ENERGETIC REQUIREMENTS AND PREY CONSUMPTION OF HARBOR SEALS (*PHOCA VITULINA*) IN THE SAN JUAN ISLANDS, WA

By

Sarah M. S. Howard

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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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A Thesis
Presented to
The Faculty of
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ABSTRACT

Harbor seals are a large-bodied and abundant predator in the San Juan Islands and eastern bays region of the Puget Sound Georgia Basin. The harbor seal population has recovered since the 1970s after passage of the Marine Mammal Protection Act and the cessation of bounties. Although there are many depressed fish stocks of conservation concern in this area, little is known on how this large predator population may impact the recovery of fish stocks in candidate marine protected areas. To quantify the links between harbor seals and their prey, a bioenergetics model was used to estimate how much prey is required by the harbor seal population during the breeding (15 June - 15 September) and non-breeding (16 September - 14 June) seasons. The model was based on an energy budget derived for three age classes for females and males in the harbor seal population (adults, subadults, and pups). I deployed 6 time-depth recorders during the fall and winter of 2007-2008 in the San Juan Islands and eastern bays region, as well as using data from 13 seals tagged in the spring of 2007. These year-round data were used to describe seasonal changes in activity budgets. I measured the percent of time tagged seals spent in three behavioral classes: hauled-out, diving, and shallow-water activity. This time budget was then applied to metabolic costs of those behaviors to estimate a field metabolic rate (FMR) for free-living harbor seals. These rates were combined with production costs to estimate total energetic requirements, which were in turn used to estimate consumption rates of harbor seals. Sensitivity analyses were also used to pinpoint the most important factors driving variation in the model. Tags were deployed for a mean of 65 ± 32 d. There were seasonal and sex differences in seal activity budgets. Females spent most of their time in shallow-water activities in the breeding season and increased their dive effort by 23% in the non-breeding season. Males increased their haul-out rates and dive effort in the non-breeding season, but were also driven by site differences. During the breeding season, males in deep-water areas typically exhibited high dive effort (> 60% of time budget) while those in shallow-water areas typically spent less time diving (< 20%). FMR-proxy rates were highest for females during the breeding season due to the costs of lactation; rates dropped for all sex and age classes in the non-breeding season by an average of approximately 16%, due in part to the overall lower cost of diving than breeding or shallow-water activities. Reproductive costs drove higher overall population energy costs in the breeding season. Salmonids and herring were the two most energetically important prey groups in terms of biomass consumed for harbor seals in both seasons. Population consumption estimates were highest for herring at 646 (±303) and 2,151 (±706) metric tons in the breeding and non-breeding seasons. Consumption estimates for the second most important prey group, salmonids, were 783 (±380) and 675 (±388) in the breeding and non-breeding seasons. This study highlighted potential differences in consumption rates between sex and age classes in the harbor seal population: predictions ranged from 1.0 - 2.9 kg day^{-1} seal^{-1}, and were highest for adult females. The highest seasonal consumption was predicted in the breeding season, although this will depend on the timing of foraging of the sex and age classes in the population. The prey consumption model was most sensitive to the input values of seal body mass and to the proportion of prey species in the diet, suggesting that future studies should focus on refining estimates of the relative importance of different prey items while still incorporating natural variation in physiological variables. While only considered a minor portion of harbor seal diet, prey groups such as rockfish may still be impacted by even low levels of predation, which will be dependent on the life-history strategy of each prey species. Consumption rates calculated by this model can be compared to current estimates and future projections of rockfish populations to measure the possible contribution of harbor seal predation to rockfish mortality rates. Harbor seals heavily depend on salmonids and herring; therefore, they may have the potential to impede the recovery of these fish species and stocks of concern, especially if they focus their predation in small areas or specialize on these prey. Harbor seal consumption rates can inform conservation managers of the potential for harbor seals to impact their prey, which can then be taken into account along with other important factors that may affect the recovery of depressed fish stocks in marine protected areas in the San Juan Islands.

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INTRODUCTION

The collapse of fisheries, marine protected areas, and impact of predators

Predators in marine ecosystems have the potential to play a critical role in shaping community structure. Top-down effects of predators through consuming prey and indirect influences, such as trophic cascades, can control the abundance of lower trophic levels, thereby greatly affecting the movement of energy through populations and communities (Terborgh 1990, Pace et al. 1999, Shears & Babcock 2002, Fanshawe et al. 2003, Halpern et al. 2006). The effects of predation in marine ecosystems are particularly strong when the predator in question is a prey specialist (Estes 1996, Fanshawe et al. 2003, Williams et al. 2004), while the effects of species that are more generalist in their food habits are dampened (Yodzis 2000).

Abundant and large-bodied organisms such as marine mammals can reasonably be expected to have an effect on prey populations (Bowen 1997), however, the exact nature of their role in food webs and the spatio-temporal variation in these effects is largely unquantified for many generalist marine predators. Harbor seals (*Phoca vitulina*) are one such abundant, generalist marine predator in the San Juan Islands, Washington. Their widespread distribution and year-round presence (Jeffries et al. 2000) make them an ideal species to examine the effects of predation in marine and estuarine ecosystems of the San Juan Islands. The San Juan Islands, part of the larger Puget Sound Georgia Basin marine ecosystem, are home to numerous fish species of conservation concern which have undergone significant declines over the past several decades (Puget Sound Action Team

2007), and thus there is a need to understand the prey requirements of predators such as harbor seals that consume these fish species.

The worldwide collapse of fishing stocks (Pauly et al. 1998, Jackson et al. 2001, Pauly & Watson 2003, Myers & Worm 2005, Pauly et al. 2005) has prompted the creation of conservation areas whose aim is the recovery of threatened marine species and habitats; however, there is a lack of knowledge on how predators affect these protected communities. A history of overfishing and habitat change has heavily impacted fish populations in the inland waters of the Pacific Northwest. Many formerly abundant fish species are now critically threatened or endangered, including Pacific salmonid species (*Oncorhynchus* spp.), forage fish stocks, and rockfish species (*Sebastes* spp.) (Mills & Rawson 2004, Penttila 2007, Puget Sound Action Team 2007). The loss of these species, which perform a critical function in regional food webs as well as having commercial and recreational value, has created a need for recovery strategies at the ecosystem level.

Marine protected areas (MPAs) in particular are important tools in the recovery of depressed fish stocks (Halpern 2003). MPAs are marine areas in which fisheries are completely closed (marine reserves), or in which fisheries are restricted while still allowing some level of harvest (Lubchenco et al. 2003). MPAs are well known for their positive influence on ecosystem processes, including larval transport, increased biomass of protected populations, and maintenance of biodiversity (Halpern & Warner 2003, Lubchenco et al. 2003). Several marine reserves have been successfully developed for rockfish recovery in Puget Sound and more have been proposed in the San Juan Islands (McConnell & Dinnel 2002, Banks 2007). Rockfish are expected to increase in size and abundance as a result of protection if the reserves are effective, yet the potential response of predators to this increase in resource availability has not been well studied (Tuya et al. 2000).

Evidence from several ecosystems suggests that understanding predator abundance and foraging behavior is important when considering the placement of conservation areas. The restoration of predators can reestablish trophic relations and restructure habitat with usually positive results (Shears & Babcock 2002, Shears et al. 2006); however, predators can also cause declines in species size and abundance inside reserves. For example, fish predation reduced body size and population density of urchins (*Paracentrotus lividus*) in the Mediterranean Sea inside reserves relative to unprotected sites, and similarly, the body size and density of red abalones were reduced in marine protected areas where sea otters (*Enhydra lutris*) were present relative to those where they were absent in California (Sala & Zabala 1996, Fanshawe et al. 2003). Marine reserves can also indirectly negatively affect the target recovery species, at least in the short term, if a predatory fish population is recovered along with the target fish species. In the San Juan Islands, Puget Sound rockfish (*Sebastes emphaeus*) are lower in abundance inside than outside reserves due to the increased size and abundance of lingcod (*Ophiodon elongatus*) which prey upon them (Eisenhardt 2001). These observations suggest that predator responses should be taken into consideration when designing and evaluating the success of marine reserves. Unfortunately, little baseline information is available on the role of mammalian predators, such as harbor seals in the San Juan Islands.

Pinnipeds (seals, sea lions, fur seals, and the walrus) are predators that conflict with human fishers as a result of entanglement in fishing gear or direct consumption of the same species targeted by commercial fisheries (Beverton 1985, Trites et al. 1997, DeMaster et al. 2001, Reeves & Reijnders 2002). Pinnipeds are thus often viewed as competitors for fish and other marine species and have been implicated in the declines of several fish stocks (Beverton 1985, Harwood & Croxall 1988, NMFS 1997, Baraff & Loughlin 2000). As a result, many efforts to assess the consumption rates of pinnipeds have been constructed for several globally important fisheries and geographic areas (Ashwell-Erickson & Elsner 1981, Lavigne et al. 1985, Olesiuk 1993, Hammill et al. 1997, Stenson et al. 1997, Croll & Tershy 1998, Bjørge et al. 2002, Furness 2002, Winship & Trites 2003, Cornick et al. 2006, Mecenero et al. 2006).

Assessing prey requirements of a population is an important first step in understanding their potential contribution to prey mortality. The energy use and prey consumption of a population of predators can then be ranked relative to the rest of the ecosystem or other predators and compared to the available prey biomass (Lavigne et al. 1982, Beverton 1985, Bax 1991, Hammill & Stenson 2000, Hansen & Harding 2006, Mecenero et al. 2006). The amount of prey consumed by pinnipeds is much smaller than that consumed by predatory fish (Bax 1991, Overholtz & Link 2007), and in many systems only a fraction of the commercial fisheries take (Harwood & Croxall 1988, Mohn & Bowen 1996, Hansen & Harding 2006, Mecenero et al. 2006). In other areas, the amount consumed is similar or larger than the amount taken by commercial fisheries (Beverton 1985). Yet, there is little evidence from marine ecosystems to suggest that pinnipeds are capable of causing a fisheries decline. However, it is difficult to assess the actual impact of pinnipeds as predators when little is known about what level of mortality these calculated consumption rates cause in prey populations (Beverton 1985, Bowen 1997, Bax 1998).

Although pinnipeds do not appear to cause prey declines, they may suppress the recovery of prey species once human fishers have depleted a fish stock. For example, the harp seal (*Phoca groenlandica*) population preyed on Atlantic cod (*Gadus morhua*), which was simultaneously fished to the point of a population collapse. Even after the fishery collapsed, the seal population continued to thrive due to its generalist food habits. If the seals continue to consume the critically depressed fish stock, then they may potentially inhibit fish recovery (DeMaster et al. 2001). In a consumption model that coupled predator energetic requirements with potential prey responses, gray seals (*Halichoerus grypus*) and harp seals appeared incapable of causing declines in an Atlantic cod stock, yet they are indeed believed to be inhibiting the recovery of cod even at low predation levels (Mohn & Bowen 1996, Bundy 2001, Fu et al. 2001, Trzcinski et al. 2006).

Uncertainty in estimates of pinniped energy use can heavily influence the outcome of these types of consumption models (Mohn & Bowen 1996, Stenson et al. 1997, Sparling & Fedak 2004). Therefore, a description of the energy needs of a wild population of pinnipeds is needed to form a realistic model of prey consumption. Previous models have relied on data from captive pinnipeds or hypothetical estimates, or lacked seasonal diet data (Hiby & Harwood 1985, Härkönen & Heide-Jørgensen 1991, Hammill et al. 1997, Warren et al. 1997). By generating models of season- and region-specific patterns of consumption with newly available data, such as used in this study, uncertainty and variation in energetic requirements of predators can be assessed and accurately described. In addition, important areas of future research needed to accurately quantify consumption can be identified, which will aid future models in estimating the response of prey to predation. Finally, this approach can quantify important predator-prey links between pinnipeds and the prey upon which they most heavily depend.

The year-round presence and generalist diet of harbor seals make them an ideal species to examine the potential interactions between a common and abundant marine predator and their commercially and recreationally important prey species. Similar to other Pacific harbor seal populations, harbor seals in the San Juan Islands take advantage of the large influx of adult salmonids in late summer and fall, and increase the diversity of their diet at other times of the year when salmon are less available (Lance & Jeffries 2007, Hauser et al. 2008). Rockfish occur in harbor seal scats in small amounts [(3-23% frequency of occurrence (FO) in scats)] in the San Juan Islands and eastern bays region (Lance & Jeffries 2006, Lance & Jeffries 2007, Luxa 2008) and in larger amounts in Oregon (21%) and California (19-50%) (NMFS 1997). Pacific herring (*Clupea pallasi*), walleye pollock (*Theragra chalcogramma*), and other estuarine species also form significant components of their diet in the San Juan Islands and nearby estuarine ecosystems (Lance & Jeffries 2007, Luxa 2008).

In addition to their feeding preferences, the relative size of any pinniped population is likely to be an important component of their ecosystem role. Harbor seal populations have been steadily increasing in Washington State after the cessation of bounty hunting in 1960 and passage of the Marine Mammal Protection Act in 1972, and are now relatively stable in numbers. From a low of approximately 3,000 seals since systematic population surveys began in 1978, the harbor seal population for the inland waters stock (Strait of Juan de Fuca, Puget Sound, and San Juan Islands) increased to 14,000 animals by 1999, with a population intrinsic rate of increase of 0.126 (Jeffries et al. 2003). This growth of the population is mirrored on a regional scale in the San Juan Islands: the population has increased from a low of approximately 1,000 seals in 1978 to approximately 8,000 seals in 2007 (Jeffries et al. 2003, Hardee 2008).

This growth of the harbor seal population has likely increased foraging pressure on their prey populations, but the extent of that impact is unknown. Due to their relatively large body size, population growth, and consumption of prey species from depleted stocks, harbor seals may have the potential to affect recovery of depressed fish populations. Indeed, harbor seals are often the focus of conflict, along with sea lions, due to their predation on endangered salmonid runs in the Pacific Northwest (NMFS 1997). In addition, marine mammal predation was identified as one of the potential factors affecting the success of rockfish reserves in the San Juan Islands (McConnell et al. 2001). In response to the uncertainty regarding predator response to MPAs, research has recently been directed at assessing the potential impacts of marine predators (Lance & Jeffries 2006, Banks 2007, Lance & Jeffries 2007, Hardee 2008, Luxa 2008, Reuland 2008). These studies are providing initial insights into the effects that mobile predators may have on the rate of recovery of protected fish species within MPAs, yet there is still little known about how harbor seals may influence prey populations, especially those of depressed species. Consumption models can provide a useful basis to build future models on the potential response of depressed fish stocks such as rockfish to predation.

Prey consumption by marine predators

Defining feeding rates and quantifying prey consumption of marine predators is problematic because feeding events are difficult to observe (London et al. 2001, Winship et al. 2002, Williams et al. 2004). Direct observation of feeding rates is possible in captive situations, but energy use and consumption by captive animals is unlikely to reflect the energy needs of a freely-living animal that employs a wide variety of strategies to forage and survive (Harwood & Croxall 1988). It is possible to make rough calculations of food consumption as a fixed percentage of body weight, but these estimates do not take into account energy density of prey or variation among individuals (Lavigne et al. 1985). Bioenergetics models are a useful tool that can overcome these problems by taking into account the factors that predict the flow of energy through individuals and populations, and have been successfully used to estimate consumption in marine mammals, birds, and fish (Lavigne et al. 1985, Grémillet et al. 2003, Harvey 2005). Bioenergetic models provide a framework to estimate energetic requirements based on data from free-living animals or they can incorporate realistic scenarios of energetic expenditures for both individual organisms and populations. Bioenergetics models account for all energy expenditures to create an energy budget for an individual organism, which, when extrapolated to the population level, can provide insight into how populations function in their ecosystems (Hoelzel 2002). These models then describe consumption based on thermodynamic laws of mass and energy balance, which predict that energy expenditures (maintenance requirements, production) must equal energy inputs (consumption), thus providing a useful measure of consumption rates by free-living animals.

I used a bioenergetics model to calculate energy use and prey consumption by the harbor seal population in the San Juan Islands. Prey consumption estimates have been made for the harbor seal population in the Georgia Basin (Olesiuk 1993); however, the two populations differ in size and diet preferences (Jeffries et al. 2003, Lance & Jeffries 2007). Thus, a regional model for the San Juan Islands is needed to accurately calculate consumption. The basic pinniped bioenergetics model calculates gross energy requirements of an individual relative to age, sex, and reproductive state according to Equation 1 (Lavigne et al. 1982, Boyd 2002):

Equation 1 $$\boldsymbol{E_{gross} = P + E_{fecal} + E_{urinary} + E_{SDA} + E_{work}}$$

where P = production, or energy that goes toward either somatic growth or reproduction (e.g., gestation, lactation),

E_{fecal} = the amount of non-absorbed chemical energy lost in solid waste,

$E_{urinary}$ = the amount of non-absorbed chemical energy lost in urine,

E_{SDA} = specific dynamic action, also called heat increment of feeding, which is work required in active digestion,

and E_{work} = basal metabolic rate (maintenance costs) plus costs of activity

Provided that an organism is in a steady state of energy balance, at least on an annual basis, and that their diet is able to supply all caloric needs, consumption is equal to gross energy requirements (Winship & Trites 2003). Bioenergetics models therefore cannot account for years when food supply is low enough to cause starvation, which to my knowledge does not currently occur in the harbor seal population residing in the inland waters of the Pacific Northwest.

Pinnipeds are generally well-studied, and many of the components needed for constructing an energy budget are readily available in the literature. I briefly describe each component in Equation 1 and how it can be accounted for in a hypothetical pinniped. 1) E_{fecal} and $E_{urinary}$. Following consumption of a food item, excretory losses through fecal and urinary losses can be estimated through the use of an efficiency term, which describes the proportion of gross energy available in food that is metabolizable. Digestive efficiency is a relatively constant 90% of energy intake among carnivores and was 90.3% for harbor seals fed a mixed fish diet (Ricklefs 1996, Trumble et al. 2003). Taken together with an available estimate of urinary losses for pinnipeds of 6-7% of digestive efficiency, the overall efficiency term is roughly 85% of gross energy (Lavigne et al. 1982). 2) E_{SDA}. The heat increment of feeding, or work required in digestion, is then estimated by decreasing the efficiency term to account for energy lost at this stage. While fecal and urinary losses are relatively constant, the heat increment of feeding is dependent upon the energy content of the diet, and increases for meals with higher protein content (Rosen & Trites 1997) - the heat increment of feeding is up to 15% of gross energy in harbor seals when fish are consumed (Markussen et al. 1994). The energy remaining at this point that was assimilated and is now available for use, approximately 70% of gross energy, is represented by the term net efficiency (Lavigne et al. 1982).

Once net efficiency is accounted for, energy is used through two main routes: work and production. 3) E_{work} can be summarized as maintenance costs plus the costs of activity.

Maintenance costs, or basal metabolic rate (BMR), for birds and mammals, are defined as the steady rate of energy use of a non-growing animal that is in a post-absorptive and thermoneutral state (Kleiber 1975). Although BMR is difficult to measure in marine mammals, it provides a minimum estimate of maintenance requirements that an animal needs to maintain cellular processes and metabolic pathways (Hoelzel 2002). The costs of activity for pinnipeds include their normal range of behaviors, from hauling-out on land to rest, give birth, and molt, as well as activities in water such as diving for food or performing display behaviors during the mating season (Scheffer & Slipp 1944, Bigg 1969, Jeffries et al. 2000). 4) P. The costs of production include growth and reproductive costs. For female pinnipeds, reproductive costs are divided into gestation (fetal growth) and lactation (nursing pups) costs, and for males are generally assumed to be negligible. Growth costs are generally estimated from known or predicted growth curves of pinnipeds from birth until they reach their maximum size and the energy content of tissues laid down (Lavigne et al. 1982, Olesiuk 1993).

The costs of work (E_{work}) and production (P) can also be combined into a field metabolic rate (FMR), or the steady rate of energy use of free-living animals (Hoelzel 2002). However, FMR is logistically challenging to obtain empirically and has currently only been measured for harbor seals during the breeding season (Reilly & Fedak 1991, Bowen et al. 1992, Coltman et al. 1998). FMR measurements also preclude the analysis of separate components of the energy budget, which can be useful for understanding how energy use varies over space and time (Sparling & Fedak 2004). A combination of field and laboratory techniques can be used as an alternative to FMR. The costs of work and production for marine mammals can be estimated separately, and can either be measured empirically or estimated based on captive animals. FMR can be approximated by gathering data on activity budgets of wild animals, and applying the metabolic costs to a time budget. Combining empirically measured metabolic costs with activity budgets has successfully been used to measure energy use in sea otters and great cormorants (*Phalacrocorax carbo*) (Grémillet et al. 2003, Yeates et al. 2007). When data for this method are not available, a generic activity multiplier can be used that extrapolates the activity and maintenance costs of a captive animal to a free-living animal with a hypothetical activity budget, or mass-predicted relationships can be used as a proxy for metabolic rate (Olesiuk 1993, Stenson et al. 1997).

A combination of field data and predictive relationships were used in this study to derive a time budget and estimate the costs of work for harbor seals. The metabolic cost of swimming is known for captive harbor seals, but it is unclear how well this reflects the activity costs of wild animals, especially while underwater (Williams & Kooyman 1985, Sparling & Fedak 2004). The capability of marine mammals to suppress their metabolic rates while underwater complicates measurements of energy use. Measurements of energy use over the duration of a dive and the following surface interval and potentially over an entire dive bout (a group of dives close in time) may be more meaningful than swimming costs (Sparling & Fedak 2004, Fahlman et al. 2008b) for free-living animals. Therefore, I used empirical evidence of diving and shallow-water activity metabolism from a closely-related species (gray seal) to estimate the cost of activity while in water, rather than either swimming costs or generic activity multipliers. The energy use while on land for harbor seals has not been measured, thus it was estimated from Kleiber's (1975) mass-predicted relationship of basal metabolic rate as a minimum cost. Rates of energy use can vary approximately two-fold between these various behaviors; therefore, it is also important to know activity budgets of wild harbor seals to be able to apply these costs appropriately. Telemetry data from free-living seals in the San Juan Islands was used in this study to estimate activity budgets as the basis for applying the metabolic costs of work.

Energy requirements depend on several factors, including sex, age, activity levels, and reproductive status. The transition from individual energy use to a population energy budget is an important step in predicting consumption of marine predators that is used to capture the variability inherent in any free-living population (Lavigne 1982, Hoelzel 2002). To include this natural variation in the model, energy requirements were estimated for different sex and age classes in the harbor seal population to make the population model as realistic as possible (Lavigne 1982, Boyd 2002, Hoelzel 2002). Once a population-level model of energy use was constructed, estimates of harbor seal efficiency and energy density of prey items in their diet, as well as the relative importance of key prey species, were used to estimate consumption. Overall, I estimated the minimum energetic cost for any given component of the energy budget to avoid overestimating energetic requirements and thus consumption. This approach allowed me to measure a lower minimum threshold of consumption, or the minimum necessary to sustain the harbor seal population, which served as the baseline prey requirements of harbor seals.

Many animals often undergo seasonal changes in energy requirements relative to changes in behavior and life history. The breeding season, which includes giving birth (pupping) and mating, is a time of high energy demand for pinnipeds (Figure 1). Sexually

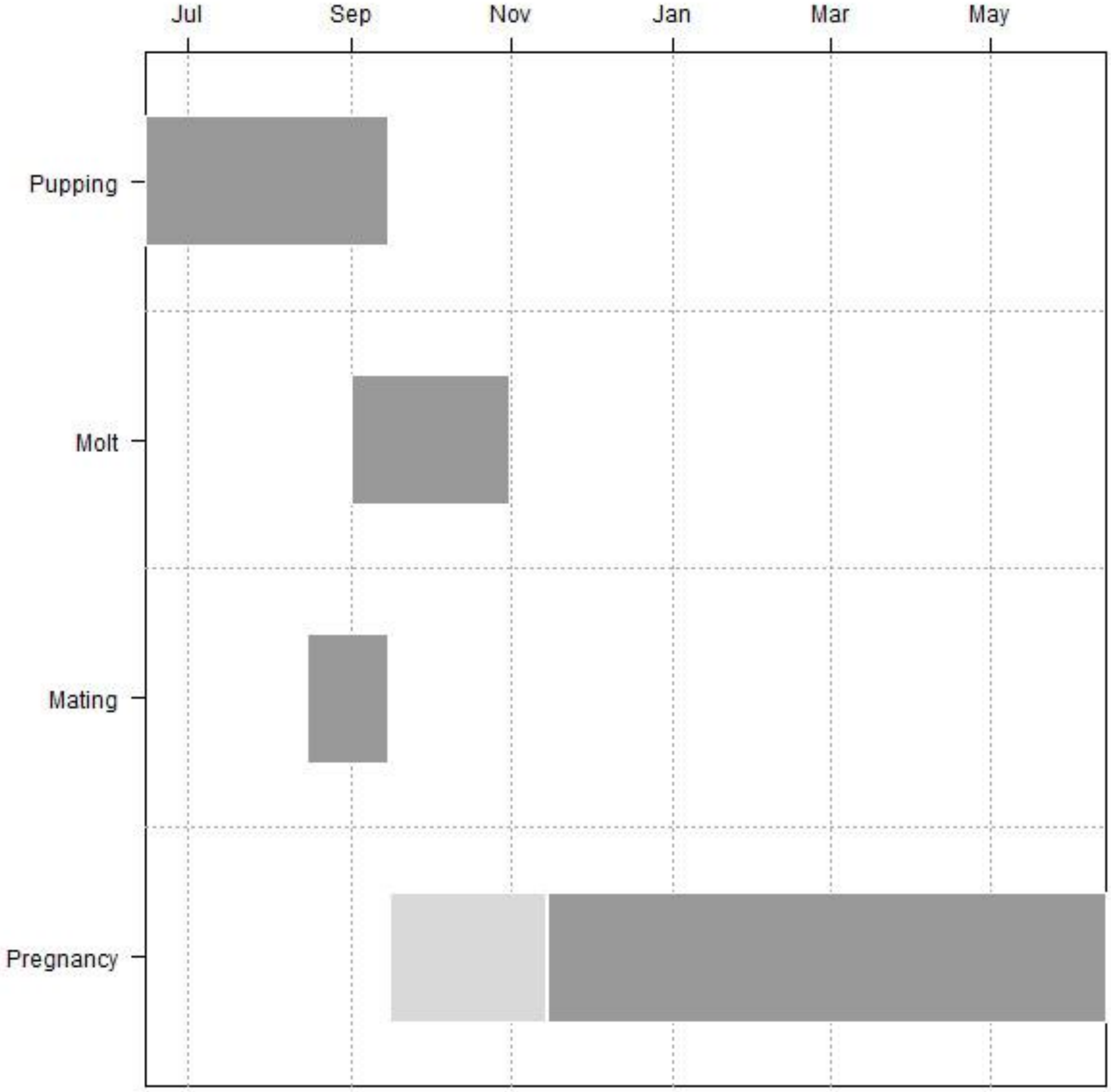

Figure 1. Annual life history stages of harbor seals in the San Juan Islands, WA. Pupping dates are from Suryan (1995), Huber et al. (2001), and Patterson and Acevedo-Gutiérrez (2008). Mating occurs shortly after pups are weaned and implantation of the embryo is delayed for approximately two months (light gray) (Scheffer & Slipp 1944, Bigg 1969).

mature females pay especially high costs in producing milk and nursing, which is believed to be more than that used by males in resource defense (Beck et al. 2003a). However, this high energy use period is not usually met by food intake, and pinnipeds must rely on body fat stores to sustain themselves. Harbor seals, for example, lose 23-33% of their body weight during the breeding season, indicating that both females and males have significant energy deficits during this time period (Bowen et al. 1992, Walker & Bowen 1993). Females and males often have different strategies to prepare for the breeding season. For example, male gray seals begin provisioning for the next breeding season later than the more conservative females. Female gray seals usually return to intensive foraging after giving birth and weaning the pup of the year, because the future survival of their next pup, as well as their own, depends on recovering their body condition relatively early in the annual cycle (Beck et al. 2003a, Beck et al. 2003b). Female harbor seals spend more time at sea after pupping and apparently also increase their foraging activity at this time (Thompson et al. 1989). The energy needs of female Steller sea lions (*Eumetopias jubatus*) increase continually after the breeding season, due to a combination of changing activity (more time in water) but also because they nurse their pups for much longer periods (330 d), while the energetic needs of male Steller sea lions remain relatively constant year-round (Hoelzel 2002, Winship et al. 2002). Immature animals may not undergo these dramatic seasonal changes and thus have yet another set of energetic requirements (Thompson et al. 1989). Thus, the combination of reproductive costs and activity levels is critical in determining when energy use is highest for any given sex and age class in a pinniped population. It is unclear in which portion of their annual cycle energy use in harbor seals is highest; however, this is critical at the individual level in determining fitness and may predict when harbor seals are at a relatively greater risk of an energy deficit. For example, if harbor seal females employ a similar recovery strategy to gray seals, they may be at a greater risk of energy depletion in early winter, thus influencing their survival. Given the variability expected between sex and age classes, it is unclear how these energetic needs translate to the population level without first quantifying energy use. Therefore, a model framework was used that considered seasonal changes in energy budgets for adults, subadults, and pups to quantify population-level energy use.

Quantifying energy needs of individuals and populations is critical not only from the predator's perspective, but also from their prey's perspective. Impacts on prey may be highest in areas of concentrated populations and during energetically expensive life-history stages of the predator (e.g. breeding season). California sea lions (*Zalophus californianus*) are thought to have the largest impact on prey during the breeding season due to their spatial concentration and high costs of lactation. However, their impact is lessened by post-breeding dispersal, indicating that both temporal and spatial scales are important when evaluating predator impacts on prey (Williams et al. 2007). In the San Juan Islands, harbor seals consume rockfish more commonly in the winter (Lance & Jeffries 2007), indicating that the relative risk of predation for their prey may change throughout the year. Therefore, I wanted to predict which season was in fact the most energetically expensive and what level of consumption is required to support the population. A seasonal comparison was used within the bioenergetics model to predict when the energy needs of the harbor seal population were highest. Variation in energetic requirements may play an important role in determining impacts on prey species, given that energetic needs and consumption (thus impacts on prey) may be temporally and spatially segregated.

The results of this model will inform managers of the potential impact of harbor seals on their prey in the San Juan Islands, including recovering fish stocks in marine protected areas. This study is the first to a) quantify harbor seal energetic requirements in the San Juan Islands, b) use metabolic costs of activities applied to time budgets of free-living seals to quantify such requirements, and c) incorporate intraspecific and seasonal variation into population-level estimates. The energetic requirements thus obtained were then used to estimate harbor seal consumption rates for five fish species of conservation concern or common in harbor seal diet to determine the amount of prey required by the harbor seal population during breeding and non-breeding seasons.

Research objectives

Given the potential of harbor seals to affect their prey populations and uncertainty in how they will respond to the establishment of MPAs within the San Juan Islands, I wanted to first quantify energy requirements and the level of consumption required to support the harbor seal population in the breeding and non-breeding seasons. Seasonal-, sex- and age-related differences within the population were compared to determine how this variation may translate to population-level energy use. For the consumption model, I selected fish species of conservation concern within the inland waters of the Pacific Northwest or common in harbor seal diet. Estimates of uncertainty were used in the model to identify areas of research needed to better predict the potential impact of harbor seals as predators.

The consumption model has three main components:

1) Individual energetic requirements: Energetic needs are primarily predicted by metabolic rates, which in turn are driven by activity levels. Therefore, I first needed to know seasonal activity budgets for each sex and age class to test the hypothesis that energetic needs vary throughout the year. Data from harbor seals tagged with time-depth recorder units were used to construct a time budget and predictive equations were used to estimate the metabolic cost of activity levels. These costs were combined with the energetic costs of reproduction and growth from the literature, using species and region-specific data where possible.

2) Population energetic requirements: To extrapolate to a population-level energetics model, I also needed to know how many individuals were present in the San Juan Islands and basic demographic parameters (fertility and mortality rates). To estimate population size, aerial surveys of harbor seal haul-outs were conducted in the San Juan Islands in 2008 and a correction factor was used to account for the proportion of the population not hauled-out during the survey. Two population series were calculated based on mortality rates for the breeding and non-breeding season in 2007 and 2008 to predict population structure and size at each season.

3) Prey consumption estimates: Seasonal diet data from the San Juan Islands were used to reconstruct the relative importance of prey items in harbor seal diet. Using estimates of harbor seal digestive efficiency and energetic density of prey from the literature, gross

energetic requirements calculated in the energetic requirements and population model components were transformed to prey consumption estimates.

METHODS

Study Site

This study was conducted in the San Juan Islands archipelago and eastern bays (Figure 2). The San Juan Islands (center 48° 35’ N, 122° 55’ W) partially consist of tidally-influenced rocky reefs and isolated rocks in the protected inland waters of Washington State. The eastern bays consist of large soft-bottomed bays from Fidalgo Bay to Bellingham Bay (center 48° 33’ N, 122° 30’ W). Harbor seals were captured in both these habitat types at three sites: 1) Padilla Bay (48° 28’ N, 122° 31’ W), a shallow bay (11,000 acres) dominated by eelgrass bed habitat and mudflats which are exposed at low tides, 2) Vendovi Island, a rocky haul-out adjacent to Padilla Bay surrounded by deep water, and 3) Bird/Belle Rocks (48º 29’ N, 122º 45’ W), isolated, exposed rocks in central Rosario Strait, with habitats typical of deep-water rocky reefs in the San Juan Islands.

Prey consumption model

A bioenergetics model was developed using regional data on activity budgets, abundance estimates, and diet data as well as data from other studies (Table 1). I compared harbor seal sex and age class energy use and consumption estimates for five particular prey species or families that harbor seals commonly consume or are species of concern in the inland waters of the Pacific Northwest: rockfish species, salmonid species, Pacific herring, walleye pollock, and shiner perch (*Cymatogaster aggregata*), a species representative of

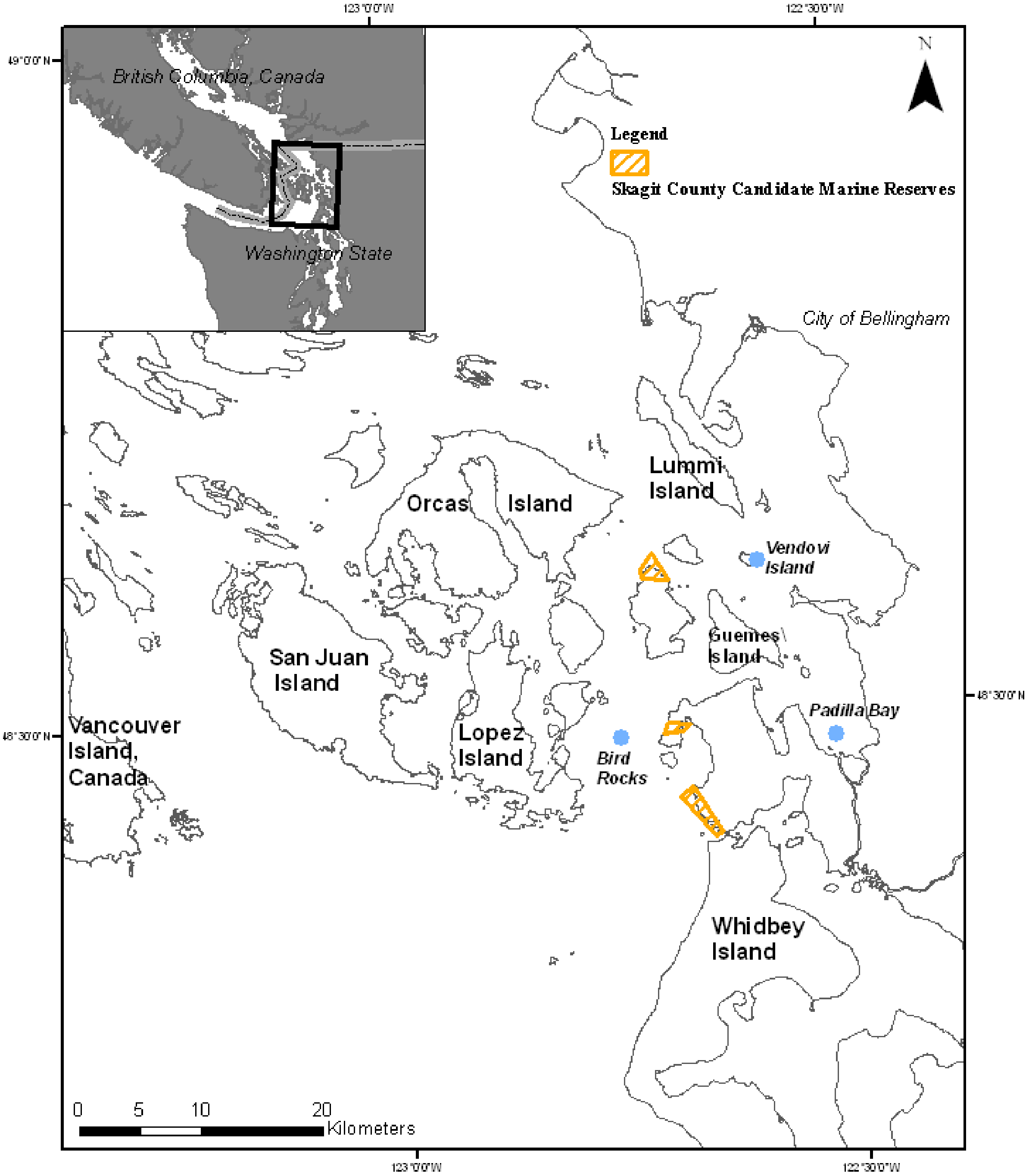

Figure 2. Study site: the San Juan Islands and eastern bays. Harbor seal tagging sites are indicated with circles and candidate marine rockfish reserves for Skagit County are indicated with cross-hatched areas.

Table 1. Datasets used in the harbor seal prey-consumption model.

Parameter Category	Dataset	[Equation]; (Source(s))	Value	Regional (San Juan I.) or species-specific
Bioenergetics	Basal metabolism	[3];(3,15)	See Results	-
	Active metabolism (dive, rest)	[4, 5];(2, 18)	See Results	-
	Activity budgets	(this study, pups: 12)	See Results	R, S
	Mass for each sex and age class	(1, 7)	Female: 24-66 kg Male: 24-89 kg	S
	Daily growth increments	[6];(7)	0.015-0.018 kg d^{-1}	S
	Apparent cost of growth	(4,5)	321 watts	S
	Cost of reproduction: lactation	[7];(6)	See Equation [7]	S
	Cost of reproduction: gestation	[8];(6)	93 MJ pup^{-1}	S
Population	Population estimates	(19, this study)	2007: 8,121 See Results	R
	Fertility rates	(1, 7)	0-0.91	S
	Mortality rates (*r*)	[9];(1, 7)	-0.17 to -0.29 y^{-1}	S
Diet	Assimilation efficiency	(17)	87.4-93.2%	S
	Heat increment of feeding	(8)	1.8-13.7%	S
	Energetic density of prey	(9-11, 13-14, 16)	2,700-11,000 j g^{-1}	
	Biomass reconstruction of proportion of prey in diet	[10]; (20, this study)	See Results	R

Sources:
(1) Bigg 1969
(2) Kleiber 1975
(3) Lavigne et al. 1986
(4) Innes et al.1987
(5) Markussen et al. 1990
(6) Bowen et al. 1992
(7) Olesiuk 1993
(8) Markussen et al. 1994
(9) Perez 1994
(10) Van Pelt et al. 1997
(11) Paul et al. 1998
(12) Bowen et al. 1999
(13) Payne et al. 1999
(14) Anthony et al. 2000
(15) Hoelzel 2002
(16) Roby et al. 2003
(17) Trumble et al. 2003
(18) Sparling & Fedak 2004
(19) Hardee 2008
(20) M. Lance, unpubl. data, WDF&W

estuarine habitats common in seal diet (Lance & Jeffries 2006, Lance & Jeffries 2007, Luxa 2008).

The model had two time steps: breeding (15 June – 15 September) and non-breeding seasons (16 September – 14 June) based on pupping phenology in the San Juan Islands (Suryan 1995, Huber et al. 2001, Patterson & Acevedo-Gutiérrez 2008). These two seasons were delineated to reflect known behavioral shifts related to pupping and breeding activities (Figure 1). Female and male subadults and adults spent 93 and 272 days in the breeding and non-breeding season, respectively. Breeding season for pups lasted only 48 d, and they were not present for the non-breeding season (i.e., they "graduated" to subadult age class). I assumed that all of their energetic requirements (including growth) during the first 45 d of life were met by nursing, to avoid overestimating their energetic requirements which had already been accounted for in the lactation component of the energy budget. Therefore, energetic requirements were not calculated for pups during the first 45 d of the breeding season, but were for the last 48 d after they were assumed to be weaned.

Model parameters were grouped into three categories: bioenergetics, population, and diet (Lavigne et al. 1982, Winship et al. 2002). Bioenergetics parameters included: 1) basal metabolic rate (BMR), 2) diving metabolic rate, 3) shallow-water metabolic rate (not actively diving below 2 m), 4) an activity budget which included proportion of time spent in three behavior classes (hauled-out, diving, and shallow-water activity), 5) weight (kg) for each sex and age class, 6) growth rates, and 7) lactation and gestation costs. The population parameters included 1) population abundance estimates and 2) fertility and mortality estimates. Diet parameters included 1) assimilation efficiency, 2) heat increment of feeding,

3) seasonal diet data [proportion of prey consumed by wet weight (kg)], and 4) energetic density of prey. (See Table 1 for parameter values with region- and species-specific data indicated. Sources for parameters are discussed in the text.) All means reported are ± (SD).

I used a matrix model written in R (vers. 2.7.1) to calculate population energy requirements and food consumption. It is possible to simply scale up from individual to population by multiplying individual energy requirements by population size. However, matrices better represent the complexity present in a given population, where food consumption depends on dynamic population size and energy requirement vectors rather than static measurements (Boyd 2002). Sex- and age-specific gross energy requirements and consumption were calculated in Equation 2 (Boyd 2002):

Equation 2.

$$\frac{EG_i = \left[\sum_{f=1}^{f=n_{activities}} (\gamma_f q_{f,i}) 86400\right] + g_i}{d_w}$$

where EG_i = energy requirements in a particular stage of the annual cycle,

γ_f = the power (watts) generated under activity f within stage i of the annual cycle,

$q_{f,i}$ = proportion of time spent in activity f

g_i = the growth increment in stage i of the annual cycle,

and d_w = the digestive efficiency of food being eaten

Growth and reproductive costs were calculated for the entire population and added after individual requirements were multiplied by a population vector composed of numbers of individuals in each sex and age class (Figure 3). All units from data taken from other literature were converted to watts (joules sec^{-1}) where appropriate.

Bioenergetic parameters

Measurements of energy expenditure in free-living harbor seals, or field metabolic rate (FMR), have only been made during the breeding season for adult seals (Hoelzel 2002). Although FMR provides accurate measurements of energy use by free-living animals, one of its disadvantages is that it averages energy use across all activity levels, thereby precluding analysis of how activity affects metabolic rate (Hoelzel 2002, Sparling & Fedak 2004). I wanted to separate the effect of behavior from other activities (such as reproductive costs that occur during breeding season) on metabolic rate. Therefore, a more detailed energy budget was constructed with costs for three behaviors for harbor seals that would allow comparisons between seasons with known behavioral differences. Following other studies (Boyd 2002, Grémillet et al. 2003, Yeates et al. 2007), this energy budget was used to estimate FMR as the cost of all behaviors, and production costs were calculated separately (see Growth and Reproduction Costs below). In addition, different predictive equations were used (see Active Metabolic Rates section below) for diving activity rather than an activity-adjusted BMR to more accurately reflect energy use and because uncertainty in activity-adjusted BMR has a significant influence on the outcome of marine mammal bioenergetics models (Shelton et al. 1997, Stenson et al. 1997, Winship et al. 2002).

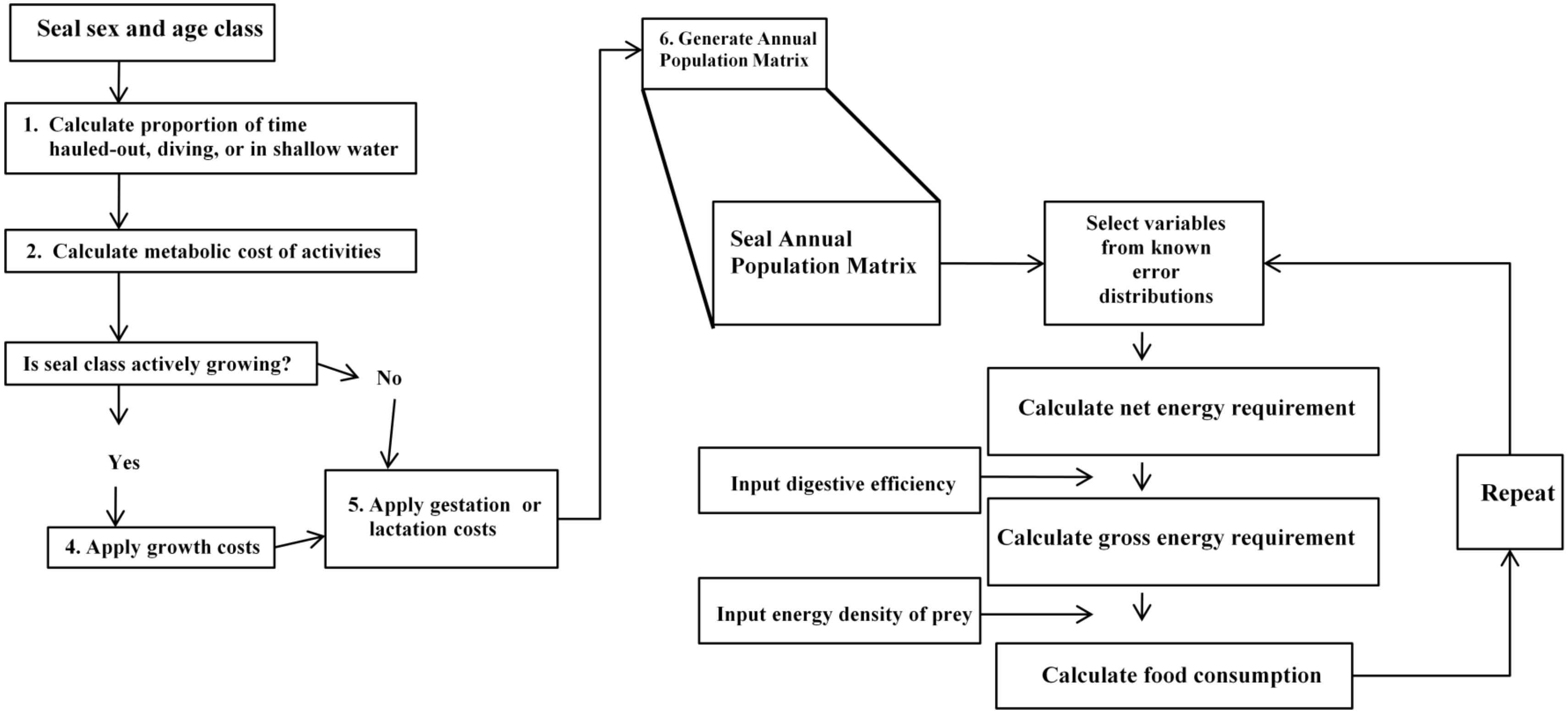

Figure 3. Sequence of steps to develop the harbor seal prey-consumption model. The annual population matrix is generated following the steps outlined on the left side and used as input into the consumption model shown to the right. A similar method to assess uncertainty in the annual population matrix is used as for consumption but is not depicted for clarity (modified from Boyd 2002).

Basal metabolism. Metabolic rates of marine mammals are the subject of much debate (Kleiber 1975, Lavigne et al. 1986, Innes et al. 1987, Williams et al. 2001, 2004). Although some of the purported higher rates for marine mammals were due to non-standard measurement techniques and terminology, animal age, and activity level, it is still unclear the extent to which marine mammals such as harbor seals vary from Kleiber's relationship (Lavigne et al. 1986, Innes et al. 1987). Metabolic depression during diving (or forced submersion in captive animals) can also affect empirical metabolic rate measurements (Butler & Jones 1997).

Despite the uncertainty inherent in measuring basal metabolic rates, the allometric relationship between body mass and metabolism (Kleiber 1975, Schmidt-Nielsen 1984, West & Brown 2004) remains a useful baseline estimate (especially because measuring metabolic rates of marine mammals is logistically challenging and expensive) and is a standard for comparison in the literature (Olesiuk 1993, Boyd 2002, Hoelzel 2002, Sparling & Fedak 2004).

Metabolic rates of hauled-out harbor seals have not been measured in the wild. However, metabolic rates of adult harbor seals resting in water and measured in captivity were 1.2 times the Kleiber prediction (Hoelzel 2002). Harbor seals spent approximately 75% of their time sleeping when hauled-out at a relatively undisturbed site in coastal California (Sullivan 1979). Metabolic rate is lower during sleep, and if similar behaviors are exhibited by San Juan Island seals, this may in part justify using BMR to represent energetic requirements during haul-out periods (Winship et al. 2002). In addition, metabolic rates for juvenile seals may be elevated above adult rates [(Innes et al. 1987) but see (Sparling &

Fedak 2004)]; however, I used the same rate as for adults to avoid overestimating energetic requirements. Equation 3 was considered to represent the minimum basal requirements, with the acknowledgement that actual rates while hauled-out may be higher. Specifically, BMR of harbor seals was assumed to conform to the relationship for phocid seals, the family to which harbor seals belong (Lavigne et al. 1986, Hoelzel 2002):

Equation 3. $$\boldsymbol{BMR = 1.93M^{0.87}}$$

where M = mass (kg)

Following Olesiuk (1993), I assumed thermoregulatory costs were negligible. Year-round air temperatures in the San Juan Islands (7.8-26.6°C as recorded by time-depth recorders on tagged seals) lie within the thermoneutral zone for harbor seals (Hansen et al. 1995). Thermoregulatory costs when hauled-out are therefore most likely neutral. Water temperature is a critical component in metabolic rate prediction for other organisms [e.g., fish: (Kitchell & Stewart 1977)] and affects the metabolic rate of freely-diving Steller sea lions when in shallow water, but thermoneutral zones in both air and water have not been defined for most pinnipeds (Rosen et al. 2007, Fahlman et al. 2008a). Water temperature was included in another harbor seal bioenergetics model, although the underlying energetics model may not accurately predict metabolic rates (Boily et al. 2000, Hoelzel 2002). In other studies, water temperature had varied effects on metabolic rates [reviewed in Olesiuk (1993) and Worthy (2001)]. Water temperatures as recorded by time-depth recorders on tagged seals ranged from 7.1-16.6°C, a range in which seal metabolic rates are not expected to change (Olesiuk 1993). In short, I assumed potential thermoregulatory costs in water were minimal or were met indirectly by other metabolic costs such as the heat increment of feeding (See Diet section) (Olesiuk 1993).

Active metabolic rates. Metabolic rates for diving and resting in water were derived from predictive equations calculated for freely-diving gray seals (Sparling & Fedak 2004). Energy use during diving depends on physiological characteristics as well as swimming or hunting strategy and the type of prey being consumed. Harbor and gray seals exhibit similar characteristics in diving behavior, such as hunting strategy and dive durations, but differ in physiological considerations such as larger body size and oxygen stores in gray seals (Thompson & Fedak 1993, Butler & Jones 1997, Thompson & Fedak 1997, Bowen et al. 2002). Swimming metabolic rate has been measured in harbor seals, but it is unclear how well this reflects energy use while freely diving in the wild (Davis et al. 1985, Sparling & Fedak 2004). Diving metabolic rate (DMR) has not been measured specifically in harbor seals, but because this may better reflect energy use while underwater, gray seal DMR was assumed to be a reasonable proxy for harbor seal DMR. DMR was calculated by Equation 4 (Sparling & Fedak 2004):

Equation 4. $$\boldsymbol{DMR = 0.016M^{0.76}}$$

where M = Mass (kg)

and DMR units are ml O_2 consumed min^{-1}

To convert oxygen consumption to energy use, the energetic equivalent of watts ml O_2^{-1} min^{-1} was assumed to be 20.1 (Butler & Jones 1997). Resting metabolic rate was calculated by Equation 5 (Kleiber 1975, Sparling & Fedak 2004):

Equation 5. $\boldsymbol{RMR = Multiplier * 3.39M^{0.76}}$

where M = mass (kg)

$Multiplier$ = factor by which metabolic rate is elevated above Kleiber estimate of BMR (1.9 for seals resting in water)

and RMR units are in watts

Activity parameters. Data loggers are often used to remotely collect behavioral data on animals that are otherwise difficult to observe (Lander et al. 2001, Hooker et al. 2007). I was able to collect behavioral data on free-ranging harbor seals in the San Juan Islands region by attaching a time-depth recorder (TDR) that continuously collected information on depth profiles, environmental temperature, and wet/dry tag status. Along with collaborators at the Washington Department of Fish & Wildlife, seals were captured and tagged from April 2007 to March 2008 following methodology in Jeffries (1993). Twenty-three of the 29 seals tagged had two units attached: 1) a satellite telemetry unit (Wildlife Computers SPOT tag) and 2) a TDR (Wildlife Computers Mk-9 and Mk-10) with embedded VHF radio transmitter to aid in location and recovery of the units. Six of the 29 tagged seals were outfitted with only a TDR. Three seals were also outfitted with a heart-rate/stomach-temperature recorder (HTR) (Table 2).

The units were attached to the seals' pelage with 5-minute epoxy and were fitted with floatation packs to allow for tag recovery after seals lost tags during their annual molt August-October. Behavioral data were therefore collected at all times of the year with the exception of the molting period, due to the temporary nature of the tag attachment method we used. Seals were tracked with boats twice a week to verify satellite locations, check tag

Table 2. Harbor seals tagged in the San Juan Islands and eastern bays region. Summary of recovered TDR data, including length of data collection period. A = Argos SPOT05 tag, H = HTR, and T = TDR. R = rocky-reef site, B = bay site.

Breeding Season Data							
Seal ID	**Sex**	**Tagging Site**	**Mass (kg)**	**Tagging Date**	**Start Date**	**End Date**	**Data Length (d)**
Y1455^{A,T}	Female	R	76.5	4/4/2007	6/15/2007	7/1/2007	16
Y1456^{T}	Female	B	55.5	4/17/2007	6/15/2007	7/19/2007	34
Y1457^{T}	Female	B	57.5	4/17/2007	6/15/2007	7/24/2007	39
Y1458^{T}	Female	B	48.5	4/17/2007	6/15/2007	8/14/2007	60
Y1459^{A,T}	Female	B	83.0	4/19/2007	6/15/2007	8/14/2007	60
Y1460^{A,T}	Female	B	62.5	4/19/2007	6/15/2007	8/6/2007	52
Y1462^{A,T}	Female	B	77.5	5/21/2007	6/15/2007	8/22/2007	68
Y1465^{T}	Female	B	103.0	5/21/2007	6/15/2007	9/9/2007	86
Y1469^{T}	Female	B	85.0	5/21/2007	6/15/2007	9/15/2007	92
B1695^{A,T}	Male	R	71.5	4/4/2007	6/15/2007	9/4/2007	81
B1699^{A,T}	Male	B	64.0	4/18/2007	6/15/2007	8/15/2007	61
B1701^{A,T}	Male	R	86.0	4/20/2007	6/15/2007	9/15/2007	92
B1712^{A,T}	Male	B	69.0	5/21/2007	6/15/2007	8/4/2007	50
B1713^{A,T}	Male	B	54.0	5/21/2007	6/15/2007	8/8/2007	54
Non-Breeding Season Data							
Y1459^{A,T}	Female	B	64.0	2/25/2008	2/26/2008	6/14/2008	109
Y1469^{T}	Female	B	85.0	5/21/2007	9/16/2007	10/5/2007	19
Y1513^{A,T}	Female	R	75.5	1/30/2008	1/31/2008	6/14/2008	135
Y1514^{A,T}	Female	R	70.5	2/25/2008	2/26/2008	6/14/2008	109
B1744^{A,H,T}	Male	R	81.5	11/20/2007	11/21/2007	2/21/2008	92
B1742^{A,H,T}	Male	R	83.0	11/19/2007	11/20/2007	12/22/2007	32
B1701^{A,T}	Male	R	86.0	4/20/2007	9/16/2007	10/6/2007	20
B1745^{A,H,T}	Male	R	83.0	1/16/2008	1/17/2008; 3/20/2008	3/7/2008; 3/28/2008	50; 8

status, and to recover tags; additional efforts to recover tags from seals that moved substantially outside of the study region (> 100 km) were made with small fixed-wing aircraft equipped with telemetry antennae.

The data collection interval for TDR units was 10 sec. TDR data were downloaded after physical recovery of the tag and processed with Wildlife Computers Data Analysis Program, which compiled instrument readings into a data file. Dives were classified with Dive Analysis software using 2 m as the minimum qualifying dive depth. Depths ≥ 2 times the tag resolution of 0.5 m, plus a safety factor of 2.0 to account for sea surface state and tag positioning, were considered representative of surface or shallow water activity (Tollit et al. 1998, Schreer et al. 2001, Baechler et al. 2002, Härkönen et al. 2008). These data were then used to summarize time spent on land and in water by the use of haul-out and dive bout classifications and depth readings.

TDR data were used to classify seal behavior with known predictive relationships between behavior and metabolic rate. Three classes of behavior were therefore identified using TDR data: 1) haul-out bouts, 2) dive bouts, and 3) shallow-water activity. Records < 24 h from the release time of the seal were removed, as were records after the last verified diving bout, to avoid including records associated with a recovery period from the tagging process (n = 19) and anesthesia given to HTR-tagged animals (n = 3), and to avoid including records after the tag had fallen off the seal, respectively.

I used a Visual Basic algorithm to identify haul-out bouts (Hardee 2008). Tags that were dry for ≥ 20 consecutive minutes were inferred to be on an animal that was hauled-out

(Austin et al. 2006, Hardee 2008) and signaled the start of a haul-out bout. A haul-out bout ended when there were two consecutive minutes of wet readings, indicating that the animal had re-entered the water.

Seals make foraging trips that are defined as the time period between leaving a haul-out and entering the sea until their return to a haul-out. Within this trip, a foraging bout can be defined as a cluster of successive dives (Austin et al. 2006). I used the term diving bout to describe time spent underwater whose primary purpose may be foraging, traveling, or other behaviors. To include very shallow dives, I identified diving bouts by modifying a Visual Basic algorithm (Reuland 2008). Bouts were defined as a series of four or more dives to greater than 2 m with surface intervals of $\leq$ 90 sec. Dives were added in an iterative fashion to the bout if the subsequent surface interval was not significantly different than the previous group of surface intervals. Otherwise, the bout was considered to have ended and the algorithm searched for a new bout.

Each time-stamped instrument reading was then matched to its respective haul-out or dive bout to allow for error-checking. Records that were erroneously classified were manually inspected and assigned to either the haul-out or dive categories. Remaining records were then placed into a shallow-water activity category. Seals also perform dives outside of bouts; these dives were first identified by their depth reading ($\geq$ 2 m) and removed from the shallow-water activity category. However, energy use during diving is most easily measured by the duration of the dive plus the post-dive surface interval. Dive bout classification allowed me to easily identify time periods of continuous diving with known post-dive surface intervals. Dive Analysis software only identifies the preceding surface interval of an individual dive. Therefore, to account for time spent in post-dive surface intervals in non-bout dives, an average surface interval of 65 sec was used for harbor seals in the San Juan Islands (Reuland 2008), multiplied by the number of non-bout dives to correct the total number of records in the dive category. These records were also removed from the shallow water activity category to ensure that all behavioral categories were mutually exclusive.

I then calculated the number of records in each activity state, averaged separately for females and males and over the breeding and non-breeding season, to estimate activity budgets for tagged seals. Behavioral activity of female and male pups was estimated using an activity budget for Nova Scotia harbor seal pups tagged with TDRs (Bowen et al. 1999).

Mass and growth. Body mass was predicted for each sex and age class following Olesiuk (1993) with a modified form of the Gompertz growth curve. The model had six sex and age classes: 1) adult females (> 6 yrs), 2) adult males (> 8 yrs), 3) subadult females (1-6 yrs), 4) subadult males (1-8 yrs), 5) female pups (age < 1), and 6) male pups (age < 1). These divisions were made on the basis of when harbor seals reach their maximum weight (approximately 66 kg and 89 kg for females and males, respectively). The daily growth increment (kg) for female and male adults and subadults was then calculated to predict differences in mass between age intervals. Daily growth increments (DGR_x) were calculated by:

Equation 6.

$$\boldsymbol{DGR_x = \frac{M_{x+1} - M_x}{d}}$$

where M_x = mass at age$_x$,

M_{x+1} = mass at next age interval

and d = number of days in cycle

Total growth costs were then calculated by multiplying DGR_x by 321 watts, an average of the apparent cost of growth for phocid seals (Innes et al. 1987, Markussen et al. 1990).

Reproduction costs. The costs of lactation and gestation were calculated for the entire population by multiplying fertility estimates in each age class by the total reproduction costs. I used the relationship described by Bowen (1992) to estimate the cost of 80% of the lactation time period for females with pups. The cost of lactation in this study could only be calculated by tracking change in body mass and proximate composition as females lost body mass during the first several weeks of lactation when they were not eating. The total cost of lactation per female will therefore be underestimated and does not include the period where females begin foraging in late lactation. Adult and subadult female lactation costs were calculated separately based on known differences in fertility rates; the total cost for lactating females in both age classes in the population was calculated by Equation 7 (Bowen et al. 1992):

Equation 7. $$\boldsymbol{Lactation_{total} = N * F * (24.2\ MJ\ *\ M^{0.75})}$$

where N = number in age class

F = fertility rate of age class (%)

M = mass of female in specific age class (kg)

and *Lactation* units are in MJ

The cost of gestation was calculated for all pregnant females in the population using an estimate of the gross energy used by females to produce a harbor seal pup (Bowen et al. 1992):

Equation 8. $$\boldsymbol{Gestation_{total} = N * F * 93\ MJ}$$

where N = number in age class

F = fertility rate of age class

and *Gestation* units are in MJ

Gestation costs were the only instance in the prey consumption model where energetic requirements may have been over- rather than under-estimated: larger females give birth to larger pups, so it is possible that gestation costs were overestimated, especially for subadult females (Bowen et al. 1994). Therefore, I measured the contribution of this factor to the overall energetic requirements through sensitivity analyses.

Population abundance

Breeding population size. Population surveys of harbor seals have been conducted annually by the Washington Department of Fish & Wildlife using fixed-wing aircraft to estimate number of animals hauled-out during the daytime lower low tide since 1978 (Jeffries et al. 2003). In collaboration with the Washington Department of Fish & Wildlife, aerial surveys of seal haul-outs were conducted in July and August 2008 in the San Juan Islands and eastern bays region in small fixed-wing aircraft by flying at an airspeed of 80 kts and at 200-300 m elevation (Figure 2). Each survey took place over two days and was flown within ± 2 h of low tide and during tidal heights ≤ 2 ft. Digital photographs were taken with a Nikon D100 with a 200 mm lens when seal numbers were > 25 individuals (Jeffries et al. 2003, Hardee 2008). Photos were enlarged with Photoshop to count all seals hauled-out on land. Seals in the water were not counted.

The estimation of seal population size based on haul-out counts requires a correction factor to account for seals in the water at the time of the survey (Huber et al. 2001, Jeffries et al. 2003). Counts were averaged for each haul-out site to obtain a mean (± SD) which were then summed to obtain a total count for each 2 d survey. The breeding season (July) correction factor of 1.53 was used for the harbor seal population in the San Juan Islands and eastern bays to obtain the total estimated population size during the pupping season (Huber et al. 2001).

Population projection. Life tables with basic demographic parameters have been constructed for harbor seals in British Columbia based on seals collected and aged in the mid-1960s (Bigg 1969). Although the seals were collected after approximately 50 yrs of control kills and commercial harvests in British Columbia and a control program in Washington State, and therefore when the population was depressed, the sample nevertheless likely represented a stable sex and age structure because of non-selective harvest methods (Bigg 1969, Olesiuk et al. 1990, Olesiuk 1993, Jeffries et al. 2003).

The harbor seal population in Washington State has recovered, and the 1960s sex and age structure may not reflect the current population status. Olesiuk (1993) noted that the harbor seal population was heavily weighted towards a young age structure by the 1980s following a period of population recovery. Now that the population has apparently stabilized, it seems likely that younger age classes have been recruited into the adult population, affecting the overall age structure (Jeffries et al. 2003). However, it is difficult to make predictions as to the current age structure due to a wide variety of influences on population dynamics.

Marine mammal population processes are highly dependent on a variety of factors, including oceanographic conditions, mortality sources, and food resources (Fowler 1981). In addition, population processes often exhibit time lags where the success of a cohort is not reflected in the population until a later time (Ricklefs 1996). Therefore, it can be difficult to infer current conditions from either the past population status or patterns in other populations. However, due to a lack of region-specific or more recent data, the mortality and fertility estimates in Bigg (1969) and Olesiuk (1993) were the best available for harbor seal population demographics in the San Juan Islands.

The age structure (number of seals present in each age class at the beginning of the breeding season) were modeled following Olesiuk (1993) by assuming an exponential decline in number of seals in age classes which distinguishes different age-dependent mortality rates. Two sets of population series were calculated for the consumption model. The population series at the beginning of the breeding season was calculated by Equation 9 (Olesiuk 1993).

Equation 9.

$$\boldsymbol{N_{S(x+t)} = N_{S(x)^{e^{-rt}}}}$$

where $N_{S(x)}$ = Number of seals in sex class S and age class x,

$-r$ = the age-dependent mortality rate,

and t = time interval between age classes

This series was adjusted by iteration to sum to the total population estimate from aerial surveys. I used the 2007 estimate of 8,121 seals from Hardee (2008) as the breeding season estimate and projected forward from this point for the second population series. This population series calculated numbers still alive in each sex and age class at the beginning of the non-breeding season, using the same age-dependent mortality rates calculated per day (instead of annually) and then multiplied by the number of days in the breeding cycle. Energy use and consumption was therefore calculated for the maximum number present in the population in each season.

Because pups were sampled non-selectively in Bigg (1969) and their mortality rate was theoretically derived, the number of pups counted in the population censuses was compared to the number calculated as discussed above. The number of pups still alive at the end of the breeding season was then added to the subadult age class for the non-breeding season.

Diet

Assimilation efficiency & heat increment of feeding. Data from the literature were used to translate net energy requirements of the harbor seal population into gross energy requirements and consumption by first taking assimilation efficiency and the heat increment of feeding into account. Values of 87.4-93.2% were used for assimilation efficiency as measured in harbor seals (Trumble et al. 2003). The heat increment of feeding is inversely related to the energetic density of prey and can be up to 15% when harbor seals consume fish. An estimate of 1.8-13.7% was used to reflect the range of possible heat increment of feeding values when energetic density of prey varies widely (range of values used in this study: approximately 3000-11,000 J g^{-1}) (Markussen et al. 1994).

Proportion of prey in diet. A biomass reconstruction technique was used to estimate the relative importance of five key prey items in harbor seal diet (Laake et al. 2002). The diet composition [frequency of occurrence (FO) of prey species in scats] of harbor seals is well known for the San Juan Islands (Lance & Jeffries 2006, 2007). Although FO data provide an index of diet composition and relative frequency of prey consumed, biomass reconstruction is necessary to evaluate the contribution of prey to harbor seal diet in energy terms (Lavigne et al. 1985, Lance et al. 2001, Luxa 2008). Otolith measurements from scat samples collected during the breeding and non-breeding seasons in 2007-2008 were used (Lance, M. WDF&W, unpubl. data), along with correction factors that account for loss of otoliths and reduction of otolith size during digestion to reconstruct the size of fish consumed (Harvey 1987, Phillips & Harvey 2005).

There were two steps in the reconstruction: 1) I first applied any available length correction factors to the otolith measurements (those known for harbor seal diet) and then used standard regressions in the literature to reconstruct fish weight from otolith length (Harvey et al. 2000), and 2) any available numerical correction factors were applied to the number of otoliths counted in samples to estimate the minimum number of individuals in the sample.

Of the “key” prey species, I lacked correction factors for herring and walleye pollock; therefore, I considered the correction factor for sardine (*Sardinops sagax*) and Pacific hake (*Merluccius productus*), respectively, to be reasonable proxies because they belong to the same taxonomic families. Measurable otoliths for salmonids are uncommon in scat samples; therefore, I used an average estimated size for adults (1589 g) and juveniles (35 g). For the reconstruction, all species of adult and juvenile salmon were combined into a "salmonids" complex, and *Clupea pallasi* and *C.* spp. were combined into a "herring" complex.

In general, biomass reconstruction was done for prey species with measurable otoliths or whose FO was $\geq$ 5, or both. A full reconstruction would require correction factors and measurable otoliths for every species in harbor seal diet to properly calculate percent contribution by wet weight to total diet (see Equation 10). However, this was not possible for diet samples due to the diversity of harbor seal diet. I generally assumed that any species that lacked at least family-level correction factors or whose FO was < 5.0, or both, contributed little to harbor seal diet by percent of wet weight. For the more dominant species (salmonids and herring), their maximum percent possible was set at 70% (non-breeding season) and 80% (breeding season) to avoid overestimating their contribution to diet (see Results). The proportion of biomass of a prey item ($\boldsymbol{\pi}_{\mathbf{i}}$) in harbor seal diet was then calculated by Equation 10 (Laake et al. 2002):

Equation 10.

$$\boldsymbol{\pi_i = \frac{n_i w_i}{\sum_{i=1}^{w} n_i w_i}}$$

where n_i = the corrected number of items (otoliths) of prey item_i

and w_i = the average weight (g) of all prey items_i

Setting the minimum and maximum values for a uniform distribution for proportion in diet as actually found in field data would have been uninformative (i.e., a range of 0-100 would imply no prior knowledge of diet composition). Many species are detected only through bone structures and if their otoliths are not present in a particular sample, it is not possible to reconstruct their weight. Therefore, the distribution parameters were set to represent a realistic range of possible values by using the between-month variation as a guide. Zero values were discarded and the minimum values for herring and salmonids were set as found in the field data, and because harbor seal diet is known to be diverse, at least 20-30% of harbor seal diet was assumed to be made up of other species and maximum was set at 70-80% (lower maximum value for non-breeding season due to increased diversity of diet). For shiner perch and walleye pollock, zero values were also discarded and the minimum possible value was assumed to be 1%, and maximum was set as found in the field data. Rockfish spp. FO was 0.5, and so was assumed to contribute nothing in energetic terms to diet during the breeding season. During the non-breeding season, rockfish FO was 1.4% (Lance, M. WDF&W, unpubl. data). However, no measurable otoliths were found, and so I set a hypothetical range for proportion of rockfish in diet from 1-2% (see Results).

Energetic density of prey. Once harbor seal population gross energy requirements were calculated, consumption was calculated by dividing gross energy requirements by the energetic density of prey items; these data were taken from the literature and converted to joules g^{-1} where appropriate (Perez 1994, Van Pelt et al. 1997, Paul et al. 1998, Payne et al. 1999, Anthony et al. 2000, Roby et al. 2003).

Incorporating error in the model

Both known and estimated variable error were incorporated into the energy and consumption estimates by using Monte Carlo simulation methods which produced a distribution of estimates (Mohn & Bowen 1996, Stenson et al. 1997, Winship et al. 2002, Mecenero et al. 2006, Bejarano et al. 2007, Overholtz & Link 2007). Sources of error are due to both measurement error (in predictive equations and in variables measured in the field) and natural variation within the seal population. Error is not necessarily normally distributed around the mean, nor can it equal all possible values around the mean (e.g., body mass cannot be a negative number). Therefore, during simulation it was important to control how parameters were chosen. I did this by describing parameters with probability distributions that best fit the assumed shape of the distribution of the data. A lognormal distribution was used for seal body mass, a triangular distribution for fertility rates, a gamma distribution for growth rates, and a uniform distribution for population size, assimilation efficiency, heat increment of feeding, energy density of prey, proportion of prey in diet, and for activity data (Otto & Day 2007, Bolker 2008). Activity variables (proportion of time diving, in shallow water, and hauled-out) were not independent; therefore, I inserted a loop that allowed the model to choose values for the “diving” and “shallow-water” proportions that were dependent on the previous proportions chosen.

Where probability distribution parameters were too complex to calculate or were not readily available (e.g., meanlog and sdlog for lognormal), a maximum-likelihood fitting procedure in R was used to estimate parameters (Bolker 2008). I ran 1,000 simulations in R such that in each simulation sets of variables were randomly chosen from their assigned distributions. These simulations allowed me to calculate a mean and standard deviation for each model output and all outputs are reported as mean (± SD).

Sensitivity analyses were used to examine which variables cause the most uncertainty in consumption estimates and to guide future research (Shelton et al. 1997, Stenson et al. 1997, Warren et al. 1997, Winship et al. 2002). This analysis was performed by allowing uncertainty in the parameter of interest, as described above, while keeping the remaining parameters constant at their average or mode (Winship et al. 2002); hereafter, referred to as “variable-parameter model.” The model was also run by fixing a parameter of interest at the first quartile (25th percentile), mean value, and third quartile (75th percentile) to graphically examine how this shifted the overall model output mean (while allowing the remaining parameters to be chosen randomly from within their distributions); hereafter, referred to as “fixed-parameter model.”

RESULTS

Activity budgets

Twenty-nine seals were tagged in 2007-2008: 15 animals (5 males, 10 females) at Padilla Bay and Vendovi Island and 14 animals (11 males, 3 females) at Bird/Belle Rocks. A total of 19 TDRs were recovered, yielding a recovery rate of 66%. Data from three seals extended over both seasons, bringing the total number of datasets to twenty-two (Table 2). One TDR malfunctioned while collecting data (seal B1745), although data collected before and after this malfunction were useable. The average data collection length period was 65 ± 32 d (Table 2).

Female haul-out activity remained relatively constant year-round; however, females consistently increased their dive effort in the non-breeding season by an average of 23%. Dive effort was high for two females during the breeding season: > 60% of time budget, or roughly equal to the non-breeding season average. Of these two females, only one had satellite location data recorded simultaneously, and she spent the majority of her time in deep-water areas; the second female did not have satellite data, but was often found inside Padilla Bay (relatively shallow waters) during field-tracking efforts. Another two females spent time in both deep and shallow water areas, and they both increased their relative dive effort by 14-20%. Time spent in shallow-water activity by females was highly variable, with most individuals just as likely to spend the majority of their time in shallow-water activity as they were in other activities (Table 3).

Table 3. Activity budgets of female and male harbor seals in the San Juan Islands and eastern bays. Proportion of time (%) individual seals spent in each behavioral class and average (± SD) for all seals. A = Argos SPOT05 tag, H = HTR, and T = TDR.

	Breeding Season			**Non-breeding Season**		
Seal ID	Hauled-out	Diving	Shallow-water	Hauled-out	Diving	Shallow-water
Y1455^{A,T}	32.5	63.6	3.9	-	-	-
Y1456^{T}	13.1	28.9	58.0	-	-	-
Y1457^{T}	11.9	60.2	27.9	-	-	-
Y1458^{T}	14.2	53.3	32.5	-	-	-
Y1459^{A,T}	26.3	51.9	21.8	17.3	72.2	10.6
Y1460^{A,T}	16.1	34.2	49.6	-	-	-
Y1462^{A,T}	10.9	14.9	74.2	-	-	-
Y1465^{T}	12.6	52.9	34.5	-	-	-
Y1469^{T}	10.6	32.1	57.3	20.6	46.1	33.3
Y1513^{A,T}	-	-	-	16.1	68.6	15.3
Y1514^{A,T}	-	-	-	13.6	81.0	5.5
Female Average	16.5 (±7.7)	43.6 (±16.5)	40.0 (±21.7)	16.9 (±2.9)	67.0 (±14.9)	16.2 (±12.1)
B1695^{A,T}	22.0	69.6	8.4	-	-	-
B1699^{A,T}	19.2	18.7	62.1	-	-	-
B1701^{A,T}	16.0	78.3	5.7	33.1	63.7	3.2
B1712^{A,T}	14.8	17.1	68.0	-	-	-
B1713^{A,T}	9.3	17.3	73.4	-	-	-
B1742^{A,H,T}	-	-	-	23.9	60.3	15.8
B1744^{A,H,T}	-	-	-	29.0	51.0	20.0
B1745^{A,H,T}	-	-	-	21.3	72.7	6.0
Male Average	16.2 (±4.7)	40.3 (±30.9)	43.5 (±33.6)	26.8 (±5.3)	61.9 (±9.0)	11.2 (±7.9)

Male seals hauled-out more often in the non-breeding than the breeding season and also increased their average absolute dive effort during the non-breeding season. However, in general, males were more variable in their activities than females. Dive effort of males that remained in deep-water areas of the San Juan Islands (n = 2) was still high (70-80% of time budget) in the breeding season. The only male with longitudinal data exhibited an inverse trend: decreased dive effort in the non-breeding season. During the breeding season, males were just as likely to spend the majority of their time in shallow-water activities as in diving activity. During the non-breeding season, males spent relatively little time in shallow-water activities (11.2% ± 7.9% of time budget) (Table 3).

Population abundance

Three sets of 2-d aerial surveys were completed during 2008: 17-18 July, 31 July-1 August, and 14-15 August. The third survey did not completely cover the study area and not included in population estimates. The average survey count over the first two surveys was 5,182 (±353) seals. After applying the correction factor for seals not hauled-out, the population estimate of harbor seals in the San Juan Islands and eastern bays from Bellingham Bay south to Similk Bay was 7,929 (±540) individuals.

Energy use

Sex- and age-related variation

Energy requirements generally increased with body size and age: adult and subadult males had greater energy requirements than females in the non-breeding season. In the breeding season, adult females had the highest energy requirements of any sex and age class in the harbor seal population. The average individual net energy rates ranged from 46 - 186 watts in the breeding season and 97 - 143 watts in the non-breeding season. Breeding season net energy rates calculated from 1,000 simulations were: 186 (±7), 157 (±7), 113 (±26), 120 (±31), and 46 (±4) watts for adult females, adult males, subadult females, subadult males, and pups, respectively. Non-breeding season net energy rates were: 125 (±4), 143 (±5), 97 (±19), 109 (±29) for adult females, adult males, subadult females, and subadult males respectively. Variability in energy use within a sex and age class was greatest for subadults (Figure 4).

Seasonal variation

Net energy requirements of the entire seal population were higher in the breeding season than the non-breeding season; instantaneous rates were approximately 0.9 (±0.1) MJ and 0.8 (±0.1) MJ, respectively (Figure 5). Per capita net energy use was similar between seasons: 112 (±12) watts in the breeding season and 108 (±14) watts in the non-breeding season. Energy use was higher during the breeding season for female and male adults and

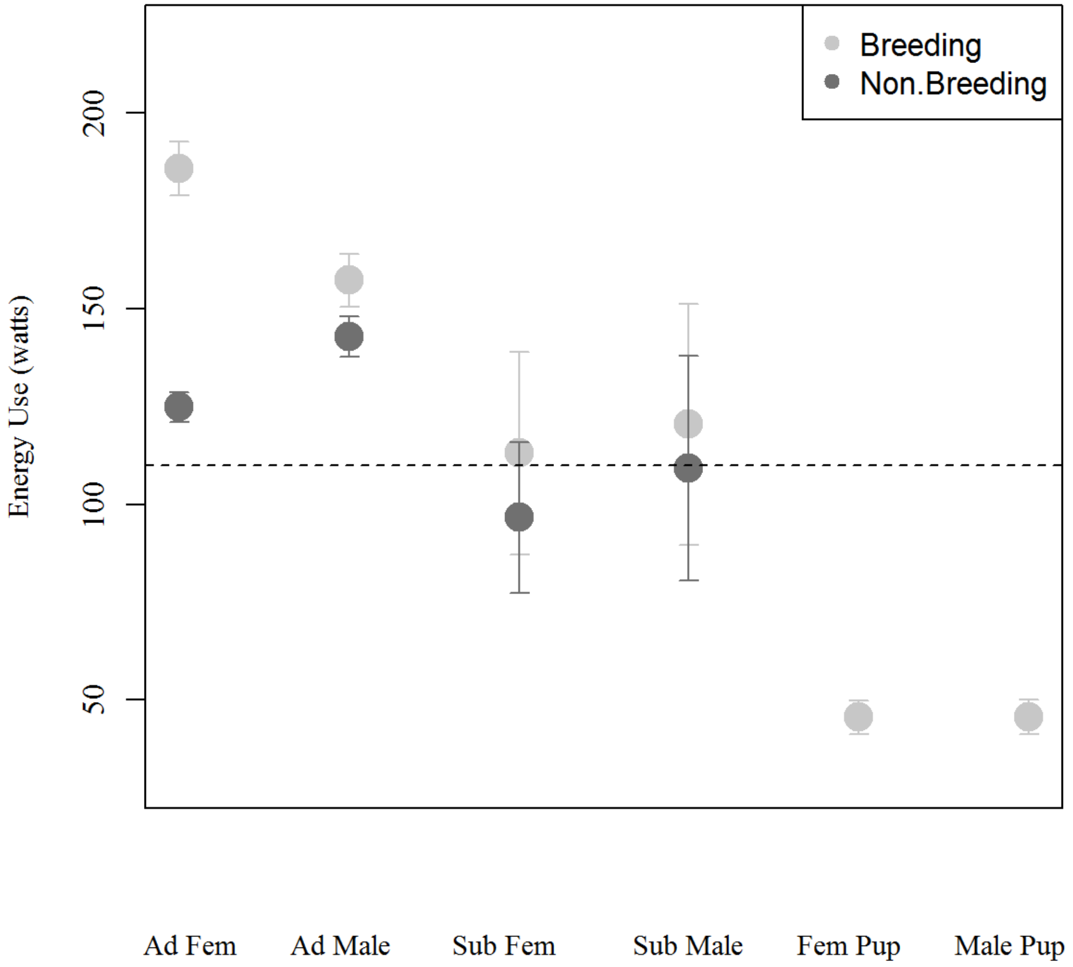

Figure 4. Variation in rates of net energy use among sex and age classes in the harbor seal population in the San Juan Islands and eastern bays. Dashed line indicates per capita rate. Error bars are SD calculated from 1,000 simulations.

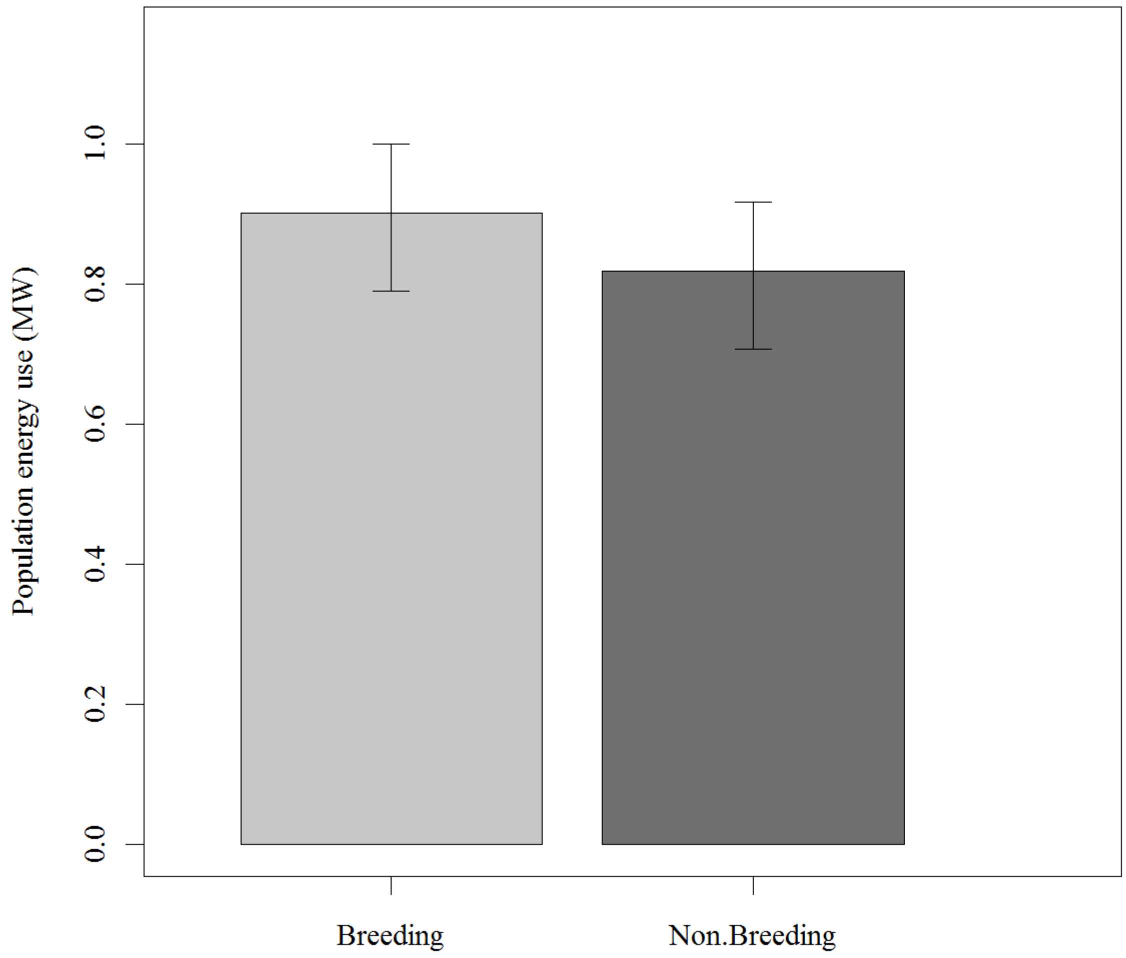

Figure 5. Instantaneous rates of net energy use by the harbor seal population in the San Juan Islands and eastern bays relative to season. Error bars are SD calculated from 1,000 simulations.

subadults than the non-breeding season, although the magnitude of difference was greatest for female adults (Figure 4).

Diet

There were 25 and 33 prey taxa identified in diet during the breeding and non-breeding seasons (Lance, M. WDF&W, unpubl. data). Herring and salmonids both comprised > 80% of the reconstructed diet samples by percent wet weight. Between-month and -site variation were large for these prey groups: in some sites scat had 0% of these groups and in others had 100% (Table 4).

Consumption

Breeding season

There were two trends evident in consumption patterns for key prey species: estimates for less common species in harbor seal diet were less variable and consumption estimates for more common species had a wider range. The average consumption for prey species calculated over 1,000 simulations was 783 (±380) metric tons of salmonids, 646 (±303) of herring, 50 (±17) of walleye pollock, and 22 (±4) of shiner perch (Figures 6-7). Subadult seals of both sexes consumed the greatest proportion of the total biomass (approximately 30-40% each), followed by adult females (27%). Adult males consumed a

Table 4. Reconstructed prey sizes and percent of wet weight in harbor seal diet in the San Juan Islands and eastern bays from biomass reconstruction of scat samples. Average percentages reported are between sampling months, and ranges in parentheses were used in the prey-consumption model. Average sizes reported are from reconstructed samples, and sizes in parentheses were hypothetical.

	Ave reconstructed (hypothetical) size (g)	**Ave % wet weight (range used in model)**	**Ave reconstructed (hypothetical) size (g)**	**Ave % wet weight (range used in model)**
	Breeding Season		**Non-breeding Season**	
Rockfish spp.	N/A	N/A	N/A	N/A (1-2)
Salmonid spp. adult	(1589)	15 (10-80)	(1589)	9 (1-25)
Salmonid spp. juvenile	(35)		(35)	
Herring spp.	63	81 (20-80)	80	85 (60-70)
Walleye pollock	57	3 (1-3)	18	0.3 (1)
Shiner perch	39	0.5 (1)	28	2 (1-2)

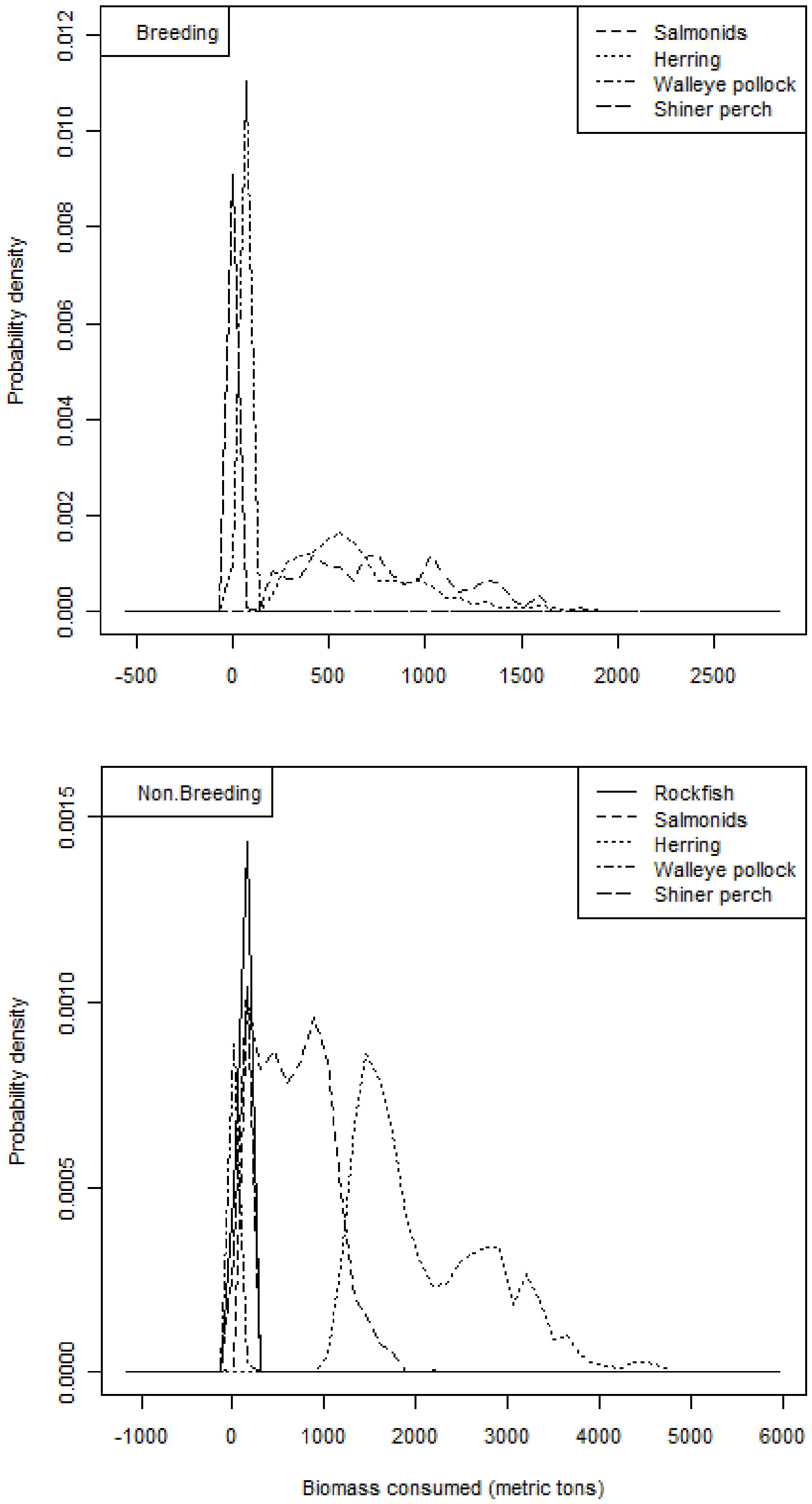

Figure 6. Probability density estimates of harbor seal biomass consumption for key prey species relative to season. Note x-axes are scaled differently.

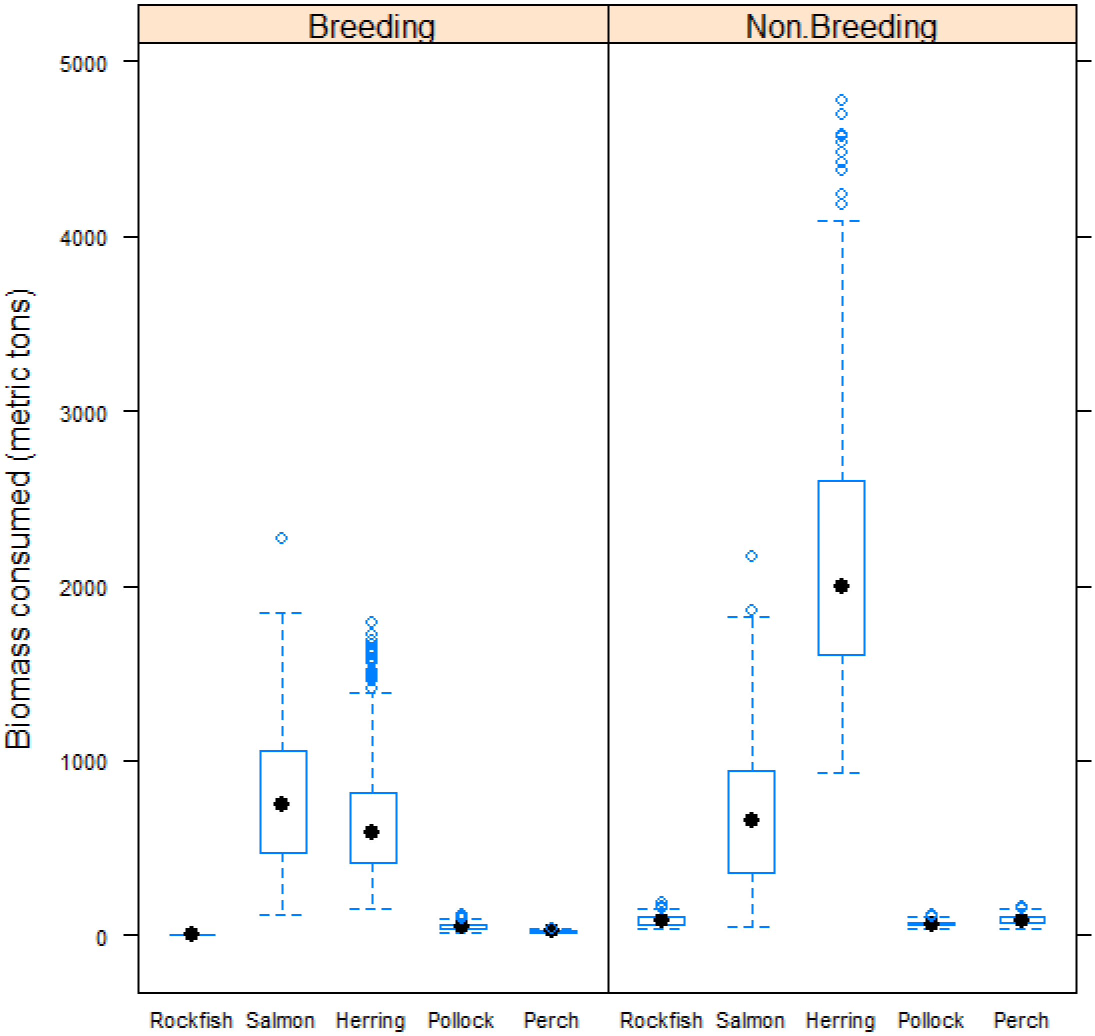

Figure 7. Consumption estimates for the harbor seal population for key prey species relative to season.

relatively small proportion of total biomass compared to adult females and subadults, and were only slightly higher than pups of both sexes (each < 10%) (Figure 8).

Non-breeding season

Herring and salmonid consumption had the widest range of values; rockfish, shiner perch, and walleye pollock were less variable. The average consumption for prey species calculated over 1,000 simulations was 84 (±26) metric tons of rockfish, 675 (±388) of salmonids, 2,151 (±706) of herring, 66 (±13) of walleye pollock, and 86 (±22) of shiner perch (Figures 6-7). Similar to the breeding season, subadults of both sexes consumed the greatest proportion of the biomass (approximately 30-45% each), followed by adult females (19%). Adult female consumption dropped slightly in the non-breeding season. Adult males consumed the smallest proportion in the population (5%) (Figure 8).

Sensitivity analyses

Energy use

Variable-parameter models. When specific parameters were allowed to vary randomly while keeping other variables fixed, variation in seal body mass had the largest effect on energy use of the population (Figure 9, Table 5). Taken together, all bioenergetics variables (mass, growth rates, and activity) accounted for the majority of the variance in the simulation model (Figure 9). Fertility rates accounted for the next-greatest variance after

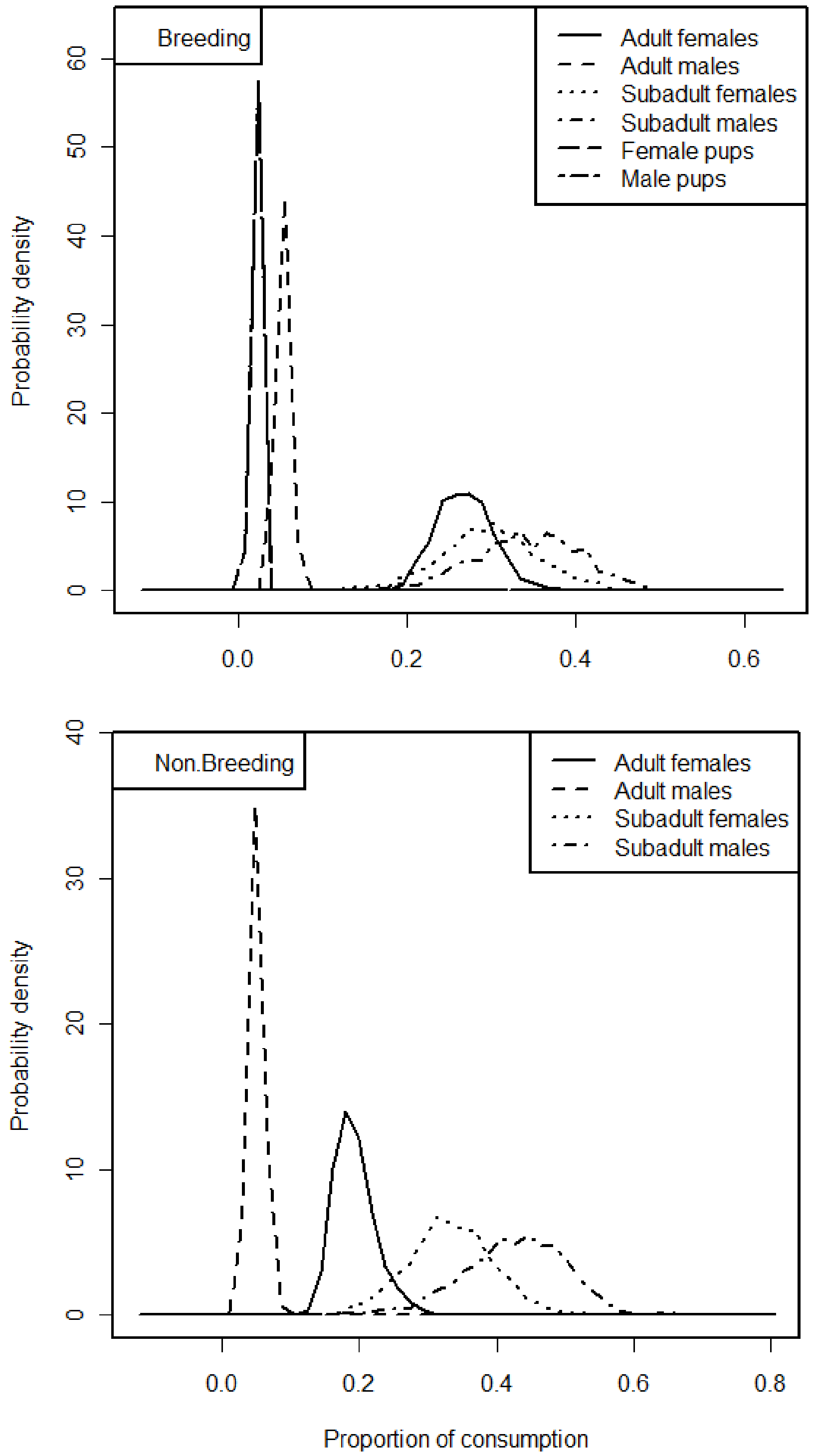

Figure 8. Probability density estimates of proportion of total biomass consumption by each sex and age class for key prey species relative to season. Female and male pup consumption on the top panel is represented by the leftmost curves which appear superimposed due to their extreme similarity.

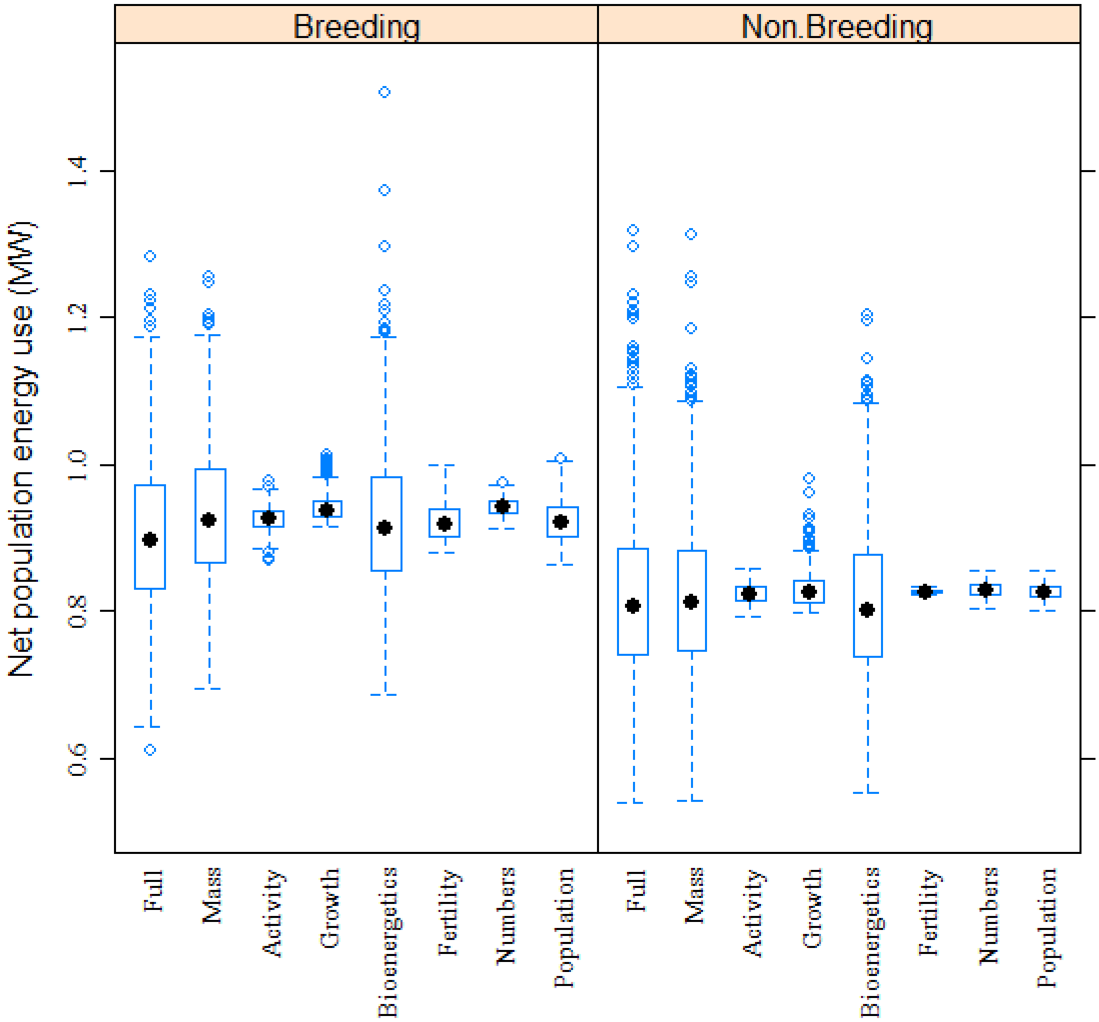

Figure 9. Effect of bioenergetics and population variables on net population energy use of harbor seals. Distribution of model outputs after running 1,000 simulations with all variables ("Full"), single (individual variables), or groups ("Bioenergetics" or "Population") of variables selected randomly. Solid circle indicates mean, solid box encloses the interquartiles, vertical dashed lines are min and max, and open circles indicate outliers. (See Table 5 for variable group definitions.)

Table 5. Proportion (%) of variance in population net energy use explained by bioenergetics and population variables relative to season. Each comparison below can be considered a separate model to compare to the full simulation model. Each such model was run separately and hence outcome can be greater than the "Full Simulation" due to interactive effects and random selection of variables.

Model Number	**Model Version**	**Breeding season**	**Non-breeding season**
1	Full Simulation	100	100
	Individual variables		
2	Mass	90.0	83.4
3	Growth Rates	3.0	3.9
4	Activity	2.7	1.3
5	Population Size ("Numbers")	1.3	0.8
6	Fertility Rates	7.3	0.04
	Groups of variables		
7	Bioenergetics variables (2-4)	>100	85.7
8	Population variables (5-6)	8.3	0.9

body mass while the second population variable (population size) contributed the least to the overall model variability (Table 5). Certain factors contributed to model variation differently in the breeding and non-breeding seasons: body growth rates contributed more to model variation in the non-breeding season, while the reverse was true for fertility rates (Table 5). As a group, population variables also contributed to model variability to a greater extent in the breeding season than in the non-breeding season (Figure 9).

Fixed-parameter models. When specific parameters were fixed while other variables were allowed to vary randomly, similar trends were seen as in the previous set of sensitivity analyses. Fixing seal body mass at different values dramatically affected the model outcome compared to other variables (Figures 10-14). Fertility rates shifted the model outcome noticeably, although to a lesser extent than body mass (Figure 13).

Consumption

Consumption estimates of salmonids and herring were most sensitive to estimates of proportion of prey in the diet and energy density of prey. There were seasonal differences in the relative importance of the contribution to model variance of these two variables. The contribution of energetic density and proportion of prey in diet was less in the breeding season than in the non-breeding season for salmonids. Proportion of prey in diet was also less important in the non-breeding season for herring. Variation in consumption estimates was low when the heat increment of feeding and assimilation efficiency were varied within their estimated range. The variance in the non-breeding season seen in the overall simulation

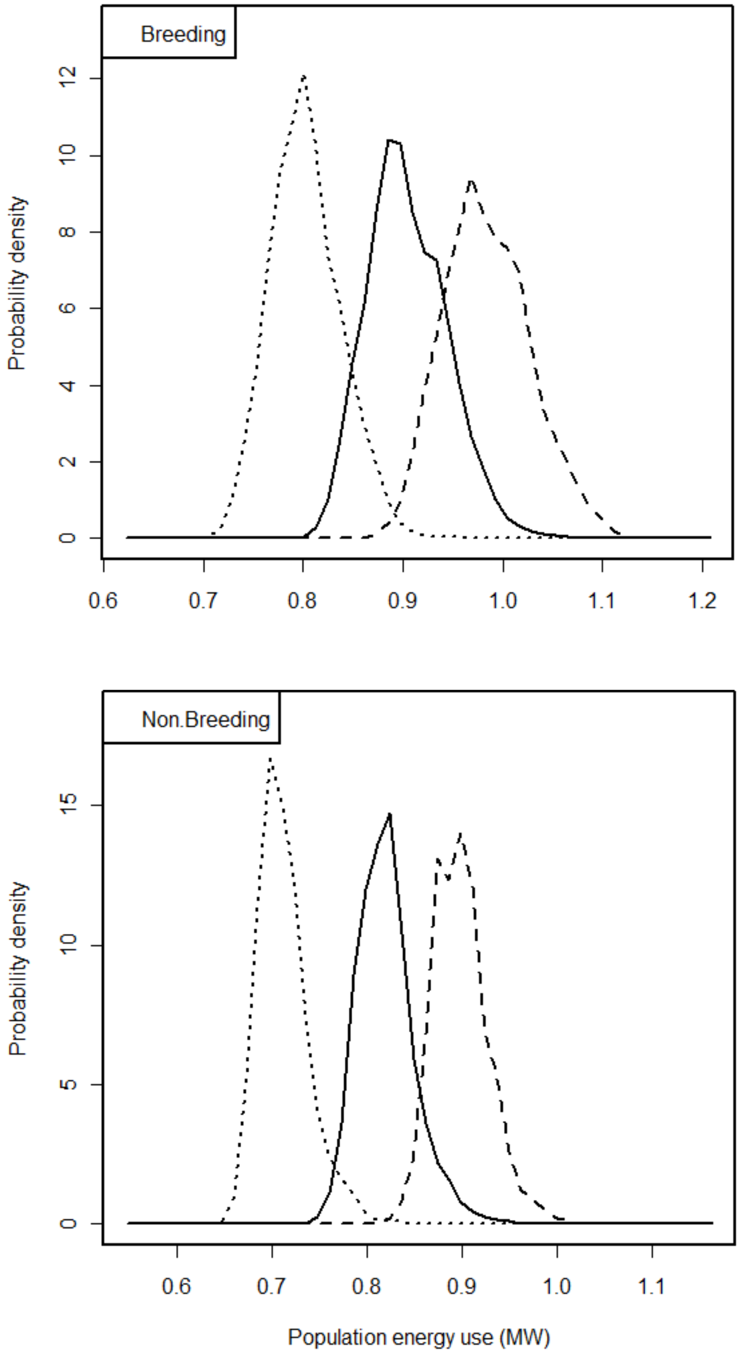

Figure 10. Influence of body mass on net population energy use relative to season. Changes in model outcome when body mass was shifted. Lines represent probability density estimates of energy use outcomes: dotted, solid, and dashed lines represent when selected variable was set at the 25th percentile, mean value, and 75th percentile, respectively.

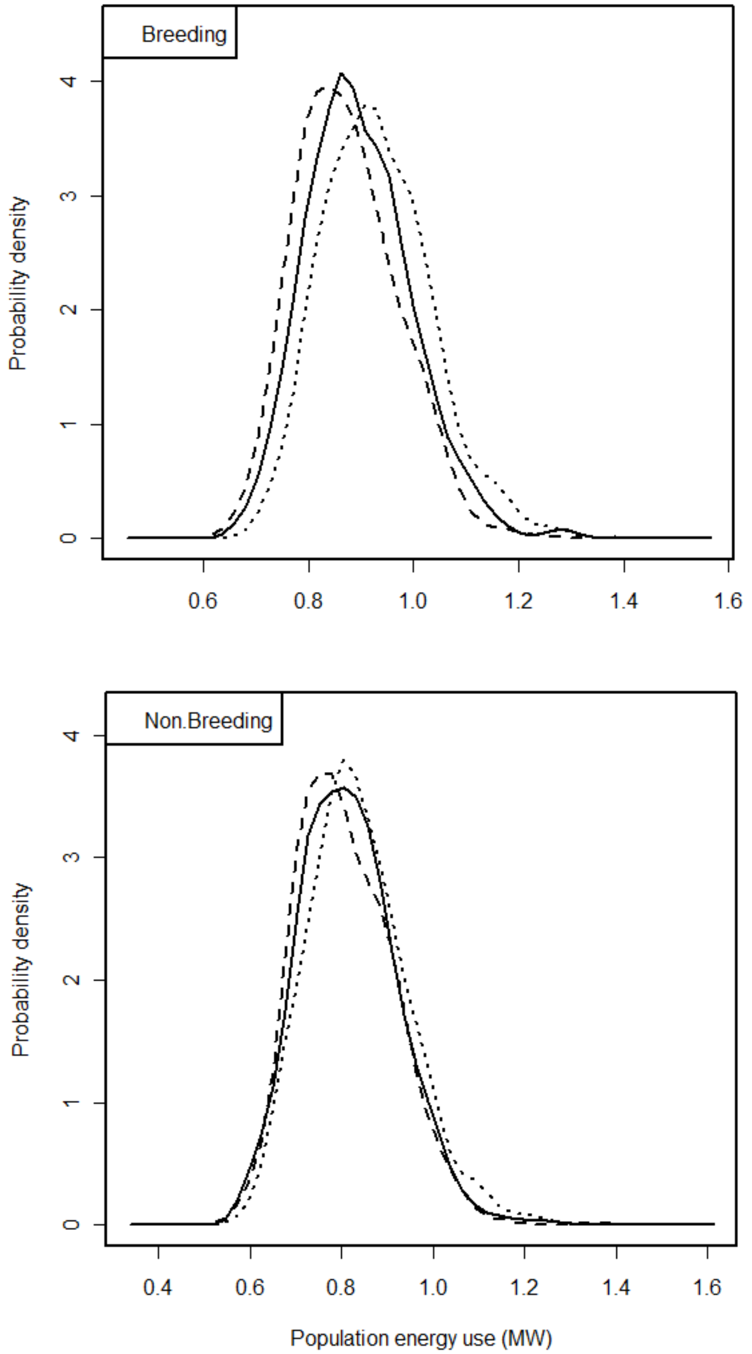

Figure 11. Influence of behavioral activity on net population energy use relative to season. Changes in model outcome when activity variables were shifted. Lines represent probability density estimates of energy use outcomes: dotted, solid, and dashed lines represent when selected variable was set at the 25th percentile, mean value, and 75th percentile, respectively. Note a shift to the left for the 75th percentile which indicates decreasing energy use.

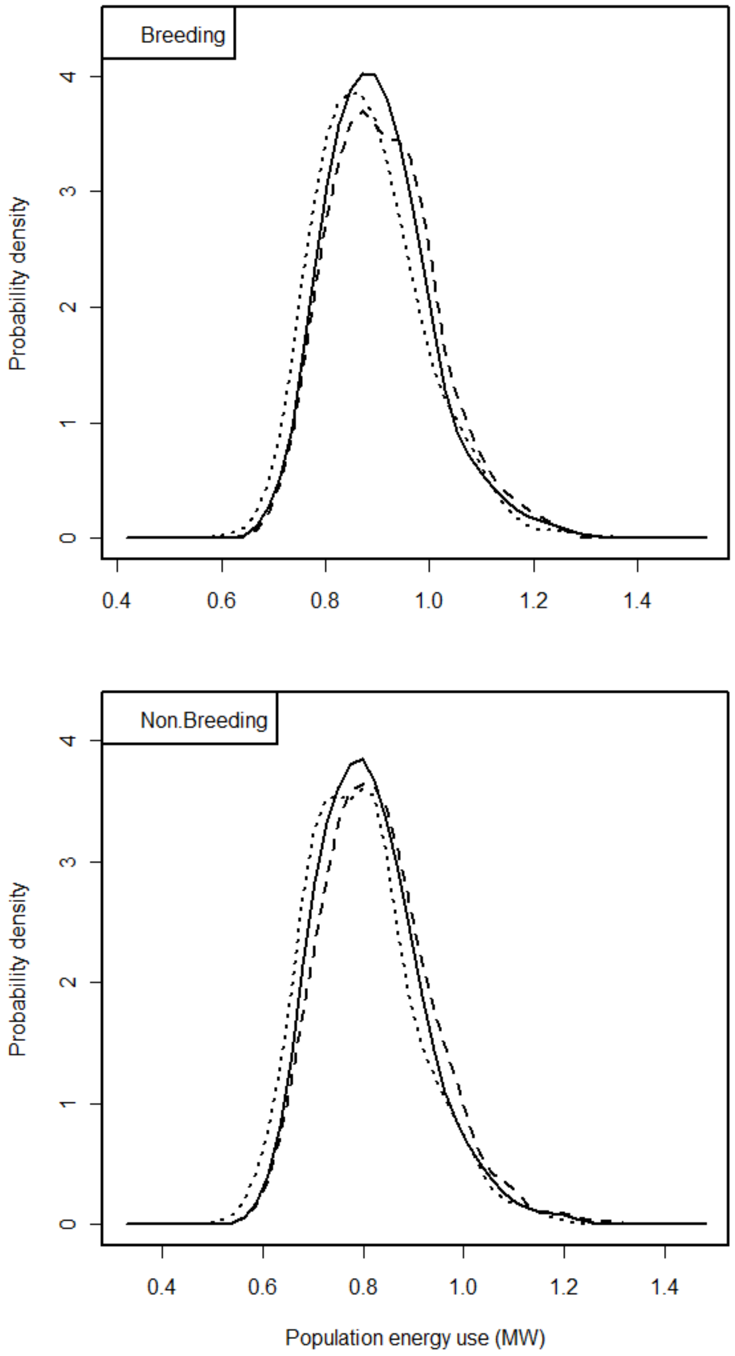

Figure 12. Influence of growth rates on net population energy use relative to season. Changes in model outcome when growth rates were shifted. Lines represent probability density estimates of energy use outcomes: dotted, solid, and dashed lines represent when selected variable was set at the 25th percentile, mean value, and 75th percentile, respectively.

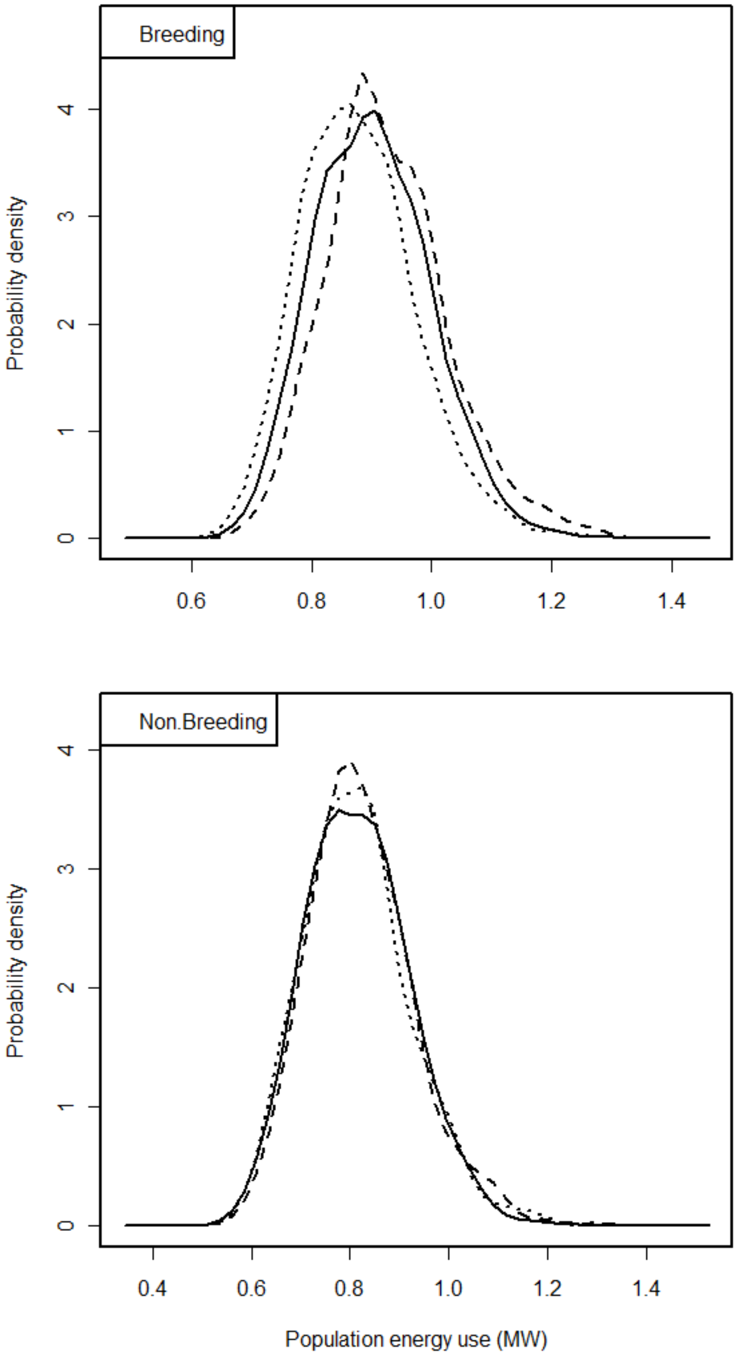

Figure 13. Influence of fertility rates on net population energy use relative to season. Changes in model outcome when fertility rates were shifted. Lines represent probability density estimates of energy use outcomes: dotted, solid, and dashed lines represent when selected variable was set at its 25th percentile, mean value, and 75th percentile, respectively.

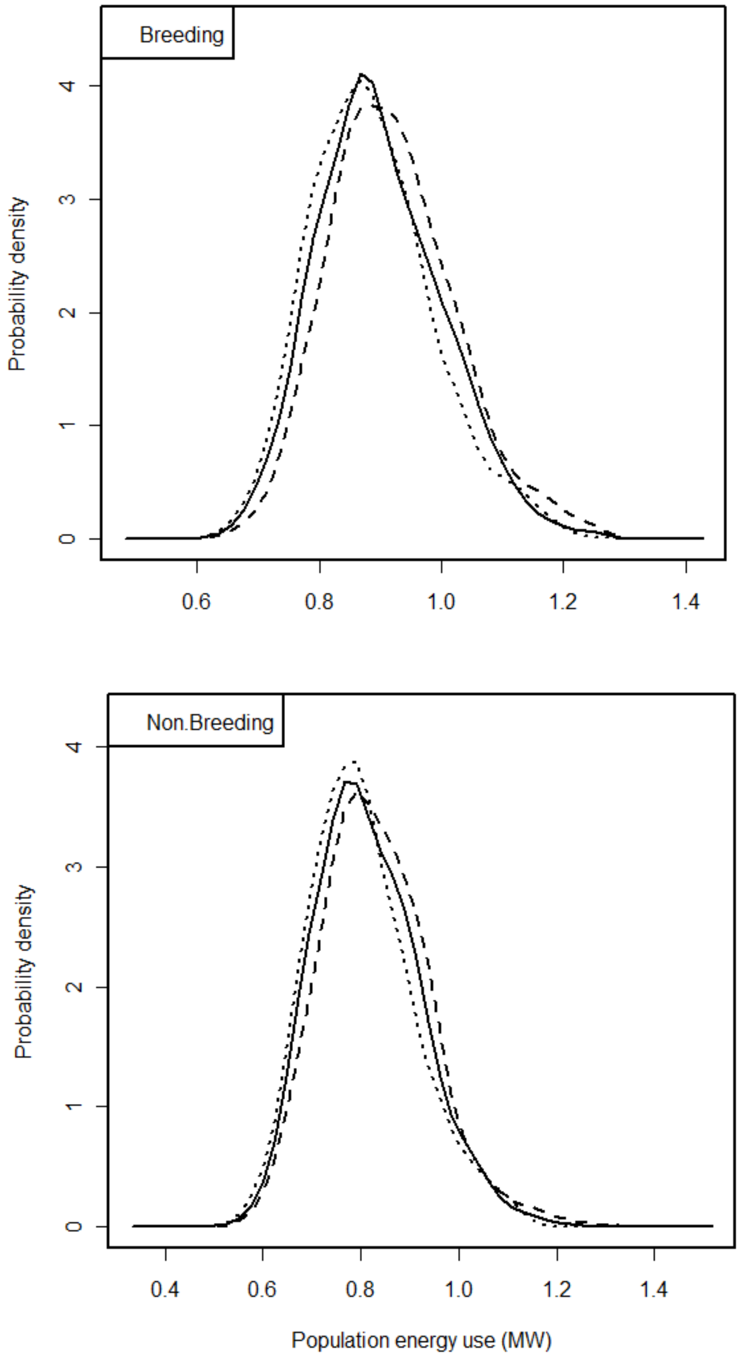

Figure 14. Influence of population size on net population energy use relative to season. Changes in model outcome when population size was shifted. Lines represent probability density estimates of energy use outcomes: solid, dashed, and dotted lines represent when selected variable was set at the 25th percentile, mean value, and 75th percentile, respectively.

model for both salmonids and herring was not well explained by any single prey variable (Figures 15-16).

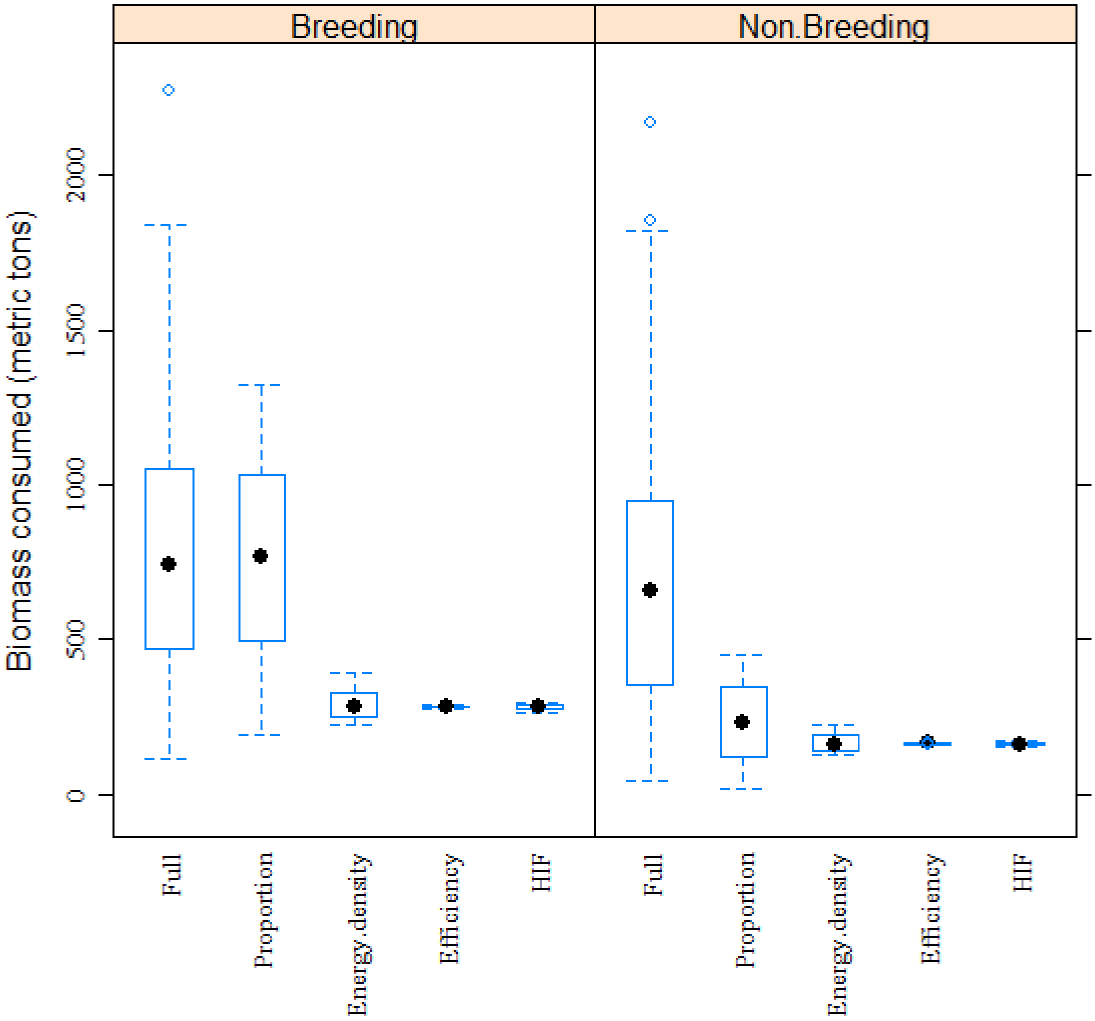

Figure 15. Effect of prey variables on salmonid consumption of harbor seals relative to season. Distribution of model outputs after running 1,000 simulations with all ("Full") or single variables selected randomly. Solid circle indicates mean, solid box encloses the interquartiles, vertical dashed lines are min and max, and open circles indicate outliers. (Note: all simulations allowed variance in seal energetic requirements.)

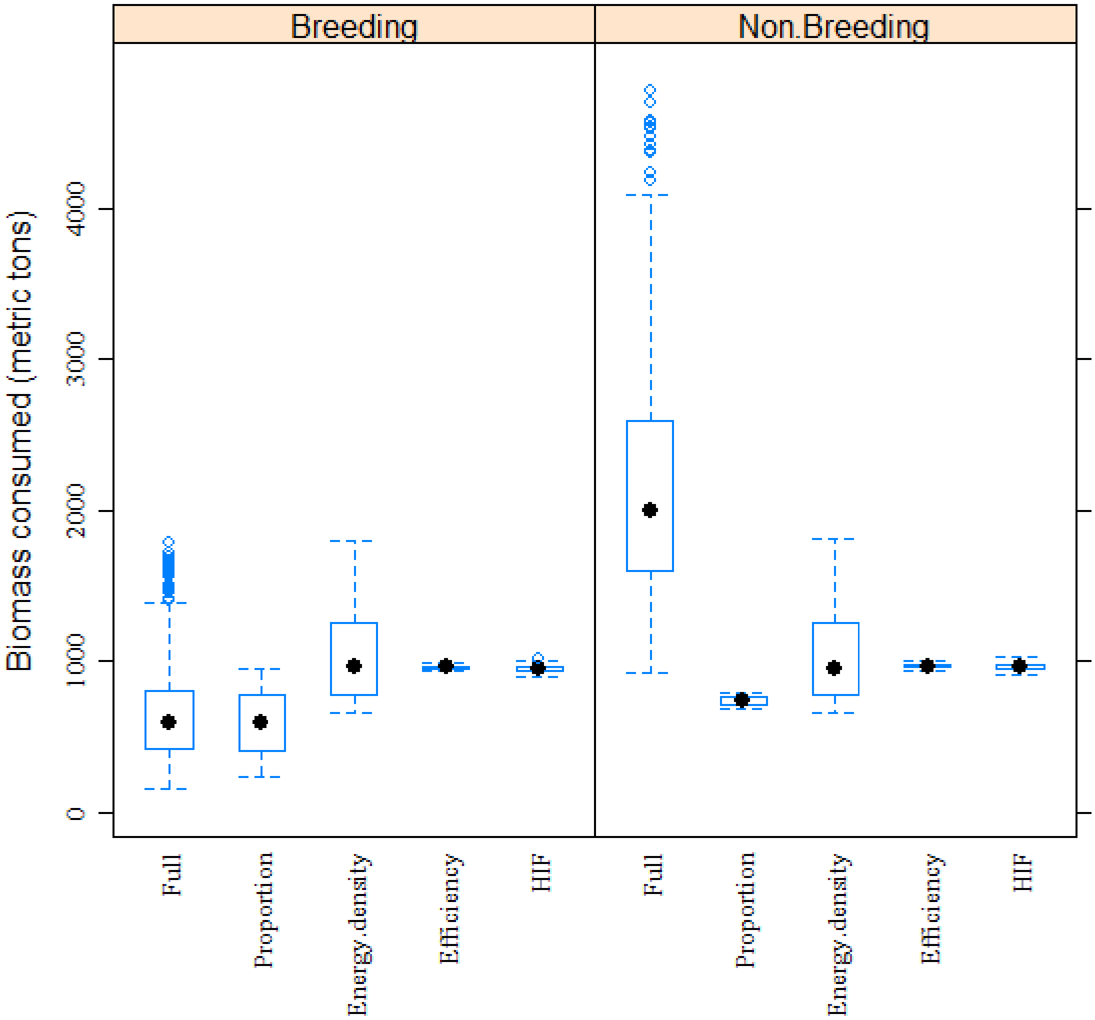

Figure 16. Effect of prey variables on herring consumption of harbor seals relative to season. Distribution of model outputs after running 1,000 simulations with all (“Full”) or single variables selected randomly. Solid circle indicates mean, solid box encloses the interquartiles, vertical dashed lines are min and max, and open circles indicate outliers. (Note: all simulations allowed variance in seal energetic requirements.)

DISCUSSION

Seasonal variation in energetic requirements and consumption

Female and male seals exhibited seasonal differences in behavior. Overall time spent at sea (diving and shallow-water activity) was almost equal between seasons for females (83% of time budget) and decreased for males in the non-breeding season from 84% to 73%. There were also seasonal differences in how seals proportioned activities within their at-sea budget. Two measures of dive effort were considered when comparing behavior between individuals and seasons: 1) absolute dive effort (proportion of time budget; high is > 60%), and 2) relative dive effort (% changes in proportion of time budget). On average, both sexes increased their dive effort in the non-breeding season and primarily spent time in shallow-water activities during the breeding season. In terms of absolute dive effort, most females exhibited low dive effort in the breeding season and high dive effort in the non-breeding season. Two females had longitudinal data, which allowed me to compare relative levels of dive effort: these also increased in the non-breeding season. On the other hand, male absolute dive effort varied greatly between individuals in the breeding season, and was generally high in the non-breeding season. I could only compare relative dive effort for one male: his dive effort actually dropped in the non-breeding season.

In general, higher dive effort was expected in the non-breeding season in the San Juan Islands, when individuals were either 1) not involved in reproductive activities, or 2) recovering from the prior or preparing for the next breeding season by diving and foraging intensively. Seasonal changes in harbor seal behavior may be driven by a variety of factors, including life history stage, prey choice, individual variation, or habitat preference (Boyd et al. 1994). Although each of these factors is predictable to some extent from year-to-year, there is also likely significant variation in the timing of each. Breeding season, for example, may extend over 3-4 months and tagged seals may have been at different stages in the breeding cycle (or not involved in breeding if immature subadults), depending on when they were captured. The molting period, another major life history stage, differs between sex and age classes (Thompson & Rothery 1987) and was observed in my study area to commence in August and last through October. Prey choices may be somewhat more predictable [for example, timing of salmonid runs (NMFS 1997)], but there may still be smaller-scale uncertainty about prey patch locations for other prey species, such as forage fish like herring. Harbor seal behavior does appear to be driven in part by prey patterns: for example, they dive deeper during the daytime in the summer when vertically migrating salmonids become abundant (Reuland 2008). The combination of all life history and prey choices should therefore predict activity budgets; it seems reasonable to expect variation between members of the population given expected differences in the timing of these activities or life history stages, as seen in this study.

Male harbor seals spend time in shallow-water behaviors during the breeding season to perform vocal displays, defend territories, and increase their chances of encountering receptive females during the late stages of lactation (Coltman et al. 1997, Van Parijs et al. 1997). Males can lose 24% of their body mass during this time period, indicating that in general, they shift attention away from foraging effort to reproductive behaviors - i.e., their total energy expenditures are not met by feeding effort (Walker & Bowen 1993). Some of the seasonal differences seen in the San Juan Islands appear to be driven by the seals' physical locations during the period of data collection, which may also be related to foraging strategy. There was a clear division between males during the breeding season: those that were captured and spent the majority of their time in rocky-reef areas exhibited high dive effort (> 60% of time budget), and the dive effort of those captured in and who favored shallow bays was much less (typically < 20% of time budget). Dive effort was high in the non-breeding season for all males, but because I lacked data on bay seals, it is difficult to assess whether they would have shifted their dive effort to the levels seen in rocky-reef seals. In addition, the division between rocky-reef and bay seals may be somewhat artificial, given that at least some males leave the bays in the non-breeding season for deeper-water areas or even the outer coast of Washington (Hardee 2008). It should also be noted that non-breeding season data for males did not always overlap in time, in contrast to the breeding season. Nevertheless, the time budgets were quite similar between individual seals.

Pregnant females haul-out frequently during the breeding season to give birth and during their 3-6 week lactation period (Bigg 1969). They also spend time diving with their pups, and likely increase dive effort soon thereafter to recover from their own loss of body mass during the breeding season (Bowen et al. 1999). It may be more important for females to forage intensively after weaning to recover their body condition (Thompson et al. 1989). Indeed, this seemed to be the case for 2 females in the San Juan Islands with longitudinal data: they both increased their dive effort by 14-20% in the non-breeding season. Female behavioral patterns were easier to discern than males due to the larger sample size; however, there was still significant inter-individual variation. Site appeared to play less of a role in predicting activity levels: females in both shallow- and deep-water areas either increased their relative dive effort from the breeding to non-breeding season, or exhibited dive effort similar to the group average in each season.

In addition to sex, age and body size also may play an important role in how seals budget their time. Due to small sample sizes, I used the same activity parameters for both subadults and adults in the prey consumption model. If it is assumed that female and male seals under 60 and 80 kg, respectively, may be subadults, there may have been 3 subadult females and 4 subadult males with activity budget data. An exploratory analysis of those data did not reveal any age-related patterns (the suspected "subadults" appeared no more similar to each other than to "adult" seals), although it should still be considered as a possibility, especially for males. Harbor seals form dominance relationships wherein larger animals have access to higher-quality haul-out sites, and subadults and pups generally spend more time in the water (Sullivan 1979). In addition, age-related differences in weight loss were seen during the breeding season in Nova Scotian harbor seals, indicating that, unlike adults, subadults continued feeding and were not involved in reproductive activities and thus may have lower energetic requirements (Walker & Bowen 1993). However, in the model, activity was less important than other factors in predicting energetic requirements and played a relatively minor role in predicting consumption.

Regardless of the drivers behind seasonal and intraspecific behavioral changes, the activity budgets used in the model provided a realistic range of possible values for harbor seal behaviors in the overall prey consumption model. Large variation between individuals may be the most realistic version of the harbor seal population, and the model structure used was able to incorporate this uncertainty (variation). Further, I purposely wanted to capture the potential range of behaviors between seals, regardless of site or other differences, so that the model reflected behaviors of both bay and rocky-reef seals, which are both present in the study area.

The metabolic rates calculated by the model can be considered a proxy for FMR, and can be compared to empirically measured-FMR to assess their accuracy. FMR has been measured in Nova Scotia's harbor seals over a one-month period during the breeding season for males and over the lactation period for females, using singly-labeled water and proximate body composition methods (Bowen et al. 1992, Coltman et al. 1998). The rates predicted by this study were approximately 20% and 120% lower for females and males, respectively, than these empirical measurements. Some of the differences could be attributed to size: harbor seals in these studies were 20-30 kg larger than harbor seals in the San Juan Islands. In addition, I predicted metabolic rate over the entire 3-month breeding season, in which the higher rates seen in Nova Scotia's seals may be balanced by reduced energy use after individual seals mate and return to regular foraging activities. The difference in rates for males may be partially explained by the fact that I was unable to measure the cost of aggressive behaviors to adult males: if these were frequently performed at or near the water's surface, they may be more energetically expensive than I accounted for. The shallow-water activity rates used in the model assumed that the seal is for the most part quiescent, which would underestimate energy use if they were in fact more active while near the water's surface. Finally, for females, lactation costs were applied after metabolic rates were calculated; therefore, the FMR-proxy actually amortized the cost of lactation over the entire female population, which would lower the overall per capita metabolic rate. Unfortunately FMR has not been measured in the non-breeding season for free-living harbor seals, precluding any direct comparisons. However, Markussen (1990) calculated an average daily metabolic rate for captive harbor seals (average weight of 38 kg) comparable to the subadult rate calculated in this study: 120 watts.

This study highlighted potential differences in consumption rates between sex and age classes in the harbor seal population: predicted fish requirements ranged from 1.0 - 2.9 kg day^{-1} $seal^{-1}$, and were highest for adult females. The highest seasonal per capita consumption was predicted in the breeding season due to the higher overall cost of shallow-water and breeding activities than diving effort, although this will depend on the timing of foraging between the sex and age classes in the population. These seasonal changes in energetic requirements in the harbor seal population can help pinpoint times in the year at which prey may be at a relatively greater risk of predation, rather than assuming equal risk throughout the year.

In species that utilize fat stores during fasting periods, such as harbor seals, inferring consumption directly from energetic requirements may be somewhat misleading. The timing of feeding may occur before the predicted energetic requirements occur (e.g., increased feeding rates to build fat stores prior to the breeding season). However, harbor seals fast or reduce feeding rates for only 2-4 weeks before resuming foraging. Therefore, their consumption may occur relatively close in time to the predicted energetic requirement, and may also fall within what was designated in this study as the breeding season. In addition, there are seasonal changes in energy intake that occur in harbor seals and other pinnipeds

(Schusterman & Gentry 1971, Rosen & Renouf 1998). Therefore, seasonal consumption estimates should be interpreted with caution until they can be confirmed with additional or alternate confirmation of the correspondence between energy requirements and food intake. Nevertheless, because these seasonal changes balance on an annual scale, annual consumption estimates provide a reliable measure of food intake of individuals in the harbor seal population.

Model sensitivity

Activity levels of free-living pinnipeds have been significant sources of uncertainty in previous prey consumption models (Lavigne et al. 1985, Hammill et al. 1997, Stenson et al. 1997, Winship et al. 2002). To address this uncertainty, I used activity budget data to build a model that predicted metabolic rates based on time budgets applied to predicted costs of activities. I varied the time spent in various activities based on data from free-living seals, rather than considering activity to be a separate component of the energy budget and varying the predicted cost of all activity, as in previous models. This study indicated that activity levels are naturally quite variable in a free-living pinniped population and thus wide confidence intervals may be a realistic input into models. Model variables can be parameterized with wide confidence intervals for two reasons: sources of uncertainty can be due to either data-poor situations or simply because the population exhibits large variation. Even when activity levels are measured from free-living animals, as they were in this study, intra-individual variation was still quite high. However, although activity levels were still a significant source of variation, they only ranked 4th (out of 5 variables) in contribution to model variance. Despite significant variation in activity levels, and the fact that in the model varying these activity levels translated to varying the cost of behaviors two-fold (i.e., shallow-water activity was approximately 2x greater cost than hauling-out), activity was a relatively minor factor in predicting overall consumption.

The prey consumption model was quite sensitive to body mass: when body mass was varied ± 10% around the average, there was a corresponding ± 10% change in the energy use outcome. Body mass controls many physiological functions in organisms, and because mass-based predictive relationships were used for metabolic rate, the model's sensitivity to body mass was not entirely unexpected. By simply accounting for body size and number of harbor seals, the model captured the bulk of energy use in the population. In fact, omitting reproduction costs (lactation and gestation costs) did not affect non-breeding season energy use estimates and lowered breeding season estimates by approximately 10%. By omitting these costs, energy use was roughly equal between seasons. Activity levels were the other variable that changed seasonally: the fact that energy use was equal between seasons by simply omitting reproductive costs confirms the idea that activity levels contributed relatively little to overall energy use calculations. However, there may have been other energy costs that could affect population-level energy use that were not accounted for, including aggressive behaviors in males or the cost of molting in harbor seals. Unless these expenditures are very large, it seems unlikely that including them would significantly change the total population energy use. Further, other consumption models have also pinpointed maintenance requirements and activity costs (comparable to the FMR-proxy rates calculated in this study) as constituting the bulk of energy requirements in harbor seal populations (Härkönen & Heide-Jørgensen 1991, Olesiuk 1993).

As a group, bioenergetics variables contributed most to sensitivity in energy requirement calculations, similar to other pinniped consumption models (Mecenero et al. 2006, Chassot et al. 2009). When the full consumption model was examined, the assumed proportion of each prey species in the diet had the largest effect on consumption outputs, also similar to other pinniped consumption models (Mohn & Bowen 1996, Shelton et al. 1997, Mecenero et al. 2006, Overholtz & Link 2007), suggesting that future effort should be focused on refining the contribution of different prey to harbor seal diet. Genetic and molecular techniques are increasingly being used to identify diet composition, although they also have their own set of assumptions (Casper et al. 2007, Deagle & Tollit 2007). Combining these techniques with scat (hard parts) analysis is likely necessary to evaluate the diet of generalist marine predators, given that they often yield different results and can answer different questions (Tollit et al. 2006). The approach I used took into account prey size, which I felt was necessary to evaluate the diet in energetic terms. Further work, including stable isotope and fatty acid analysis, should yield data to test the assumptions about the relative importance of salmonids and herring compared to other species in harbor seal diet.

Other prey consumption models have identified population variables (offspring production, mortality rates) as those with the strongest effects, in part because they influenced the prediction of population size (Mohn & Bowen 1996, Boyd 2002). I only addressed intraannual error in population size (e.g., range of estimates made in 2007 for population size) which in general was much smaller than the interannual variation used in other models. This model could be extended to incorporate interannual uncertainty in harbor seal population size, which could help ascertain how consumption may vary in subsequent years. Because consumption was for the most part proportional to the biomass of the seal population, the 2.3% decrease in population estimates from 2007 to 2008 would correspond to a roughly equal percent decrease in estimated consumption. This prediction assumes that all other model variables were similar between years, which seems reasonable given the similarity in population sizes. Nevertheless, at dramatically different population sizes, there may be different behavioral or population changes that would need to be taken into account (for instance, individual prey preferences, intraspecific competition, fertility rates, mortality rates) to predict population consumption.

In contrast to the other population variables, only point estimates were used for mortality rates. The age structure of the harbor seal population calculated in this study was heavily dominated by subadults (roughly 80% of the population) and the population structure was based on data from a time period when the harbor seal population was depressed in size. If the increase in population size since the 1970s has led to decreased juvenile survival rates, as is predicted to be the case for marine mammals, then future models may need to incorporate a more recently derived age structure to assess how this affects population consumption (Fowler 1981, Hiby & Harwood 1985).

Implications for prey populations

Harbor seal population consumption estimates for rockfish species, a group of species of concern in the Puget Sound Georgia Basin, constituted a relatively minor proportion of total consumption by harbor seals. There are over 26 species of rockfish that occur in the inland waters of Washington State, with many listed as state-endangered. The two most dominant species, copper (*Sebastes caurinus*) and quillback rockfish (*Sebastes maliger*), for which abundance data are best documented, have both undergone serious declines and are now being considered for federal threatened and endangered status in the southern portion of Puget Sound (Mills & Rawson 2004, Puget Sound Action Team 2007). For depressed species such as these, even small amounts of predation may be significant. If we assume an average size of 1 kg for a rockfish in harbor seal diet (ignoring age- or species-size differences), then harbor seals hypothetically consumed 84,000 rockfish individuals in 2007 in the San Juan Islands and eastern bays. However, to illustrate the importance of age or species preference by harbor seals, if we assume that harbor seals eat only Puget Sound rockfish (the smallest of the rockfish at ca. 40 g), then they could have consumed over 2 million individuals, a number that presumably can impact the rockfish population. It seems clear that prey that constitute even a minor proportion of harbor seal diet may be affected by predation, if such predation increases their natural mortality rates.

Overall, this study suggested a strong potential for harbor seals to affect their prey if they focus their predation in either small areas or on depressed fish species that are low in numbers. Despite the very low frequency with which prey like rockfish occur in harbor seal diet, this source of mortality may still be significant. Salmonids and herring are currently the major prey items for harbor seals; however, other prey that are consumed less frequently may still be impacted. If rockfish recover, harbor seals may also respond by increasing their predation rates of rockfish due to the increased availability of prey. Consumption rates calculated by this model can be compared to current estimates and future projections of rockfish population sizes to measure the possible contribution of harbor seal predation to rockfish mortality rates.

This study emphasized the importance of herring and salmonids to the harbor seal population, and quantified important predator-prey links between harbor seals and the prey upon which they heavily depend. These prey items also form a critical component of the diet of a wide variety of terrestrial and marine predators, including sea lions, whales, bears, and predatory fish (Gende et al. 2001, Lindstrøm et al. 2002, Gende & Sigler 2006, Overholtz & Link 2007). Harbor seal consumption of other species may depend in part on the availability of these two prey items. Harbor seals consume seasonally abundant prey and diversify their diet in the winter, when adult salmonids decrease in abundance (Lance & Jeffries 2007). Therefore, any future changes in herring and salmonid stock sizes has the potential to affect harbor seals, and would theoretically increase predation rates on other species. Future models could test these assumptions by using the consumption levels documented in this study and comparing them to availability of preferred and alternate prey.

Incorporating variation in all model variables to calculate consumption rates was essential to defining realistic lower and upper limits of harbor seal consumption rates. Even at the lower limits of consumption rates, harbor seals consumed large amounts of salmonids and herring, two prey groups that are also of great importance both to the Puget Sound

Georgia Basin food web and to recreational and commercial fishing. Many herring stocks in Puget Sound have undergone critical declines, and there is concern that pinniped predation may have increased the natural mortality rate of herring in some areas (Musick et al. 2000, Stick et al. 2005, Puget Sound Action Team 2007), although it is acknowledged that there are likely many factors that contributed to the decline of herring (Puget Sound Action Team 2007). If herring continues to decline, harbor seals may either respond by increasing their predation rates of other species, or alternatively, may continue to prefer herring regardless of their abundance (Luxa 2008, Reuland 2008). Thus, changes in the herring population may have wide-reaching consequences for both harbor seals and their prey. Similar to herring, salmon populations have undergone serious declines in Puget Sound, with several stocks federally or state-listed as threatened, critical, or depressed (Puget Sound Action Team 2007), and there is also concern that pinnipeds may affect salmon recovery (NMFS 1997, London et al. 2001). Thus, further efforts to understand and model how harbor seals interact with their prey, particularly depressed fish species, merits further attention to examine what proportion of natural mortality may be caused by harbor seals.

The model's predicted per capita fish consumption (key species plus a generic "other prey" category) of 2.1 kg day^{-1} seal^{-1} (annual average 2.9, 2.8, 2.0, 2.2, and 1.0 kg for adult females, adult males, subadult females, subadult males and pups, respectively) fell within the range estimated for the British Columbian and Norwegian harbor seal populations: 1.9 kg and 4 kg, respectively (Härkönen & Heide-Jørgensen 1991, Olesiuk 1993, Bjørge et al. 2002). The average body mass in the model was 50 kg, which was equivalent to a per capita consumption of approximately 4% of seal body weight day^{-1}, although it should be noted that

% body weight estimates are unreliable because they ignore energetic density of prey items. This study highlighted the differences in consumption between sex and age classes: notably, adult females consumed similar (or greater in the breeding season) per capita amounts as adult males, despite their smaller body size, due to lactation costs. Subadult males consumed approximately 20% less than their adult counterparts, despite weighing roughly 33% less, which was attributed to the allometric scaling of energetic requirements to body size (Schmidt-Nielsen 1984). Subadult females, however, weighed roughly 33% less than their adult counterparts and also consumed 33% less, most likely because the cost of lactation was amortized over all females. At the population level, adult males consumed the smallest amount, mostly due to their small numbers in the population. Subadults were numerically dominant and thus consumed the greatest proportion of biomass, while adult females fell in between adult males and subadults. Thus, larger body size alone did not always equal greater consumption rates when the population was considered as a whole unit.

Such sex- and age-related differences in consumption rates may play an important role in predicting predator-prey interactions. Further modeling of these interactions should take into account potential differences in the population’s behavior, as impacts on prey may differ greatly if the sex and age classes prefer different prey (i.e., have different foraging strategies) or consume prey at different rates during the year. If harbor seals prepare for the breeding season earlier in the year by increasing their consumption rates, the risk of predation for prey may also be higher at those times. These ranges in consumption rates can inform conservation managers of the potential for harbor seals to impact their prey, which can then taken into account along with other important factors that may affect recovering depressed fish stocks in the San Juan Islands.

Conclusions

Harbor seals are a large-bodied and abundant predator in the San Juan Islands and adjacent eastern bays region of the Puget Sound Georgia Basin and may impact the success of marine protected areas by preying on recovering fish species. Thus, there is a need to understand the energetic and prey requirements of predators such as harbor seals which consume these fish species. In the prey consumption model, there was seasonal variation in energetic requirements: reproductive costs drove higher overall population energy costs in the breeding season. The highest seasonal consumption was predicted in the breeding season, suggesting that impacts on prey may differ seasonally. Adult females had the highest consumption rates of any sex and age class in the population, due to the cost of lactation. Further exploration of the foraging strategies employed by different sex and age classes in the harbor seal population in different seasons should help predict times of intensive foraging by harbor seals, and conversely, identify times of the year when seals are possibly at a greater risk of depleting their energy stores, and thus are more heavily influenced by their prey.

The prey consumption model was most sensitive to the input values of seal body mass and to the estimated proportion of prey species in the diet, suggesting that these two factors were responsible for most of the variation in consumption estimates. Body size of seals was a more powerful predictor than any other model variable. Future diet studies that use genetic and molecular techniques could help refine estimates of the proportion of prey in diet (Deagle & Tollit 2007), and increase the accuracy of consumption estimates.

The harbor seal population in the San Juan Islands and eastern bays region seems to have stabilized in numbers after a period of population recovery since the 1970s, and thus consumption rates have likely also been more or less stable in recent years. Nevertheless, research at smaller spatial scales can help clarify how harbor seal foraging effort is distributed over this area and predict areas of greater potential impact by harbor seals. While only considered a minor portion of harbor seal diet, prey groups such as rockfish may still be impacted by even low levels of predation, which will be dependent on the life-history strategy of each prey species. Harbor seals heavily depend on salmonids and herring, which were the two most energetically important prey groups in terms of biomass consumed for harbor seals during both the breeding and non-breeding seasons. Therefore, harbor seals may have the potential to impede the recovery of other fish species and stocks of concern, especially if they focus their predation in small areas or specialize on these prey (Middlemas et al. 2006, Williams et al. 2007, Wright et al. 2007). Future models that incorporate prey demographics, other important fish predators, and the response of harbor seals to different levels of prey abundance should further inform managers of the potential for harbor seals to impact the recovery of fish stocks.

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