



(Photograph by G. E. Davis)

Harbor seal species profile

Encyclopedia of Puget Sound

June 9, 2014

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Table of Contents

Introduction	3
Distribution	3
Global.....	3
Local	4

Populations	4
Genetic diversity.....	4
Population size.....	5
Longevity and survival	6
Physical Characteristics	6
Size and coloration	6
Molting.....	6
Whiskers.....	7
Eyes.....	7
Behavior	9
Haul-out	9
<i>Haul-out frequency</i>	9
<i>Haul-out site fidelity</i>	10
<i>Hauling-out for predator avoidance</i>	11
<i>Competition for haul-out space</i>	12
Home Range	12
<i>Adults</i>	12
<i>Pups</i>	13
Diving	13
Foraging	14
Navigation.....	15
Diet	15
Impact on Depressed Fish Stocks.....	18
Reproduction	20
Mating.....	20
Pupping.....	20
<i>Pup development</i>	23
<i>Maternal effects on pup health</i>	24
<i>Pup effects on maternal health</i>	24
Mother-pup interactions	24
<i>Fostering</i>	24
<i>Diving and Foraging</i>	25
Threats	26
Historic Culling	26
Predation.....	26
Disease.....	28
Toxins	34
Disturbance.....	35
Rehabilitation	37
Literature Cited	38
Acknowledgements	55

Introduction

The harbor seal (*Phoca vitulina*) is the most commonly seen marine mammal in the Salish Sea and can be found throughout the region year round (Gaydos and Pearson, 2011). They have been intensively studied within the Salish Sea and this species profile provides an overview of what is known about them.

Harbor seals are a widely distributed, small phocid species. The pinnipeds, or the “feather-footed” seals, sea lions, and walruses, lie within the order Carnivora (Committee on Taxonomy, 2014). Here, the phocids (family Phocidae) are the “true” or “earless” seals (Committee on Taxonomy, 2014). Harbor seals can be found along the temperate coastal regions of Europe, North America, and Asia. The subspecies *P. v. richardii* inhabits the majority of North America’s Pacific coastline, including the Salish Sea. Originally named *Halicyon richardii* in 1864 by John Edward Gray in honor of Captain George Henry Richards, leader of the 1861 to 1862 British survey expedition along Vancouver Island (Scheffer and Slipp 1944), the Latin name for the harbor seal was changed to *P. richardii* in 1902, *P. v. richardsi* in 1904, and finally *P. v. richardii* in 1942 (Scheffer 1958). In his comprehensive review of harbor seals, Bigg (1969a) used *P. v. richardi*. The Latin names *Phoca vitulina richardsi* (Huber et al., 2012 and 2010) and *Phoca vitulina richardii* (Carretta et al., 2013) are both currently used.

Distribution

Global

Phoca vitulina is divided into five subspecies. In the North Pacific, *P. v. stejnegeri* and *P. v. richardii* are recognized, with *P. v. stejnegeri* being found in the western North Pacific and *P. v. richardii* in the eastern North Pacific. *Phoca vitulina stejnegeri* typically has a larger body size, a more massive skull, and darker pelage than the *P. v. richardii*. The three subspecies found along Atlantic Ocean coastlines are *P. v. concolor* in the western Atlantic, *P. v. vitulina* in the eastern Atlantic, and *P. v. mellonae* around the Ungava Peninsula of northeast Canada (Berta and Churchill, 2012).

Phoca vitulina richardii is distributed from the eastern Aleutian and Pribilof Islands in Alaska south to Baja California, Mexico (Berta and Churchill, 2012). Warm, ambient air temperatures likely dictate the southern limit of harbor seal populations. In a study that looked at body temperature, metabolic rate and skin temperature, Hansen et al. (1995) demonstrated that harbor seals experience hyperthermia at 32.5 °C and at this warm temperature, had a mean metabolic rate 1.6 times higher than the expected rate for mammals of the same body mass.

Local

The harbor seal is the most commonly seen marine mammal in the Salish Sea and can be found throughout the region year round (Gaydos and Pearson, 2011). Depending on the tide and time of year, harbor seals will come out of the water to rest on land, a behavior termed “hauling-out.” They use more than a thousand sites throughout the region, including sand bars, mudflats, tideflats, rocks, reefs, ledges, all types of beaches, islands, logbooms, docks, and floats (DFO 2010, Jeffries et al. 2000). Nearly 1,400 haul-out sites have been identified in British Columbia alone (DFO 2010). Seals usually remain within 20 kilometers of the coast but have been detected as far as 100 kilometers from shore (DFO 2010). They are capable of using freshwater habitat as well as salt water and have been documented 250 kilometers up the Skeena River and 500 kilometers up the Fraser River (DFO 2010). Olesiuk (2010) assembled a series of 40 haul-out site maps for British Columbia. The Washington Department of Fish and Wildlife’s Atlas of Seal and Sea Lion Haulout Sites in Washington (Jeffries et al. 2000) documents the locations of 507 haul-out sites throughout Washington State waters.

Populations

Genetic diversity

Genetic variation in harbor seal mitochondrial DNA increases with increasing distance along the Pacific coast of Washington, Oregon, and California (Lamont 1996). Although some male harbor seals travel between the Salish Sea and Washington’s outer coast (Peterson et al. 2012), harbor seals in the Salish Sea are genetically distinct from those found on the outer coast (Lamont 1996). It has been hypothesized that this is a result of reproductive isolation during the Pleistocene when the Cordilleran ice sheet might have isolated what is now the inland population of seals in a giant freshwater lake (Lamont 1996). Potentially a consequence of genetic differences, seals within the Salish Sea also exhibit later reproductive timing than coastal populations (Seekins 2009, Lamont 1996).

Reflecting the genetic distinction between outer coast and inland waters harbor seals, the United States National Oceanic and Atmospheric Administration (NOAA) currently manages them as two distinct stocks, the Oregon-Washington Coastal Stock and Washington Inland Stock (Carretta et al. 2013; Huber et al. 2012). Further genetic analysis of the nuclear and mitochondrial DNA of Washington Inland harbor seals suggests that the stock should be subdivided into three geographically and genetically separate stocks: North Inland Waters, Hood Canal, and South Puget Sound (Huber et al. 2012, Huber et al. 2010). Stock structure of harbor seals in British Columbia is unknown, so the Canadian Department of Fisheries and Oceans (DFO) manages the British Columbian harbor seal population without an emphasis on subpopulations (DFO 2010). However, based on observed differences in reproductive timing and high haul-out region fidelity, genetically isolated subpopulations probably do exist in the region (DFO 2010).

Population size

Bounty hunters began reducing harbor seal populations in the Northeast Pacific Ocean in the 1870s. Off the coast of British Columbia, up to half a million harbor seals were killed for pelts or bounty from the 1870s until the 1970s (Olesiuk 2010, Bigg 1969a, Fisher 1952). Between 1943 and 1960, at least 17,133 harbor seals were killed in Washington State (Newby 1973, Scheffer and Slipp 1944). Both U.S. and Canadian harbor seal populations were protected in the 1970s, in the United States by the 1972 Marine Mammal Protection Act (NOAA 2013a) and in Canada under the 1970 Marine Mammal Regulations in the Fisheries Act (Government of Canada 2013, DFO 2010).

From 1972 into the 1980s, harbor seal stocks grew exponentially at a rate of about 6% per year. Since the mid-1990s, the Salish Sea population seems to have reached carrying capacity and has remained relatively stable (DFO 2010, Jeffries et al. 2003). The inland Washington harbor seal stock is estimated to be over 12,000 (Carretta et al. 2013), while the Strait of Georgia sustains approximately 39,000 harbor seals (Olesiuk 2010). Combining those figures, the total population of harbor seals in the Salish Sea is over 50,000. The Salish Sea covers 16,925 square kilometers of marine water (Gaydos et al. 2008), making the harbor seal density of almost 3 harbor seals per square kilometer of ocean possibly one of the most dense harbor seal populations in the world.

Assessments of population size are usually carried out via aerial surveys of hauled-out harbor seals (Thompson and Harwood 1990). Aerial surveys are generally carried out at low tide during the pupping season when the highest proportions of harbor seals are hauled-out (DFO 2010). Because only a portion of harbor seals is hauled out at a low tide, these counts must be corrected to estimate total population size. Huber et al. (2001) used VHF radio tagging to determine the ratio of hauled-out seals to submerged seals in Washington and Oregon stocks yielding a correction factor of 1.53 to estimate the total population from the counts of seals hauled-out. However, because haul-out behavior generally varies by date, time, tide state, and location, this correction factor is only applicable to Washington and Oregon harbor seals during the pupping season, the time and location specific to this study. Reflecting the sensitivity of hauling-out behavior to local conditions, correction factors for smaller areas within the study region vary from 1.85 in the Strait of Juan de Fuca/San Juan Islands to 1.36 in Puget Sound (Huber et al. 2001). The correction factor for estimating the harbor seal population from aerial surveys of haul out sites in British Columbia harbor seals is 1.63 (DFO 2010).

As the radio-tagging method to estimate correction factors assumes a high level of haul-out site fidelity during the pupping season, a mathematical method for determining correction factors has been developed as an alternative (Cowles et al. 2013). Cowles et al. (2013) determined which environmental factors influence haul-out of local harbor seals (hour of day, ebb current speed, and tide height) and used these factors to develop a haul-out model and correction factor for

Protection Island, Washington. This method is of limited value because extensive data must be collected for each haul-out site and it is only applicable to the relatively few haul-out sites that are available for hauling-out at all tide levels.

Longevity and survival

Average longevity of female harbor seals is 10 years while males live an average of 8 years, although wild female and male harbor seals have been known to live as long as 30 and 20 years, respectively (DFO 2010, Osborne et al. 1998, Bigg 1969a). In captivity, harbor seals may live into their early 30s (Walker 1999, Osborne et al. 1998). Based on fecundity estimates and a population sample of 245 seals collected just prior to the pupping season in British Columbia, Bigg (1969a) projects an overall annual mortality rate of 20%. By constructing life tables, it is estimated that from birth to 5 years of age, males and female mortality rate was around 20%, but after 5 years of age, female mortality drops to 15% while male mortality climbs to 29% (Bigg 1969a). Harbor seal survival was also studied on Tugidak Island in the northern Gulf of Alaska by Hastings et al. (2012) using mark-recapture methods. Their results complement Bigg (1969a), showing that annual survival is higher for females than males. They also found that the most vulnerable life stage is from birth to weaning (approximately the first month of life), with an average mortality of 26% males and females.

Physical Characteristics

Size and coloration

Harbor seals are the second smallest of the phocids, only slightly larger than Ringed seals (*Phoca hispida*) (Smith et al. 1990). Harbor seals exhibit a striking spectrum of black and white pelage coloration ranging from pale white to nearly black coats with light or dark spots, rings, and splotches. (DFO 2010, Jeffries et al. 2000, Scheffer and Slipp 1944). Within the North Pacific there appears to be a geographic gradient of pelage. In the south there is a higher proportion of seals with dark coats (often described as light on dark) while in the north there is a higher proportion of light coats (often called dark on light) (Shaughnessy and Fay 1977, Stutz 1967a). Harbor seals exhibit slight sexual dimorphism with males weighing an average of 27% more than females (Bowen et al. 2001). Adult females typically reach a length of 147 centimeters and have an average mass of 59 kilograms whereas adult males grow to an average of 161 centimeters and 73 kilograms (Bigg 1969a, Scheffer and Slipp 1944). Scheffer and Slipp (1944) note a particularly large male specimen weighing 116 kilograms and 170 centimeters in length, measured as a straight line from nose to tail.

Molting

Harbor seals molt, or shed their pelage, annually at the end of the mating season in mid- to late summer (Daniel et al. 2003, Walker 1999, Ling 1972, Stutz 1967b). Molting in phocids is a relatively quick process (Ling 1972); Scheffer and Slipp (1944) describe how the molting of a 4-year-old male in captivity ensued for at least a month, his old, brownish hair replaced by a silvery gray coat with dark, defined rings and spots. Daniel et al. (2003) tracked the progression of molting in

yearling, subadult, and adult harbor seals on Tugidak Island, Alaska. The dates of molting were identical for yearlings and subadults between 1997 and 1999, but adults molted 3 to 6 days later in 1999 than in 1997 or 1998. Yearlings were the first to molt, followed by subadults and finally adults. Daniel et al. (2003) hypothesize that adults may have delayed molting due to poor body condition. Sexually mature seals lose mass during the mating period, resulting in poorer nutritional state. Hormones may also play a role in the timing of molting (Daniel et al. 2003).

Daniel et al. (2003) describe the progression of the molt in fairly well defined stages. During the premolt, the pelage fades or bleaches to a uniform brown or tan and the spots and rings become indiscernible. Next, small patches of new hair begin to show, starting around the navel and scar tissue, then continuing on the face, neck, flippers, anal and urogenital openings, and along the dorsal midline and dorsum. The dorso-lateral sides are the final patches to molt. Post-molt, seals are shiny with well-defined spots and rings. Yearlings and subadults virtually always molt according to this progression, but adults show more individual variation (Daniel et al. 2003).

Whiskers

Adult harbor seals have approximately 42 vibrissae beside each nostril, each up to 125 millimeters long (Scheffer and Slipp 1944). Whiskers are held in an abducted position while swimming (Hanke et al. 2010). Mystacial vibrissae in harbor seals can detect objects by touch and are essential for hydrodynamic trail following, tracking water disturbances over a greater distance than can be done by sight or hearing (Hanke et al. 2010). Harbor seal whiskers have an undulated surface structure, which reduces water flow resistance while swimming and also decreases consequent vortices back on the whiskers by an order of magnitude as compared to sea lion whiskers, which are not undulated (Hanke et al. 2010).

Eyes

Harbor seals are thought to be L-cone monochromats, meaning the only color they see is red, but they may have mesopic color vision (Hanke et al. 2009, 2008). Hanke et al. (2009) reviewed harbor seal vision and found that they have many adaptations for seeing in air and under water. Above the water's surface, harbor seals have vision equivalent to terrestrial mammals. Harbor seals have multifocal lenses, allowing for high-resolution eyesight over a broad range of ambient light. Like carnivores such as cats, wolves, and dogs, the retina in harbor seals has both a visual streak and an area centralis, which allows for good peripheral detection of movement. The retinas of other pinnipeds do not have this combination. Harbor seals also have high contrast sensitivity, enabling them to detect objects and movement as effectively as a cat (Hanke et al. 2009).

Unlike terrestrial mammals, harbor seals' vertical and horizontal optokinetic nystagmuses (OKN) are symmetrical, which means that their eyes track movement equally well in all planes (Hanke et al. 2009). This helps them maneuver in the 3-dimensional aquatic environment. Terrestrial mammals, on the

other hand, have asymmetrical vertical OKN, which is an adaptation for walking over an irregular surface (Hanke et al. 2009).

Harbor seal eyes are very sensitive and can adapt rapidly to changes in light. The pupil is circular and has a low focal ratio when fully dilated, but the pupil becomes a vertical slit and finally a tiny pinhole as it constricts in the presence of light (Hanke et al. 2009). The retina is characterized by light sensitive rods and is backed by a tapetum cellulosum, a type of tapetum lucidum, which results in the glowing eyeshine seen in many vertebrates at night (Hanke et al. 2009). The tapetum cellulosum reflects light back through the retina, improving harbor seals' night vision. This is important for diving, as harbor seal vision needs to accommodate the rapid change from bright daylight to the darkness hundreds of meters below the ocean's surface (Hanke et al. 2009).

The cornea is adapted to suit sight in both the air and water, with a flattened vertical meridian. This interacts with the slit-shaped pupil to allow for a sharp image in air as long as the pupil does not extend past the flat portion of the cornea (Hanke et al. 2009). Hanke et al. (2006) conducted refractive measurements of harbor seal eyes, finding emmetropic (normal) or slightly hyperopic (far-sighted) vision under water and myopic (near-sighted) vision with astigmatism in air. However, this study did not take into account the aforementioned interaction between the corneal topography and slit pupil, which could skew the results (Hanke et al. 2009).

Harbor seals' eyes are situated dorsally, which affords them a wide visual field (Fig. 1). This may also allow them to keep their eyes above water while swimming at the water's surface. However, the ventral field of vision is more limited; for this reason, harbor seals swim upside down to look below them while foraging (Hanke et al. 2009).

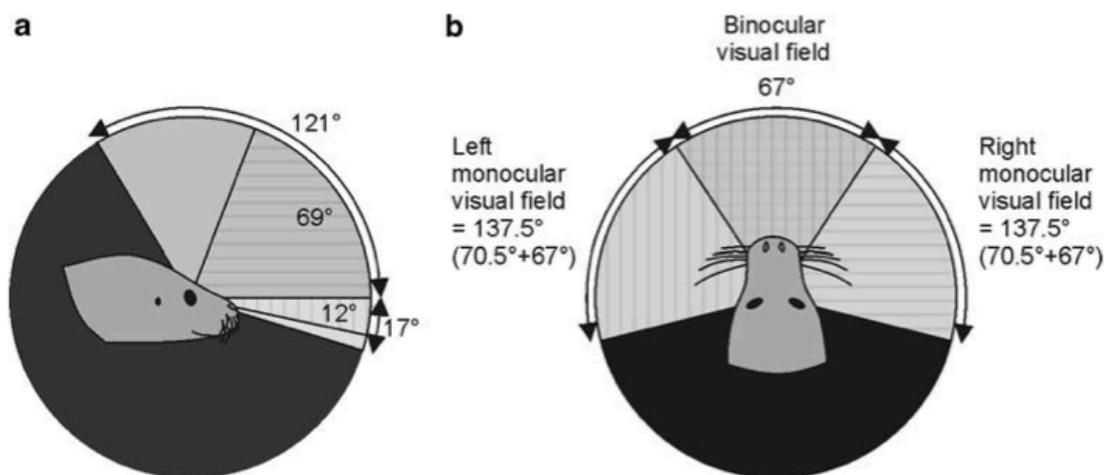


Figure 1: Monocular and binocular visual fields of a harbor seal in air (Hanke et al. 2009)

Behavior

Haul-out

Harbor seals haul-out on land year round (Watts 1996) and use haul-outs to molt, give birth, nurse, socialize, and rest (S Jeffries unpubl. data). The metabolic costs of sleeping on land are less than that of sleeping in water (Watts 1996). When haul-out sites are unavailable due to high tide, harbor seals can sleep in the water, either completely submerged or floating with their head above water, but they must wake frequently to breathe (Riedman 1990).

Islands, beaches, rocks, reefs, docks, logbooms, sand bars, and other areas commonly used by seals as haul out sites are mapped for Washington (Jeffries et al. 2000) and for British Columbia (Olesiuk 2010).

Haul-out frequency

Numbers of hauled-out harbor seals tend to peak during the summer months, particularly during molting season (Patterson and Acevedo-Gutiérrez 2008, Harris et al. 2003). Harbor seals may haul-out more frequently while molting because they have reduced food requirements or because blood flow increases in peripheral tissues throughout molting, so resting on land reduces the energy spent on thermoregulation (Watts 1996). Except in noisy areas of high urban development, harbor seals typically follow a diurnal haul-out cycle, with numbers of seals on shore peaking around midday or at low tide in the afternoon and evening (Cowles et al. 2013, Cunningham et al. 2009, Patterson and Acevedo-Gutiérrez 2008, Simpkins et al. 2003, Watts 1996, Thompson et al. 1989). The proportion of seals hauled-out at a given time varies between the sexes and among age groups and also depends on environmental factors. Time of day, season, tide level, weather, and human disturbances are some of the many variables known to affect haul-out patterns (London et al. 2012, Acevedo-Gutiérrez and Zarelli 2011, Patterson and Acevedo-Gutiérrez 2008, Härkönen et al. 1999, Watts 1996, Thompson et al. 1989). Thus, specific haul-out behavior may differ among harbor seal populations in different areas, as well as among individual harbor seals.

Harbor seals in different areas within the Salish Sea show variation in haul-out patterns. In Hood Canal, harbor seals haul-out nocturnally from June through September due to high human disturbance levels, but return to daylight haul-outs by the quieter months of October and November (London et al. 2012). The effect of the tide on haul-out behavior is evident around Hood Canal; many ideal haul-out locations are exposed during the 2 hours before and 2 hours after low tide, so maximum numbers of harbor seals are found hauled-out during these hours on rocky reefs and mudflats, especially in the 1.5 hours after low tide (London et al. 2012, Huber et al. 2001). Harbor seals around Bellingham maintain a nocturnal haul-out schedule year-round because of high human-generated noise levels during the day (Acevedo-Gutiérrez and Zarelli 2011). Numbers of hauled-out harbor seals around Bellingham peak between July and September 9, during the pupping and breeding seasons (Farrer and Acevedo-Gutiérrez 2010).

Researchers have observed haul-out patterns for harbor seals in different areas outside of the Salish Sea as well. In Northwest Scotland, more harbor seals hauled-out from late winter through early summer than during the rest of the year (Cunningham et al. 2009). Females hauled-out more frequently than males between June and September but less frequently from October through May. Individuals devoted between 11% and 27% of their time on haul-outs, the durations of which lasted on average 4.77 hours, with a maximum haul-out of a lengthy 24.6 hours. Only between May and July was there a marked diurnal pattern with a strong midday preference for hauling-out (Cunningham et al. 2009). A similar seasonal trend was observed in the Gulf of Maine, where the highest numbers of harbor seals hauled-out in August during the molting season and the fewest in January (Harris et al. 2003). In Nanvak Bay and Grand Island, (AK), harbor seals hauled-out most frequently in early September at midday on days without rain and wind speeds near 16 kilometers per hour (Simpkins et al. 2003). At a haul-out site on Prudence Island, Rhode Island, the diurnal trend was much weaker from February through April. On average, 22 harbor seals hauled-out during the day and 16 hauled-out at night. Neither temperature nor wind affected haul-out turnouts significantly (Norris 2007).

Haul-out behavior was studied in Swedish harbor seals and revealed that peak haul-out frequency varied significantly between the sexes and among age groups (Härkönen et al. 1999). Harbor seal pups were caught, branded, and monitored over 12 years. Several trends were found, but most interestingly, 4 to 5 year old primiparous females hauled-out 70% less than older females. Spending more time at sea to feed frequently during lactation, these young harbor seal mothers spend less time with their newborn pups, resulting in high frequencies of mother-pup separation. Also notable was a peak in haul-out activity in 5-year-old males during the July mating period. These young males presumably haul-out more to dodge the aggressive older males (Härkönen et al. 1999). Around Orkney, Scotland, male and female harbor seals also demonstrated different haul-out patterns (Thompson et al. 1989). Male harbor seals were observed to haul-out more at the beginning of the molting period, while females did not have a marked peak in haul-out behavior. Rather, females hauled-out less after they finished lactating. Male and female seals hauled-out regularly day and night throughout the winter (Thompson et al. 1989).

Haul-out site fidelity

Haul-out site fidelity varies greatly among individual harbor seals, but the norm is high fidelity (DFO 2010, Hardee 2008). Using results from VHF radiotag telemetry in the San Juan Islands, Suryan and Harvey (1998) found that 69% of harbor seals manifested a haul-out fidelity of 75% or greater. Using satellite tag-linked GPS telemetry data, Hardee (2008) compared haul-out site fidelity between harbor seals at rocky reef sites throughout the Salish Sea versus seals in the estuarine habitat of Padilla Bay, also within the Salish Sea. Male seals from the rocky reef sites had low haul-out site fidelity and a very broad spatial distribution of many haul-out regions, as far as 120 kilometers apart. All Padilla

Bay seals, male and female, remained within 10 kilometers of the bay, and half of the seals had 100% haul-out site fidelity (Hardee 2008). Padilla Bay is an important harbor seal pupping area and high site fidelity is likely associated with pupping and nursing at these haul-out sites (S Jeffries unpub. data).

Hauling-out for predator avoidance

Hauling-out allows harbor seals to evade aquatic predators, including transient killer whales (*Orcinus orca*). The amount of time spent hauling out can be a direct reflection of predation pressure. In 2003 and 2005, transient killer whales visited Hood Canal and preyed upon an estimated 1,000 harbor seals (London et al. 2012). Compared to pre-killer whale exposure in 2002, harbor seal haul-out probability increased 40% to 50% by 2005. After the transient killer whales left Hood Canal in 2006, harbor seals resumed pre-2005 haul-out behavior (London et al. 2012).

While hauled-out, harbor seals remain vigilant of potential threats and predators by continually scanning their environment. They may be displaced from the haul-out when a potential predator or threat is spotted. Johnson and Acevedo-Gutiérrez (2007) monitored human disturbances of harbor seals from Yellow Island in the San Juan Islands. During their study, hauled-out harbor seals were disturbed by boaters 14 times. Passing powerboats never disturbed the seals, but stopped powerboats and kayaks were seen as threats and caused seals to be displaced from their haul-out from distances that ranged from 27 to 371 meters. Hauled-out harbor seal numbers recovered within 60 minutes after only 50% of disturbances (Johnson and Acevedo-Gutiérrez 2007). Suryan and Harvey (1999) also observed disturbances of harbor seals at three locations in the San Juan Islands, Puffin Island, Clements Reef, and Skipjack Island. Disturbances caused by powerboats, bald eagles (*Haliaeetus leucocephalus*), and unknown sources were frequent, occurring on at least 71% of survey days during the pupping season. Harbor seals on Puffin Island only fully recovered after 19% of disturbances, compared to the other 2 locations, which had full recoveries after 54% and 45% of disturbances (Clements Reef and Skipjack Island, respectively). Puffin Island hosted a higher percentage of pups than the other locations, which could account for the increased apprehension after detection of a predator (Suryan and Harvey 1999).

Olson (2013) found that Salish Sea harbor seals occupying haul-out sites with frequent human exposure have become habituated to high levels of disturbance and exhibit less of an anti-predatory response than harbor seals at sites of low human exposure. Harbor seals at high anthropogenic exposure sites reacted (alert behavior or flushing into the water) to only 45.45% of bald eagle interactions compared to seals at low exposure sites, which reacted to 77.17% of bald eagle interactions. Habituated harbor seals save energy by not flushing into the water at the approach of (usually harmless) boat traffic. However, reduced sensitivity to disturbances increases the risk of natural predation (Olson 2013).

Scanning behavior of harbor seals has been studied outside the Salish Sea. On Prudence Island, Rhode Island, individual harbor seals scanned for themselves when in groups smaller than 7 seals (Norris 2007). In groups of 10 to 40 seals, there were approximately 2 to 4 constant scanners looking out for the whole group (Norris 2007). In the Bay of Fundy, where historically harbor seals have been terrestrially threatened by dogs, fishermen, and bounty hunters, harbor seals spend 82% of their time scanning their surroundings (Terhune 1985). However, individuals reduce that commitment to 27% of their time when in groups of 41 to 54 harbor seals (Terhune 1985).

Competition for haul-out space

Harbor seals engage in more aggressive encounters when haul-out space is limited. At a site with limited space in Humboldt County (California), harbor seals spent an average of 4.96 seconds per hour on agonistic behaviors, compared to 1.03 seconds per hour per seal at a site with virtually unlimited haul-out space (Neumann 1999). Social hierarchy and aggressive interactions are more pronounced when haul-out space is a limited resource (Neumann 1999).

Harbor seals defend their haul-out space by communicating with their forelimbs and muzzle. On Abalone Beach (California), 8 typical social signals were observed (Sullivan 1982). Submissive seals yielded to larger intruders with a “move away” signal. Aggressive behaviors included the “head up-stare,” “extended foreflipper,” “foreflipper wave,” “foreflipper scratch,” “growling,” “closed-mouth head thrust,” and the most aggressive “open-mouth head thrust.” These interactions sustained well-developed hierarchies, with large adult males dominating other individuals. Larger, older individuals typically displaced younger, smaller opponents in brief encounters. Different age groups utilized certain social signals more than others and encounters often included common two-step and three-step signal sequences (Sullivan 1982).

Home Range

Adults

Harbor seals are non-migratory, typically moving and foraging within 30 kilometers of primary haul-out sites in the Salish Sea (Peterson et al. 2012, DFO 2010). However, there is a high degree of individual variation in home range in adult harbor seals. Males have been documented to travel much farther than females. Using satellite tags, Peterson et al. (2012) tracked 20 wild adult seals in the San Juan Islands. The female harbor seals tracked during this study remained within 41.6 kilometers of the capture site, with some females traveling a maximum distance of only 6.0 kilometers from the capture site. Conversely, 8 males traveled more than 100 kilometers from the capture site at least once during the study period. Peterson et al. (2012) did not find any distinct pattern in these long-range movements; for example, 1 seal traveled from Bird Rocks in the San Juan Islands over 100 kilometers to southern Puget Sound 3 times, another seal traveled from Bird Rocks to Belle Chain and Quadra Island in British Columbia, and 2 seals traveled well over 200 kilometers to the outer coast of

Washington State. These trips over 200 kilometers lasted between 7 and 56 days and ended within 10 kilometers of the original capture site (Peterson et al. 2012).

Cunningham et al. (2009) observed similar trends in adult harbor seal movements in Scotland, also using satellite transmitters. Some harbor seals (unspecified sex) in this study traveled more than 9 days and 100 kilometers from the capture site, but 50% of trips were within 25 kilometers of a primary haul-out site and lasted only 12 to 24 hours (Cunningham et al. 2009).

Pups

A comparison of the movements of wild and rehabilitated harbor seal pups suggests that wild pups learn foraging behaviors within their first 32 days of life (pre-weaning) (Gaydos et al. 2012). Rehabilitated pups traveled nearly 3 times farther than wild pups on a daily basis and had less haul-out site fidelity than wild pups. Rehabilitated pups also ventured three times farther than wild pups, 98.9 to 324.9 kilometers from the release site (Gaydos et al. 2012). Wild pups learn to forage near their primary haul-out site and move less daily within their 3 to 6 week nursing period, the length of which varies by location (Cottrell et al. 2002, Stein 1989, Bigg 1969a, Scheffer and Slipp 1944).

Diving

Harbor seals in the San Juan Islands dive as deep as 90 meters and for as long as about 6 minutes (Wilson et al. 2014). The small, non-rotatable flippers that limit harbor seals to awkward shuffling on land allow harbor seals to be very agile swimmers (Riedman 1990). Williams and Kooyman (1985) measured speeds of harbor seals swimming in tanks, with averages ranging from 1 to 5 meters per second. The researchers also compared the drag of a swimming seal to that of a human and found that seals experienced 5 times less drag than human swimmers. The streamlined shape and mostly internalized limbs of seals allow them to be more efficient swimmers (Williams and Kooyman 1985).

Harbor seals have other adaptations to diving. Harbor seals can tolerate considerable carbon dioxide and lactic acid buildup in the blood (Walker 1999). Like other marine mammals, harbor seals can induce bradycardia, slowing their heart rate from 55 to 120 beats per minute to 4 to 15 beats per minute to conserve oxygen while diving (Walker 1999). Reducing blood circulation to peripheral blood vessels conserves oxygen for the brain and the heart (Walker 1999). Larger seals can dive deeper and for significantly longer time periods than smaller seals (McFarland 2013, Eguchi and Harvey 2005). Unlike more sexually dimorphic pinniped species, sex is not a factor in harbor seal diving ability, since males are only slightly larger than females (McFarland 2013, Bigg 1969a, Scheffer and Slipp 1944).

In the San Juan Islands and Hood Canal, harbor seals spend about 100 hours a week diving, amounting to around 1,500 dives at depths averaging between 10 meters and 50 meters (McFarland 2013). Suryan (1995) and Suryan and Harvey (1999) observed diving behavior of harbor seals in the San Juan Islands,

characterizing it as “milling” (foraging), traveling, resting, or spending time near shore. Suryan (1995) found that the average lengths of these dives were 4.00 to 6.22 minutes, 3.15 to 3.57 minutes, 2.88 minutes, and 1.52 to 3.59 minutes, respectively. The average depth of water while milling was 110 meters, while traveling and near shore activities occurred in water 70 meters and 40 meters deep, respectively (Suryan and Harvey 1999).

In Monterey Bay, California, 80% of observed dives of harbor seals were associated with foraging (Eguchi and Harvey, 2005). The deepest of these was 481 meters and the longest lasted 32.25 minutes, but average dive depth and duration were considerably shorter; seals most commonly foraged at intermediate depths of 50 to 200 meters for approximately 2 to 15 minutes. Heavier seals were found to dive deeper and longer on average than lighter seals, possibly resulting in vertical resource partitioning based on size (Eguchi and Harvey, 2005).

In Prince William Sound, Alaska, harbor seals exhibit seasonal variations in diving behavior (Frost et al. 2001). Between September and April seals spend up to 75% of the time in the water, corresponding with lower haul-out frequencies. The reverse is true throughout the late spring and summer months, when harbor seals spend 60% of their total time in water in May and only 40% in July. In September, harbor seals spend 80% of the night diving, while only 50% of July nights are spent diving. Dive depths are deepest during the winter when prey is found in deeper water (Frost et al. 2001).

Foraging

In the Salish Sea, harbor seals typically forage within 4 kilometers of primary haul-out sites throughout the day and night, but especially during flooding tides (Zamon 2001, Suryan and Harvey 1999, Suryan 1995). However, harbor seals also can undertake long distance trips to areas of seasonal prey abundance (Peterson et al. 2012). Peterson et al. (2012) documented adult male harbor seals from Bird Rocks in the San Juan Islands traveling more than 400 kilometers to the outer coast of Washington State, likely to follow prey. However, none of the 6 seals from Padilla Bay tracked in the same study traveled outside of their core haul-out areas, indicating that they had different foraging behavior than the Bird Rocks seals, foraging only locally (Peterson et al. 2012). During summer, seals use the relatively shallow waters in Padilla Bay as a preferred pupping and nursery area, which may explain the differences between rocky habitats in deep water and shallow estuaries as well (S Jeffries, Unpub. data).

Harbor seals seem to adjust their foraging behaviors according to their physical environment and prey availability. In one area near Cattle Pass in the San Juan Island, seals aggregated near a channel constriction where tidal currents concentrate prey during the incoming tide (Zamon 2001). Under these conditions, harbor seals foraged on maximum numbers of salmon and schooling fish (Zamon 2001). Suryan and Harvey (1999) also reported that harbor seals take advantage of the rip tides to help capture prey, as they noted that most foraging areas had a

shoaling seafloor and reefs, which create rip currents. Thomas et al. (2011) observed harbor seal foraging behavior relative to the seasonal spawning of herring (*Clupea pallasii*) in the Strait of Juan de Fuca. The study found that during the spawn season when adult herring cease to forage and lose mass, harbor seals consumed more juvenile herring, taking advantage of the lower handling cost associated with easily-caught juvenile herring, which provide a comparable amount of nutrition to spawn-season adult herring. However, post-spawn, harbor seals switched their diet to a higher proportion of adult herring as well as Pacific sand lance (*Ammodytes hexapterus*). Thomas et al. (2011) also observed a marked increase in nocturnal diving and regular foraging on buried sand lance after the spawning season (Pacific sand lance bury themselves in sand and gravel to avoid predation).

Navigation

Harbor seals are capable of celestial navigation and might orient themselves using lodestars while traveling at night if terrestrial landmarks are not available (Mauck et al. 2008). (Mauck et al. 2008) trained two harbor seals to locate the azimuth of a lodestar in a custom swimming planetarium with 100% accuracy. The harbor seals could locate the lodestar Sirius on a projection of approximately 6,000 stars of the northern hemisphere night sky, randomly oriented for each trial, and touch their snouts at Sirius' azimuth.

Diet

As generalist and opportunistic predators, harbor seals have a highly diverse diet, feeding on at least 60 different species of fish as well as several species of crustaceans and mollusks in the Salish Sea (Tables 1, 2 and 3). In one rare instance, birdwatchers witnessed a harbor seal attack and apparently consume a harlequin duck (*Histrionicus histrionicus*) near San Juan Island (Tallman and Sullivan, 2004). Remains of mammals (possibly American mink, *Neovison vison*) and unidentified nereid worms also have been detected in harbor seal scat (Luxa and Acevedo-Gutiérrez, 2013). Perhaps harbor seals are too generalist at times; between 2006 and 2011, 7 harbor seals were found dead, their esophagi or stomachs having been perforated by the poisonous dorsal fin spines of their lethal meal, the spotted ratfish (*Hydrolagus colliei*) (Akmajian et al. 2012). More benign fish species, including gadoids, herring, salmonids, and plainfin midshipmen, compose the bulk of the harbor seal diet seasonally (Luxa and Acevedo-Gutiérrez 2013, Lance et al. 2012, Olesiuk 1993, Everitt et al. 1981).

There are several different techniques researchers utilize to evaluate feeding habits of harbor seals. Scheffer and Sperry (1931) studied the diet of harbor seals by acquiring dead harbor seals, often with the help of bounty hunters, and identifying the contents of their stomachs. Scheffer and Slipp (1944) used stomach content analysis as well. In recent years, less invasive means of diet analysis have been developed, including scat analysis (e.g., Luxa and Acevedo-Gutiérrez 2013, Lance et al. 2012, Olesiuk 1993, Everitt et al. 1981) and fatty acid signature analysis of blubber samples (e.g., Bromaghin et al. 2013).

Table 1: Teleost fishes eaten by harbor seals

Family	Species	Publication
Agonidae	Unidentified poacher	C
Ammodytidae	Pacific sand lance, <i>Ammodytes hexapterus</i>	A, B, D, E, F
Anarhichadidae	Wolf eel, <i>Anarhichthys ocellatus</i>	D
Argentinidae	Argentines, unidentified argentinids	D
Bathymasteridae	Northern ronquil, <i>Ronquilus jordani</i>	D
Batrachoididae	Plainfin midshipman, <i>Porichthys notatus</i>	A, C, D, E, F
Bothidae	Unidentified Lefteye flounders	D
Clupeidae	Unidentified clupeid	B, C
	American shad, <i>Alosa sapidissima</i>	B, C, D
	Pacific herring, <i>Clupea pallasii</i>	A, C, D, E, F
	Pacific sardine, <i>Sardinops sagax</i>	C, D
Cottidae	Unidentified sculpins	C, E, F
	Buffalo sculpin, <i>Aspicottus bison</i>	D
	Great sculpin, <i>Myoxocephalus polyacanthocephalus</i>	F
	Irish lords, <i>Hemilepidotus</i> spp.	D
	Pacific staghorn sculpin, <i>Leptocottus armatus</i>	A, B, C, D, F
Cyprinidae	Northern pikeminnow, <i>Ptychocheilus oregonensis</i>	C
Cryptacanthodidae	Giant wrymouth, <i>Cryptacanthodes giganteus</i>	D
Embiotocidae	Unidentified surfperches	C, E, F
	Pile perch, <i>Rhacochilus vacca</i>	C, F
	Shiner perch, <i>Cymatogaster aggregate</i>	A, B, C, D, F
Engraulidae	Northern anchovy, <i>Engraulis mordax</i>	A, C, D
Gadidae	Unidentified gadid	B, C
	Pacific cod, <i>Gadus macrocephalus</i>	C, D, E, F
	Pacific tomcod, <i>Microgadus proximus</i>	D, E, F
	Walleye Pollock, <i>Theragra chalcogramma</i>	A, B, C, D, E, F
Gasterosteidae	Threespine stickleback, <i>Gasterosteus aculeatus</i>	C, D
Gobiidae	Unidentified goby	C
Hexagrammidae	Greenlings, Hexagrammid spp.	C, D
	Kelp Greenling (<i>Hexagrammos decagrammus</i>)	A
	Lingcod, <i>Ophiodon elongatus</i>	D, E, F
Liparidae	Snailfishes, unidentified liparidids	D
Merlucciidae	Pacific hake, <i>Merluccius productus</i>	D, E, F
Myctophidae	California headlight fish, <i>Diaphus theta</i>	D
	Northern lampfish, <i>Stenobranchius leucopsarus</i>	D
Osmeridae	Smelts, unidentified osmerids	C, D, E
	Eulachon, <i>Thaleichthys pacificus</i>	D
	Surf smelt, <i>Hypomesus pretiosus</i>	D
Pholidae	Unidentified gunnels	C, D

Pleuronectidae	Unidentified Righteye flounders	D
	Butter sole, <i>Isopsetta isolepis</i>	D
	Dover sole, <i>Microstomus pacificus</i>	D
	English sole, <i>Pleuronectes vetulus</i>	D
	Flathead sole, <i>Hippoglossoides elassodon</i>	F
	Pacific sand sole, <i>Psettichthys melanostictus</i>	D
	Rex sole, <i>Errex zachirus</i>	D
	Starry flounder, <i>Platichthys stellatus</i>	A, D
Pleuronectiformes ¹	Unspecified flatfishes	C, D, E, F
Salmonidae	Unspecified <i>Oncorhynchus</i> spp.	B, C, E, F
	Coho salmon, <i>Oncorhynchus kisutch</i>	A, D
	Chinook salmon, <i>Oncorhynchus tshawytscha</i>	A, B, D
	Chum salmon, <i>Oncorhynchus keta</i>	A, D
	Pink salmon, <i>Oncorhynchus gorbuscha</i>	A, D
	Sockeye salmon, <i>Oncorhynchus nerka</i>	A, D
Scombridae	Chub mackerel, <i>Scomber japonicas</i>	D
Sebastidae	Unidentified rockfishes	B, C, D, E, F
	Black rockfish, <i>Sebastes melanops</i>	A
	Copper rockfish, <i>Sebastes caurinus</i>	A
	Puget Sound rockfish, <i>Sebastes emphaeus</i>	A
	Yellowtail rockfish, <i>Sebastes flavidus</i>	A
Stichaeidae	Unidentified pricklebacks	C, D
	Snake prickleback, <i>Lumpenus sagitta</i>	C
Syngnathidae	Bay pipefish, <i>Syngnathus leptorhynchus</i>	C
Trichodontidae	Pacific sandfish, <i>Trichodon trichodon</i>	C
Zoarcidae	Unidentified eelpouts	C

¹Pleuronectiformes is an order, not a family, of flatfish.

Literature Cited: A: Bromaghin et al. 2013; B: Howard et al. 2013; C: Luxa and Acevedo-Gutiérrez, 2013; D: Lance et al. 2012; E: Olesiuk 1993; F: Scheffer and Sperry 1931.

Table 2: Chondrichthyes consumed by harbor seals

Family	Species	Publication
Chimaeridae	Spotted ratfish, <i>Hydrolagus colliei</i>	F
Elasmobranchii ²	Unidentified elasmobranch	C
Petromyzontidae	Unidentified lampreys	C, D
	Pacific lamprey, <i>Entosphenus tridentatus</i>	F
	River lamprey, <i>Lamptera ayresii</i>	C
Rajidae	Unidentified skates	B, C, D
Squalidae	Spiny dogfish, <i>Squalus acanthias</i>	A, D

²Elasmobranchii is a subclass of cartilaginous fishes that includes sharks, rays, and skates.

Literature Cited: A: Bromaghin et al. 2013; B: Howard et al. 2013; C: Luxa and Acevedo-Gutiérrez, 2013; D: Lance et al. 2012; E: Olesiuk 1993; F: Scheffer and Sperry 1931.

Table 3: Crustaceans and mollusks consumed by harbor seals

Classification	Species	Publication
Crustacea	Unidentified crustaceans	D, F
Callinassidae	Bay ghost shrimp, <i>Neotrypaea californiensis</i>	F
	Dungeness crab, <i>Metacarcinus magister</i>	F
	Graceful rock crab, <i>Metacarcinus gracilis</i>	F
Cancridae	Pygmy rock crab, <i>Glebocarcinus oregonensis</i>	F
Paguridae	Unidentified hermit crabs	F
Pandalidae	Prawn, <i>Pandalus danae</i>	F
Pinnotheroidea	Schmitt pea crab, <i>Pinnixa schmitti</i>	F
	Flattop crab, <i>Petrolisthes eriomerus</i>	F
	Porcelain crab, <i>Petrolisthes cinctipes</i>	F
Upogebia	Blue mud shrimp, <i>Upogebia pugettensis</i>	F
Varunidae	Yellow shore crab, <i>Hemigrapsus oregonensis</i>	F
Mollusca		
Capulidae	Unidentified snail	F
Cephalopoda	Unidentified cephalopod	C, E
	Clawed armhook squid, <i>Gonatus onyx</i>	D
	Magister armhook squid, <i>Berryteuthis magister</i>	D
Loliginidae	Opalescent Inshore squid, <i>Doryteuthis opalescens</i>	A, D
Octopodidae	Pacific red octopus, <i>Octopus rubescens</i>	D, F
Teuthida	Unidentified squid	C
Yoldiidae	Comb yoldia, <i>Yoldia myalis</i>	F

Literature Cited: A: Bromaghin et al. 2013; B: Howard et al. 2013; C: Luxa and Acevedo-Gutiérrez, 2013; D: Lance et al. 2012; E: Olesiuk 1993; F: Scheffer and Sperry 1931.

Impact on Depressed Fish Stocks

The Salish Sea has one of the highest densities of harbor seals in the world and numerous species of fish in decline, raising concern about the role of these predators in causing or exacerbating fisheries declines or hindering recovery of depleted fish stocks (Ward et al. 2012). Harbor seals consume 14 of the 31 fish species in the Salish Sea listed as threatened, endangered or candidate for listing and possibly prey upon more than the two rockfish (*Sebastes* spp.) species noted (Table 4; Gaydos and Brown 2011). In terms of biomass, salmonids, herring, and hake are the most important prey groups (Howard et al. 2013, Olesiuk 1993). Howard et al. (2013) used a bioenergetics model to estimate the impact of harbor seals in the San Juan Islands on prey species. The authors estimate that harbor seals consume 403 to 1,163 metric tons of salmonids and 343 to 949 metric tons of herring in the harbor seal breeding season, while consumption shifts to 283 to 1,063 metric tons of salmonids and 1,445 to 2,857 metric tons of herring during the non-breeding season. Olesiuk (1993) conducted a similar study of harbor seals in the Strait of Georgia in 1988, estimating annual consumptions of hake, herring, and salmonids to be 4,214 metric tons, 3,206 metric tons, and 398 metric tons, respectively. Rockfish is also

a significant prey group, comprising 58 to 110 metric tons consumed by harbor seals in the non-breeding season (Howard et al. 2013). Bromaghin et al. (2013) found that the harbor seal diet consists primarily of black and yellowtail rockfish, Chinook salmon, adult Pacific herring, and shiner perch. Understanding which rockfish species (in addition to black and yellowtail) are being consumed is critical for determining potential impact on rockfish recovery.

Table 4: Fish species of concern in the Salish Sea consumed by harbor seals* (modified from Gaydos and Brown, 2011)

Species	British Columbia	Washington State	Canada	U.S.A.
Eulachon (<i>Thaleichthys pacificus</i>)	Blue List	Candidate		Threatened
Pacific cod (<i>Gadus macrocephalus</i>), South & Central Puget Sound		Candidate		Species of Concern
Pacific hake (<i>Merluccius productus</i>), Puget Sound / Georgia Basin		Candidate		Species of Concern
Pacific herring (<i>Clupea pallasii</i>)		Candidate		
Pacific sardine (<i>Sardinops sagax</i>)			Species Concern (SARA ²)	
Rockfish, Black (<i>Sebastes melanops</i>)		Candidate		
Rockfish, Yellowtail (<i>Sebastes flavidus</i>)		Candidate	Candidate (COSEWIC)	
Salmon, Chinook (<i>Oncorhynchus tshawytscha</i>), no DPS or ESU ³			Candidate (COSEWIC)	
Salmon, Chinook (<i>Oncorhynchus tshawytscha</i>), Puget Sound		Candidate		Threatened
Salmon, Chum (<i>Oncorhynchus keta</i>), no DPS or ESU			Candidate (COSEWIC)	
Salmon, Chum (<i>Oncorhynchus keta</i>), Summer Run Hood Canal		Candidate		Threatened
Salmon, Coho (<i>Oncorhynchus kisutch</i>), no DPS or ESU			Candidate (COSEWIC)	
Salmon, Coho (<i>Oncorhynchus kisutch</i>), Interior Frasier River			Endangered (COSEWIC)	
Salmon, Coho (<i>Oncorhynchus kisutch</i>), Puget Sound and Strait of Georgia				Species of Concern
Salmon, Pink (<i>Oncorhynchus gorbuscha</i>)			Candidate (COSEWIC)	
Salmon, Sockeye (<i>Oncorhynchus nerka</i>), Cultus Lake			Endangered (COSEWIC)	
Salmon, Sockeye (<i>Oncorhynchus nerka</i>), Fraser River Drainage			Candidate (COSEWIC)	
Salmon, Sockeye (<i>Oncorhynchus nerka</i>), Sakinaw Lake			Endangered (COSEWIC)	
Surf Smelt (<i>Hypomesus pretiosus</i>)			Candidate (COSEWIC)	
Walleye Pollock (<i>Theragra chalcogramma</i>), S. Puget Sound		Candidate		

*Species of concern in the Salish Sea are evaluated through different protocols by British Columbia, Washington State, Canada, and the United States. The terms “Blue List,” “Candidate,” “Endangered,” “Special Concern,” “Threatened,” and “Species of Concern” all indicate a need for conservation but at varying levels beyond the scope necessary for this paper. Please refer to “Species of Concern within the Salish Sea: changes from 2002 to 2011” (Gaydos and Brown, 2011) for further information.

¹Committee on the Status of Endangered Wildlife in Canada

²Species at Risk Act

³Distinct population segment; Evolutionarily Significant Unit

Reproduction

Mating

Harbor seals are mildly polygynous (Hayes et al. 2006, Sullivan 1982). The environments occupied by harbor seals do not promote terrestrial territoriality or harem formation as mating systems (Sullivan 1982). Male harbor seals cannot effectively establish and defend territories or harems on land due to the limited space available on many haul-out sites, nor in water, a boundless, airless, three-dimensional medium. Similarly, females cannot aggregate when the tide forces them to abandon a haul-out site and they must constantly surface for air while in the water (Sullivan 1982). Females also become highly dispersed, up to 45 kilometers from the primary haul-out site, as they resume foraging at the end of lactation and beginning of the mating season (Thompson et al. 1994).

Mating begins after weaning, usually in September or October depending on the location (Bigg 1969a, Scheffer and Slipp 1944). Sullivan (1981) describes aquatic displays and their possible role in mating. Adult male harbor seals interact in aquatic displays at the water's surface, which are thought to be sparring sessions to attract females. These interactions last an average of about 5 minutes and include rolling, flipper splashing, lobtailing, scratching, mounted riding, biting, growling, and bubble blowing. A receptive female can assess the fitness of males in these sessions and may instigate an aquatic encounter with a male. These male-female interactions resemble male-male interactions, but are generally less aggressive, last between 17 and 74 minutes, and the male does all riding (Sullivan 1981). Copulation is believed to occur underwater (Sullivan 1981, Thompson et al. 1994).

Male harbor seals in British Columbia become sexually mature between 3 and 6 years of age and are sexually active, having sperm in the tubules of the epididymis, from March through November, although most mating occurs only in September (Bigg 1969a). Average male harbor seals might sire 1 pup per year, while more successful males may father 2 pups per year. Females become sexually mature between 2 and 5 years of age and ovulate mostly in September (Bigg 1969a) and are limited to carrying 1 pup per year (Hayes et al. 2006). After fertilization, implantation and development of the blastocyst is arrested for about 2.5 months until about mid-November in what is termed embryonic diapause, or delayed implantation (Temte 1985, Bigg 1969a). Older females may have higher fecundity than younger females. Bigg (1969a) examined 66 adult female harbor seals, in which implantation had taken place. Females aged 2 to 7 years had 80% fecundity while individuals 8 to 29 years old had 97% fecundity (Bigg 1969a).

Pupping

Bigg (1969b) describes clines in pupping seasons across the range of *Phoca vitulina*. Along the Asian coast, the pupping season occurs from late January to mid-April in Japan and from late April to early May in the Commander Islands (Russia). A similar trend is present on the east coast of North America, with the

pupping season occurring later in the north than in the south. Pupping occurs in New England from late March to early June, while pups are born from late June to early July on Baffin Island. A recognizable pupping cline does not exist in European harbor seals. On the west coast of North America, pupping occurs progressively later from Alaska to Washington and progressively earlier from Washington to Mexico (Bigg 1969b). Within the Salish Sea, pups are born an average of 88 days later than pups born on Washington's outer coast (Temte 1985). The Washington Department of Fish and Wildlife Harbor Seal Pupping Timeframes in Washington State (Seekins 2009) shows the annual pupping seasons by region (Fig. 2). In the San Juan Islands, premature harbor seal pups with lanugo fur have been sighted as early as 4 May and as late as 11 July. The first full term pups were born in the second week in June and first week in September, but most pupping took place between late June and early July (Suryan 1995). The highest numbers of harbor seals can be seen ashore in the San Juan Islands during the last week of July and the first week of August (Suryan 1995). Consistency in the date of parturition has been documented in captive harbor seals. A captive female harbor seal gave birth to 4 pups in 5 years and parturition dates had a range of only 3 days (Temte 1985).

Pupping in Atlantic harbor seals (*P. v. concolor*) has been observed in detail on the Island of Miquelon, 19 kilometers southeast of Newfoundland, by Lawson and Renouf (1985). Parturition occurred on land between 6:00 am and 4:25 pm during low tide. Females ready to give birth, having an obviously rounded belly, were very alert. A female in the birthing position lay on her belly with the vaginal slit and hind flippers raised slightly and foreflippers held close to her sides. In 80% of births observed, the pup's head emerged first and was still enclosed within the amniotic sac. One pup was born hind flippers first and one emerged with its left side first. Duration of labor varied from 38 seconds to 21 minutes with a mean duration of 3.5 minutes. Females delayed delivery after being disturbed by an approaching seal in 8 instances, 3 of which continued to parturition after the female relocated and resumed labor after a few minutes. In the other 5 cases, the female halted delivery and entered the water, presumably to attempt birthing at another time (Lawson and Renouf 1985).

Pups are precocious and quite active immediately after birth (DFO 2010, Jeffries et al. 2000). For pups born on the Island of Miquelon (Newfoundland), pups first nursed between 3 and 138 minutes after parturition with an average time of 40.1 minutes, depending on how well the pup could crawl and locate its mother's nipple (Lawson and Renouf 1985). Nursing bouts of pups on Gertrude Island in southern Puget Sound lasted an average of 72.5 seconds and pups nursed every 3 to 4 hours (Newby 1973). Vocalizations begin several hours after birth (Lawson and Renouf 1985). Vocalizations of pups on Gertrude Island in Washington State sound like "ma-a-a" or "kroo-roo" (Newby 1973). A harbor seal pup ringtone can be downloaded at www.seadocsociety.org. Pups are hesitant at first to enter the water but as the tide covers their intertidal haul-out site, they soon swim with their

mothers and can be seen riding on their mothers' backs during their first few weeks of life (Lawson and Renouf 1985).

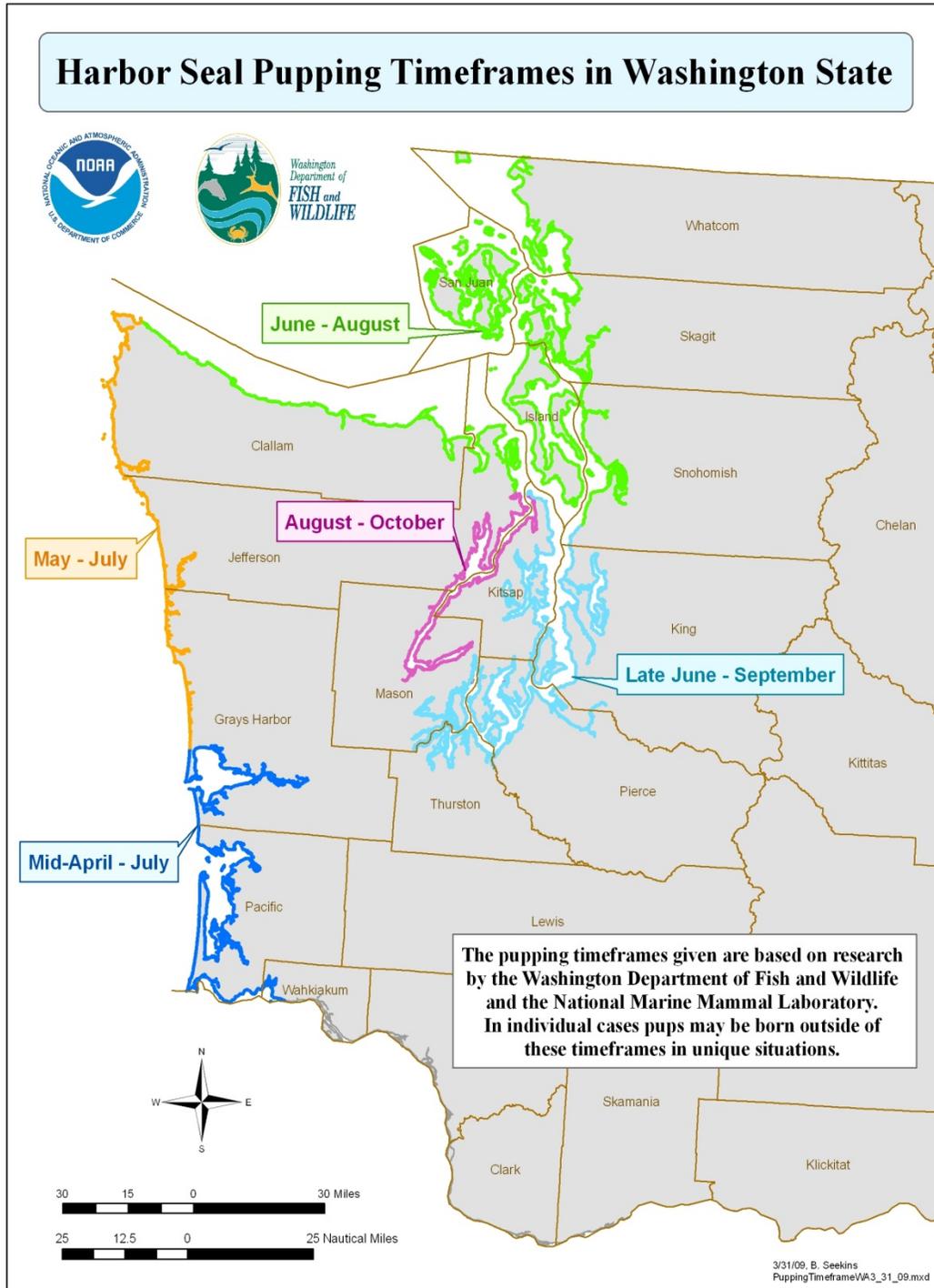


Figure 2: Harbor Seal Popping Timeframes in Washington State (Seekins 2009)

Pup development

Harbor seals pups born in the Salish Sea weigh on average between 10.9 and 11.5 kilograms (Cottrell et al. 2002). Males weigh approximately 3.7% to 4.6% more than females at birth, a sign of early sexual dimorphism, but males and females gain mass at equal rates (Bowen et al. 2001, Ellis et al. 2000, Bowen et al. 1993). Roughly 20% of pups are born with lanugo, the fetal hair typically molted in-utero before birth. These animals are generally smaller, weighing between 9.4 and 10.2 kilograms (Cottrell et al. 2002).

The nursing period for *P. v. richardii* spans 30.5 to 33.5 days, which corresponds with neonatal growth rates of 0.368 to 0.420 kilograms per day (Cottrell et al. 2002). Typical girth and length of harbor seal pups at birth are 52.4 to 55.6 centimeters and 76.1 to 79.9 centimeters, respectively, and girth increases at a rate of 5.8 to 7.0 millimeters per day during the nursing period (Cottrell et al. 2002). *P. v. richardii* pups in rehabilitation, however, are fed an artificial milk replacer formula and gain weight much slower than wild pups, at an average rate of 0.211 kilograms per day (Fig. 3; Briese et al. 2012). In contrast, *P. v. concolor* residents of Sable Island, Nova Scotia, manifest a daily mass gain twice as large as wild *P. v. richardii* pups and consequently nurse over a shorter period (Bowen et al. 2001).

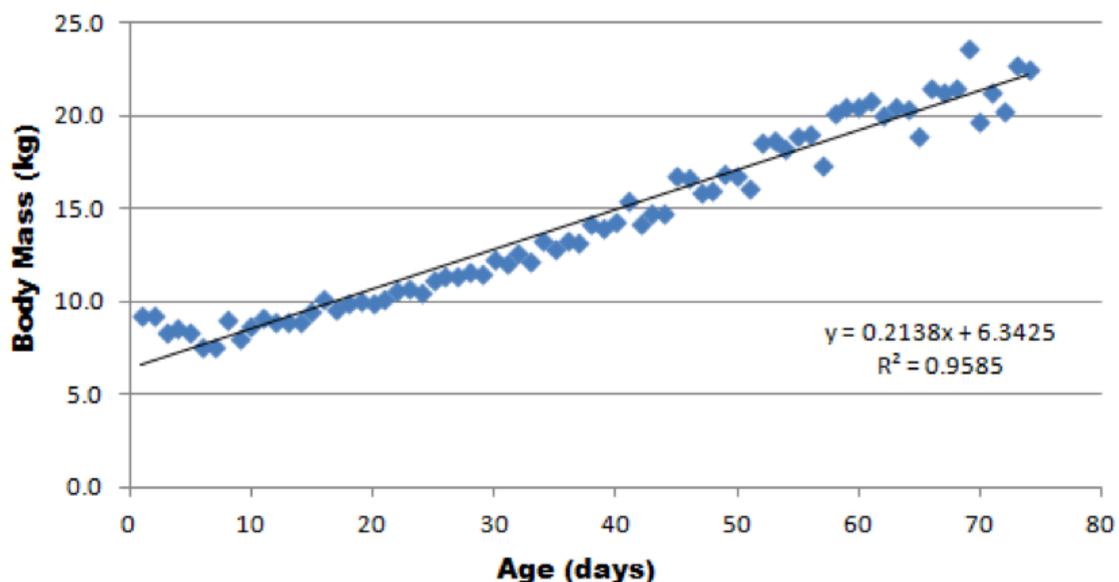


Figure 3: Growth rates of captive harbor seal pups at Wolf Hollow Rehabilitation Center, 0 to 75 days (Briese et al. 2012)

In the Salish Sea, pups are weaned at an average mass of 24 kilograms (Bowen et al. 2001, Bigg 1969a). Male pups are around 7.1% heavier than females at

weaning age (Bowen et al. 2001). Pups fast for the 14 to 17 days after weaning and lose 21% of weaning mass by 5 weeks post-weaning. By about a month after weaning, the content of pup body fat decreases from 32.8% to 12% while water content increases from 47.7% to 63.0% (Muelbert and Bowen 1993).

Adult harbor seals have a dental formula of (i 3/2, c 1/1, pc 5/5) X 2 = 34. Information about harbor seal dental eruption is scarce. Pups can have resorbing deciduous teeth at birth (Meyer and Matzke 2004; Scheffer and Slipp 1944). The deciduous teeth have vestigial characteristics, developing rapidly yet incompletely when the harbor seal fetus is three months old. Deciduous teeth can last up to 4 weeks post-parturition (Meyer and Matzke 2004) and are quickly replaced by permanent teeth to facilitate normal feeding after the very short nursing period (Meyer and Matzke 2004).

Maternal effects on pup health

Maternal age has a large impact on pup health and pup birth mass increases with maternal age (Bowen et al. 2001, Ellis et al. 2000). In a study of harbor seals on Sable Island, Nova Scotia, 13 out of 14 premature pups (with lanugo coats) were born to young, primiparous mothers early in the season and weighed 20% less than non-lanugo pups (Ellis et al. 2000). Smaller, premature pups are likely to have less subcutaneous fat than normal full term pups and may have increased energy expenditures to offset thermal losses due to their high surface to volume ratio. Combined, these factors present significant challenges for small pups (Bowen et al. 1993). At the same study site on Sable Island, pups of young females aged 4 to 6 years gained mass at a lower rate (0.56 kilograms per day) than pups of older females, which grew at a rate of 0.74 to 0.78 kilograms per day through mid-lactation (Bowen et al. 1993).

Pup effects on maternal health

Female harbor seals lose an average of 30.8 kilograms during lactation at a rate of 0.7 to 2.0 kilograms per day with young females losing about 2.5 kilograms more than older females overall (Bowen et al. 2001). This is primarily a consequence of the high percentage of milk fat in the seal's milk and the energetic costs of lactation. In female harbor seals on Sable Island, Nova Scotia, milk fat content was 40.8% at parturition but increased to 50.2% by the first week after parturition and remained constant throughout lactation (Lang et al. 2005). Protein content averaged 9% throughout lactation (Lang et al. 2005). The milk fat content of females separated from their pups for 4 to 6 days decreased by 20% to 23% while the milk protein content increased by 6% to 11%, representing a rapid response in mammary gland function when nursing stops and suggesting that females cannot leave pups to forage for long time periods without negatively affecting pup growth (Lang et al. 2005).

Mother-pup interactions

Fostering

Stein (1989) observed mother-pup interactions in Grays Harbor and noted that abandoned harbor seal pups frequently attempted to nurse with another female

but were usually rejected. Sometimes females would bite or shake the abandoned pups. Some pups were successful in nursing from unaware, sleeping females for more than 30 seconds (Stein 1989).

On Sable Island, Nova Scotia, approximately 10% of females foster pups during the lactation period (Boness et al. 1992). Only females who had lost their own pups fostered and females only cared for one pup at a time, although pups were sometimes cared for by more than two females (Schaeff et al. 1999, Boness et al. 1992). Younger females became separated from their pups more often than older females. At the study site in Nova Scotia, most separations occurred within a day of a storm, with strong wind causing surface currents, swells, and noise (Boness et al. 1992).

Schaeff et al. (1999) investigated fostering behavior as kin selection in a population of harbor seals on Sable Island, Nova Scotia. Kin selection does not seem to be the driving force behind harbor seal fostering behavior. Breeding harbor seals display high natal philopatry, returning to their birthplace to breed. However, related individuals do not cluster within colonies. Because relatives were not grouped together, there was a very low chance that a female would preferentially choose a relative pup to foster, thereby increasing her own inclusive fitness. However, the study colony had a high level of relatedness; this could be a sign of a bottleneck event or perhaps kin selection acting at the level of the colony (Schaeff et al. 1999).

Diving and Foraging

Precocious harbor seal pups begin swimming and diving soon after birth. However, the muscles of young pups are not fully developed until well after weaning (Prewitt et al. 2010). Pup muscle has relatively poor aerobic and anaerobic performance (due to low levels of myoglobin and the enzymes citrate synthase and lactate dehydrogenase necessary for respiration), contributing to immature diving ability. Muscle biochemistry develops as the pup grows and practices diving, eventually reaching the muscle endurance typical of adult harbor seals (Prewitt et al. 2010).

During lactation, female harbor seals on Sable Island spent 55.4% of time at sea while pups spent 39.8% of time at sea. Mothers and pups began diving within 3 days after parturition, especially at night through the early morning. Dives lasted between 1 and 2.25 minutes, although dive durations were slightly shorter for pups. Females sometimes dove solo, but pups never dove without their mothers (Bowen et al. 1999).

Threats

Historic Culling

Harbor seal abundance was reduced drastically in British Columbia and Washington State from the 1870s until the 1970s. Washington's culling program was instituted to protect commercial and sport fishermen (Huber and Laake 2002). In British Columbia, harbor seals were killed for pelts from 1879 to 1914 and from 1962 to 1968, with at least 172,649 pelts harvested commercially during these periods (Olesiuk 2010). Harbor seals in British Columbia were also killed for population control as a bounty program from 1914 until June 30, 1964, with at least 114,903 bounties paid for seal snouts (Olesiuk 2010). After the bounty program ended, at least another 5,500 harbor seals were killed by Canadian Department of Fisheries and Oceans (DFO) staff for predator control (Olesiuk 2010). These figures are low estimates of the total number of harbor seals killed; after they are shot, harbor seal carcasses often sink. Recovery rates of killed harbor seals have been estimated to be between 48% and 75%, indicating that at least 0.5 million harbor seals were killed between 1879 and 1970, reducing the total abundance of harbor seals in British Columbian waters to a mere 10,000 by the late 1960s (Olesiuk 2010). Between 1943 and June 30, 1960, an estimated 17,133 harbor seals were killed in Washington State, this figure accounting for a 40% pelt recovery rate (NOAA 2003, Newby 1973). In the early 1940s, harbor seals may have numbered up to 10,000 in Washington State (Scheffer and Slipp 1944). Canadian harbor seals were protected in 1970 (Olesiuk 2010). In the U.S., the Marine Mammal Protection Act of 1972 mandates that marine mammal populations including harbor seals should not fall below optimum sustainable numbers.

Culling programs of marine mammals are typically instituted to protect commercially valuable fish stocks from predators, however a review of marine mammal culls found that the impacts of culling on prey populations have never been evaluated (Bowen and Lidgard 2013). They found that while culls can significantly reduce predator density, they most often are enacted without measurable objectives in place. Predator-prey interactions are often complex, so culls can have unintended consequences. It is unknown what effects the culling programs in British Columbia and Washington State had on fisheries and the ecosystem at large (Bowen and Lidgard 2013).

Predation

The most significant predators of harbor seals within the Salish Sea are marine mammal-eating transient, or Bigg's, killer whales (*Orcinus orca*) (Ford et al. 2000, Scheffer and Slipp 1944). Sightings of transient killer whales, especially near shore and haul-out sites, peak during the harbor seal pupping season due to increased prey availability (Baird and Dill 1996). During 434 hours of observations, Baird and Dill (1996) observed 138 attacks of transient killer whales on marine mammals, 130 of which were successful attacks on harbor seals. Harbor seal pups were the most vulnerable to transient killer whale attack, with pups accounting for 34/57 of harbor seals whose ages could be determined,

while 12/57 were adults and 11/57 were juveniles (Baird and Dill 1996). Transient killer whales may also kill harbor seals for purposes other than consumption, perhaps as surplus killing or play behavior (Gaydos et al. 2005).

In 2003 and 2005, transient killer whales foraged in Hood Canal, an infrequent occurrence. London et al. (2012) found a marked response in Hood Canal harbor seals to the arrival of killer whales. In 2005, harbor seals hauled-out 40% to 50% more compared to 2002 to avoid killer whales, and after the departure of the whales, haul-out frequency returned to pre-2005 levels (London et al. 2012). Killer whales are large-scale predators, needing nearly 300,000 kilocalories per day for basic metabolic demands; a pod of killer whales has the power to wipe out whole populations of small marine mammals (Williams et al. 2004). Luckily for Salish Sea harbor seals, resident pods of killer whales primarily consume fish, not harbor seals (London et al. 2012).

Sharks are a significant predator of harbor seals outside of the Salish Sea (Scheffer and Slipp 1944). Great white sharks (*Carcharodon carcharias*) feed primarily on pinnipeds, including harbor seals (Anderson et al. 2008, Scheffer and Slipp 1944). Pacific sleeper sharks (*Somniosus pacificus*), another harbor seal predator, are hypothesized by Taggart et al. (2005) to be contributing to the large decline in harbor seal populations in Glacier Bay, Alaska, over the past decade. However, harbor seals composed only a small percentage (3.1% mass) of sleeper shark diet in a study in the Gulf of Alaska (Sigler et al. 2006).

Recently, Steller sea lions (*Eumetopias jubatus*) emerged as a predator of harbor seals in Glacier Bay, Alaska (Mathews and Adkison 2010). The Glacier Bay harbor seal population declined 65% from 1992 to 2002, and Steller sea lions are thought to be contributors to that decline. Mathews and Adkison (2010) noted 13 direct observations of Steller sea lion attacks on harbor seals in which the sea lions usually bit and flung the seal violently from side to side. Observers reported that the events lasted between 20 and 60 minutes, involved lots of blood and ripping of tissue, and ended with the sea lions chewing and swallowing the harbor seal meat. The authors hypothesize that observed rates of Steller sea lion predation could remove approximately 33% of harbor seal pups in some years, but could not be solely responsible for the 12.4% rate of decline in the harbor seal population from 1992 to 2008. However, harbor seals may have suffered from reduced fitness due to efforts of predator avoidance. Harbor seals may be subsisting on nutritionally inferior food sources as a result of avoiding Steller sea lions at optimal foraging locations (Mathews and Adkison 2010). Steller sea lions are not known to prey on harbor seals in the Salish Sea, but the two species overlap spatially in the area, presenting the opportunity for such an occurrence.

While hauled-out, harbor seals are vulnerable to terrestrial predators. Steiger et al. (1989) found a high rate of coyote (*Canis latrans*) predation on harbor seal pups hauled-out on Gertrude Island in southern Puget Sound. Harbor seal carcasses are eaten by a variety of terrestrial scavengers, including turkey

vultures (*Cathartes aura*) and bald eagles (*Haliaeetus leucocephalus*) (Steiger et al. 1989) and these animals have been seen picking at moribund seal pups. Depending on the location of seals within the Salish Sea, other terrestrial predators may include Grizzly and Black bears (*Ursus arctos horribilis* and *Ursus americanus*, respectively), wolves (*Canis lupus*), and domestic dogs (*Canis lupus familiaris*) (London et al. 2012).

Disease

Like all mammals, harbor seals can be infected with a variety of infectious diseases. Based on data from dead harbor seal pups collected at various haul out sites in Washington State, Steiger et al. (1989) found that the primary causes of harbor seal pup death were premature parturition, starvation, terrestrial predation, and human caused mortality. Table 5 details some of the pathogens that have been reported to infect harbor seals. Some of these diseases are zoonotic and can be transmitted to humans. Others have the capability to be transmitted to domestic or other wild species.

Table 5: Pathogens identified in harbor seals

Pathogen	Wild (Salish Sea)	Wild (Elsewhere)	Captive
Viruses			
Coronavirus		Harbor Seal Coronavirus California (Nollens et al. 2010)	
Eastern equine encephalitis virus			Zoo Massachusetts (McBride et al. 2008)
Influenza A		H7N7, New England coast (Geraci et al. 1982), H4N5, New England coast (Hinshaw et al. 1984), H4N6 & H3N3, New England coast (Callan et al. 1995), H3N8, New England (Anthony et al. 2012)	
Influenza B		Netherlands (Osterhaus et al. 2000)	
Dolphin Morbillivirus		Netherlands (Osinga et al. 2012), Japan (Fujii et al. 2006)	Zoos & Aquariums USA (Clancy et al. 2013)
Phocine Herpesvirus-1	Himworth et al. 2010	PhHV-1 Netherlands (Maness et al. 2011), East & West Coast US and Canada (Goldstein et al., 2003)	Rehabilitation centers coastal North East Pacific (Himworth et al. 2010)
Seal anellovirus		California (Ng et al. 2011)	
Sealpox virus (parapox)	Raverty et al., 2011; Nollens et al. 2006	USA (Pacific & Atlantic) (Roess et al. 2011), North Sea (Becher et al. 2002)	Rehabilitation centers USA (Roess et al. 2011), Rehabilitation center Germany (Becher et al. 2002)
West Nile Virus			Aquarium New Jersey (Del Piero et al. 2006)

Bacteria			
<u>Gram positive</u>			
<i>Arcanobacterium spp.</i>	Lockwood et al. 2006	<i>A. phocae</i> Scotland (Ramos et al. 1997), California (Johnson et al. 2003)	
β -hemolytic <i>Streptococcus spp.</i>	Lockwood et al. 2006	North Sea (Vossen et al. 2004), California (Thornton et al. 1998)	
<i>Clostridium perfringens</i>		Germany (Siebert et al. 2007)	(Dierauf & Gulland 2001)
<i>Corynebacterium spp.</i>	<i>C. pseudotuberculosis</i> Lockwood et al. 2006	California (Thornton et al. 1998), Germany (Siebert et al. 2007), Scotland (Munro et al. 1992)	
<i>Enterococcus spp.</i>	Lockwood et al. 2006	California (Thornton et al. 1998)	
<i>Erysipelothrix rhusiopathiae</i>		Sweden (Eriksson et al. 2009), Germany (Siebert et al. 2007)	(Opriessnig et al. 2013)
<i>Listeria ivanovii</i>		California (Thornton et al. 1998)	
Methicillin Resistant <i>Staphylococcus aureus (MRSA)</i>	Raverty et al. 2011	California (Fravel et al. 2011)	Sanctuary Ireland (Fravel et al. 2011)
<i>Staphylococcus epidermidis</i>		Germany (Siebert et al. 2007)	
<i>Staphylococcus aureus</i>	Kersh et al. 2012	UK (van Elk et al. 2012), California (Thornton et al. 1998)	Rehab center California (Thornton et al. 1998), Rehab center Alaska (Van Pelt and Dieterich, 1973)
<i>Streptococcus spp.</i>	α -hemolytic strep Steiger et al. 1989	<i>S. viridans</i> , California (Thornton et al. 1998), <i>S. zooepidemicus</i> , Germany (Siebert et al. 2007), <i>S. phocae</i> , Norway (Hassan et al. 2006)	
<u>Gram negative</u>			
<i>Acholeplasma spp.</i>		Baltic & North Seas (Giebel et al. 1991)	
<i>Acinetobacter spp.</i>	Steiger et al. 1989	<i>A. baumannii</i> California (Thornton et al. 1998)	
<i>Aeromonas spp.</i>	Lockwood et al. 2006	<i>A. hydrophila</i> California (Thornton et al. 1998)	Rehabilitation center California (Thornton et al. 1998), <i>A. hydrophila</i> , Zoo in Padua, Italy (Mazzariol et al. 2013)
<i>Bartonella spp.</i>			Rehabilitation center Netherlands (Morick et al. 2009)
<i>Bisgaardia spp.</i>		California (Hansen et al. 2013), UK (Sundeep et al.	Zoos & Aquariums Canada, Holland, Denmark (Hansen et

		2011)	al. 2012)
<i>Bordetella bronchiseptica</i>		Scotland (Munro et al. 1992)	
<i>Brucella pinnipedialis</i>	Lambourn et al., <i>In Press</i> ; Garner et al. 1997	SE Alaska (Hueffer et al. 2013), Scotland (Garner et al. 1997), North Sea (Prenger-Berninghoff et al. 2008), New England coast (Maratea et al. 2003)	
<i>Chryseobacterium spp.</i>	Lockwood et al. 2006		
<i>Citrobacter spp.</i>	Lockwood et al. 2006	<i>C. diversus</i> California (Thornton et al. 1998)	
<i>Coxiella burnetii</i>	Kersh et al. 2012	Pacific Northwest (Kersh et al. 2012), California (Lapointe et al. 1999)	
<i>Edwardsiella tarda</i>		California (Thornton et al. 1998)	
<i>Enterobacter spp.</i>	Lockwood et al. 2006	California (Thornton et al. 1998)	
<i>Escherichia coli</i> [^]	Lockwood et al. 2006	California (Thornton et al. 1998), Germany (Siebert et al. 2007)	Rehab centers (Thornton et al. 1998)
<i>Klebsiella spp.</i> [^]	Lockwood et al. 2006	California (Thornton et al. 1998)	
<i>Leptospira spp.</i>	Lambourn et al., 1998 (antibodies)	Alaska (Hueffer et al. 2011), California (Stevens et al. 1999)	Rehab center California (Stamper et al. 1998), Rehab center Netherlands (Kik et al. 2006)
<i>Moraxella spp.</i>		California (Thornton et al. 1998)	Rehab center California (Thornton et al. 1998)
<i>Morganella morganii</i>	Lockwood et al. 2006	California (Thornton et al. 1998)	Rehab center California (Thornton et al. 1998)
<i>Mycoplasma spp.</i>		New England coast (Geraci et al. 1982), Baltic & North Seas (Giebel et al. 1991)	Sanctuary in UK (Ayling et al. 2011)
<i>Pasteurella spp.</i>	Lockwood et al. 2006	<i>P. multocida</i> California (Johnson et al. 1998)	Dolfinarium Holland (Hansen et al. 2012)
<i>Plesiomonas shigelloides</i>		California (Thornton et al. 1998)	
<i>Proteus spp.</i>	Lockwood et al. 2006	California (Thornton et al. 1998)	Rehab center California (Thornton et al. 1998), Rehab center Alaska (Van Pelt and

			Dieterich 1973)
<i>Providentia stuartii</i>		California (Thornton et al. 1998)	
<i>Pseudomonas spp.</i>	<i>P. aeruginosa</i> Lockwood et al. 2006	California (Thornton et al. 1998)	Rehab center California (Thornton et al. 1998), Rehab center Alaska (Van Pelt and Dieterich 1973)
<i>Salmonella spp.</i>		California (Thornton et al. 1998)	
<i>Serratia liquefaciens</i>		California (Thornton et al. 1998)	
<i>Serratia marcescens</i>	Lockwood et al. 2006		
<i>Shewanella spp.</i>	Lockwood et al. 2006		
<i>Vibrio spp.</i>		California (Hughes et al. 2013, Thornton et al. 1998) <i>V. damsela</i> Germany (Siebert et al. 2007)	Rehab center California (Thornton et al. 1998)
Gram indeterminate (acid fast)			
<i>Mycobacterium avium</i>		Scotland (Foster et al. 2013)	
Fungi			
<i>Candida spp.</i>			Zoo in Japan (Higgins et al. 2000), Tennessee (Pollock et al. 2000)
<i>Trichophyton mentagrophytes</i>			Zoo in Tennessee (Pollock et al. 2000)
Parasites			
Acanthocephalans			
<i>Bolbosoma spp.</i>		Bering Sea* northern fur seals (Kuzmina et al. 2012)	
<i>Corynosoma spp.</i>	Garner et al. 1997	Alaska (Shults et al. 1982), Oregon (Stroud et al. 1978), <i>C. strumosum</i> Western & Eastern Atlantic (Leidenberger et al. 2007)	
Cestodes			
<i>Anophryocephalus ochotensis</i>		Alaska (Shults et al. 1982)	
<i>Diphyllobothrium cordatum</i>		Eastern Atlantic (Leidenberger et al. 2007)	

<i>Diphyllobothrium elegans</i>		Eastern Atlantic (Leidenberger et al. 2007)	
Nematodes			
<i>Acanthocheilonema (Dipetalonema) spirocauda</i>		New England coast (Geraci et al. 1982), German & Danish North Sea, Baltic, Wadden, Irish Sea, Iceland, Netherlands, Sweden, Japan, Nova Scotia, Oregon, Gray's Harbor WA, East & West Atlantic (Leidenberger et al. 2007), Alaska & Bering Sea (Shults et al. 1982), California, Atlantic Canada (Dunn & Wolke 1976), Oregon (Stroud et al. 1978)	Zoo Washington (MacDonald et al. 1969), Marineland California (Taylor et al. 1961)
<i>Diriofilaria immitis</i>			In endemic areas (Dierauf & Gulland 2001, Medway & Wieland 1975)
<i>Parafilaroides spp.</i>	Lambourn et al., In Press (see pub for species); Garner et al. 1997	<i>P. gymnurus</i> in Netherlands (Osinga et al. 2012), Baltic & North Seas (Lehnert et al. 2010), <i>P. gymnurus</i> West & East Atlantic (Leidenberger et al. 2007)	
<i>Otostrongylus circumlitus</i>	Lambourn et al., In Press	Netherlands (Osinga et al. 2012), New England coast (Geraci et al. 1982), Baltic & North Seas (Lehnert et al. 2010), California (Elson-Riggins et al. 2004), West & East Atlantic (Leidenberger et al. 2007)	
<i>Diocotophyme renale</i>		New Jersey (Hoffman et al. 2004)	
<i>Anisakis simplex</i>		Oregon (Stroud et al. 1978), East & West Atlantic (Leidenberger et al. 2007)	
<i>Contraecaecum osculatum</i>		Germany (Siebert et al. 2007), Oregon (Stroud et al. 1978), Eastern & Western Atlantic (Leidenberger et al. 2007)	
<i>Phocasaris cystophorae/spp.</i>		Eastern & Western Atlantic (Leidenberger et al. 2007)	
<i>Pseudoterranova (Phocanema) decipiens</i>		Atlantic Canadian Coast (McClelland et al. 1980), Germany (Siebert et al. 2007), California (Nadler et al. 2005), Norway (Aspholm et al. 1994), Oregon (Stroud et al. 1978), West & East Atlantic (Leidenberger et al. 2007)	

Trematodes			
<i>Cryptocotyle lingua</i>		Eastern Atlantic (Leidenberger et al. 2007)	
<i>Phagicola septentrionalis</i>		Eastern Atlantic (Leidenberger et al. 2007)	
<i>Pricetrema zalophi</i>		Oregon (Stroud et al. 1978)	
<i>Rossicotrema venustum</i>		Oregon (Stroud et al. 1978)	
Protozoa			
Coccidia "C"	Gibson et al., 2011		
<i>Cryptosporidium spp.</i>		Maine (Bass et al. 2012)	
<i>Eimeria phocae</i>		Western & Eastern Atlantic (van Bolhuis et al. 2007)	Rehab center Netherlands (van Bolhuis et al. 2007), University Maryland (Hsu et al. 1974)
<i>Giardia duodenalis</i>	Gaydos et al. 2008	Alaska (Hueffer et al. 2011), New England coast (Lasek-Nesselquist et al. 2010)	
<i>Neospora caninum</i>		Japan (Antibodies) (Fujii et al. 2007)	
<i>Sarcocystis neurona</i>	Gibson et al., 2011	California (Miller et al. 2001)	Zoo Illinois (Mylniczenko et al. 2008)
<i>Toxoplasma gondii</i>	Gibson et al., 2011; Lambourn et al. 2001,	California (Miller et al. 2001), Japan (Fujii et al. 2007), UK & France (Cabezón et al. 2011), Eastern Canada (Measures et al. 2004)	
Ectoparasites			
<i>Echinophthirius horridus</i>		Germany (Seibert et al. 2007), Gray's Harbor WA & Scotland (Thompson et al. 1998), West & East Atlantic, North & Wadden Seas, UK, Denmark, Netherlands, Norway, Sweden, New England coast, Florida, Nova Scotia, Virginia,	Rehab center Netherlands (Morick et al. 2009)

<i>Halarachne spp.</i>		California (Leidenberger et al. 2007) <i>H. baumanii</i> Scotland (Munro et al. 1992), <i>H. miroungae</i> Oregon (Stroud et al. 1978)	
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Toxins

Core sediment samples suggest that human activity began polluting the Salish Sea with lead, mercury, silver, copper, and hydrocarbons in the late 1800s (Lefkovitz et al. 1997). Persistent organic pollutants (POPs) such as polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichlorethane (DDT) began to appear in the 1930s and peaked in the 1960s (Lefkovitz et al. 1997). Both DDT and PCBs were banned in the U.S. and Canada in the 1970s because of their toxicity (Ross 2006). Polybrominated diphenyl ethers (PBDEs) are flame retardant chemicals that replaced PCBs, but are also toxic (Ross 2006, Washington State Department of Ecology 2013). Most uses of PBDEs were banned in the state of Washington in 2008 and 2011 (Washington State Department of Ecology 2013). POPs and heavy metals are lipophilic and do not break down quickly. This allows them to bioaccumulate in the fat of organisms and within food webs, reaching high concentrations within upper trophic level marine mammals such as harbor seals (Tabuchi et al. 2006).

Ross et al. (2013) compared PCB and PBDE concentrations in wild harbor seal pups at four locations in the Salish Sea. Reflecting a diet of the more highly contaminated fish stocks, harbor seals on Gertrude Island in southern Puget Sound were 4 to 5 times more contaminated with PCBs than harbor seals from Smith Island in northern Puget Sound and Hornby Island and the Fraser River estuary in British Columbia. Among the four sites, PCB concentrations were highest, followed by PBDEs. Small concentrations (>0.5% of total contamination) of polychlorinated diphenylethers (PCDEs) and polychlorinated naphthalenes (PCNs) were also detected. Ross et al. (2013) evaluated contaminant trends in harbor seals from 1984 to 2009. PBDE concentrations doubled every 3.1 years from 1984 to 2003, but declined by 71% from 2003 to 2009. Legacy PCB concentrations dropped 81% from 1984 to 2003. Ross et al. (2013) estimate that the 53,000 harbor seals in the Salish Sea in 2009 together held 2.6 kilograms of PCBs and 1.0 kilogram of PBDEs.

PCBs target the harbor seal immune system. Ross et al. (1996) compared indicators of immune system health of harbor seals fed contaminated Baltic Sea herring to harbor seals fed relatively uncontaminated Atlantic Ocean herring. The researchers found that increased PCB contamination impaired natural killer cell activity, T-lymphocyte function, and antigen-specific lymphocyte proliferation. Mos et al. (2006) also assessed the immunotoxicity of harbor seals in the Salish Sea by analyzing blood and blubber samples for PCB levels and immune function. Increasing concentrations of PCBs reduced the immune response of harbor seals. Supporting the results of Ross et al. (1996), Mos et al. (2006) found that PCBs reduced T lymphocyte function and proliferation and decreased

percentages of lymphocytes in white blood cell counts. Overall these effects can reduce harbor seals' ability to defend against pathogens.

PCBs also affect the growth and development of harbor seals. Tabuchi et al. (2006) studied the effects of PCBs on thyroid hormones (THs) in harbor seals in Washington State and British Columbia. PCBs were found to interfere with TH signaling and TH gene expression, which could in turn alter the structure and function of blubber. Blubber in harbor seals is specialized for energy storage, insulation, buoyancy control, and nutrient storage (Tabuchi et al. 2006).

Acute hydrocarbon exposure can be a source of mortality in harbor seals. After the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska, counts of harbor seals at 25 seal haul out sites in Prince William Sound declined by 4.6% per year between 1990 to 1997, amounting to an overall population reduction of 63% (Hoover-Miller et al. 2001, Frost et al. 1999). Although the harbor seal population in this area started declining in 1984, the tanker spill of 35,000 metric tons of oil is held responsible for at least 300 harbor seal deaths (Hoover-Miller et al. 2001).

Disturbance

People, animals, and natural occurrences such as falling trees frequently disturb hauled-out harbor seals (Calambokidis et al. 1991). In Bellingham, harbor seals seem to have adjusted their behavior to human disturbance, avoiding the continual, high diurnal noise levels of their urban environment by hauling-out nocturnally (Acevedo-Gutiérrez and Zarelli, 2011). However, harbor seals are also affected by ephemeral disturbances, mainly vessels that approach closely to haul-out sites, and particularly kayakers. These disturbances cause harbor seals to flush into the sea, prematurely ending their time of rest. Johnson and Acevedo-Gutiérrez (2007) monitored disturbances of hauled-out seals from Yellow Island, in the San Juan archipelago. They reported that 85.7% of kayakers, 57.1% of stopped powerboats, and 4.6% of passing powerboats encroached within the 100 yard (91 meter) NOAA buffer zone around marine mammals. Harbor seals were disturbed by kayakers and stopped powerboats at an average distance of 91.0 meters and 190.5 meters, respectively. Harbor seals were affected least by moving powerboats, which passed as close as 39 meters without disturbing the hauled-out seals. Johnson and Acevedo-Gutiérrez (2007) suggest increasing the buffer zone to prevent disturbances.

Other studies conducted in Washington State have observed similar trends. Calambokidis et al. (1991) recorded 0.33 disturbances per observation hour at a haul-out site in Woodard Bay, Washington. Sources of disturbance included motorboats, skiffs, canoes, kayakers, aircraft, deer (*Odocoileus hemionus columbianus*), herons (*Ardea herodias*), and a natural tree fall. Calambokidis et al. (1991) also found that harbor seals reacted to kayakers and canoes at a greater distance compared to motorboats and skiffs. At Puffin Island, Clements Reef, and Skipjack Island in the northern San Juan Islands, Suryan and Harvey (1999) observed harbor seal disturbances on at least 71% of survey days. Powerboats, unknown factors, and bald eagles (*Haliaeetus leucocephalus*) were the top three

most common sources of disturbance. They noted that, although kayakers caused few disturbances in absolute terms, they posed a greater potential disturbance to hauled-out harbor seals. Only 9% of powerboaters disturbed seals within 1 kilometer of the haul-out site, whereas 55% of kayakers within the same range caused a disturbance. Suryan and Harvey (1999) did not observe any trends considering powerboat speed, but found that powerboats caused disturbances at a range of 28 meters to 260 meters. Powerboats that passed parallel to haul-out sites without abruptly adjusting speed or course caused minimal disturbance (Suryan and Harvey 1999). Full recoveries (all seals returning to the haul-out) after a disturbance was more common before low tide when the intertidal haul-out is still being exposed, but after low tide when the incoming tide is covering the intertidal sites, partial recoveries and no recoveries were most common (Suryan 1995). Recovery time varied from 7 to 228 minutes for full and partial recoveries (Suryan 1995).

Disturbances of harbor seals at haul out sites also have been evaluated in Alaska. Hoover-Miller et al. (2013) conducted a study in Aialik Bay, Alaska, and reported that only 19% of kayakers approached close to seals and 12% caused disturbances, in contrast to higher rates in Washington State. Although kayakers still caused the greatest proportion of disturbances, Hoover-Miller et al. (2013) noted that the disturbances caused by kayakers has declined since 2006, likely in response to increased training of guides. Harbor seals in Alaska must also contend with cruise ships. It is recommended that cruise ships remain at least 91 meters from seals in Alaska, but Jansen et al. (2010) found that harbor seals were disturbed when ships were as far as 500 meters. Risk of disturbing harbor seals was 25 times greater when ships were within 100 meters and 4 times greater when ships approached directly rather than abeam. Jansen et al. (2010) recommend that cruise ships stay at least 500 meters from hauled-out harbor seals.

Disturbances may cause more than a mere momentary change in harbor seal behavior (Calambokidis et al. 1991). Aside from altering haul-out times as described above in Bellingham (Acevedo-Gutiérrez and Zarelli, 2011), disturbances may drive harbor seals to permanently abandon preferred haul-out sites. Disturbances increase stress during pupping, mating, or molting. Mother-pup pairs may also be more sensitive to disturbances during the initial bonding period, as they face the risk of becoming separated. Mother-pup pairs on Puffin Island in the San Juan Islands showed a lower recovery (returning to the haul-out site after a disturbance) and were more vigilant than other seals (Suryan and Harvey 1999, 1999). Disturbances also reduce anti-predatory responses in harbor seals, making them more vulnerable to bald eagle predation (Olson 2013). In the Salish Sea, harbor seals at sites with greater anthropogenic exposure responded less to bald eagles than harbor seals at sites with less human exposure (Olson 2013). Of course, if boats approach too close to harbor seals, the result can be fatal. Bexton et al. (2012) reported that 76 dead pinnipeds had washed ashore the UK coast between 2008 and 2010 with

“corkscrew injuries,” caused when seals were drawn through the ducted propellers of boats. Propeller strikes have also been detected in stranded harbor seals in the Salish Sea (Gaydos, Unpub. data).

Rehabilitation

Although the harbor seal population in the Salish Sea is at or near carrying capacity (Jeffries et al. 2003) and often-expensive efforts to bolster non-endangered species through rehabilitation are controversial, a number of stranded harbor seal pups are rehabilitated each summer in the Salish Sea with strong public support (Gaydos 2012). Hotlines are maintained in Washington State and British Columbia, with which beachgoers can report strandings of harbor seals or other marine mammals (NOAA 2013b). Often the general public is concerned about unattended harbor seal pups, unaware that harbor seal mothers routinely leave their pups ashore while foraging. These “abandoned” pups should be observed for signs of injury or the return of the mother, but otherwise left alone at a distance of at least 100 yards (DFO 2006, NOAA 2013b).

If an appropriate authority determines that a harbor seal is in need of rehabilitation, the seal is taken to a rehabilitation center (Whaley and Borkowski 2009, DFO 2006). In British Columbia, the Vancouver Aquarium Marine Mammal Rescue Centre is authorized by DFO to rehabilitate many harbor seals every summer (DFO 2006). NOAA authorizes several rehabilitation centers in the San Juan Islands and Puget Sound to care for harbor seals, including Wolf Hollow Wildlife Rehabilitation Center on San Juan Island (NOAA 2013b).

In the U.S., release conditions for marine mammal species have been standardized since the 1990s through NOAA’s National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (FWS). The list of required historical, developmental, behavioral, ecological, and medical criteria is extensive, and includes measures to ensure that the seal is capable of surviving in the wild and will not be a threat to other organisms. For example, releasable seals can hunt and feed themselves, swim and dive effectively, and pass a health test conducted by a veterinarian. Seals with visual or auditory dysfunction or a reportable disease are not releasable. The release site should be chosen to maximize survivability of the released seal; this is often at a haul-out near the stranding site, where the seal may rejoin its genetic stock and natural home range. NMFS and FWS mandate that all released pinnipeds must be flipper tagged for post-release identification (Whaley and Borkowski 2009). The general protocol established by the Vancouver Aquarium for rehabilitating harbor seals is largely the same as in the U.S. (Vancouver Aquarium 2013).

Some differences in hematology and serum chemistry have been detected between rehabilitated and wild harbor seal pups (Gaydos et al., 2012; Greig et al. 2010). Döhle bodies, an indicator of infection in humans, appeared in the leukocytes of 15% to 22% of pups in rehabilitation but were not found in any of

the wild seals. Compared to rehabilitated pups, wild harbor seals had lower thresholds for total alanine aminotransferase (ALT), albumin, cholesterol, globulin, glucose, leukocytes, neutrophils, phosphorous, potassium, total protein, and sodium. However, wild harbor seal pups had higher thresholds for mean cell volume, chloride, creatine kinase, hematocrit (HCT), and hemoglobin (HGB) (Greig et al. 2010).

In an effort to determine if rehabilitated harbor seals behaved similarly to wild cohort-matched seal pups, Gaydos et al. (2012) compared the movements of 10 wild harbor seal pups to 10 rehabilitated harbor seals pups using satellite transmitters. The study found that, compared to wild pups, rehabilitated pups traveled nearly 3 times as far daily and dispersed over 3 times as far from the release site. This suggests that wild seals imprinted on foraging areas during their first month of life with their mothers, a learning experience that seals in rehabilitation lacked. In addition, satellite tags on rehabilitated pups transmitted half as long as those on wild seals, which could be attributed to seal death or transmitter loss or defect. If transmission time is used as a proxy for lifespan, neither cohort had high survival. The rehabilitated seal pups in this study would have had a 100% mortality rate, compared to a 90% mortality rate in the wild harbor seals. Although conclusions about rehabilitated harbor seal survival cannot be drawn from this study, it does effectively demonstrate that rehabilitated harbor seals in the Salish Sea behave differently from their wild counterparts (Gaydos et al. 2012).

Few other mark-recapture studies regarding the success of rehabilitated seals have been conducted. Harvey et al. (1983) reports post-release sightings of two rehabilitated harbor seals in Washington and Oregon, each more than 70 kilometers from their original release site. Two studies conducted further outside of the Salish Sea area did not detect difference between wild and rehabilitated pups (Morrison et al. 2011; Lander et al. 2002) suggesting that location-specific factors such as population carrying capacity and differences in both prey availability and predators could influence behavior differences between wild and rehabilitated seal pups (Gaydos et al. 2012).

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Acknowledgements

We thank the numerous SeaDoc Society summer research interns that helped acquire this information, including G. Bishop, A. Briese, S. Heidelberg and S. Smolley. Interns L. Anderson and K. Wicinas helped compile the list of pathogens and parasites. Several external reviewers, including S. Jeffries, M. Haulena, and D. Lambourn, provided external review and comments that strengthened the manuscript. Support for this work was provided by the SeaDoc Society (www.seadocsociety.org) and the Puget Sound Institute (www.urbanwaters.org/psi/). Gary E. Davis took the harbor seal cover photo.