

**THE BEHAVIORAL RESPONSE OF HARBOR SEALS TO
SEASONAL PREY PULSES OF SPAWNING PACIFIC HERRING**

By

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Accepted in Partial Completion
of the Requirements for the Degree
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MASTER'S THESIS

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A Thesis

Presented to

The Faculty of

Western Washington University

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Of the Requirements for the Degree

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ABSTRACT

The Pacific harbor seal (*Phoca vitulina*) is a noteworthy omission from the list of predators that aggregate at herring spawning sites, despite strong suggestive evidence that they are likely to respond to herring pulses. Working with the hypothesis that spawning herring aggregations are seasonally important prey for harbor seals, we tested several predictions using an analysis of harbor seal prey remains, GPS telemetry, and satellite-linked time/depth recorder data. Contrary to predictions, herring in harbor seal diet was comprised of 77% juveniles and 23% adults in the spawn season, versus 33% juveniles and 67% adults in the post-spawn season. Seal diving focus peaked at night during the post-spawn season, and seals exhibited less diving effort during the spawn season. Harbor seals did not however appear to alter their foraging behaviors to take advantage of spawning herring aggregations. The lack of response by harbor seals to spawning herring pulses is likely explained by seasonal differences in adult herring profitability, the availability of alternative prey, or a decline in local herring biomass.

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INTRODUCTION

Resource pulses

A substantial portion of ecological theory is based on observations of ecosystems during periods of resource variability, which often lead to complex trophic dynamics (Odum 1969, Stephens and Krebs 1986, Chesson 1994). Certain large magnitude variations in resource availability, termed resource pulses, are of recent interest due to their previously underestimated ability to influence ecological communities (Ostfeld and Keesing 2000, Holt 2008, Nowlin et al. 2008, Yang et al. 2008). Resource pulses are dramatic increases in resource availability characterized by high intensity, relatively low frequency, and short overall duration (Yang et al. 2008). Common examples of resource pulses include increased plant production as a result of precipitation induced by El Niño Southern-Oscillation (ENSO) events (Lima et al. 1999, Ostfeld and Keesing 2000, Holmgren et al. 2001), mast seeding by plants resulting in a superabundance of seeds for primary consumers (Kelly 1994, Herrera et al. 1998), and the infrequent emergence of large insect populations such as periodical cicadas and locusts (Yang 2004, Sánchez-Zapata 2007).

Resource pulses commonly have bottom-up effects in ecosystems followed by subsequent top-down effects as a result of increased predator abundance (McShea 2000, Ostfeld and Keesing 2000, Schmidt and Ostfeld 2008). For example, the number of songbird nests predated by rodents increases in years following a large oak tree mast seeding event (McShea 2000). The increased nest predation was attributed to an overabundance of rodent predators as a result of the excessive acorn food supply available to rodents in the previous autumn (McShea 2000). This example illustrates a simple and relatively intuitive result of a resource pulse.

However, the trophic interactions in pulsed resource communities can be much more complex. For instance, Schmidt and Ostfeld (2003) pointed out that the relationship between songbird populations and rodent abundance in forest communities is not always strictly monotonic. They observed that in low mast seed years, songbird populations were under increased raptor predation pressure because rodent populations were low, whereas in high mast years songbirds were under increased nest predation pressure from rodents (as in the previous example). This complex trophic dynamic resulted in the highest songbird abundance during conditions of intermediate mast production. The second example illustrates that resource pulses can have complex cascading effects in ecosystems, often dependent upon the qualities of the resource pulse such as pulse magnitude.

Not all consumers are well adapted to take advantage of the periodical superabundance of resources. Generalist consumers are the most likely to respond to resource pulses because they are able to take advantage of temporary increases in resource abundance and feed on alternative food sources when the pulse is absent (Ostfeld and Keesing 2000). Additionally, consumers must also exhibit a rapid functional or numeric response to the presence of a resource pulse in order to fully utilize it. As a result, consumer species able to temporarily increase resource consumption and to move effortlessly over long distances are best adapted to take advantage of resource pulses (Rose and Polis 1998). In some instances, consumers anticipate these infrequent events by increasing reproductive output in advance of the resource pulse to levels that would otherwise be unsustainable (Boutin et al. 2006, Yang et al. 2008). Therefore the ability to predict the occurrence of a resource pulse yields distinct fitness advantages for consumers.

While most conceptual work on resource pulses has focused on terrestrial ecosystems, several recent studies have evaluated resource pulses occurring in aquatic ecosystems (Willson

and Womble 2006, Nowlin et al. 2008, Yang et al. 2010). These studies have highlighted that resource pulses are common in aquatic ecosystems, including events such as periodic upwelling of nutrient-rich water into the euphotic zone (Adams et al. 2000, Longhurst 2001), guano deposition by migrating waterbirds and subsequent nutrient release (Kitchell et al. 1999), episodic blue mussel settlement eliciting an aggregative response by sea stars (Bologna et al. 2005), and large aggregations of spawning fish providing an important seasonal energy input to consumers, ranging from microbes to top predators (Willson and Halupka 1995, Helfield and Naiman 2001, Naiman et al. 2002). Aquatic and terrestrial ecosystems appear to respond to resource pulses in many of the same ways; however there is some evidence that consumers in aquatic ecosystems are able to respond more quickly to pulse events than those in terrestrial ecosystems (Nowlin et al. 2008, Yang et al. 2010).

The importance of salmonid spawning events as a resource pulse in estuarine and riparian communities is widely recognized and well studied (Helfield and Naiman 2001, Naiman et al. 2002, Nowlin et al. 2008, Yang et al. 2010). However, the ecosystem impacts of other fish spawning events operating on a similar temporal scale have not received as much attention (Willson and Womble 2006). In addition to salmonids, spawning eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*) are all important to the foraging ecology of numerous vertebrate consumers (Willson and Womble 2006). Fish spawning events differ from many examples of resource pulses in the conceptual literature in the frequency with which events occur relative to the life span of the consumer (Ostfeld and Keesing 2000, Yang et al. 2008). For example, many fish spawning events occur seasonally and are utilized by long-lived consumers, whereas the classic example of nutrient input from periodical cicadas occurs only every 17 years and is utilized by microbes and small forest plants (Yang

2004). Nonetheless, many fish spawning aggregations are excellent examples of resource pulses in marine ecosystems, because they are relatively brief, infrequent events of high resource availability for consumers. Pacific herring spawning aggregations are a particularly good example of a resource pulse, providing a superabundance of energy-rich prey for seabirds, cetaceans, and pinnipeds.

Spawning pacific herring as a resource pulse

Pacific herring are an abundant, energy-rich forage fish in the North Pacific Ocean that have received much attention due to their ecological and economic importance (Hourston and Haegele 1980, Gustafson et al. 2006, Therriault et al. 2009). They are considered forage fish because they are among a class of small, schooling fishes that are important prey for larger fish and wildlife. The documented geographic range of Pacific herring extends from the Baja California Peninsula to the Alaskan Arctic in the eastern Pacific, and from Korea to the Russian Arctic in the western Pacific (Hourston and Haegele 1980). Herring in the north Pacific are generally divided into separate stocks based loosely on regional differences in spawn timing, spawn location and genetic data. In some regions there is an active fishery for adult Pacific herring and roe, although concerns about the impact of fisheries on herring populations have led to heavy regulation and closure of herring fisheries in many areas (Stout et al. 2001).

Pacific herring have an interesting life history that involves seasonal spawning migrations. During the spring months, herring eggs are primarily deposited on marine vegetation in the shallow intertidal areas of protected bays and inlets (Haegel and Schweigert 1985). In the first six months of development, Pacific herring remain near the shallow waters of the spawning grounds where they feed on locally available zooplankton. Larval herring metamorphose into

juveniles after approximately 13 wks and then form progressively larger schools that eventually migrate to the offshore feeding grounds after their second summer (Hourston and Haegele 1980, Therriault et al. 2009). Immature herring remain in the offshore feeding grounds until they reach sexual maturity between ages 2-5 yrs (Lassuy 1989), after which they begin making yearly migrations to the inshore spawning areas. However, some herring do not make the initial offshore migration at the juvenile stage, but rather remain in the inland waters throughout their entire life (Stevenson 1955, Lassuy 1989). In the late fall, adult herring migrate en masse to the spawning grounds, where they form densely aggregated schools in pre-spawner holding areas approximately 3-4 wks prior to spawning (Stick 2005, Stick and Lindquist 2009). Spawning occurs in waves over the course of several days in early spring, after which the spent herring immediately migrate back toward the offshore feeding areas (Haegele and Schweigert 1985).

During the weeks when they are spawning, Pacific herring experience high predation rates on both adult fish and their eggs (Hourston and Haegele 1980, Lassuy 1989, Willson and Womble 2006). Referring to the predation pressure experienced by herring on Canada's Pacific coast, Hourston and Haegele (1980) wrote: "They are most susceptible when massed on the spawning grounds and preoccupied with spawning activities. Large herds of seals and sea lions, pods of killer whales, flocks of gulls, cormorants and puffins, and schools of dogfish gather from miles around to eat their fill from the bounteous supply of herring which is so readily accessible." In fact it has been hypothesized that the mass spawning strategy of Pacific herring evolved to saturate predators with more biomass than can be consumed, thereby assuring reproductive success in spite of high predation rates (Pianka 1978). Natural mortality for Pacific herring has been estimated to be approximately 30% per year for adults (Hourston and Haegele

1980) and egg mortality from seabirds alone is estimated up to 40% annually (Outram 1958, Haegele and Schweigert 1985).

Pacific herring spawning aggregations and their eggs together form an important annual resource pulse that delivers high energy food to many consumers. Excluding fish, at least 25 vertebrate species forage in large numbers on adult herring and eggs at Pacific herring spawning sites (Willson and Womble 2006). The vast majority of those species are birds, which primarily forage on deposited eggs during low tide. Spawning herring can deliver exceedingly large quantities of stored energy from the ocean to coastal consumers in the form of roe. The eggs deposited by one spawning stock of Atlantic herring (*Clupea harengus*) constitute the world's largest flux of biological energy caused by a single population (Varpe et al. 2005). In some regions of the north Pacific, herring are the most important fish prey species for seabirds (Therriault et al. 2009), and strong links exist between herring reproduction and seabird foraging ecology. For example, surf scoters (*Melanitta perspicillata*) alter their foraging behavior and habitat use in response to the availability of herring roe, forming aggregations up to 75 000 individuals at a single herring spawning site (Lok et al. 2008). And access to large quantities of herring spawn may be crucial for certain migratory seabirds to replenish depleted energy reserves (Anderson et al. 2009).

Far fewer marine mammals than seabirds have been documented foraging in large numbers at Pacific herring spawning sites; however, herring aggregations are particularly important for certain marine mammal populations. At least four marine mammal species prey on herring aggregations: grey whales (*Eschrichtius robustus*), humpback whales (*Megaptera novaengliae*), killer whales (*Orcinus orcas*), and Steller sea lions (*Eumetopias jubatus*) (Willson and Womble 2006). Of these species, the relationship between Steller sea lions and herring

aggregations has been the most studied (Womble et al. 2005, Gende and Sigler 2006, Womble and Sigler 2006, Sigler et al. 2009, Womble et al. 2009). Foraging on herring spawning and overwintering aggregations is an important part of a seasonal foraging strategy used by Steller sea lions to attain good body condition prior to the breeding season (Womble et al. 2005, Womble et al. 2009) and is likely linked to their reproductive success (Costa et al. 1989). Furthermore, it has been hypothesized that a dramatic decline in the western stock of Alaska Steller sea lions is due to a dietary shift from highly nutritive forage fish, such as herring and capelin, to low-energy gadids (Trites and Donnelly 2003, Rosen and Trites 2005).

The Pacific harbor seal (*Phoca vitulina*) is a noteworthy omission from the list of predators that aggregate at herring spawning sites (Norcross et al. 2001, Willson and Womble 2006). Steller sea lions and harbor seals have largely overlapping diets and geographic distributions (Bigg 1981, Schusterman 1981a), and both have been observed foraging in large numbers at the spawning sites of other marine forage fish (Marston et al. 2002). Additionally, herring are frequently observed in the diets of harbor seals throughout much of their range (Thompson et al. 1991, Olesiuk 1993, Andersen et al. 2007, Lance and Jeffries 2007) and herring are a preferred prey of harbor seals when they are available (Lunneryd 2001). Given the obvious predator-prey relationship between seals and herring, it seems likely that harbor seals would also respond to herring spawning aggregations.

Harbor seal foraging ecology

Harbor seals are a regionally abundant, high-level predator in marine and estuarine environments, ranging throughout the temperate and subarctic waters of the North Pacific and North Atlantic oceans (Bigg 1981). These small phocid seals primarily occupy the littoral zone,

often spending lengthy periods hauled out in near-shore areas on rocky or sandy substrates. While they occasionally perform long-distance movements (Lowry et al. 2001, Lessage et al. 2004, Hardee 2008), harbor seals are considered non-migratory central place foragers, making repeated short foraging trips from a preferred haul-out location. They are generalist predators that feed on a variety of locally available fish and invertebrate species; however, their diet is dominated by a few select species (Tollit et al. 1997).

Harbor seal diet and foraging behavior are influenced by a variety of factors including sex (Thompson et al. 1998), age (Hastings et al. 2004), season (Lowry et al. 2001), time of day (Frost et al. 2001), haul-out type (Hardee 2008, Reuland 2008), and dominant prey species (Tollit et al. 1997). Among these factors, the dominant prey species has a particularly strong influence on the foraging strategy adopted by harbor seals. For example, harbor seals that fed on cryptic prey such as flounder use a “cruising” foraging strategy, i.e. they swim slowly along the sea floor attempting to disturb well camouflaged prey, whereas harbor seals foraging on conspicuous prey such as schooling sand lance pursue the schools at high speed attempting to separate and consume small groups of fish (Bowen et al. 2002). In addition, seasonal or annual changes in the distribution and abundance of preferred prey can change the overall foraging strategy adopted by harbor seals. Harbor seals in Moray Firth, Scotland, feed in pelagic waters in years when overwintering Atlantic herring are abundant, and in demersal waters when herring are not abundant (Tollit et al. 1997).

Seasonal changes in the foraging behavior of harbor seals related to the abundance of preferred prey are detectable in the diving behavior and horizontal movements of seals. Multiple investigations of harbor seal diving behavior have observed strong diurnal dive depth patterns in certain seasons, suggesting that harbor seals follow vertically-migrating prey in the water column

when such prey are regionally abundant (Thompson et al. 1991, Hastings et al. 2004, Reuland 2008). A strong correlation between the fall distributions of harbor seals and the locations where English sole (*Parophrys vetulus*) are seasonally aggregated has also been observed (Grigg et al. 2009). While these studies indirectly determined seal foraging on seasonally available prey, the methods used are particularly powerful when combined with an analysis of prey remains (Sigler et al. 2009).

It is surprising that the relationship between harbor seal foraging behavior and spawning aggregations of Pacific herring remains poorly understood. Herring are amongst the highest energy-density forage fish available to harbor seals (Anthony et al. 2000) and comprise a large portion of the Pacific harbor seal diet (> 90% by frequency of occurrence) in some regions (Lance and Jeffries 2007). In Scotland, harbor seals modify their haul-out use and foraging patterns to take advantage of overwintering schools of Atlantic herring, leading to increased seal body condition in the following spring (Thompson et al. 1996). Herring in the diet of harbor seals in Limfjord, Denmark, peaked when herring entered the fjord to spawn, comprising 90% of the weight consumed by seals during that time (Andersen et al. 2007). In San Francisco Bay, harbor seal locations were correlated with herring spawning sites during the months when herring spawn, and several hauled-out seals were observed covered in herring eggs (Grigg et al. 2009). These findings strongly suggest that harbor seals take advantage of seasonal pulses of spawning herring.

Harbor seals are likely to respond to seasonal pulses of spawning herring for several reasons, beyond a simple preference for herring prey. Because harbor seals are generalist predators, they are among those species most able to switch quickly between prey species depending on which one is most abundant and readily available. Harbor seals are also highly

mobile predators, traveling up to 500 km between haul-out sites (Lowry et al. 2001). High mobility enables consumers to respond quickly to resource pulses with an aggregative response, and may explain why some harbor seals exhibit long-range movements. For instance, harbor seals in southeastern Alaska aggregate during spring spawning runs of energy-rich eulachon (*Thaleichthys pacificus*) (Marston et al. 2002), and harbor seals display both functional and aggregative responses to the presence of migrating salmonids (Middlemas et al. 2006). Lastly, harbor seals are relatively long lived predators with a high learning capacity (Schusterman 1981b), and the ability to memorize locations using a variety of cues including landscape information (Mauck and Dehnhardt 2007). Harbor seals are therefore likely able to predict the timing and locations of annual fish prey pulses such as spawning herring aggregations.

Harbor seals and Pacific herring in the Salish Sea

The Salish Sea is a trans-boundary inland body of water that includes the Strait of Georgia, Puget Sound, and the Strait of Juan de Fuca (Fig. 1). Pacific herring are the most studied of the forage fishes in the Salish Sea, with active survey efforts and management practices on both sides of the Canada and U.S.A. border. Historically, there was a large reduction fishery for Pacific herring in this region, which was used to produce fish meal and oil (Hourston and Haegele 1980). However, due to concerns about declining herring populations, the herring fishery in Washington State is almost completely closed. On the Canadian side of the border, there continue to be well regulated fisheries for bait herring and roe. Population estimates of herring in the Salish Sea are typically performed during the months when herring are spawning, and are based on a combination of acoustic surveys and spawn deposition analysis. In Washington State, most spawning occurs between mid January to early April (Fig. 2), and

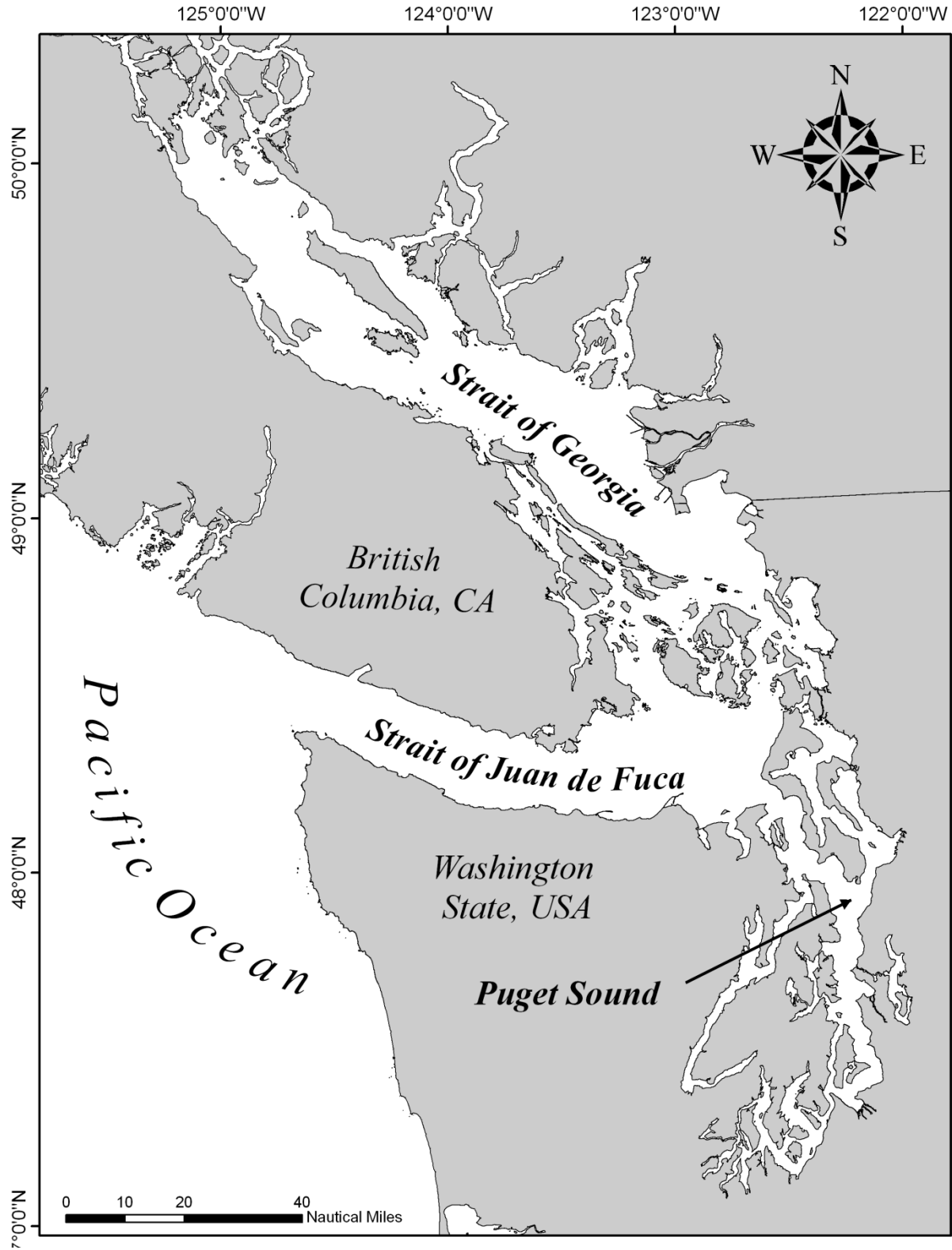


Figure 1. The Salish Sea and its three major bodies of water: the Strait of Georgia, the Strait of Juan de Fuca, and Puget Sound.

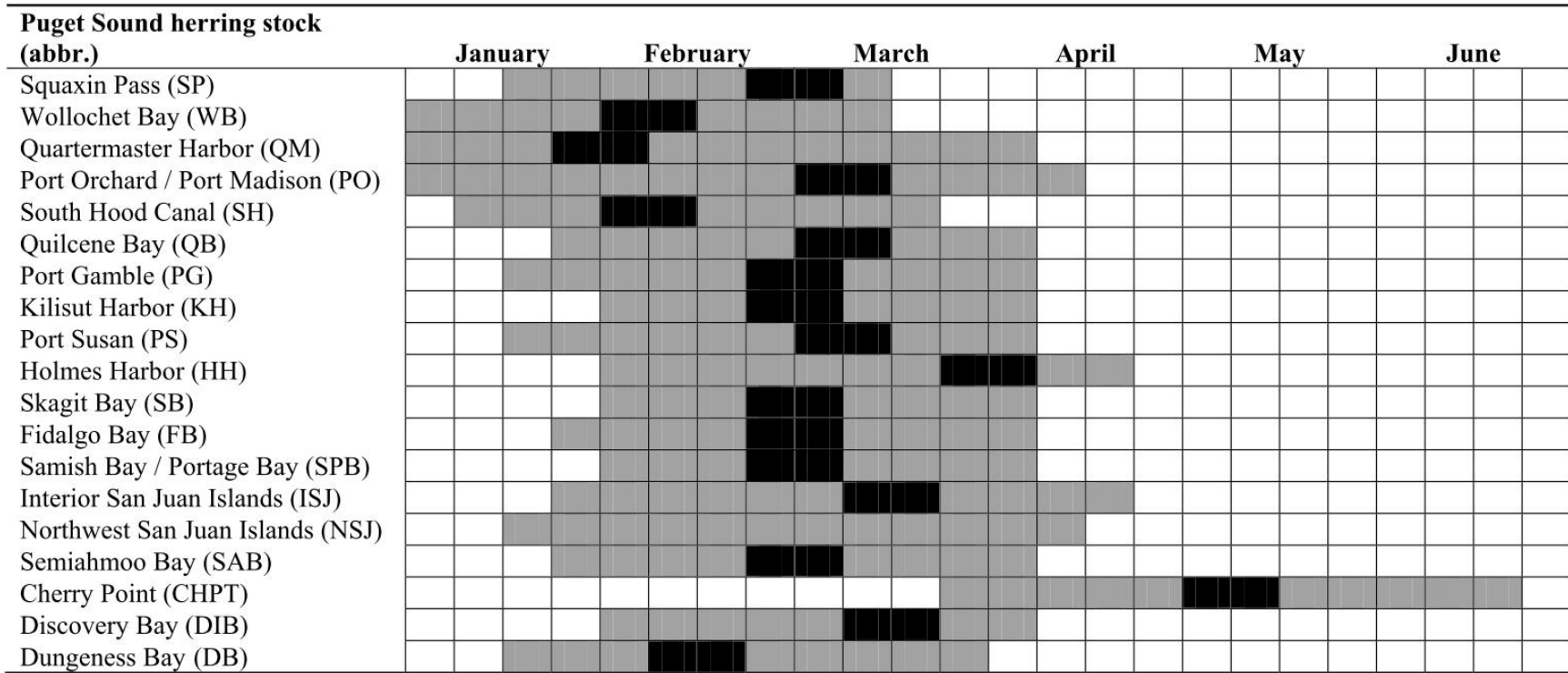


Figure 2. Range (gray shading) and peak (black shading) of documented spawn timing for WDFW Puget Sound Pacific herring stocks. Figure used with the permission of Gustafson et al. (2006)

spawning locations are relatively consistent and well documented (Stick 2005). Recent concerns about the rapid decline of the once-large Cherry Point herring stock in Washington have instigated two extensive reviews by the U.S. National Marine Fisheries service on the status of Pacific herring in the Salish Sea (Stout et al. 2001, Gustafson et al. 2006). Based on a wide variety of evidence, the authors concluded that the Salish Sea contains a single distinct population segment (DPS) of Pacific herring, despite some regional differences in spawn timing and evidence of ‘homing’ to specific spawning locations. The authors also concluded that the Salish Sea Pacific herring DPS is overall healthy, although they admitted that certain potential subpopulations within the DPS are in decline. Conversely, harbor seal populations are healthy throughout the Salish Sea, having rebounded substantially since their protection by law in 1970 in Canada and in 1972 in the United States (Olesiuk et al. 1990, Jeffries et al. 1999). Harbor seal populations in the Strait of Georgia experienced logistic growth during the 1970’s and 80’s, showing an average growth rate of 11.5% per annum during that time period (Olesiuk 1999). The same general trend was observed in Washington waters, where harbor seals populations in Washington State appear to be near carrying capacity (Jeffries et al. 2003).

In some regions within the Salish Sea, the inverse correlation between the size of herring and harbor seal subpopulations is quite striking. In the Strait of Juan de Fuca for example, there has been a consistent decline in herring spawner biomass since the mid 1980’s (Fig. 3), whereas the harbor seal populations in that area have experienced a rapid increase during the same time period (Fig.4). The decline in herring stock biomass in the Strait of Juan de Fuca is primarily driven by the collapse of the historically abundant Discovery Bay herring stock (Gustafson et al. 2006). Local resource managers speculated that the Discovery Bay herring stock decline may

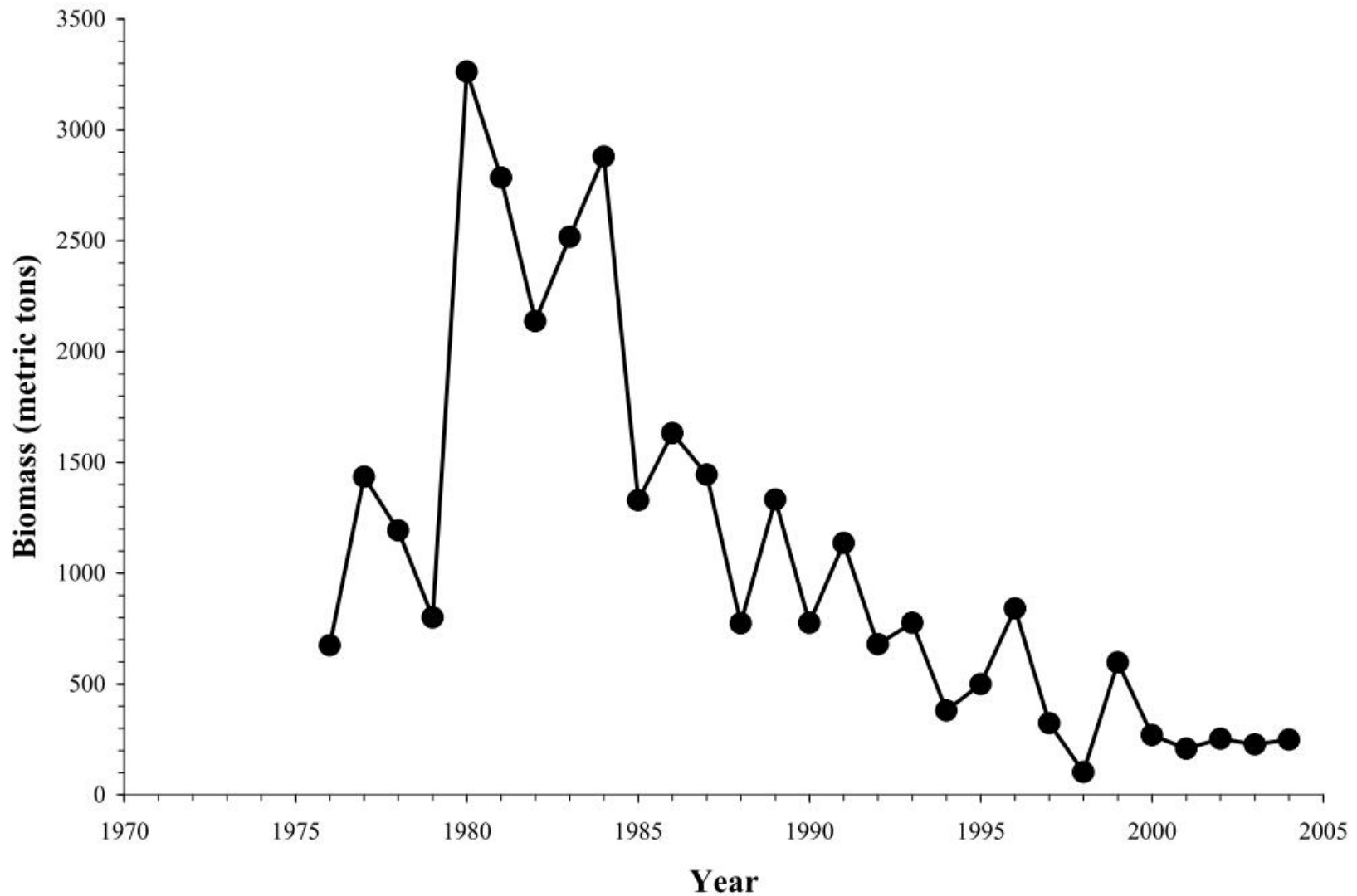


Figure 3. Pacific herring spawning biomass (metric tons) from 1973 to 2004 in the Strait of Juan de Fuca. Figure used with the permission of Gustafson et al. (2006).

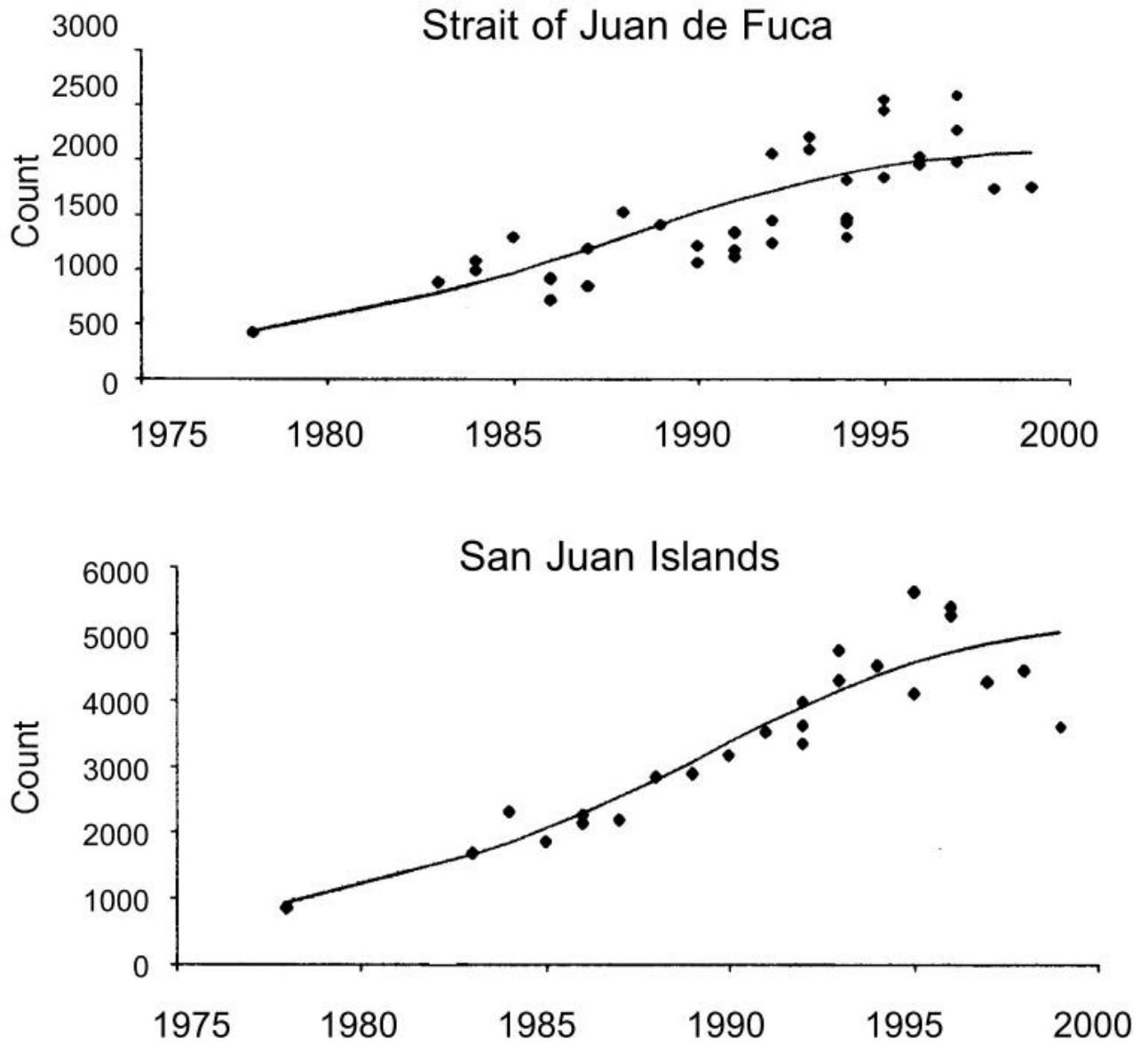


Figure 4. Generalized logistic growth curves of harbor seals in the Washington, inland waters stock. Data presented for the Strait of Juan de Fuca stock (above), and the nearby San Juan Island stock (below). Figures used with the permission of Jeffries et al. (2003).

have been a result of pinniped predation, particularly from animals using the nearby Protection Island haul-out (Stick 2005). Similarly, increased pinniped predation was identified as one of the major risk factors to the survival of Pacific herring in the Salish Sea (Stout et al. 2001).

Because harbor seals are so abundant and herring so well monitored in the Salish Sea, the region is ideal to study the response of harbor seals to seasonal aggregations of spawning herring. Working with the hypothesis that spawning herring aggregations are seasonally important prey for harbor seals, our objective was to measure the seasonal changes in harbor seal diet, foraging distribution, and diving behavior relative to spawning herring aggregations. We monitored the behavioral response of harbor seals on Protection Island, WA, to seasonal changes in herring distribution using a combination of satellite tags, time depth recorders, and seal scat analysis. Specifically, we predicted that: 1) harbor seal consumption of adult herring peaks during the season when herring are spawning, 2) harbor seals seasonally change their foraging areas to take advantage of spawning herring aggregations, and 3) seal diving behavior reflects the vertical distribution of herring in the water column when herring are spawning.

METHODS

Study location

Protection Island (48°07'40"N, 122°55'50"W) is a small National Wildlife Refuge located in the eastern Strait of Juan de Fuca, USA, (Fig. 5) that is known for its extensive seabird colonies and high quality marine habitat. We chose Protection Island for our study due to its proximity to important herring spawning areas (Stick and Lindquist 2009) and its relative importance as a harbor seal haul-out site (Jeffries et al. 2000). Two sandy spits extending eastward and westward from the island are used by up to 1,000 harbor seals during all tidal phases (Jeffries et al. 2000). Discovery Bay, situated approximately 3.5 km south of Protection Island, is the spawning site of the Discovery Bay herring stock. It was once the second largest herring stock in Washington State but has experienced a dramatic decline in recent decades, possibly due to harbor seal predation (Stick 2005). To the west of Protection Island two other small herring spawning grounds make up the Dungeness/Sequim Bay herring stock. While these two stocks are the closest to Protection Island, all of Washington's inland herring spawning locations are within foraging distance of Protection Island harbor seals (Hardee 2008).

Harbor seal diet

Harbor seal fecal samples (scats) were collected on a single day during each of two herring-related seasons: spawn (16 March) and post-spawn (22 July). The seasons were defined based on the local spawn timing (Stick 2005, Penttila 2007). Scats were collected on both island spits, during daytime low tides, with a target sample size of 60 scats for each collection period

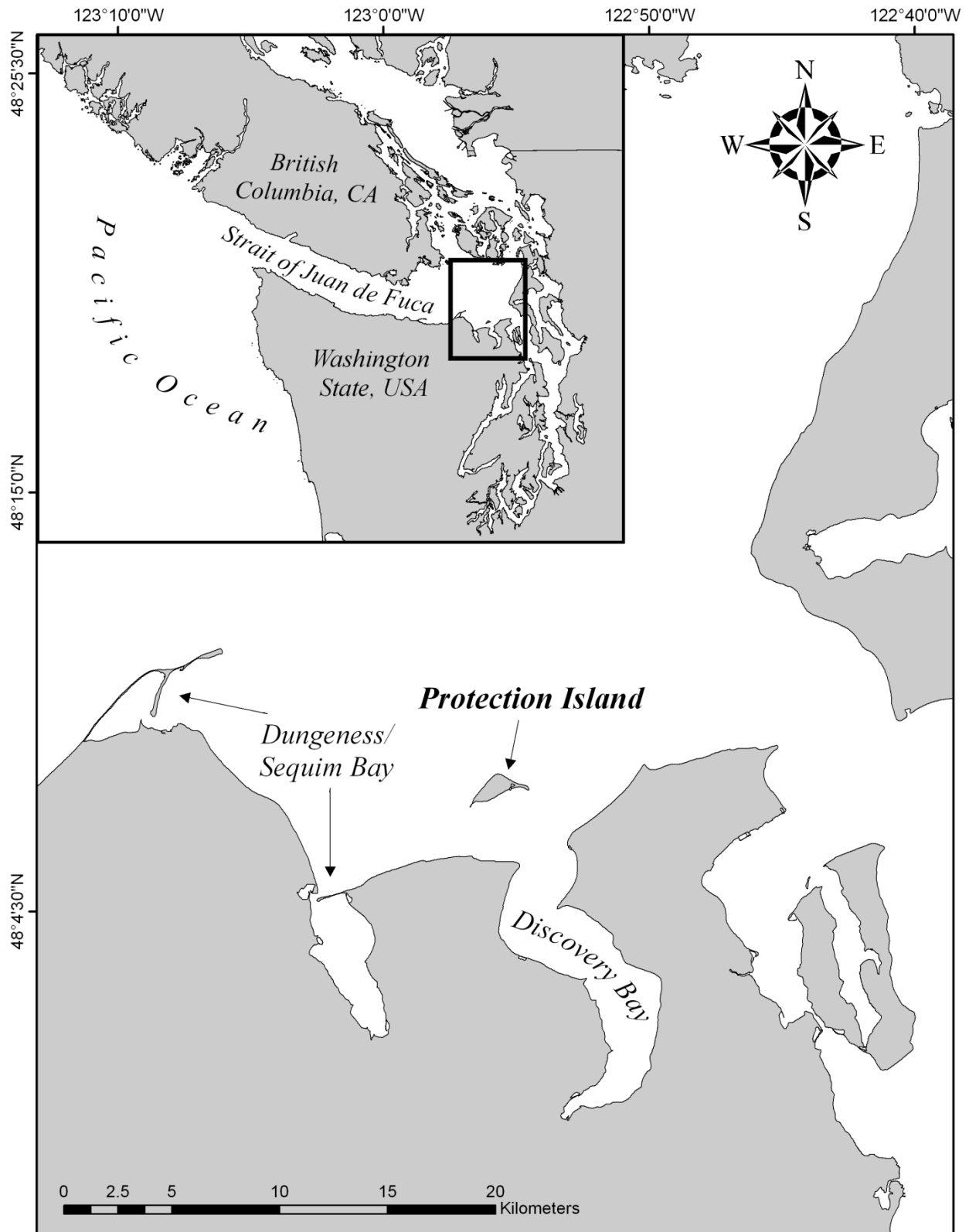


Figure 5. Protection Island, the site where harbor seals were tagged and scat collected. Nearby bays used by spawning Pacific herring are also indicated.

(Trites and Joy 2005). Samples were collected in plastic ‘Whirlpak’ bags and frozen until processing.

Samples were washed using nest sieves (Lance et al. 2001). Prey were identified to the lowest possible taxon using a dissecting microscope, reference fish bones from Washington and Oregon, and published fish bone, otolith, and cephalopod beak keys (Kashiwada et al. 1979, Morrow 1979, Wolff 1982, Clarke 1986, Cannon 1987, Harvey et al. 2000, Lance et al. 2001). Otoliths were measured using an ocular micrometer and graded according to Tollit et al. (2004). Only otoliths graded good (no or minimal erosion) and fair (small amount of erosion) were measured. Data were entered into an Access database.

Diet data are presented as percent frequency of occurrence for each season (spawn and post-spawn). To account for differences in sample sizes among seasons, we present an unweighted average that was calculated by taking the mean percent Frequency of Occurrence (FO) within each season for each prey species. When a sample contained hard parts identifiable to the species level and other parts only identifiable to the family level (but within same family), we included both the species category (e.g. Pacific herring) and the family category (e.g. Unidentified clupeids) only when prey parts were different size (age) classes. Top prey species were identified as those with frequency of occurrence $\geq 25\%$ during one of the two seasons (Luxa 2008).

To estimate the age and size classes of Pacific herring consumed by harbor seals we used a three-step calculation. First, we applied grade-specific length correction factors (g-LCFs) to herring otoliths from seal scats to correct for digestion erosion. Because appropriate correction factors for Pacific herring were not available, we used the mixed diet correction factors for the closely related species Pacific sardine (*Sardinops sagax*) to generate corrected otolith lengths

(Phillips and Harvey 2009). Second, we estimated herring lengths from corrected otolith lengths using a published species-specific regression equation (Harvey et al. 2000). Lastly, consumed herring age classes were calculated by comparing our estimated herring lengths to size at age data for Pacific herring in the region (Schweigert et al. 2009). Juvenile herring were differentiated from adults as those with an estimated age class < 3 (Hay 1985, Gustafson 2006). Values are reported as mean \pm SD.

Tag deployment and programming

On January 12th and 13th of 2008, harbor seals were captured on Protection Island using the beach-seine method (Jeffries et al. 1993) (MMPA Permit No. 782-1702-05). All animals were weighed, measured and flipper tagged with a unique identification number. Five adult seals (2 males, 3 females) received a combined satellite-linked Time Depth Recorder (TDR) and Fastloc GPS receiver (model MK10AF, Wildlife Computers, Redmond, USA) that was attached to the pelage using 5-min epoxy. We placed the instruments on the dorsal midline on the animals such that the tag would be exposed to the air when the back of the seal reached the water surface. During Jan 12-July 3, 2008, we received regular transmissions from all five tags via the Argos satellite network that contained compressed TDR and Fastloc GPS data. Messages were processed using Wildlife Computers' software (DAP Processor 2008) and the progress of the animals was monitored using the Satellite Tracking and Analysis Tool (Coyne and Godley 2005).

To conserve battery life, we limited the number of fastGPS measurement attempts to a maximum of 4 per h or 100 per d. The TDR sensor was set to sample every 10s and record only dives >2m in depth or >30s in duration. The tags automatically summarized the diving behavior

of the animals each day into four 6-h time periods: morning (0400-0959), day (1000-1559), evening (1600-2159), and night (2200-0359) local time. Throughout the study, local sunrise always occurred in the morning period and sunset always occurred during the evening period. Transmitted maximum dive depth histograms tallied dives into twelve depth bins: 2-10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250, 250-300, 300-350, 350-400, 400-500, >500m. Only those depth bins that contained data for at least one animal were used in subsequent analyses.

Similar to scat collection, all transmitted GPS locations and TDR histograms were separated into two herring-related seasons of equal duration (84 d each): spawn (Jan 14-Apr 7) and post-spawn (Apr 8 – Jun 30) based on the spawn timing of local Pacific herring (Stick 2005, Penttila 2007).

Seal foraging areas

After the fastloc GPS locations were solved using the DAP processor, we imported for initial inspection the location data into GIS (ArcView 9.3 – ESRI, Redlands, USA). We removed extreme erroneous locations using a combination of two methods used in other GPS studies of diving marine animals (Schofield et al. 2009, Costa et al. 2010). First, the data were filtered using the `grpSpeedFilter` function in the R package “`diveMove`” (Luque and Liaw 2009), which applies the first stage of the filtering algorithm described in Austin et al. (2003). For this function we used the species-specific speed threshold of 2 m s^{-1} applied in previous harbor seal studies (Williams and Kooyman 1985, Lessage et al. 1999, Hardee 2008). Second, we subjectively removed any additional locations that passed the speed filter but were obviously erroneous because they fell on land (Schofield et al. 2009). Because our interest was in the foraging distribution of harbor seals, we eliminated locations associated with haul-out behavior.

Thompson et al. (1998) defined harbor seal foraging locations as any identified location $> 2\text{km}$ from a haul-out site. However, based upon our observations of seals around Protection Island and the abundance of high quality fish habitat $< 2\text{km}$ of the island, we concluded that a 2km buffer would be far too conservative and therefore chose to eliminate locations $< 0.5\text{km}$ of the documented haul-out sites (Jeffries et al. 2000).

To address the questions of seal space use in this study, we calculated two foraging Utilization Distributions (UDs) for each seal and for each herring-related season. To quantify changes in space use between seasons, the first UD calculated was a fixed kernel density estimate, which was later used in the calculation of overlap indices (Fieberg and Kochanny 2005). For the fixed kernel estimates we used the *ad hoc* method of bandwidth selection (Worton 1995, Calenge 2006) because the Least Square Cross Validation method failed to minimize for our data. While fixed kernel UD are useful for quantifying UD similarity, they are less effective for describing actual areas used by animals in close proximity to hard boundaries such as coastlines (Getz et al. 2007). To better estimate the sizes and locations of seal foraging areas, the second UD calculated was an adaptive local convex hull (*a*-LoCoH) (Getz et al. 2007, Huck et al. 2008). The resulting 95% contour was used to describe the overall foraging area used by each seal, and the 50% contour defined core foraging areas (Ostfeld 1986, Hyrenbach 2002, Hardee 2008).

Using the fixed kernel density estimates, we calculated an index of UD overlap to assess whether seals used different foraging areas between the spawn and post-spawn seasons. An extensive review of UD overlap indices concluded that the Utilization Distribution Overlap Index (UDOI) is the most appropriate for analyses of space-use sharing (Fieberg and Kochanny 2005). In general, UDOI values < 1 indicate less overlap than would be expected from

overlapping uniform distributions, whereas values >1 indicate greater UD overlap than would be expected from overlapping uniform distributions. To statistically compare UDs between seasons we created a set of reference values for UDOI by generating a null distribution of overlap indices from 10 000 simulated, completely overlapping, random, uniform distributions. Using the simulated overlaps, we calculated a p-value for each seal's overlap statistic i.e. the probability of obtaining a value \leq the observed overlap value from the null distribution.

Lastly, we quantified harbor seal use of herring habitat by calculating the amount of overlap between each seal's *a*-LoCoH UDs and two publically available herring datasets: (1) the documented locations where herring aggregate prior to spawning (holding areas), and (2) documented locations where herring regularly deposit eggs (spawning areas) (Stick 2005, Stick and Lindquist 2009). While the timing of herring spawn is quite consistent between years, there is moderate between-year variability in the locations of herring holding areas (K.C. Stick, Washington Department of Fish and Wildlife, La Conner, Washington, personal communication, 2008). Thus, caution should be exercised in the interpretation of the UD/herring area overlap calculations. All values are reported as mean \pm SD.

Seal diving behavior

We calculated three diving variables from the maximum dive-depth histograms to describe seal diving behavior during the four 6-h periods. Any histograms that contained <10 dives/histogram were excluded from the analysis to prevent small sample size bias (Hastings et al. 2004).

Dive depth focus. The degree to which harbor seals focused their diving to a single depth bin was assessed by calculating the dive depth focus (F) within each histogram (Frost et al. 2001, Hastings et al. 2004):

$$F = \sum \{[n_i (n_i - 1)]/[N (N - 1)]\}$$

With n being the number of dives per meter in bin i and N being the total number of dives in the histogram (Hastings et al. 2004). Values of dive depth focus ranged from 1.0 (high focus) to 0.167 (low focus) with values > 0.5 indicating that most dives within the histogram were to a single depth bin.

Modal dive depth. Previous studies of harbor seal diving behavior that used satellite data recorders found that modes are strongly representative of seal diving behavior (Frost et al. 2001, Hastings et al. 2004). Thus, harbor seal use of the water column was summarized by calculating the modal dive depth, i.e. the depth bin with the highest number of dives per meter within a histogram. In the rare case when a mode could not be identified because two depth bins had equal dives per meter, that histogram was removed from subsequent analyses. To perform statistical analyses on the modal dive depth we rescaled the depth bins to integers (1-12) from the shallowest to the deepest bin.

Dive frequency. As a metric of overall foraging effort, we used dive frequency, i.e. the number of dives per hour during each 6-h histogram. Differences in harbor seal dive frequency between seasons may also be attributed to seasonal changes in seal behaviors other than foraging; however harbor seals in the study region do not appear to undergo major life history changes during the study period (Huber et al. 2001). Hence, we believe that changes in diving frequency between the herring-related seasons can be attributed to changes in foraging behavior.

We used linear mixed effects models to test the effects of season (spawn, post-spawn) and period (morning, day, evening, night) on the three dive parameters with the R package lme4 (Bates and Maechler 2009). Of the two fixed effects, period was nested within season, and both were nested within the random effect of seal. For each dive parameter we compared the fit of models that contained an interaction between the fixed effects and models containing each separate main effect. Model fit was compared using Akaike Information Criterion, and the model with the lowest AIC value is reported for each parameter.

RESULTS

Harbor seal diet

We collected 126 harbor seals scats from Protection Island between the two seasons (spawn: n = 61, post-spawn: n = 65, Table 1). The average number of species per scat was 2.5 ± 1.4 during the spawn season, and 2.2 ± 1.3 during the post-spawn season; the maximum number of prey species identified in a single scat was eight. Overall harbor seal diet included at least 21 species from 16 families. In both seasons the top prey species were Pacific herring, Walleye pollock (*Theragra chalcogramma*), and Pacific sand lance (*Ammodytes hexapteras*); however the importance of each top prey species varied between seasons. In the spawn season the dominant prey species was Walleye pollock (FO = 62%) followed by Pacific herring (FO = 43%) and Pacific sand lance (FO = 28%). Whereas the opposite trend was observed in the post-spawn season, with the most important prey species being Pacific sand lance (FO = 42%) followed by Pacific herring (FO = 40%) and Walleye pollock (FO = 25%). We observed only a minor difference (3% FO) in the amount of herring consumed by harbor seals between the spawn and post-spawn seasons.

Table 1. The percent frequency of occurrence (FO) of prey species in harbor seal scats collected on Protection Island during the spawn (16 March) and post-spawn (22 July) seasons.

Phylum	Family	Group or <i>Species</i>	Common Name	spawn		post-spawn	
				n=61	%FO	n=65	%FO
Chordata							
	Gadidae			50	82	24	37
		Unidentified gadids	Codfishes	9	15	6	9
		<i>Theragra chalcogramma</i>	Walleye pollock	38	62	16	25
		<i>Merluccius productus</i>	Pacific hake	0	0	1	2
		<i>Gadus macrocephalus</i>	Pacific cod	3	5	1	2
	Clupeidae			36	59	42	65
		Unidentified clupeids	Herrings	9	15	16	25
		<i>Clupea pallasii</i>	Pacific herring	26	43	26	40
		<i>Alosa sapidissima</i>	American Shad	1	1.6	0	0
	Salmonidae			12	20	21	32
		Unidentified salmonids	Salmon	11	18	21	32
		<i>Oncorhynchus tshawytscha</i>	Chinook salmon	1	16	0	0
	Cottidae			5	8	2	3
		Unidentified cottids	Sculpins	2	3	1	2
		<i>Leptocottus armatus</i>	Staghorn sculpin	3	5	1	2
	Ammodytidae	<i>Ammodytes hexapteras</i>	Pacific sand lance	17	28	27	42
	Embiotocidae	<i>Cymatogaster aggregata</i>	Shiner perch	11	18	2	3
	Engraulidae	<i>Engraulis mordax</i>	Northern anchovy	2	3	1	2
	Pleuronectidae	Unidentified pleuronectids	Righteye flounders	2	3	5	8
	Liparidae	Unidentified liparidids	Snailfishes	1	2	0	0
	Rajidae	Unidentified rajids	Skates	1	2	5	8
	Osmeridae	Unidentified osmerids	Smelts	1	2	0	0
	Scorpaenidae	Unidentified scorpaenids	Rockfishes	0	0	1	2
	Zoarcidae	Unidentified zoarcids	Eelpouts	2	3	2	3
	Pholidae	Unidentified pholids	Gunnels	1	2	0	0
		Unidentified fish spp.		1	2	5	8
		Not identifiable fish spp.		3	5	0	0
Mollusca							
	Octopodidae	<i>Octopus rubescens</i>	Pacific red octopus	3	5	4	6
	Loliginidae	<i>Loligo opalescens</i>	Market squid	2	3	1	2
Arthropoda							
		Unidentifiable crustaceans		2	3	1	2

A total of 230 herring otoliths were recovered from harbor seal scats between seasons (spawn: n = 109, post-spawn: n = 121). Corrected otolith lengths (mean = 3.3 ± 0.93 mm) were on average 28.9% larger than the uncorrected otolith lengths (mean = 2.5 ± 0.53 mm), equating to an estimated average fish length of 15.4 ± 4.9 cm for herring consumed by harbor seals during the study period. There was a remarkable difference in the estimated age classes of herring consumed between the two seasons (Fig.7a-b). During the spawn season, herring in harbor seal diet was comprised of 77% juveniles (estimated age class < 3) and 23% adults, versus the post-spawn season in which 33% were juveniles and 67% were adults. Most (83%) of the juvenile herring consumed during the spawn season were < 2 yrs in age. Of the adult herring consumed during the spawn season, the large majority were age >7 yrs; whereas seals consumed a variety of adult herring age classes during the post-spawn season.

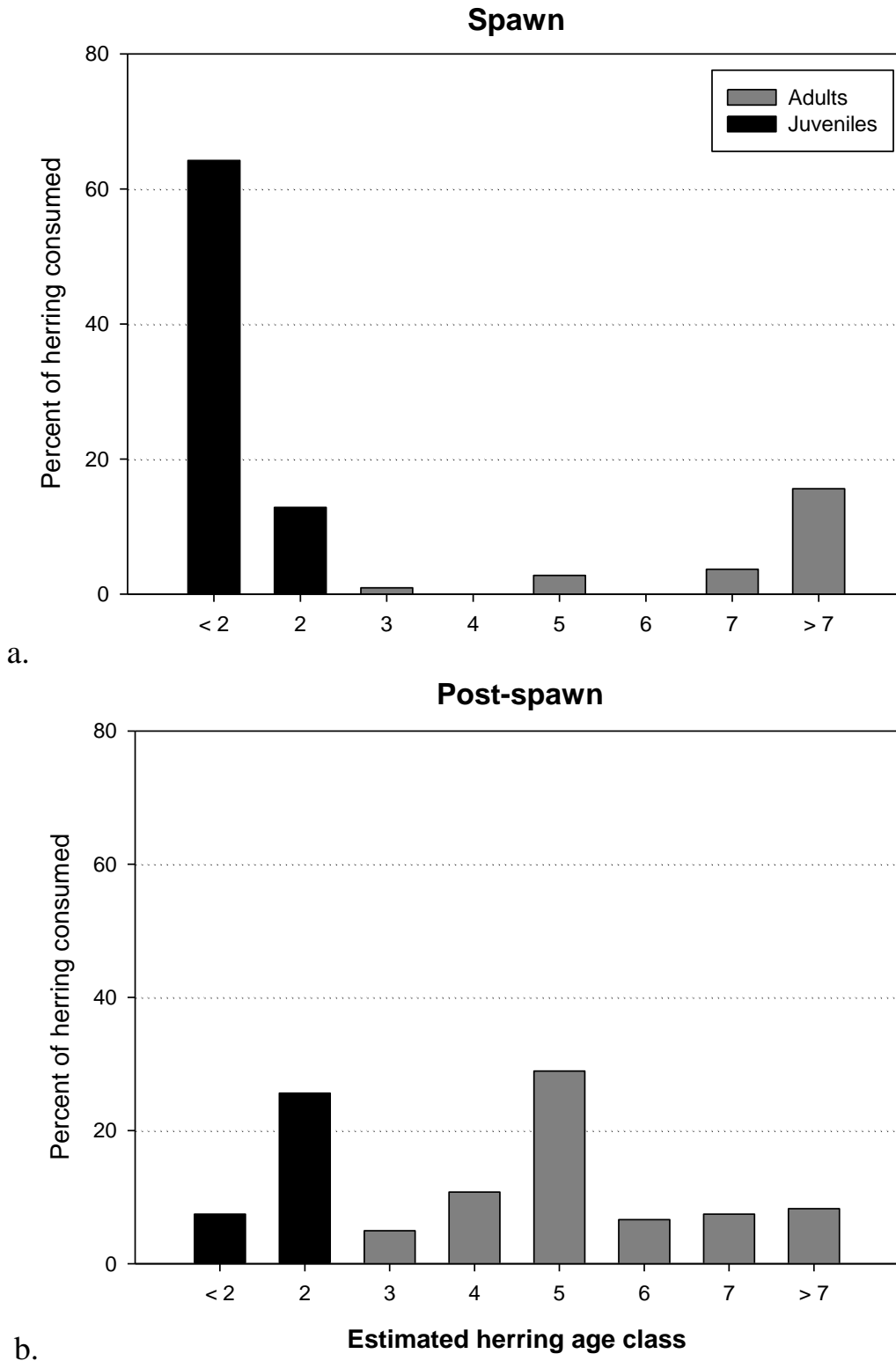


Figure 6. Estimated age classes of herring consumed by harbor seals during the spawn (a) and post-spawn (b) seasons. Black bars indicate herring estimated to be juveniles and grey bars indicate adults.

Seal foraging areas

All tags performed well during the study period with an average of 998 ± 229 GPS locations per seal (range = 840-1397) or approximately 6 locations per day. Filtering steps removed 1.5% of locations, and an additional 32% of locations were identified as haul-out behavior and removed before calculation of the foraging utilization distributions. There were no significant differences in the sizes of harbor seal foraging UD_s between the spawn and post-spawn seasons for the overall foraging areas: 95% a-LoCoH (spawn: 57.59 ± 42.28 km², post-spawn: 39.48 ± 11.29 km²; paired $t = 1.22$, $df = 4$, $p = 0.29$); and the core foraging areas: 50% a-LoCoH (spawn: 6.95 ± 3.93 km², post spawn: 7.19 ± 3.87 km²; paired $t = -0.16$, $df = 4$, $p = 0.88$). There was however a high degree of individual variability in the sizes of foraging UD_s (Fig. 7a-e).

The UDOI index of UD overlap indicated three of the five seals showed significantly less UD overlap between seasons than would be expected from completely overlapping uniform distributions at the 95 and 50% contour levels (Table 2). However, two of those three seals that were identified as having changed their foraging areas between the spawn and post-spawn seasons exhibited only minor foraging area differences between seasons (Fig. 7c1-c2, d1-d2). Only one of the five seals foraged in a largely different region of the Strait of Juan de Fuca between the spawn and post-spawn seasons (Fig. 7a1-a2).

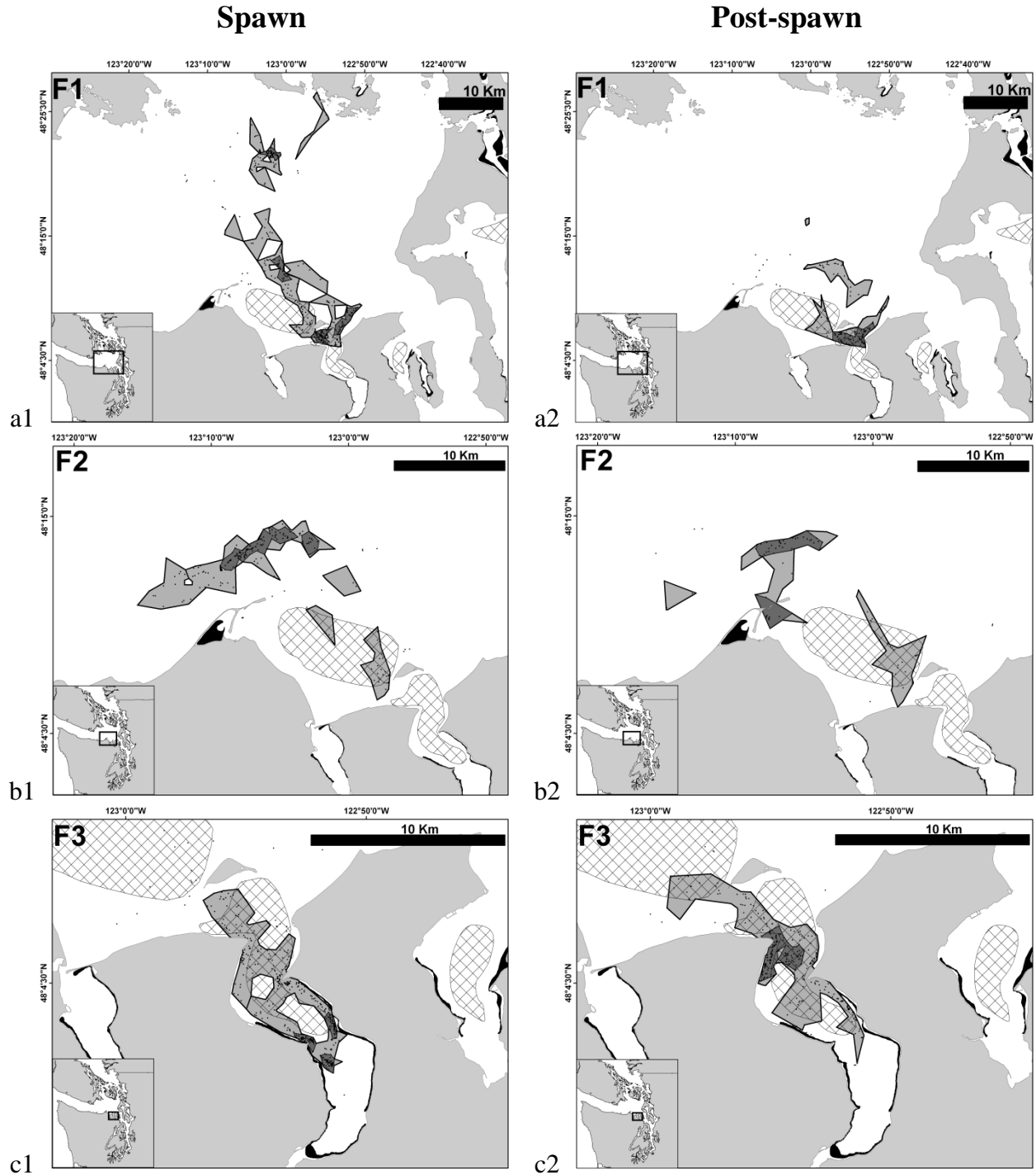


Figure 7. Foraging areas of GPS-tagged harbor seals during the spawn (left) and post-spawn (right) seasons. Symbols indicate GPS locations (•), overall foraging areas (95% a-LoCoH) (■), core foraging areas (50% a-LoCoH) (■), herring holding areas (▨), and herring spawning areas (■). Seal sex and ID are indicated in the upper left (F = female, M = male). Herring data provided by Washington Department of Fish and Wildlife.

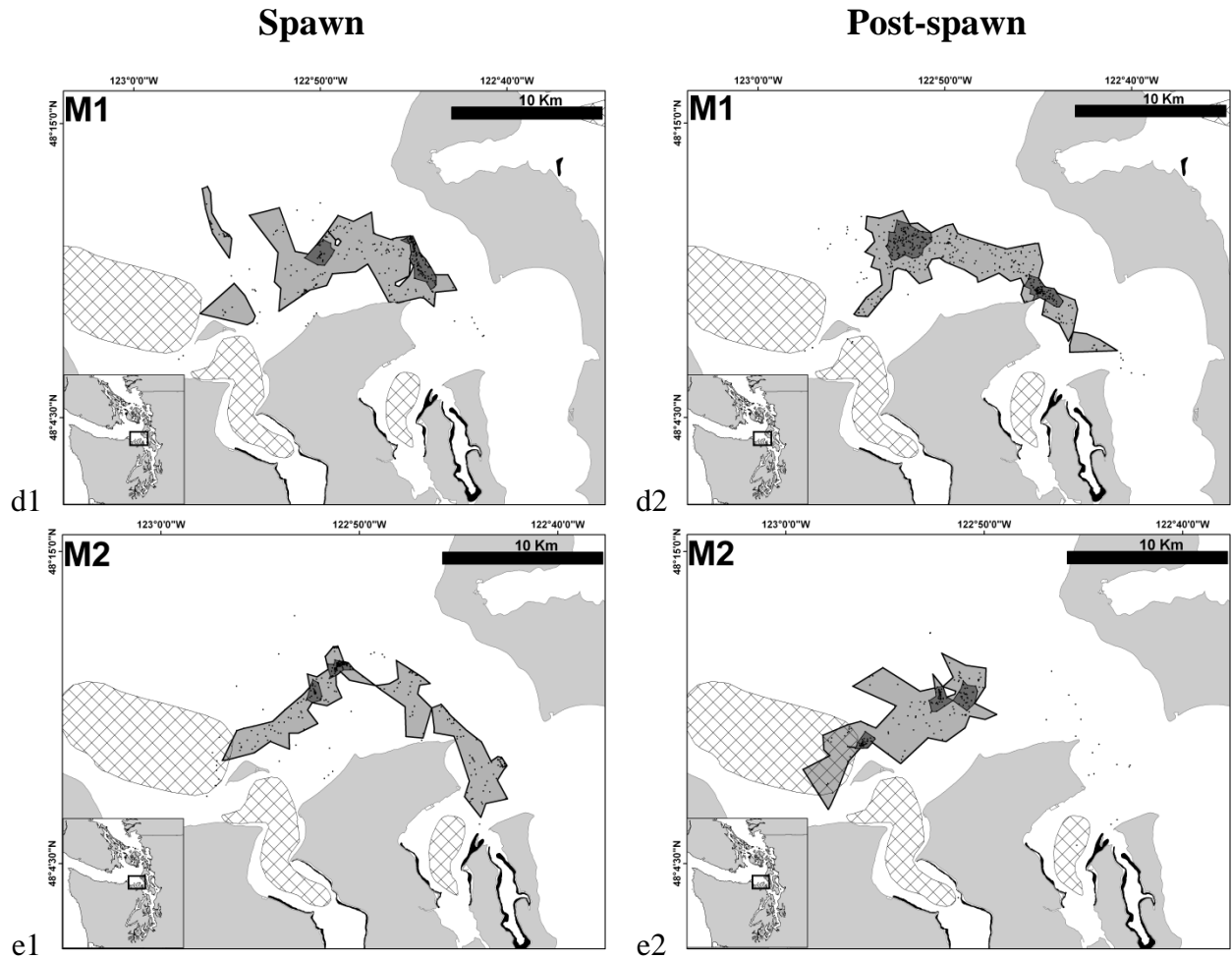


Figure 7 (continued). Foraging areas of GPS-tagged harbor seals during the spawn (left) and post-spawn (right) seasons. Symbols indicate GPS locations (•), overall foraging areas (95% a-LoCoH) (■), core foraging areas (50% a-LoCoH) (■), herring holding areas (▨), and herring spawning areas (■). Seal sex and ID are indicated in the upper left (F = female, M = male). Herring data provided by Washington Department of Fish and Wildlife.

Table 2. The utilization distribution overlap index UDOI between seasons (spawn, post-spawn) for each tagged harbor seal. Overlap index values are presented for the 95 and 50% conditional UDs. P values represent the probability of obtaining an overlap value \leq the observed overlap value from a null distribution of 10 000 completely overlapping uniform distributions.

Seal ID	UDOI 95	P value	UDOI 50	P value
F1	0.812	< 0.001	0.099	0.045
F2	1.183	1.000	0.151	0.711
F3	0.892	< 0.001	0.014	< 0.001
M1	0.929	< 0.001	0.043	< 0.001
M2	1.185	1.000	0.104	0.071

The amount of overlap between the a-LoCoH UD's and the herring holding/spawning areas was not significantly different between the spawn and post-spawn seasons for either contour level (Fig. 7a-e) i.e. between holding areas and the 95% contours (spawn: 7.24 ± 7.30 km², post spawn: 10.17 ± 6.74 km²; paired $t = -2.11$, $df = 4$, $p = 0.10$), between holding areas and the 50% contours (spawn: 0.60 ± 1.26 km², post spawn: 1.65 ± 2.79 km²; paired $t = -1.52$, $df = 4$, $p = 0.22$), between spawning areas and the 95% contours (spawn: 0.02 ± 0.05 km², post spawn: 0.02 ± 0.05 km²; paired $t = 1.00$, $df = 4$, $p = 0.37$), and between spawning areas and the 50% contours (spawn: 0.01 ± 0.02 km², post spawn: 0.00 ± 0.00 km²; paired $t = 1.00$, $df = 4$, $p = 0.37$). Two of the five seals had core foraging areas that overlapped with herring holding areas during both seasons (Fig. 7a1-a2, c1-c2); whereas only one seal's core foraging area overlapped slightly with documented herring spawning areas (Fig. 7c1), and it occurred during the spawn season.

Seal diving behavior

After removing dive depth histograms with fewer than 10 dives, the average number of histograms per seal was 220 ± 33 for the study period. Overall average values for the calculated diving variables were: 0.60 ± 0.08 for dive depth focus (range from 0.167 indicating an even dive distribution across all depth bins, to 1.0 indicating all dives were to a single depth bin), 2.1 ± 0.61 for modal dive depth (i.e. the rescaled depth bin value), and 5.1 ± 0.31 dives/hr for diving frequency.

Based on AIC values, the best model fit for the dive depth focus variable included an interaction between season and time of day (Fig. 8a). In the spawn season, diving focus was greatest during the day but only slightly higher than the other three time periods. The most

dramatic difference in dive depth focus occurred during the post spawn season, in which diving focus was much greater during the night than any other time period. The best model for the modal dive depth variable (Fig. 8b) contained only the random factor of individual seal. Lastly, variation in diving frequency was best described by the effect of season, indicated by a proportionally large difference in diving frequency between the spawn and post spawn seasons (Fig. 8c). Harbor seals on average dove 1.1 dives h^{-1} less (20% change) during the spawn season than they did during the post-spawn season (spawn = 4.43 ± 0.35 dives h^{-1} , post-spawn = 5.53 ± 0.53 dives h^{-1}).

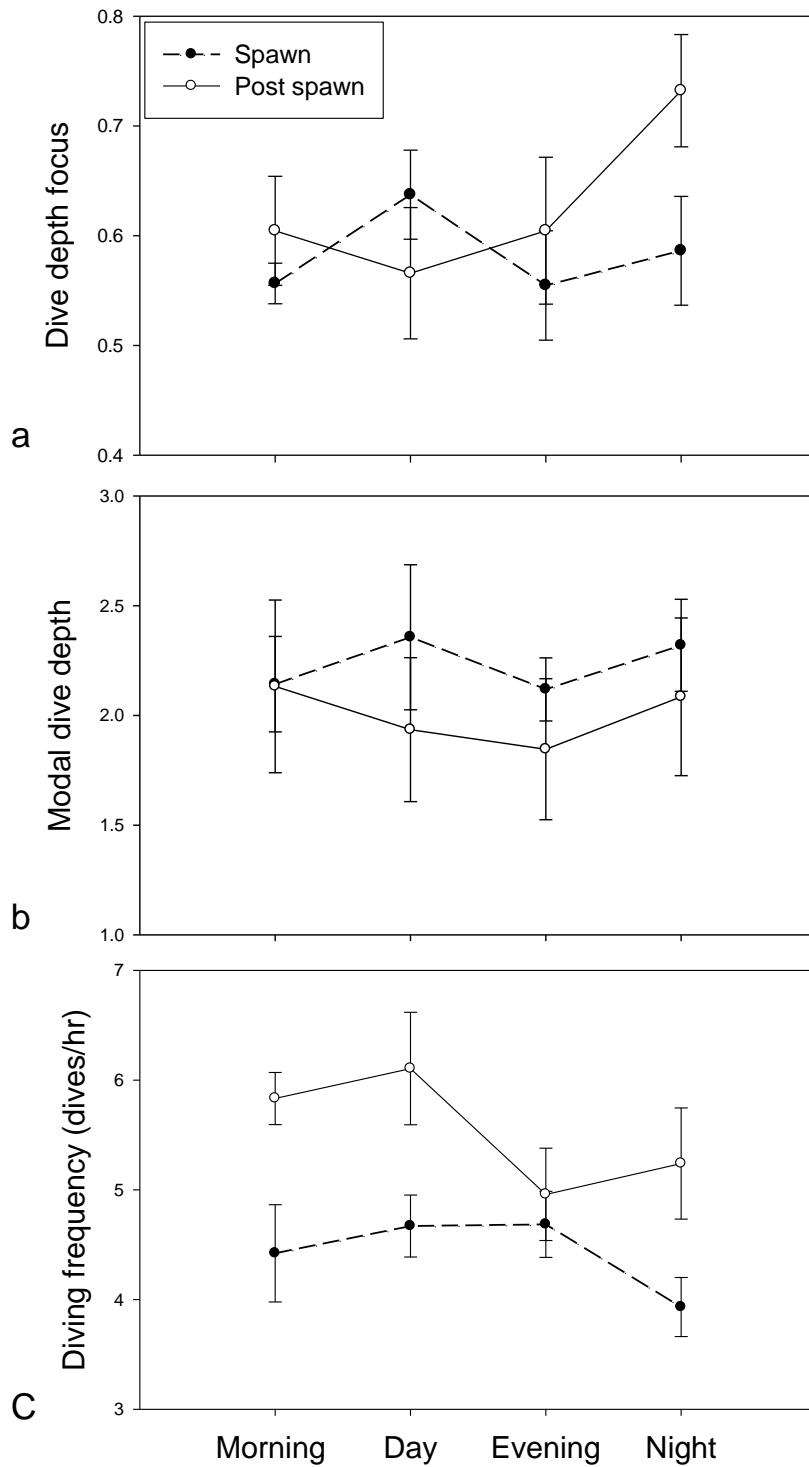


Figure 8. Diurnal variation in harbor seal dive depth focus (a), modal dive depth (b), and diving frequency (c) between seasons (spawn and post-spawn). Morning (0400-0959), day (1000-1559), evening (1600-2159), and night (2200-0359). See text for details on dive variables.

DISCUSSION

Harbor seal diet

We detected two major differences in harbor seal diet between the spawn and post-spawn seasons. The first was a shift from a diet dominated by Walleye pollock during the spawn season to a diet that included a higher percentage of Pacific sand lance and a lower percentage of pollock during the post-spawn season. The second major change was a shift from eating almost entirely juvenile herring in the spawn season to eating mostly adult herring in the post-spawn season (Fig. 6); although there was very little difference in the overall herring percent frequency of occurrence between seasons. These observations are counter to our predictions that herring in harbor seal diet would peak during the spawn season, and that the herring consumed by harbor seals during the spawn season would primarily be spawning adults.

Several explanations could account for why Protection Island harbor seals did not consume many adult herring during the spawn season. The first and most likely explanation is that foraging on spawning herring is less profitable for harbor seals during the spawn season than foraging on juvenile herring or pollock. When herring migrate into the inshore waters to spawn, they cease foraging and largely rely on stored energy for gamete production and bodily maintenance. This leads to a large decrease in herring energy density during the spawn season, equating to a reduction of approximately 40% of their total somatic energy content (Paul et al. 1998). Juvenile herring however are only slightly less energy dense than adults during the spawn season, but likely require substantially less handling time and are regionally abundant in the spawn season (Paul et al. 1998). Given that handling times increase rapidly with prey size, some authors have suggested that small prey are retained in the diets of large predators because they are actually more profitable for predators when the energetic costs of prey acquisition are

considered (Scharf et al. 2001). Thus the decision by harbor seals to forage on juvenile herring during the spawn season can be explained by the relative capturability of juveniles, combined with the large proportional decrease in adult herring energy density during that season. This finding implies that seasonal changes in the pulsed prey energy density and the availability of profitable alternate prey, may both affect the likelihood that a predator will respond to the prey pulse.

A less likely yet intuitive explanation for why harbor seals primarily consumed juvenile herring during the spawn season is that spawning herring in the Strait of Juan de Fuca may no longer be abundant enough to elicit a response from harbor seals. In the early 1980's a large spawning population of Pacific herring occupied the area, but since then there has been a consistent decline in spawning herring biomass in the Strait of Juan de Fuca (Stick 2005, Gustafson et al. 2006, Stick and Lindquist 2009). Because a fundamental component of the resource pulse definition includes a large magnitude increase in resource availability, it is possible that spawning herring in the Strait of Juan de Fuca are no longer an effective resource pulse (Ostfeld and Keesing 2000, Nowlin et al. 2008, Yang et al. 2008, Yang et al. 2010). If that is the case, then we would not expect harbor seals in the Strait of Juan de Fuca to change their foraging behavior during the spawn season and/or consume a higher proportion of adult herring. However we would still expect local herring abundance to peak during the spawning season in the Strait of Juan de Fuca. Thus this second explanation does not account for the observed increase in harbor seal foraging on adult herring during the post-spawn season.

Additionally, if harbor seals only respond to large-magnitude spawning herring aggregations, then we would expect that Protection Island harbor seals consumed a large proportion of herring during the spawn season when Strait of Juan de Fuca herring were

historically abundant. Interestingly, historical harbor seal diet data from Protection Island in 1981 shows that harbor seals consumed more herring during the summer (55% frequency of occurrence) than they did during the winter (29% frequency of occurrence) when herring were spawning (Everitt et al. 1981). At that time spawning herring biomass in the Strait of Juan de Fuca was approximately ten times larger than it is currently (Gustafson et al. 2006). Since harbor seals chose to consume more herring during the post-spawn even when spawning herring in the Strait of Juan de Fuca were extremely abundant, it lends further support to our first explanation that foraging on adult herring may be more profitable for Protection Island seals during the post-spawn season.

Seal foraging areas

Based on the UDOI index, a large proportion of harbor seals from Protection Island (40%) showed high foraging site fidelity between seasons (Table 2). Of the seals that did use different foraging areas between seasons, only one appeared to forage in a noticeably different region within the Strait of Juan de Fuca (Fig. 7a1-a2). These results are somewhat counter to our prediction that harbor seals use different foraging areas when herring are spawning versus when they are not spawning. However, these results are consistent with the findings of other researchers who have detected high foraging area fidelity in harbor seals (Suryan and Harvey 1998, Tollit et al. 1998).

Also contrary to our predictions, there was no seasonal difference in harbor seal use of documented herring holding areas or spawning areas. Foraging areas of seals overlapped with herring areas in both seasons, suggesting that portions of herring spawning habitat are important foraging areas for harbor seals regardless of the presence of herring. The only two herring areas

that overlapped with harbor seal foraging areas were those closest to the haul-out site. While all of the inshore herring spawning areas are within the foraging range of harbor seals on Protection Island, none of the distant spawning areas were used by tagged seals. If Strait of Juan de Fuca herring populations were indeed insufficient to elicit a response from Protection Island harbor seals, it is noteworthy that those seals did not change their foraging areas to be in other locations of high spawning herring abundance within their range. This implies that harbor seals on Protection Island were either unaware of the availability of the other spawning aggregations, or foraging on those aggregations is not profitable enough to elicit an aggregative response from distant harbor seals. Due to the variability of herring holding areas and our small sample size we hesitate to draw firm conclusions from these results. However our data suggest that despite their high mobility and therefore high likelihood of exhibiting a numeric response to prey pulses (Rose and Polis 1998, Ostfeld and Keesing 2000), harbor seals did not appear to alter their foraging areas to utilize seasonal pulses of spawning herring.

Seal diving behavior

Despite the small sample size, we detected strong seasonal and diurnal variations in harbor seal diving focus and frequency during the study period (Fig. 8a, 9c). In the herring spawn season harbor seal dive depth focus peaked during the day, and diving was overall less frequent during this period. These results are consistent with our prediction that harbor seal diving behavior during the spawn season would reflect the distribution of diurnally migrating prey. However, during the spawn season harbor seals primarily consumed Walleye pollock and juvenile herring, rather than consuming adult herring as we had expected (Fig. 6). Pollock of the size class eaten by harbor seals and juvenile herring both occupy nearshore waters and perform

daily vertical migrations; during the day they form dense shoals near the sea floor, and then disperse into the upper water column at night to feed (Lowry et al. 1988, Gustafson et al. 2000). The peak in daytime dive depth focus during the spawn season suggests that seals adopted a benthic or demersal foraging strategy, likely targeting dense schools of young herring and pollock. However, we did not observe a corresponding pattern in harbor seal dive depths that would support that conclusion. This may be due to the highly variable bathymetry in the study region and the large individual variability in harbor seal foraging areas (Suryan and Harvey 1998, Hardee 2008). In fact, the inclusion of diving focus as a factor in pinniped studies that incorporate binned dive data was partially driven by the goal of detecting benthic foraging in habitats with highly variable bathymetry (Frost et al. 2001). Given the bathymetric complexity of the habitat surrounding Protection Island, it is not surprising that we did not detect a consistent pattern of depths used across all seals.

The most striking difference in diving behavior between seasons was the large peak in nighttime diving focus during the post-spawn season (Fig. 8a), accompanied by an increase in overall diving effort (Fig. 8c). During the post-spawn season we also observed a decrease in the importance of pollock in seal diet and an increase in sand lance consumption. The peak in nighttime diving focus is likely related to the observed increase in foraging on sand lance during the post-spawn season. Sand lance bury themselves in sea floor and remain dormant throughout most of the winter until food availability increases the following spring. Once active, sand lance forage in large schools during the day and migrate nightly into the substrate to avoid predation (Robards et al. 1999). Harbor seals regularly forage on buried sand lance by disturbing them out of the sediment, and it has been demonstrated that this benthic foraging strategy is more profitable for seals than pursuing daytime schools of sand lance (Bowen et al. 2002). The peak

in harbor seal diving focus during the post-spawn season is therefore likely due to an increase in nighttime benthic foraging on sand lance during that season.

Given the harbor seal diet differences between seasons, the overall decrease in harbor seal diving effort during the spawn season is more difficult to interpret. We expected that seal diving frequency would be lower during the spawn season because less effort would be required to meet energetic needs when foraging on densely aggregated adult herring. However, while we did observe lower diving effort during the spawn season, we also found that seals did not consume many adult herring at that time (Fig. 6). One possible explanation for the reduction in diving effort during the spawn season is that juvenile herring and pollock require less handling time than adults, and several prey could be acquired within a single dive. Therefore fewer dives may actually be required for harbor seals to meet their energetic needs when foraging on juvenile fish. Whereas, the increased diving frequency in the post-spawn season could reflect the greater effort required to catch adult herring and other energy-rich prey e.g. salmonids, available during that season. However the increase in foraging effort during the post-spawn season is likely offset by the high energy density of their prey at that time. This clearly demonstrates the usefulness of concurrent diet analysis when interpreting pinniped telemetry data, and emphasizes the importance of a multi-level approach to understanding predator responses to changes in prey availability.

Conclusions

Protection island harbor seals exhibited several behavioral differences between the spawn and post-spawn seasons while some behaviors did not change. First and foremost, harbor seals consumed primarily juvenile herring and pollock in the spawn season, and then switched to adult

herring and sand lance in the post-spawn season. Harbor seal diving focus was greatest in the day during the spawn season, and peaked at night during the post-spawn season combined with an increase in overall diving effort (i.e. frequency). Three of the five tagged seals changed their foraging utilization distributions between seasons; however only one seal used a largely different foraging area during the spawn season. Lastly, harbor seal foraging areas only overlapped with herring holding and spawning areas that were closest to the haul-out site, and did so in both seasons.

Pacific herring spawning aggregations are an important seasonal resource pulse for a wide variety of consumers including pinnipeds (Hourston and Haegele 1980, Lassuy 1989, Willson and Womble 2006, Therriault et al. 2009). However, despite suggestive evidence that harbor seals are likely to utilize these seasonal aggregations, our data did not indicate that spawning herring are important prey for Protection Island harbor seals. Instead we found that juvenile herring and Walleye pollock were the key prey species for harbor seals during the season when herring are spawning. These findings are consistent with another herring resource pulse study that did not identify harbor seals as responding to spawning herring aggregations (Willson and Womble 2006). However they are inconsistent with a study that reported harbor seal consumption of herring peaked during the herring spawn season in the north Atlantic (Andersen et al. 2007). While our results may be partially explained by a large reduction in herring spawner biomass in the Strait of Juan de Fuca, there is also strong evidence that adult herring are less profitable for harbor seals during the spawn season than they are at other times of year.

Our study indicates that future resource pulse investigations that focus on the response of predators should take into account several aspects of a resource pulse, such as seasonal changes

in prey energy density, prey handling time, and availability of alternative prey, which are all likely to affect the response of predators to seasonal prey pulses. A similar study design to this one that incorporates a concurrent survey of prey availability between seasons could yield substantial additional insight into the relationship between harbor seals and their herring prey.

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