AN ABSTRACT OF THE THESIS OF

<u>Sheanna M. Steingass</u> for the degree of <u>Master of Science</u> in <u>Wildlife Science</u> presented on <u>March 7, 2014</u>.

Title: Foraging Behavior of the Pacific Harbor Seal (*Phoca vitulina richardii*) in the Pacific Northwest and Potential Impacts of Coastal Hypoxia on Foraging Efficiency.

Abstract approved:

Markus Horning

In the last decade, the California Current Large Marine Ecosystem (CCLME) has experienced a trend of increased severity of upwelling-driven coastal hypoxia. This thesis strove to examine the potential upper trophic level impacts of moderate and severe hypoxia in the CCLME. Initially I conducted a literature review of Pacific harbor seal (*Phoca vitulina richardii*) diet in the regions of Oregon and Washington. Thirteen papers were reviewed which detailed harbor seal foraging studies in Washington, Oregon and the Columbia River from 1931 until 2012. Throughout this region, 148 prey species or genera were described in harbor seal diet. Accordingly, I created energetic individual-based models of harbor seal spatial foraging behavior in response to hypoxia-related habitat compression for three predominant prey species, Pacific herring (*Clupea pallasii*), English sole (*Parophyrs vetulus*) and Pacific sandlance (*Ammodytes hexapterus*). The model was composed of three submodels which simulated hypoxia and spatial foraging, foraging energetics, and dive mechanics. Hypoxia was scaled from 0 to a level of 1, which represented a severe inner-shelf hypoxic or anoxic event in which up to 80% of the inner shelf water column was hypoxic, and species lost 50% of their horizontal habitat. Response variables were also evaluated at the intermediate hypoxia levels of 0.25 and 0.75.

A sensitivity analysis was conducted to illuminate which predictor variables drove a variety of response variables. Hypoxia strongly drove energetic balance, travel cost to foraging locations and time spent foraging at depth for all three prey species. Caloric content of prey, as parameterized, did not contribute significantly to model output. For smaller harbor seals, energetic gains were maximized by foraging on Pacific herring or sandlance during normoxia, and sandlance during severe hypoxia. Larger adult harbor seals benefitted most from a herring- or sole-based diet during normoxia, herring and sandlance during moderate to severe hypoxia. The results suggest that shifts in spatial foraging behaviors during hypoxia may be readily apparent upon spatial analysis of behavioral telemetry data. The information gathered in this thesis will be used in the experimental design of a field-based study of the effects of coastal hypoxia on harbor seal foraging behavior. © Copyright by Sheanna M. Steingass

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Foraging Behavior of the Pacific Harbor Seal (*Phoca vitulina richardii*) in the Pacific Northwest and Potential Impacts of Coastal Hypoxia on Foraging Efficiency.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Sheanna M. Steingass, Author

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FORAGING BEHAVIOR OF THE PACIFIC HARBOR SEAL (*PHOCA VITULINA RICHARDII*) IN THE PACIFIC NORTHWEST AND POTENTIAL IMPACTS OF COASTAL HYPOXIA ON FORAGING EFFICIENCY.

CHAPTER 1: INTRODUCTION

Harbor Seal Distribution and Evolution

Harbor seals (*Phoca vitulina*) are found on coastlines throughout the northern hemisphere from latitudes 30°N to as far as 85° N (Courbis 2009), making them one of the most widely distributed pinniped species. There are five global subspecies identified by geographic range as described by Scheffer (1958): Eastern Atlantic harbor seals (*P. vitulina vitulina*) (Linnaeus, 1758); Western Atlantic harbor seals (*P. vitulina vitulina*) (Linnaeus, 1758); Western Atlantic harbor seals (*P. vitulina vitulina*) (Eastern Pacific harbor seals (*P. vitulina richardii*) (Gray 1984); Western Pacific harbor seals (*P. vitulina stejnegeri*) (Allen, 1902); and Ungava seals (*P. vitulina mellonae*), (Doutt, 1942).

All five subspecies are opportunistic marine predators (Scheffer 1958) which are particularly philopatric, or loyal to their haul-out sites. Evaluation of mitochondrial differentiation in harbor seals from the Pacific and Atlantic oceans suggest that harbor seals appear to be spatially predictable on the scale of several hundred kilometers (Stanley et al. 1996). As a result of this strong site fidelity, harbor seals between haul-out locations display notable genetic differentiation (Stanley et al. 1996, Burg et al. 1999).

Harbor seal life history

Harbor seals are one of the smallest phocids, and as a result share life history characteristics with other phocids as well as otariids. For instance, harbor seals employ a mixed-strategy reproductive method, displaying weaning tactics somewhat intermediary between strictly capital-breeding (maternal fasting during nursing) phocids and income-breeding (foraging during nursing) otariids (Boyd 2000, Stephens et al. 2009). Harbor seal pups are generally born relatively precocial and able to swim (Bigg 1981). Examinations of the foraging behaviors of nursing harbor seal mothers and pups found that mothers forage primarily alone until the mid-late lactation period, although mothers and pups were noted as foraging together as early as zero to three (0-3) days postpartum (Lawson and Renouf 1985, Bowen et al. 1999). Lactation period varies among females and years but is generally between two to six weeks (Bigg 1981). The nursing stage is the only stage in the harbor seal's life where it shows strong interaction and bond with other individuals, as harbor seals are not especially social as adults. Despite hauling out together, very little interaction occurs besides agonistic behaviors to maintain individual distance (Sullivan 1982), although these behaviors do not have a strongly hierarchical organization as in otariids (Bigg 1981).

The harbor seal reproductive cycle is largely annual. After lactation, ovulation and mating take place, followed by a delayed implantation period of one to three months, and a gestation of 9 to 11 months (Bigg 1981). Harbor seal reproductive timing varies between subspecies and populations but is synchronous within populations (Courbis 2009); for harbor seals on the Oregon coast, pupping season is primarily in the spring months of March through June, when the largest numbers of animals can be found in protected bays and shorelines (Harvey 1987). The body mass of adult male Pacific harbor seals averages around 73 kilograms, while adult females tend to be about 25% lighter at 58.5 kilograms (Scheffer and Slipp 1944). This is variable between individuals and on a seasonal basis; the numbers previously stated were for individuals measured in Washington State around the calendar year. The largest male measured by Scheffer and Slipp (1944) was 116 kg. The heaviest female recorded, was pregnant at the time and weighed 110 kg. The average length of 5 measured adult harbor seal males was 154 cm, and the average of 37 females was 142 cm. Pacific harbor seal pups weigh 10 kg upon birth, and after the period of weaning (usually 4 to 6 weeks), weigh approximately 24 kg (King 1964, Bigg 1969).

Harbor Seal Behavioral Ecology

As homeotherms utilizing an aquatic environment, harbor seals and other marine mammals are uniquely constrained in a number of physiological processes including thermoregulation, reproduction, foraging ecology and dive capacity (Kooyman et al. 1981, Rosen et al. 2007, Womble 2012). For pinnipeds in particular, dive capacity is scaled to metabolic rate, suggesting that deeper-diving animals can be constrained by their aerobic capacities as breath holders (Boyd and Croxall 1996). The point in dive duration at which a primarily aerobic diving animal begins to accumulate lactic acid is known as aerobic dive limit (ADL) (Kooyman et al. 1980, Horning 2012). Most pinniped species, including harbor seals, tend to remain within their predicted ADL during foraging, with few dives exceeding this threshold (Feldkamp et al. 1989, Kooyman 1989, Boyd and Croxall 1996).

Metabolic rate and available oxygen stores of diving mammals have been shown to scale to body mass (Kooyman et al. 1981, Horning 2012), and ultimately define the diving behaviors and abilities in harbor seals and other marine mammals. A study of nursing harbor seal pups by Jorgenson et al. (2001) confirmed that as pups grew and matured, key components of dive capacity such as dive depth, duration, and bottom time increased significantly. As a result of reduced dive capacity, young harbor seals often forage on benthic invertebrates found further inshore than the pelagic and benthic prey favored by adults (Scheffer 1958). Similarly, Kooyman et al. (1983) noted that juvenile Weddell seals had a reduced dive capacity as compared to adult seals, but also rarely performed anaerobic dive. The authors concluded that body size and age were significantly limiting for diving capacity.

Harbor seal foraging tactics are opportunistic, with diets that largely reflect the prey distribution and bathymetry of their environment (Sergeant 1951). For instance, studies of dietary contents from seals in The Wash and Blakeney Coast of Norfolk, of two proximate foraging locations in the United Kingdom showed that harbor seal diet closely reflected available local natural resources. In The Wash, where common whelks (*Buccinum undatum*) were prominent within the ecosystem, harbor seal stomach contents were disproportionately represented by whelk opercula; whereas

seals from Blakeney fed primarily on flatfish with no evidence of whelk consumption (Hall et al. 1998). Similar dietary studies (Brown and Mate 1983, Courbis 2009, Grigg et al. 2009, Gibble 2011) have also demonstrated that harbor seal diet is largely variable and opportunistic based on individual foraging tactics and patchy distribution of prey resources (Sharples et al. 2012, Womble 2012).

Despite wide-ranging distributions, all five subspecies of harbor seals display similarities in spatial foraging habits, dietary variability, and habitat use. This review highlights the regional similarities and differences in harbor seal foraging behaviors in a way that makes it more evident which traits are highly universal within species, and which vary highly according to region. Many studies have found that although strong haulout fidelity results in apparent regional differences between harbor seal populations, inter-individual variation is also very high, suggesting that foraging is a highly learned behavior as in other marine mammal species.

Harbor Seal Foraging Behavior

As noted in the introduction, harbor seals are particularly versatile foragers, often using whichever resource is readily available (Stanley and Shaffer 1995, Orr et al. 2004, Wright et al. 2007). However, many of their prey items can be categorized into basic groupings of benthic, epibenthic, schooling, and pelagic species (Brown and Mate 1983). Additionally, even though their diet is largely variable, it can still be somewhat predictable as certain species tend to make up a large component of

individual diet. A literature review of quantitative harbor seal prey species revealed that there are at least 148 species or genera in the northern CCLME that can be identified as harbor seal prey (Sperry 1931, Everitt et al. 1981, Graybill 1981a, Brown and Mate 1983, Roffe and Mate 1984, Beach et al. 1985, Browne et al. 2002, Orr et al. 2004, Lance and Jeffries 2007, Wright et al. 2007, Lance and Jeffries 2009, Thomas et al. 2011, Lance et al. 2012).

Harbor Seal Dive Behavior and Physiology

Harbor seals are one of the smallest pinniped species, and as such they tend to dive more shallowly and nearshore than their Otariid counterparts in the northern CCLME (Schreer and Kovacs 1997). Tollit et al. (1998) concluded that the choice of optimal dive depth (and therefore realized dive depth in the field) for harbor seals depends on four major factors: (1) local bathymetric conditions, (2) the ability to maximize the proportion of dive time spent foraging, (3) the availability of prey geographically and spatially in the water column, and (4) the cost and benefits of feeding on different species.

Eguchi and Harvey (2005) conducted a study of harbor seal dive behaviors in Monterey Bay, California. Sixteen individual seals were analyzed over a course of 13,063 dives, which were then divided into five subsequent types, as described by Schreer and Testa (1996) for Weddell seals. Eguchi and Harvey found that dive depth was significantly correlated with body mass of the seal, and the median dive depths for males was 5-100 meters for males, and 5-86 meters for females. Similarly, the median dive duration for males was 2.5-8.5 minutes for males and 2.75-7.25 minutes for females. The greatest dive duration, although highly atypical, was 35.25 minutes. They also found that as productivity in Monterey Bay increased, harbor seals appeared to switch from a mostly benthic to pelagic-based diet, indicating that harbor seals are in fact opportunistic foragers.

Womble (2012) conducted similar studies of harbor seal foraging behaviors in Glacier Bay, Alaska. Her analysis included 572,106 dive records from 25 female harbor seals. Although a completely different ecological system was being studied, her calculated mean dive duration was similar to Eguchi and Harvey's findings at 2.8 ± 0.5 minutes. The maximum dive time measured in her study was 17.7 minutes, which exceeds the 8.9 minute theoretical aerobic dive limit (ADL) of an adult female harbor seal established by Bowen et al. (1999).

Harbor seals in Oregon State

Harbor seals are abundant along the Oregon and Washington coasts, being found in most estuaries and bays, as well as rocky areas. They also commonly travel up rivers to feed on salmon and other seasonally-abundant resources (Roffe and Mate 1984, Orr et al. 2004). Harbor seals population numbers have grown greatly since the institution of the Marine Mammal Protection Act (MMPA) of 1972. Population estimates taken in 1967 and 1968 revealed approximately 500 individuals along the entirety of the Oregon coast (Pearson and Verts 1970). This small number was largely due to the bounty placed upon harbor seals by the state, which encouraged harvesting of animals that were seen as 'pests' to fisheries. The \$5-25 bounty payment resulted in hundreds of animals being harvested annually in the 1930's and 40's, until that number dropped drastically in the 1960's. Shortly thereafter, the MMPA was enacted. Harvey et al. (1990) conducted a harbor seal census in Oregon from 1975-1983 and observed seals at 32 haulout locations throughout the Oregon coast. A notable difference, the Cape Arago site alone hosted more than 985 individuals, with the total count at 28 sites being 3,419 individuals. A more recent stock assessment by Brown et al. (2005) estimated 10,087 (95% CI: 8,445-12,046) individuals inhabiting the Oregon coast during the 2002 reproductive year, which the authors estimate as within the range of carrying capacity. Although aerial and visual surveys can be subject to errors of detection probability (Huber et al. 2001, Brown et al. 2005b), a general population estimate of approximately 10,000 is still informative.

As was noted in Scheffer (1944), the diet of harbor seals often echoes that of the local commercial fishing industry. Harbor seals in Oregon are no exception. Numerous dietary surveys have been conducted for harbor seals in the Pacific Northwest, in riverine environments, estuaries, and offshore. Harbor seals in Oregon and other locations have been noted to take advantage of seasonally-available resources, including Chinook (*Oncorhynchus tshawytschai*), coho (*Oncorhynchus kisutch*), and steelhead or rainbow trout (*Oncorhynchus mykiss*) which spawn in

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several river systems (Roffe and Mate 1984, Orr et al. 2004). However, even harbor seals which swam upriver also fed on marine prey items including flounders (Pleuronectidae), Pacific hake (*Merluccius productus*), Pacific staghorn sculpin (*Leptocottus armatus*), smelts (Osmeridae) and shiner surfperch (*Cymatogaster aggregata*) (Roffe and Mate 1984). Although harbor seals do travel upriver on a seasonal basis, many individuals forage primarily in the marine estuarine or coastal environments.

Harbor Seals in Washington State and the Columbia River

Washington's coastal geography is widely dominated by the Puget Sound and a number of larger bays throughout the coastline. A large percent of the state's population of harbor seals resides within the Puget Sound area, hauling out along shorelines and islands within. Similarly, there are a number of harbor seal haulouts along the Columbia River, including the Desdemona Sands area.

Harbor seals in Washington are divided into two stocks for management purposes by the National Marine Fisheries Service (NMFS): inland and coastal (Jeffries et al. 2003). Harbor seal haulout sites are located throughout the state, along Hood Canal, the Eastern Bays of the Puget Sound, the San Juan Islands, the Strait of Juan de Fuca, and along coastal bays and shorelines. Much like Oregon, bounty programs instituted from 1943-1960 resulted in the reported harvest of more than 10,000 seals and sea lions; 95% of which were harbor seals (Newby 1973). Newby (1973) further estimated that due to sinking losses after shooting, at least 17,000 individuals were harvested during that time. When the MMPA was enacted in 1972, there were as few as 2,000 individuals left in the state (Newby 1973, Jeffries et al. 2003).

Harbor seal populations in Washington have been continually monitored since that date, and have shown strong population growth. Due to extrapolation from visual surveys, confidence intervals predicting the actual population can be quite wide. Nevertheless, harbor seals have shown strong logistical population growth since the 1970's (Jeffries et al. 2003). From 1978 to 1999, Jeffries et al. (2003) found that harbor seal populations in the state had tripled from an estimated 6,786 to 19,379. This number is nearly double of that of Oregon; however, Washington's dynamic coastlines including Puget Sound range for more than 3,000 miles while Oregon's coastline covers a distance of approximately 1,400 miles. Populations in all areas but the Hood Canal fit a logistical growth pattern; Hood Canal populations held somewhat steady for the duration of the investigation. Results suggest that during the time of the study, harbor seals were nearing their estimated carrying capacity. Population estimates of harbor seals in Washington from 1999 to more recent years, much like that of Oregon, are not readily available.

Less information exists as to harbor seal populations along the Columbia River; however the number of harbor seals inhabiting the Desdemona Sands haulout site was approximately 1,500 animals in 2010 (Scordino 2010). In 1985, Beach et al. estimated that approximately 6,000 to 7,000 animals inhabited 78 sites along the Columbia River. Interactions of marine mammals and commercial fisheries is of considerable interest, especially near the area of the Bonneville Dam, a critical fish passage point for spawning salmon located 145 miles from the mouth of the river. In all three locations of this study, harbor seal populations were once heavily monitored and regulated; however recent reliable population estimates are no longer conducted and published as frequently as they once were. Whether population levels will continue to grow or level out at current estimates of carrying capacity remains to be seen, and has important implications for management.

Hypoxia in the California Current Large Marine Ecosystem

The CCLME is one of four highly productive eastern boundary current systems in the world. Eastern boundary systems support approximately 20% of the world-wide fishery landings, making them especially important in terms of biodiversity, as well as fisheries production (Pauly and Christensen 1995). A major driver of productivity in the CCLME is coastal upwelling, in which northerly winds drive Ekman transport of nutrient-rich but oxygen-poor water upward through the water column during summer months (Figure 1.1) (Park et al. 1962, Carr and Kearns 2003).



Figure 1.1. Wind-driven upwelling as it occurs in the CCLME. Northerly winds drive coastward upwelling of cold, nutrient rich water inshore. Graphic: Wikimedia commons.

Episodic hypoxic zones (areas with < 1.4 ml dissolved oxygen per liter of water) have been documented in coastal oceans for more than three decades (Jewett et al. 2010). For Oregon and the surrounding coastal area, the severity of hypoxia is highly correlated with the strength and duration of annual upwelling events and wind index (Rabalais et al. 2010a). In extreme cases, anoxia (<0.5 ml/l dissolved oxygen) has resulted in 'dead zones' with the 'near complete mortality of macroscopic invertebrates' as reported off the Oregon coast in 2006 (Chan et al. 2008b). Unlike most hypoxic zones that are driven by anthropogenic-caused eutrophication and algal blooms, the CCLME water-column shelf hypoxia appears driven by atmospheric and oceanic circulation, altered nutrient transport and increased near-shore respiration that can likely be linked to changing climate (Chan et al. 2008b, Jewett et al. 2010).

Hypoxic events near the Oregon coast have been noted annually in the historical record as early as the 1960's (Brown and Power 2011) and are just one global instance of hypoxia in a coastal ecosystem. Farther offshore, the Oxygen Minimum Zone (OMZ) hosts regularly low dissolved oxygen in deeper waters (Gibson and Atkinson 2003), but oxygen levels within shallow coastal regions usually remain above biologically detrimental levels. Oregon's hypoxia has grown notably more severe in the recent decade, in both decreased levels of dissolved oxygen, approaching anoxia, spatial extent, and the encroaching of hypoxic and anoxic water onto the commercially and ecologically-important continental shelf region (Chan et al. 2008b, PISCO 2014). The global count of near-shore hypoxic zones - now numbering more than 400's - has roughly doubled every decade since the 1960s (Diaz and Rosenberg 2008, Jewett et al. 2010) and largely reflects increasing human perturbations of terrestrial nutrient cycles (Jewett et al. 2010, Rabalais et al. 2010b). Finally, severity, extent, persistence and frequency of hypoxic events have also increased (Chan et al. 2008b, Jewett et al. 2010). Global trends hint towards increased levels of hypoxia in the near future, and it is especially important to continue to work towards a comprehensive understanding of hypoxia and its social and ecological implications before the problem reaches unmanageable levels (Cooley 2012).

Hypoxia has the potential to cause large ecosystem-level regime shifts, as have been demonstrated in systems described by Monteiro et al. (2008), Stramma et al. (2010) and Zhang et al. (2010). While the physical forcing of coastal ocean conditions, and lower trophic level impacts have been investigated in a continuing effort, very little is known about impacts of hypoxia on mesopredators, and next to nothing is known about the impact on uppermost trophic levels (Jewett et al. 2010, Keller et al. 2010). Many recent publications have examined impacts of hypoxia on various fish species (Diaz and Rosenberg 1995a, Domenici et al. 2000, Bell et al. 2003, Behrens et al. 2007, Domenici et al. 2007, Brandt et al. 2011), adaptations of mobile vertebrates (Ludsin et al. 2009, Craig 2012), and invertebrate population-level effects (Craig 2012, Roman et al. 2012). However, no recent publications examine the indirect effects on air breathing predatory marine mammals. Studies of hypoxic events have revealed that low-oxygen bottom water often forces mobile vertebrates and invertebrates inshore, and higher into the water column (Eby and Crowder 2002, Zhang et al. 2009, Craig 2012). Inshore movement results in concentrated populations of potential prey for upper level predators, as well as easier accessibility (Diaz and Rosenberg 2008).

Other possible ecosystem impacts of hypoxia include reduced predation of more tolerant species which remain in the low-oxygen zones (Altieri 2008). Additional hypotheses point to increased prey for highly mobile mesopredators, such as Humboldt squid, which feed both on live fauna, as well as detritus created during mortality events (Hunt Jr et al. 1990, Hunt 1991, Ainley et al. 1995, Ainley et al. 2005, Tynan et al. 2005). Harbor seals are generalist predators that remain on the Oregon coast year round, unlike many other local pinniped species that migrate north and south along the eastern Pacific coast. Their highly varied diet consists predominantly of benthic, epibenthic and schooling fish, and pelagic species (Brown and Mate 1983, Tollit et al. 1998, Orr et al. 2004, Grigg et al. 2009). Common harbor seal prey species in the eastern Pacific include sole (and other flatfish), hake, sculpin, surfperch, sandlance, herring, anchovy (Brown 1980, Graybill 1981a, Harvey 1987, Browne et al. 2002, Orr et al. 2004, Wright et al. 2007) and seasonally-available salmonids (Orr et al. 2004, Wright et al. 2007) - all of which are likely impacted to some degree by hypoxia. Additionally, young harbor seals with reduced diving capacity prefer invertebrates, such as crabs, that have also been shown to experience mortality or pronounced inshore movement during hypoxic events (Bell et al. 2003, Grigg et al. 2009).

Research Objectives

Few dietary or spatial studies of harbor seal foraging behavior have been conducted for the coastal Pacific Northwest in the last two decades. Additionally, although investigations of hypoxia's impacts on fish populations have been pursued, species-specific information in the wild is still largely unknown (Keller et al. 2010). By comparing foraging efficiency of harbor seals at the simulated onset, climax, and dissipation of hypoxic events, I hope to illustrate possible effects of hypoxia on *Phoca vitulina* in terms of foraging efficiency, which will be translated to bioenergetic gains. Other studies which will be used to parameterize the model have demonstrated the role of hypoxia in habitat compression, aggregation effects, and shunting of prey species to near-shore areas where they will be more easily accessible to foraging harbor seals and other predators (Diaz and Rosenberg 1995b, Ritter and Montagna 1999, Rabalais et al. 2001, Eby et al. 2005, Diaz and Rosenberg 2008, Vaquer-Sunyer and Duarte 2008, Jewett et al. 2010).

As prey may move inshore, I expect that hypoxia has the potential to positively affect harbor seals in that many prey species will be higher in patch density and also more accessible during hypoxic events as a result of habitat compression and displacement. Patch sizes may not only become larger and more dense (more individuals per cubic area), but patches themselves may also become more closely distributed. If this is the case, then there could be implications for many fish species, as they are both impacted by bottom-up effects (hypoxia and habitat compression), and top-down effects (increased predation pressure by marine mammals or other predatory species). Many species that are potentially impacted by hypoxia are also economically important (Keller et al. 2010).

The first chapter of this thesis will begin with a review of the dietary habits of harbor seals in Washington and Oregon, which is a necessary first step in determining which prey types should be used in a modeling effort. Prey type is especially important when examining the impacts of coastal hypoxia, as different species inhabit different areas of the water column and have different sensitivities to low oxygen conditions. The second chapter describes the initial, conceptually-modeled assessment of possible energetic and behavioral effects of recurring shelf hypoxia on the Oregon Coast on the Pacific harbor seal (*Phoca vitulina richardii*). It is possible that severe hypoxia has the potential to significantly affect foraging behaviors of harbor seals, and may demonstrate a strong bottom-up effect. Additionally, it has thus far been unclear whether these effects may be positive, negative, or negligible on an individual basis.

Studying behavioral and energetic implications for harbor seals is an important first step towards a comprehensive understanding of the full implications of hypoxia for ecosystems. Gathering baseline data and creating preliminary biological models are essential steps in developing a continuing approach to monitoring ecological implications of hypoxic events globally. This thesis aims to integrate an examination of a unique oceanographic phenomenon with the behavioral ecology of a common predatory marine mammal species.

CHAPTER 2: A REVIEW OF FEEDING AND BEHAVIORAL ECOLOGY OF PACIFIC HARBOR SEALS (*PHOCA VITULINA RICHARDII*) IN THE NORTHERN CALIFORNIA CURRENT LARGE MARINE ECOSYSTEM

Abstract

A review of harbor seal dietary composition within the regions of Oregon, Washington and the Columbia River was conducted. Papers examining quantitative dietary information using visual observations, stomach content analyses, or fecal hard part analyses were used to create a comprehensive view of harbor seal foraging in the northern California Current Larger Marine Ecosystem of Oregon and Washington, also referred to here as the Pacific Northwest. Overall, 13 papers from the years 1931 to 2012 were compiled to get a quantitative estimate of harbor seal diet based on fecal hard parts analysis.

Harbor seals were found to consume a seasonally and spatially-varied diet, which included more than 148 species between the three areas. Harbor seal diet in Washington State was the most diverse, with 139 prey types consumed. Seals in Oregon were reported to consume 86 prey types, and seal diet in the Columbia River included 49 prey types. Prey species consumed in all three regions consisted largely of commercially-important teleost fish. The top three prey types in Oregon, as reported by percent frequency of occurrence were Pacific herring (5.91%) and fish of the families Osmeridae or smelt species (21.13%), and Rajidae or skate species (6.36%). The top three prey types in Washington consisted of North Pacific hake (20.42%), Pacific herring (17.97%) and Salmonidae (10.28%). Within the Columbia River region, 47 of 49 species were also found in either Washington or Oregon, the top three of which were Pacific herring (14.06%), Staghorn sculpin (11.70%), and Pacific eulachon (9.07%). Harbor seal diet in Washington State included 12 prey taxa, while Oregon harbor seal diet only represented 6 taxa. The large number of prey species and site-to-site variance is reflective of opportunistic and regionally-variable foraging behavior in harbor seals.

Introduction

Harbor seals (*Phoca vitulina*) are found in most oceans from latitudes 30°N to 85° N (Courbis 2009). The subspecies *Phoca vitulina richardii* is found all along the California Current Large Marine Ecosystem (CCLME), which stretches south to Baja and north to Washington State. Phoca vitulina richardii is also found along the Alaskan Coast. Until the Marine Mammal Protection Act (MMPA) was enacted in 1972, P. vitulina richardii population numbers dropped precipitously due to active hunting and state-issued bounties to remedy suspected conflicts with fisheries. Censuses in Oregon from 1967 and 1968 revealed the population had been reduced to only 500 individuals along the entire Oregon coast (Pearson and Verts 1970). Since the enactment of the MMPA, harbor seal numbers along the CCLME have increased dramatically. Population estimates of harbor seals in Oregon in 1977 through 2003 revealed an average statewide population growth rate of 8.1% per annum (Brown et al. 2005b). Previously numbering in the hundreds, harbor seals in Oregon now number above 10,000 individuals (Brown et al. 2005b). Seal in Washington state were estimated to have an estimated maximum population growth value of $12.6\% (\pm 2.3)$ per annum for seals inhabiting the Puget Sound, and a maximum population growth value of 18.5% (\pm 3.7) on Washington state's exterior coastline (Jeffries et al. 2003). This significant population growth of harbor seals represents increased biomass, predator impacts and potential management implications for fisheries species of

commercial interest in the CCLME, one of four most highly productive eastern boundary upwelling ecosystems of the world.

The CCLME is generally partitioned into four regions north to south: the Pacific Northwest (Oregon and Washington) northern; Central California; the Southern California Bight; and Baja California. Each region has notably different upwelling patterns and therefore ecosystem dynamics. The productive fisheries areas of coastal Washington and Oregon have often raised the issue of pinniped predatory impacts on commercial fisheries (Zamon 2001, Orr et al. 2004, Lance and Jeffries 2006, Scordino 2010, Lance et al. 2012). Several independent studies have been conducted on harbor seal foraging behaviors and dietary composition, including as recently as 2012. However, studies of harbor seal behavioral ecology in Oregon and Washington are lacking in 1) recent evaluation, and 2) a comparative review on an ecosystem and statewide basis. For these reasons, I have conducted a review of literature regarding harbor seal foraging ecology in the Pacific Northwest region of the CCLME. The review reveals that even within the Pacific Northwest, habitats and therefore foraging habits of *P. v. richardii* are extremely diverse.

Regions of Interest

Oregon's marine geography is defined by numerous bays and river inlets, as well as rocky volcanic reef, rocky intertidal and sandy shore bottom zones. Oregon has more than 22 bays, many of which are locations of harbor seal haul outs and breeding sites (Brown et al. 2005a). The continental shelf in Oregon typically extends 12-17 nautical miles offshore with one exception of the Heceta Bank, on the central Oregon coast, which extends approximately 78 nautical miles from shore (ArcGIS 10.2) and results in a particularly productive shelf area. Oregon's continental shelf areas become particularly productive during the upwelling season, but conversely so during severe hypoxia due to oxygen deprivation of marine fauna (Grantham et al. 2004). The severely hypoxic years of 2002 and 2006 saw mass invertebrate mortalities and emigration of fish species from primary habitat, including rockfish (*Sebastes spp*), which normally occupied the inner continental shelf (Chan et al. 2008a). Oregon's marine fisheries are a major component of the coastal and state economy. Additionally, many commercially-important fisheries species are consumed by harbor seals, including flatfish (*Pleuronectiformes spp*.), Pacific whiting (*Merluccius productus*), Dungeness crab (*Cancer magister*), salmonids (*Salmonidae spp*.), and Pacific sardines (*Engraulis mordax*) (COMES 2012).

Washington includes both estuarine and coastal habitat, as well as the 2,642 square kilometer Puget Sound. Puget Sound, including the ecologically-rich San Juan Islands, creates a unique inland marine ecosystem for harbor seals and their prey. In Puget Sound, harbor seals are the most abundant species of pinniped with more than 15,000 individuals estimated (Lance and Jeffries 2006;2009). Harbor seals residing in the San Juan Islands number over 4,000 and reside at more than 150 haul out locations (Lance and Jeffries 2009). Harbor seals consume numerous species prevalent in the

San Juan Islands, including rockfish, lingcod (*Ophiodon elongatus*), bottomfish, schooling fish, and cephalopods (Lance and Jeffries 2006, Lance et al. 2012).

Lastly, the Columbia River represents a unique high-volume riverine ecosystem which shares many species of coastal Oregon and Washington, including harbor seals. It is the largest river in the Pacific Northwest, and the seventh largest river in the United States, discharging into a drainage area of 28,000 square miles (Kammerer 1990). The Columbia River has many harbor seal haul out sites, including Desdemona Sands, Baker Bay, South Jetty, Grays Bay, Green Island, Miller Sands, Welch Island, and Wallace Island (Beach et al. 1985). As a result, the issue of fisheries management of local salmon, commercially-important fish and sturgeon populations are of concern as they relate to local pinniped predation and management (Beach et al. 1985). It is worth examining the primary differences in food sources between inland, riverine and coastal populations of harbor seals in the Pacific Northwest.

Methods

A literature review was conducted on Google Scholar (© Google) and Web of Science (© Thomson Reuters) search platforms. I utilized keywords relating to harbor seal diet, including the terms: 'foraging', 'fecal analysis', 'dietary', 'ecology', 'predation', 'diet', 'dive or diving', 'diet composition'. The results yielded 28 papers directly relevant to the topic for their descriptions of spatial behavior, quantitative dietary analysis, qualitative dietary analysis, or examination of potential fisheries interactions within the Pacific Northwest region.

Of the papers examined, 13 contained detailed, quantitative information on dietary composition primarily through percent frequency of occurrence (%FO) in fecal hard parts analysis (Sperry 1931, Everitt et al. 1981, Graybill 1981a, Brown and Mate 1983, Roffe and Mate 1984, Beach et al. 1985, Browne et al. 2002, Orr et al. 2004, Lance and Jeffries 2007, Wright et al. 2007, Lance and Jeffries 2009, Thomas et al. 2011, Lance et al. 2012) (Figure 2.1). The remaining 15 papers described harbor seal behavior in terms of visual observations of predation (Bayer 1985, Zamon 2001, Tallman et al. 2004), population studies (Pearson and Verts 1970, Antonelis Jr and Fiscus 1980, Jeffries et al. 2003), captive dietary studies (Harvey 1989, Cottrell et al. 1996, Eguchi and Harvey 2005, Phillips and Harvey 2009), spatial telemetry data (Grigg et al. 2009, Peterson et al. 2012), two technical reports (Region 1997, Scordino 2010) regarding harbor seal predation on salmonids and commercially important fish species, and lastly a modeled feeding experiment (Trites and Joy 2005). The latter 15 papers, excepting Tallman et al. (2004) are informative for their descriptions of harbor seal behavior in the Pacific Northwest region, but are not examined here due to a lack of comparable quantitative data. All dietary information in this review is given in terms of %FO obtained from the 13 papers examining dietary habits of wild harbor seals, as well as a visual examination by Tallman et al. (2004). Data were divided regionally into Oregon, Washington, or Columbia River studies. The Columbia River

was treated as a separate habitat from Washington and Oregon as it is a unique highvolume riverine ecosystem running between the two states of interest.



Figure 2.1. Map of approximate locations of scat collection for the 13 quantitative papers (plus Tallman et al. 2004) examined in this review. Note that (F) and (G) had overlapping locations; duplicates were removed for clarity.

Dietary Analysis

Due to the large period of time between the oldest (1931) and the newest (2012) papers, different scientific names for species were used. All species were standardized to their most common or currently accepted scientific classification.
When papers classified prey items to their nearest taxonomic groupings- including class, order, family, genus, species, subphylum or group within a subphylum (i.e. 'shrimp'), this grouping was retained as it was presented in the literature. Therefore, some papers might have used the categorization 'Salmonidae' while another used a particular species. All groups of species were standardized by spelling and counted as one individual character unit within Microsoft Excel ©. To broadly categorize prey types for more basic comparison, I have reduced prey species to 11 encompassing categories: 'teleost fish', 'cephalopod', 'crustacean' (crabs and non-shrimp decapods), 'shrimp', 'bird', 'bivalve', 'lamprey', 'gastropod', 'hagfish', 'skate' and 'wolf eel'.

Results

Washington State

Most of the quantitative papers reviewed were based in inland waters, including locations within Puget Sound such as the San Juan Islands (Sperry 1931, Tallman et al. 2004, Lance and Jeffries 2007;2009, Lance et al. 2012), the Eastern Bays of Puget Sound (Lance and Jeffries 2007), and Protection and Gertrude Island (Everitt et al. 1981, Thomas et al. 2011). However, data also exists for various riverine locations including Hood Canal, Quilcene Bay, Dosewallips River, Duckabush River, Hamma Hamma River, and the Skokomish River (Figure 2.2) (Lance and Jeffries 2009).





Washington: Between-Site Differences in Dietary Composition

Lance et al. (2012) examined harbor seal diet year-round within Puget Sound from 2005 to 2008. Seasonal effects were examined by dividing collection periods into summer/fall (July through September), winter (January and February), and spring (March through June) seasons. These data are part of a longer term dataset collected to

determine the spatial and temporal variability of harbor seal diet in Puget Sound and Washington State, and were also used for earlier publications (Lance and Jeffries 2007;2009). This particular study focused exclusively on harbor seal predation in the San Juan Islands and Northern Puget Sound, as it related to the implementation of marine reserves in the area in an effort to provide protection for depressed fish stocks. In total, 1,723 scat samples were collected in the San Juan Island region, and 1,683 of these contained identifiable remains. The authors found that the most commonlyconsumed prey item was the Pacific herring (Clupea pallasii), which was demonstrated by a 28.74% FO in summer/fall seasons, 38.84% FO in winter, and 63.06% FO in spring. It should be noted, however, that salmon (Salmonidae) were the primary prey item identified in summer/fall, with a %FO of 51.37%. Pacific sandlance (Ammodytes hexapterus) were also commonly prevalent in the diet, occurring with 16.06% FO in summer/fall, 32.83% in winter, and 25.02% in the spring season. Lance et al. (2012) found that the mean number of prey species per scat was 1.98, indicating that while harbor seal foraging is highly variable within populations, individual meals themselves often consist of only a few species. In total, 67 different prey types were identified as harbor seal prey in the San Juan Islands over this time period. The study also indicates that dietary composition varied seasonally and regionally. The authors also examined seasonal prey associations, and determined that these groupings were not in fact random, and showed seals either feeding on seasonally-abundant schooling prey (salmonids in fall/summer and herring in the spring and winter), or single non-schooling individual fish year round.

Beach et al. (1985) examined sites along Oregon, Washington and the Columbia River from 1980-1982. The sites in Washington State included Willapa Bay and Grays Harbor, where scat was collected in most months. In Grays Harbor, prey base showed a high degree of variability from month to month, however the northern anchovy appeared to be a consistently-important prey item, being the primary prey type in May 1981, July 1980 and 1981, and August 1980 and 1981. The seven species found in more than 5% of scats year-round included the Pacific staghorn sculpin (Leptocottus armatus), English sole, Pacific tomcod, Pacific sandlance, shiner perch, and starry flounder. Species that occurred to be seasonally-prevalent included the northern anchovy (*Engraulis mordax*), longfin smelt (*Spirinchus thaleichthys*), Pacific herring (*Clupea pallasii*), rex sole (*Glyptocephalus zachirus*), and bay goby (Lepidogobius lepidus). The predation of salmonids occurred at moderate numbers, and peaked in July 1981, where steelhead (Oncorhynchus mykiss) otoliths appeared in 14.3% of scats. Chinook salmon also occurred as a dietary component, in 6.7% of scats in June 1981.

Willapa Bay had a similar prey composition to Grays Harbor, with the top seven species included northern anchovy, Pacific staghorn sculpin, shiner perch, English sole, Pacific tomcod, starry flounder, bay goby and sand sole (*Psettichthys melanostictus*). Seasonal prey items included Pacific herring, lingcod, steelhead trout, petrale sole (*Eopsetta jordani*), snake prickleback (*Lumpenus sagittal*), and white surfperch (*Phanerodon furcatus*). Anchovies appeared once again as the top prey item in several months including June 1980 (40% FO), June 1981 (100% FO), August 1980 (58.5% FO), and September 1980 (29.4% FO). Pacific staghorn sculpins were highly prevalent in July 1980 (50% FO) and August 1981 (34% FO), and were highly prevalent in other months.

Authors Lance and Jeffries (2009) also created a report for the State of Washington to outline harbor seal diet in Hood Canal, South Puget Sound, and the San Juan Islands. Harbor seals in Hood Canal numbered over 1,000 individuals at five primary haul out locations. In the south Puget sound, the animals numbered approximately 1,200 and inhabit five primary haul out locations. Lastly, Puget Sound seals in the eastern bay areas (Samish, Skagit, Padilla and Bellingham) and Gulf Islands, British Columbia numbered 3,000 individuals at the time of the study.

In Hood Canal, where Lance and Jeffries' collections took place in the fall from 1998-2004, diet was largely composed of Pacific hake (79% FO), Pacific herring (30%), and adult salmonids (26%). In the spring, diet shifted to 85% Pacific hake, 26% Pacific herring, 35% northern anchovy, and only 8% adult salmonids. South Puget Sound represented notably different diet composition. In fall, there was a 99% FO of gadid species (family Gadidae), specifically Pacific tomcod and hake. Clupeids such as herring occurred at 69%, followed by plainfin midshipmen (*Porichthys notatus*) (47% FO) and flatfish (Pleuronectiformes) (33%). Harbor seals in the San Juan Islands had a more variable diet, which was reflected seasonally. Pacific herring was the most important species overall in all seasons (57% FO), with gadids and Pacific sandlance being important in winter and spring, adult salmonids being prevalent in summer and fall, and northern anchovy being prevalent only in winter.

Like many regional studies in the Pacific Northwest, Pacific herring (Clupea *pallasii*) was an overall important aspect of the diet. Authors Lance and Jeffries (2009) reiterate that harbor seal diet is largely opportunistic and can be used as a useful indicator of species composition and prey availability throughout the year in a region. A similar but shorter study was conducted on Gertrude and Protection Islands from 1978-1979 by Everitt et al. (1981). Scats were collected at the two haulout sites, and examined for prey composition, as measured by %FO. More than 29 different fish species – including 9 species of flatfish and 2 species of salmonid – were identified. For seals in Protection Island, WA, the two most dominant prey species were found to be walleye pollock (*Theragra chalcogramma*) and English sole. Pacific herring (Clupea harengus or Clupea pallasii) were also a very prevalent prey item overall (8.6%), and in all seasons except spring. Shiner perch were overwhelmingly present in winter (63.6% FO), but not in other seasons at the Protection Island site. For Gertrude Island, the prevalent prey item during all seasons was Pacific hake, representing 55.6% FO overall in 1979, 51.2% in summer, and 60.0% in fall 1979. The second most prevalent prey item in this study was the plainfin midshipman (Porichthys notatus), occurring with 13.6% FO in all seasons, followed by 11.0% and 16.10% in summer and fall 1979, respectively. The shiner perch was similarly present in Gertrude Island, with 9.8% FO in all seasons and 15.6% in summer, followed by

4.2% in fall. The authors recognize the fact that, as first described by (Scheffer and Slipp 1944), harbor seals consume smaller prey more or less whole, while larger species may be underrepresented in dietary analyses due to tearing into smaller pieces before ingestion.

Lance and Jeffries (2007) specifically examined the dietary habits of harbor seals within the vicinity of the San Juan Island archipelago, as well as east of the islands in the 'Eastern Bays' – Bellingham Bay and Padilla Bay, Washington. Data were collected from 2005-2006 as part of the longer-term data set presented in Lance and Jeffries (2009). The collection period was divided into seasons, defined as spring, summer/fall and winter. In total, 398 scats were collected, of which 392 contained identifiable remains. The overall findings of the study demonstrate that Pacific herring was a dominant prey item within this region, occurring in 57% of fecal samples, and appearing as the top prey item in every collection period. Other prey items were more seasonal, but overall adult salmonids (19% FO overall) and walleye pollock (15% FO overall) were the dominant species. Other species that were important as reported by Lance and Jeffries included rockfish (12% FO), threespine stickleback (Gasterosteus aculeatus) (12% FO), cephalopods (11% FO), shiner perch (11% FO), Pacific sandlance (10% FO), codfish species (Gadidae) (9% FO), herrings and shad (Clupidae spp.) (9% FO), Northern anchovy (8% FO), skates (family Rajidae) (6% FO), sculpins (6% FO), and eelpouts (5% FO). The eastern bays were somewhat similar in prey composition to the San Juan Island and Channel, with Pacific herring predominating.

In total, 44 prey types were identified as consumed by harbor seals in these regions. This is notably smaller than the 67 identified in Lance et al (2012), suggesting that a longer study period and increased sample size in the 2012 study led to a greater variability of detected prey.

Thomas et al. (2011) examined harbor seal foraging response to a local prey spawning pulse, the Pacific herring (*Clupea pallasii*). The authors sought to determine whether a seasonally-prevalent resource (spawning herring) would be reflected in harbor seal foraging behaviors, and therefore dietary composition. The authors collected scat samples in the region of Protection Island in the Strait of Juan de Fuca, the western entrance to Puget Sound. A select number of seals were also tagged with satellite telemetry devices in order to gauge spatial foraging behavior. Dietary studies revealed that Pacific herring was indeed an important prey resource, occurring in 43% of fecal samples in the March 16, 2009 collections, and in 40% of fecal samples collected on July 22, 2009. The average number of species per scat was 2.5 (± 1.4) , closely reflecting a study conducted by Lance et al (2012), which had an average of 1.98 prey types or species per scat. Overall, 126 scats were collected (125 of which were used in analysis), and prey representing 21 species from 16 families were present in the dietary contents. In both spring and summer collections, the primary three prey species were Pacific herring, walleye pollock, and Pacific sandlance. In the spawning season (spring), herring was in fact not the top species, as walleye pollock was present in 62% of samples, followed by Pacific herring (43%)

FO), then Pacific sandlance (28% FO). Conversely, in the summer post-spawning season, Pacific sandlance was the primary dietary component (42% FO), followed by Pacific herring (40% FO) and then walleye pollock (25% FO). Surprisingly, harbor seals did not appear to directly target the spawning aggregation, as there was very little variation in the dietary role of herring between seasons. Therefore it appears that harbor seals were instead focused on other prey species, or perhaps younger non-reproductive herring as primary food sources. Other important species in the diet included herrings, salmonids (including Chinook salmon and other unidentified species), codfishes, northern anchovy, and shiner perch.

Washington: Anomalous and Secondarily-Consumed Species

As opportunistic predators, harbor seals have sometimes been noted to consume prey items that might be considered secondary, coincidental, or purely abnormal. Sperry (1941) noted that the stomachs of harbor seals sometimes contained various gastropods, which were considered to be consumed accidentally during the predation of other species. In 2004, Tallman et al. observed the anomalous and purposeful predation of a harlequin duck (*Histrionicus histrionicus*) in the San Juan Islands, Washington. This is to my knowledge the only published account of a harbor seal consuming a bird species; however other anecdotal evidence of harbor seals feeding on seabirds exists.

Oregon State

The species that were repeatedly present in harbor seal diet between studies included the Pacific herring (*Clupea pallasii*), flatfish (*Pleuronectiformes*), Pacific staghorn sculpin (*Leptocottus armatus*), English sole (*Parophyrs vetulus*), rex sole (*Glyptocephalus zachirus*), Pacific hake or whiting (*Merluccius productus*), Pacific tomcod (*Microgadus proximus*), Shiner surfperch (*Cymatogaster aggregata*), Pacific sardine (*Sardinops sagax*), and Pacific sandlance (*Ammodytes hexapterus*), to name a few. However, the harbor seal diet within Oregon was widely varied and consisted of 96 species, which primarily consisted of fish. Salmonids figured prominently in harbor seal diet in Oregon, occurring frequently by way of both adults and juveniles. However, the %FO for salmonids was relatively low, and never represented more than 23.10% occurrence of diet. This 23.10% occurrence was by way of a stomach content analysis conducted by Roffe and Mate (1984) with a relatively small sample size (n=14).

Oregon-based studies have been highly variable in terms of method, time period and location. Studies have tended to focus on multiple sample collection sites for fecal analysis, and also range from 1980 to 2007. The specific sites examined include the Alsea River (Wright et al. 2007), Netarts Bay (Brown and Mate 1983), Coos Bay (Graybill 1981a), and the Rogue River (Roffe and Mate 1984). Comprehensive studies including multiple regional haulout sites include papers by Beach (1985), Orr et al. (2004), and Browne et al. (2002). Publications specific to one location also tended to employ different methods, including visual analysis and stomach content analysis; however, there are 7 papers with quantitative %FO data available.

Oregon harbor seals were found to consume a handful of invertebrate and nonteleost fish species, including cephalopods, lamprey, skate and crustacean species. However, the diversity of invertebrates cataloged were much less than those documented in Washington-based studies. Out of 95 documented species, 88 of these (91.7%) were teleost fish. The four groups of invertebrates consumed included various crustaceans (recorded by Graybill (1981) but not described past this rough taxonomic grouping), and three groupings of cephalopod- various species, market squids (*Loligo spp.*), and octopus species (*Octopus spp.*). Additionally, both river (Orr et al. 2004) and Pacific (Graybill 1981a, Roffe and Mate 1984, Beach et al. 1985, Orr et al. 2004) lamprey were recorded. Browne et al. (2002) and Wright et al. (2007) additionally recorded unidentified *Lampetra spp*. Lastly, skates (*Rajidae* species) were recorded by Wright et al. (2007) and Orr et al. (2004).

Teleost fish composed the majority of species consumed by harbor seals in Oregon. The variety of species was quite large and comparable to that of Washington State (85 species). Species that were commonly prevalent between studies included the Pacific Staghorn Sculpin (*Leptocottus armatus*), Pacific herring (*Clupea pallasii*), Shiner perch (*Cymatogaster aggregata*), English sole (*Parophrys vetulus*), Pacific sandlance (*Ammodytes hexapterus*), American shad (*Alosa sapidissima*), rex sole (*Glyptocephalus zachirus*), and various species of salmonids (*Salmonidae*).

The study conducted by Beach et al (1985) illuminated a wider variety of species in Oregon than others in this review, which is not surprising since the samples were collected at a greater variety of sites. The other studies in Oregon focused on specific estuarine haul out locations, including the Umpqua River (Orr et al. 2004), Columbia River (Browne et al. 2002), Alsea River (Wright et al. 2007), Netarts Bay (Brown and Mate 1983), Coos Bay (Graybill 1981b), and Rogue River (Roffe and Mate 1984).

Oregon: Between-Site Differences in Dietary Composition

Roffe and Mate's study varied considerably from others in Oregon, as it employed stomach content analysis with a relatively small sample size (n=14). Pacific lamprey, Steelhead salmon, Eulachon (*Thaleichthys pacificus*), and white croaker (*Genyonemus lineatus*) were particularly prominent in these samples, showing 92.3% FO (lamprey) and 23.1% FO (all others), respectively. There were seven additional species of teleost fish found in these samples.

Orr et al. (2004) examined harbor seal dietary composition on the Umpqua River in an effort to examine foraging effects on salmonids in that location. At the time of the study, the Umpqua estuary was home to approximately 600-1,000 harbor seals (although this has likely increased since publication of that paper), residing at two locations approximately 4.8 km from the river mouth. A considerably large sample size (n=119 in Fall 1997, n=219 in Spring 1997, and n=313 in Fall 1998, including only scats with identifiable remains) allows for a more thorough description of harbor seal foraging habits.

The study found various unidentified flatfish species (Pleuronectiformes) as a predominant prey type in Fall 1997 (FO = 38.5%), but were much less significant in Spring 1997 (FO = 20.2%), and Fall 1998 (FO = 14.8%). The next of the top five prev species in Fall 1997 were Pacific hake, rex sole, Pacific staghorn sculpin, and English sole. There were a total of 33 species found this season. Fall 1998 dietary composition was similar, but not identical to this, with 36 prey types, the top five being Pacific hake (41.6% FO), Pacific herring (35.9% FO), rex sole (19.9 %FO), smelt species (Osmeridae) (19.5 %FO), and Pacific sardine (17.9% FO). The Pacific sardine was followed closely by English sole, with an FO of 17.5%. Spring was somewhat dissimilar in prey composition, consisting of 34 prey types, with the five predominant types being shiner surfperch (23.6% FO), Pacific staghorn sculpin (21% FO), Pacific lamprey (20.5% FO), unidentified flatfish (20.2% FO), and Pacific hake (17%). The study found that 76% of the species recorded inhabit marine waters exclusively, demonstrating that the seals foraged primarily at sea, while resting onshore at the estuarine haul out location.

Additionally, Orr et al. (2004) found that salmonid remains were in 39 of the samples (6%) but this may not be entirely indicative of salmonid dietary prevalence,

due to issues in fecal analysis of hard parts of larger fish species. The researchers utilized various hard parts, rather than just otolith analysis, and in fact found that 37 of the 39 samples contained salmonid bones but no otoliths. Genetic analysis was employed on these samples to find that 90% were Chinook or coho salmon or steelhead trout, outlining the benefit in the new methods of non-otolith and genetic analysis in identification of salmonid species.

Wright et al. (2007) examined harbor seal diet in the Alsea River, in order to once again examine harbor seal predatory pressure on salmonids. The study was largely based upon visual observations, which concluded that harbor seals consumed approximately 21% (with a large range of uncertainty – 3-63%) of the prespawning population of salmon. The authors noted that a large percent of this predation likely occurred upriver by a small proportion (~12.5%) of individuals. In addition to visual methods, acoustic telemetry, molecular genetics and scat analysis were also conducted. Scat collection was conducted at two haul out locations, and found 36 prey types consumed by seals in the Alsea River. The upper haulout yielded few samples (n=6), so the two sites were included together in an overall analysis.

Primarily, harbor seal diet was dominated by two species – Pacific herring (41.9% FO), and English sole (36.8% FO), but also included 10 species that were found at 10% or greater %FO, including rex sole (19.7%), Dover sole (15.4%), Pacific sandlance (14.5%), Pacific tomcod (12.8%), Flatfish, sanddab species (*Citharichthys species*), smelt species (all 11.1%), and butter sole (*Isopsetta isolepis*) (10.3%). Adult

salmonids were found in 9.4% of the samples, and juvenile salmonids figured relatively low in terms of dietary composition, being present in 0.8% of samples. Considering the low number of individuals estimated to predate on salmon, it appears that a large amount of salmon consumption is due to a few individuals that appear to focus heavily on this prey source.

Brown and Mate (1983) examined the foraging habits of harbor seals within Netarts Bay, Oregon in order to determine relative seal predation upon salmonids and other fishes in the estuarine habitat. Visual observations were a primary method of investigation, and were conducted twice monthly from May 1977 until November 1981 in Netarts Bay, and in Tillamook Bay from June 1978 until November 1981. In addition to visual surveys, radio telemetry was utilized to determine spatial habitat use of harbor seals, as well as hard part (otoliths and teeth) scat analysis. The authors found a large component of harbor seal diet in the Netarts Bay area consisted of flatfish. Of the ten species of flatfish identified as harbor seal prey, five of these including the English sole, rex sole, Pacific sanddab, Dover sole, and slender sole (Lyopsetta exilis) ranked as five of the top seven most-prevalent prey types consumed. These top seven most prevalent prev were: Pacific sandlance (38.9% FO), English sole (31.6% FO), Rex sole (Glyptocephalus zachirus) (26.3% FO), Pacific sanddab (Citharichthys sordidus) (17.9%), Staghorn sculpin (16.9% FO), Pacific dove sole (*Microstomus pacificus*) (16.9%), and Slender sole (*Lyopsetta exilis*) (11.6%). It was

also noted that the high frequency of flatfish in harbor seal diet appears in other studies, including ones mentioned in this review (Sperry 1931, Graybill 1981a).

The authors noted that the peak abundance of harbor seals coincided with the seasonal return of chum salmon (*Oncorhynchus keta*) in fall. Interestingly, the only salmonid that appeared upon fecal hard parts analysis was *Oncorhynchus mykiss* – the steelhead trout - even though seals were observed to predate upon chum salmon during observations. Predatory losses of chum salmon were estimated to be approximately 1.5-7.2% per year, which was deemed a serious loss at the time, as the stock was in the process of being built up to a sustainable level by managers. The study highlights the importance of using a variety of methods while determining predation rates on salmonids, especially when making management decisions. Additionally, genetic methods can be particularly useful in determining rate of predation, as visual observations are often inherently inadequate, therefore one must use caution when using them to ultimately determine population-level predatory impacts.

Graybill (1981a) examined the foraging habitats and haul out patterns of harbor seals in Coos Bay, Oregon. A total of 296 scats were collected from July 1978 until March 1981 in two locations of the Coos Bay area: North Spit and Pigeon Point. Of these, 230 (78%) contained fish remains with identifiable otoliths. In total, 45 species of teleost fish representing an estimated 1,695 individuals were identified. Of these, 880 (52%) were bottom dwellers, while 47% were midwater types. The top five species of prey by %FO were Pacific staghorn sculpin (29%), English sole (22%), shiner perch (20%), Pacific herring (19%), and various cephalopods (14%). The speckled sanddab (*Citharichthys stigmaeus*) was also relatively prevalent, with a %FO of 13%.

Of the 45 prey species identified, 33 made a relatively small contribution to dietary composition, leaving 12 to compose a majority of the diet. The families that contributed the most were *Pleuronectidae*, *Cottidae*, *and Embioticidae*, contributing 27.0, 21.0, and 23.0 percent of the total number of fish consumed, respectively. Graybill's findings are consistent with the fact that harbor seals tend to consume primarily benthic flatfish, if available, followed by midwater pelagic fish species. This is likely due to the relatively high caloric density of certain flatfish in comparison to other common prey species (Dygert 1990).

Beach et al. (1985) conducted a review of harbor seal foraging at a number of sites in Oregon, Washington, and the Columbia River between 1980-1982. The study involved the collection of scat at 121 individual survey events at five sites along the Pacific Northwest coast, including Grays Harbor, Washington (n = 403), Willapa Bay, Washington (n = 211), the Columbia River (n = 436), Tillamook Bay (n = 38), and Netarts Bay (n = 5). The study categorized prey types into 'primary' (prey likely purposely consumed by seals as a caloric source), and 'secondary' (invertebrate epifauna likely consumed secondarily by seals). In total between all sites, 61 prey types were identified in the harbor seal diet.

The primary species that were noted to be consumed by harbor seals across all sites were Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), whitebait smelt (*Allosmerus elongatus*), longfin smelt (*Spirinchus thaleichthys*), Pacific tomcod (*Microgadus proximus*), shiner perch (*Cymatogaster aggregata*), Pacific staghorn sculpin (*Leptocottus armatus*), English sole (*Parophrys vetulus*), and starry flounder (*Platichthys stellatus*). In Tillamook Bay, one of the most commonlyconsumed prey was the rex sole (*Errex zachirus*), with a dietary %FO of 24% in September 1981 (n=25), and a %FO of 23.1% in October 1981 (n=13). Various crabs (*Cancer spp.*) were consumed primarily in October (30.8% FO), but were not as prevalent in September (12% FO). The other primary prey types that appeared in September were not as prevalent the following month. These included English sole (16% FO), Pacific sanddab (16% FO), northern anchovy (12% FO), and Pacific sandlance (12% FO). The remainder of Beach's samples were based in Washington and the Columbia River, and are summarized in their respective sections.

Sperry (1931) is perhaps one of the earliest examinations of harbor seal foraging in the Pacific Northwest. Reflecting the historical circumstances under which it was written, dietary analyses were created not from scat samples but rather taken directly from stomachs of animals lethally harvested under bounty. Despite a difference in collection method, dietary contents are very similar to those found in other papers with less-invasive methods. In total, 81 stomachs were gathered from 1927-1930 in the Puget Sound area. The top five prey items found included Pacific tomcod (27.16% FO), various flounder (Pleuronectidae) species (28.40% FO), Pacific hake (22.22% FO), squids (*Loligo spp.*) (22.22% FO), and sculpins (Cottidae) (20.99% FO). Other species that composed more than 10% of the overall diet included shrimp (*Crangon spp.*) (17.28% FO), shiner perch (13.58% FO), walleye pollock (12.35% FO), Pacific cod (11.11% FO) and lingcod (11.11% FO). In total, this study found 33 prey types being consumed by harbor seals.

Columbia River

Two authors in this research review examined harbor seal diet within the Columbia River. The first, Browne et al. (2002), examined harbor seal diet in Desdemona Sands, a primary harbor seal haulout (Figure 2.3). This haul out is located approximately 26 km from the river mouth and is the largest harbor seal haul out on the lower Columbia river.

In Browne et al. (2002), scats were collected at times which correlated with Columbia River runs of Chinook salmon. Of the analyzed scat samples, more than 45 prey taxa were identified, with prey from 17 groups primarily composing the diet. Forty prey taxa were listed in terms of quantitative %FO that were utilizable for this review.



Figure 2.3. Location of Desdemona Sands, a large harbor seal haulout site located 26 miles from the mouth of the Columbia River.

Salmon were consumed by harbor seals during all sampling times in some amount, most notably in spring; however the dietary composition of adult salmonids tended to be relatively low as estimated by %FO. In spring, juvenile salmonids had a frequency of occurrence of 19%, while adult salmonids showed up 6% of the time. In summer, juvenile and adult salmonids showed up in relatively small amounts, being 5% and 4% respectively. Lastly, fall numbers of salmonid consumption were moderately higher, being 10% for adult salmonids and 5% for juveniles. The authors noted that the inclusion of all hard parts, rather than just otoliths, increased the prominence of many larger prey species upon analysis, including salmonids, Pacific hake, Pacific tomcod, American shad, hexagrammids, elasmobranchs, and lampreys. The most prominent prey species varied by season. The five most common prey types in spring were the Pacific staghorn sculpin (FO = 41%), Pacific herring (FO = 36%), starry flounder (*Platichthys stellatus*) (FO = 30%), smelt species (FO = 28%), and lamprey species (FO = 28%). Summer's top prey included Pacific herring (FO = 57%), lamprey species (FO = 25%), American shad (*Alosa sapidissima*) (FO = 19%), Pacific staghorn sculpin (FO = 19%), and smelt species (FO = 18%). Lastly, the five most common prey species in fall were Pacific tomcod (FO = 39%), smelt species (FO = 25%), Pacific hake (FO = 28%), Pacific staghorn sculpin (FO = 25%), and American shad (FO = 22%).

Beach et al. (1985) also examined harbor seal foraging along the Columbia River, and gathered data year-round from 1980 until 1981. Monthly collections highlighted seasonal variations in prey base. In January through April, the eulachon (*Anoplopoma fimbria*) was constantly present in scat at a relatively high %FO. In January 1981 and 1982, the eulachon appeared in 50% of scats (n = 18 and 12, respectively). They dominated in February 1982 with a %FO of 86.7%, and were also prevalent in March 1981 (16.7% FO) and March 1982 (100% FO of 3 samples). They were found in 10.7% of samples in April 1981, and 20% of samples in April 1982. In the rest of the samples, they are noticeably absent or in low numbers. Northern anchovies (*Engraulis mordax*) appear to be highly prevalent in the months May through September, and appear as the top food item in May 1981 (89.5% FO), June 1980 and 1981 (25% and 20% FO, respectively), July 1981 (36.3% FO), August 1981 (46.9% FO), and September 1981 (15.3% FO).

Numbers of fecal samples taken monthly were highly variable and dependent on the availability of scats during collection times. While smaller samples likely do not fully represent the full scale of diet variability, they are still informative in terms of qualitative dietary content. Seven species of bony fish were identified in more than 5% of scats collected during the study. These included the Pacific staghorn sculpin, longfin smelt, Pacific tomcod, snake prickleback, starry flounder, English sole, and Pacific herring. Seasonal prey included northern anchovies, eulachon, whitebait smelt, and Pacific hake. Pacific and river lamprey were commonly consumed by harbor seals; Pacific lamprey consumption peaked in March and April, while river lamprey consumption peaked in July and August. In terms of salmonid consumption, only otoliths were examined and therefore salmon appeared to compose a very small proportion of harbor seal diet- however this may not be entirely representative of true consumption rates.

Overall, the dietary composition of harbor seals in the Columbia River contains primarily species that are also found in the harbor seal diet in Washington or Oregon, or both. There are only two unique recorded species in the Columbia River, the *Cyprinidae* (carp) family, and the sculpin genus *Icelus*. However, the proportional dietary composition of harbor seals within the River system is unique when compared to that of Washington or Oregon coastlines and inland waters (Figure 2.1).

Discussion

Limitations of Fecal Analysis

Hard parts-based quantitative dietary analysis is not without inherent biases. However, it still remains an informative method for describing prey composition, comparing regional effects, and some forms of quantitative dietary analysis, when used with estimated correction factors. Fecal analysis, stomach contents analysis, and visual observation are all subject to inherent biases that must be considered when performing dietary studies or comparisons (Browne et al. 2002). When consuming larger prey, such as salmonids, harbor seals have been commonly observed bringing prey to the surface and consuming most of the fish, while leaving the head (Scheffer and Slipp 1944). Utilizing otolith identification as the primary means of fecal analysis will result in a bias against large fish species, and may yield very little useful information when examining harbor seal predation on salmonids, which are often consumed as larger, reproductive adults. Small prey are much more often consumed below the surface, as few visual observations exist to the contrary (Antonelis Jr and Fiscus 1980, Zamon 2001). However, the digestive process may result in a different bias against smaller, less bony, or cartilaginous prey items, as they may be more completely digested and therefore not be fully represented as hard parts in fecal samples (Harvey 1989). Thus, smaller prey items may also be underestimated.

Studies have been conducted to attempt to estimate a correction factor and best methodology for fecal analysis (Cottrell et al. 1996, Tollit et al. 1997, Browne et al.

2002, Tollit et al. 2003, Trites and Joy 2005, Phillips and Harvey 2009). However, studies tend to differ in their outcomes, and due to their design were often conducted with a limited number of prey species.

In pinnipeds, defecation may not occur entirely on land, and therefore fecal sampling may be a form of biased subsampling reflecting predominantly feeding during the preceding six hours or less, based on average gut-passage times (Markussen 1993). A study by Phillips and Harvey (2009) found that in captivity, only 5% of scats from a harbor seal were collected from the enclosure's haul out platform, while the remainder were collected from the water portion of the enclosure. Therefore, caution must be utilized when applying scat analysis as a means of dietary evaluation. However, land-based scat collection is often the only available method of directly measuring prey composition. Emerging genetic evaluation methods (Reed et al. 1997, Tollit et al. 2009) represent a fine scale method of prey identification that resolves some of the issues of hard parts analysis, through identification of hard parts that may not be readily identifiable to species through visual examination. However, because fecal-based genetic methods are subject to the same sampling methods as hard parts analysis, they are subject to the same biases. Broad-scale analyses, such as stable isotope analysis (Newsome et al. 2007) and quantitative fatty acid signature analysis (Iverson et al. 2004) can eliminate sampling bias, but only resolve dietary composition to a trophic-level basis and are more difficult to quantify when predators feed on

multiple prey species within the same level. Therefore, fecal hard-parts analysis is often employed as the most practical and least costly method of dietary analysis.

Summary of Results

Within the papers reviewed, there are a reported 148 species or groups of species identified as being consumed by harbor seals. A majority of identified prey species are teleost fish, consisting of 113 unique species or groups in Washington, Oregon and the Columbia River combined. Fish that reoccurred repeatedly within the top 50% of the diet for harbor seals in all three regions were the Pacific herring (17.97% in Washington State, 14.06% in the Columbia River) and 5.91% in Oregon State), the Pacific hake (20.42% in Washington, 4.72% in Oregon), and the Pacific staghorn sculpin (11.70% in the Columbia River, 4.90% in Oregon). Salmonids functioned as a major part of the diet in Washington (10.28%) but were either rare in the diet or had a low rate of detection in Oregon and the Columbia River (Figure 2.4).



Figure 2.4. Top 50% prey species of Pacific harbor seals in Oregon, Washington and Columbia River by %FO overall.

Washington alone had 128 species present, with 94 being teleost fish, ten crustaceans, nine cephalopods, five shrimps, four groupings of lamprey species (including 2 broad unknown groupings), and one each of: unidentified agnathan fish (hagfish or lamprey), bivalve, skate, wolf eel, hagfish, gastropod, and bird species (Figure 2.5). Washington's unique species (species found only in Washington and not Oregon State or the Columbia River) numbered 60, and included 37 species of teleost

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fish, six cephalopods, eight crustaceans, three shrimps, two lampreys, and one species each of bird, bivalve, gastropod and wolf eel.



Figure 2.5. Recorded species composition of harbor seal prey in Washington State (n = 129 species).

Oregon had 86 species present upon dietary analysis, including 74 species of teleost fish, three types of lamprey (river, Pacific, and unidentified), three species of cephalopods, two shrimp, two crustaceans, and one hagfish species (Figure 2.6). Oregon's 18 unique prey types included 17 species of teleost fish consumed by harbor seals, and *Eptatretus stoutii*, the hagfish. A total of 57 species were identified in both Washington and Oregon, including 57 species of teleost fish, three species of cephalopods, two crustaceans, three shrimp, a hagfish, three lampreys (river, Pacific, and unidentified), and one unidentified agnathan fish. While there is a high degree of

synonymy between the two states, there are also a number of unique species to each, largely attributable to different habitat types as examined by the papers.





The Columbia River represented a smaller biodiversity of prey described. In total, samples taken from the Columbia River contained remains of 49 total prey types, 38 of which were teleost fish, two were crustaceans, two were cephalopods, three were River, Pacific, or unidentified lamprey species, two were shrimp, one was an unidentified agnathan fish, and one was a hagfish (Figure 2.7). The only two species types unique to the Columbia River were fish of the *Cyprinidae* (carp) family and the genus *Icelus*. It can therefore be stated that although the Columbia River is a significant freshwater ecosystem, many prey species consumed in or near the river by harbor seals are species that are found elsewhere on the Washington and Oregon coastlines.



Figure 2.7. Recorded species composition of harbor seal prey in the Columbia River (n = 49).

The findings of this review reflect that harbor seals are highly diverse in their foraging behaviors from region to region, however are highly opportunistic predators which eat locally- and seasonally-available resources. Harbor seals in Oregon, Washington and the Columbia River tend to consume commercially-important fish species, however it is not known what the true population-level impacts of this predation is. Hard parts fecal analysis is a useful first step towards understanding primary dietary composition of this predator species, however it must be applied in conjunction with other behavioral, dietary, and population evaluation methods in order to provide an understanding of the full ecological role of a biologically important predator species such as the Pacific harbor seal.

APPENDIX I: PREY TYPE LISTS

PREY TYPES REPORTED IN WASHINGTON (N=128)

Scientific Name	Common Name	Category
Agnathan spp**	Agnathan spp.	Lamprey
Allosmerus elongatus	Whitebait smelt	Tel. Fish
Alosa sapidissima	American shad	Tel. Fish
Ammodytes hexapterus	Pacific sandlance	Tel. Fish
Ammodytes personatus**	Sandlance	Tel. Fish
Amphistichus rhodoterus**	Redtail surfperch	Tel. Fish
Anarrhichthys ocellatus**	Wolf eel	Wolf Eel
Anoplopoma fimbria	Sablefish	Tel. Fish
Argentinid spp**	Argentines	Tel. Fish
Atheresthes stomias	Arrowtooth flounder	Tel. Fish
Bathymasteridae**	Bathymasteridae	Tel. Fish
Berryteuthis magister**	Magister armhook squid	Cephalopod
Berryteuthis spp**	Armhook squid	Cephalopod
Bothidae**	Lefteye flounders	Tel. Fish
Brachyistius frenatus**	Kelp perch	Tel. Fish
Callianassa californiensis	Bay ghost shrimp	Shrimp
Cancer gracilis**	Graceful rock crab	Crustacean
Cancer magister**	Dungeness crab	Crustacean
Cancer oregonensis**	Hairy crab	Crustacean
Cancer spp	Crabs (Cancer spp.)	Crustacean
Cephalopoda	Unidentified Cephalopods	Cephalopod
Chitonotus pugetensis	Roughback sculpin	Tel. Fish
Citharichthys sordidus	Pacific sanddab	Tel. Fish
Citharichthys stigmaeus	Speckled sanddab	Tel. Fish
Clupea pallasii	Pacific Herring	Tel. Fish
Clupeidae	Herrings	Tel. Fish
Cottidae	Sculpins	Tel. Fish
Crangon spp	Crangon shrimp	Shrimp
Crustacea	Crustacea	Crustacean
Cryptacanthodes giganteus**	Giant wrymouth	Tel. Fish
Cymatogaster aggregata	Shiner surfperch	Tel. Fish

Damalichthys vacca	Pile perch	Tel. Fish
Diaphus theta**	California headlight fish	Tel. Fish
Embiotocidae	Surfperch species	Tel. Fish
Engraulis mordax	Northern anchovy	Tel. Fish
Enophrys bison**	Buffalo sculpin	Tel. Fish
Enophrys spp**	Sculpin	Tel. Fish
Eopsetta jordani	Petrale sole	Tel. Fish
Eptatretus stoutii	Hagfish	Hagfish
Errex zachirus	Rex sole	Tel. Fish
Gadidae	Codfishes	Tel. Fish
Gadus macrocephalus	Pacific cod	Tel. Fish
Gasterosteus aculeatus	Threespine sticklebacks	Tel. Fish
Glyptocephalus zachirus	Rex sole	Tel. Fish
Gonatus onyx**	Clawed armhook squid	Cephalopod
Gonatus spp**	Gonatus spp	Cephalopod
Hemigrapsus oregonensis**	Shore crab	Crustacean
Hemilepidotus spinosus**	Brown Irish Lord	Tel. Fish
Hemilepidotus spp	Irish lords	Tel. Fish
Hexagrammidae	Greenlings	Tel. Fish
Hexagrammos decagrammus	Kelp greenling	Tel. Fish
Hippoglossoides elassodon	Flathead sole	Tel. Fish
Histrionicus histrionicus**	Harlequin Duck	Tel. Fish
Hydrolagus colliei**	Ratfish	Tel. Fish
Hypomesus pretiosus	Surf smelt	Tel. Fish
Isopsetta isolepis	Butter sole	Tel. Fish
Lampetra ayresii	River Lamprey	Lamprey
Lampetra spp	Lamprey	Lamprey
Lampetra tridentate	Western lamprey	Lamprey
Lepidogobius lepidus	Bay goby	Tel. Fish
Lepidopsetta bilineata	Rock sole	Tel. Fish
Leptocottus armatus	Pacific staghorn sculpin	Tel. Fish
Liparidae**	Snailfishes	Tel. Fish
Loligo opalescens**	Market squid	Cephalopod
Loligo spp	Squid spp	Cephalopod
Lumpenus lampretaeformis**	Blenny	Tel. Fish
Lumpenus sagitta**	Snake prickleback	Tel. Fish

Lycodopis pacifica**	Blackbelly eelpout	Tel. Fish
Lyopsetta exilis	Slender sole	Tel. Fish
Merluccius productus	Pacific hake	Tel. Fish
Microgadus proximus	Pacific tomcod	Tel. Fish
Microstomus pacificus	Dover sole	Tel. Fish
Myoxocephalus spp**	Sculpins	Tel. Fish
Nautichthys oculofasciatus**	Sailfin sculpin	Tel. Fish
Octopus rubescens**	Pacific red octopus	Cephalopod
Octopus spp	Benthic octopus	Cephalopod
Oncorhynchus gorbuscha**	Pink salmon adult	Tel. Fish
Oncorhynchus keta**	Chum salmon adult	Tel. Fish
Oncorhynchus kisutch	Coho salmon adult	Tel. Fish
Oncorhynchus kisutch (juv)**	Coho salmon juvenile	Tel. Fish
Oncorhynchus mykiss	Steelhead	Tel. Fish
Oncorhynchus nerka**	Sockeye salmon adult	Tel. Fish
Oncorhynchus nerka (juv)**	Sockeye salmon juvenile	Tel. Fish
Oncorhynchus tshawytscha**	Chinook salmon adult	Tel. Fish
Oncorhynchus tshawytscha (juv)	Chinook salmon juvenile	Tel. Fish
Ophiodon elongatus	Lingcod	Tel. Fish
Osmeridae	Smelts	Tel. Fish
Osmerus mordax**	Rainbow smelt	Tel. Fish
Pagurus spp**	Hermit crab	Crustacean
Pandalus danae**	Prawn	Shrimp
Parophrys vetulus	English Sole	Tel. Fish
Peprilis simillimus**	Pacific butterfish	Tel. Fish
Petrolisthes cinctipes**	Porcelain crab	Crustacean
Petrolisthes eriomerus**	Flat-topped crab	Crustacean
Petromyzontidae**	Lampreys	Lamprey
Phanerodon furcatus	White surfperch	Tel. Fish
Pholidae	Gunnels	Tel. Fish
Pinnixa schmitti**	Pea crab	Crustacean
Platichthys stellatus	Starry flounder	Tel. Fish
Plectobranchus evides**	Bluebarred prickleback	Tel. Fish
Pleuronectidae	Righteye flounders	Tel. Fish
Pleuronectiformes	Flatfish	Tel. Fish
Pleuronichthys coenosus**	C-O Sole	Tel. Fish
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Porichthys notatus**	Plainfin midshipman	Tel. Fish
Poroclinus rothrocki	Whitebarred prickleback	Tel. Fish
Psettichthys melanostictus	Sand sole	Tel. Fish
Rajidae	Skates	Skate
Rhacochilus vacca**	Pile perch	Tel. Fish
Ronquilus jordani**	Northern ronquil	Tel. Fish
Salmonidae	Unidentified Salmon adult	Tel. Fish
Salmonidae (juv)	Unidentified Salmon juvenile	Tel. Fish
Sardinops sagax	Sardine	Tel. Fish
Scomber japonicus	Chub mackeral	Tel. Fish
Sebastes spp	Rockfish (adult)	Tel. Fish
Sebastes spp (juv)**	Rockfish (juvenile)	Tel. Fish
Sebastes spp (various)**	Rockfish (various)	Tel. Fish
Shrimp**	Shrimp	Shrimp
Spirinchus thaleichthys	Longfin smelt	Tel. Fish
Squalus acanthias**	Spiny dogfish	Tel. Fish
Stenobrachius leucopsarus**	Northern lampfish	Tel. Fish
Stichaeidae**	Pricklebacks	Tel. Fish
Thaleichthys pacificus	Eulachon	Tel. Fish
Theragra chalcogramma**	walleye pollock	Tel. Fish
Trichodon Trichodon	Sandfish	Tel. Fish
Trichotropis spp**	Snail	Gastropod
Upogebia pugettensis**	Blue mud shrimp	Shrimp
Yoldia myalis**	Bivalve	Bivalve
Zoarcidae	Eelpouts	Tel. Fish

PREY TYPES REPORTED IN OREGON (N=86)

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species with a	denotes a prey type reported	i caciusivery ili Or	egon

Scientific Name	Common Name	Category
Agonidae**	Poacher spp	Tel. Fish
Allosmerus elongatus	Whitebait Smelt	Tel. Fish
Alosa sapidissima	American shad	Tel. Fish
Ammodytes hexapterus	Pacific sandlance	Tel. Fish

Anoplopoma fimbria	Sablefish	Tel. Fish
Artedius spp.**	Sculpins	Tel. Fish
Atheresthes stomias	Arrowtoothed Flounder	Tel. Fish
Callianassa californiensis	Ghost shrimp	Shrimp
Cancer spp	Crabs (Cancer spp)	Crustacea
Cephalopoda	Cephalopods	Cephalopod
Chilara taylori**	Spotted cusk eel	Tel. Fish
Chitonotus pugetensis	Roughback sculpin	Tel. Fish
Citharichthys sordidus	Pacific sanddab	Tel. Fish
Citharichthys spp**	Sanddab Spp	Tel. Fish
Citharichthys stigmaeus	Speckled sanddab	Tel. Fish
Clevelandia ios**	Arrow goby	Tel. Fish
Clupea pallasii	Pacific herring	Tel. Fish
Clupeidae	Herring/Shad	Tel. Fish
Coryphopterus nicholsi**	Blackeye goby	Tel. Fish
Cottidae	unidentified cottid	Tel. Fish
Crangon spp	Crangon shrimp	Shrimp
Crustacea	Decapods various	Crustacea
Cymatogaster aggregata	Shiner surfperch	Tel. Fish
Damalichthys vacca	Pile Perch	Tel. Fish
Embiotoca lateralis**	Striped surfperch	Tel. Fish
Embiotocidae	Surfperch spp	Tel. Fish
Embiotocidae (juv)**	Surfperch (juv)	Tel. Fish
Engraulis mordax	Northern anchovy	Tel. Fish
Eopsetta jordani	Petrale sole	Tel. Fish
Eptatretus spp**	Hagfish	Hagfish
Eptatretus stoutii	Pacific hagfish	Hagfish
Errex zachirus	Rex sole	Tel. Fish
Gadidae	Codfishes	Tel. Fish
Gadus macrocephalus	Pacific cod	Tel. Fish
Gasterosteus aculeatus	Threespine stickleback	Tel. Fish
Genyonemus lineatus**	White croaker	Tel. Fish
Glyptocephalus zachirus	Rex sole	Tel. Fish
Gobiidae**	Unidentified gobiid	Tel. Fish
Hemilepidotus spp	Irish lord	Tel. Fish
Hexagrammidae	Greenling	Tel. Fish

Hexagrammos decagrammus	Kelp Greenling	Tel. Fish
Hippoglossoides elassodon	Flathead sole	Tel. Fish
Hyperprosopon ellipticum**	Silver surfperch	Tel. Fish
Hypomesus pretiosus	Surf smelt	Tel. Fish
Isopsetta isolepis	Butter sole	Tel. Fish
Lampetra ayresii	River lamprey	Lamprey
Lampetra spp	Lamprey spp	Lamprey
Lampetra tridentata	Pacific Lamprey	Lamprey
Lepidogobius lepidus	Bay goby	Tel. Fish
Lepidopsetta bilineata	Rock sole	Tel. Fish
Leptocottus armatus	Staghorn sculpin	Tel. Fish
Loligo spp	Market squid	Cephalopod
Lyopsetta exilis	Slender sole	Tel. Fish
Merluccius productus	Pacific hake	Tel. Fish
Microgadus proximus	Pacific tomcod	Tel. Fish
Microstomus pacificus	Dover sole	Tel. Fish
Mylocheilus caurinus**	Peamouth chub	Tel. Fish
Octopus spp	Octopus rubescens	Cephalopod
Oncorhynchus kisutch	Coho salmon	Tel. Fish
Oncorhynchus mykiss	Steelhead or Rainbow Trout	Tel. Fish
Oncorhynchus tshawytscha	Chinook salmon	Tel. Fish
Ophiodon elongatus	Lingcod	Tel. Fish
Osmeridae	Osmeridae	Tel. Fish
Parophyrs vetulus	English sole	Tel. Fish
Phanerodon furcatus	White Surfperch	Tel. Fish
Pholidae	Gunnel spp	Tel. Fish
Pholis ornata**	Saddleback gunnel	Tel. Fish
Platichthys stellatus	Starry flounder	Tel. Fish
Pleuronectidae	Flatfish	Tel. Fish
Pleuronectiformes	Unidentified flatfish	Tel. Fish
Poroclinus rothrocki	Whitebarred prickleback	Tel. Fish
Psettichthys melanostictus	Sand Sole	Tel. Fish
Radulinus asprellus**	Slim Sculpin	Tel. Fish
Rajidae	Unidentified rajid	Tel. Fish
Salmonidae	Unidentified Salmon	Tel. Fish
Salmonidae (juv)	Unidentified juv salmon	Tel. Fish
Sardinops sagax	Pacific sardine	Tel. Fish
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Scomber japonicus	Pacific mackerel	Tel. Fish
Scorpaenichthys marmoratus**	Cabezon	Tel. Fish
Sebastes spp	Rockfish species	Tel. Fish
Spirinchus starksi	Night Smelt	Tel. Fish
Spirinchus thaleichthys	Longfin smelt	Tel. Fish
Thaleichthys pacificus	Eulachon	Tel. Fish
Trachurus symmetricus	Jack mackeral	Tel. Fish
Trichodon trichodon	Pacific sandfish	Tel. Fish
Zoarcidae	Unidentified zoarcid	Tel. Fish
Sebastes spp	Rockfish	Tel. Fish
Sebastidae	Rockfish spp	Tel. Fish
Spirinchus starski**	Nightsmelt	Tel. Fish
Spirinchus thaleichthys	Longfin smelt	Tel. Fish
Thaleichthys pacificus	Eulachon	Tel. Fish
Trachurus symmetricus**	Jack mackeral	Tel. Fish
Trichodon trichodon	Pacific sand fish	Tel. Fish
Zoarcidae	Eelpout spp	Tel. Fish

PREY TYPES REPORTED IN THE COLUMBIA RIVER (N=49)

S	pecies	with	a **	denotes a	prey	type	reported	exc	lusive	ly i	n tl	ne (Colun	ıbia	l R	iver
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Scientific Name	Common Name	Category		
Agnathan spp	Agnathan spp	Lamprey		
Allosmerus elongatus	Whitebait smelt	Tel. Fish		
Alosa sapidissima	American shad	Tel. Fish		
Ammodytes personatus	Pacific sandlance	Tel. Fish		
Amphistichus rhodoterus	Redtail surfperch	Tel. Fish		
Anoplopoma fimbria	Eulachon	Tel. Fish		
Callianassa californiensis	Ghost shrimp	Shrimp		
Cancer spp	Crabs (Cancer spp)	Crustacean		
Citharichthys sordidus	Pacific sanddab	Tel. Fish		
Citharichthys stigmaeus	Speckled sanddab	Tel. Fish		
Clupea pallasii	Pacific herring	Tel. Fish		
Crangon spp	Crangon shrimp	Shrimp		
Crustacea	Crabs various	Crustacean		

Cymatogaster aggregataShiner perchTel. FishCyprinidae***CarpTel. FishEngraulis mordaxNorthern anchovyTel. FishEopsetta jordaniPetrale soleTel. FishEptatretus stoutiiHagfishHagfishBrex zachirusRex soleTel. FishHemilepidotus sppIrish lordTel. FishHypomesus pretiosusSurf smeltTel. FishIcelus spp**SculpinTel. FishIsopetta isolepisButter soleTel. FishLampetra ayresiiRiver lampreyLampreyLampetra ayresiiRiver lampreyLampreyLampetra ayresiiStaghorn sculpinTel. FishLoigo opalescensMarket squidCephalopodLumpenus sagittaSnake pricklebackTel. FishMicrogadus proximusPacific tomcodTel. FishMicrostomus pacificusDover soleTel. FishOncorhynchus mykissSteelhead troutTel. FishOncorhynchus nerkaSockeye salmonTel. FishParoficus staffStary flounderTel. FishParonenctidaeRightye flounderTel. FishPholidaeGunnel sppTel. FishPholidaeStary flounderTel. FishPleuronectidaeRightye flounderTel. FishPleutichthys stellatusStary flounderTel. FishProoclinus rothrockiWhitebarred pricklebackTel. FishPlatichthys melanostictusSand soleTel. FishSalmonidaeAdult salmonids <th></th> <th></th> <th></th>			
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	Trichodon trichodon	Sandfish	Tel. Fish

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CHAPTER 3: A CONCEPTUAL MODEL OF PROXIMATE ENERGETIC EFFECTS OF COASTAL HYPOXIA ON THE PACIFIC HARBOR SEAL, PHOCA VITULINA RICHARDII.

Abstract

A conceptual energetic individual-based model was created to simulate the possible energetic implications of coastal hypoxia on the spatial foraging behaviors and overall foraging efficiency of the Pacific harbor seal (Phoca vitulina richardii). The model was based on the daily energy budget of a male Pacific harbor seal at an adult maintenance body mass. In an effort to determine the potential energetic effects of coastal hypoxia, habitat compression of representative prey fish taxa was simulated at varying degrees of hypoxic events using STELLA Modeling Software ([©] iSee Systems). Hypoxia ranged from 'normoxia', or normal dissolved oxygen levels; to 'severe' in which up to 80% of the water column was affected, and approximately half of each species' horizontal habitat was lost. Pacific sandlance (Ammodytes *hexapterus*), Pacific herring (*Clupea pallasii*), and English sole (*Parophrys* vetulus) were chosen as three model species which best represented common prey types within the diet of the Pacific harbor seal. The factors of spatial foraging most affected by coastal hypoxia were travel distance to foraging grounds, total time spent at depth during foraging dives, and total energy balance. As travel cost to foraging decreased, overall energy balance increased.

For larger harbor seals (80kg and 100kg), English sole were the most efficient species on which to forage during normoxia (2.49% and 7.19% growth, respectively),

however during moderate to severe hypoxia sandlance are the most energeticallybeneficial prey species (up to 23.13% and 23.33% seal growth by percent body mass). For smaller harbor seals (60kg), Pacific herring represented the most energetically efficient prey species during normoxia, but during moderate to severe hypoxia, sandlance become the most energetically-beneficial prey species (21.29% growth). Sandlance represented the highest increase in foraging efficiency during severe hypoxic events for all three body masses of harbor seals. Smaller adult harbor seals shifted from generalized foraging on neritic schooling fishes to foraging closer inshore on smaller forage fish during increasing levels of hypoxia. Larger adult harbor seals shifted from foraging on calorically-rich groundfish species to schooling neritic fishes as hypoxia increased. Increases in individual foraging efficiency and changes in spatial foraging behaviors have the potential for population-level impacts and merit field-based quantitative study.

Introduction

Since 2002, unusually severe and prolonged hypoxic events have been occurring in the northern California Current Large Marine Ecosystem (CCLME), one of the four major eastern boundary current systems in the world (Chan et al. 2008b). Recurrent anoxia and hypoxia has occurred annually, and even as recently as summer 2013 (PISCO 2014). The CCLME, including the Oregon Coast, composes one of the four major Eastern boundary current marine ecosystems which support approximately 20% of the world-wide fishery landings, making them especially important in terms of biodiversity, as well as fisheries production (Pauly and Christensen 1995). Episodic hypoxic zones (areas w. < 1.4 ml dissolved oxygen per liter of water, or 30% saturation) have been documented in coastal oceans for more than three decades (Jewett et al. 2010). Locally, the Oregon coast is subject to annual hypoxic events, the strength of which is highly correlated with the strength and duration of annual upwelling events (Rabalais et al. 2010). In extreme cases, anoxia (<0.5 ml/l dissolved oxygen) has resulted in 'dead zones' with the 'near complete mortality of macroscopic invertebrates' as reported off the Oregon coast in 2006 (Chan et al. 2008b). Strong upwelling events represent altered nutrient transport and increased near-shore respiration that may be potentially linked to changing climate and physical processes (Chan et al. 2008b, Jewett et al. 2010).

In Oregon, a number of upper trophic level marine predator species, including several species of pinniped feed on a variety of commercially important fish species.

Of these pinniped species, the only one which remains reliably present year-round in Oregon is the Pacific harbor seal (*Phoca vitulina richardii*), which forages in nearshore waters that are susceptible to severe hypoxic events. Numbering more than 10,000 (Brown et al. 2005), harbor seals in Oregon represent a significant unit of biomass in the coastal ecosystem, and serve as important predators for a wide variety of schooling, salmonid, and flatfish species. While many of these species may be well-adapted for moderate hypoxic events, most are biologically unable to cope with dissolved oxygen levels below 1.4 ml/l (Vaquer-Sunyer and Duarte 2008). Therefore, it is predicted that habitat compression occurs when species avoid hypoxia by moving inshore and higher in the water column, resulting in increased risk of predation (Breitburg 2002, Eby and Crowder 2002, Zhang et al. 2009).

To the current date, the impacts of coastal hypoxia-induced fish habitat compression on piscivorous marine mammals have not been studied. Potentially important questions are whether compressed prey distributions translate to significant individual energetic effects for marine predators, and whether these effects translate to population-level impacts. The first step in addressing these problems is to determine whether hypoxic events elicit individual energetic changes for predators based on costs of foraging and transport. To determine whether this is a possibility, I have created a conceptual, qualitative model which simulates harbor seal foraging during varying levels of hypoxia. The span of severity ranges from 'zero' - in which normoxia occurs and species are found in their normally-inhabited spatial zones- to 'severe', where hypoxia encompasses up to 80% of the near-shore water column (Chan et al. 2008a). Three types of prey species were selected based on evidence of dietary importance, particularly in the summer months (Steingass, manu. in prog.); available literature on their reaction to variant dissolved oxygen levels; and for their gross representation of primary prey types of harbor seals. These types include schooling neritic fishes, bottom-dwelling flatfish, and dielly-cycling schooling and burrowing neritic fish. Each category of fish displays unique habitat and spatial use patterns, and each has a different adaptive response to varying levels of hypoxia, as described below. Prey tolerance to and reaction to hypoxia has been preliminarily documented for all three species of interest. Additionally, predator avoidance behaviors and reactions of these species are well-known. However, the combination of prey behavior in relation to both hypoxia and predator avoidance is not as readily apparent. Therefore, while my model does include some behavioral responses, I account for increased susceptibility of fish to predation on a largely spatial scale.

The species chosen for investigation were the Pacific herring (*Clupea pallasii*), the English sole (*Parophrys vetulus*), and the Pacific sandlance (*Ammodytes hexapterus*). Pacific sandlance (*Ammodytes hexapterus*) are a predominant Pacific harbor seal prey, and common inhabitants of estuaries and the continental shelf. Sandlance burrow into sandy substrate at night and disperse into the water column in schools of varying size during the day, (Eschmeyer and Herald 1999). Diurnal vertical migrations and burrowing rates of sandlance are shown to be affected by hypoxia, as shown by Behrens and Steffensen (Behrens and Steffensen 2007). Additionally, an oxygen gradient increasing shoreward would likely shift sandlance inshore, as well as higher in the water column.

English sole (*Parophrys vetulus*) are very commonly found in the diet of the Pacific harbor seal, and have a life history representative of other flatfishes that harbor seals are known to prey upon. Adult flatfishes are non-schooling and patchily distributed in sandy substrate during both day and night. They may also migrate epibenthically through the water column to feed (Clemens and Wilby 1961). Being a bottom-dwelling species, heavy upwelling-related hypoxia would likely result in compression of this species inshore, along the floor of the continental shelf.

Pacific herring (*Clupea pallasii*) are a highly school-oriented neritic fish species that exhibits spectacular grouping behaviors, resulting in a patchy aggregate resource (Whitehead 1985). Herring are proliferative and are commonly found in harbor seal diets around the globe, including the Pacific Northwest. A schooling fish species such as herring would likely be subject to both vertical and horizontal habitat compression (Eby and Crowder 2002, Keller et al. 2010).

Juvenile harbor seals have been noted to feed on different prey sources than adult seals, as they are relatively restricted in their diving capacity (Burns et al. 2005) and are also documented to spend less time offshore (Thompson et al. 1998a). Juvenile harbor seals have been noted to feed on crustaceans and estuarine fish which may also be affected by hypoxia. However, to reduce unnecessary model variation, my model focusses on adult, non-reproductive male harbor seals at maintenance weight. The average body mass of interest in this study is 80.0 kg, but seals of masses 60kg and 100kg were also examined. Once more data is gathered, modeling reproductive, nursing, or juvenile animals may be useful.

Individual-Based Modeling in Ecology

I have chosen to create a conceptual model for application in answering preliminary research questions about the system of interest. While not appropriate for answering applied quantitative questions in ecology, conceptual models can provide an elementary understanding of qualitative mechanisms for an ecological process (Grimm 1999). In cases of preliminary investigations where data does not exist, conceptual models are most appropriate when beginning to gather information about a system. In the case of the upper trophic level impacts of hypoxia, initiating a field study without any prior information can be particularly difficult and costly. For this reason, a conceptual model is a useful first step for designing a field-based study. Conceptual models can be more accurately parameterized per individual rather than on a large-scale basis. Therefore, they usually illuminate causes and effects as they relate to individual animals or single ecological units (Grimm and Railsback 2005).

Individual-based ecological models have been applied in a variety of topics, including foraging efficiency (Roese et al. 1991), bioenergetics (Malavear 2002), and cost of transport and senescence (Williams et al. 2004, Hindle and Horning 2010). In my creation of a conceptual model, I intended to create a model that is simple enough to be applied to future studies of harbor seal dive energetics and foraging, but also correctly parameterized that it may provide a clear picture of prey reaction and resultant effects on harbor seals during various hypoxia scenarios. The design of a field-based spatial foraging study in relation to hypoxia is particularly novel, and a working model will help guide experimental design. Factors that appear to have had the most significant implications in harbor seal foraging energetics were noted for field observation.

My model was parameterized using data collected regarding the spatial distributions of the three fish species, as well as physiological parameters of harbor seal physiology and behavior garnered from a review of harbor seal foraging behaviors. Harbor seal energetic budgets were determined from existing literature on metabolic rates and activity costs at maintenance (Markussen et al. 1990, Markussen et al. 1994) and costs of transport (Davis et al. 1985, Butler and Jones 1997). I hypothesized that, due primarily to decreased cost of transport and increased prey per unit area during hypoxic events, the foraging efficiency of harbor seals significantly increases during severe hypoxia (<30% saturation, 1.4 ml/l). I also proposed that during events of moderate hypoxia (30-75% saturation), foraging efficiency does not increase in an energetically significant way. While the model output is quantitative, my conclusions drawn are qualitative.

Methods

A computerized model was created using STELLA Modeling Software, v. 10.0.4 (© 2014 iSee Systems, Lebanon, NH). STELLA uses a combination of operational graphics and mathematical functions as a platform for the creation of dynamic models. I chose a 24 hour period as the span of one full simulation in my model, as harbor seals fairly reliably cycle their activities on a daily basis, returning to haul out sites nightly to rest. Using a day as a time period also allowed me to track growth on a daily and monthly basis. In the simulation of a full 24-hour period, the model was subsequently divided into time allotment of various activities. Primarily, the model was divided into time spent hauled out and resting ("dry") and time spent in the water ("wet"). The time spent wet was further divided into time actively foraging and time recovering on the surface between dives. Each time period had a unique metabolic rate associated with the corresponding activity level. For harbor seals in Oregon in the summer months, seals were assumed to be within their thermoneutral zone, and the costs of thermoregulation were therefore negligible (Hansen et al. 1995). Basal metabolic rate in Watts was calculated using Kleiber's equation (Kleiber 1961):

$BMR(W) = 3.39 \times (Mass(kg))^{0.75}$

Calculations regarding the BMR of harbor seals and other marine mammal species do exist (Lavigne et al. 1986), but they are not significantly different than Kleiber's original law and are based on limited data (Hoelzel 2009). Based on

previous studies of harbor seal time-energy budgets, modeled harbor seals were estimated to spend five hours resting exclusively on land (Yochem et al. 1987, Howard 2009), and the remaining nineteen hours submerged in the water. Of the time in water, 1/5 was assumed to be 'recovery time'; time spent between dives resting on the surface of the water, as this appears to be a consistent pattern for harbor seals and grey seals (Thompson et al. 1991). The remaining time was spent actively swimming to foraging locations or performing foraging dives.

General Model Structure

The primary structure of the model as created in STELLA © was divided into three submodels: "Foraging Energetics", "Hypoxia and Spatial Foraging", and "Dive Mechanics". Each addresses a different aspect of behavior or physiology, and is mechanistically linked to the other two components. The Foraging Energetics submodel is a daily energy budget for a foraging harbor seal at maintenance. It includes foraging costs, travel costs, metabolic rates, foraging gains, body mass, dive capabilities and metabolizable energy. This submodel is the central component of the model and its ultimate output, "Cumulative Energy Balance", was the final model output which was determinative of foraging efficiency. The Dive Parameters submodel consists of time-allocated dive parameters based on dive constraints as predicted by the body mass component of the Foraging Energetics submodel because dive abilities have been shown to link to body mass. It also provides outputs to the Foraging Energetics component by way of time allocation of diving versus simply swimming which ultimately impacts metabolic expenditures.

The Hypoxia and Spatial Foraging submodel addresses the spatial components of harbor seal foraging driven by prey distribution, as well as how they are potentially impacted by hypoxic events. There are three versions of the submodel, one for each prey species. Parameters include prey depth, distance from shore, school and individual density, and chance of encounter (successful dive). Additionally, this component includes a hypoxia component which is scaled from 0 to 1. Hypoxia impacts both the prey per square unit area, as well as the two spatial components of prey distribution; distance from shore and depth in the water column.

Submodel: Foraging Energetics

Very little work has been done regarding the swimming metabolism and cost of transport for harbor seals during foraging. Therefore, based on measurements by Davis et al. (1985) and Lesage et al. (1999), I assumed seals traveled and dove at the minimum cost of transport (MCT), 1.4 m/s. The cost for traveling at this velocity was estimated by Davis et al. to be approximately 2.3 J/m⁻¹/kg⁻¹ for an adult seal. As energetic rates were presented in most cases as rates per kilogram body mass per meter traveled, I had to translate distance back into a velocity that could be multiplied by time in order to get the overall energy expenditure over a 24-hour period. Using

this information, I was able to calculate transport costs during diving for seals by multiplying 2.3 $J/m^{-1}/kg^{-1}$ by distance traveled, shown below:

Active Travel Cost = 2.3 J/kg⁻¹/(1.4
$$\frac{M}{s}$$
 × TIME (s))⁻¹

The costs of transport were added to metabolic rates to obtain an activity cost. However, cost of transport was only utilized at one of either the ascent or descent phase of the dive. This is because it is highly unlikely that animals are neutrally buoyant; therefore, either their ascent or descent is likely in 'drift' phase and requires little additional energy (Williams et al. 2000). The other leg of vertical travel during the dive was considered to be at resting metabolic rate while swimming (SMR), as explained below. While diving, seals were assumed to travel vertically downwards, rather than at a specified grade or skew during diving.

For the remaining ~3.8 hours spent resting on the surface, I utilized Davis et al.'s (1985) estimated Resting Metabolic Rate (RMR) while swimming, which equaled $1.1 \text{ J/m}^{-1}/\text{kg}^{-1}$. Similarly, I calculated the distance traveled while under RMR utilizing the lower end of the MCT as calculated by Davis et al., being 1.0 m/s, and multiplied this times $1.1 \text{ J/m}^{-1}/\text{kg}^{-1}$ to obtain travel costs for this:

Resting Travel Cost =
$$1.1 \text{ J/kg}^{-1}/(1.0 \frac{M}{s} \times TIME(s))^{-1}$$

The total energy expenditure for 24 hours was obtained by adding the constituent metabolic rates plus the additional travel costs as dictated by travel distances generated by the model. Therefore, although the basal metabolic costs remained the same day to day, the overall energy expenditure differed variably due to the variability built into the diving and foraging components of the model. Foraging of the harbor seal was dictated by the Foraging Energetics and Hypoxia component of the model; prey encounter rates were built around various probabilities, and therefore differed from day to day; some days were more successful in capturing prey than others.

As many studies on harbor seals were performed utilizing different standard energy measures, various conversion factors were used. First and primarily, the measure of joules was considered to be the standard SI energetic measure for my model. Watts were a common unit of energy measure utilized by physiological studies on harbor seals which I used to parameterize the model; however, mL O^2 / time were also commonly used as it is one of the most easily measured energetic currencies in a laboratory environment. Therefore, I utilized the conversion used by Butler and Jones (1997) and Howard (2009) which calculated a conversion factor of 20.1 Watts per mL O^2 / min. Additionally, as pinnipeds in maintenance condition generally catabolize and metabolize adipose tissue (Hoelzel 2009), I assumed that any body mass change throughout the day was due to adipose addition or loss. Therefore, energy (J) was converted to body mass change (g) in a ratio of 39,300 J/g, or 39.3 kJ/g body mass (Schmidt-Nielsen 1997). For the three primary prey species, caloric content was based on empirically measured energy density from previous sources.

For pinnipeds consuming a large number of smaller, less energetically dense prey, the effect of satiation is an important consideration when calculating daily consumption rates. In the light of optimal foraging, seals would likely stop foraging if digestive satiation was reached. According to Rosen and Trites (2004), satiation was indeed a factor for captive Steller sea lions (*Eumatopias jubatus*) after consuming fish to14-16% of body mass. Considering the average weight by length of several prey species as determined by Vermeer and Devito (1986), the number of individual prey items consumed per feeding bout is unlikely to reach even the lowest point of satiety (11.5% body mass) (Table 3.1).

Table 3.1. Estimated number of individuals of common prey items of the Pacific harbor seal required to reach a level of satiety. Prey data as described in Vermeer and Devito (1986).

Common Prey Item	Individuals to Reach Satiety (rounded):
2 nd Year pacific herring	167
2 nd Year + Pacific Sandlance	544
Widow rockfishes	1631
Sockeye salmon	424
1 st year herring	2864
1 st year sandlance	4509

It could be argued that an actively foraging seal consuming fish throughout the day is subject to different physiological mechanisms and feedbacks than an individual being meal-fed in captivity. For this reason, I did not consider satiation effects within my model. Energy densities of prey were taken from Vermeer and Devito (1986) and Dygert (1990) as shown in Table 3.2 and 3.3.

Table 3.2. Mean energy contents of female English sole sampled by Dygert (1990) in Blaine, Washington 1983-1984.

Sampling Date	Mean Energy Content (kJ) of individual English Sole
June 6th	2336.8
July 22nd	2636.3

Cumulative Energy Balances

Over a twenty-four hour period, the cumulative energy balance was defined as the final balance in KJ from net metabolizable energy of prey consumed minus the additive energetic costs of basal metabolic rate and cost of transport during foraging and traveling. Metabolizable energy was defined as the energy available after digestion (fecal and urinary losses) for storage or growth, and was estimated to be 84.6% of gross energy consumed, as calculated by Boulva (1973).

Table 3.3. Conversion of caloric densities of fish from Calories per gram to KJ values per fish. Caloric density values obtained from Vermeer and Devito (1986).

Fish Species (Auklet Prey)	Mass (g) by Length	Calories Per Gram	Length (cm)	Expected Caloric Value (cal.)	Expected Energy Content (Kcal)	Expected Energy Content (KJ)
2 nd Year Pacific	59.7739922	6051	175	361692.4268	361.6924268	1513.321114
herring						
2 nd Year + Pacific	18.37951044	5383	155	98936.9047	98.9369047	413.9520093
Sandlance						
1 st year herring	3.485414995	4763	72	16601.03162	16.60103162	69.45871631
1 st year sandlance	2.213912557	4700	80	10405.38902	10.40538902	43.53614765

Diving Mechanics

The Diving Mechanics submodel contained the mechanisms relative to the diving and foraging habits of the modeled seal over a 24 hour basis. This submodel consisted of the time the animal spent in the water, and linked with the spatial foraging and hypoxia component to determine time allotment of dives as determined by dive depth and success, as well as time allotment between actively foraging and swimming on the water's surface between dives. To account for body mass-correlated dive abilities, dive times were based on proposed dive duration (DD). Dive duration as used here was considered to be the maximum amount of time a harbor seal would likely spend underwater for one foraging dive, based on empirical measurements by Lesage et al. (1999) and Womble (2012). Womble found a mean dive duration for harbor seals in Glacier Bay, Alaska (n = 572,106 dives) was 2.8 ± 0.5 minutes. Similarly, Eguchi and Harvey (2005) described median dive durations of male harbor seals in Monterey Bay, California of 2.75 to 7.25 minutes. As per (Bigg 1981), the theoretical Aerobic Dive Limit for an adult female (lactating) harbor seal, was 8.9 minutes. Dive duration and aerobic capacity are generally linked to body mass in marine mammals, and was shown in Eguchi and Harvey (2005). Utilizing data from Womble (2012) and Eguchi and Harvey (2005), dive duration was assumed to relate linearly to body mass, and was calculated as follows:

Maximum Dive Duration = $0.102 \times Mass(kg)$

The term 'maximum dive duration' (MDD) was used, rather than theoretical aerobic dive limit (TADL), as harbor seals are shorter-duration divers which generally operate well within their aerobic dive limits (Bigg 1981). Rather, the DD was considered to be a fraction of MDD. Successful dives and non-successful dives differed in their durations, as various authors have demonstrated that successful dives last longer on average than unsuccessful or search dives (Horning and Trillmich 1997, Weise et al. 2006, Hindle and Horning 2010, Womble 2012). Successful dives were assumed to last at 0.50*MDD; while unsuccessful dives were assumed to be 0.25*MDD. This yielded dive durations that fell well within the limits of previous data collected on *P. vitulina*, and the average correlated with Womble's mean dive duration value of 2.8 minutes (Boyd and Croxall 1996, Lesage et al. 1999, Womble 2012). For an 80 kg seal in my model, the average dive duration equaled 2.72 minutes.

The time a seal spent foraging at depth (TAD) could be deduced by subtracting time spent ascending plus descending from the total dive time of an individual dive (Figure 3.1):

TAD = Total Dive Time - (Ascent Time + Descent Time)



Figure 3.1. Typical U-shaped dive pattern as modeled; dive time was determinant on MDD, and time spent foraging at depth was considered to be dependent on ascent and descent time.

Therefore, because successful dives were longer and seals could therefore spend proportionately more time on the bottom, they are also considered to be more efficient (Kramer 1988). Prey were only considered to be encountered during successful dives. Because it is not realistic to assume exactly one prey item was consumed per minute at depth, a 'handling time' factor was used to estimate a realistic number of individual prey fish caught over time while foraging. Handling time was partially determined by fish size (smaller fish had shorter handling times), schooling or patchy distributions (English sole were often only captured once per dive, while multiple herring and sandlance could be captured), and afterwards adjusted in order to create a balanced daily energetic budget over a 24 hour period for an 80kg seal. Based on patch dynamics, a seal was assumed to be more likely to have subsequent foraging success if a previous dive was successful- especially in schooling species. Therefore, each subsequent dive after a successful dive was given an additional 25% chance of success. Once an unsuccessful dive occurred, this process reset itself.

Diving mechanics in the model were based on a time counter system, where the total time diving and recovering at the surface of the water totaled 19 hours per day; 15.2 hours of this time allotment was spent actively foraging, and 3.8 hours of this was considered to be time spent recovering at the water's surface between dives. The time allotment in the model was not parameterized to be variable, as increased variability in this component would not have served to answer any research questions regarding my general hypothesis. However, other parts of the model do include variability factors. As dive time was linked to aerobic dive capacity, smaller seals had resultantly smaller dive durations on average than larger seals. Therefore, foraging success was linked to the ability to dive to and forage at depth.

Total diving times, recovery times, and times at depth were totaled throughout the day to determine caloric expenditures by seals in the water. The total energy expended while recovering at the surface (SMR) was also totaled. At nineteen hours, the seal was assumed to return to the haulout site for the night, and returned to a basal metabolic rate.

Submodel: Hypoxia and Spatial Foraging

The third submodel was the "Hypoxia and Spatial Distribution" submodel which defined the spatial characteristics of prey distribution and resultantly, the foraging of the harbor seal on a two-dimensional basis: the depth and horizontal distance from shore at which prey were found, as well as the prey per square meter. This submodel also included hypoxia, the model's primary parameter of interest. The prey distance from shore and depth were determined using average values from literature, as well as some general estimations. This submodel has one version for each of the three prey species. Each model was created based specifically on the life history and habitat use traits of the prey species of interest, as noted in the introduction. One complete model with submodels was created and run for each species; and each was parameterized so that at normoxia, an adult harbor seal could subsist exclusively on that one prey item with minimal energy loss or gain overall. Although harbor seals are opportunistic foragers, a mixed prey model was not run. Rather, the results of the prey-specific models were compared individually to determine which types of foraging and prey sources appeared to be the most energetically beneficial in different hypoxia scenarios. Additionally, because harbor seals appear to consume only a few prey types per foraging bout (approximately 1.98 as shown by Lance et al. (2012) and the model was run over a 24-hour period, it is not an unrealistic expectation that prey types of one day may consist largely of one species.

Vertical prey distribution in the water column for sandlance and herring distribution were created using a Weibull Distribution in Microsoft Excel ©. Weibull distributions are continuous probability distributions which are defined by a shape parameter (k) and a scale parameter (λ). More dynamic than normal distribution functions, Weibull distributions can be altered to span any scale of values, and can be altered to reflect skewness. While traditionally utilized in applications of engineering, Weibull distributions can lend themselves well to biological applications (Pinder III et al. 1978). Separate Weibull distributions were created for depth distributions of herring and sandlance, and a distance from shore distribution was created for English sole. A mathematical function was utilized to link the distributions to hypoxia. The depth of highest density in the distribution was exported to STELLA and used as the terminal foraging depth for seals. In the case of sandlance and herring, harbor seals began foraging bouts with search dives of a depth of five meters, and with each dive depth increased by five meters until the maximum density depth was reached, where the seal would remain foraging for the duration of that diving bout. A diving bout was considered to be the series of dives of similar characteristics once it reaches foraging grounds.

Prey Distribution: English Sole (Parophrys vetulus)

English sole density distributions were assumed to be mostly one-dimensional; that is, even with severe hypoxia, sole were unlikely to be far above the seafloor.
However, there was a mild vertical component to English sole distribution. The topography of the seafloor at the Newport Hydrographic (NH) Line was graphically mapped in STELLA to give a realistic bathymetry of fish depth, and therefore dive depth in accordance to distance from shore (Figure 3.2). Therefore, the major compression component was horizontal as fish were forced closer inshore due to hypoxia (Figures 3.3, 3.4). English sole were assumed to inhabit depths of 60 meters or deeper, at an average of 15 kilometers from shore based on data by the West Coast Ground Trawl Survey (Keller et al. 2013). At maximum hypoxia ('Hypoxia = 1' in the model), fish were assumed to have lost 50% of horizontal habitat.



Figure 3.2. Graphical function of general bathymetry of the NH-Line, off Newport Oregon.



Figure 3.3. English sole distribution at Hypoxia = 0. Peak density function equals the distance from shore at which the maximum density of fish occurs.



Figure 3.4. English sole distribution at Hypoxia = 1.

Prey Distribution: Pacific Herring (Clupea pallasii)

Pacific herring spatial distributions were two-dimensional, described in both vertical distribution in the water column as well as horizontal distance from shore. A random distribution of 8,000 to 10,000 meters was chosen as the distance of fish from shore. For vertical distribution in the water column, a Weibull distribution with a shape parameter (k = 2) and a scale parameter ($\lambda = (80/Hypoxia + 1)$) was used, which made the distribution a function of hypoxia, and shifted fish nearshore during low oxygen events (Figures 3.5, 3.6).



Figure 3.5. Vertical Pacific herring distribution at Hypoxia = 0.



Figure 3.6. Vertical distribution of Pacific herring in severe hypoxia (Hypoxia = 1)

The original maximum encounter probability of Pacific herring during normoxia (the probability of encounter at the depth with most fish per unit area squared) was determined by the Weibull distribution, and parameterized based on Misund and Øvredal (1988). However, estimated school sizes in this study were highly variable so rather a reasonably smaller estimated range was used.

For all three prey species, harbor seals were assumed to travel one primarily long distance at MCT to a foraging ground, then remain in that proximity for the remainder of that foraging for the day, as per Thompson et al. (1998b). The energy expended in traveling to a foraging site was determined by multiplying the cost of transport times the final distance from shore at which the simulated foraging ground was located. During a hypoxic event, resultant distance from shore was determined by dividing the original distance from shore by the 'inshore coefficient' to obtain a new compressed value.

Inshore coefficient = 1 + Hypoxia_Value

This compressed depth value was multiplied by the compressed vertical distribution value to obtain the new habitat area of prey. Therefore, during severe or anoxic events (Hypoxia = 1), horizontal habitat was assumed to half, and the same number of fish were forced into a smaller habitat area, thereby increasing the probability of prey encounter. The increased likelihood of encounter was determined by dividing the original habitat area (at Hypoxia = 0) by the compressed habitat area (at Hypoxia = 1) to determine the multiplicative value for increased prey per unit area, which increased the likelihood of a random prey encounter:

$Increased \ likelihood \ of \ Encounter = \frac{Original \ Habitat \ Area}{Compressed \ Habitat \ Area}$

Increased likelihood of encounter was multiplied to the original maximum encounter probability plus a random chance variable of 0 to 75% to obtain the "Final Chance of Encounter". For three prey species, any value of the final chance of encounter that was greater than 0.5 (50%) was considered to be a successful dive; any value less than 50% was considered to be unsuccessful.

Prey Distribution: Pacific sandlance (Ammodytes hexapterus)

Sandlance have a unique life history and habitat utilization as compared to the other two categories of prey. They are a dielly-cycling forage fish which often burrow into substrate nocturnally to avoid predators and emerge into the water column to swim in schools during the day (Behrens and Steffensen 2007). Sandlance are comparatively low in caloric value as compared to Pacific herring and English sole (Table 3.2, 3.3). However, as they are quite small and exhibit schooling behaviors, sandlance were assumed to have a shorter handling time than larger prey. Sandlance are generally not burrowed in the daytime, when harbor seal foraging was assumed to take place. However, it has been shown that increasing hypoxia can affect the burrowing behavior of sandlance. Behrens and Steffensen (2007) noted the lesser sandlance (Ammodytes tobianus) exhibited altered burrowing behaviors during varying levels of dissolved oxygen. During moderate hypoxia sandlance were 10% more likely to be burrowed. However, in events of severe hypoxia, sandlance were 40% more likely to be actively swimming in the water column than during normoxia. Therefore, I assumed that there was a 10% reduction in the likelihood of foraging success in moderate hypoxia, and in severe hypoxia I multiplied the final probability of encounter by an additional factor of up to 1.40 in cases of moderate to severe hypoxia (Figure 3.9). Vertical distribution in the water column was determined by the Weibull function with shape parameter k = 10 and scale parameter $\lambda = 85/(Hypoxia +$ 1) (Figures 3.7, 3.8).



Figure 3.7. Vertical distribution of sandlance in the water column during normoxia. Most fish were assumed to be near the sandy bottom.



Figure 3.8. Vertical distribution of sandlance in the water column during severe hypoxia or anoxia. Fish are forced away from the bottom due to lethal levels of low DO.



Figure 3.9. Graphical function of sandlance burrowing during increasing hypoxia. Fish are more likely to seek burrows during moderate events, but less so in severe hypoxia.

Final distance of sandlance prey from shore was estimated similarly to other fish, however they were assumed to be nearer shore than other prey, as they are often found near intertidal zones (Eschmeyer and Herald 1999); the original distance offshore of 100 meters was divided by the inshore coefficient (1 + Hypoxia), effectively halving horizontal habitat during severe events. Final chance of encounter was determined as in other fish, with additional consideration for the burrowing coefficient:

Final Chance of Encounter =
$$\left(\left(random(0, 50) + \frac{MEP}{100}\right) * ILE\right) * BEC$$

Where MEP = Max Encounter of Probability ILE = Increased Likelihood of Encounter, and

BEC = *Burrow Emergence Coefficient (graphical function)*

All of the parameters combined to create a dynamic submodel with varying vertical and horizontal distributions, as well as dynamic probability of encounter for harbor seals. The results of the submodel, including dive depth and chance of encounter, were input into the 'Diving Mechanisms' submodel to determine time allotment of dives, as well as whether dives were successful or unsuccessful, which ultimately drove the dive time of each dive. Additionally, spatial foraging outputs from this submodel were input into the Foraging Energetics submodel as energetic costs of transport.

Model Verification and Validation

After basic construction and parameterization of thye model, it was calibrated to be energetically neutral as possible for an 80kg harbor seal at normoxia; that is, daily energetic gains or losses were minimal for each species. Daily mass gains/losses were cross-checked for plausibility with existing data as to harbor seal mass loss and gains at maintenance (0.3-0.4 kg per day) (Markussen et al. 1990). Additionally, the model was run for 30 consecutive 'days' (simulated 24 hour periods) and the monthly mass/gains were tallied.

The maximum and minimum daily growth values for a 60kg, 80kg, and 100kg harbor seal per day at normoxia are shown in Table 3.4.

Prey Species	Harbor Seal	Daily Mass Loss/Gain (kg)
	Mass (kg)	
English Sole (Parophrys vetulus)	60.0	Minimum: -0.050 (Loss)
		Maximum: -0.149 (Loss)
	80.0	Minimum: -0.061 (Loss)
		Maximum: 0.175
	100.0	Minimum: 0.013
		Maximum: 0.098
Pacific herring (Clupea pallasii)	60.0	Minimum: -0.092 (Loss)
		Maximum: 0.032
	80.0	Minimum: -0.101 (Loss)
		Maximum: 0.049
	100.0	Minimum: 0.033
		Maximum: 0.419
Pacific sandlance (Ammodytes	60.0	Minimum: -0.044 (Loss)
hexapterus)		Maximum: -0.107 (Loss)
	80.0	Minimum: -0.082 (Loss)
		Maximum: 0.015
	100.0	Minimum: -0.085 (Loss)
		Maximum: 0.06

Table 3.4. Growth and loss (kg) mass values for harbor seals during normoxia. Daily growth and loss values were calculated for three body masses of seals, using a conversion value of 39.3 kJ/g (Schmidt-Nielsen 1997).

All mass gains and losses were within the growth limits described by Markussen et al. (1990). In order to determine which parameters were particularly important for the ultimate outcome of the model (cumulative energy balance), various sensitivity analyses were run for each species of fish. Parameters were varied by 10% of their expected or modeled range, and outcomes were analyzed in R. For each sensitivity analysis, 50 24-hour simulations were conducted to capture a range of variability. The parameters tested via sensitivity analysis were: Total Time Spent Foraging at Depth vs. Seal Mass (kg); Total Energy Balance (KJ) vs. Seal Mass (kg); Total Time Spent Foraging at Depth vs. Hypoxia; Total Energy Balance (KJ) vs. Hypoxia; Total Energetic Balance (KJ) vs. Fish KJ Value (KJ value for each individual prey fish consumed); and Travel Cost to Foraging (KJ) vs. Hypoxia.

Results

Sensitivity Analyses

English Sole

For English sole, Total Time at Depth was particularly sensitive to Seal Mass $(p = 1.176 \times 10^{-6}, r = 0.3916)$ and Hypoxia $(p = 1.119 \times 10^{-6}, r = 0.3928)$ (Figure 3.10). Total Energy Balance was not significantly sensitive to Seal Mass (p = 0.05437, r = 0.075), but was sensitive to Hypoxia $(p = 4.249 \times 10^{-5}, r = 0.2972)$, as was Travel Cost to Foraging (p = 0.00019, r = 0.2538). Total Energetic Balance was not sensitive to the Fish KJ Value (p = 0.6652, r = 0.0039). For English Sole, body mass and hypoxia both explained a large amount of the variance for predictor variables.



Figure 3.10. Sensitivity analysis results for English sole. Total time at depth (min) and travel cost to foraging (KJ) were most strongly correlated with hypoxia. Seal mass (kg) did not strongly drive response variables in comparison. Energy balance was not sensitive to fish energy content (KJ).

Herring

For Pacific herring, Total Time at Depth was very sensitive to Seal Mass (p= 2.2×10^{-16} , r = 0.7585), as was Total Energy Balance (p = 1.5×10^{-9} , r = 0.5363). Total Time at Depth (p = 8.925×10^{-12} , r = .6244), Total Energy Balance (p = 3.389×10^{-11} , r = 0.6032) and Travel Cost to Foraging (p = 1.128×10^{-6} , r = 0.3926) were sensitive to Hypoxia. Lastly, Total Energetic Balance was not sensitive to Fish KJ Value (p = 0.09375, r = 0.0574). For Pacific herring, seal body mass most strongly explained the variance in response variables for the model (Figure 3.11).



Figure 3.11. Sensitivity analysis results for Pacific herring. Both seal mass (kg) and hypoxia strongly drove the response variables of total energy balance (KJ), time at depth (min) and travel cost to foraging (KJ). Energy balance was not sensitive to fish energy content (KJ).

Sandlance

In the sandlance model, Total Energy Balance was sensitive Seal Mass (p = 0.0056, r = 0.1494), but Total Time at Depth not (p =0.3702, r = 0.0168), Total Time at Depth was quite sensitive to Hypoxia (1.391 x 10^{-14} , r = 0.7123), as was Total Energy Balance (1.298 x 10^{-11} , r = 0.6185) and Travel Cost to Foraging (p = 1.027 x 10^{-5} , r = 0.336). Total Energetic Balance was not sensitive to Fish KJ Value (p = 0.0996, r = 0.0555). Hypoxia explained the majority of variance in response variables for sandlance (Figure 3.12).

Overall Sensitivity Results

Overall, sensitivity results were similar between species. The total energy balance in the English sole and sandlance models was less sensitive to seal mass than the herring model, suggesting that mechanisms of foraging efficiency differ between species. Travel cost to foraging was strongly linked to hypoxia and consisted of a large percentage of the daily energy budget of the modeled harbor seal.



Figure 3.12. Hypoxia strongly drove total energy balance (KJ), time at depth (min), and travel cost to foraging (KJ). Those factors were more weakly driven by seal mass (kg). Energy balance was not sensitive to fish energy content (KJ).

Growth and Energetic Balances

The results of the three prey-specific models inspire a variety of questions, potential mechanisms, and parameters of interest for future field-based studies. Primarily, from the results of the models, it can be suggested that for all three species (prey types), there was an increase in a positive energetic balance for a harbor seal foraging in increasingly hypoxic conditions. This was largely driven by prey compression inshore and therefore reduced travel costs to foraging. Secondarily, increased foraging success resulted in seals capturing more prey and therefore obtaining a higher net KJ intake per day. Larger seals (80kg, 100kg) tended to benefit more energetically than smaller seals (60kg) simulated in the model scenarios. This is perhaps because a smaller adult seal's dive capacity is already limited to shorter, nearshore dives as compared to larger adults. Large adult seals which have a higher dive capacity are able to benefit more from increased prey densities on a per-dive basis. Even in scenarios of severe hypoxia, smaller seals were limited in their dive capacities. The projected monthly growth values for seals were different for each prey species and seal body mass; English sole- and herring-based growth curves were Sshaped, while the sandlance-based growth curve was logistic and showed signs of leveling or maximizing at higher levels of hypoxia. Except in the case of the 60kg individual, Pacific herring proved to be the most energetically-beneficial species to forage on during severe hypoxia (Figure 3.14, Table 3.9). For the smaller seal, sandlance appeared to be the most energetically-beneficial (Figure 3.15, Table 3.10).

While English sole were the largest and most calorically-rich prey species, they were also distributed strictly on the seafloor of the continental shelf, and therefore did not experience two-dimensional habitat compression as strongly as sandlance or herring (Figure 3.13, Table 3.8). Overall, all three sizes of seals benefited somewhat from even moderate hypoxia.

Spatial Foraging Behaviors

Several energetically-important factors were impacted by hypoxia, including travel cost to foraging (KJ), time at depth (min), travel distance to foraging (m), and terminal dive depth (m). The terminal dive depth was the depth at which the highest density of prey was located, and was the depth at which the harbor seal ultimately reached and remained at for the duration of the dive bout. Travel costs between normoxia and severe hypoxia (Hypoxia = 1) roughly halved for all three species (Tables 3.5, 3.6, 3.7). Time at depth varied between species, and the foraging model for Pacific sandlance showed the most dramatic responses, with seals experiencing an increase of time at depth between 2.541 and 3.589. This leads to increased foraging efficiency, as the ratio of time at depth per total dive time increases accordingly.

Harbor seal travel distance to foraging roughly halved for all species of prey, and terminal dive depth change was equal for all seal masses in the Pacific sandlance and English sole models, but was greater for seals of mass 100kg (0.50) than for seals of mass 60kg (0.80) in the Pacific herring model. This was due to parameterization; English sole depth was not determined by the Weibull distribution as the two other species; additionally smaller (60kg) seals were limited in their capacity to dive for Pacific herring and therefore were less affected by hypoxia than larger 100kg seals. The results suggest potentially significant alterations in spatial foraging behaviors during prey habitat compression that could be readily apparent in collected spatial data.

Table 3.5. Change in Response Variables (Value at Hypoxia = 1 / Value at Hypoxia =0) for English sole (*Parophrys vetulus*)

Seal Mass	Travel Cost (KJ)	Time at Depth (min)	Travel Distance to Foraging (m)	Terminal Dive Depth (m)
60kg	0.498	3.589	.498	0.375
80kg	0.502	2.756	.502	0.375
100kg	0.490	2.541	0.490	0.375

Table 3.6. Change in Response Variables (Value at Hypoxia = 1 / Value at Hypoxia =0) for Pacific herring (*Clupea pallasii*)

Seal Mass	Travel Cost	Time at Depth	Travel Distance	Terminal Dive
	(KJ)	(min)	to Foraging (m)	Depth (m)
60kg	0.474	0.965	0.474	1
80kg	0.474	1.013	0.474	1
100kg	0.474	0.965	0.474	1

Table 3.7. Change in Response Variables (Value at Hypoxia = 1 / Value at Hypoxia =0) for Pacific sandlance (*A. hexapterus*)

Seal Mass	Travel Cost	Time at Depth	Travel Distance	Terminal Dive
	(KJ)	(min)	to Foraging (m)	Depth (m)
60kg	0.507	2.04	0.507	0.80
80kg	0.512	2.474	0.512	0.40
100kg	0.495	1.695	0.495	0.50



Figure 3.13. Harbor seal individual growth with an English sole-based diet in four hypoxia gradients.

Initial Body	Hypoxia	Growth or		% Body Mass
Mass (kg)	(0 to 1)	Loss (kg)	$\pm STDEV$	Change
60.00	0.00	-3.13	0.0294	-5.21
60.00	0.25	-2.99	0.0374	-4.98
60.00	0.75	-2.70	0.0333	-4.49
60.00	1.00	-1.89	0.0264	-3.15
80.00	0.00	1.99	0.0649	2.49
80.00	0.25	3.54	0.0573	4.43
80.00	0.75	2.63	0.0671	3.28
80.00	1.00	4.38	0.0645	5.48
100.00	0.00	7.19	0.0977	7.19
100.00	0.25	8.42	0.1046	8.42
100.00	0.75	7.81	0.0928	7.81
100.00	1.00	8.94	0.1116	8.94

Table 3.8. Changes in mass for hypoxia scenarios on an English sole diet.



Figure 3.14. Harbor seal individual growth with a Pacific herring-based diet in four hypoxia gradients.

Initial Body	Hypoxia	Growth or		% Body Mass
Mass (kg)	(0 to 1)	Loss (kg)	± STDEV	Change
60.00	0.00	-0.78	0.0316	-1.30
60.00	0.25	4.94	0.0245	8.24
60.00	0.75	7.67	0.0213	12.78
60.00	1.00	8.44	0.0288	14.07
80.00	0.00	0.04	0.0491	0.05
80.00	0.25	7.39	0.0697	9.24
80.00	0.75	18.60	0.0317	23.25
80.00	1.00	19.78	0.0298	24.72
100.00	0.00	6.75	0.0803	6.75
100.00	0.25	9.76	0.0635	9.76
100.00	0.75	23.11	0.0353	23.11
100.00	1.00	23.96	0.0326	23.96

Table 3.9. Changes in mass for hypoxia scenarios on a Pacific herring diet.



Figure 3.15. Harbor seal individual growth with a Pacific sandlance-based diet in four hypoxia gradients.

Table 3.1	10	Changes	in mass	for	hypoxia	scenarios	on a	Pacific	sandlance	diet
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Initial Body	Hypoxia	Growth of		% Body Mass
Mass (kg)	(0 to 1)	Loss (kg)	± STDEV	Change
60.00	0.00	-1.68	0.0205	-2.81
60.00	0.25	5.23	0.0133	8.72
60.00	0.75	10.75	0.0002	17.91
60.00	1.00	12.77	0.0002	21.29
80.00	0.00	0.29	0.0420	0.36
80.00	0.25	10.16	0.0187	12.71
80.00	0.75	16.52	0.0003	20.64
80.00	1.00	18.51	0.0002	23.13
100.00	0.00	1.43	0.0440	1.43
100.00	0.25	14.26	0.0259	14.26
100.00	0.75	21.37	0.0005	21.37
100.00	1.00	23.33	0.0002	23.33

Discussion

Models are created to simulate familiar environments in unfamiliar or difficultto-examine conditions. As a result, all models require that assumptions be made, as replicating a system exactly in its entirety defeats the purpose and usefulness of the model. A conceptual model has additional assumptions, as data is very preliminary or retrospective. My goal was to create a conceptual, individual based model that could be used in the design of future field studies regarding the energetic effects of coastal hypoxia on harbor seal foraging behaviors. Specifically, I sought to obtain enough information to determine whether hypoxic events could have significant energetic impacts on harbor seals, and which variables were most important for such impacts. For seals of all body masses, hypoxic events resulted in increased energetic balances which increased with the severity of the event. Energetic gains and resultant growth were less for smaller seals, which foraged at shallower depths that were not as heavily affected by hypoxia. For 60kg seals, significant energetic gains only occurred at higher levels of hypoxia (0.75 to 1). However, for seals feeding on nearshore sandlance, growth by percent body mass was comparable for all three masses of seals. The data gathered suggests that moderate to severe hypoxic events could cause alterations in spatial foraging behaviors of harbor seals, as prey move inshore and closer to the water's surface in order to avoid low oxygen conditions. Model results also suggest that energy expenditures based on spatial distribution of prey are considerably more important than the dietary composition itself. The idea that

environmental variables may be more predictive than prey-based models for marine mammals has also been suggested by Torres et al. (2008). However, scat-based analyses or less fine scale methods of dietary analysis such as stable isotope analysis or fatty acid quantitative analysis might secondarily provide evidence for shifts in foraging behavior. If hypoxia does in fact cause heavy habitat compression of prey species of harbor seals, it has a high potential to cause changes in energetic balance for individuals. This would merit further field studies and examinations of spatial foraging behaviors of harbor seals during normoxia and hypoxic events.

Each prey model produced results unique to the spatial distribution of that prey species. For sandlance which were distributed nearshore, and high in the water column, physiological limitations of body mass had little effect on overall energetic balance or time spent foraging at depth for the foraging harbor seal. Physiological limitations were apparent for Pacific herring, as smaller seals spent twice as much time foraging at depth during severe hypoxia as did larger seals. However, decreased travel costs and dive capacity still resulted in larger mass gains of heavier seals. The sandlance model demonstrated a stronger correlation to hypoxia in terms of overall foraging success, which highlights the fact that the burrowing and behavioral component of the model likely also impacted the final result. This demonstrates that environmentally-forced behavioral modification of prey (such as decreased predator avoidance during hypoxia-induced physiological stress) can be especially impactful on predator foraging efficiency as well as prey mortality. Due to limited information, fine-scale aspects of prey behavior are potentially very important, but particularly difficult to incorporate into a foraging model without adequate data (Domenici et al. 2002, Behrens and Steffensen 2007, Domenici et al. 2007, Behrens et al. 2010).

During severe hypoxia, 80kg and 100kg seals benefitted more than smaller 60kg seals, as demonstrated by projected monthly growth. For smaller seals, Pacific sandlance represented the most beneficial prey during moderate-high and severe hypoxia, but Pacific herring were equally beneficial during moderate (25%) hypoxia. This suggests that a small adult harbor seal may shift from generalized foraging to foraging on inshore schooling species, such as sandlance, during moderate and severe hypoxia. For 80kg and 100kg seals, Pacific herring represented the most advantageous species to forage on during severe hypoxia, followed closely by sandlance. In moderate hypoxic events, sandlance was the most beneficial species. English sole represented a modest increase in caloric benefit for all three body sizes of seals in any level of hypoxia, however represented an efficient prey resource at normoxia for larger seals. The fact that English sole quickly become inefficient during any level of hypoxia suggests that a shift in dietary consumption might occur as adult harbor seals begin to focus on schooling forage fish. Larger adult harbor seals may switch from foraging on calorically-dense bottom fish to schooling fish during hypoxia. During normoxic conditions, sandlance are not particularly beneficial for 60kg seals, but become so during moderate to high hypoxia likely due to increased availability very close to shore. Small harbor seals that forage on a mix of schooling

neritic fish during normoxia may benefit from shifting to nearshore foraging of small forage fish such as sandlance. In all cases, the daily total energetic balance (energetic gains minus metabolic and activity costs) was not strongly sensitive to fish energetic content, demonstrating that energetic balance of the modeled harbor seal had less to do with which particular prey item they are foraging on, and more to do with the spatial distribution, vertical depth, and handling time/density of individuals of that species.

The primary goal of this model was to create a framework for the collection of field data in the most efficient and applicable way possible. The underlying mechanisms outlined by the model suggest that the examination of coastal hypoxia on uppermost trophic levels is a problem worth examining, as individual energetics ultimately has the potential to translate to population- and ecosystem-level effects. Based on the results of this model, I suggest that a preliminary examination of harbor seal foraging behaviors before, during and after coastal hypoxia events could begin to illuminate potentially important, but under examined seasonal ecological impacts. The model suggests that changes in spatial foraging behavior, as well as dietary composition, may occur for all masses of adult male harbor seals during hypoxic events. The collection of field data relating to spatial foraging and overall dietary composition during hypoxic events may yield distinct patterns for a highly opportunistic and unpredictable predator. I predict inshore shifts in foraging, especially for smaller harbor seals, and a shift from groundfish to schooling neritic fishes for seals of intermediate to large adult mass. For smaller seals, I predict that

foraging behaviors will shift even closer inshore as seals shift from schooling neritic forage fish to inshore smaller species.

Once preliminary time-depth recorder (TDR) data for harbor seals is gathered and analyzed in relation to hypoxia, the model can be re-parameterized in order to create a more accurate and applicable model. Ultimately, TDR data can be combined with other environmental components including sea surface temperature (SST), upwelling index (a primary driver of hypoxia), direct dissolved oxygen measures, and productivity to create a predictive habitat model for harbor seals. Predictive habitat modeling can be particularly useful in spatial planning efforts that are taking place along the eastern Pacific coastline in the form of marine protected areas, marine reserve, and wave energy platforms. The collection of baseline data regarding harbor seal spatial ecology is also particularly important, as very little current data exists for harbor seals in the CCLME. Illuminating upper trophic level impacts of coastal hypoxia is an important step towards understanding bottom-up forcing of ecosystems and food webs within the marine environment, particularly as unprecedented changes continue to occur in marine areas important to management, conservation, and natural resources.

APPENDIX II: SUBMODELS

Submodel: Foraging Energetics. Diagrammatic representation of the basic inputs or converters (ovals), outputs or stocks (rectangles) and action connectors (arrows) as utilized in STELLA.



Submodel: Dive Mechanics. Diagrammatic representation of the basic inputs or converters (ovals), outputs or stocks (rectangles) and action connectors (arrows) as utilized in STELLA.



Submodel: Hypoxia/Spatial Foraging. Diagrammatic representation of the basic inputs or converters (ovals), outputs or stocks (rectangles) and action connectors (arrows) as utilized in STELLA.



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CHAPTER 4: CONCLUSIONS

The purpose of this thesis was to examine the foraging behavior of the Pacific harbor seal (*Phoca vitulina richardii*) in the Pacific Northwest region of the United States as it relates to the environmental factor of upwelling-driven coastal hypoxia. While coastal hypoxia is a normal occurrence within the California Current Large Marine Ecosystem, recent increases in duration, spatial extent, and severity suggest that examining ecosystem-level impacts of bottom-up forcing will be particularly important issue for future management. In this aspect, the impacts of coastal hypoxia on upper trophic level predators are poorly researched and understood globally. The Pacific harbor seal was chosen as a model study species because it remains in the regions of Oregon and Washington year-round, and forages nearshore in areas that are likely affected by coastal hypoxia, particularly during severe events.

My literature review of harbor seal dietary habits revealed that harbor seals feed on a number of commercially-important fish species, and therefore represent an important predator species within coastal ecosystems. Harbor seal diet was found to be particularly diverse and contained at least 148 prey types from 11 taxa with the Pacific Northwest region. Seals in Oregon consumed 86 species from 2 taxa, while seals from Washington State consumed 128 prey types from all 11 taxa. Lastly, harbor seals consumed 49 described prey types from 7 taxa, most of which were present in Washington and Oregon.

I created an energetic individual based conceptual model for harbor seal foraging in the Pacific Northwest during events of normoxia and moderate to severe coastal hypoxia. From my literature review, I selected three representative prey species to be modeled as a gross representation of prey types in the harbor seal diet; English sole (Parophyrs vetulus), Pacific herring (Clupea pallasii), and Pacific sandlance (Ammodytes hexapterus). For each species of prey, a separate model of harbor seal spatial foraging behavior was created. The hypothesis that intermediate and severe hypoxia increase foraging efficiency was tested for three body masses of harbor seals- 60kg, 80kg and 100kg, as well as four different gradients of hypoxia – 'normoxia' (0), 'moderate' hypoxia (0.25), 'moderate-severe' hypoxia (0.50), and 'severe' hypoxia or 'anoxia' (1.0). Foraging efficiency for all three masses of seals did increase with increased hypoxia, although differently for each prey species and seal mass. For each mass, distance to foraging grounds roughly halved between normoxia and anoxia, and the efficiency of diving (time spent foraging at depth per dive) increased. For seals 80kg and 100kg, English sole represented the most efficient prey species during normoxia. However, during moderate hypoxia, Pacific herring was the most efficient species, followed closely by Pacific sandlance. For all three masses of seals, Pacific sandlance was the most efficient prey species during anoxia. Smaller harbor seals (60kg) benefited the most from foraging on Pacific herring
during normoxia, but quickly became more successful when foraging on sandlance during moderate and severe hypoxia. These results suggest that during events of hypoxia, larger harbor seals could benefit from a potential shift from a diet of calorically-dense groundfish to patchily-distributed neritic schooling fish such as herring or sandlance which experience pronounced vertical and horizontal habitat compression. Similarly, small harbor seals may have a more generalized diet during normoxia and shift foraging to inshore, shallower areas during periods of increasing hypoxia.

The results gathered from both chapters suggest that harbor seals may change diet based on significant environmental perturbations such as severe inshore hypoxia. These shifts should be readily apparent in the collection and analysis of field-based TDR data of harbor seals prior to, during, and after the formation of hypoxic events. Specifically, a change in spatial foraging as it relates to distance from shore, time spent foraging at depth, and dive depth may translate to important individual energetic impacts for harbor seals. As these individual impacts may translate to population- or ecosystem- level impacts, gathering field-based data is vital to understanding the upper trophic level impacts of coastal hypoxia. The model created here, as well as my literature review of harbor seal dietary composition in the Pacific Northwest provide some preliminary hypotheses and parameters of interest for the continued examination of the impacts of bottom-up forcing on a marine predator species.

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