FOOD HABITS OF HARBOR SEALS (*PHOCA VITULINA*) IN TWO ESTUARIES IN NORTHERN PUGET SOUND, WASHINGTON

By

Kathryn Luxa

Accepted in Partial Completion

Of the Requirements for the Degree

Master of Science

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MASTER'S THESIS

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FOOD HABITS OF HARBOR SEALS (*PHOCA VITULINA*) IN TWO ESTUARIES IN NORTHERN PUGET SOUND, WASHINGTON

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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ABSTRACT

There is a long-held belief that marine mammals are a threat to fishery resources. In Puget Sound, there is particular concern about the potential impacts of pinniped predation on depleted or recovering populations of rocky reef bottomfish. To understand the potential effects of pinnipeds on fish stocks, it is necessary first to describe the types of prey that they consume. The goal of this study was to describe the seasonal diet composition of the Pacific harbor seal (*Phoca vitulina*) in two estuaries, Padilla Bay and Drayton Harbor. Fecal samples ("scats") were collected from haul-out sites during pre-pupping (May – June) and pupping (July – September) seasons in 2006. Otoliths and other diagnostic skeletal structures were used to identify prey to the lowest possible taxon. Frequency of occurrence (% FO) was calculated for all prey taxa, and occurrences of the top (> 25% FO) prey species were compared between seasons (Drayton Harbor pre-pupping and pupping), years (Drayton Harbor 1992 and 2006), and sites (Padilla Bay and Drayton Harbor). I also compared seal diet from Padilla Bay and Drayton Harbor with that from non-estuarine haul-out sites in the San Juan Islands. Overall, 40 prey taxa, representing at least 26 taxonomic families, were identified in 198 harbor seal scats from the estuaries. In Padilla Bay, the most common prey were gunnel (family Pholidae), snake prickleback (*Lumpenus sagitta*), Pacific staghorn sculpin (*Leptocottus armatus*), and shiner perch (*Cymatogaster aggregata*). Threespine stickleback (*Gasterosteus aculeatus*) and Pacific herring (*Clupea pallasi*) were the most frequently consumed species in Drayton Harbor, and shiner perch, snake prickleback, Pacific staghorn sculpin, mammal, and flatfish also each occurred in more than 50% of samples from at least one season. The majority (> 85%) of samples contained demersal and benthopelagic taxa; pelagic prey were also common in Drayton Harbor diet. Occurrences of top prey taxa varied by season, year, and site. Most top prey species were consumed more frequently during pupping season in Drayton Harbor. The diversity of Drayton Harbor pupping season diet (9.3 ± 2.99 prey taxa/sample) was also significantly higher than pre-pupping season (6.1 ± 2.82 prey taxa/sample) and Padilla Bay pupping season (4.0 ± 1.68 prey taxa/sample) diets. All top prey taxa differed significantly between estuarine and non-estuarine haul-out sites. Diet composition suggested that harbor seals in Padilla Bay and Drayton Harbor foraged primarily within estuarine habitats, such as those found near the haul-out sites, and some Drayton Harbor seals occasionally fed in other habitats (e.g., freshwater). Temporal and spatial variations in diet appeared to reflect differences in the availability of prey taxa, but this was not always the case (e.g., increased predation on Pacific herring between 1992 and 2006). Drayton Harbor represents the first account of mammals as harbor seal prey. Considering the proximity of some northern Puget Sound estuaries to rocky habitats, including the candidate marine reserves in Skagit County, it is necessary to monitor the food habits of harbor seals in various habitats near marine reserves to assess more accurately the degree of predation on depressed fish stocks.

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Acevedo-Gutiérrez. Field and lab methods were also approved by Western Washington University's Animal Care and Use Committee (Protocol No. 06-001).

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INTRODUCTION

Marine ecosystems worldwide have been dramatically modified by human disturbances, particularly overfishing. To meet the global demands for food and fishmeal, millions of tons of fish are removed from the oceans annually (FAO 2007). This intensive harvest places incredible pressure on marine communities and, consequently, may alter their structure and functioning (Blaber *et al.* 2000; Jackson *et al.* 2001; Pauly *et al.* 2002; Frank *et al.* 2005). It has even been suggested that overfishing will catalyze the collapse of coastal ecosystems (Jackson *et al.* 2001). In Puget Sound, fish stocks have declined dramatically and many species, including rockfish (*Sebastes* spp.), are in critical condition (PSAT 2007; WDFW 2008).

Marine reserves have become an increasingly popular conservation and management tool in coastal ecosystems because of their rapid and long-lasting benefits to marine species (Halpern and Warner 2002). Reserves are a special class of marine protected areas in which fishing and other extractive activities are not allowed (Lubchenco *et al.* 2003). Population density and biomass, as well as overall species diversity, are significantly greater inside than outside reserves (Halpern 2003). Additionally, marine reserves may augment nearby fisheries through spillover of juveniles and adults (Alcala and Russ 1990; Gell and Roberts 2003). Several marine reserves exist in Puget Sound and, recently, three candidate reserve sites were identified for the recovery of rocky reef bottomfish in Skagit County (Weispfenning 2006).

Marine reserves effectively place limits on human activities; however, marine predators may affect the abundance of prey species within reserves (Fanshawe *et al.* 2003). In response to increases in prey density, predators are expected to increase both their abundance (aggregative response) and frequency of foraging (functional response; Solomon 1949; Hassell 1966). To understand the potential impact of predators on depleted or recovering populations, it is first necessary to describe the types of prey that they consume. Such data provide a quantitative foundation on which to generate testable hypotheses about diet variation, prey choice, and ultimately how predators influence prey abundance.

Pinnipeds (suborder Pinnipedia: seals, sea lions, and the walrus) are important marine predators that consume a variety of fish and cephalopods. In Puget Sound, the Pacific harbor seal (*Phoca vitulina*) is the most abundant pinniped species (Jeffries *et al.* 2000). An examination of temporal and spatial variation in seal diet is currently underway in rocky habitats (Lance and Jeffries 2007), but little is known about the food habits of harbor seals in estuarine environments. Hence, this study aimed to provide baseline data on the seasonal diet composition of an upper-level marine predator, the harbor seal, in two estuaries in northern Puget Sound.

Overfishing and fisheries collapse: Puget Sound

Over the last three decades, populations of salmonids, forage fish, and groundfish have undergone significant declines in Puget Sound. The Puget Sound runs of chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) are listed as Threatened under the federal Endangered Species Act (WDFW 2008), while other stocks are considered Depressed or Critical (WDFW 2002). Nine stocks of Pacific herring (*Clupea pallasi*) are similarly depleted, including the Cherry Point stock which was once the largest population in Washington State (Bargmann 1998; Stick 2005). In addition, Pacific cod (*Gadus* *macrocephalus*), walleye pollock (*Theragra chalcogramma*), and Pacific hake (*Merluccius productus*) are in Poor or Critical condition (PSAT 2007).

Rockfish, lingcod (*Ophiodon elongatus*), and other rocky reef bottomfish populations were greatly reduced after Washington Department of Fish and Wildlife (WDFW) encouraged bottomfishing to help alleviate pressure on already stressed salmon stocks in the 1970s (McConnell *et al.* 2001). Some rockfish species may now be at less than 10% of their historic reproductive potential (Palsson 1998) and several are listed as Species of Concern in Washington State (WDFW 2008). In addition to more traditional fishery management methods, such as bag limits, several "no-take" marine reserves were established for bottomfish protection (Palsson 2002). Rockfish and lingcod are excellent candidates for reserve protection due to their high site fidelity and small home ranges (Matthews 1990a; Love *et al.* 2002). Indeed, in monitoring surveys conducted at Brackett's Landing Shoreline Sanctuary Conservation Area (formerly Edmonds Underwater Park) and at sites in the San Juan Islands Marine Preserves, copper rockfish (*S. caurinus*) and lingcod were larger and more abundant than in nearby fished areas (Palsson 1998; Eisenhardt 2001).

Following the apparent success of existing reserves, the Skagit County Marine Resources Committee (MRC) has recommended three candidate reserve sites for bottomfish protection in western Skagit County (Weispfenning 2006). Should a site eventually be designated as a reserve, its success will depend on a range of social and biological factors, including stakeholder support and compliance, habitat characteristics, and predation by pinnipeds (McConnell and Dinnel 2002). The potential effects of predators on bottomfish species within reserves are of particular interest as predators are expected to increase both their abundance (aggregative response) and frequency of foraging (functional response) in areas of high prey density (Solomon 1949; Hassell 1966). However, to predict the effects of pinniped predation on the recovery of rocky reef bottomfish and other Puget Sound fisheries, it is critical to understand their food habits.

Pinniped impacts on prey populations

Marine mammals are important predators of fish, cephalopods, and crustaceans, including commercially valuable species. As a result, there is a long-held belief that marine mammals, especially pinnipeds, are significant threats to fishery resources (Harwood and Croxall 1988; Harwood 1992; Baraff and Loughlin 2000). Recent increases in pinniped populations and the redistribution of fishing effort to inshore waters have greatly increased the potential for interactions between pinnipeds and fishing fleets (Harwood 1987). Seals and sea lions are often seen foraging near boats and fishing equipment, and have been observed raiding gear for trapped fish (Harwood 1983; Shaughnessy 1985; Königson *et al.* 2006). There is also a large overlap in prey items taken by pinnipeds and commercial fisheries, more so than the one observed with other marine mammals (Trites *et al.* 1997). Largely for these reasons, pinnipeds have been implicated in the declines of numerous Atlantic and Pacific Ocean fisheries (Scheffer and Sperry 1931; Beverton 1985; Myers *et al.* 1997; NMFS 1997; Baraff and Loughlin 2000; Carter *et al.* 2001; Hansen and Harding 2006).

The effects of pinniped predation on fisheries are of considerable economical and biological interest, yet they are still poorly understood. In marine communities, predator-prey relationships are rarely linear, and pinnipeds interact with their prey through direct and indirect pathways (Bax 1998; Trites *et al.* 2006). As a result, much information is needed to adequately assess the impacts of pinniped predation, including species, quantity, and size classes of consumed prey and their variation over space and time; however, these data are often incomplete or unavailable (Clark 1985; Harwood and Croxall 1988; Matthiopoulos *et al.* 2008). In their place, consumption estimates are used as a crude indicator of impact (Northridge and Beddington 1992). Such estimates suggest that pinnipeds typically remove less prey biomass than fisheries (Harwood and Croxall 1988; Furness 2002; Hansen and Harding 2006) and much less than predatory fish (Bax 1991; Overholtz and Link 2007). Even where predation by pinnipeds is equal to or exceeds commercial harvest (e.g., Shaughnessy 1985), it is difficult to conclude that pinniped predation actually drives changes in fish populations (Bowen 1997; Bax 1998). In a review of marine mammal-fishery interactions, Beverton (1985) found no instances of pinnipeds negatively affecting the abundance of a commercially valuable species, and could provide only one example in which seal predation may have caused a decrease in a non-targeted fish population. In that study, fish communities were compared between Lower Seal Lake, Quebec, which supported a population of freshwater harbor seals, and nearby lakes where seals were not present (Power and Gregoire 1978). Lake trout (*Salvelinus namaycush*) in Lower Seal Lake exhibited signs of severe exploitation, including smaller size, higher growth rate, and younger age-at-maturity than trout in the other lakes.

Pinnipeds with specialized feeding habits, especially those that consume slow-moving or sessile species, may be more likely to control prey population dynamics than generalist predators (Northridge and Beddington 1992). This has been documented in Pacific walrus (*Odobenus rosmarus*) foraging on bivalves in Alaska (Oliver *et al.* 1985) and in other non-pinniped specialists, such as gray whales (*Eschrichtius robustus*; Oliver and Slattery 1985) and sea otters (*Enhydra lutris*; Estes and Palmisano 1974). Generalist predators, however, may switch to a different prey item when the abundance of preferred prey falls below a certain level of availability; therefore, they are less likely to have a regulatory effect on prey abundance (Bax 1998). For example, grey seals (*Halichoerus grypus*) in the North Sea are assumed to have little impact on their prey because their diet includes a number of different species and the mortality they cause to any given species is generally small compared to that caused by the fishery (Harwood and Croxall 1988; Hansen and Harding 2006).

Pinnipeds may not be responsible for declines in fisheries; however, there is emerging evidence that, regardless of their feeding habits, they may suppress the recovery of depleted prey populations. In eastern Canada, predation by grey seals appears to be an important factor affecting the recovery of Atlantic cod (*Gadus morhua*; Fu *et al.* 2001; Trzcinski *et al.* 2006), even though cod accounts for less than 5% of adult grey seal diet (Beck *et al.* 2007). Similarly, a model that simulated interactions between fish, fishers, and seals in a theoretical marine reserve concluded that seals would reduce fish biomass, thus negating the conservation effects of the reserve and reducing benefits to fishers (Boncoeur *et al.* 2002).

One conclusion derived from this review is that we first need to describe the diet of pinnipeds to understand their potential impacts on prey populations and marine reserves. California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), northern elephant seals (*Mirounga angustirostris*), and harbor seals all occur in Puget Sound waters (Calambokidis and Baird 1994). The harbor seal, however, is the most abundant and widely-distributed of these species, utilizing more than 250 haul-out sites in the region, and is 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 and 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 by 7 – 10 times (Jeffries *et al.* 2003). During the last decade, seal predation was identified as a potential major stressor in the declines of Pacific herring, Pacific hake, and walleye pollock fisheries in Puget Sound (West 1997). In addition, seals may also impose significant predation on out-migrating juvenile and returning adult salmonids (NMFS 1997; Yurk and Trites 2000). Given their potential to impact prey populations in Puget Sound, I chose to focus my study on harbor seals.

The foraging behavior of harbor seals

Harbor seals can be considered central place foragers that return to a centralized location (a haul-out site) between foraging bouts to rest, socialize, and nurture their young (Thompson and Miller 1990; Nickel 2003). Individuals generally exhibit fidelity to a single haul-out site, particularly during the breeding and molting seasons (Yochem *et al.* 1987; Suryan and Harvey 1998); however, use of one or two neighboring sites is not uncommon (Pitcher and McAllister 1981; Thompson *et al.* 1994; Olesiuk 1999; Nickel 2003). Most adult harbor seals forage within 20 km of their haul-out site (Thompson *et al.* 1998; Tollit *et al.* 1998; Wright *et al.* 2007), with the majority of foraging activity within 5 – 10 km (Brown and Mate 1983; Stewart *et al.* 1989; Frost *et al.* 2001; Nickel 2003). In the Strait of Georgia, British Columbia, over 90% of foraging dives occurred within 10 km of haul-out sites (Olesiuk 1999). Similar results were reported for male harbor seals in the San Juan Islands during the mating season (Suryan and Harvey 1998). Individuals may also undertake longer foraging trips (Thompson and Miller 1990; Thompson *et al.* 1998; Lowry *et al.* 2001). For instance, a subadult male tagged in San Francisco Bay made repeated trips to offshore locations, approximately 50 km away from its haul-out site (Nickel 2003).

The location, timing, and duration of harbor seal foraging trips are influenced by numerous factors including seal sex and body size, prey availability, bathymetry, and reproductive, tidal, and diel cycles (Pauli and Terhune 1987; Thompson *et al.* 1991; Thompson *et al.* 1994; Ries *et al.* 1997; Thompson *et al.* 1998; Zamon 2001; Boness *et al.* 2006; Reuland 2008). A recent study in northern Puget Sound indicates that harbor seal foraging trip duration is also related to haul-out site type (Reuland 2008). In this region, harbor seals use two general types of haul-out sites: estuarine, which are found in shallow, soft-bottomed bays, and 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). Average foraging trip duration from estuarine haul-out sites in northern Puget Sound was shorter than from non-estuarine sites (Reuland 2008). Seals from the estuarine haul-out sites also had smaller, more contiguous home ranges (Hardee 2008).

Harbor seals are opportunistic predators that feed on a variety of fish and cephalopods, with more abundant species comprising the majority of the diet (Thompson *et al.* 1991; Tollit *et al.* 1997; Wilson *et al.* 2002). Diet composition tends to reflect differences in prey communities in distinct habitats (Härkönen 1987; Bowen and Harrison 1996). In southern New England, harbor seal diet, assessed via fecal sample analysis, varied between rocky and sandy habitats (Payne and Selzer 1989). The diet of seals at haul-out sites in sandy habitats was dominated by American sand lance (*Ammodytes americanus*), while gadiform fishes (order Gadiformes), rockfish (family Scorpaenidae), flatfish (order Pleuronectiformes), and Atlantic herring (*Clupea harengus*) were consumed most frequently by seals at rocky sites (Payne and Selzer 1989). In a similar study in the Strait of Georgia, salmonids were more important in harbor seal diet inside estuaries than outside estuaries (Olesiuk *et al.* 1990). More generally, though, diet composition can be used to identify the foraging habitats of seals (Brown and Mate 1983; Carter *et al.* 2001). For example, most prey species consumed by harbor seals at haul-out sites along the Umpqua River in Oregon (less than 5 km from the river's mouth) were exclusively marine (e.g., Pacific hake) or found in marine and estuarine habitats (e.g., anadromous species), while exclusively riverine-estuarine species (e.g., cyprinids) were rare (Orr *et al.* 2004). In Hood Canal, Washington, harbor seal fecal samples collected from several estuaries contained remains of chinook salmon (extremely rare in the sampled river systems), indicating that seals had also foraged in "open water" habitats (London *et al.* 2001). In regions where habitats are diverse, such as northern Puget Sound, it is likely that harbor seals forage in a range of habitats (e.g., Bjørge *et al.* 1995). Consequently, it is important to describe diet in different habitats.

Seasonal and interannual variations in harbor seal diet are typically associated with local changes in the abundance and availability of prey species (Olesiuk *et al.* 1990; Pierce *et al.* 1991; Tollit and Thompson 1996; Hall *et al.* 1998; Brown *et al.* 2001). Seasonal changes are often related to migratory movements of prey species (Brown and Pierce 1997; 1998). In British Columbia, harbor seals consume Pacific hake primarily during April – November, but switch to Pacific herring the rest of the year (Olesiuk *et al.* 1990). This switch coincides with the arrival of pre-spawning herring from offshore waters. The return of anadromous species to estuaries and rivers, e.g., salmonids (Pitcher 1980; Middlemas *et al.* 2006), eulachon (*Thaleichthys pacificus*; Marston *et al.* 2002), or Pacific lamprey (*Lampetra tridentata*; Roffe and Mate 1984), is also important. In the San Juan Islands, harbor seal predation on salmonids increases in the summer and fall, as large numbers of these fish pass through the region on the way to their natal streams (Lance and Jeffries 2007). In addition, Reuland (2008) reports the development of a diurnal foraging pattern, suggestive of concentrated foraging effort on vertically migrating prey species (e.g., Pacific herring, salmonids), as salmonids return to this region. Finally, interannual differences in diet may be a reflection of variability in fish stock abundance (Thompson *et al.* 1996), or may indicate large-scale changes in ecosystem health (e.g., increased abundance of prey in marine reserves). Therefore, to better understand harbor seal predation on local fish populations, diet must be examined over short and long temporal scales.

Harbor seal diet in Puget Sound estuaries

Harbor seal diet in Puget Sound is diverse, including dozens of species of fish, as well as squid and octopus. The main prey species in all regions (Hood Canal, northern and southern Puget Sound) are Pacific herring and gadiform fishes (gadids and Pacific hake), and salmonids are seasonally important; flatfish, surfperches (family Embiotocidae), eelpouts (family Zoarcidae), sculpins (family Cottidae), Pacific sand lance (*Ammodytes hexapterus*), northern anchovy (*Engraulis mordax*), and plainfin midshipman (*Porichthys notatus*) are also frequently consumed (Scheffer and Sperry 1931; Calambokidis *et al.* 1978; Everitt *et al.* 1981; London *et al.* 2001; Zamon 2001; Lance and Jeffries 2007).

Within the last five years, the diet of harbor seals at non-estuarine haul-out sites in the San Juan Islands has been studied extensively (Lance and Jeffries 2007), but the diet of harbor seals in estuaries in northern Puget Sound is not well-known. Previous investigations included some data from estuaries in southern Puget Sound and Hood Canal (e.g., Scheffer and Sperry 1931; Calambokidis *et al.* 1978); however the analyses are over 20 years old (but see London *et al.* 2001). Therefore, diet estimates are unlikely to reflect recent trends in prey abundance and availability in estuaries in northern Puget Sound. The most recent description of diet in a northern Puget Sound estuary comes from scat samples collected from a haul-out site in Drayton Harbor in June – September 1992 (WDFW unpublished data). The most common prey items (> 25% frequency of occurrence) were threespine stickleback (*Gasterosteus aculeatus*), Pacific staghorn sculpin (*Leptocottus armatus*), snake prickleback (*Lumpenus sagitta*), Pacific herring, and shiner perch (*Cymatogaster aggregata*). It is expected that harbor seals foraging in other, nearby estuaries will consume similar, estuary-associated organisms. However, considering the proximity of some northern Puget Sound estuaries to rocky habitats, including the candidate marine reserves in Skagit County, it is possible that seals utilizing estuarine haul-out sites also forage in non-estuarine habitats. If our intent is to understand harbor seal predation on rockfish and other depleted populations, it is necessary to investigate the diet of harbor seals in all habitats, including estuaries.

Research objectives

Despite the potential impact of harbor seals on fish populations, little is known about their foraging habits in soft-bottomed, estuarine habitats of northern Puget Sound. Yet, understanding diet composition and how it varies over time and space is important for predicting how predation will affect prey populations. Hence, I examined temporal and spatial variation in the diet of harbor seals in two estuaries in northern Puget Sound, Padilla Bay and Drayton Harbor. To accomplish these goals I described:

1) The prey species consumed by harbor seals during pre-pupping and pupping seasons by using fecal (“scat”) sample analysis.

2) The short-term temporal variation in the diet of harbor seals in Drayton Harbor by comparing pre-pupping and pupping seasons.

3) The long-term temporal variation in the diet of harbor seals by comparing seal diet in Drayton Harbor during 2006 with that described in 1992 (WDFW unpublished data).

4) The spatial variation in the diet of harbor seals at estuarine haul-out sites by comparing pupping season prey species in Padilla Bay to Drayton Harbor.

5) The spatial variation in the summer (July – August) diet of harbor seals in different habitats by comparing diet from soft-bottomed, estuarine (Padilla Bay, Drayton Harbor) and rocky, non-estuarine (San Juan Islands; Lance and Jeffries 2007) haul-out sites.

STUDY AREA

Padilla Bay

Padilla Bay (48^{o} 27' to 48^{o} 35' N, 122^{o} 28' to 122^{o} 34' W; Figure 1) is an extremely shallow bay located in Skagit County, Washington. 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). Unlike other Puget Sound estuaries, Padilla Bay lacks a single, large source of fresh water (i.e., a river). Instead, freshwater comes from small agricultural sloughs and the nearby Skagit River and Samish River estuaries. To the west, the bay is bisected by the Swinomish Channel, a dredged waterway that connects Padilla Bay to Skagit Bay in the south. The Swinomish Channel also represents the western boundary of the Padilla Bay National Estuarine Research Reserve, which encompasses approximately 45 km^2 of submerged and coastal habitat. The eelgrass habitats serve as important nurseries for young fish (Jeffrey 1976) and spawning substrates for Pacific herring (Penttila 2007). Other forage fish species, including surf smelt (*Hypomesus pretiosus*) and Pacific sand lance, spawn on beaches around the bay (Penttila 2007). During the summer, shiner perch, threespine stickleback, snake prickleback, and bay pipefish (*Syngnathus leptorhynchus*) are the most abundant fish species (Penaluna 2006).

At low tide, almost the entire bay is emptied, revealing an expansive network of mudflats and shallow tidal channels. Harbor seals haul out along the edges of these channels and are therefore only present at low water. I collected scat samples from two southern haul-out sites, East Swinomish (48^{o} 28.93'N, 122^{o} 30.97'W) and West Swinomish (48^{o} 29.09'N, 122^{o} 32.22'W). These sites were selected to maximize the potential for scat deposition,

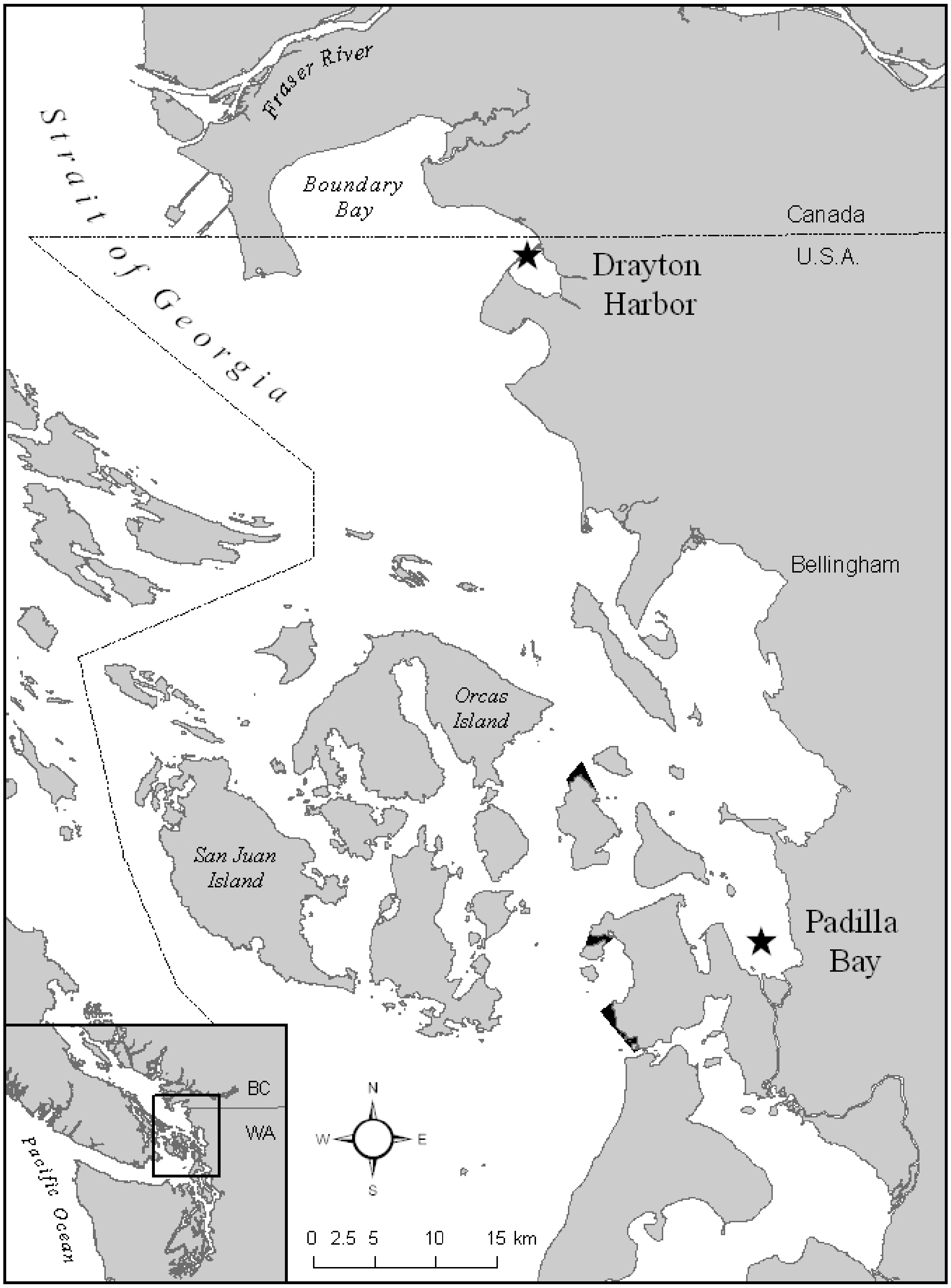

Figure 1. Map of northern Puget Sound. Harbor seal scats were collected from haul-out sites in Padilla Bay and Drayton Harbor (indicated by a star). Candidate marine reserve sites recommended by the Skagit County Marine Resources Committee are shown in black boxes (Weispfenning 2006).

based on haul-out site abundance estimates (Jeffries *et al.* 2000; Banks 2007), and for the ease with which they could be reached for collection activities.

Padilla Bay is an ideal site for describing the spatial variation of harbor seal diet in relation to marine reserves. The bay is close to the candidate marine reserve sites (Figure 1), as well as rocky, non-estuarine habitats where seal diet has been studied by WDFW (Lance and Jeffries 2007). Thus, my data will assist in providing a more complete description of harbor seal diet in Skagit County and be applicable to the Skagit MRC's efforts to restore rocky reef bottomfish. For instance, if rocky reef bottomfish, or other species that associate with rocky habitat and deep water, appear in seal diet, one could safely assume that seals in the region – regardless of whether their haul-out site is rocky or estuarine – may exploit prey in candidate marine reserves.

Drayton Harbor

Drayton Harbor (48° 58' to 49° 0' N, 122° 44' to 122° 48' W; Figure 1) is a 6.5-km^2 estuary located just south of the United States-Canada border. The bay is sheltered by Semiahmoo Spit, which separates it from Boundary Bay. Like Padilla Bay, Drayton Harbor is an intertidal estuary that includes large eelgrass meadows; however, to my knowledge there are no estimates of the area covered by eelgrass within or adjacent to the bay. Dakota Creek and California Creek are the primary freshwater inputs for the estuary. Steelhead return to Dakota Creek to spawn between February and June; chum salmon (*O. keta*) and coho salmon (*O. kisutch*) have been reported in Dakota and California creeks during October – January (WDFW 2002). Chinook salmon and sea-run cutthroat trout (*O. clarki*) may also spawn here (Whatcom County 2003). In addition, steelhead, coho, chinook, chum, and pink

(*O. gorbuscha*) salmon spawn in rivers that drain into the Boundary Bay estuary. Drayton Harbor is a documented spawning area for Pacific herring (January – April), surf smelt (year-round), and Pacific sand lance (WDFW 1997; Penttila 2007), and these species also spawn in Boundary Bay (de Graaf 2007; Hay and McCarter 2007).

I collected scat samples from the floating breakwater that surrounds Semiahmoo Marina at the east end of Semiahmoo Spit (48^{o} 59.11' N, 122^{o} 46.42' W). In the summer, the haul-out site is utilized by up to 200 harbor seals, including females and their pups (Patterson and Acevedo-Gutiérrez 2008). This haul-out site was desirable for this study because it is a reliable source of scats. Unlike Padilla Bay, the haul-out site is available at all tide levels, providing unlimited time for seals to deposit scats without risk of them being washed away before they can be collected. There was also the opportunity to examine between-year variation in harbor seal diet because scat samples were collected from this haul-out site in 1992 (WDFW unpublished data).

METHODS

There are various approaches to investigating pinniped diet including: direct observation (Bowen *et al.* 2002); identification of hard prey parts from stomach contents, regurgitates, or fecal samples (Scheffer and Sperry 1931; Hume *et al.* 2004; Orr *et al.* 2004); stable isotope analysis of blubber (Iverson *et al.* 2004); and genetic analyses of prey remains or the fecal matrix (Deagle *et al.* 2005; Kvitrud *et al.* 2005). Analysis of hard parts from fecal samples was selected for this study because scat collection is minimally intrusive to harbor seals, scats are readily available at haul-out sites, and numerous samples can be collected in a relatively short period of time (Lance *et al.* 2001; Orr *et al.* 2004). For sample collection, processing, and prey identification methods, I followed the protocol described by Lance *et al.* (2001).

Sample collection

Scat sample collection was attempted during two seasons in 2006: pre-pupping (late March through June) and pupping (July through September). Pupping season was determined by the onset of harbor seal pupping in this region (Huber *et al.* 2001), although some pups appeared in Drayton Harbor in June (Patterson and Acevedo-Gutiérrez 2008). Harbor seals are thought to mate shortly after lactation (Thompson 1988), approximately 4 – 6 weeks after females give birth to pups (Bigg 1973; Newby 1973), and molt soon after mating (Bigg 1981; Huber *et al.* 2001). Thus, pupping season also included these other life history phases. For each study area, I attempted to collect at least 100 scats per season (Trites and Joy 2005).

Padilla Bay

Scat collection trips were conducted from 30 March to 7 September 2006 in Padilla Bay. The length of the sample period was determined by the first and last low, daytime tides of the year. Trips were attempted every 10 – 14 days during tidal "windows", or periods of consecutive days with daytime negative low tides. Late-July and late-September sampling trips were eliminated to avoid disturbing seals during peaks in pupping and molting. Within a tidal window, I planned trips on days with the lowest tides occurring during daylight hours, with a maximum of three trips per tidal window. The shallow channels and unstable substrate in Padilla Bay made it necessary to use a kayak to reach my study sites. As a consequence, collection trips were further restricted to days with wind speeds less than 10 knots.

The timing of a trip within a day was based on the tide so that a site was reached at or soon after low tide, and after the predicted peak in hauled-out seals (Hayward *et al.* 2005). In theory, this not only maximized the number of harbor seals that had utilized the haul-out site, but also maximized the amount of time available for seals to deposit scat. Due to the timing of collection trips, however, only one haul-out site could be visited per trip. In 2005, the highest average counts of non-pup (subadult and adult) seals were recorded in April and August at East Swinomish and West Swinomish, respectively (Banks 2007). Thus, collection efforts tended to be focused on East Swinomish during pre-pupping season and West Swinomish during pupping season. Samples were pooled for diet analyses because the two haul-out sites are relatively close to one another (within 2.2 km) and surrounded by similar habitats (e.g., sandy/muddy substrate, eelgrass). Additionally, fish communities within eelgrass beds in Padilla Bay do not differ spatially (Penaluna 2006), therefore prey availability was likely similar near the haul-out sites.

Prior to collection, I recorded the numbers of pup and non-pup seals present at the haul-out sites. Scats were collected with spoons, tongue depressors, and putty knives and placed in Reaves® 124 μm nylon mesh paint strainers (Orr *et al.* 2003). Whenever possible, I collected all scats present at the haul-out sites. On some collection trips to West Swinomish, very small quantities of fecal matter were found scattered across the beach. It is unknown how scats could have been spread out in this way, although large waves created by boats traveling in Swinomish Channel may have been involved; indeed, on one trip, one scat was found floating in the water. To avoid over-estimating my sample size, "mini scats" that were within 1 m of one another and had similar color and texture were collected as a single sample. Samples were immediately returned to the lab, gently rinsed, placed in 1 gallon Ziploc® bags, and stored frozen.

Drayton Harbor

Collection trips to Drayton Harbor were attempted up to four times per month (one trip per week) from 2 May to 30 September 2006. To prevent disturbance to hauled-out individuals, I conducted most collection trips at night after all seals had left the marina breakwater, or avoided sections of the breakwater where seals were hauled out. Collection trips were also constrained by the availability of a boat for transportation to and from the breakwater.

Scats were collected with spoons, tongue depressors, and putty knives and placed in Whirl-pak® sample bags (May – June) or Reaves® 124 μm mesh nylon bags (July –

September). Since this site is available regardless of tidal height, scats tended to accumulate over time. To minimize the amount of time between scat deposition and collection, I 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 samples were returned to the lab and stored frozen.

Sample processing

To separate prey parts from unwanted fecal materials, all samples were rinsed through a series of nested mesh sieves: 2.0 mm, 1.0 mm, and 0.71 mm (Riemer and Mikus 2006; Lance and Jeffries 2007). As an additional means of removing organic matter, those samples collected in mesh bags were first processed in a washing machine on a "gentle" cycle (Orr *et al.* 2003). Padilla Bay samples were generally small and contained little fecal matter, so although they were collected in mesh bags, they were not placed in the washing machine. Prey remains, including fish otoliths and skeletal bones, cartilaginous parts of elasmobranchs and lampreys (family Petromyzontidae), and cephalopod beaks, were recovered from the sieves using forceps. Other invertebrate remains were discarded as it was impossible to determine whether they were primary or secondary prey species (Orr *et al.* 2004). I also retained mammal and bird structures, although these organisms are not typically consumed by harbor seals (but see MacKenzie 2000; Tallman and Sullivan 2004). Prey remains were stored in glass vials with a 70% isopropyl alcohol solution (Browne *et al.* 2002). After approximately two weeks, the alcohol was poured off and samples were dried in a drying oven on the lowest setting. Cephalopod beaks were placed in separate vials prior to drying and stored in alcohol to prevent distortion (Lance *et al.* 2001).

Prey identification and analysis

To ensure accurate identification of prey remains, I was trained by personnel with extensive experience in fish bone identification at Pacific Identifications Inc., Victoria, BC, Canada. Identifications of all structures in thirty samples (15% of all samples) were verified by Pacific Identifications using an extensive reference collection at the University of Victoria; other identifications from approximately 45 samples were verified as needed. Prey remains were examined under a dissecting microscope and identified to the lowest possible taxonomic level using published bone and otolith identification keys (Morrow 1979; Cannon 1987; Harvey *et al.* 2000; Lance *et al.* 2001) and the comparative reference collection at the National Marine Mammal Laboratory in Seattle, Washington. I identified mammal fragments by comparing their texture to mammal structures confirmed by Pacific Identifications. It is possible that fragments of bird bones could have been mistaken for mammal, although this was likely an uncommon occurrence. All fish and cephalopod identifications were assigned a two-digit code to reflect the confidence of the identification to the family level (first digit) and to genus and species (second digit; Table 1). Within a sample, I did not report structures that were identified to both the species level (e.g., Pacific staghorn sculpin) and family level (unidentified sculpin) unless they were obviously different from one another (e.g., different otoliths). 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). "Unidentified fish"

Table 1. Prey identification confidence codes and their corresponding levels of identification. The first digit of the code expresses confidence in the identification of the family; the second digit refers to genus and species. Modified from Lernau (1996) and S. Crockford (personal communication[1]).

Code	Confidence description	Identification level
22	100% certain to species	Species
21	100% certain to family; similar to genus/species	Family
20	100% certain to family only; genus/species tentative	Family
18	Identification certain to a group of families	Subclass, Class, or Order
10	Identification tentative to family	Unidentified fish
00	n/a	Mammal or Bird

[1] Dr. Susan Crockford; Pacific Identifications Inc.; 6011 Oldfield Road R.R. #3, Victoria, BC Canada V9E 2J4; 19 March 2007

hard parts either belonged to species that were not represented in the reference collections, or were too eroded or indistinctive, and thus could not be identified. Therefore, this category probably included prey species that had been identified in other samples, as well as unique taxa. Taxonomic groups described in this study were based on the Integrated Taxonomic Information System online database (2008) and FishBase (2008).

Whenever possible, I noted the presence of structures from juvenile prey, which I determined either by comparing the structures to reference specimens with known lengths or by examining the relative size differences of structures within and between samples. Only juvenile and adult salmonids were entered as separate taxa because the size (age) classes behave very differently; adults pass through estuaries on their way to spawn in natal streams, while juveniles use estuaries as they transition to life in saltwater (Wydoski and Whitney 2003). Additionally, I used three terms to characterize the habitat preferences of fish taxa: 1) “demersal”, or fish that live and feed on or near the sea-bed, 2) “benthopelagic”, or fish that live and feed on or near the sea-bed as well as within the water column, and 3) “pelagic”, or fish that live and feed in open water. Fish taxa were assigned to these categories based on information available on the FishBase website (2008). All non-fish taxa (e.g., unidentified bird) and taxa that include fish species with different habitat preferences (e.g., unidentified gadid) were assigned to an “other” category.

Prey identifications were entered in an Access database and exported to an Excel spreadsheet for analysis. To describe diet composition, I calculated percent frequency of occurrence (% FO). This measurement expresses the percentage of samples that contain a particular species:

$$\%FO_i = \frac{\sum_{k=1}^{s} O_{ik}}{n} \text{ x } 100$$

where O_{ik} = 0 if taxon i is absent in scat k
1 if taxon i is present in scat k
n = total number of fecal samples that contained prey

Percent frequency of occurrence is useful for discerning which prey taxa are commonly and rarely consumed, but does not provide information about the quantity (e.g., number, biomass) of prey consumed (Lance *et al.* 2001). Despite this disadvantage, it is a widely-used index of pinniped diet composition, and has been used to describe the food habits of seals and sea lions in many regions of the world, including Washington and Oregon (Gales *et al.* 1993; Berg *et al.* 2002; Hall-Aspland and Rogers 2004; Lance and Jeffries 2007; Trites *et al.* 2007; Wright *et al.* 2007). I described the diversity of harbor seal diet relative to site and season by calculating the mean number of taxa per scat sample (Lance and Jeffries 2007). I tested for differences in diet diversity between seasons and between estuaries by using a Kruskal-Wallis rank sum test (Zar 1996).

To estimate temporal and spatial variation in diet composition, I used contingency table analyses (Pearson χ^2) to compare the number of occurrences of prey taxa. Due to small sample sizes, analyses were limited to the most frequently occurring (“top”) prey taxa. I defined the top prey as taxa that occurred in more than 25% of samples from a given season, year, or site. Samples collected in Drayton Harbor were used for seasonal comparisons. Between-year comparisons of diet were based on the top taxa in samples collected from Drayton Harbor during June – September 1992 (WDFW unpublished data) and 2006. To compare top prey between estuaries, I used samples collected from Padilla Bay and Drayton

Harbor during pupping season. Samples collected July – August 2006 were used for comparison between estuarine (Padilla Bay and Drayton Harbor) and non-estuarine (San Juan Islands; Lance and Jeffries 2007) diets. For all comparisons, expected values were proportional to sample size to account for differences in the number of samples collected in each season, year, and site. To compensate for multiple comparisons, I adjusted alpha (α) for each taxon using a Bonferroni correction (Zar 1996).

RESULTS

Diet composition

Padilla Bay

I collected a total of 44 scats in Padilla Bay (Appendix 1). No samples were found at the haul-out sites during pre-pupping season. All scats collected during pupping season contained identifiable remains of ray-finned fishes; no evidence of cephalopods, cartilaginous fish, or other vertebrates was found (Table 2). Samples contained 4.0 ± 1.68 prey taxa (mean ± SD) and no samples had more than eight taxa. Overall, 21 prey taxa, representing at least 15 taxonomic families, were identified.

The taxa that were most frequently consumed by seals were gunnel (family Pholidae; 88.6%), snake prickleback (59.1%), Pacific staghorn sculpin (50.0%), and shiner perch (47.7%). Threespine stickleback and bay pipefish, which are abundant in Padilla Bay during the summer (Penaluna 2006), occurred in 18.2% and 4.5% of samples, respectively. Remains of juvenile salmonids were found in two samples. Demersal (90.9%) and benthopelagic (86.4%) taxa were most common in Padilla Bay diet, and pelagic prey were occasionally consumed (Figure 2).

Drayton Harbor

Collection trips in Drayton Harbor yielded a total 154 scats (Appendix 1). All scats collected during pre-pupping (n = 35) and pupping (n = 119) seasons contained identifiable prey remains (Table 3). Ray-finned fish taxa were found in all samples; mammal (56.5%), lamprey (7.8%), cephalopod (6.5%), elasmobranch (5.2%), and bird (0.6%) remains were

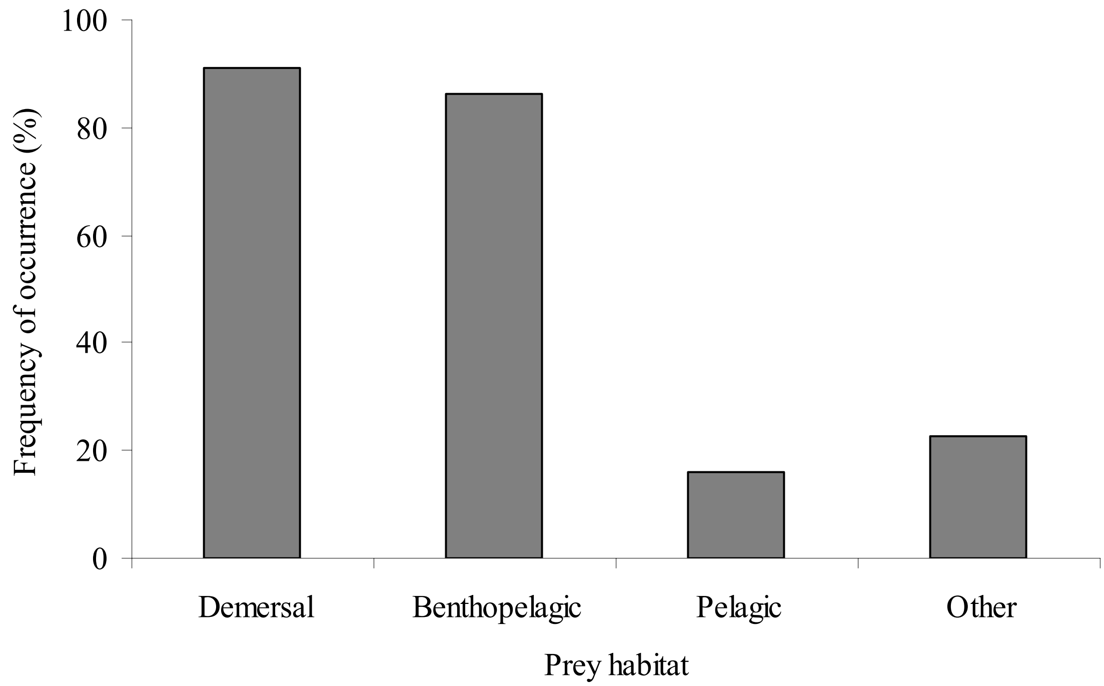

Figure 2. The frequency of occurrence of demersal, benthopelagic, and pelagic prey taxa in harbor seal scats from Padilla Bay. See Methods for definitions of prey habitats. Habitat preferences of prey taxa are provided in Appendix 2.

also present. Approximately 40 prey taxa, from at least 26 taxonomic families, were identified in samples collected from Drayton Harbor.

Pre-pupping season (May – June). On average, pre-pupping season samples contained 6.1 ± 2.82 prey taxa, although some had as many as thirteen taxa. Threespine stickleback (88.6%), Pacific herring (68.6%), and goby (family Gobiidae; 45.7%) were the most frequently consumed prey taxa (Table 3). Mammal remains were found in 42.9% of samples. One structure was tentatively identified as American mink (*Mustela vison*), but most of the remains were too fragmented and eroded to be identified to species. Their size and texture were consistent with juvenile small mammals (S. Campbell, personal communication[2]). Flatfish, plainfin midshipman, shiner perch, gunnel, adult salmonid, and smelt (family Osmeridae) were also common prey, each occurring in > 25% of samples. Remains of rockfish (probably adults) were found in eight samples (22.9%). Juvenile Pacific herring and shiner perch were present, but with low (< 10%) frequency (K. Luxa, unpublished data). Prey that prefer benthopelagic habitats (e.g., threespine stickleback) occurred in nearly all samples (97.1%), although demersal (85.7%) and pelagic (71.4%) taxa were also quite common (Figure 3). Approximately half of pre-pupping season samples contained prey in the "other" habitat category (e.g., mammal).

Pupping season (July – September). Pupping season samples contained 9.3 ± 2.99 prey taxa. No samples had fewer than two taxa and one sample contained eighteen taxa. Threespine stickleback, Pacific herring, shiner perch, snake prickleback, Pacific staghorn sculpin, and mammal were the most frequently consumed prey, all occurring in at least 60% of samples (Table 3). Other common prey included flatfish (50.4%), Pacific sand lance

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[2] Dr. Sarah Campbell; Department of Anthropology, Western Washington University; 516 High Street; Bellingham, WA 98225; 16 April 2008.

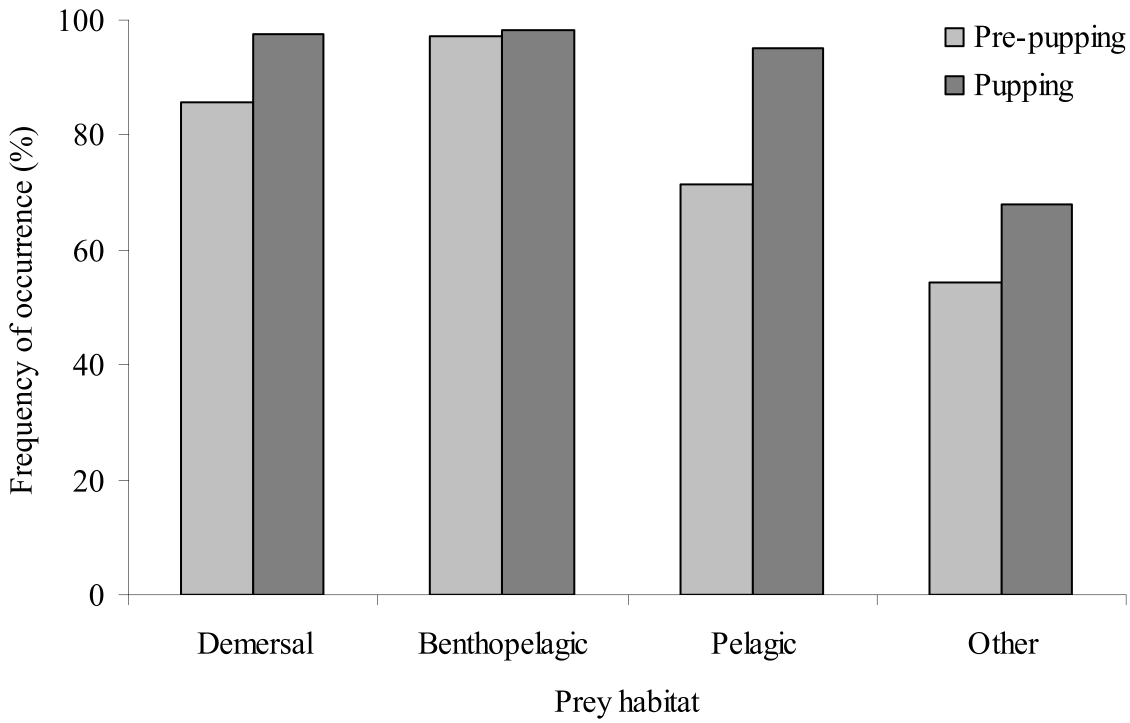

Figure 3. The frequency of occurrence of demersal, benthopelagic, and pelagic prey taxa in harbor seal scats collected from Drayton Harbor relative to season. See Methods for definitions of prey habitats. Habitat preferences of prey taxa are provided in Appendix 2.

(49.6%), adult salmonid (47.1%), smelt (42.9%), juvenile salmonid (36.1%), northern anchovy (35.3%), goby (29.4%), and plainfin midshipman (26.1%). More than 86% of samples contained juvenile prey, such as snake prickleback, shiner perch, and flatfish; however, juvenile Pacific herring were found most often (71.4%; K. Luxa, unpublished data). Rockfish remains were found in 10 samples (8.4%; Table 3); 30% of those occurrences appeared to be juveniles (K. Luxa, unpublished data). Overall, demersal, benthopelagic, and pelagic prey had similar frequencies of occurrence, and a very high proportion of samples contained prey in each of these three habitat preference categories (Figure 3). Prey that prefer other habitats occurred in approximately 68% of samples.

Temporal variation in seal diet: Drayton Harbor

Seasonal variation

Fifteen prey taxa occurred in more than 25% of samples from at least one season in Drayton Harbor (Figure 4; Appendix 4). Frequencies of occurrence of all fifteen top (> 25% FO) taxa were higher during pupping season than pre-pupping season. Of these, shiner perch, northern anchovy, Pacific staghorn sculpin, and snake prickleback were found in significantly more pupping season than pre-pupping season samples. Frequencies of occurrence of these species increased by approximately 3 – 4 times, except for Pacific staghorn sculpin which increased by eight times. Diet diversity was also significantly higher during pupping season than pre-pupping season (Kruskal-Wallis $\chi^2 = 27.53$, df = 1, $p < 0.001$).

Between-year variation

Thirteen prey taxa occurred in more than 25% of samples from at least one year in Drayton Harbor (Figure 5; Appendix 5). Frequencies of occurrence of all thirteen top taxa were higher during 2006 than 1992, and eight taxa occurred in significantly more samples from 2006 than 1992. Pacific sand lance, northern anchovy, goby, and mammal occurred in 30.2% – 61.2% of samples from 2006, but were absent from 1992 samples. Of the taxa that were consumed in both years, occurrences of salmonids (adults and juveniles), Pacific herring, and shiner perch increased the most between the 1992 and 2006.

Spatial variation in seal diet: estuaries and non-estuaries

Drayton Harbor and Padilla Bay

Fifteen prey taxa occurred in more than 25% of samples from at least one estuary during pupping season (Figure 6; Appendix 6). Only three of these taxa (shiner perch, snake prickleback, and Pacific staghorn sculpin) 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. Of these, nine taxa were consumed significantly more often in Drayton Harbor, and one taxon (gunnel) occurred in significantly more Padilla Bay samples. Northern anchovy, goby, mammal, and adult salmonid were only found in the diet of 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 pupping season, harbor seal diet in Drayton Harbor was significantly more diverse than in Padilla Bay (Kruskal-Wallis $\chi^2 = 73.88$, df = 1, $p < 0.001$).

Estuaries and non-estuaries

Twelve prey taxa occurred in more than 25% of samples from at least one habitat (Figure 7; Appendix 7). Just two of these, Pacific herring and adult salmonids, were top prey in both habitats. All top taxa differed significantly between estuarine and non-estuarine habitats. Gadiform fishes (gadids and Pacific hake) and adult salmonids were more common in the diet of seals in the San Juan Islands; all other taxa were consumed more frequently by seals from Padilla Bay and Drayton Harbor. Snake prickleback and mammal were not reported in non-estuarine diet. Diet diversity could not be statistically compared between habitats; however, samples from non-estuarine haul-out sites contained an average of 2.20 prey taxa (Lance and Jeffries 2007), while estuarine samples had 7.6 ± 3.69 prey taxa.

DISCUSSION

Analysis of hard parts in harbor seal scats from two estuaries in northern Puget Sound facilitated the identification of cephalopod, fish, bird, and mammal remains, representing at least 26 taxonomic families. In Padilla Bay, the most common prey taxa in harbor seal diet, in decreasing order, were gunnel, snake prickleback, Pacific staghorn sculpin, and shiner perch. Threespine stickleback and Pacific herring were the most frequently consumed prey in Drayton Harbor during pre-pupping and pupping seasons, and shiner perch, snake prickleback, Pacific staghorn sculpin, mammal, flatfish, Pacific sand lance, adult salmonid, goby, smelt, juvenile salmonid, northern anchovy, plainfin midshipman, and gunnel also each occurred in more than 25% of samples from at least one season. For both Padilla Bay and Drayton Harbor, the majority of samples were composed of demersal (e.g., Pacific staghorn sculpin) and benthopelagic (e.g., threespine stickleback) taxa; in Drayton Harbor, more than 70% of samples also contained pelagic prey (e.g., Pacific herring).

Occurrences of top (> 25% FO) prey taxa in harbor seal diet varied by season, year, and site. Top prey, including shiner perch, threespine stickleback, and Pacific herring were generally more common in samples collected from Drayton Harbor during pupping season in 2006. Diversity (taxa/sample) of Drayton Harbor pupping season diet was also significantly higher than pre-pupping season and Padilla Bay diets. All top prey taxa differed significantly between estuarine and non-estuarine haul-out sites. With the exception of gadiforms (gadids and Pacific hake) and adult salmonids, top prey taxa were more frequently consumed by harbor seals in Drayton Harbor and Padilla Bay than in the San Juan Islands (Lance and Jeffries 2007).

Diet composition in estuaries

The 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 diversities (average prey taxa per sample) in this study are among the highest for harbor seals in any habitat (Olesiuk *et al.* 1990; Thompson *et al.* 1991; Bowen and Harrison 1996; Tollit and Thompson 1996; Andersen *et al.* 2004; Orr *et al.* 2004; Lance and Jeffries 2006). Pupping season samples from Drayton Harbor contained an average of 9.3 ± 2.99 prey taxa, and one sample included remains from 18 different taxa. In contrast, scat samples collected from rocky haul-out sites in the San Juan Islands contained one to three taxa and occasionally had as many as nine taxa (Lance and Jeffries 2007). The high diet diversity measured in Padilla Bay and Drayton Harbor may be a reflection of high productivity near the haul-out sites. Estuaries are some of the most productive ecosystems on earth, and they play critical roles as spawning grounds and nurseries for fish (Correll 1978). Eelgrass habitats, in particular, support high levels of biodiversity and fish abundance (Bayer 1981; Murphy *et al.* 2000).

Diet composition suggests that harbor seals in Padilla Bay and Drayton Harbor foraged primarily within soft-bottomed, estuarine habitats, such as those found near the haul-out sites. Gunnel species, which occurred in 88.6% of samples from Padilla Bay, prefer habitats with sandy or muddy substrate and dense eelgrass beds (Eschmeyer *et al.* 1983; Lamb and Edgell 1986). Shiner perch and snake prickleback were important prey in both Padilla Bay and Drayton Harbor, and are two of the most abundant fish species in Padilla Bay during the summer (Penaluna 2006). Indeed, all of the top prey taxa in seal diet, as well as many others that were consumed less frequently (e.g., pile perch, *Rhacochilus vacca*), commonly occur in estuaries in Puget Sound (Fresh 1979; Lamb and Edgell 1986; Wydoski and Whitney 2003; Penttila 2007). These results are consistent with previous studies indicating that harbor seals prey on locally abundant populations (Härkönen 1987; Thompson *et al.* 1991; Tollit *et al.* 1997; Wilson *et al.* 2002).

The foraging activities of harbor seals may have been concentrated in the estuaries during the study period (summer) because of major life history phases that take place during that season. The haul-out sites in Padilla Bay and Drayton Harbor are used as nurseries for harbor seal pups (Jeffries *et al.* 2000; Patterson and Acevedo-Gutiérrez 2008). Due to their small body size, female harbor seals must forage during lactation (Boness *et al.* 1994; Thompson *et al.* 1994). Foraging dives typically commence during mid- to late-lactation (Boness *et al.* 1994; Bowen *et al.* 1999). At this time, foraging ranges of females are likely restricted to habitats near their haul-out site. In a study in the Moray Firth, Scotland, females with pups were found within 2 km of haul-out sites on each day of the study period (Thompson *et al.* 1994). Later in the summer, as pups are weaned and females come into estrus, male harbor seals reduce their foraging effort and remain closer to haul-out sites to attract females (Van Parijs *et al.* 1997; Boness *et al.* 2006). Finally, harbor seals spend more time ashore during the molting period (Thompson 1989; Frost *et al.* 2001; Huber *et al.* 2001; Banks 2007), and are less likely to make long foraging excursions. If foraging ranges during the summer months are smaller than in other months, it is possible that the diet of seals in Padilla Bay and Drayton Harbor will differ at other times of the year.

Harbor seals in Drayton Harbor may have occasionally foraged in non-estuarine habitats. Remains of northern pikeminnow (*Ptychocheilus oregonensis*), a freshwater fish, appeared in 6 samples (5.0%) during pupping season. This species inhabits lakes and streams in Washington (Wydoski and Whitney 2003), and is the dominant predator of out-migrating salmonids in the Columbia River (Knutsen and Ward 1999). Harbor seals may have entered freshwater to feed on salmonids, much like seals in other regions (London *et al.* 2001; Middlemas *et al.* 2006; Wright *et al.* 2007), and incidentally encountered northern pikeminnow. Indeed, samples with northern pikeminnow also contained juvenile salmonid, adult salmonid, or both. While in freshwater, Drayton Harbor seals may have also consumed other anadromous species (e.g., American shad, *Alosa sapidissima*, river lamprey, *Lampetra ayresii*) or species that regularly move between marine and freshwater environments (e.g., Pacific staghorn sculpin, threespine stickleback; Eschmeyer *et al.* 1983; Wydoski and Whitney 2003).

Rockfish prefer rocky reefs and other complex, hard-substrate habitats, yet they were found in 8.4% – 22.9% of samples from Drayton Harbor. Harbor seals at other estuarine haul-out sites in Washington (Jeffries 1984; Browne *et al.* 2002), British Columbia (Olesiuk *et al.* 1990), and Oregon (Brown and Mate 1983; Orr *et al.* 2004; Wright *et al.* 2007) also consume rockfish, so rockfish predation is not unique to seals in Drayton Harbor. However, the average frequency of occurrence of rockfish in Drayton Harbor diet (11.7%) was higher than in the spring and summer/fall diets of seals in the San Juan Islands (6.2%; Lance and Jeffries 2007). There are several potential explanations for the occurrence of rockfish in Drayton Harbor diet. First, rockfish could have been present in the estuarine habitats around the haul-out site. Juveniles of several rockfish species (e.g., copper rockfish, black rockfish, *S. melanops*) settle in estuaries or eelgrass beds (Murphy *et al.* 2000; Love *et al.* 2002; Gallagher 2007), and adults will occasionally enter shallow, soft-bottomed habitats during the summer (Matthews 1990b). Most of the rockfish structures recovered from harbor seal scats appeared to be from adults, although three pupping season samples contained juveniles only (K. Luxa, unpublished data). Another possibility is that harbor seals sometimes foraged in nearby rocky, non-estuarine habitats; for example, off Point Roberts, approximately 20 km from the haul-out site (Appendix 8). Little is known about the distribution of rockfish near Point Roberts, but the bathymetry in this region suggests that high-relief substrata, which are preferred by some rockfish species (Love *et al.* 2002), may be available. It is also possible that harbor seals traveled to more distant (over 25 km away) rocky habitats in the San Juan Islands or Canadian Gulf Islands. Similar long-distance movements by seals have been observed in the Moray Firth (Thompson and Miller 1990; Tollit and Thompson 1996; Thompson *et al.* 1998; Tollit *et al.* 1998), the San Juan Islands (Suryan and Harvey 1998; Hardee 2008), and other regions (Lowry *et al.* 2001; Nickel 2003). Alternatively, seals that typically used haul-out sites and foraged in rocky, non-estuarine habitats (like Point Roberts or the San Juan Islands) may have intermittently rested and deposited scat at the haul-out site in Drayton Harbor. Of these scenarios, it seems least likely that the rockfish were consumed in habitats that are far away from Drayton Harbor. If seals consumed prey at more distant locations, remains from those meals were less likely to be deposited at the haul-out site. Long-distance foraging trips may last several days (Thompson and Miller 1990; Thompson *et al.* 1998; Nickel 2003), but most prey remains are evacuated from the seals' body after 24 – 48 hours (Harvey 1989; Deagle *et al.* 2005; Phillips 2005). Additionally, remains of medium- and large-sized (i.e., adult) rockfish were consistently found in river otter scats collected at Semiahmoo Marina (K. Luxa, unpublished data). River otter home ranges vary between 10 and 40 km of shoreline (Bowyer *et al.* 1995; Blundell *et al.* 2000; Bowyer *et al.* 2003), and frequent foraging trips to distant rocky habitats may be unfeasible. Analysis of harbor seal movements or rockfish surveys may help to elucidate the non-estuarine foraging habitats of seals in this region.

The majority of samples collected from Padilla Bay and Drayton Harbor contained demersal and benthopelagic prey. Similar trends have been observed in the diet composition and diving behavior of harbor seals in other regions (Brown and Mate 1983; Bjørge *et al.* 1995; Tollit *et al.* 1998; Andersen *et al.* 2004). At Sable Island, Nova Scotia, adult male harbor seals use two foraging strategies when searching for demersal prey in a sandy habitat (Bowen *et al.* 2002). Most males use a tactic called "cruising": swimming approximately 1 – 2 m above the sea-bed, they catch prey by quickly thrusting their head towards the bottom, or by using their snout to rout in the sediment. Less often, they use one or both of their front flippers to dig through the sand and disturb prey. Given the importance of demersal and benthopelagic prey in their diet, harbor seals in Padilla Bay and Drayton Harbor may have utilized similar demersal foraging strategies.

While seals in both estuaries exploited pelagic prey, they were much more common in Drayton Harbor diet. In that estuary, Pacific herring and northern anchovy were the most frequently consumed pelagic taxa. Presence of pelagic species in harbor seal diet suggests that some foraging activities may have occurred at night because several prey species (e.g., Pacific herring, northern anchovy, Pacific hake, Pacific sardine, *Sardinops sagax*) are more abundant in surface waters (< 25 m) at that time (Krutzikowsky and Emmett 2005). In the San Juan Islands, harbor seal foraging bouts are thought to increase during twilight hours in response to diurnal vertical migrations of Pacific herring and salmonids (Reuland 2008).

The unusually high diet diversity observed in the study estuaries likely resulted from seals using a variety of foraging tactics that enabled them to encounter and capture schooling fish (e.g., Pacific herring, shiner perch), as well as more solitary species (e.g., plainfin midshipman, Pacific sandfish, *Trichodon trichodon*). In addition to searching throughout the water column, seals may have focused their foraging effort near topographic features in the estuaries, such as tidal and shipping channels, where prey may become concentrated by currents or incoming tides (Ries *et al.* 1997; Nickel 2003). Harbor seals foraging in the Wadden Sea repeatedly dove along the edges of shallow (< 5 – 10 m deep) tidal channels (Ries *et al.* 1997). Similarly, in non-estuarine habitats, harbor seals frequently forage in constricted channels between islands or near shoals (Suryan and Harvey 1998; Zamon 2001; Banks 2007). Swinomish Channel (Padilla Bay) or the narrow (< 0.5 km) entrance to Drayton Harbor might concentrate prey in similar ways.

Harbor seal diet diversity was likely affected by the size and energy density of prey taxa. When seals consume small species (e.g., threespine stickleback) and juvenile fish, they must compensate for the size of their prey by eating more individuals or by foraging for longer periods of time. For example, a harbor seal can fulfill its daily energy requirement by consuming a single adult salmonid, but they must consume more than 4×10^3 juvenile Pacific herring (mean wet mass = 2.2 g) to obtain the same amount of energy (Zamon 2001). Many of the fish species consumed by harbor seals in Padilla Bay and Drayton Harbor (e.g., threespine stickleback, shiner perch, goby) tend to be relatively small (< 15 cm in length; FishBase 2008), hence longer foraging bouts may have been necessary to meet their energetic demands. Given the high species diversity of estuaries (Murphy *et al.* 2000), it is reasonable to assume that seals encountered (and consumed) more prey species the longer they foraged.

Gadiform fishes are important prey of harbor seals in estuaries in Washington, Oregon, and British Columbia (Olesiuk *et al.* 1990; London *et al.* 2001; Browne *et al.* 2002; Orr *et al.* 2004), but were rarely consumed by harbor seals in Padilla Bay and Drayton Harbor. Juvenile Pacific hake and Pacific cod settle in shallow bays and estuaries, including eelgrass beds, and young Pacific tomcod (*Microgadus proximus*) and walleye pollock swarm in shallow waters in the summer and fall (Cohen *et al.* 1990; Love 1996; Gustafson *et al.* 2000). Individuals move to deeper water (50 − 500 m) as they get older. Walleye pollock and Pacific tomcod were two of the most abundant species in a bottom trawl survey conducted in northern Puget Sound and the San Juan Islands, but no gadiform species were found near the harbor seal haul-out sites sampled in my study (Palsson *et al.* 2003). Hence, despite the apparent importance of shallow, estuarine environments to juveniles, the lack of gadiforms in seal diet was probably due to their low abundance in shallow habitats near the haul-out sites.

Adult and juvenile salmonids were top prey taxa in Drayton Harbor, where harbor seals have access to important spawning streams. In contrast, salmonid remains were found in just two samples from Padilla Bay. Swinomish Channel is thought to be a migratory pathway for Skagit River salmonids and juveniles may use Padilla Bay for refuge and feeding (Quinn 2005; Grossman *et al.* 2007), but there are no natal streams in Padilla Bay (WDFW 2002). It is unclear why adult salmonids were not found in harbor seal scats from Padilla Bay because several species, including chinook salmon and chum salmon, were likely returning to the Skagit River to spawn during the study period (WDFW 2002). Indeed, adult salmonids were the dominant prey of harbor seals in the San Juan Islands between July and August 2006 (Lance and Jeffries 2007). The distribution and abundance of adult salmonids in Padilla Bay is not currently monitored, and it is possible that few salmonids used Padilla Bay as a migration corridor, decreasing the likelihood that seals would have encountered them while foraging. In 2007, a diurnal pattern in the diving bouts of seals from Padilla Bay suggested that seals foraged on salmonids during pupping season (Reuland 2008). However, it is unknown if this is because salmonids were more abundant in Padilla Bay that year, or because seals foraged at greater distances from their haul-out sites in 2007 than 2006. Juvenile salmonids were not found in surveys conducted in Padilla Bay between December 2003 and July 2004 (Penaluna 2006), although they were observed at low frequencies in earlier studies (Simenstad *et al.* 1988; Micucci 2000 in Penaluna 2006). Few juvenile salmonids may survive the journey from Skagit Bay to refuge habitats in Padilla Bay, due to excessive osmotic (Grossman *et al.* 2007) or thermal stress (Quinn 2005) in Swinomish Channel. Salmonid predation by Padilla Bay seals may vary depending on environmental (e.g., salinity) and temporal (e.g., interannual differences in salmonid abundance) factors.

Numerous studies have described the importance of herring and other clupeids in harbor seal diet (Scheffer and Sperry 1931; Thompson *et al.* 1991; Thompson *et al.* 1996; Iverson *et al.* 1997). Pacific herring was one of the top two prey species for harbor seals in Drayton Harbor, but only occurred in approximately 10% of samples collected during pupping season in Padilla Bay. In Drayton Harbor, seals consumed Pacific herring in all months of the study period. Juvenile herring, possibly young-of-the-year, increased from a single occurrence in pre-pupping season to 71.4% of pupping season samples (K. Luxa, unpublished data). Pacific herring spawn in the Drayton Harbor area between January and June (Stick 2005), prior to pre-pupping and pupping seasons, thus they may also be important harbor seal prey during other times of the year. Abundances of herring stocks near the haul-out site have declined over the last 25 years (Stick 2005). The Cherry Point herring stock was once the largest in Puget Sound, but it is now critically depleted, meaning that the stock's abundance is so low that recruitment failure is likely or has already occurred. Since 2000, Cherry Point herring spawning biomass has increased slightly (Stick 2005), but predation by harbor seals may impede the stocks' recovery (e.g., Trzcinski *et al.* 2006). Future study of harbor seal predation on herring in the Drayton Harbor area may help to determine if predation significantly affects stock abundance. The relative unimportance of Pacific herring in Padilla Bay seal diet is probably due to seasonal variation in availability, as well as decreases in the abundance of the Fidalgo Bay herring stock (Stick 2005; Penaluna 2006). As in Drayton Harbor, it is possible that Pacific herring is a more important prey species for Padilla Bay harbor seals during January – March, when adult herring return to this area to spawn (Stick 2005).

To my knowledge, this study is the first to identify mammals as harbor seal prey. Remains of small mammals, probably juveniles, were found in 42.9% of pre-pupping season samples and 60.5% of pupping season samples. One structure was tentatively identified as a sacrum from a young American mink. Mammals are unusual prey items for harbor seals (D. Tollit, personal communication[3]); I could find no reports of harbor seals attacking mammals or of mammal remains being found in scats or stomach contents, even in trace amounts. Indeed, harbor seals rarely consume vertebrates other than fish (but see MacKenzie 2000; Tallman and Sullivan 2004). Predation on mammals is relatively uncommon among other pinnipeds, although Steller sea lions will consume harbor seals and young California sea

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lions (Byrnes and Hood 1994; Mathews and Pendleton 2006), and some walruses eat seals (Lowry and Fay 1984). Other small aquatic or semi-aquatic mammals that may occur in Drayton Harbor include river otters, muskrats (*Ondatra zibethicus*), raccoons (*Procyon lotor*), and beavers (*Castor canadensis*). Harbor seals consuming mammals may have foraged in any of the tidal streams that flow into Drayton Harbor or nearby estuaries (Appendix 8). Field observations at two of these streams (California and Dakota Creeks) revealed abundant riparian habitat, suggesting that these mammals are likely to be present in the intertidal zone. I considered the possibility that mammal remains were deposited by other predators and accidentally collected with seal scats. To explain the high frequency of occurrence of mammal in scat samples, mammal remains would need to be regularly deposited on the breakwater, and seals would have to consistently deposit scat on top of those remains. Besides harbor seals, the breakwater at Semiahmoo Marina is used by river otters, bald eagles (*Haliaeetus leucocephalus*), and predatory seabirds. I think it is unlikely that the mammal remains were deposited by one of these predators, given that mammals are not a major component of river otter diet (Larsen 1984; Jones 2000; J. Gaydos, personal communication[4]; K. Luxa, unpublished data) or bald eagle diet (Stinson *et al.* 2001) in Puget Sound. Gulls (*Larus* spp.) in coastal regions rarely consume mammals (Vermeer 1982; Kubetzki and Garthe 2003). Thus, the most parsimonious explanation is that some harbor seals in Drayton Harbor took advantage of a novel, locally abundant food resource. Further study is required to determine why this strategy may be preferred by some seals, and whether or not this is common year-round.

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Temporal variation in seal diet: Drayton Harbor

Four top prey taxa (shiner perch, snake prickleback, Pacific staghorn sculpin, and northern anchovy) occurred in significantly more samples in pupping season than pre-pupping season. Increased consumption of these taxa during pupping season coincided with periods of increased availability, such as spawning, seasonal migrations, or the arrival of young-of-the-year fishes in estuaries (Lamb and Edgell 1986; Wydoski and Whitney 2003; Penttila 2007). For example, shiner perch aggregate in shallow bays and estuaries to feed, mate and give birth during the summer (Wydoski and Whitney 2003). Fully-developed young are born primarily in July and August, and the juvenile fish remain in estuaries through the late fall. In Drayton Harbor, the frequency of occurrence of shiner perch in harbor seal samples approximately tripled between pre-pupping and pupping seasons. Remains of juvenile shiner perch were found in a few samples from June, whereas approximately half of all shiner perch occurrences during pupping season included juveniles (K. Luxa, unpublished data). 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 and Thompson 1996; Hall *et al.* 1998; Lance and Jeffries 2006).

Occurrences of eight top prey taxa were significantly higher in 2006 than in 1992, although the reasons for these differences are unclear. In other regions, between-year variation in harbor seal diet is related to changes in prey population abundance (Tollit and Thompson 1996; Brown *et al.* 2001; Wilson *et al.* 2002). In the Moray Firth, extreme variability in the abundance of overwintering clupeids is reflected in harbor seal diet (Thompson *et al.* 1996). In “good” years, when clupeids are abundant, they account for at least 60% of diet, but they are less than 10% of diet during “bad” years. It is possible that abundances of Pacific sand lance, shiner perch, threespine stickleback, northern anchovy, mammal, and goby near Drayton Harbor have increased since 1992, but their populations are not currently monitored. Another possibility is that harbor seals actively selected these taxa in 2006. In Mousa, Shetland, harbor seals apparently use a “mixed diet selection strategy”; that is, they consumed temporally abundant prey, and selected other species (Brown *et al.* 2001). However, estimates of prey abundance in Drayton Harbor would be necessary to make this conclusion.

Despite declines in stock abundance, Pacific herring occurred in significantly more samples in 2006 than in 1992. Reuland (2008) hypothesized that harbor seals near candidate marine reserves in Skagit County may reduce their consumption of Pacific herring and switch to alternate species, such as rockfish, as herring stock abundances continue to decline. In Drayton Harbor, however, the opposite was observed. Semiahmoo Bay and Cherry Point herring stock sizes decreased by more than 50% between 1992 and 2004 (Stick 2005), but the frequency of occurrence of Pacific herring in seal diet was 2.5 times greater in 2006 than in 1992. Salmonids declined over the same time period (WDFW 2002), and were also more frequently consumed in 2006. Harbor seals’ exploitation of Pacific herring and salmonids, even at lower population abundances, suggests that these taxa may be preferred prey of seals in Drayton Harbor.

Temporal differences in harbor seal diet may have been influenced by the size of top prey. As previously discussed, seals that consume small species or juvenile fish must eat more individuals or forage for longer periods of time to fulfill their daily energy requirements. If harbor seals in Drayton Harbor tended to forage on small fish, this might explain why frequencies of occurrence of all top prey taxa were higher in pupping season than pre-pupping season, and higher in 2006 than 1992. Occurrences of juvenile shiner perch and Pacific herring increased between pre-pupping and pupping seasons in 2006, and I also found evidence of juvenile snake prickleback, Pacific sand lance, threespine stickleback, flatfish, and Pacific staghorn sculpin in pupping season samples, but not in pre-pupping samples (K. Luxa, unpublished data). The frequency of occurrence of juvenile fish in samples collected in 1992 is unknown; however, two small prey taxa, Pacific sand lance and goby, did not appear in any samples collected during 1992. Analysis of the number and size of individuals in harbor seal scats would provide further insight into the seasonal and between-year trends observed in Drayton Harbor diet.

Spatial variation in seal diet: estuaries and non-estuaries

Spatial variation in seal diet has been found in previous studies, but typically where seals forage in different habitat types (Härkönen 1987; Payne and Selzer 1989; Olesiuk *et al.* 1990; Bowen and 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 significantly between the estuaries during pupping season. As previously discussed, greater frequencies of Pacific herring and salmonids in Drayton Harbor diet were likely due to differences in prey availability between the estuaries or prey preferences of harbor seals, and predation of mammals appears to be a unique behavior of some seals in Drayton Harbor. 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). Some gunnel species (e.g., saddleback gunnel, *Pholis ornata*) prefer habitats with dense eelgrass beds (Lamb and Edgell 1986), and therefore gunnels may be more abundant and widely distributed in Padilla Bay. Threespine stickleback, goby, flatfish, and plainfin midshipman were more frequently consumed in Drayton Harbor than Padilla Bay, but the reasons for these differences are less apparent. It is unclear if top prey taxa would be more or less similar during other times of the year. Results of these comparisons highlight the importance of considering within-habitat type (e.g., estuary) differences in harbor seal diet when investigating seals' potential impacts on prey populations.

Differences in top prey taxa between the estuaries may have been related to differences in the age and sex structures of the seal populations at the haul-out sites during pupping season. Females with pups were observed at the haul-out sites in both estuaries, but the Padilla Bay sites may be more important as nurseries, and therefore used more exclusively by females with pups (e.g., Johnson and Jeffries 1983; Kovacs *et al.* 1990), than the haul-out site in Drayton Harbor (S. Jeffries, personal communication[5]). Mothers and pups in Drayton Harbor may prefer to haul out on exposed mudflats during low tide (as in Padilla Bay and other northern Puget Sound estuaries; Jeffries *et al.* 2000) instead of the floating breakwater at Semiahmoo Marina, which may be difficult for pups to access. Under this scenario, the haul-out site in Drayton Harbor could have included more subadults and adult males, and since females forage closer to their haul-out site during lactation (Thompson *et al.* 1994), the average foraging range of seals in Padilla Bay may have been smaller than Drayton Harbor. This may also explain why Padilla Bay diet composition described in this

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[5] Steve Jeffries; Washington Department of Fish and Wildlife; 7801 Phillips Road SW, Tacoma, WA 98498; 25 July 2008

study differs so greatly from diet data collected from Eliza Rock and Vendovi Island (Lance and Jeffries 2007). The haul-out sites at Eliza Rock and Vendovi Island are non-estuarine, yet they are frequently visited by seals that were tagged at haul-out sites in Padilla Bay (M. Lance, personal communication[6]). During July and August 2006, scats collected from the two islands mainly included salmonids, clupeids, rockfish, and gadiforms, and the top prey taxa in Padilla Bay diet (gunnel, snake prickleback, Pacific staghorn sculpin, and shiner perch) each occurred in less than 15% of samples (Lance and Jeffries 2007). It is possible that my results for Padilla Bay were biased toward female harbor seals with pups, rather than being representative of the population as a whole; however, to reach such a conclusion would require knowledge of the sexes and ages of seals at the haul-out sites sampled in this study and that of Lance and Jeffries (2007).

All top prey taxa differed significantly between the diets of 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 more than 25% of samples from both habitats, but it was nevertheless more common in estuarine diet than 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 and 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 significantly more samples from the San Juan Islands. Each year, large numbers of adult salmonids pass through that region as they return to their natal streams throughout Washington and British Columbia (Quinn 2005). Predation by harbor seals in estuaries may

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increase once adult salmonids reach begin to 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, unpublished data). Variation in other prey taxa is likely to persist year-round because of differences in prey communities between estuarine and non-estuarine habitats (e.g., Payne and Selzer 1989; Bowen and Harrison 1996). As previously discussed, gadiforms were rarely consumed by seals from Padilla Bay and Drayton Harbor because they tend to be distributed in deeper water. Gadiforms were significantly more common in 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 and 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.

Conclusions

To predict the potential impacts of harbor seals on prey populations, it is important to understand their diet composition and how it varies over time and space. In this study, harbor seals in Padilla Bay and Drayton Harbor foraged primarily in estuarine habitats such as those surrounding their haul-out sites. Overall, their diet included prey from more than two dozen taxonomic families, and diet diversity was among the highest reported for harbor seals in any region.

It is possible that some harbor seals foraged in non-estuarine habitats, as suggested by the presence of a freshwater species and rockfish in the diet of Drayton Harbor seals. Hence, marine reserve site selection might benefit from considering the effects of predation by harbor seals beyond the immediate area. McConnell and Dinnel (2002) estimated the potential impacts of pinniped predation at candidate reserve sites in Skagit County based on the presence or absence of harbor seal haul-out sites. The results of this study suggest that seals from haul-out sites in other habitats may forage in those areas and their potential impact should also be considered. Long-distance foraging trips, coupled with the temporal variation in seal diet observed in Drayton Harbor (driven by changes in prey availability and abundance), may result in increased predation of rockfish after reserves are created.

Similarly, harbor seal predation may impact the recovery of depleted Pacific herring stocks near Drayton Harbor. Enumeration and measurement of Pacific herring otoliths would make it possible to estimate the herring biomass consumed by harbor seals each season. In addition, Cherry Point herring are genetically distinct from other herring stocks in Puget Sound and British Columbia (Stick *et al.* 2005). Hence, genetic analyses could be employed to identify their presence in seal scat samples (e.g., Kvitrud *et al.* 2005).

Rockfish were consumed by harbor seals and river otters in Drayton Harbor, but their distribution and abundance in this region are currently unknown. Year-round diet studies coupled with rocky reef bottomfish surveys and satellite-tracking of seals will reveal the location of foraging areas and assist in determining the potential impact on rockfish stocks. This information would inform the prioritization of potential sites for marine reserves in Whatcom County.

Harbor seals exhibited strong temporal and spatial variation in diet. There were significant differences in prey consumed between pre-pupping and pupping seasons and between 1992 and 2006 in Drayton Harbor. To gain further understanding of temporal variation in the diet of harbor seals at estuarine haul-out sites, it will be necessary to collect scat samples year-round. The haul-out site in Drayton Harbor is ideal for such an analysis because it is available at all tide levels and can be easily accessed for scat collection. In particular, trends in the importance of mammal, Pacific herring, and non-estuarine prey taxa warrant additional investigation. There were also significant differences in prey consumed between Padilla Bay and Drayton Harbor and between haul-out sites in estuarine and non-estuarine habitats. Spatial variations in diet suggest that harbor seals feed on locally abundant prey, thus their food habits should also be described at the numerous estuarine haul-out sites in northern Puget Sound to determine top prey taxa and potential impacts to species of interest to management.

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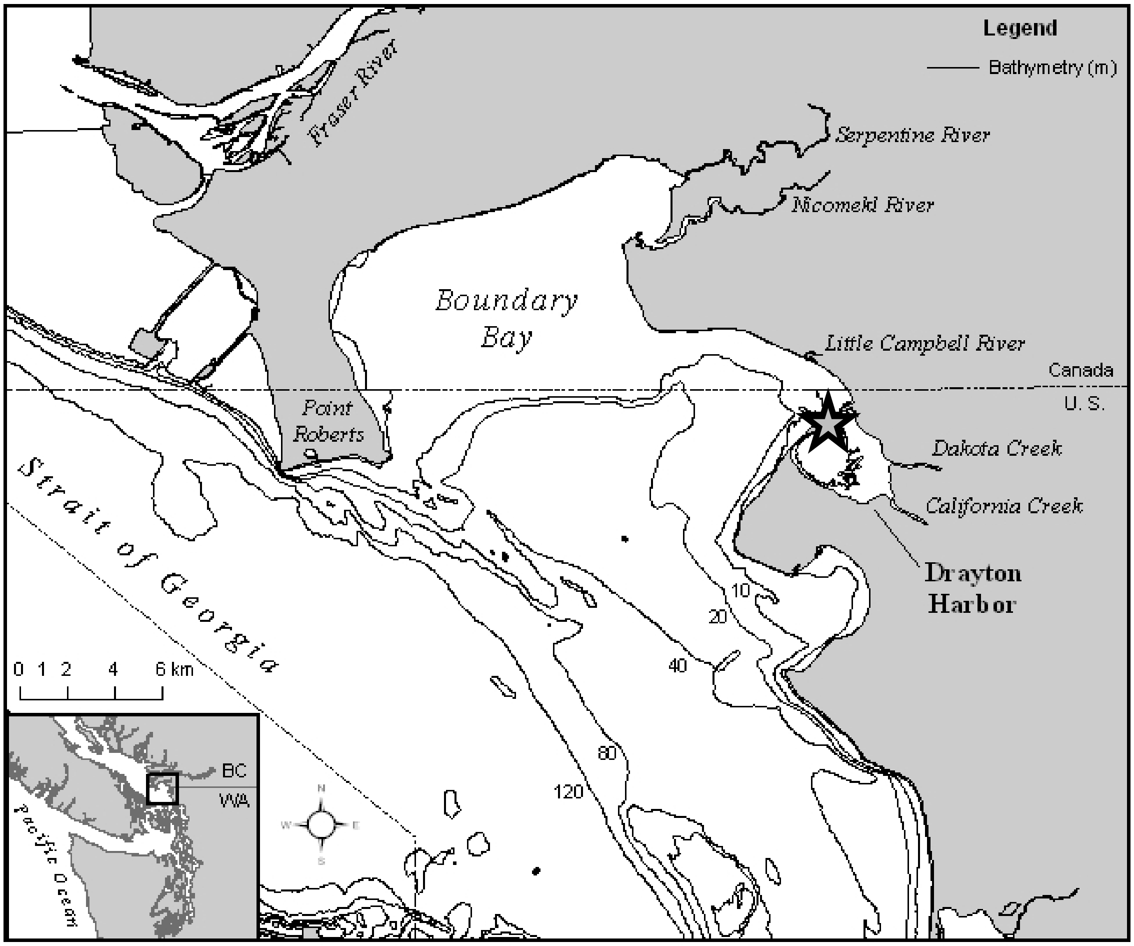
Appendix 3. Prey taxa abbreviations used in figures. Taxa that begin with "all" (e.g., all gadids and Pacific hake) include prey that are identified to the family level and to species (unidentified gadid, walleye pollock, Pacific cod, Pacific tomcod, and Pacific hake). Taxa that begin with "unidentified" (e.g., unidentified goby) include prey that are only identified to the family level.

Abbreviation	Taxon
Ammhex	Pacific sand lance
Clupal	Pacific herring
Cymagg	Shiner perch
Engmor	Northern anchovy
Gadfrm	all gadids and Pacific hake
Gasacu	Threespine stickleback
Gobiid	unidentified goby
Leparm	Pacific staghorn sculpin
Lumsag	Snake prickleback
Mammal	unidentified mammal
Osmer	all smelts
Pholid	unidentified gunnel
Pleuro	all flatfishes
Pornot	Plainfin midshipman
SalmA	all salmonids – adult
SalmJ	all salmonids – juvenile
Salmon	all salmonids – adult and juvenile



Appendix 8. Map of the Drayton Harbor and Boundary Bay estuaries. The harbor seal haul-out site at Semiahmoo Marina (Drayton Harbor) is indicated by a star.