

**Seasonal Variation in the Foraging Behavior of Harbor Seals in the Georgia Basin:
Implications for Marine Reserves**

By
Kenady Reuland

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Moheb A. Ghali, Dean of the Graduate School

ADVISORY COMMITTEE

Chair, Dr. Alejandro Acevedo-Gutiérrez

Dr. Deborah Donovan

Dr. Benjamin Miner

MASTER'S THESIS

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**Seasonal Variation in the Foraging Behavior of Harbor Seals in the Georgia Basin:
Implications for Marine Reserves**

**A Thesis
Presented to
The Faculty of
Western Washington University**

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

**By
Kenady Reuland
April 2008**

ABSTRACT

Marine reserves help manage fisheries and marine resources by increasing the biomass of exploited species both within and adjacent to their boundaries. The designation of marine reserves in Skagit County, Washington, has been proposed as a means of replenishing rockfish (*Sebastes* spp.) stocks. With the designation of new reserves, it is expected that rockfish abundance will increase and, consequently, that predators will respond to this change by altering their foraging behavior. To accurately predict the response of local marine predators to increases in rockfish densities as well as their potential impact on marine reserves one must first understand their current foraging behavior. This study aimed to develop baseline data on the foraging behavior of the Pacific harbor seal (*Phoca vitulina*), a resident marine predator in the inland waters of Washington and Canada. I used time-depth recorders (TDRs) to examine variations in foraging behavior during the pre-pupping (April-June) and pupping (July-September) seasons. I deployed 26 TDRs at three haul-out sites in the Georgia Basin (7 at Bird Rocks, 8 at the Belle Chain Islets, and 11 in Padilla Bay). I classified harbor seal dive types to examine foraging behavior on two temporal scales: bouts of diving and foraging trips. Seals dove to an average dive depth of $30.0 \pm \text{SE } 0.07$ m. On a profile of time and depth, six dive types were identified based on depth, duration, speed of ascent and descent, and vertical movements within the bottom portion of the dive. Dive types were used to classify three bout types: 1) long and deep (24.3 %), 2), short and shallow (24.7 %), and 3) short and deep (51.0 %). Short/Deep bouts were the predominant type used throughout the study; however, variation in the use of different bout types was observed relative to haul-out site, season, and time of day. A diurnal pattern in diving was observed

during the pupping season with an increase in shallow bouts at night and deep bouts during the day. Foraging trip duration decreased during the pupping season at all haul-out sites. Diving bouts and foraging trips varied both spatially and temporally, suggesting differences in foraging behavior between haul-out sites and across seasons in association with fluctuations in prey abundance or life history. Forage fish, preferred prey items for harbor seals, are expected to decrease in abundance in the Georgia Basin with potential recruitment failure of Pacific herring (*Clupea pallasii*) in both 2008 and 2010. Intra-annual variation in harbor seal diet, with an increase in rockfish and a decrease in herring consumption during the winter, has been documented in the San Juan Islands. The duration of this switch and thus, the predation pressure of seals on rockfish, may increase if forage fish abundances in the Georgia Basin continue to decline. The baseline data collected in this study, coupled with concurrent diet and home range analysis, will help facilitate the determination of the aggregative and functional responses of harbor seals to future variations in prey abundances, and hence will offer insight on the potential impact of harbor seals on the success of marine reserves in the Georgia Basin.

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INTRODUCTION

Background

The state of the world's oceans has come to the forefront of environmental policy within the last twenty years as the effects of global warming, pollution, and fishery exploitation become apparent. The United Nations Food and Agriculture Organization reported that 69% of the world's fish stocks were fully exploited, overexploited, or depleted by the mid 1990's (UNFAO 1995). This decrease in marine stocks is due to multiple stressors including overfishing, pollution, coastal development, and habitat loss; however, the general consensus by fisheries experts is that ineffective management is the fundamental cause (Milazzo 1998). Traditional management tools, such as maximum sustainable yield estimates, are unable to address the numerous anthropogenic impacts on marine organisms and fish stocks (Halpern 2003); likewise, they do not take into account various other ecosystem influences on stock recruitment such as prey availability and the impact of predators.

The World Summit on Sustainable Development (WSSD) held in Johannesburg in 2002 developed a plan to implement sustainable development around the world. A major component of this plan includes providing environmental protection and highlighting the importance of marine ecosystems as critical for sustainable fisheries and global food security (Kaiser et al. 2005). The WSSD plan developed a commitment to improve marine conservation, including the application of ecosystem-based management around the globe by 2010. Ecosystem-based management is intended to 'integrate management of human activities, based on knowledge of ecosystem dynamics, to achieve sustainable use of

ecosystem goods and services, and maintain ecosystem integrity' (Kaiser et al. 2005). Marine Protected Areas (MPAs) have become increasingly popular with fisheries management and conservation biologists as a tool for ecosystem-based management and the protection of renewable marine resources. Although protection varies depending on the goal of the MPA and local regulations, a rapid increase in the biomass, abundance, and average size of exploited species within area boundaries is generally observed (Eichbaum et al. 1996, Thompson et al. 2001, Gell & Roberts 2003).

Marine predators may affect the distribution and abundance of prey species within protected areas. In response to the increases in size, abundance, and biomass of prey species in MPAs, one would expect predators to respond by increasing, in these areas, their abundance (aggregative response), frequency of foraging (functional response), or both (Middlemas et al. 2006). As a consequence, predators may potentially inhibit the recovery of exploited species (Fu et al. 2001). Understanding the current influence of marine predators on local prey populations is important for determining their potential impact on the recovery of exploited species after the designation of MPAs.

Marine Reserves

MPAs are defined as 'areas of the coastal zone or open ocean that are the target of management for the broad purpose of conservation and sustainable use' (Eichbaum et al. 1996). They have been proposed as an efficient way to maintain and manage fisheries while simultaneously preserving biodiversity, meeting conservation objectives, and satisfying human needs (Tuya et al. 2000, Halpern & Warner 2003). Marine reserves are MPAs with zero extraction regulations (Lubchenco et al. 2003), allowing for the protection of any

species that falls within the reserve boundaries. Marine reserves are currently gaining popularity due to their success in increasing the biomass, average size, and abundance of exploited species within their boundaries (Halpern & Warner 2003). In addition, areas adjacent to reserves tend to benefit as well due to the ‘spill-over’ of fish biomass and larval transport that occurs when animals leave or migrate outside the reserve (Gell & Roberts 2003). However, the response of marine predators to increased prey biomass poses a potential threat to the recovery of exploited prey species and realization of reserve goals.

Marine Reserves in Puget Sound

Historically, groundfish in Puget Sound, Washington, supported thriving commercial and recreational fisheries (Palsson et al. 1998). In the 1970’s Puget Sound fisheries landed more than 27 million pounds of groundfish in a year; however, more recent landings, without a decrease in effort, have recorded < 5 million pounds, the lowest numbers in 50 years (Figure 1) (Palsson et al. 1998). The decline in groundfish species, including rockfish (*Sebastes* spp.), is due to multiple stressors including overfishing and environmental toxins (PSAT 2007). Rockfish stocks in Puget Sound have been listed in critical condition since 2005 (PSAT 2007), prompting both local and federal entities to implement management and conservation projects, such as marine reserves, to aid in the recovery of these valuable stocks.

Currently, there are several established marine reserves in Puget Sound (Tuya et al. 2000) and three other candidates for future designation in the eastern San Juan Islands, Skagit County (Weispenning 2006) (Figure 2). The potential establishment of reserves in

Figure 1. Historical groundfish catch from Puget Sound (excluding Neah Bay) during 1921-1996. Taken from Palsson et al. (1998).

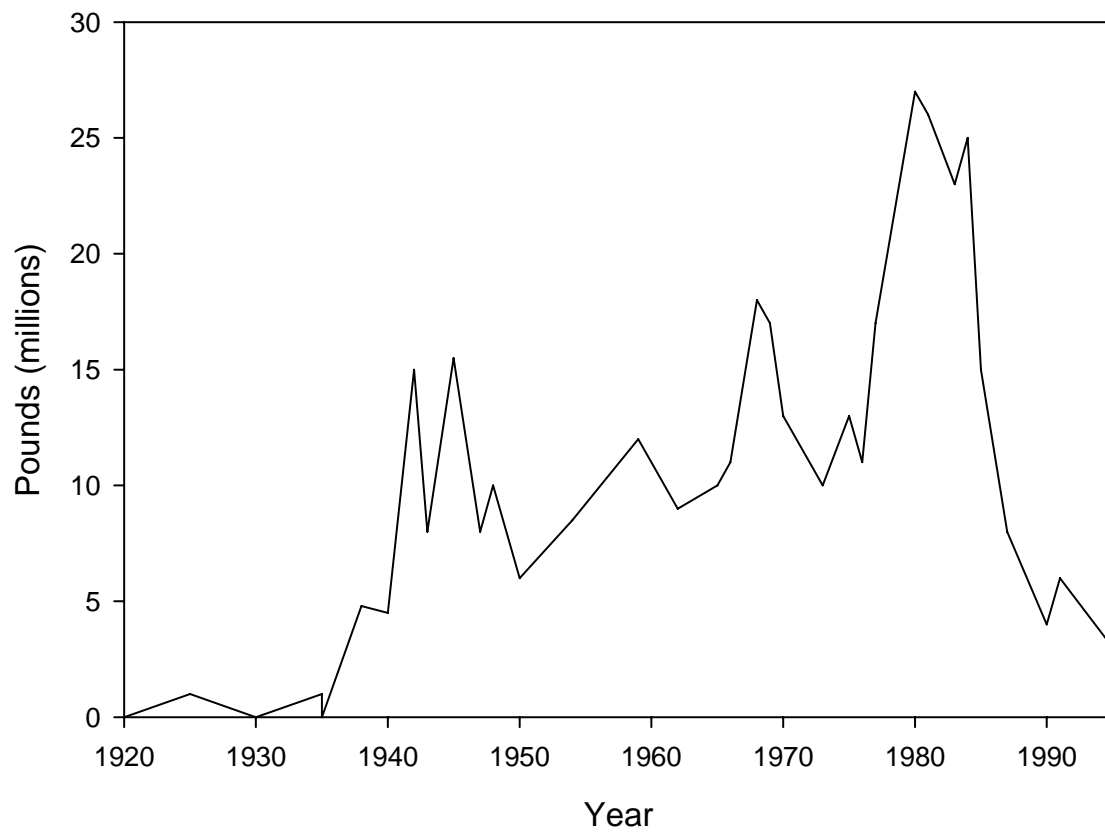
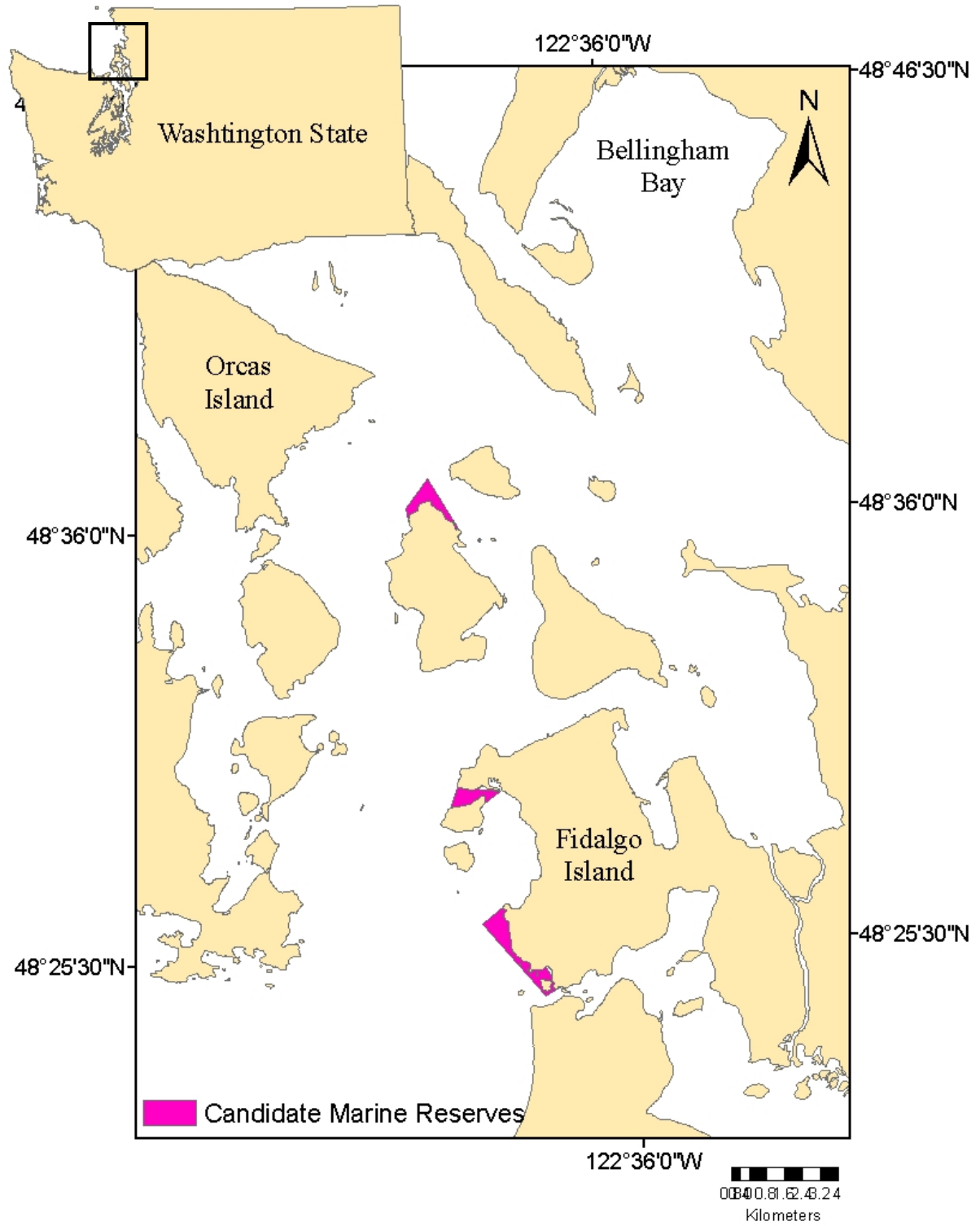


Figure 2. Candidate marine reserve sites in Washington State. Data from Weispfenning (2006).



-the eastern San Juan Islands is motivated by a grass roots recovery plan for rocky reef bottomfish, particularly rockfish and lingcod (*Ophiodon elongates*) (McConnell et al. 2001) by the Skagit County Marine Resource Committee (SCMRC). With the possibility of establishing additional reserves in the San Juan Islands to aid in bottomfish recovery (Dinnel & McConnell 2001), it is necessary to determine the foraging behavior and diet of local marine predators to evaluate their potential impact on stock recovery and the future success of the reserves.

Pinnipeds in the Georgia Basin

Marine mammals, most notably pinnipeds (seals, sea lions, fur seals, and the walrus), are viewed as a threat to local fisheries in many areas, including the Georgia Basin (Harwod & Croxall 1988, Bekkby & Bjørge 1995, Bjørge et al. 2002). Recently, grey seals (*Halichoerus grypus*) were cited as one factor in the failed recovery of Atlantic cod (*Gadus morhua*) and the diminished success of marine reserves in Nova Scotia (Fu et al. 2001). In Puget Sound, harbor seals were blamed for declines in bottomfish catches in the 1940's and 1950's, leading to a state-financed bounty and control program (Newby 1973); and California sea lions (*Zalophus californianus*) were recently being removed from the Ballard Locks in Seattle due to predation on endangered and commercially important salmonid species (NMFS 1997). Rocky-reef bottomfish, a recovery priority in northern Puget Sound, have numerous marine predators including resident pinniped species (Olesiuk 1993, Brown et al. 2002, Lance & Jeffries 2007). However, the actual impact of pinniped predation on bottomfish populations is not well documented.

Multiple pinniped species are observed in the Georgia Basin throughout the year with the potential to affect bottomfish populations. Northern elephant seals (*Mirounga angustirostris*) and California sea lions are observed in the inland waters of Washington and British Columbia, but are not year-round residents and are rarely found in northern Puget Sound and the San Juan Islands (Jeffries et al. 2000). Steller sea lions (*Eumetopias jubatus*) are observed in the San Juan Islands during the fall and winter, but typically occur in very low numbers (peak counts of 1,000 animals) (Jeffries et al. 2000). Harbor seals, on the other hand, are widely distributed and abundant in the inland waters with well-known, year-round, haul-out sites throughout the San Juan Islands (Jeffries et al. 2000) and the Strait of Georgia (Olesiuk 1993). With greater spatial and temporal abundance throughout Puget Sound than other pinnipeds, harbor seals appear to pose the greatest potential threat to the recovery of rockfish and the success of marine reserves in the San Juan Islands and are therefore the focus of my study.

Harbor Seals

Harbor seals, the only breeding pinniped species in Washington State (Brown et al. 2002, Jeffries et al. 2003), currently have a state-wide population in excess of 30,000 animals, with an estimated 14,000 inhabiting inland waters (Jeffries et al. 2003). They are opportunistic predators that feed on locally abundant prey species and commonly exhibit switching behaviors as prey abundances change seasonally and annually (Middlemas et al. 2006). Switching between prey types typically results from adopting different foraging locations or strategies, such as dive or search behavior, as prey availability changes (Middlemas et al. 2006). Switching behaviors are apparent when analyzing the spatial and

temporal variation in dive patterns (McConnell et al. 1992), and might be indicative of an aggregative and/or functional response to variations in prey type or abundance.

Harbor seals consume rockfish in Oregon and British Columbia (Olesiuk 1993, NMFS 1997), but a recent diet analysis indicates that rockfish account for less than 12% of their overall diet in Puget Sound, with seasonal variations in its occurrence (Lance & Jeffries 2007). Currently, rockfish in Puget Sound are listed in critical condition (Dinnel et al. 2003, PSAT 2007) and have low abundances when compared with historical records (Palsson et al. 1998). This decrease in abundance may be one reason for a lower frequency of occurrence of rockfish in the harbor seal diet in Puget Sound. As rockfish abundances potentially increase with the designation of marine reserves, harbor seals, given their foraging habits and abundance in the area, may consequently increase their consumption of rockfish. It is still unclear what impact the current predation rate of harbor seals has on depleted rockfish stocks; however, an increase consumption of rockfish may pose a threat to stock recovery.

Foraging Ecology and Behavior of Pinnipeds

Habitat use by marine predators is assumed to reflect the depth and distribution of prey as prey availability is generally correlated with the physical and biological properties of the ocean (Austin et al. 2006b). Vertical movements in the water column enable a predator to encounter prey, thus reflecting the depth and spatial distribution of prey patches on a fine scale. Horizontal movements reflect search tactics and predator behavior as well as prey distribution over a large scale (Bell 1991). Although some pinnipeds dive for reasons unrelated to foraging, such as mating or dominance displays, diving is thought to accurately

demonstrate foraging activity (Boyd et al. 1994, Beck et al. 2003). It incorporates both the horizontal and vertical components of foraging: searching for, encountering, and consuming prey. Diving predators can modify their foraging behavior on multiple temporal scales depending on prey abundance and availability (Baechler et al. 2002, Austin et al. 2006b). The foraging behavior of pinnipeds, including harbor seals, can be organized along three temporal scales: 1) foraging trips: defined as the period between entering the water after an extended period of dry time and returning to haul-out on land (Austin et al. 2006b); 2) bouts of diving: clusters of continuous dives (Baechler et al. 2002); and 3) individual dives: excursions from the surface (Boyd et al. 1994).

Fine-scale analysis of foraging behavior —detailing habitat use, movements (vertical and horizontal), and dive patterns while searching for and capturing prey— has helped elucidate predator-prey interactions in pinnipeds (Costa et al. 1989). Knowing when and where predators feed offers insight into how they respond to the abundance of local prey species (Austin et al. 2006b). However, without baseline data with which to base an analysis of foraging behavior it is difficult to accurately identify changes in predator-prey interactions.

Harbor Seal Foraging Behavior

Harbor seal foraging behavior varies both seasonally and annually and differs by sex and age classes (Boness et al. 1994, Coltman et al. 1997, Thompson et al. 1998, Frost et al. 2001, Baechler et al. 2002). Harbor seal dives average 2 - 4 min and the two-dimensional profile of time and depth is generally a variant of a square or V- shape. Previous studies

have identified five and seven dive types for harbor seals in Alaska and Canada with distinct fluctuations in the use of different dive types over time (Lesage et al. 1999, Frost et al. 2001, Baechler et al. 2002). The inferred functions of these dive types is somewhat circumstantial; however, recent studies using stomach-temperature telemetry (STT) indicate that square-shaped dives are commonly used during foraging activities (Lesage et al. 1999, Austin et al. 2006b). There is high variability in the foraging behavior of harbor seals. Some studies support the hypothesis that harbor seals feed mostly on benthic prey with little diurnal variation in dive depths or types (Bjørge et al. 1995, Tollit et al. 1998). Other studies indicate that foraging occurs more often at dusk and that seals show a distinct diurnal foraging pattern, using square-shaped dives as they follow the diurnal vertical migration of prey (Bowen et al. 1999, Lesage et al. 1999, Hastings et al. 2004). Multiple studies have shown that diving and foraging behaviors also vary between individuals, age, and sex classes (Coltman et al. 1997, Thompson et al. 1998, Härkönen et al. 1999, Frost et al. 2001, Hastings et al. 2001, Beck et al. 2003). In Nova Scotia, adult males perform long and deep dives more often before the breeding season and then switch to short and shallow dives during the breeding season to remain close to the haul-out site and increase the likelihood of encountering a female in estrous (Coltman et al. 1997). Female harbor seals do not fast while nursing, but continue to forage throughout the year (Boness et al. 1994, Thompson et al. 1994, Bowen et al. 1999, Bowen et al. 2001). In Scotland, they adjust their foraging behavior throughout the lactation period, making shorter trips during early lactation and longer trips during late lactation to maintain their own body mass and that of their pup (Boness et al. 1994, Bowen et al. 1999). All of the aforementioned studies highlight

seasonal, spatial, and diel variation in foraging behavior, suggesting that foraging behavior may differ both among and between harbor seal populations.

Harbor seals in the inland waters of Washington and Canada have numerous haul-out sites ranging from southern Puget Sound north through the Strait of Georgia. These sites tend to fall into two broad categories: estuarine (soft-bottomed bays) and non-estuarine (rocky-reef islands) (Olesiuk 1993, Jeffries et al. 2000). The presence and abundance of prey species is typically correlated with available habitat and sediment type (Payne & Selzer 1989). Therefore, the variation in prey associated with different haul-out sites (rocky vs. sandy), suggests that the foraging behavior and diet of harbor seals may vary between site types. Identifying differences in seal foraging behavior between haul-out sites from different locations (Puget Sound and the Strait of Georgia) and habitat types (rocky vs. sandy) is an important step in developing baseline data on the foraging behavior of a locally abundant marine predator. These data will aid in determining the potential negative impact of harbor seals on the recovery of local rockfish populations and also play a significant role in predicting the success of marine reserves near known harbor seal haul-out sites.

Research Objectives

I examined the diving behavior of harbor seals to develop baseline data on their foraging behavior in the Georgia Basin. Correlating changes in foraging behavior to changes in diet or prey abundance develops a useful baseline of harbor seal foraging that may be used to monitor prey fluctuations and ecosystem dynamics in the future. Specifically, I wanted to know how foraging behavior differed between the pre-pupping (April-August) and pupping

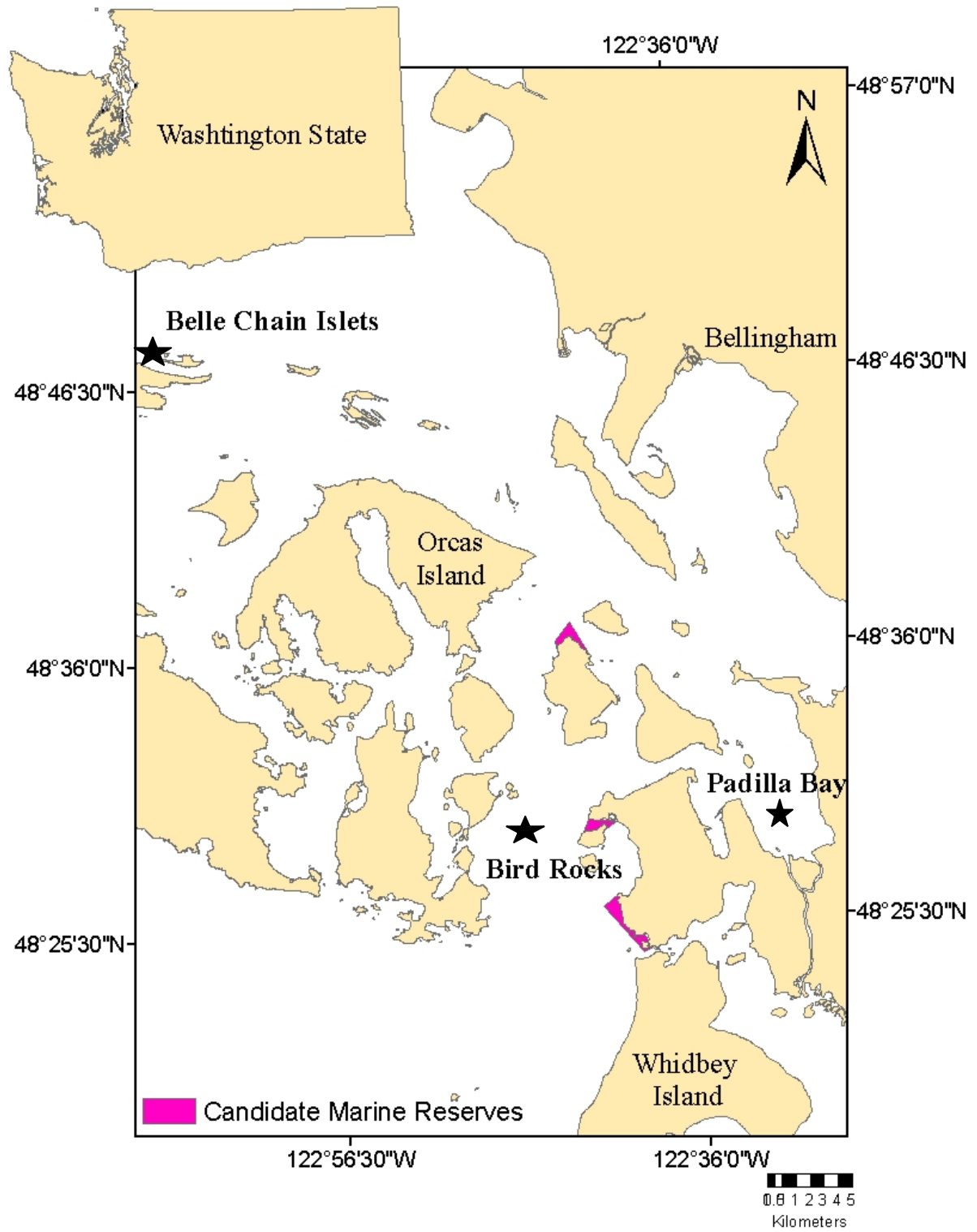
seasons (July-August) and between haul-out sites, or both. I examined changes in dive behavior during the spring and summer of 2007 by identifying diving bout types and analyzing their frequency of occurrence throughout the day and during two seasons (pre-pupping and pupping). I also examined changes in foraging trip duration between the two seasons. Changes in dive behavior and time spent searching for and capturing prey (foraging trip duration) generally indicates switching between prey types or foraging locations (McConnell et al. 1992) and may be indicative of an aggregative or functional response to changes in prey abundances. Identifying these changes will help develop a baseline of current foraging behaviors for harbor seals in the Georgia Basin and will aid in measuring changes in the future if prey abundances increase with the designation of marine reserves. Analysis of harbor seal foraging locations and movements will not be addressed in this document.

METHODS

Study Site

Twenty six instruments were deployed on harbor seals (*Phoca vitulina*) in the spring of 2007 at three sites: Padilla Bay National Estuarine Research Reserve (hereafter Padilla Bay) (n = 11) and Bird/Belle Rocks (n = 7) in Puget Sound, and the Belle Chain Islets (n = 8) in the Strait of Georgia, Canada (Figure 4). Padilla Bay is a large soft-bottomed estuarine bay situated near the historic mouth of the Skagit River (center at 48° 31' 22" N, 122° 31' 40" W). There are 3-5 harbor seal haul-out sites in the bay and use of these sites varies depending on time of year (Jeffries et al. 2000). Bird and Belle Rocks are rocky reef, non-estuarine haul-out sites located in Rosario Strait. Bird Rocks (48° 29' 10" N, 122° 45' 36" W) is a congregation of three rocky reef islands used year round by harbor seals and during the winter months by Steller sea lions (*Eumetopias jubatus*). Belle Rock (48° 29' 36" N, 122° 45' 05" W) is a rocky reef located < 1 km from Bird Rocks and is exposed only during low tide. Given their close proximity, data from Bird and Belle Rocks were combined for analysis and will from now on be referred to only as Bird Rocks. The Belle Chain Islets in the Strait of Georgia are a chain of small rocky reef islets located just east of Samuel Island (center at 48° 49' 42" N, 123° 15' 42" W). This chain of rocky islets is part of the Gulf Islands National Park Reserve and is highly valued for its marine mammal haul-out and sea bird nesting sites. All three sites are located in the Georgia Basin, a designation for the area encompassing the Strait of Juan de Fuca, the Strait of Georgia, and Puget Sound.

Figure 3. Tagging locations of *Phoca vitulina* in the Georgia Basin during spring 2007.



Instrument Deployment

Adult harbor seals were captured in April and May of 2007 following the methods of Jeffries et al. (1993) under the leadership of the Washington Department of Fish and Wildlife (WDFW) and, when tagging in Canada, under the leadership of Department of Fisheries and Oceans (DFO). After capture, weight to the nearest 0.5 kg and dorsal strait length to the nearest 0.5 cm was measured, blood and blubber biopsies were taken, and time-depth recorders (TDRs; Wildlife Computers, Redmond, WA, Mk-9, Mk-10F, or Splash) and either a Spot 05 satellite tag (Wildlife Computers) or a VHF head tag (ATS, Isanti, MN) were attached to each seal. Tags were glued to the pelage of the animal using 5-min epoxy. TDR tags were placed along the dorsal midline of the animal between the shoulders, satellite and VHF tags were placed on top of the head.

Tags were expected to come off with the annual fall molt and were set to record data every day as the battery life would not be exhausted during this six-month duration. Spot tags were set to transmit every second hour of every day with a maximum of 350 transmissions per day. TDR tags were set to record time, pressure (depth), light level, and temperature (tag temp. for Mk-9, water temp. for Mk-10F) every 10 sec. Mk-10F tags were also set to record GPS positions continuously during the first two weeks of April, May, and June, and during the entire month of July, August, and September with a maximum number of 150 acquisitions per day. TDR tags (Mk-9, Mk-10F, and Splash) were equipped with an Eco-tech floatation pack and a VHF transmitter. The instrument package was positively buoyant and balanced to float with the VHF antenna upright to allow for tracking and recovery after it became detached during the seals annual molt between August and October of 2007.

Data Collection

Seals were tracked using boat-based radio telemetry to verify satellite locations, identify non-satellite tagged animals, and recover tags after they molted off. To find individuals, we traveled by boat to the last known position of the animal and then moved between nearby haul-out sites until the animal was located. For safety concerns, boat-based operations were limited to a 35-km radius of Shannon Point Marine Center (48° 30'32" N, 122° 40' 58" W). Therefore, not all tagged individuals were observed during each tracking session. Seals were tracked 2-4 times per week from April through October 2007. An average of $5.8 \pm \text{SE } 0.61$ seals ($n=18$) were observed during each session allowing us to see every animal within our range at least once per week. Seals that regularly traveled outside the 35-km range were not observed regularly and the tags were recovered with the assistance of WDFW and DFO ($n=3$).

Data Processing

Individual seals were tracked manually via VHF telemetry and automatically via data collected by polar orbiting satellites operated by Service Argos. TDR data were downloaded and processed using software provided by Wildlife Computers (Redmond, WA). All dives were corrected using Zero-offset correction software to account for drift in the TDR's pressure transducer, which estimates water depth. However, the program was unable to account for all instrument noise introduced by sea surface conditions; therefore, only dives ≥ 5 m were analyzed in this study to follow the standard protocol of pinniped diving studies (Schreer & Testa 1995, Tollit et al. 1998, Lesage et al. 1999, Baechler et al. 2002).

Wildlife Computers' dive analysis software was used to analyze the corrected dive records and to classify the following variables for each dive: maximum depth, duration, bottom time (time spent at more than 85% of the maximum depth of the dive), wiggles (the number of vertical movements within the bottom portion of the dive), and average ascent and descent rates. Five additional variables were used for dive classification: skew1 (the ratio of average ascent rate to average descent rate), skew2 (the ratio of average descent rate to average ascent rate), the ratio of bottom time to dive duration (BTD), the ratio of bottom time to maximum depth (BTM), and the ratio of maximum depth to dive duration (MDD) (Schreer & Testa 1996, Lesage et al. 1999, Baechler et al. 2002).

Dive Behavior

Dive Classification

Diving by air breathing marine predators, such as harbor seals, can be viewed as excursions from the surface to search for and/or consume prey (Austin et al. 2006b) and can be characterized by multiple factors. In this study, eleven dive variables were used to classify dives and determine the dive shapes of harbor seals in the study area: 1) maximum depth, 2) duration, 3) bottom time, 4) wiggles, 5) average ascent rate, 6) average descent rate, 7) skew 1, 8) skew 2, 9) BTD, 10) BTM, and 11) MDD. Wiggle count was a defining characteristic of wiggle-dives and was therefore deemed categorical, where all dives with a wiggle count > 0 were considered wiggle dives. As none of the variables were normally distributed, non-categorical data were log or square root transformed prior to analysis. Transformation did not result in normality, but did reduce the skew in the distribution;

therefore, the square root or logarithm of each non-categorical variable was used in subsequent analyses. Wiggle count was not transformed. Concern over multivariate normality was not warranted as analyses were exploratory and intended to describe patterns and not as statistical inference techniques (McGraigal et al. 2000).

To generate a smaller set of uncorrelated variables, the ten numerical dive variables were initially run through a Principle Components Analysis (PCA), which produced a set of three uncorrelated factors (Lesage et al. 1999). A varimax rotation was applied to the factors to simplify the interpretation of the results. Multivariate-normal missing-value imputation was used for missing values (Hintze 2000). I selected factors using the percent of eigenvalues method in which 80% of the total variance must be explained by the selected number of factors. The resultant three factor scores from the PCA plus the wiggle-dive variable were then introduced into a k-means cluster analysis (Schreer & Testa 1995, Schreer et al. 1998, Lesage et al. 1999). Previous studies have identified between five and seven dive types for pinniped species (Schreer & Testa 1996, Austin et al. 2006b) and five and seven dive types specifically for harbor seals (Lesage et al. 1999, Baechler et al. 2002). The optimum number of clusters for this study was determined by analyzing the cluster solutions of five, six, and seven clusters. The cluster solutions were validated using a discriminant function analysis (Schreer & Testa 1995, 1996, Lesage et al. 1999) and the appropriate number of clusters was determined as the most parsimonious solution, the one with the fewest number of clusters and the highest percent classification accuracy.

Foraging Behavior

Identifying foraging trips and bouts. To better understand the foraging behavior of harbor seals in the Georgia Basin, I examined diving behavior at two temporal scales: foraging trips and bouts of diving (Boyd et al. 1994, Austin et al. 2006b). To identify diving bouts, I used a modified version of Boyd's (1994) iterative statistical method for classifying bouts of diving. Following Boness et al. (1994), I operationally defined the beginning of a harbor seal bout as a minimum of four consecutive (surface interval between dives ≤ 90 s) dives to at least 6 m. After the start of a bout, subsequent dives were added to the bout if the next surface interval was not significantly greater than the mean surface intervals from the previous dives within the bout according to a t-test with an alpha value of 0.05 (Boyd et al. 1994, Beck et al. 2003). The bout ended when the subsequent surface interval was significantly greater than the previous surface intervals in the bout. After examining the dive records, foraging trips were defined as the time in water occurring between two haul-out periods ≥ 15 min and including at least one diving bout.

Diving bout classification. Bouts were classified using eight bout variables: 1) number of dives within the bout; 2) mean dive depth; 3) mean dive duration; 4) mean surface interval; 5) bout duration; 6) percent of time spent at depth; 7) percent of square-shaped dives; and 8) percent of V-shaped dives. According to a Shapiro-Wilk's test, the first five variables were not normally distributed and hence were log-transformed. Although transformation did not result in normalization, it did reduce the skew in the dataset. The same procedure described to identify individual dives was used to identify diving bout types. Bout variables were run through a PCA to produce a smaller set of uncorrelated variables, then PCA factor scores were input into a k-means cluster analysis. The cluster

solutions were validated using a discriminant function analysis and the most parsimonious cluster solution was accepted.

Statistical analysis. I analyzed foraging trips and diving bouts using Linear Mixed Effects Models (LMEM) to account for repeated measures and unequal variance in the data. Specifically, I compared seasonal and diurnal variation among and between haul-out site groups for bout type and foraging trip duration. The different life history stages that occurred during the study period were divided into pre-pupping (April-June) and pupping (July-September) seasons. Because I was interested in the effects of haul-out site, season, time of day, bout type, and month on dive behavior I included these factors as fixed effects in these models whereas, individual seal was included as a random effects to account to account for its confounding influence (Austin et al. 2006a). When analyzing foraging trips the number of dives per trip was added as a random effect and bout type was removed. Although sex differences in dive behavior have been documented in harbor seals (Thompson et al. 1998, Härkönen et al. 1999, Hastings et al. 2004), sex was not included as a factor in these models due to unequal and small sample sizes. Two variations of models were run, one with haul-out site, time of day, bout type, and season as fixed effects, and the other with haul-out site, time of day, and month as fixed effects. Month was separated from season in an attempt to identify changes in bout type on a smaller time scale than season. The lowest Akaike's Information Criterion (AIC) was used to select the models with the best fit. A delta AIC value (Δ_i) < 2 was used to identify models with considerable support (Mazerolle 2004). Independent contrasts were run when significant interactions were identified. *P* values were Bonferroni-corrected when multiple comparisons were made. All analyses were performed with NCSS97 (Hintze 2000) and R version 2.6.1.

RESULTS

Twenty-six seals were tagged at the three Georgia Basin sites. Twenty animals were equipped with both a TDR (Mk-9, Mk-10F, or Splash) and an instrument that transmitted satellite locations (Spot5 or Splash). The remaining six animals were equipped with a TDR (Mk-9) and a VHF head tag, which allowed me to manually locate the animals.

All TDR packages deployed in the Padilla Bay National Estuarine Research Reserve were recovered (n=11), four TDR packages were recovered from Bird Rocks, and two Splash tags were recovered from the Belle Chain Islets. A total of 216,087 dives were recorded for 9 adult females, and 8 adult males (Table 1). Due to variable molt times, only two seals retained their tags through the duration of the pupping season (July-September); therefore, data recorded after August 31 were not included in analysis. Preliminary analysis of movement patterns shows that seals either return to or do not travel far from their respective tagging sites (S. Hardee, personal communication¹). This behavior suggests that pooling seals by their tagging sites accurately identifies where they were hauling-out during this study.

¹ Sarah Hardee, personal communication March, 2008

Dive Behavior

Dive Classification

The PCA run on the ten transformed dive variables suggested the selection of three factors, which accounted for 86.45% of the total variance. All the dive variables loaded significantly on at least one principal component factor and were therefore all included in subsequent analyses (Appendix 7). After excluding dives with > 50% of the values missing, a total of 191,554 (90.0%) dives were classified. After running the factor scores plus the wiggle dive variable through a k-means cluster analysis, discriminant analysis indicated that six clusters was the appropriate number to accept with 88.5% of the dives classified correctly.

The six clusters (dive types) were assigned a dive shape after visual inspection of the results (Table 2). Four of the six dive types were square-shaped, with a mean bottom time (85% of time spent in the bottom portion of the dive) > 50% of the total dive duration (Table 3). The remaining two dive types (types 1 and 3) were considered V-shaped dives with a mean bottom time < 33% of the total dive duration. Type 2 and type 5 dives were considered deep dives (≥ 20 m) and were similar in depth, duration, and bottom time (Table 3); however, type 2 dives were classified as wiggle dives and type 5 dives were not (Table 2). Dive types 4 and 6 were considered shallow (< 20 m) and were also separated by wiggles. Type 4 dives were classified as wiggle dives and type 6 dives were not. Type 1 and type 3 dives, the V-shaped dives, were similar in depth and duration (Table 3), but differed in skew. Type 3 dives were skewed to the left indicating a slow descent rate compared to ascent rate, and type 1 dives were skewed to the right indicating a slower ascent rate (Table 2).

Table 1. Data collected from each tagged *Phoca vitulina* relative to capture site.

Site and ID	Sex	Mass (kg)	TDR	Recovery	# Dives	Location Tag	# days of dive data
Bird Rocks							
B1695	M	71.5	Mk-10	Y	38,576	Spot 5	152
B1696	M	74.5	Mk-10	Y	14,513	Spot 5	57
B1697	M	96.0	Mk-9	N	-	Spot 5	-
B1698	M	90.0	Mk-9	N	-	Spot 5	-
B1700	M	86.0	Mk-9	Y	9,476	VHF	52
B1701	M	81.5	Mk-10	N	-	Spot 5	-
Y1455	F	76.5	Mk-10	Y	13,419	Spot 5	88
Total	6M, 1F			4	75,984		
Belle Chain							
B1702	M	81.5	Splash	N	-	Splash	-
B1703	M	66.5	Splash	N	-	Splash	-
B1704	M	72	Splash	N	-	Splash	-
B1706	M	90.5	Splash	N	-	Splash	-
B1707	M	58.5	Splash	Y	26,459	Splash	102
B1709	M	92	Splash	Y	17,909	Splash	96
B1710	M	77	Splash	N	-	Splash	-
B1711	M	70.5	Splash	N	-	Splash	-
Total	8M			2	44,368		
Padilla Bay							
B1699	M	64.0	Mk-9	Y	5,516	Spot 5	119
B1712	M	69.0	Mk-9	Y	2,377	Spot 5	75
B1713	M	54.0	Mk-9	Y	3,266	Spot 5	76
Y1456	F	55.5	Mk-9	Y	4,268	VHF	94
Y1457	F	57.5	Mk-9	Y	17,305	VHF	99
Y1458	F	48.5	Mk-9	Y	14,210	VHF	119
Y1459	F	83.0	Mk-9	Y	19,643	Spot 5	127
Y1460	F	62.5	Mk-9	Y	8,262	Spot 5	93
Y1462	F	77.5	Mk-9	Y	1,172	Spot 5	92
Y1465	F	103.0	Mk-9	Y	15,329	VHF	92
Y1469	F	85.0	Mk-9	Y	5,143	VHF	137
Total	3M, 8 F			11	96,491		

Table 2. Dive shapes and general characteristics of *Phoca vitulina* dives in the Georgia Basin.

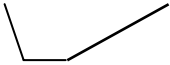

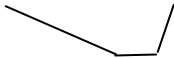


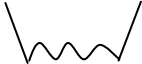
Dive Type	Characteristics	Dive Shape	Percent of Total Dives
Type 1	Short, Shallow, V-shape, Skewed Right		9.6%
Type 2	Long, Deep, Square, Wiggles		24.3%
Type 3	Short, Shallow, V-shape, Skewed Left		9.8%
Type 4	Short, Shallow, Square		17.6%
Type 5	Long, Deep, Square		17.9%
Type 6	Short, Shallow, Square, Wiggles		20.8%

Table 3. Mean (\pm SE) values of *Phoca vitulina* dive types in the Georgia Basin.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Max Depth (m)	13.6 \pm 0.20	64.0 \pm 0.66	15.7 \pm 0.23	11.1 \pm 0.14	54.1 \pm 0.60	11.7 \pm 0.15
Duration (s)	157.0 \pm 1.60	287.4 \pm 2.15	158.6 \pm 1.65	200.1 \pm 1.88	263.2 \pm 1.96	215.0 \pm 2.06
Bottom Time (s)	50.6 \pm 0.98	147.3 \pm 1.80	49.6 \pm 0.99	139.5 \pm 1.73	142.7 \pm 1.69	149.6 \pm 1.82
Wiggles	0.35 \pm 0.01	1 \pm 0	0.5 \pm 0.01	0 \pm 0	0 \pm 0	1.0 \pm 0
Avg. Descent Rate (m·s ⁻¹)	0.6 \pm 0.01	1.1 \pm 0.01	0.3 \pm 0.003	0.5 \pm 0.004	1.0 \pm 0.01	0.5 \pm 0.004
Avg. Ascent Rate (m·s ⁻¹)	0.2 \pm 0.002	0.9 \pm 0.01	0.6 \pm 0.01	0.4 \pm 0.004	0.9 \pm 0.01	0.4 \pm 0.004
Skew 1	0.4 \pm 0.001	0.9 \pm 0.01	2.3 \pm 0.02	1.0 \pm 0.01	0.9 \pm 0.01	1.0 \pm 0.01
Skew 2	2.9 \pm 0.06	1.2 \pm 0.01	0.5 \pm 0.004	1.2 \pm 0.01	1.2 \pm 0.01	1.3 \pm 0.01

Diving Bouts

A total of 27,171 bouts were identified with an average duration of $1,900.3 \pm \text{SE } 11.93 \text{ s}$ ($32 \pm \text{SE } 0.20 \text{ min}$). The PCA recommended the retention of four factors, which accounted for 90.49% of the total variance. All of the bout variables were included in the analysis as they all loaded significantly on at least one factor. Discriminant analysis of the cluster solutions indicated that three clusters was the most parsimonious solution, correctly classifying 98.6% of the bouts. The characteristics of each bout type were identified after manual inspection of the results (Table 4). Diving bouts were broadly separated by duration and depth. A long bout had a duration $\geq 1,800 \text{ s}$ (30 min), and a deep bout had a mean dive depth $\geq 20 \text{ m}$. Bout types 1 and 3 were both classified as deep and were composed of mostly square-shaped dives ($> 80\%$), but differed dramatically in duration (Table 4). Type 2 bouts were classified as short and shallow and contained a mixture of dive types (49% square-shaped and 51% V-shaped) (Table 4).

Bout type by season. The following model was used to examine variation in bout use across seasons:

$$Y = \mu + \text{Site} + \text{Season} * \text{Time} * \text{BoutType} + \text{Site} * \text{Time} + \text{Site} * \text{BoutType} + \text{Seal} + \text{NumBouts}$$

Haul-out site, time of day, and bout type all significantly influenced the number of bouts performed (Table 5). Season did not influence bout use as an independent factor, but did have a significant affect when interacting with both time of day and bout type. The number of short/shallow bouts increased significantly during the pupping season ($P = 0.03$) and the number of short/deep bouts decreased ($P < 0.03$). Looking at interaction of season with time of day there was a significant change in the use of different bout types. During the pre-pupping season there were more short/deep bouts used throughout the day than any other

bout type. During the pupping season there was an increase in short/shallow bouts and a decrease in short/deep bouts at night, making shallow bouts the predominant type used at night during this season ($P = 0.03$) (Figure 4). The interaction of haul-out site and time of day identified differences in bout effort throughout the day ($P = 0.03$) (Figure 5). Bird Rocks and Padilla Bay showed similar patterns with more bouts occurring from 0:00 – 5:59 h. The Belle Chain Islets seals were different with more bouts occurring from 6:00 – 10:59 h. All sites had an additional increase in abundance of bouts from 16:00 – 20:59 h and the fewest number of bouts occurred during the middle of the day (11:00 – 15:59 h) and a night (21:00 – 23:59 h). The use of each bout type also varied significantly at each haul-out site ($P < 0.001$). The relative proportion of each bout type at each site was similar with more short/deep bouts being performed at all sites (Figure 6). However, the use of short/deep bouts varied significantly between Padilla Bay and the other two sites ($P < 0.001$). Additionally, the Belle Chain Islet seals were the only seals to perform more short/shallow bouts than short/deep bouts (Figure 6).

Bout type by month. The following model was used to examine the variation in harbor seal bout use by month:

$$Y = \mu + \text{Site} * \text{Time} * \text{BoutType} + \text{Seal} + \text{NumBouts}$$

All models including month as a factor had a delta AIC score (Δ_i) > 2 and therefore did not provide considerable support for examining variation in bout use. The interaction of haul-out site, time of day, and bout type and the interaction of haul-out site and bout type did significantly affect the number of each bout type used; however, both of these interactions were described previously when examining bout use by season. Therefore, from this point forward I will only refer to variation in bout use by season.

Table 4. Mean (\pm SE) values of *Phoca vitulina* bout types in the Georgia Basin.

	Type 1 Long/Deep	Type 2 Short/Shallow	Type 3 Short/Deep
Number of Dives	9.7 \pm 0.043	6.1 \pm 0.01	5.7 \pm 0.007
Dive Depth (m)	29.0 \pm 0.30	16.5 \pm 0.13	42.7 \pm 0.25
Dive Duration (s)	229.2 \pm 1.11	157.6 \pm 0.88	253.1 \pm 0.79
Surface Intv. Duration (s)	104.1 \pm 6.53	51.0 \pm 2.22	39.6 \pm 0.33
Bout Duration (s)	3003.4 \pm 41.96	1250.0 \pm 13.83	1667.2 \pm 5.61
Time at Depth (%)	0.8 \pm 0.002	0.8 \pm 0.002	0.9 \pm 0.001
Square-shaped (%)	0.9 \pm 0.002	0.4 \pm 0.002	0.9 \pm 0.001
V-shaped (%)	0.1 \pm 0.002	0.4 \pm 0.002	0.04 \pm 0.001

Table 5. ANOVA output for linear mixed effect model examining the association of site, season, and time of day with *Phoca vitulina* bout types in the Georgia Basin. Bold font indicates significant interactions.

	num DF	den DF	F-Value	P-Value
Site	2	14	6.85	0.01
Season	1	929	3.25	0.07
Time	4	929	12.29	< 0.001
Bout Type	2	929	65.80	< 0.001
Season : Time	4	929	0.67	0.61
Season : Bout Type	2	929	5.13	0.01
Time : Bout Type	8	929	1.87	0.06
Site : Time	8	929	2.20	0.03
Site : Bout Type	4	929	22.58	< 0.001
Season : Time : Bout Type	8	929	2.21	0.03

Figure 4. Distribution of *Phoca vitulina* bout types relative to season and time of day. The pre-pupping season is from April-June and the pupping season is from July-August.

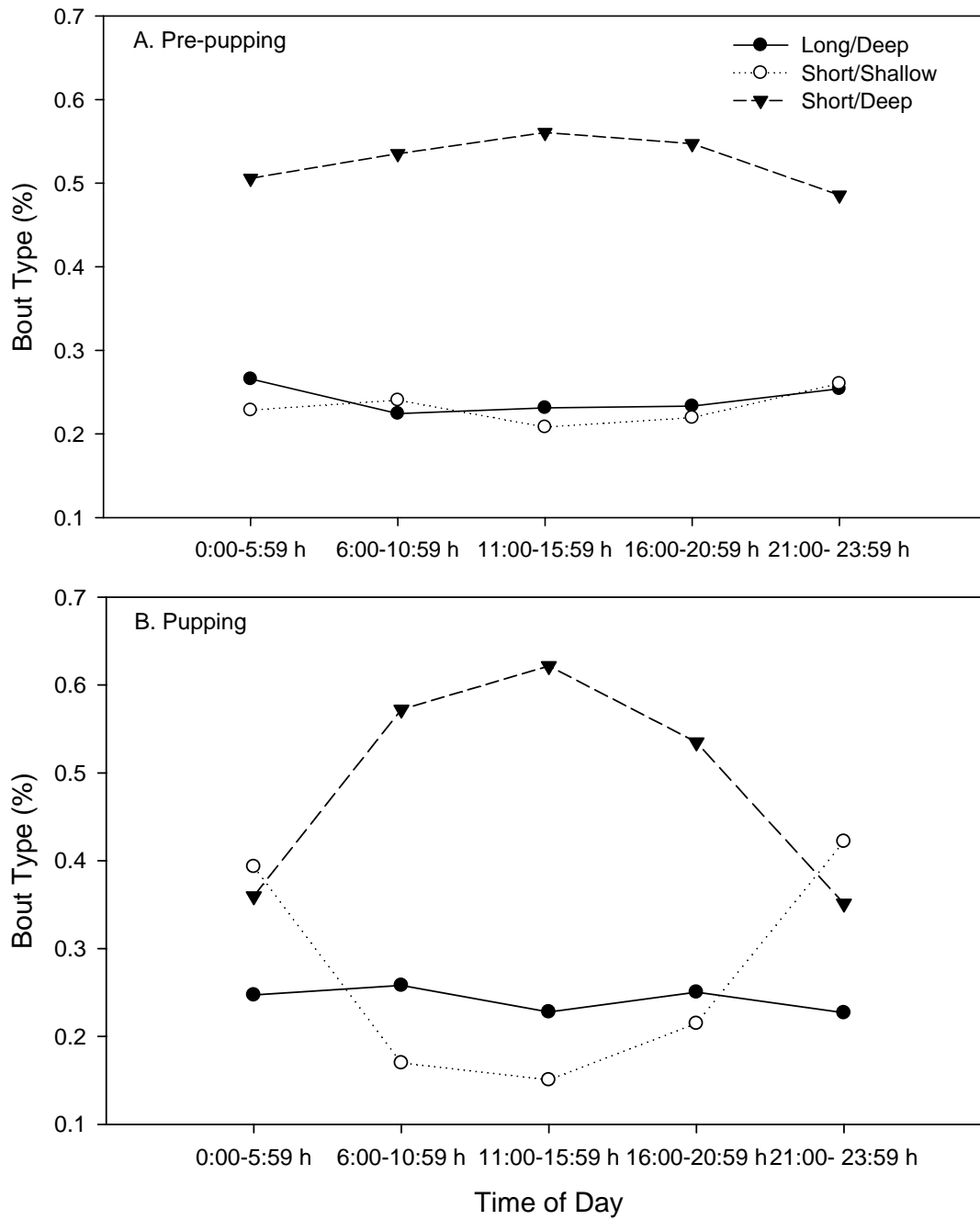


Figure 5. Distribution of *Phoca vitulina* bout types relative to seals per haul-out site and time of day.

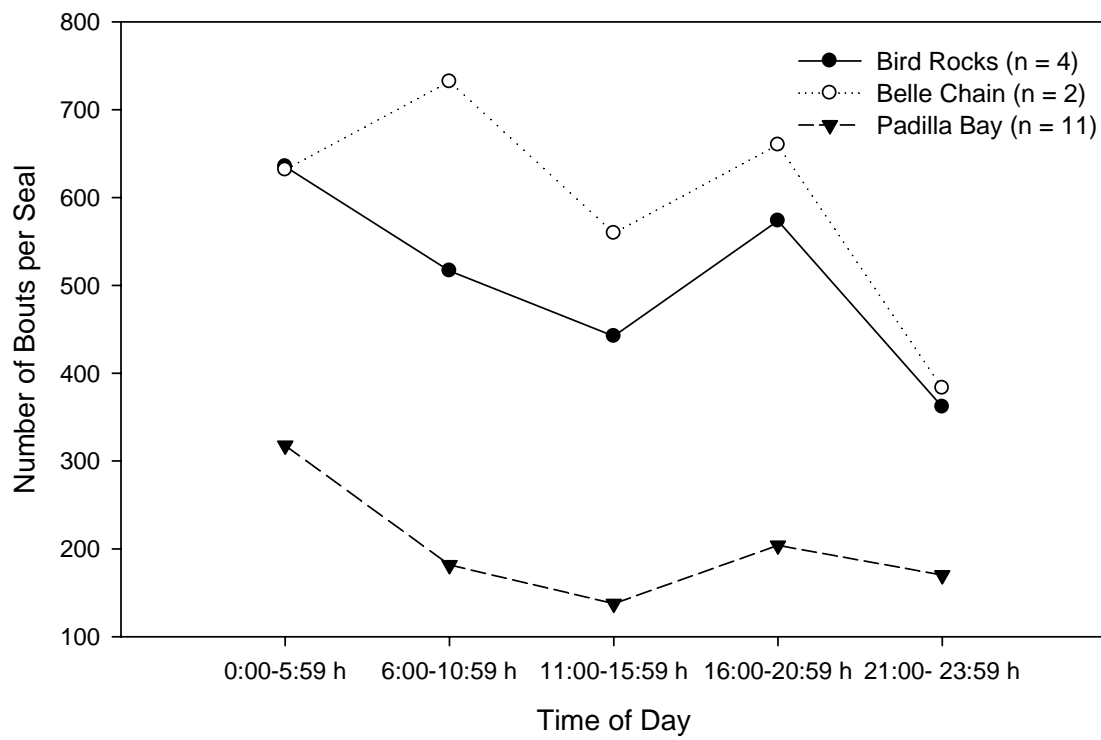


Figure 6. Distribution of *Phoca vitulina* bout types relative to haul-out site.

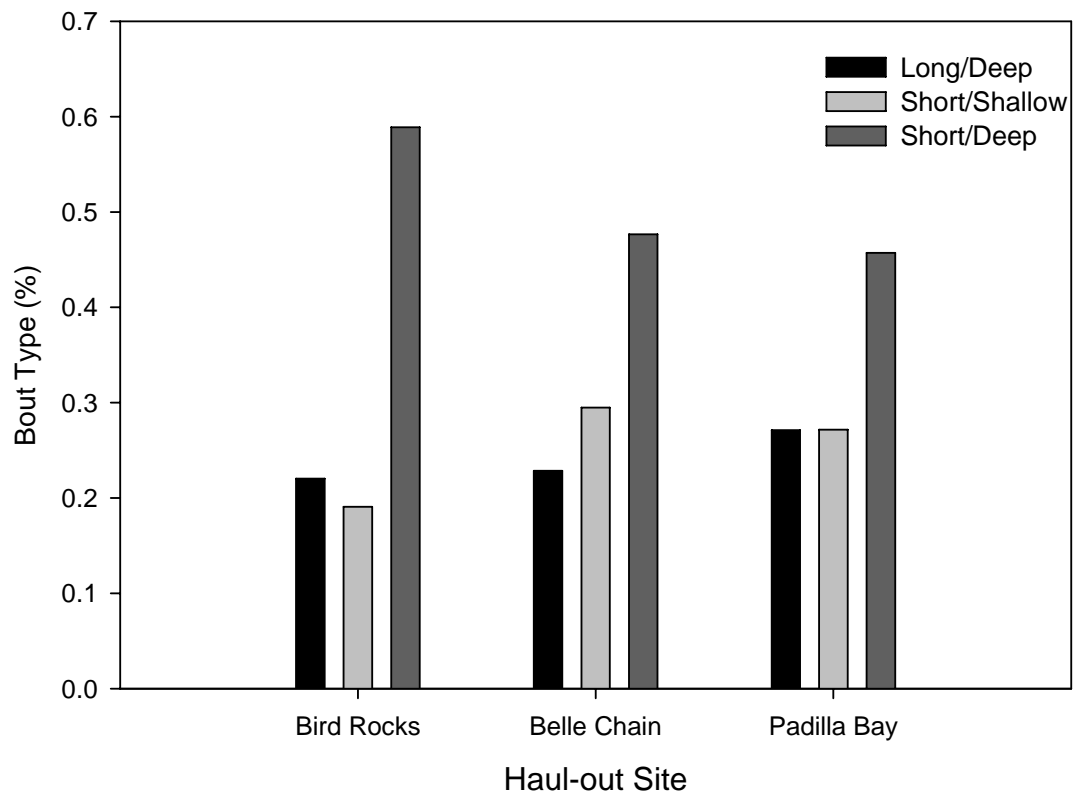


Table 4. ANOVA output for linear mixed effect models examining the association of site, month, and time of day with *Phoca vitulina* bout types in the Georgia Basin. Bold font indicates the significant interactions.

	Num DF	Den DF	F-Value	P-Value
Site	2	14	6.94	0.01
Time	4	928	11.89	< 0.001
Bout Type	2	928	64.25	< 0.001
Site : Time	8	928	2.09	0.03
Site : Bout Type	4	928	23.62	< 0.001
Time : Bout Type	8	928	1.84	0.07
Site : Time : Bout Type	16	928	0.44	0.97

Foraging Trips

A total of 2,699 foraging trips were identified for all 17 seals. Each trip included an average of $61.9 \pm \text{SE } 1.53$ dives with a mean duration of $6.2 \pm \text{SE } 0.13$ h. The mean trip duration per haul-out site was representative of the means for individual seals and was therefore used in analysis (Table 8). Linear mixed effects models indicated that the interaction between haul-out site and season or the interaction between haul-out site and month were the best models for explaining foraging trip duration (Tables 9 and 10). Time of day was not a significant factor in explaining trip duration. When examining trip duration by month April was excluded because not all seals were tagged until May generating an unequal sample size across sites for the month of April.

Trip duration by season. Trip duration decreased when moving from the pre-pupping season (April-June) into the pupping season (July-August) (Figure 7). Independent contrasts indicated that the change in trip duration between seasons was significantly greater at Bird Rocks than at both the Belle Chain Islets and Padilla Bay ($P < 0.001$) (Figure 8). During the pre-pupping season trip duration at Bird Rocks was significantly longer than at the other two sites ($P < 0.001$). However, during the pupping season trip duration at Padilla Bay was significantly less than at both Bird Rocks and the Belle Chain Islets ($P < 0.001$).

Trip duration by month. The same trend was observed by month as by season at Bird Rocks and Padilla Bay: trip duration decreased in July at the beginning of the pupping season. The Belle Chain Islets were different; the average trip duration in July (the beginning of the pupping season) is slightly higher than the average durations in both May and June. Duration at this site did not decrease until August, when it dropped from 7.0 h to 3.9 h (Figure 9).

Table 5. Mean (\pm SE) values of *Phoca vitulina* foraging trips relative to haul-out site in the Georgia Basin. Bold font indicates the trip characteristics averaged for each haul-out site.

Seal ID	Number of Trips	Avg. Trip Duration (h)	Avg. Number of Dives per Trip
Bird Rocks	141	9.9 \pm 8.83	108.5 \pm 99.26
B1695	265	8.4 \pm 8.16	112.1 \pm 105.39
B1696	107	8.3 \pm 7.98	108.0 \pm 111.66
B1700	114	12.4 \pm 7.83	101.4 \pm 67.7
Y1455	79	13.4 \pm 11.42	107.4 \pm 99.73
Belle Chain	231	6.4 \pm 5.99	76.3 \pm 88.62
B1707	238	6.9 \pm 6.74	92.6 \pm 101.56
B1709	224	5.9 \pm 5.04	58.9 \pm 68.44
Padilla Bay	152	4.9 \pm 5.63	42.2 \pm 59.71
Y1456	114	2.8 \pm 3.01	26.0 \pm 38.76
Y1457	173	6.9 \pm 6.75	75.4 \pm 79.04
Y1458	386	3.5 \pm 3.67	30.0 \pm 38.92
Y1459	247	6.7 \pm 5.82	55.0 \pm 55.25
Y1460	251	2.5 \pm 2.57	22.8 \pm 30.86
Y1462	40	6.5 \pm 7.01	19.7 \pm 21.38
Y1465	175	8.1 \pm 8.39	76.6 \pm 86.60
Y1469	86	3.9 \pm 5.21	13.4 \pm 14.83
B1699	74	5.1 \pm 5.48	51.2 \pm 68.25
B1712	88	4.5 \pm 5.09	18.9 \pm 24.45
B1713	38	6.2 \pm 6.73	75.2 \pm 127.42

Table 6. ANOVA output for linear mixed effect models examining the association of site and season with *Phoca vitulina* trip duration in the Georgia Basin. Bold font indicates significant interactions.

	num DF	den DF	F- Value	<i>P</i> -Value
Site	2	14	0.26	0.78
Season	1	2679	37.81	< 0.001
Site : Season	2	2679	11.04	< 0.001

Figure 7. Mean foraging trip duration for *Phoca vitulina* in the Georgia Basin relative to season. The pre-pupping season is from April-June and the pupping season is from July-August.

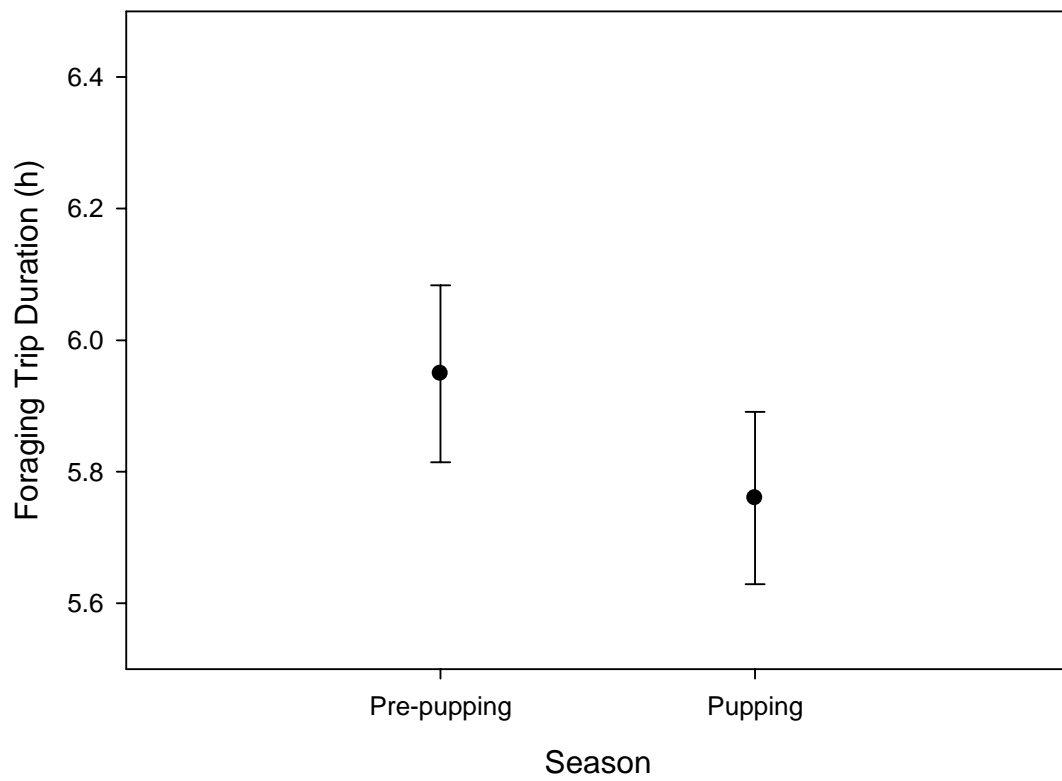


Figure 8. Mean (\pm SE) foraging trip duration of *Phoca vitulina* relative to haul-out site in the Georgia Basin. The pre-pupping season is from April-June and the pupping season is from July-August.

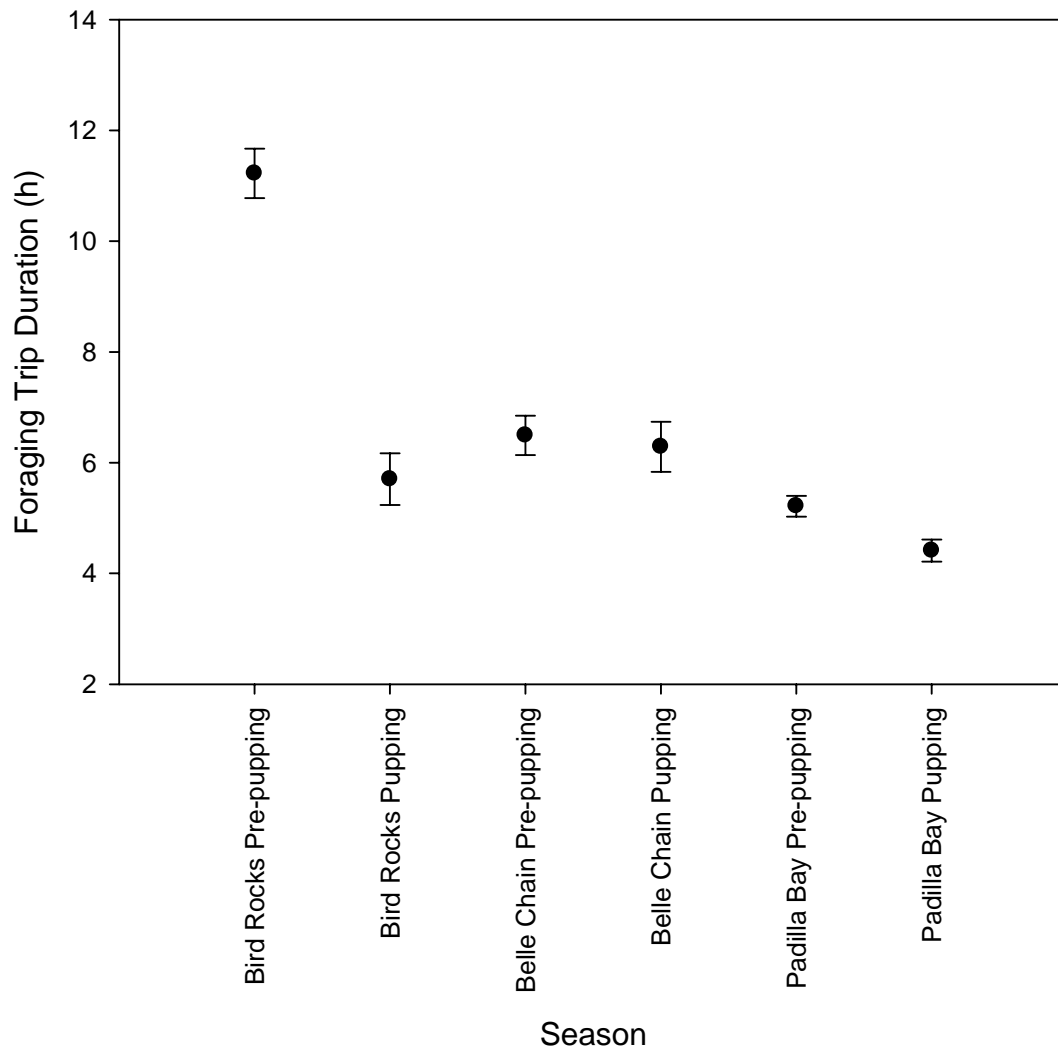
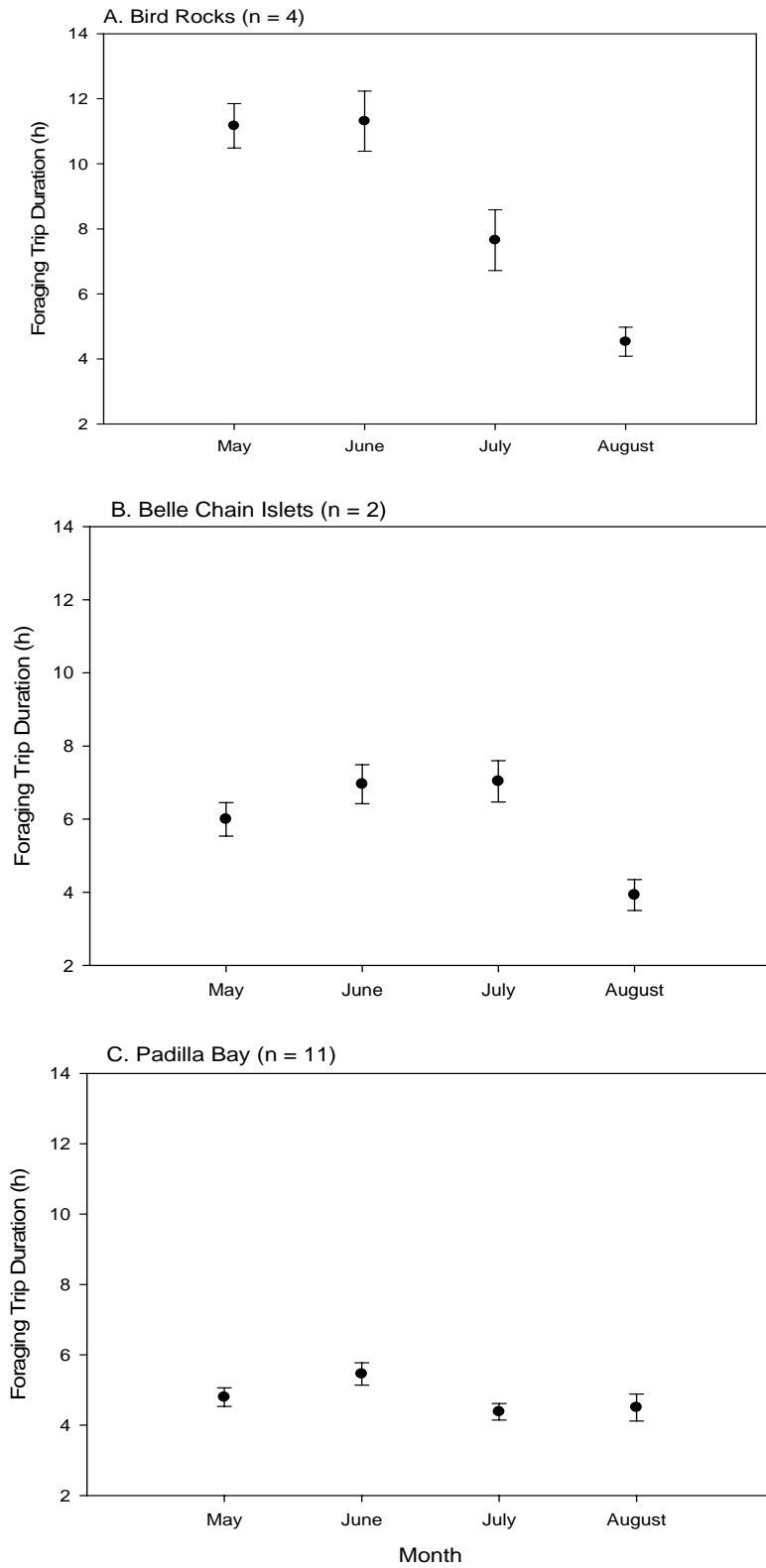


Table 7. ANOVA output for linear mixed effect models examining the association of site and month with *Phoca vitulina* trip duration in the Georgia Basin. Bold font indicates significant interactions.

	num DF	den DF	F-Value	P-Value
Site	2	14	0.27	0.77
Month	3	2345	10.79	< 0.001
Site : Month	6	2345	5.32	< 0.001

Figure 9. Foraging trip duration of *Phoca vitulina* relative to haul-out site and month in the Georgia Basin.



DISCUSSION

In determining the management and designation of marine reserves aimed to aid in the recovery of prey species, the impact of local predators on these prey populations needs to be considered. This study was able to document both seasonal and diurnal variation in the use of different bout types and seasonal variation in foraging trip duration at three haul-out sites in the Georgia Basin. There was high variability between haul-out sites and seasons, apparently in association with fluctuations in prey abundances. Variation in bout use and foraging trip duration suggests that seals switched the predominant prey in their diet, as the switches in behavior coincided with prey fluctuations in the study area. My results support diet analysis from the area, which indicates that harbor seal diet varies based on prey fluctuations (Lance & Jeffries 2007).

I examined the foraging behavior of harbor seals (*Phoca vitulina*) in the Georgia Basin on two temporal scales: diving bouts and foraging trips. To determine diving bouts and foraging trips I first classified individual dive types. Diving bouts were examined to identify changes in foraging behavior on a small scale and potentially identify a switch in the prey consumed throughout the day. Foraging trips were examined to identify changes in duration and therefore effort spent searching for prey across seasons and months. By combining these analyses I was able to correlate variations in foraging behavior with fluctuations in prey abundance throughout the Georgia Basin and between haul-out sites while developing a cohesive picture of harbor seal foraging behavior during the pre-pupping and pupping seasons.

Six dive types were identified in this study: four square-shaped dives varying in depth, duration, and wiggle occurrence, and two V-shaped dives varying in skew. The number and shape of these dives were similar to those reported for harbor seals in other areas (Lesage et al. 1999, Baechler et al. 2002). Three bout types were classified based on the six dive types: long/deep, short/shallow, and short/deep. These bout types were used to examine variation in foraging behavior across the pre-pupping and pupping seasons. The proportion of each bout type used varied by haul-out site, season, and time of day suggesting that diving bouts were affected both spatially and temporally. The duration of foraging trips decreased at all haul-out sites during the pupping season, a result similar to that reported in other studies (Thompson et al. 1994, Coltman et al. 1997). The magnitude of decrease was smaller at both the Belle Chain Islets and Padilla Bay than at Bird Rocks suggesting differences in foraging strategies or prey selection between seals from different haul-out sites. When examining overall foraging behavior, combining analyses of diving bouts and foraging trips, each haul-out site was unique. As previous studies have shown that foraging behavior between nearby sites is similar, this study proposes interesting variation related either to haul-out site or sex in the Georgia Basin.

Harbor seal diet analyses in the study area have been restricted to August through April, leaving a data gap in the middle of my study (May-July). However, data collected in 2005 and 2006 suggest that herring (*Clupea spp.*) was the dominant prey of harbor seals in April, the month in which I began my study, and that there was a switch to salmon (*Oncorhynchus spp.*) as the dominant prey item by the beginning of August (Lance & Jeffries 2007). While herring are available year-round in Puget Sound, salmon do not come into the area until July (Quinn 2005). Hence, the temporal and spatial variation in both bout types

and foraging trip duration may represent variation in prey availability. Seals switched the predominant prey in their diet over time thus changing their foraging behavior and seals from different sites fed on different prey items explaining variability between sites. Under this scenario, seals exploited readily available prey by adopting different foraging strategies during different seasons or when foraging in specific locations.

Dive Behavior

Dive Classification

I identified six dive shapes for harbor seals in the Georgia Basin. Studies examining pinniped diving behavior have usually identified four to seven dive types (Boyd et al. 1994, Schreer & Testa 1996, Lesage et al. 1999, Frost et al. 2001, Baechler et al. 2002, Austin et al. 2006b). Among these classifications, two dive shapes are commonly observed: square- and V-shaped dives, while the remaining dives are a variation of these core shapes. All of the classified dives in this study resembled one of the core dive shapes and differed either in skewness (ratio of ascent and descent rates), depth, duration, or the occurrence of wiggles.

It is difficult to assign function to an individual dive or to a dive type. Previous studies have attempted to assign functions to different dive shapes by combining dive profiles, stomach-temperature telemetry, and swim speed to their analyses (Lesage et al. 1999, Baechler et al. 2002). These studies have suggested that skewed dives, with longer ascent or descent phases, may be attributed to a seal increasing the horizontal search component of the dive, or simply swimming along a bottom that progressively changes in depth (Lesage et al. 1999). Square-shaped dives have consistently been associated with foraging behavior as the diver spends more time at depth thus increasing the likelihood of

encountering prey (Le Boeuf et al. 1988, Schreer & Testa 1996, Lesage et al. 1999, Baechler et al. 2002). V-shaped dives may be related to exploratory behavior or travelling depending on the depth or skew of the dive respectively. Although multiple studies have been able to attribute dive shapes to specific dive functions, the authors have also acknowledged that the association of one dive type to only one behavior is largely anecdotal. Recent studies have shown that it is difficult to infer specific behaviors based on dive shape alone and that examining bouts of diving more accurately represents changes in foraging patterns and behavior (Boness et al. 1994, Boyd et al. 1994, Baechler et al. 2002, Beck et al. 2003, Austin et al. 2006b). Consequently, dives were used to identify different bout types and were not compared individually in this study.

Diving Bouts

The behavior of harbor seals is organized into clusters or bouts of diving. In this study, only 8.1% of dives occurred outside of these bouts. I identified three bout types differing primarily in depth and duration, but also in the percentage of square- and V-shaped dives occurring within the bout. These results are similar to those found in grey seals (*Halichoerus grypus*), Antarctic fur seals (*Arctocephalus gazella*), and harbor seals in other areas (Boness et al. 1994, Boyd et al. 1994, Beck et al. 2003). The differences in duration, dive shape, and percent of time spent at depth between bout types, may suggest that each type represented a different behavior. Determining the exact nature of these behaviors remains difficult and limited (Boyd et al. 1994, Austin et al. 2006b); however, studies using stomach-temperature telemetry to identify feeding events, indicate that bouts of diving with a

high percentage of time spent at depth (with a high percentage of square-shaped dives) are correlated with foraging activities (Lesage et al. 1999, Austin et al. 2006b). I identified two bout types with a high percentage of time spent at depth (short/deep and long/deep). The majority of dives occurring within these bouts were square-shaped with > 80% of the entire bout duration spent at depth (in the bottom portion of the dive).

Wiggle dives have also been correlated with foraging behavior as vertical movement in the bottom portion of the dive can be attributed to movements within a prey patch (Lesage et al. 1999). In all three bout types identified in this study, > 50% of the dives within each bout were classified as wiggle dives. Short/shallow bouts contained nearly equal proportions of both square and V-shaped dives.

Shallow diving bouts (Boyd et al. 1994) as well as V-shaped dives (Lesage et al. 1999) have previously been associated with exploratory behavior while searching for a prey patch and feeding near the surface (< 20 m). V-shaped dives have been attributed to a number of different activities including traveling, predator avoidance, and exploration as animals are able to reduce drag and increase their chances of encountering prey by diving while traveling instead of swimming at the surface (Williams & Kooyman 1985, Schreer & Testa 1996, Lesage et al. 1999, Williams 1999).

In this study, short/shallow bouts contained both square and V-shaped dives, and may therefore be associated with searching for and then feeding within prey patches located in shallow waters (< 20 m). The median dive depth in these shallow bouts was 13.3 m with an average depth of $16.5 \pm \text{SE } 0.13$ m. Both the long/deep and short/deep bouts had a high proportion of time spent at depth and may be attributed to foraging in deep waters (≥ 20 m) (Coltman et al. 1997). The majority of dives within these bout types were square-shaped

with wiggles, indicating a high proportion of time spent at depth while feeding within a prey patch. While both of these bout types represent foraging in deep waters the duration of the bouts differed on average by 22 min. The surface interval between dives in long/deep bouts was on average 64 s longer than those in short/deep bouts and the median dive depth was 21.0 m with an average depth of $29.0 \pm \text{SE } 0.30$ m.

Short/deep bouts, with deeper dives (median = 36.8 m, average = $42.7 \pm \text{SE } 0.25$) and shorter inter-dive surface periods, likely represented continuous foraging within a tightly aggregated prey patch where the seal returned briefly to the surface to replenish its oxygen stores before returning to feed.

Long/deep bouts also represented foraging at depth; however, the differences in dive depth and inter-dive surface intervals indicate a different foraging strategy than that suggested for short/deep bouts. Seals may have been foraging on more loosely aggregated or larger prey resulting in more time spent at the surface between dives.

Variation in bout use. The number of bouts performed was significantly influenced by haul-out site, season, bout type, and time of day; indicating that foraging behavior was affected both spatially and temporally. Bout effort data, with an increase in effort during twilight periods, suggests that seals from all of the study sites were feeding on vertically-migrating prey, an explanation offered to explain similar variations in effort for other pinnipeds (Le Boeuf et al. 1988, Williams et al. 1992, Boyd & Croxall 1996, Lesage et al. 1999). Vertically-migrating prey, such as herring (*Clupea spp.*), tend to form more dense aggregations during dawn and dusk than at other times of day (Muntz 1983, Lesage et al. 1999). Hence, the capture success of seals would increase by foraging when prey form these large aggregations.

Further support for the idea that harbor seals in the Georgia Basin consumed vertically-migrating prey is seen when examining the interaction of season, time of day, and bout type. A diurnal pattern developed during the pupping season (July-August), with an increase in deep bouts (≥ 20 m) during the day and an increase in shallow bouts (< 20 m) at night. Harbor seals are opportunistic predators; however, a large portion of prey in their diet (herring, salmon, and sand lance) follow a diurnal vertical migration remaining at depth during the day and moving towards the surface at night to feed (Groot & Margolis 1928, Orr et al. 2003, Lance & Jeffries 2007). The observed pattern in the use of different bout types would indicate that the seals were following the vertical migration of their prey. A diurnal pattern in diving bout types has been observed in marine predators including whales, pinnipeds, and marine birds; however, only one other study has identified deeper diving during the day for harbor seals (Hastings et al. 2004). Harbor seals in Southeast Alaska and in Prince William Sound dove deeper during the day than at night during the post-molt and winter seasons. Seals in the Georgia Basin most likely benefit from deeper diving during the day in the summer because the predominant prey in their diet, herring and salmon (*Oncorhynchus spp.*), tend to form tightly aggregated groups deeper in the water column during the day at this time of year (Brodeur & Wilson 1996, Quinn 2005).

Diet analysis in Puget Sound indicates that harbor seals in 2005 (a pink salmon year) switched from consuming nearly 80% herring to 80% salmon at the end of July (Lance & Jeffries 2007). Salmon return to the Georgia Basin in July and August (Quinn 2005). Certain species of salmon (pink, sockeye, and chum) typically remain at depths of 6 - 36 m as they return from the open ocean and make their way back to their natal streams (Groot & Margolis 1928). These species also follow a diurnal vertical migration typically staying in

the deeper end of their range during the day and moving into shallower waters at night (< 20 m). This study was conducted during a pink salmon (*O. gorbuscha*) year, which leads me to conclude that the diurnal pattern observed during the pupping season, coupled with an increase in shallow diving, may be correlated with a switch in the predominant prey consumed (from herring to salmon).

During their diurnal vertical migration, herring and sandlance (*Ammodytes hexapteras*) aggregate in deeper waters at night and disperse in shallower waters during the day. This behavior is likely why I observed an increased bout effort during twilight hours across both seasons (indicative of foraging on diurnally migrating prey). The lack of a distinct diurnal pattern in bout use during the pre-pupping season when seals were theoretically feeding on herring, is difficult to explain because diet data for these sites from May-July are limited.

One study on the diet of harbor seals in Padilla Bay was able to collect data during the pre-pupping season (April-June); however, data were collected in 2006 when pink salmon were not running in the area. This study indicates that harbor seals from estuarine areas have a more diverse diet than those outside the estuary. In Padilla Bay, herring, salmon, and small schooling fish are consumed by harbor seals; however, seals also readily consume a number of benthic estuarine species such as gunnel (*Pholid spp.*), snake prickleback (*Lumpenus sagitta*), Pacific staghorn sculpin (*Leptocottus armatus*), plainfin midshipman (*Porichthys notatus*), and eelpout (*Zoarcid spp.*) (Luxa, personal communication²). Rocky-reef sites located just outside estuaries, likely used by estuarine seals (Lance, personal communication³), also show a more varied diet than that of rocky-reef

² Katie Luxa, personal communication March 12, 2008

³ Monique Lance, personal communication February 9, 2008

sites away from estuaries (Lance & Jeffries 2007). The increased variety in diet near estuaries and the regular consumption of benthic estuarine prey may be why a diurnal pattern in bout behavior was not observed in Padilla Bay until a shift in prey availability was observed and salmon began to run in late July. Other studies of harbor seals from estuarine bays indicate that seals typically forage in the benthos and that no diurnal pattern in dive behavior is observed in those areas (Boness et al. 1994, Tollit et al. 1998, Lesage et al. 1999). Individual seals may develop preferences for different foraging strategies, prey selection, or foraging locations (Boyd et al. 1994) and seals in Padilla Bay likely exploit both the estuarine habitat and the seasonal increases in salmon abundance. Preliminary analysis of harbor seal movement patterns in the Georgia Basin shows that seals from Padilla Bay typically remained < 5 km from the estuary during the pre-pupping and pupping seasons, while seals from both Bird Rocks and the Belle Chain Islets made multiple trips > 10 km from their tagging site (Hardee et al. 2008). Under this scenario, seals hauling-out in Padilla Bay foraged preferentially within the estuarine habitat. Foraging in the benthos throughout the year, and exploiting the salmon run during the summer, would explain the lack of a diurnal pattern during the pre-pupping season, the diurnal diving pattern during the pupping season, and why short/deep bouts were the predominant bout type used during both seasons in Padilla Bay.

The absence of a diurnal pattern during the pre-pupping season is more difficult to explain at Bird Rocks and the Belle Chain Islets. In analyzing foraging behavior using bouts instead of individual dives, a more biologically relevant analysis was completed; however, details such as the difference between wiggle and non-wiggle square-shaped diving may have been excluded. Studies examining individual dives indicate that deep (≥ 20 m), square-

shaped dives without wiggles may indicate foraging in the benthos (Le Boeuf et al. 1992, Schreer & Testa 1996, Lesage et al. 1999). Benthic-dwelling prey are present in the harbor seal diet from rocky-reef sites, including Bird Rocks and the Belle Chain Islets; however, a large majority of their diet is comprised of vertically-migrating schooling fish such as herring, Pacific hake (*Merluccius productus*), and salmon (Lance & Jeffries 2007). At both of these sites 18-30 % of the dives during the pre-pupping season were deep (≥ 20 m) and square-shaped without wiggles (Appendix 1), potentially indicating benthic foraging. Although harbor seals typically consume more pelagic prey in this area, consumption of prey that does not undergo a diurnal vertical migration (i.e. rockfish) does occur and seals from these sites may have exploited this type of prey during the pre-pupping season. The use of both wiggle and non-wiggle square-shaped diving was observed during this time potentially indicating that seals were foraging both in the benthos and on pelagic schooling prey. The use of both dive types during the pre-pupping season, before diurnally migrating salmon return to Puget Sound, may be why a distinct diurnal pattern in the use of different bout types was not observed until the pupping season.

Foraging Trips

Trip duration differed both between seasons and between haul-out sites in the Georgia Basin. To my knowledge, no study has examined these temporal and spatial variations in foraging trips in this area. Previous studies have focused on the effects of trip duration on post-trip haul-out duration (Austin et al. 2006b), the characteristics of maternal foraging trips during lactation (Bowen et al. 1999), the types of diving bouts that comprise foraging trips

(Boyd et al. 1994, Austin et al. 2006a, Austin et al. 2006b), and the influence of size and sex (Thompson et al. 1998).

Predator search behavior is generally correlated with prey patch characteristics; therefore, more time spent at sea (a longer foraging trip) will theoretically increase the chances of a seal encountering prey (Austin et al. 2006b). However, foraging trip duration also varies as prey abundances change. It has been suggested for both Steller sea lions (*Eumetopias jubatus*) and harbor seals in Alaska, that less time is spent foraging in the spring and summer because prey become more abundant near haul-out sites (Merrick & Loughlin 1997, Frost et al. 2001). Energy-rich prey such as capelin (*Mallotus villosus*) and sand lance (Appendix 2) become readily available and move closer to shore during the summer months in the Georgia Basin, suggesting that harbor seals can obtain more energy with less time spent foraging during this time (Anthony et al. 2000, Frost et al. 2001).

In this study, foraging trip duration varied both between haul-out sites and over time. There was a significant difference in trip duration between the pre-pupping and pupping seasons; however, when looking at each site individually, Bird Rocks was the only site with a significant decrease in trip duration by season. Trip durations at both the Belle Chain Islets and Padilla Bay decreased minimally during the pupping season, but seals from Bird Rocks decreased their trip duration by almost 50%. Similar to Alaska, energy-rich prey in the Georgia Basin, such as herring and salmon, become more abundant and move closer to shore during the summer months (Groot & Margolis 1928, Anthony et al. 2000). This increase in prey abundance near shore may be one reason for the overall decrease in trip duration at all sites. Under this scenario, seals were able to ingest more energy with less time spent

foraging. However, this does not address the minimal of lack of variation at both the Belle Chain Islets and Padilla Bay.

The magnitude of change in foraging trip duration across seasons varied between haul-out sites suggesting preferences for different foraging strategies or prey selection by seals from different haul-out site groups (Boyd et al. 1994). Seals from the Belle Chain Islets and Padilla Bay may have had prey readily available and abundant throughout the study period and did not need to adjust their search effort or trip duration during the pupping season, while the seals from Bird Rocks did. Additionally, when examining trip duration by month I was able to examine variation on a smaller scale. Although the Belle Chain Islets did not decrease trip duration significantly between seasons, there was a significant decrease in duration between July and August. The mating season for harbor seals in this area typically begins in August. Both seals tagged at the Belle Chain Islets were adult males, who typically make shorter foraging trips during the mating season (Coltman et al. 1997). Identifying intra-annual variation between haul-out sites suggests variation among individuals from different groups within a population, which has not previously been described for harbor seals in this area. These differences should be considered when extrapolating to the population level as different haul-out sites may exhibit more behavioral variations that were not described here. Additionally, the duration of foraging trips identified in this study appear to be shorter than previously identified for harbor seals. In Padilla Bay, haul-out availability is limited by tidal cycle, which, during extreme tides may make haul-out sites in the estuary inaccessible. With foraging trip duration shorter than some of the tidal cycles, the data suggest that some seals are moving to other locations during high tide. This will be interesting to investigate when examining foraging locations and movement patterns.

Foraging Behavior of Harbor Seals in the Georgia Basin

Analysis of variation in both diving bouts and foraging trips enabled me to examine harbor seal foraging behavior on two temporal scales: diving bouts and foraging trips. Both analyses suggest prey switching in association with fluctuations in prey abundance throughout the year. When looking at overall foraging behavior we see that each haul-out site is unique and that variations in behavior may be related to fluctuations in prey abundances, life history, or both. By combining these analyses I was able to identify between-site differences, which may allude to larger behavioral differences, such as prey specialization or habitat exploitation by different haul-out site groups. Prey specialization, with forage fish specialists and salmon specialists, has already been documented for harbor seals in southern Puget Sound (London et al. 2001) and likely explains the variation in diet and foraging behavior observed for harbor seals in this study.

These baseline data suggest differences in foraging behavior for haul-out sites located in close proximity to each other (15-55 km). Bird Rocks and Padilla Bay showed similar variations in the use of different bout types; however, seals from Padilla Bay and the Belle Chain Islets were more similar in the variation of foraging trip duration. When looking at diving bouts and foraging trips (the overall foraging behavior), the results suggest that each site is unique. Future studies should continue to document the foraging behavior at these sites to determine if these differences can be attributed to individual variability or to haul-out habitat exploitation. If seals adjust their foraging strategies based on prey abundance, then their foraging behavior may be highly correlated with haul-out site habitat as seals will likely exploit prey located near their primary haul-out site. The data presented here provide an opportunity to continually monitor and determine the relative importance of habitat

characteristics on variations in harbor seal foraging behavior. Comparing haul-out habitat to foraging area habitat may allude to either a correlation between foraging behavior and haul-out site type or to the degree of individual variability in foraging behaviors within the population. Either result will provide managers with important information regarding the foraging behavior of harbor seals allowing them to identify behavioral changes for harbor seals in the future and determine the regulatory influence of harbor seals on rockfish populations.

Beyond changes in prey abundance and/or profitability, behavioral changes that occur during the pupping and mating seasons may also influence foraging behavior. Although site was a significant factor in the analysis of foraging trip duration one should keep in mind that only one of four seals from Bird Rocks retained its TDR tag through the duration of the pupping season. Therefore, the data presented for Bird Rocks during the pupping season are strongly skewed towards the behavior of one individual (B1695), an adult male. Adult male harbor seals typically spend more time at sea and dive to deeper depths before the mating season to build up energy stores and then begin making shorter foraging trips with shallower dives during the mating season (Coltman et al. 1997). In this study, I did not include mating season as an important life-history stage; however, a female harbor seal becomes oestrous shortly after weaning a pup. As the nursing period for harbor seals is roughly four-five weeks (Allen 1985, Bowen 1991, Thompson et al. 1994), depending on how early in the season a female pups, the mating season and the pupping season may coincide. This coincidence may be responsible for the observed decrease in trip duration during the pupping season at Bird Rocks. Additionally, when looking at trip duration by month only a slight decrease was observed in July, at the beginning of the pupping season, and a more dramatic

decrease was observed in August at both Bird Rocks and the Belle Chain Islets. This later decrease in trip duration more likely coincides with the beginning of the mating season in the Georgia Basin and is another explanation for the dramatic decrease in foraging trip duration at these sites. In Padilla Bay, only a slight decrease in trip duration was observed during the pupping season. Unlike many phocids (true seals), harbor seals continue to forage while nursing (Boness et al. 1994) and make repeated trips to sea to dive. During the pupping season, females will likely make shorter trips or remain relatively close to their haul-out site so as not to leave their pup unattended longer than necessary. In this study, I did not test for sex differences in bout type or foraging trip duration; however, an exploratory analysis of sex differences at Padilla Bay identified a decrease in trip duration in July and August (the pupping season) when males were removed (Appendix 6). By decreasing foraging trip duration seals were able to continue foraging without leaving pups unattended for extended periods of time. The observed changes in foraging behavior may be explained as a mechanism for both increasing the potential of finding a mate and making shorter foraging trips to increase pup survivorship or for taking advantage of changes in prey abundance. However, the sex ratio both among and between haul-out sites was unequal so it is difficult to attribute the variation in foraging behavior solely to mating and/or pupping behaviors. Additionally, the behaviors observed are better explained by prey availability than by changes in life history. Therefore, as behavioral changes related to life history may influence foraging behavior, changes in prey availability likely have a stronger influence and are the most logical explanation for the changes observed in this study.

As an upper trophic-level predator harbor seals have the ability to serve as indicator species for ecosystem changes as variation in their foraging behavior may indicate prey

switching and, potentially, changes in prey abundances. Continued monitoring of harbor seal dive behavior will allow for future determination of changes in foraging behavior as well as their potential impact on local prey populations.

Implications for Marine Reserves

Candidate marine reserve sites in Puget Sound are being considered as an ecosystem management tool to aid in the recovery of rockfish. Currently, rockfish make up < 12% of the year-round harbor seal diet in the San Juan Islands (Lance & Jeffries 2007) and dive data suggest that seals fed on vertically-migrating prey as well as on benthos, but not exclusively on benthic prey, such as rockfish. Additionally, preliminary analyses have identified that the core foraging areas of harbor seals were located > 10 km from candidate reserve sites (Reuland et al. 2008). Hence, neither rockfish appeared to be an important prey item for harbor seals nor did seals appear to forage regularly within candidate reserve sites. Although seals do not appear to consume a large amount of rockfish, successful recovery of this important stock will be determined by how rockfish respond to seal predation and not by the abundance of rockfish in the harbor seal diet. There are multiple ways that rockfish populations can respond to predation and reserve designation. If a change in the foraging behavior of harbor seals is not observed and rockfish abundances do not increase after reserve designation, harbor seal foraging likely does not affect rockfish populations. However, if a change in foraging behavior indicating an increase in benthic foraging or aggregations within reserve boundaries, coupled with no increase in rockfish abundances then harbor seals may affect rockfish recovery. Lastly, if both a change in foraging behavior

and an increase in rockfish abundance are observed then seals may potentially affect, but not inhibit rockfish recovery as the rockfish population would still increase. It will be important to monitor rockfish populations both before and after reserve designation in order to determine this response and the actual influence seals have on rockfish population dynamics.

When exploring potential threats to recovering prey populations it is important to look at predicted prey abundances as well as past and present abundances for the entire ecosystem. Forage fishes, such as herring, comprise a large part of the harbor seal diet and fluctuations in the abundance of these fishes may have direct impacts on these upper trophic-level predators (Lance & Jeffries 2007). Recent surveys of herring spawn in the Georgia Basin have found almost no 0+ herring during both the 2005 and the 2007 survey years (Therriault, personal communication⁴). These surveys suggest potential recruitment failure for both 2008 and 2010, with a dramatic decrease in adult herring abundance. With a decrease in Pacific herring within the Georgia Basin, harbor seals may switch from what appear to be their preferred prey to something else that is readily available. This switch from forage fish to rockfish has already been observed in the San Juan Islands during the winter months (Lance & Jeffries 2007), the duration of which may last longer as forage fish abundances continue to decline throughout the year. Although harbor seals do not currently appear to consume a large quantity of rockfish, this ratio may change as the abundance of other prey within the ecosystem changes over time. Continued monitoring of this expected change in prey abundance and the foraging behavior of harbor seals may elucidate the intra-annual switching behaviors for harbor seals in the Georgia Basin under current prey conditions allowing for inter-annual changes to be identified in the future.

⁴ Tom Therriault, personal communication March 13, 2008

Identifying variations in the foraging behavior of harbor seals is crucial when considering the designation of marine reserves, especially with a potential decline in the abundance of their primary prey source. Monitoring harbor seal foraging behavior and general movement patterns throughout the Georgia Basin, both before and after the designation of reserves, will be important for identifying the functional and aggregative responses of harbor seals as prey abundances change in these areas as well as determining how rockfish respond to seal predation. Dive behavior and movements should be monitored throughout the year to determine intra-annual variation in foraging behavior under current prey abundances. Data from this study suggest prey switching as prey availability changes as well as the consumption of both vertically-migrating and benthic-dwelling prey. Continued monitoring of rockfish populations in marine reserves and seals from these three haul-out sites, as well as other similar sites throughout the Georgia Basin, will test this hypothesis and provide state and federal agencies with important information to consider when monitoring prey abundances within marine reserves after designation.

LITERATURE CITED

- Allen SG (1985) Mating behaviour in the harbor seal. *Marine Mammal Science* 1:84-87
- Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* 248:53-78
- Austin D, Bowen WD, Mcmillan JI, Boness DJ (2006a) Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology* 75:408-420
- Austin D, Bowen WD, McMillan JI, Iverson SJ (2006b) Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* 87:3095-3108
- Baechler J, Beck CA, Bowen WD (2002) Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbor seals (*Phoca vitulina*). *Canadian Journal of Zoology* 80:1569-1577
- Beck CA, Bowen WD, Mcmillan JI, Iverson SJ (2003) Sex differences in diving at multiple temporal scales in a size-dimorphic capital breeder. *Journal of Animal Ecology* 72:979-993
- Bekkby T, Bjørge AJ (1995) Variation in stomach temperature as an indicator of meal size in the harbour seal, *Phoca vitulina*. *ICES Journal of Marine Science* 12:1-6
- Bell WJ (1991) Searching behaviour: the behavioural ecology of finding resources, 1. Chapman and Hall, London, UK
- Bjørge AJ, Bekkby T, Bakkestuen V, Framstad E (2002) Interactions between harbour seals, *Phoca vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information System (GIS) and energetics modeling. *ICES. Journal of Marine Science* 59:29-42
- Bjørge AJ, Thompson D, Hammond PS, Fedak MA, Bryant E, Aarefjord H, Roen R, Olsen M (1995) Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In: Walløe I, Ulltang Ø (eds) Whales, seals, fish and man. Elsevier, Norway, p 211-223
- Boness DJ, Bowen WD, Oftedal OT (1994) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioral Ecology and Sociobiology* 34:95-104
- Bowen WD (1991) Behavioural ecology of pinniped neonates. In: Renouf D (ed) Behaviour of pinnipeds. Chapman and Hall, London, UK, p 66-127

- Bowen WD, Boness DJ, Iverson SJ (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. *Canadian Journal of Zoology* 77:978-988
- Bowen WD, Iverson SJ, Boness DJ, Oftedal OT (2001) Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* 15:325-334
- Boyd IL, Arnould JPY, Barton TR, Croxall JP (1994) Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* 63:703-713
- Boyd IL, Croxall JP (1996) Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* 74:1696-1705
- Brodeur RD, Wilson MT (1996) A review of the distribution, ecology, and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography* 5:148-166
- Brown P, Laake J, DeLong R (2002) Diet of harbor seals (*Phoca vitulina*) on the Columbia River, 1995-1997. *Fishery Bulletin* 100:423-433
- Coltman DW, Bowen WD, Boness DJ, Iverson SJ (1997) Balancing foraging and reproduction in the male harbor seal, an aquatically mating pinniped. *Animal Behavior* 54:663-678
- Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70:596-606
- Dinnel P, McConnell M (2001) Potential of marine protected areas for rocky reef bottomfish in Skagit County, WA, Skagit County Marine Resource Committee
- Dinnel P, McConnell M, Dolph I, Ramaglia J, Sato M (2003) Rocky reef bottomfish reserves for Skagit County, Washington?, Skagit County Marine Resources Committee, Anacortes, WA
- Eichbaum WM, Crosby MP, Agardy MT, Laskin SA (1996) The role of marine and coastal protected areas in the conservation and sustainable use of biological diversity. *Oceanography* 9:60-70
- Frost KJ, Simpkins MA, Lowry LF (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science* 17:813-834
- Fu C, Mohn R, Fanning PL (2001) Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1613-1623
- Gell F, Roberts C (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution* 18:448-455

- Groot G, Margolis L (1928) Pacific salmon life histories, 1. UBC Press, Vancouver, Canada
- Halpern BS (2003) The impact of marine reserves: do reserves work and does reserve size matter? *Ecological Applications* 13:S117-S137
- Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London B* 270:1871-1878
- Hardee S, Reuland K, Lance MM, Jeffries SJ, Olesiuk PF, Acevedo-Gutiérrez A (2008) Harbor seal movements and hot spots in the Georgia Basin revealed through the use of satellite-telemetry 2008 Ocean Sciences Meeting, Orlando, FL
- Härkönen TJ, Harding KC, Lunneryd SG (1999) Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *Journal of Applied Ecology* 36:825-841
- Harwod J, Croxall JP (1988) The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Marine Mammal Science* 4:13-33
- Hastings KK, Frost KJ, Simpkins MA, Pendleton GW, Swain UG, Small RJ (2004) Regional differences in diving behavior of harbor seals in the Gulf of Alaska. *Canadian Journal of Zoology* 82:1755-1773
- Hastings KK, Small RJ, Simpkins MA, Swain UG (2001) Dive behavior of adult and subadult harbor seals from Kodiak Island and Southeast Alaska, Alaska Department of Fish and Game, Anchorage, AK
- Hintze JL (2000) NCSS 2000 User's Guide. Number Cruncher Statistical Systems, Kaysville, UT
- Jeffries SJ, Brown RF, Harvey JT (1993) Techniques for capturing, handling and marking harbor seals. *Aquatic Mammals* 19:21-25
- Jeffries SJ, Gearin PJ, Huber HR, Saul DL, Pruett DA (2000) Atlas of seal and sea lion haulout sites in Washington, Washington Department of Fish and Wildlife, Wildlife Science Division, Olympia, WA
- Jeffries SJ, Huber HR, Calambokidis J, Laake J (2003) Trends and status of harbor seals in Washington State: 1978-1999. *Journal of Wildlife Management* 67:208-219
- Kaiser MJ, Attrill MJ, Jennings S, Thomas DN, Barnes DKA, Brierley AS, Polunin NVC, Raffaelli DG, Williams P (2005) *Marine ecology: processes, systems, and impacts*, 1. Oxford University Press, New York, NY
- Lance MM, Jeffries SJ (2007) Temporal and spatial variability of harbor seal diet in the San Juan Island archipelago, Washington Department of Fish and Wildlife, Lakewood, WA

- Le Boeuf BJ, Costa DP, Huntley AC, Feldkamp SD (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. Canadian Journal of Zoology 66:446-458
- Le Boeuf BJ, Naito Y, Asaga T, Crocker DE, Costa DP (1992) Swim speed in a female northern elephant seal: metabolic and foraging implications. Canadian Journal of Zoology 70:786-795
- Lesage V, Hammill MO, Kovacs KM (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. Canadian Journal of Zoology 77:74-87
- London JM, Lance MM, Jeffries SJ (2001) Observations of harbor seal predation on Hood Canal salmonids from 1998 to 2000, Studies of expanding pinniped populations NOAA Grant No. NA17FX1630, WDFW, PSMFC Contract No. 02-15, Seattle, WA
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13:S3-S7
- Mazerolle MJ (2004) Mouvements et reproduction des amphibiens en tourbières perturbées. PhD dissertation, Université Laval, Québec, Canada
- McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. Antarctic Science 4:393-398
- McConnell ML, Dinnel P, Dolph I, Robinette J, Semrau D (2001) Rocky reef bottomfish recovery in Skagit County, Washington, Phase I Final Report: marine protected areas - preliminary assessment and public input, Skagit County Marine Resource Committee
- McGraigal K, Cushman S, Stafford S (2000) Multivariate Statistics for Wildlife and Ecology Research. Springer-Verlag New York, Inc., New York
- Merrick RL, Loughlin TR (1997) Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Canadian Journal of Zoology 75:776-786
- Middlemas SJ, Barton TR, Armstrong JD, Thompson PM (2006) Functional and aggregative responses of harbour seals to changes in salmonid abundance. Proceedings of the Royal Society of London B 273:193-198
- Milazzo M (1998) Subsidies in world fisheries: A re-examination World Bank Technical Paper no. 406. Fisheries Series. The World Bank, Washington D.C.
- Muntz WRA (1983) Bioluminescence and vision. In: Macdonald AG, Priede IG (eds) Experimental Biology at Sea. Academic Press, New York

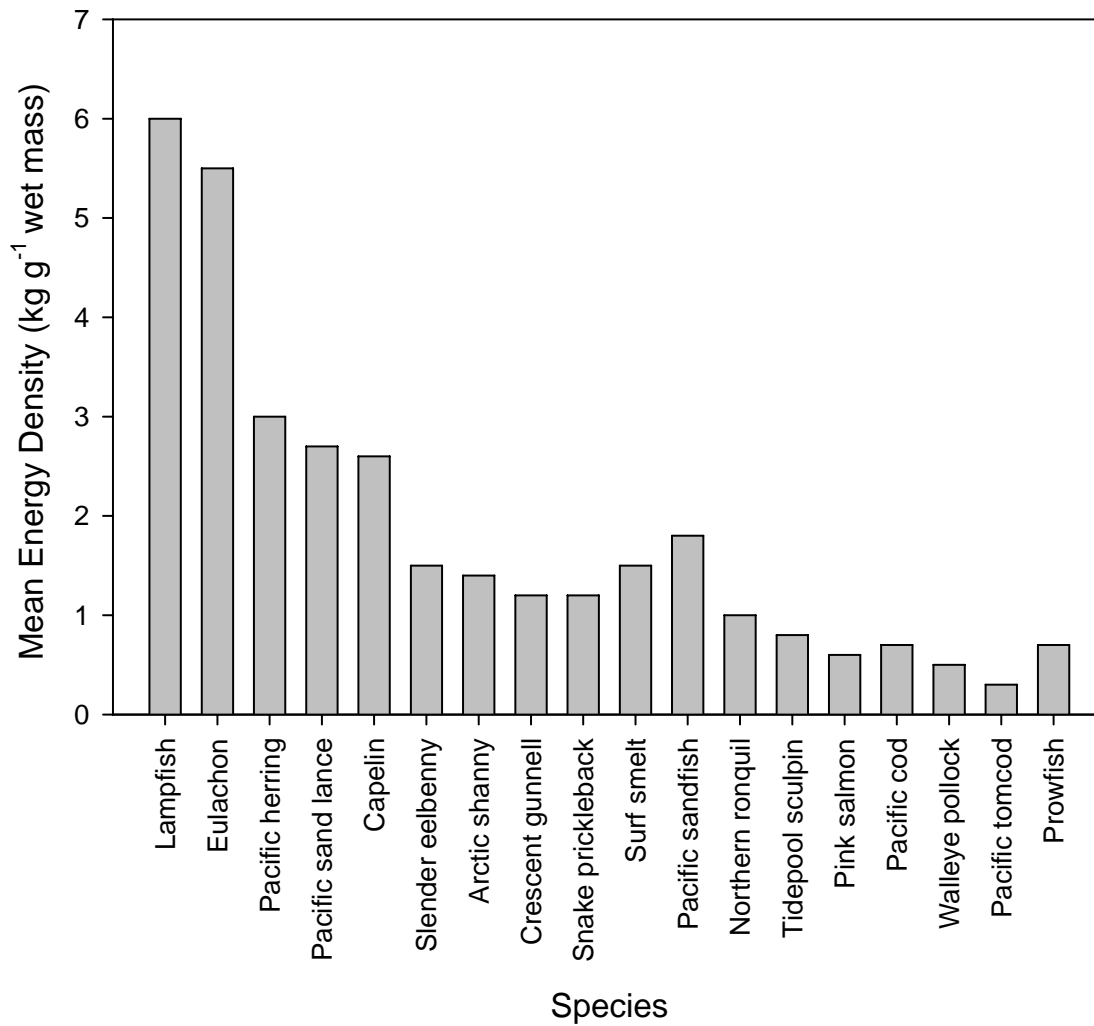
- Newby TC (1973) Changes in Washington State harbor seal population, 1942-1972. *Murrelet* 54:5-6
- NMFS (1997) Investigation of scientific information on the impacts of California sea lions and Pacific harbor seals on salmonids and on the coastal ecosystems of Washington, Oregon, and California, NMFS-NWFSC-28, Seattle, WA
- Olesiuk PF (1993) Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin* 91:491-515
- Orr AJ, Banks AS, Mellman S, Huber HR, DeLong RL, Brown RF (2003) Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids. *Fishery Bulletin* 102:108-117
- Palsson WA, Northrup TJ, Barker MW (1998) Puget Sound groundfish management plan (revised). Technical Report by Washington Department of Fish and Wildlife, Marine Resources Division, Olympia, WA
- Payne PM, Selzer LA (1989) The distribution, abundance and selected prey of the harbour seal *Phoca vitulina concolor*, in S. New England. *Marine Mammal Science* 5:173-192
- PSAT (2007) 2007 Puget Sound Update: Ninth Report of the Puget Sound Ambient Monitoring Program. Puget Sound Action Team, Olympia, WA
- Quinn TP (2005) The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, WA
- Reuland K, Hardee S, Lance MM, Jeffries SJ, Acevedo-Gutiérrez A (2008) Habitat characteristics of harbor seal foraging locations in the Georgia Basin 2008 Ocean Sciences Meeting, Orlando, FL
- Schreer JF, O'Hara Hines RJ, Kovacs KM (1998) Classification of dive profiles: A comparison of statistical clustering techniques and unsupervised artificial neural networks. *Journal of Agricultural, Biological, and Environmental Statistics* 3:383-404
- Schreer JF, Testa JW (1995) Statistical classification of diving behavior. *Marine Mammal Science* 11:85-93
- Schreer JF, Testa JW (1996) Classification of weddell seal diving behavior. *Marine Mammal Science* 12:227-250
- Thompson PM, Mackay A, Tollit DJ, Enderby S, Hammond PS (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology* 76:1044-1053

- Thompson PM, Miller D, Cooper R, Hammond PS (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *Journal of Animal Ecology* 63:24-30
- Thompson PM, Van Parijs S, Kovacs KM (2001) Local declines in the abundance of harbor seals: implications for the designation and monitoring of protected areas. *Journal of Applied Ecology* 38:117-125
- Tollit DJ, Black AD, Thompson PM, Mackay A, Corpe HM, Wilson B, Van Parijs S, Grellier K, Parlane S (1998) Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology*:209-222
- Tuya FC, Soboil ML, Kiddo J (2000) An assessment of the effectiveness of Marine Protected Areas in the San Juan Islands, Washington, USA. *ICES Journal of Marine Science* 57:1218-1226
- UNFAO (1995) The state of world fisheries and aquaculture, Rome, Italy
- Weispfenning A (2006) Survey of nearshore demersal fishes within candidate marine reserves in Skagit County, Washington. MS thesis, Western Washington University, Bellingham, WA, Bellingham, WA
- Williams TM (1999) The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Proceedings of the Royal Society of London B*. 354:193-201
- Williams TM, Briggs DR, Croxall JP, Naito Y, Kato A (1992) Diving pattern and performance in relation to foraging ecology in the Gentoo penguin, *Pygoscelis papua*. *Journal of zoology* 227:211-230
- Williams TM, Kooyman GL (1985) Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology* 58:576-589

Appendix 1. Percent of dive types used by each *Phoca vitulina* relative to season in the Georgia Basin. Bold font indicates overall percentages for the haul-out site.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
	Short/Shallow V, skew Right	Long/Deep square, wiggles	Short/Shallow V, skew Left	Short/Shallow square	Long/Deep square	Short/Shallow square, wiggles
Bird Rocks	7.68	34.58	7.24	12.81	27.49	10.20
Pre-pupping	7.10	34.31	4.98	13.38	29.95	10.26
B1695	5.51	51.35	5.12	7.96	23.67	6.40
B1696	10.36	38.14	7.23	8.38	24.54	11.37
Y1455	2.75	19.23	3.65	22.21	43.02	9.14
B1700	11.75	15.17	3.47	19.20	32.34	18.06
Pupping	9.66	35.46	14.88	10.85	19.15	10.00
B1695	9.68	35.61	14.97	10.87	18.81	10.05
Y1455	5.56	10.00	0.00	6.67	76.67	1.11
Belle Chain	8.51	26.20	9.69	13.42	19.75	22.44
Pre-pupping	8.29	30.58	9.36	10.95	18.49	22.33
B1707	8.35	31.53	10.38	10.04	21.44	18.26
B1709	8.20	28.92	7.55	12.56	13.26	29.52
Pupping	8.79	20.54	10.12	16.60	21.37	22.58
B1707	8.71	31.94	12.42	4.02	34.34	8.57
B1709	8.87	8.13	7.62	30.31	7.25	37.83
Padilla Bay	11.32	15.29	11.26	23.58	9.53	29.03
Pre-pupping	11.39	14.96	11.01	21.86	10.36	30.42
Y1456	17.30	1.54	12.44	39.32	3.05	26.35
Y1457	3.60	17.75	5.36	20.68	13.20	39.41
Y1458	11.72	7.49	7.00	33.04	11.23	29.51
Y1459	8.25	25.28	10.56	15.57	13.97	26.36
Y1460	18.87	0.79	15.38	26.97	2.47	35.53
Y1462	13.06	3.44	6.19	40.21	3.09	34.02
Y1465	9.35	34.31	9.87	12.54	11.27	22.66
Y1459	16.64	3.56	21.34	17.07	1.28	40.11
B1699	18.63	13.84	16.92	13.10	13.22	24.29
B1712	27.44	11.43	25.20	8.98	5.66	21.29
B1713	19.03	3.86	31.00	12.67	5.60	27.84
Pupping	11.18	15.86	11.70	26.56	8.09	26.61
Y1456	21.41	0.11	16.00	50.55	2.21	9.71
Y1457	3.71	0.00	4.54	34.01	0.06	57.69
Y1458	7.12	0.00	4.44	61.70	0.10	26.64
Y1459	13.47	17.19	15.88	18.75	16.48	18.24
Y1460	16.99	0.00	14.72	35.18	0.00	33.11
Y1462	12.11	0.30	7.32	35.72	1.79	42.75
Y1465	10.28	41.54	12.67	7.98	14.62	12.91
Y1459	20.76	1.24	26.65	20.76	0.31	30.27
B1699	23.37	0.00	23.19	15.04	0.36	38.04

Appendix 2. Relative contributions of lipid content toward total energy density ($\text{kg}\cdot\text{g}^{-1}$ wet mass) of forage fishes (≥ 100 mm) in the northern Gulf of Alaska in 1995 and 1996. Taken from Anthony et al. (2000).



Appendix 3. Mean dive depth (m) for each *Phoca vitulina* relative to season in the Georgia Basin. Bold font indicates haul-out site averages.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
	Short/Shallow V, skew Right	Long/Deep p square, wiggles	Short/Shallow V, skew Left	Short/Shallow square	Long/Deep square	Short/Shallow square, wiggles
Bird Rocks	17.38	63.07	17.26	16.22	51.46	16.70
Pre-pupping	18.73	63.85	20.67	17.52	51.85	18.19
B1695	17.75	68.74	18.94	13.04	64.50	15.72
B1696	19.16	61.47	20.05	10.25	60.22	14.13
Y1455	23.35	55.35	27.12	23.60	42.60	26.47
B1700	17.70	53.17	18.40	16.07	41.21	17.75
Pupping	14.02	60.53	13.41	10.83	49.35	11.57
B1695	14.00	60.57	13.41	10.79	49.66	11.56
Y1455	21.20	36.56		21.50	36.23	17.00
Belle Chain	14.82	81.13	18.77	9.27	68.34	10.45
Pre-pupping	14.19	91.57	18.24	9.04	81.28	10.06
B1707	14.68	64.73	18.36	8.50	62.21	10.12
B1709	13.30	143.25	17.95	9.81	135.72	10.00
Pupping	15.58	61.08	19.39	9.47	53.92	10.94
B1707	17.38	59.07	22.43	11.50	55.07	12.88
B1709	13.65	69.71	13.99	9.17	47.97	10.46
Padilla Bay	11.18	52.31	13.67	9.35	47.03	10.73
Pre-pupping	11.82	51.53	13.80	10.28	47.38	11.70
Y1456	7.85	37.55	7.92	7.97	31.85	7.72
Y1457	11.13	46.55	16.51	8.09	47.34	7.68
Y1458	9.40	39.85	9.37	8.81	40.45	10.45
Y1459	17.45	52.90	21.13	17.96	61.77	22.52
Y1460	8.34	25.17	8.00	7.60	22.24	7.07
Y1462	11.71	45.20	11.17	7.96	43.67	11.91
Y1465	16.73	70.67	18.00	16.06	61.10	16.53
Y1459	9.12	31.68	11.21	6.83	25.89	7.57
B1699	14.87	29.65	15.00	13.50	27.01	14.15
B1712	13.07	22.99	12.36	7.68	21.28	12.29
B1713	10.97	19.23	12.12	11.95	19.21	10.25
Pupping	10.04	53.60	13.45	8.02	46.24	8.80
Y1456	6.88	10.00	6.78	6.39	13.35	6.48
Y1457	7.04		7.10	7.34	7.00	7.25
Y1458	6.26		5.98	6.41	11.25	6.28
Y1459	12.21	40.13	13.69	12.00	45.75	13.56
Y1460	5.95		6.14	5.68		5.75
Y1462	9.81	41.00	9.18	10.33	22.67	9.89
Y1465	13.20	58.09	21.23	11.52	47.90	12.55
Y1459	7.40	25.00	7.72	6.69	19.67	7.28
B1699	6.05		5.84	5.87	11.00	6.07

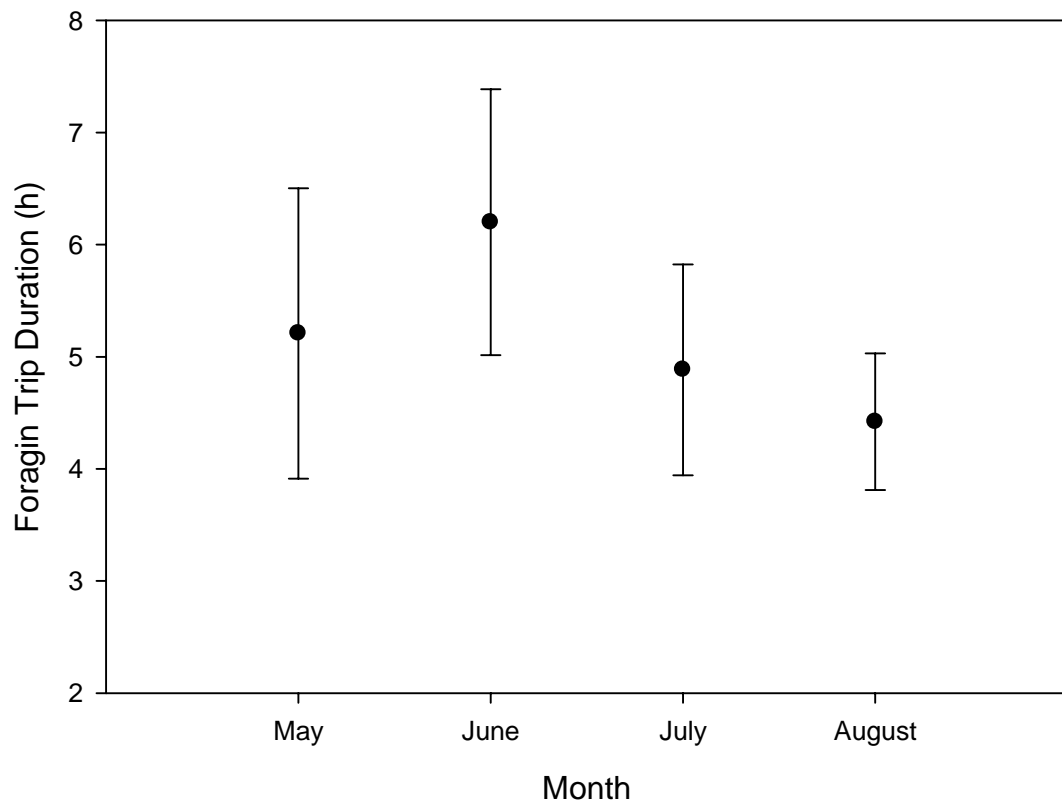
Appendix 4. Mean dive bottom time (s) for each *Phoca vitulina* relative to season in the Georgia Basin. Bold font indicates haul-out site averages.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
	Short/Shallow V, skew Right	Long/Deep square, wiggles	Short/Shallow V, skew Left	Short/Shallow square	Long/Deep square	Short/Shallow square, wiggles
Bird Rocks	175.20	278.27	162.79	255.85	267.29	271.78
Pre-pupping	196.79	294.54	198.76	282.41	280.68	304.82
B1695	177.37	274.79	169.16	194.24	268.59	218.63
B1696	151.91	277.18	179.54	178.81	253.56	222.06
Y1455	245.25	380.02	279.00	316.83	309.03	393.13
B1700	253.25	342.15	226.95	363.40	275.54	376.48
Pupping	121.57	225.06	122.08	145.04	196.48	157.17
B1695	121.26	224.97	122.08	144.64	194.50	157.13
Y1455	212.00	277.78		258.33	279.57	210.00
Belle Chain	160.24	307.22	162.34	172.98	249.58	212.71
Pre-pupping	168.84	341.47	163.85	185.74	284.43	225.75
B1707	149.88	243.54	154.06	152.15	215.68	183.53
B1709	202.93	530.06	187.64	233.18	480.77	271.87
Pupping	149.78	241.46	160.54	162.13	210.71	196.08
B1707	143.76	232.06	163.08	156.54	212.90	180.70
B1709	156.22	281.69	156.04	162.93	199.42	199.87
Padilla Bay	145.84	288.81	155.04	182.43	266.21	199.51
Pre-pupping	153.27	303.13	161.00	192.79	282.26	210.86
Y1456	124.35	216.17	126.54	144.67	193.12	172.18
Y1457	149.32	256.13	157.65	167.87	264.02	176.36
Y1458	139.40	280.80	140.52	170.62	273.61	188.55
Y1459	226.79	352.41	231.15	307.29	369.61	316.76
Y1460	128.54	182.50	129.90	157.64	164.13	171.64
Y1462	213.42	403.00	208.33	217.78	384.44	268.08
Y1465	202.46	348.51	200.44	274.31	342.16	272.14
Y1459	150.77	237.20	179.67	184.25	203.33	226.13
B1699	143.25	201.77	150.32	200.02	159.53	201.92
B1712	134.27	160.26	119.96	169.46	108.97	192.80
B1713	116.17	137.04	122.39	228.84	102.33	182.32
Pupping	132.71	265.37	145.32	167.64	230.53	176.99
Y1456	86.44	60.00	90.14	95.94	108.00	101.93
Y1457	127.60		125.79	147.83	50.00	155.89
Y1458	147.76		130.77	178.89	107.50	191.27
Y1459	139.49	237.14	152.23	191.83	231.65	195.58
Y1460	120.43		129.55	150.70		164.12
Y1462	164.07	395.00	154.49	268.49	211.67	273.85
Y1465	138.41	274.68	165.89	177.87	233.32	184.38
Y1459	139.75	222.50	136.74	159.05	173.33	180.27
B1699	116.12		113.52	147.59	60.00	186.10

Appendix 5. Mean dive duration (s) for each *Phoca vitulina* relative to season in the Georgia Basin. Bold font indicates haul-out site averages.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
	Short/Shallow V, skew Right	Long/Deep square, wiggles	Short/Shallow V, skew Left	Short/Shallow square	Long/Deep square	Short/Shallow square, wiggles
Bird Rocks	175.2047	278.2663	162.789	255.8459	267.2858	271.7788
Pre-pupping	196.7898	294.5371	198.7634	282.4135	280.6811	304.8182
B1695	177.3669	274.7943	169.1614	194.2389	268.5934	218.6333
B1696	151.9126	277.181	179.5414	178.8127	253.5618	222.0555
Y1455	245.2507	380.0211	279	316.8336	309.0262	393.1261
B1700	253.2528	342.1454	226.9497	363.3959	275.5405	376.4791
Pupping	121.5673	225.0593	122.0774	145.0447	196.4775	157.1669
B1695	121.2634	224.9726	122.0774	144.6379	194.4952	157.1327
Y1455	212	277.7778		258.3333	279.5652	210
Belle Chain	160.2441	307.22	162.3413	172.9788	249.5819	212.7071
Pre-pupping	168.8426	341.4685	163.8504	185.7383	284.4297	225.7463
B1707	149.8758	243.5392	154.0585	152.1534	215.6837	183.528
B1709	202.9346	530.0633	187.643	233.1771	480.7692	271.8742
Pupping	149.7779	241.4574	160.5422	162.1263	210.7076	196.0762
B1707	143.7584	232.0579	163.0791	156.5407	212.8951	180.6958
B1709	156.2213	281.6928	156.0368	162.934	199.42	199.8721
Padilla Bay	145.8446	288.8133	155.0442	182.4315	266.2144	199.51
Pre-pupping	153.2736	303.1266	160.9978	192.7864	282.2642	210.8644
Y1456	124.3454	216.1702	126.5435	144.6745	193.1183	172.1793
Y1457	149.3154	256.131	157.6519	167.8705	264.0227	176.3575
Y1458	139.3973	280.8	140.5199	170.6187	273.613	188.5491
Y1459	226.7857	352.4146	231.1538	307.2929	369.6145	316.7592
Y1460	128.544	182.5	129.9037	157.6402	164.1333	171.6435
Y1462	213.4211	403	208.3333	217.7778	384.4444	268.0808
Y1465	202.46	348.5123	200.4356	274.307	342.1559	272.137
Y1459	150.7692	237.2	179.6667	184.25	203.3333	226.1348
B1699	143.249	201.7742	150.3226	200.0189	159.531	201.9203
B1712	134.2705	160.2564	119.9612	169.4565	108.9655	192.7982
B1713	116.1714	137.0423	122.386	228.8412	102.3301	182.3242
Pupping	132.7105	265.3744	145.3225	167.6371	230.5274	176.9888
Y1456	86.4433	60	90.13793	95.93886	108	101.9318
Y1457	127.602		125.7917	147.8309	50	155.8918
Y1458	147.7586		130.7735	178.8898	107.5	191.2719
Y1459	139.4886	237.1355	152.2345	191.8296	231.6459	195.5788
Y1460	120.4331		129.5455	150.7034		164.1212
Y1462	164.0741	395	154.4898	268.4937	211.6667	273.8462
Y1465	138.4129	274.6815	165.8866	177.8714	233.3151	184.3816
Y1459	139.7512	222.5	136.7442	159.0547	173.3333	180.273
B1699	116.124		113.5156	147.5904	60	186.0952

Appendix 6. Foraging trip duration for female *Phoca vitulina* tagged at Padilla Bay.



Appendix 7. PCA factor loadings for *Phoca vitulina* dives after varimax rotation. Bold font indicates significant loading.

Variables	Factor1	Factor2	Factor3
Max Depth	-0.922968	-0.210550	-0.016641
Duration	-0.680354	0.535641	-0.002974
BottomTime	-0.516447	0.828779	-0.017979
Avg. Descent Rate	-0.887616	0.112007	-0.242613
Avg. Ascent Rate	-0.870358	0.102253	0.309048
Skew1	0.065526	-0.043644	0.959520
Skew2	0.062068	-0.015349	-0.961519
Bottom Time/Duration	-0.254186	0.873374	-0.019538
Bottom Time/Max Depth	0.250031	0.913121	-0.019837
Max Depth/Duration	-0.530101	-0.678267	-0.026297