top taxa, except gunnel, had higher frequencies of occurrence in samples collected from Drayton Harbor than Padilla Bay. Goby, mammal, northern anchovy, and adult salmonid were only found in the diet of harbor seals from Drayton Harbor. Of the taxa that were consumed in both estuaries, occurrences of gunnel, Pacific herring, and threespine stickleback differed the most between Padilla Bay and Drayton Harbor. During summer/fall, the diet in Drayton Harbor was more species-rich than in Padilla Bay.

Sixteen prey taxa occurred in ≥ 25% of samples from at least one habitat (Figure 4). Just two of these, Pacific herring and adult salmonids, were top prey in both habitats. Gadiform fishes (gadids and Pacific hake) and adult salmonids were more common in the diet of harbor seals in the San Juan Islands; all other taxa were consumed more frequently by harbor seals from Padilla Bay and Drayton Harbor. Goby, mammal, and snake prickleback were not reported in non-estuarine diets during July and August. Samples from non-estuarine haul-out sites contained an average of 2.2 prey taxa (Lance & Jeffries, 2007), whereas estuarine samples had 7.6 ± 3.6 prey taxa.

Discussion

Diet Composition and Richness
The total number of prey taxa consumed by harbor seals in Padilla Bay and Drayton Harbor is comparable to other studies in Pacific Northwest estuaries (London et al., 2001; Browne et al., 2002; Orr et al., 2004; Wright et al., 2007). However, the diet richness (average prey taxa per sample) described herein is among the highest for harbor seals in any habitat (Olesiuk et al., 1990; Thompson et al., 1991; Orr et al., 2004; Hauser et al., 2008). Harbor seal scats typically contain less than five species, and rarely exceed 10 taxa (e.g., Orr et al., 2004; Lance & Jeffries, 2007). In contrast, summer/fall samples from Drayton Harbor contained an average of 9.2 ± 3.0 prey taxa, and one sample

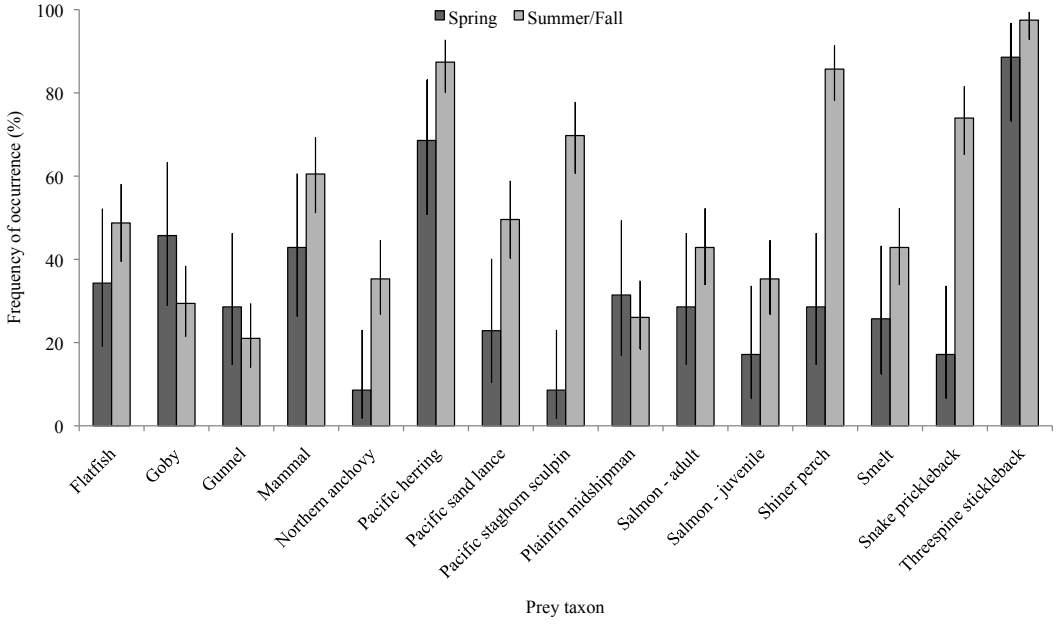

Figure 2. Top prey taxa in harbor seal diet from Drayton Harbor in spring (n = 35) and summer/fall (n = 119); top prey taxa were defined as taxa that occurred in ≥ 25% of samples from at least one season. Error bars are exact 95% binomial confidence intervals.

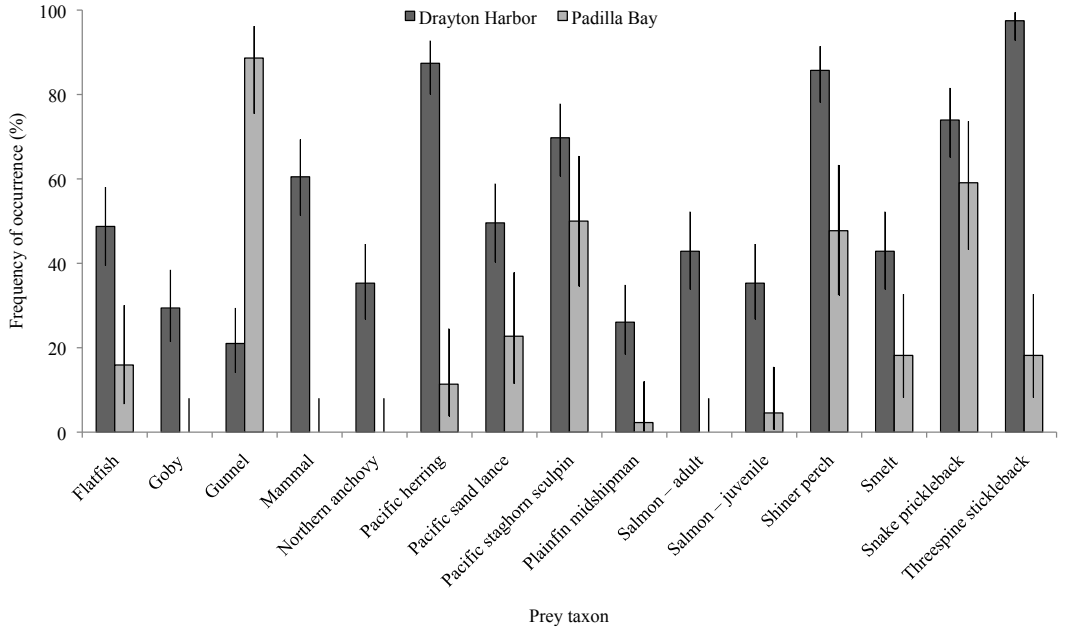

Figure 3. Top prey taxa in harbor seal diet from Padilla Bay (n = 44) and Drayton Harbor (n = 119) during summer/fall; top prey taxa were defined as taxa that occurred in ≥ 25% of samples from at least one estuary. Error bars are exact 95% binomial confidence intervals.

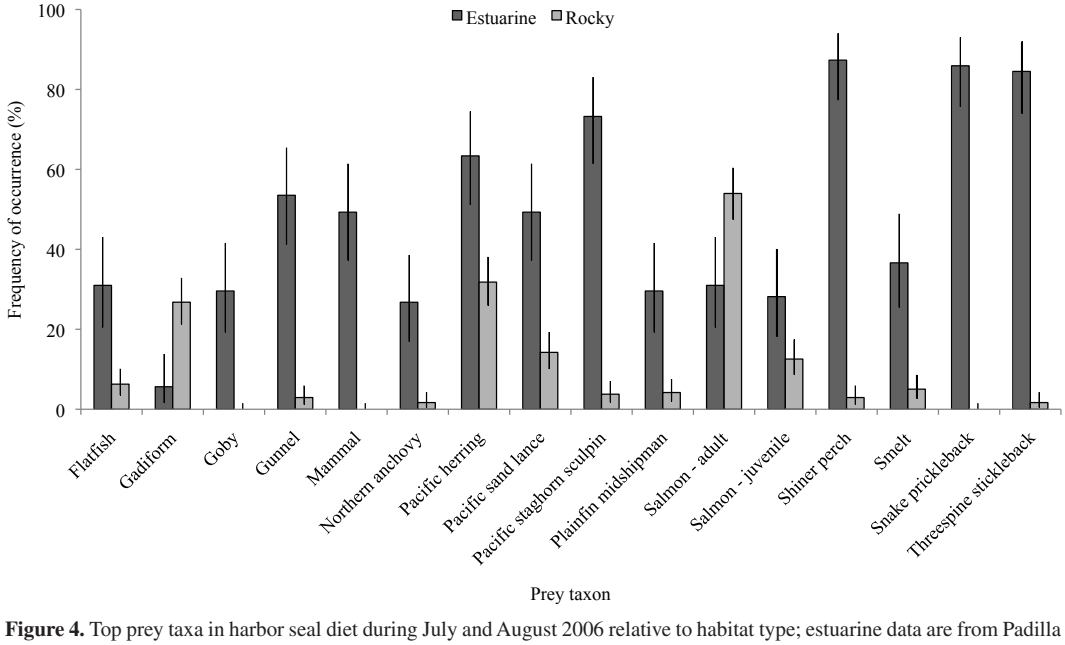

Figure 4. Top prey taxa in harbor seal diet during July and August 2006 relative to habitat type; estuarine data are from Padilla Bay and Drayton Harbor (n = 71); non-estuarine data are from the San Juan Islands (n = 239; Lance & Jeffries, 2007). Top prey taxa were defined as taxa that occurred in ≥ 25% of samples from at least one habitat. Gadoid includes all species from family Gadidae and Pacific hake. Number of occurrences for smelt was unavailable; the maximum number of occurrences was estimated by summing occurrences of all species within the taxon. Error bars are exact 95% binomial confidence intervals.

included remains from 18 different taxa. Diet richness was likely influenced by the high diversity of fish species in estuaries (Bayer, 1981; Murphy et al., 2000) and the opportunistic foraging habits of harbor seals; that is, harbor seals likely encountered (and consumed) more prey species during foraging bouts in or near Padilla Bay and Drayton Harbor.

Diet composition suggests that harbor seals in Padilla Bay and Drayton Harbor foraged primarily within estuarine habitats such as those surrounding their haul-out sites. Shiner perch and snake prickleback were important prey in both Padilla Bay and Drayton Harbor, and they are two of the most abundant fish species in Padilla Bay during the summer (Penaluna, 2006). All of the top prey taxa described in this study, as well as many others that were consumed less frequently (e.g., pile perch [*Rhacochilus vacca*]), commonly occur in estuaries in the Salish Sea (Fresh, 1979; Lamb & Edgell, 1986; Wydoski & Whitney, 2003; Penttila, 2007). These results are consistent with previous studies indicating that harbor seals prey on locally abundant populations (Härkönen, 1987; Payne & Selzer, 1989; Tollit et al., 1997; Hall et al., 1998). The foraging range of Drayton Harbor seals is unknown, but core areas used by satellite-tagged harbor seals from Padilla Bay all fall within the boundaries of Padilla Bay (Peterson et al., 2012). Foraging activity was likely concentrated near the estuaries during the study period, particularly summer/fall, because pupping, mating, and molting occur during those months (Huber et al., 2001). These three activities are associated with smaller foraging ranges of harbor seals (Boness et al., 1994, 2006; Thompson et al., 1994; Van Parijs et al., 1997). If foraging ranges during the summer months are smaller than in other months, it is possible that the diet of harbor seals in Padilla Bay and Drayton Harbor will differ at other times of the year.

To our knowledge, this study is the first to identify mammals as harbor seal prey. Remains of small mammals, possibly juveniles, were found in 42.9% of spring samples and 60.5% of summer/fall samples from Drayton Harbor. Harbor seals rarely consume vertebrates other than fish (but see MacKenzie, 2000; Tallman & Sullivan, 2004). Predation on mammals is relatively uncommon among pinnipeds, although Steller sea lions (*Eumetopias jubatus*), leopard seals (*Hydrurga leptonyx*), and walruses (*Odobenus rosmarus*) will sometimes consume other pinnipeds (Lowry & Fay, 1984; Hiruki et al., 1999; Mathews & Adkison, 2010). Most recently, grey seals (*Halichoerus grypus*) have been described as a possible predator of harbor porpoise (*Phocoena phocoena*; Haelters et al., 2012). Potential semi-aquatic mammal prey in this region include American mink, river otter (*Lontra canadensis*), muskrat (*Ondatra zibethicus*), raccoon (*Procyon lotor*), and various other small rodents (e.g., vole [*Microtus* spp.]). In fact, one structure was tentatively identified as the sacrum from a young American mink. It is possible that mammal remains were deposited at the haul-out site by other predators (e.g., river otter, bald eagle [*Haliaeetus leucocephalus*], or predatory seabirds) and accidentally collected with harbor seal scats. However, to explain the high frequency of occurrence of mammals in scat samples, mammal remains would need to be regularly deposited on the marina breakwater, and harbor seals would have to consistently deposit scat on top of those remains. We believe it is unlikely that the mammal remains were deposited by one of these other predators given that these predators are not present at the haul-out site as much as harbor seals, and mammals are not major components of their diets in coastal regions (Vermeer, 1982; Jones, 2000; Collis et al., 2002; Watson, 2002; Penland & Black, 2009). Still, the unprecedented occurrence of mammal in harbor seal diet requires further study to determine the source of these remains and how they came to be collected with the scats.

Temporal Variation in Harbor Seal Diet

In Drayton Harbor, 12 top prey taxa occurred in more samples in summer/fall than in spring. Increased consumption of shiner perch, snake prickleback, Pacific staghorn sculpin, and northern anchovy coincided with periods of increased availability such as spawning, seasonal migrations, or the arrival of young-of-the-year fishes in estuaries (Lamb & Edgell, 1986; Wydoski & Whitney, 2003; Penttila, 2007). For example, shiner perch aggregate in shallow bays and estuaries to feed, mate, and give birth during the summer (Wydoski & Whitney, 2003). The frequency of occurrence of this species in harbor seal samples tripled between spring and summer/fall. Seasonal differences in Drayton Harbor diet composition suggest that harbor seals foraged on temporally abundant prey as has been described in other studies (Olesiuk et al., 1990; Pierce et al., 1991; Tollit & Thompson, 1996; Hall et al., 1998; Lance et al., 2012).

Spatial Variation in Harbor Seal Diet

Spatial variation in harbor seal diet has been described in previous studies, typically in regions where harbor seals forage in different habitat types (Härkönen, 1987; Payne & Selzer, 1989; Olesiuk et al., 1990; Bowen & Harrison, 1996; Tollit et al., 1998). The harbor seal haul-out sites in Padilla Bay and Drayton Harbor appear to be surrounded by similar habitats, but most top prey taxa differed between the estuaries during

summer/fall. Pacific herring was consumed more frequently in Drayton Harbor, probably due to a difference in availability between the estuaries (Penaluna, 2006; Stick & Lindquist, 2009). It is less clear why adult salmonids were not consumed by Padilla Bay harbor seals because several species, including chinook salmon (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*), were returning to the central Salish Sea to spawn during the study period (Washington Department of Fish and Wildlife [WDFW], 2002). Indeed, adult salmonids were also the dominant prey of harbor seals in the nearby San Juan Islands between July and August 2006 (Lance & Jeffries, 2007). One possible explanation is that, unlike Drayton Harbor, there are no natal streams in Padilla Bay (WDFW, 2002), although it is thought to be a migratory pathway for Skagit River salmonids (Quinn, 2005). The distribution and abundance of adult salmonids in Padilla Bay is not currently monitored, and it is possible that few fish used Padilla Bay as a migration corridor, decreasing the likelihood that harbor seals would have encountered them while foraging. Variation in other taxa may have been related to seasonal movements of species or habitat availability. For example, northern anchovy may not occur in Padilla Bay during the summer months because they are concentrated near spawning areas in the southern Strait of Georgia and southern Puget Sound (Penttila, 2007). Finally, the tentative inclusion of mammals in harbor seal diet appears to be unique to Drayton Harbor and, as previously noted, requires further investigation. These comparisons highlight the importance of considering within-habitat type (e.g., estuary) differences in harbor seal diet when investigating harbor seals' potential impacts on prey populations.

For July and August 2006, all top prey taxa varied greatly between the diets of harbor seals at soft-bottomed, estuarine (Padilla Bay, Drayton Harbor) and rocky, non-estuarine (San Juan Islands) haul-out sites. Pacific herring was one of the only taxa that occurred in ≥ 25% of samples from both habitats, but it was nevertheless more common in the estuarine diet than the non-estuarine diet. In the San Juan Islands, spring and winter diets were dominated by herring, but harbor seals switched to a salmonid-dominated diet during July and August (Lance & Jeffries, 2007). Frequencies of occurrence of herring may be more similar between habitat types at different times of the year. Adult salmonids were also top prey in both habitats, but they occurred in more samples from the San Juan Islands. Predation by harbor seals in estuaries may increase as more adult salmonids swim upstream to spawn; indeed, frequency of occurrence of adult salmonids increased by approximately 25% between August and September in samples from Drayton Harbor (K. Luxa, unpub. data). Differences in other prey taxa are likely to persist year-round because of differences in prey communities between estuarine and non-estuarine habitats. Gadiform fishes, which tend to be distributed in deeper water (Gustafson et al., 2000), were more common in the harbor seal diet from the San Juan Islands where haul-out sites are surrounded by deep water. Conversely, species such as shiner perch, threespine stickleback, and Pacific staghorn sculpin prefer shallow, soft-bottomed bays and estuaries (Eschmeyer et al., 1983; Wydoski & Whitney, 2003). Thus, to understand the potential impacts of harbor seal predation on prey populations, it is not only important to compare diets within similar habitats, but also across different habitats.

Biases and Limitations

Hard parts recovered from scat samples are commonly used to describe the diet of pinnipeds, and the limitations of this method are well-documented (Pierce & Boyle, 1991; Tollit et al., 2003; Bowen & Iverson, in press). The central assumption of scat analysis is that prey remains identified from samples represent all species consumed by the study population. At the population level, diet composition is affected by the number of scats collected (Trites & Joy, 2005) and by the size of samples as smaller scats contain fewer prey remains (Olesiuk et al., 1990; Arim & Naya, 2003). Prey identification is biased toward skeletal structures that are recognizable after digestion, a factor which varies by prey species and prey length within species (Cottrell et al., 1996; Bowen, 2000; Phillips & Harvey, 2009).

We were unable to collect the numbers of samples recommended by Trites & Joy (2005), and many of the scats collected in Padilla Bay were unusually small. It is likely that some rare prey species never appeared in the scats that were collected; this is supported by our species discovery curves for Padilla Bay, Drayton Harbor spring, and Drayton Harbor summer/fall, all of which did not reach prolonged asymptotes. Despite insufficient sample sizes, gross differences in diet may still be detected between populations (Bowen & Iverson, in press), hence, our conservative decision to use only the most frequently occurring prey taxa for temporal and spatial comparisons. Another potential source of bias in this study is contamination of samples at the Drayton Harbor haul-out site, a floating marina breakwater that is never covered during high tide and, therefore, never "cleaned" between collection dates. It is possible that some older harbor seal prey remains or remains deposited by other animals (e.g., river

otter) were incidentally collected with fresh scats, but we expect that such occurrences would be random and do not consider this to be a major source of error. Finally, % FO is a simple, useful metric for determining common and rare prey taxa, but it offers no indication of the quantity of prey consumed (Lance et al., 2001). Enumeration and measurement of hard parts are time-intensive, and length correction factors may not be available for all prey species (Bowen & Iverson, in press). We believe % FO was appropriate for this initial description of harbor seal diet in Padilla Bay and Drayton Harbor; however, to draw any meaningful conclusions about the impact of harbor seals on prey populations, future studies should attempt to estimate biomass consumed, particularly for prey species of interest.

Conclusions

Harbor seals in Padilla Bay and Drayton Harbor foraged primarily in estuarine habitats such as those surrounding their haul-out sites. Their diet included prey from more than two dozen taxonomic families; diet richness was among the highest reported for harbor seals in any region; and the presence of unidentified mammals in Drayton Harbor samples is a finding that warrants further investigation. Temporal and spatial variations in diet suggest that harbor seals from Padilla Bay and Drayton Harbor fed on seasonally and locally abundant prey. Our results call for additional studies on the food habits of harbor seals at these and other estuarine haul-out sites in the central Salish Sea to expand our knowledge of harbor seal diet and to take the next step in identifying potential impacts on prey species by incorporating more detailed analyses (i.e., prey enumeration and biomass reconstruction).

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