ASSESSMENT OF THE REPRODUCTIVE ECOLOGY OF HARBOR SEALS *(PHOCA VITULINA*) AND NORTHERN SEA OTTERS (*ENHYDRA LUTRIS KENYONI*) IN ALASKA USING SUBSISTENCE BIOSAMPLING PROGRAMS

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A

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By

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Abstract

Harbor seals (*Phoca vitulina*) and northern sea otters (*Enhydra lutris kenyoni*) in Alaska have experienced extreme fluctuations in abundance in recent decades. The purpose of this study was to examine growth and determine the age and size at sexual maturity in populations of these two species, as spatial and temporal variations in environmental conditions and changes in ecological constraints as a result of population fluctuations can influence growth and reproductive characteristics of individuals. All samples for this research were collected via biosampling, the collection of measurements and biological tissue samples, as a component of subsistence harvesting by Alaska Natives. In Chapter 1, morphometric measurements and reproductive tracts were collected by the Alaska Native Harbor Seal Commission's Biosampling Program from female harbor seals harvested throughout the Gulf of Alaska from 1998 through 2005. Seals attained an asymptotic standard length (SE) of 147.7 ± 2.6 cm and body mass of 82.2 ± 4.8 kg. Female harbor seals did not mature until a minimum age of 3 yr, a standard length of 122 cm, and a weight of 48 kg. The average age of sexual maturity was 4.2 ± 0.7 yr (95% CI). Fetal growth was measured by standard length, curvilinear length, axillary girth, the cube root of fetal mass, skull length, condylobasal length, zygomatic width, and skull width against the day of the year the mother was harvested. The x-intercept of the linear regression of each fetal growth measurement against the day of the year produced estimates of the implantation date that ranged from September 22nd to October 17th, with a mean date of September 30th ± 8 d (SD). Harbor seals from this study are smaller in length, have a later implantation date, and are larger at sexual maturity compared to harbor seals in the Gulf of Alaska from the 1960s. In Chapter 2, morphometric measurements and reproductive tracts were collected by a Native Alaskan subsistence hunter from 40 male sea otters near Gustavus, in Southeast Alaska. The maximum recorded standard length and axillary girth were 160 cm and 78.7 cm, respectively. Sexual maturity was assessed by the histological examination of the testes and epididymides and the subsequent measurement and characterization of the seminiferous tubules. Male sea otters in the region reached sexual maturity at 3 to 4 yr of age, after attaining a standard body length of 130 cm, a mean seminiferous tubule diameter of 140 µm, and a baculum length of 14 cm. Sea otters outside Gustavus, Alaska exhibit increased body size and lower ages of sexual maturity compared to sea otters in other regions of Alaska, suggesting that resources are abundant and are not limiting maturation rates of male sea otters near Glacier Bay. In the future, as anthropogenic influences continue to increase and environmental conditions fluctuate, biosampling programs will be an invaluable tool for continued monitoring of marine mammals in Alaska.

Table of Contents

Page

Signature Page i

Title Page iii

Abstract v

Table of Contents vii

List of Figures ix

List of Tables xi

Acknowledgements xiii

General Introduction 1

Literature Cited 7

Chapter 1: Female growth, reproductive characteristics, and fetal growth of harbor seals (*Phoca vitulina*) in the Gulf of Alaska 15

1.1 Abstract 15

1.2 Introduction 16

1.3 Materials and Methods 20

1.3.1 Study Area and Animals 20

1.3.2 Laboratory Analyses 21

1.3.3 Data Analysis 22

1.4 Results 24

1.4.1 Postnatal Growth 24

1.4.2 Fetal Growth 25

1.4.3 Sexual Maturity 26

Page

1.5 Discussion 27
  1.5.1 Sampling Biases and Limitations 27
  1.5.2 Postnatal Growth 27
  1.5.3 Fetal Growth 29
  1.5.4 Reproductive Maturity 31
1.6 Literature Cited 34

Chapter 2: Growth and sexual maturation in male northern sea otters (*Enhydra lutris kenyoni*) from Gustavus, Alaska 55

2.1 Abstract 55
2.2 Introduction 56
2.3 Materials and Methods 61
  2.3.1 Study Area and Animals 61
  2.3.2 Laboratory Analyses 61
  2.3.3 Data Analysis 63
2.4 Results 64
2.5 Discussion 66
2.6 Literature Cited 71

General Conclusion 91
  Literature Cited 95

List of Figures

Page

Figure 1.1. Locations of subsistence-harvested harbor seals used in this study 45

Figure 1.2. Von Bertalanffy growth curves fitted to (a) standard body length (n=65) and (b) body mass (n=63)...46

Figure 1.3. First year growth (±SD) in (a) standard length (n=15) and (b) body mass (n=15) 47

Figure 1.4. Harbor seal fetal body growth 48

Figure 1.5. Harbor seal fetal skull growth 49

Figure 1.6. Total number of corpora in the ovaries of immature and mature harbor seals............50

Figure 2.1. Map of the sea otter harvest area near Gustavus, Alaska 81

Figure 2.2. Representative seminiferous tubules of (a) immature, (b) pubertal, and (c) mature sea otters...82

Figure 2.3. Gompertz growth curves fitted to (a) standard body length (n=29) and (b) axillary girth (n=29) 83

Figure 2.4. Gompertz growth curves fitted to (a) baculum length (n=31) and (b) baculum mass (n=31)..84

Figure 2.5. Gompertz growth curves fitted to baculum diameter (n=31) at the (a) head, (b) middle, and (c) base 85

Figure 2.6. Gompertz growth curves fitted to mean testes (a) length, (b) width, (c) volume, and (d) mass versus age (n = 30) 86

Figure 2.7. Mean seminiferous tubule diameter (STD) versus (a) age (n = 30), (b) standard body length (n=36), (c) baculum length (n=38), and (d) mean testes length (n=38)....................87

Figure 2.8. Sea otter (a) baculum length (n=38) and (b) mean testes mass (n=37) versus standard body length 88

List of Tables

Page

Table 1.1. Parameter estimates (±SE) of von Bertalanffy growth functions for standard length and body mass 51

Table 1.2. ANCOVA results and estimated implantation dates and growth rates for fetal measurements 52

Table 1.3. Mean values for body mass (kg), standard length (cm), ovary mass (g), and ovary volume (cm^3) by reproductive status 53

Table 2.1. Parameter estimates (±SE) for Gompertz growth functions 89

Table 2.2. ANOVA results, mean, standard deviation (SD), range, and sample size (n) for body size and reproductive measurements for immature, pubertal, and mature sea otters 90

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General Introduction

During the 1960s to the 1980s populations of numerous marine mammal species, including northern fur seals (*Callorhinus ursinus*), Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and northern sea otters (*Enhydra lutris kenyoni*) declined precipitously in southwest Alaska, including the western Gulf of Alaska (GOA), the Aleutian Islands, and the eastern Bering Sea (Braham *et al.* 1980, Trites 1992, Trites & Larkin 1996, Doroff *et al.* 2003, Burn & Doroff 2005, Estes *et al.* 2005, Small *et al.* 2008). Harbor seals also declined dramatically in the central GOA at Tugidak Island starting in the mid-1970s, Aialik Bay in the late 1970s, and Prince William Sound in the mid-1980s; however, these populations are now showing signs of recovery and are likely increasing (Pitcher 1990, Frost *et al.* 1999, Jemison *et al.* 2006, Hoover-Miller *et al.* 2011, Allen & Angliss 2013). Contrastingly, in Southeast Alaska harbor seals, as well as the eastern distinct population unit of Steller sea lions, have been stable or increasing in most areas (Calkins *et al.* 1999, Sease *et al.* 2001, Small *et al.* 2003). In Glacier Bay, however, large declines in harbor seal abundance have been documented since the 1990s (Mathews & Pendleton 2006, Womble *et al.* 2010).

Sea otters in Alaska were hunted extensively by Russian fur traders beginning in the late 1700s (Kenyon 1969). By the time they were protected under the North Pacific Fur Seal Treaty of 1911, they had been hunted to near extinction and were locally extirpated from Southeast Alaska (Kenyon 1969, Jameson *et al.* 1982). Although the Southwest Alaska stock of sea otters recovered following federal protection, it began to decline rapidly in the 1980s, which led to the stock being listed as Threatened under the Endangered Species Act in 2005 (Doroff *et al.* 2003, Estes *et al.* 2005, Doroff *et al.* 2011). Between 1965 and 1969 the Alaska Department of Fish and Game (ADF&G), with the assistance of other state and federal agencies, reintroduced 412 sea otters from Prince William Sound and Amchitka Island to six sites in Southeast Alaska. Sea otter abundance in Southeast Alaska has since increased in many regions, including Glacier Bay where population growth is so high there is likely a significant amount of immigration from adjacent areas (Bodkin *et al.* 2002, Bodkin *et al.* 2006, Esslinger & Bodkin 2009).

It is largely unknown why a multitude of marine mammal species are declining in the western GOA and why there are such contrasting population trends in portions of the central and eastern GOA. It is likely the result of a combination of factors including spatial and temporal changes in environmental conditions, prey availability, predation, and anthropogenic effects that can all affect survival and reproduction (Trites 1992, Merrick *et al.* 1997, Anderson & Piatt 1999, Doroff *et al.* 2003, Heise *et al.* 2003, Miller *et al.* 2005, Mathews & Pendleton 2006, Trites *et al.* 2007, Atkinson *et al.* 2008).

Life history characteristics such as growth, survival, and reproduction are affected by population density and environmental conditions. Population density plays a crucial role in determining the reproductive characteristics in mammals (Fowler 1987, Fowler 1990, Wauters & Lens 1995, Bonenfant *et al.* 2002, Williams *et al.* 2013). As population density increases, the per-capita prey availability typically declines and organisms must make trade-offs between survival, growth, and reproduction (Stearns 1989). Life history theory predicts that growth should be slower and sexual maturity achieved later as resources become limiting (Stearns 1992). The growth and reproductive characteristics of populations can therefore yield inferences on population status and environmental conditions. As population density increases, the body mass of individuals typically declines and animals often reduce the amount of energy allocated to reproduction, increasing the age of first reproduction and reducing reproductive success (Scheffer 1955, Bengtson & Laws 1985, Fowler 1990, Wauters & Lens 1995, Festa-Bianchet &

Jorgenson 1998, Williams *et al.* 2013). In populations in which declines are driven by bottom-up causes, such as resource limitation, one expects to see slow growth and delayed mean age of sexual maturity (Stearns 1976). In populations driven by top-down influences, such as predation, one expects to see rapid growth and early maturity (Stearns 1976). Early maturation at a large body size may also indicate rapid growth and good environmental conditions due to low population density and/or plentiful resources (Stearns & Koella 1986). Consequently, understanding growth and reproduction of marine mammal populations is not only important for management, but also can provide insight into population density and/or prey availability including changes over time and space. The large fluctuations in population size and density of marine mammal populations in Alaska has likely caused changes in growth and reproductive characteristics, which has implications on the future status of these populations.

The Marine Mammal Protection Act (MMPA) was established in 1972, prohibiting the take of marine mammals with the purpose of maintaining healthy and stable populations and ecosystems (16 U.S.C. § 1361 et. seq.). Obtaining scientific samples from marine mammals has become a difficult task since the enactment of the MMPA, due to the restrictions on lethal study methods and the requirement of a permit for any sample collections that are considered a "take". "Takes" include tagging, disturbing, restraining, collecting dead marine mammals, or collecting samples from live or dead animals. Alaska Natives are exempt from the prohibition of the take of marine mammals under the MMPA, section 101(6), and are permitted to harvest marine mammals for subsistence purposes providing that it is done in a non-wasteful manner and there are no hunting restrictions imposed by the Endangered Species Act.

Marine mammals are an important source of food and income in the form of handicrafts for Native Alaskan communities. The health of those species is essential to provide for Alaska

Native harvests to sustain their cultural and traditional ways of life. Biosampling, or the collection of measurements and biological tissue samples, from these harvested animals provides valuable information that allows scientists and resource managers to monitor the health and condition of marine mammals over time and space. Biosampling subsistence-harvested animals can produce large sample sizes and allow access to data that otherwise would be difficult or impossible to collect, creating a comprehensive understanding of marine mammal populations in Alaska. Biosampling programs are mutually beneficial to both scientists and Alaskan Natives, by providing samples to assess the health and status of marine mammal populations and supplying important information on the food safety and sustainable use of the marine mammals that Alaska Natives consume.

Alaska is ideally suited for biosampling of subsistence harvested animals with its large populations of marine mammals and numerous coastal communities in which Alaskan Natives rely on marine mammals for subsistence. Biosampling programs can take multiple forms. The Alaska Native Harbor Seal Commission (ANHSC) ran a structured Biosampling Program from 1996 to 2006, over which time they trained and certified 155 biosampling technicians and collected samples from over 500 harbor seals (Alaska Native Harbor Seal Commission; http://harborsealcommission.org/). A formal biosampling manual was created and harvesters and technicians were trained and certified in proper methods for recording data and collecting, storing, and shipping tissue samples (Vanek 2001, Hoover-Miller 2013a). Samples from the biosampling program have contributed to research on harbor seal health and condition, growth, population structure, contaminants, diet, and reproduction. The program was suspended in 2006 due to a lack of funding. In April, 2013 the ANHSC hosted a biosampling workshop in Seward, Alaska, with the goal of identifying ways of re-establishing the biosampling program (Hoover-Miller 2013b).

The collection of biosamples can be less structured than programs such as the ANHSC Biosampling Program. Sea otter samples for this research were collected by a single Native Alaska sea otter subsistence hunter. This type of relationship still requires a substantial level of training in data recording and standardized sample collection, but when constrained in scope, can be much less expensive, and can provide an adequate number of samples for a targeted research project. Regardless of the format of the biosampling program, the data that can be gained from physical samples and traditional ecological knowledge are valuable for evaluating the health and condition of free-ranging animals and managing human interactions with marine mammals in Alaska. Biosampling of subsistence harvested animals provides an opportunity for resource users, managers, and scientists to collectively learn about, and track over time, the health and condition of harvested animals and the populations they represent.

In Chapter 1, morphometric measurements and reproductive tracts from 85 female harbor seals were collected by Alaska Native subsistence hunters as part of the ANHSC's Biosampling Program. Collected between 1998 and 2005 from locations throughout the GOA, these samples were examined macroscopically to describe female growth and sexual maturity, and fetal growth. The specific objectives were to 1) examine both prenatal and postnatal growth and 2) characterize sexual maturity as a function of age and body size. Changes in body growth and reproductive characteristics often correspond to spatial and temporal variations in environmental parameters and/or population dynamics. Understanding the growth and reproductive characteristics of harbor seal populations in Alaska, in light of the population fluctuations over recent decades, is crucial for understanding past and future changes.

In Chapter 2, morphometric measurements and reproductive samples collected from 40 sea otters by an Alaska Native subsistence hunter were examined to evaluate the growth and sexual maturity of male sea otters near Glacier Bay, in Southeast Alaska outside Gustavus. The objectives were to determine (1) age and size at sexual maturity and (2) morphometric changes based on age and reproductive state for male sea otters. This research compliments and expands on previous work to create a clearer and more detailed understanding of the reproductive strategies of sea otters in Southeast Alaska, specifically those otters at the forefront of the population expansion.

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Chapter 1:

Female growth, reproductive characteristics, and fetal growth of harbor seals (*Phoca vitulina*) in the Gulf of Alaska[1]

1.1 Abstract

Harbor seals *(Phoca vitulina)* in Alaska have experienced extreme fluctuations in abundance in recent decades. Significant changes in population size can lead to changes in ecological constraints that influence growth and reproductive characteristics of individuals. This study assesses pre- and postnatal growth and sexual maturity of harbor seals in the Gulf of Alaska using morphometric measurements, reproductive tracts (n = 85), and fetuses (n= 27) collected by subsistence hunters as part of the Alaska Native Harbor Seal Commission's Biosampling Program from 1998 through 2005. Female seals attained an asymptotic standard length (SE) of 147.7 ± 2.6 cm and body mass of 82.2 ± 4.8 kg. Fetuses increased 0.33 cm d^{-1} in standard length and 0.09 $g^{1/3}$ d^{-1} in mass. There were no significant differences in growth between male and female fetuses. Based on the inverse regressions of fetal growth on day of the year, implantation date ranged from September 22nd to October 17th, with the mean date of September 30th ± 8 d (SD). Female harbor seals matured at a minimum age of 3 yr, a standard length of 122 cm, and a mass of 48 kg. The average age of sexual maturity was 4.2 ± 0.7 yr (95% CI).

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[1] Hutchinson, E.A., S. Atkinson, and A. Hoover-Miller. (2014). Female growth, reproductive characteristics, and fetal growth of harbor seals (*Phoca vitulina*) in the Gulf of Alaska. In preparation for Marine Mammal Science.

1.2 Introduction

Harbor seals (*Phoca vitulina*) are a widely distributed coastal pinniped that inhabit temperate, subarctic, and arctic waters in both the northern Atlantic and Pacific oceans. The timing of harbor seal breeding and birthing varies geographically, but within a particular region is highly synchronized (Bigg 1969a, Temte *et al.* 1991, Temte 1994). In the Gulf of Alaska (GOA), pups are born from May through mid-July (Pitcher & Calkins 1979, Jemison & Kelly 2001). After birth, the mother nurses her pup for approximately 4 to 6 weeks (Bigg 1969b, Bigg & Fisher 1974, Pitcher & Calkins 1979). Female harbor seals come into estrus and mate shortly after weaning (Bigg & Fisher 1974, Pitcher & Calkins 1979). The development of the embryo is suspended at the blastocyst stage for approximately 1.5 to 3 months, in a process referred to as embryonic diapause, ensuring that pups are born when environmental conditions are most favorable to their survival (Fisher 1954, Bishop 1967, Bigg 1969b, Bigg & Fisher 1974, Pitcher & Calkins 1979, Boyd 1991, Atkinson 1997). Following embryonic diapause, the blastocyst attaches to the uterine wall and continues to develop for 8 to 9 months of active fetal development, also referred to as placental gestation (Bigg & Fisher 1974, Boyd 1991).

Harbor seals in Alaska have experienced large fluctuations in abundance in recent decades. At Tugidak Island (Central GOA), the population of harbor seals declined by an estimated 85% between 1976 and 1988 (Pitcher 1990). In Prince William Sound, abundance declined by approximately 63% between 1984 and 1997 (Frost *et al.* 1999). Aialik Bay, a tidewater glacial fjord, also experienced large declines beginning in the late 1970s (Hoover-Miller *et al.* 2011). The populations of harbor seals at Tugidak Island, Prince William Sound, and Aialik Bay have stabilized since the mid-1990s, early 2000s, and late 1980s, respectively, and all show indications of increasing trends (Jemison *et al.* 2006, Hoover-Miller *et al.* 2011, Allen & Angliss 2013). Harbor seals in areas of Southeast Alaska, such as Ketchikan and Sitka, have been stable or increasing (Small *et al.* 2003). However, in Glacier Bay, harbor seals declined by up to 75% from 1992 to 2002 and they continue to decline (Mathews & Pendleton 2006, Womble *et al.* 2010). What exactly caused these declines, and why Glacier Bay continues to decline at an alarming rate despite ecological and anthropogenic protections is largely unknown (Mathews & Pendleton 2006, Womble *et al.* 2010). Significant changes in population size can produce profound changes in individual growth and reproductive characteristics through the influence on ecological constraints such as prey resource availability, which can determine the future status of these harbor seal populations (Hood & Ono 1997, Laidre *et al.* 2006, Holmes *et al.* 2007).

Studies of life history characteristics are vital for assessing the health and condition of wild animals. This is valuable for scientific research, managing human interactions with wild populations, cultural wellbeing, and may provide insights into the dynamics of the ecosystems of those animals. The energy that organisms allocate to growth and reproduction can aid in understanding population status, climate conditions, resource availability, and the predation pressures on the subject population (Stearns 1976, Stearns & Koella 1986, Reiter & Le Boeuf 1991). As population density increases, the per-capita prey availability typically declines and organisms must make trade-offs between survival, growth, and reproduction (Stearns 1989). As resources become limited, life history theory predicts that growth should be slower and sexual maturity achieved later (Stearns 1992). As population density increases, the body mass of individuals typically declines and animals often reduce energy allocated to reproduction, increasing the age of first reproduction and reducing reproductive success (Scheffer 1955, Fowler 1990, Wauters & Lens 1995, Festa-Bianchet & Jorgenson 1998, Williams *et al.* 2013).

Slow growth and a later age at sexual maturity can therefore indicate a scarcity of food resources due to high population density and/or poor environmental conditions (Bengtson & Laws 1985, Trippel 1995). A population in decline that exhibits these characteristics may be subject to food limitation or environmental stress. Conversely, a population with rapid growth and an early age at sexual maturity can indicate abundant nutrient resources and good environmental conditions (Bengtson & Laws 1985). In growing populations that are below carrying capacity, it is expected that age at sexual maturity be reduced due to resources not being fully exploited, while in declining populations, the opposite would be expected, with sexual maturity being delayed (Stearns 1976). Monitoring growth and reproduction over time and space can therefore provide insight into possible causes of population fluctuations and are vital for informing management decisions.

The northeast Pacific has experienced significant changes over the last several decades. Global climate change has produced warming of the majority of the earth's surface, with particular influence on northern ecosystems (Oechel & Vourlitis 1997, Jorgenson *et al.* 2001, Walther *et al.* 2002, Hinzman *et al.* 2005). In addition to this general warming trend, the northeast Pacific experienced an abrupt increase in temperature in the late-1970s, which has been associated with a widespread marine ecological regime shift involving a transition in the Pacific Decadal Oscillation from a cold to warm phase (Anderson & Piatt 1999, Hare & Mantua 2000). This shift was associated with a decline in forage species such as shrimp and capelin and an increase in groundfish recruitment and pacific salmon catches in the GOA (Anderson & Piatt 1999). The regime shift coincided with documented declines in the harbor seal populations at Tugidak Island, Aialik Bay, and the Aleutian Islands (Pitcher 1990, Jemison *et al.* 2006, Small *et al.* 2008, Hoover-Miller *et al.* 2011). A further regime shift occurred in 1989, yet the changes were not as prevalent as the 1977 shift and did not represent a simple shift back to pre-1977 conditions (Hare & Mantua 2000). Changes in prey composition, abundance, and distribution as a result of these ecosystem-level changes may be a potential cause or a contributing factor in the harbor seal population fluctuations (Hinzman *et al.* 2005, Ware 2007, Overland *et al.* 2008). Documenting the growth and reproductive success of harbor seals over time and across different habitats/ecosystems provides a means of monitoring population fluctuations and evaluating their potential causes. Marine mammals are often viewed as sentinels of ocean health (Jessup *et al.* 2004, Moore 2008). As harbor seals are exposed to a changing climate and increasing anthropogenic disturbances, monitoring their population status and individual health is a valuable means of monitoring ocean conditions and potential impacts on food security for Alaskan Natives who harvest seal populations for consumption.

In the past, reproduction in marine mammals was traditionally studied using lethal methods and gross macroscopic and microscopic examinations of the reproductive tracts. Collecting biological samples from marine mammals became much more challenging after the enactment of the Marine Mammal Protection Act (MMPA) in 1972. Most data on harbor seal reproductive characteristics and fetal growth were collected before the MMPA (Bishop 1967, Bigg 1969b, Pitcher & Calkins 1979, Pitcher & Calkins 1981). Post-MMPA, data on marine mammal reproduction have mostly been obtained from stranded or captive animals (Bodkin *et al.* 1993, Pietraszek & Atkinson 1994, Iwasa & Atkinson 1996, Gardiner *et al.* 1999). Such animals are unlikely to be representative samples of healthy, wild populations.

The data and samples utilized for the present research came from wild and presumed healthy harbor seals harvested for subsistence purposes by Alaska Natives and collected by the Alaska Native Harbor Seal Commission’s (ANHSC) Biosampling Program. From 1996 to 2006 the ANHSC Biosampling Program trained and certified hunters and other technicians on standardized scientific protocols for the collection of morphometric measurements and tissue samples from subsistence harvested harbor seals. Biosamples from subsistence-harvested animals provides tissues and associated data necessary to assess reproductive characteristics of healthy, wild harbor seals. The contributions of subsistence harvesters provides access to vital life history data for assessing the health and condition of seals, without the need to sacrifice individuals strictly for scientific purposes and abides by current MMPA regulations.

This study investigates female growth and reproductive biology and fetal growth of harbor seals from the GOA. We used morphometric measurements and reproductive tracts collected from subsistence-harvested animals to: 1) examine both prenatal and postnatal growth and 2) characterize sexual maturity as a function of age and body size. Changes in body growth and reproductive rates often correspond to spatial and temporal variations in environmental parameters and/or population dynamics. Understanding the growth and reproductive characteristics of harbor seal populations in Alaska, in light of the population fluctuations over recent decades, is crucial for understanding past and future changes.

1.3 Materials and Methods

1.3.1 Study Area and Animals

Between 1996 and 2006 the ANHSC's Biosampling Program certified 155 biosampling technicians from 40 native villages, who voluntarily collected biological samples from more than 500 subsistence-harvested harbor seals. Samples and associated data are managed by the University of Alaska Museum of the North. A subset of those samples were used in this research, including reproductive tracts from 85 female harbor seals and 27 fetuses collected between 1998 and 2005 throughout the GOA (Fig. 1.1). Sample sizes in some comparisons may be smaller due to incomplete measurements or tissue collections for some seals. In the field, each female reproductive tract was removed in its entirety, including the uterus and both ovaries. If the seal was pregnant and a fetus was present, the fetus typically was left in the uterus; some near-term fetuses were removed from the uterus. The entire reproductive tract was placed in a Ziplock bag and frozen before being shipped for analysis. In addition to the reproductive tract, the biosampler collected data on date, location, body mass, standard length, evidence of lactation, and any abnormalities of the harvested seal. Body mass was measured to the nearest pound using a hanging scale. Standard length was measured to the nearest cm from the tip of the nose to the tip of the tail along a flat surface with the seal on its back. A canine tooth for most individuals, and an incisor for some were collected and sent to Matson’s Laboratory in Missoula, Montana for aging (Blundell & Pendleton 2008).

1.3.2 Laboratory Analyses

Each reproductive tract was thawed before examination in the laboratory. The right and left ovaries were separated from the reproductive tracts and weighed individually to the nearest 0.1 g. The length, width, and depth of each ovary were measured using dial calipers to the nearest 0.1 cm. The ovaries were bisected and examined under a dissecting microscope for evidence of corpora lutea and corpora albicantia. The number of corpora lutea and corpora albicantia in each ovary were counted and recorded and then combined for both ovaries.

After being excised from the uterine horn, each fetus was weighed and the sex determined. The mass of the fetus was measured to the nearest g. Standard length, curvilinear length, and axillary girth were all measured to the nearest 0.1 cm using a flexible vinyl measuring tape. Standard length was measured identically to that of older seals. Curvilinear length was measured from the tip of the nose to the tip of the tail following the curve of the body, and axillary girth was measured around the body of the fetus just under the pectoral flippers. On each fetal skull, four cranial measurements were taken to the nearest 0.1 cm using dial calipers. These measurements included 1) the skull length from the back of the skull to the anterior extent of the zygomatic process, 2) the condylobasal length (CBL) from the tip of the nose to the back of the skull, 3) the maximum skull width measured at the base of the skull, and 4) the zygomatic width measured across the skull from the distal extent of the zygomatic process.

1.3.3 Data Analysis

The reproductive cycle of harbor seals is highly synchronized within a specific geographic location (Bigg 1969a, Temte *et al.* 1991, Temte 1994). As a result, reproductive events such as breeding, implantation, and birth occur approximately at the same time within a population. Although there is some variation (Jemison *et al.* 2006), for the purposes of this research, we assumed a birth date of June 1st based on the literature and previous research (Bigg 1969a, Pitcher & Calkins 1979, Calambokidis *et al.* 1987, Jemison *et al.* 2006, Hoover-Miller *et al.* 2011). To examine first year growth, all seals under 1 year of age, as determined by the growth layers in the cementum of the teeth, were aged to the month using the assumed birth date of June 1st and the date the animal was harvested. Mean ± SD of standard length and body mass were calculated for each month and a simple linear regression model was fit to the data.

Postnatal growth was described using von Bertalanffy growth curves (von Bertalanffy 1957, Lydersen & Kovacs 2005). Growth curves for standard length and body mass were of the form:

$$L_x\,(or\ M_x) = L_\infty(or\ M_\infty)[1 - e^{-a(x-x_0)}]^b, \qquad (1.1)$$

where L_∞ and M_∞ are the asymptotic length (cm) and mass (kg), L_x and M_x are the length and mass at time x, x is the age of the seal in years, x_0 is an estimated time before birth when the embryo begins to grow after embryonic diapause (McLaren 1993), e is a mathematical constant that is the base of the natural logarithm (2.71828), and a and b are both constants where a describes the rate of approach to the horizontal asymptote and b describes the curvilinearity of that approach (McLaren 1993). A value of -0.63 was chosen for x_0 based on data for harbor seals in the GOA in McLaren (1993), and was also supported by our fetal data. Growth models were fit in R, version 3.0.2 (R Core Team 2013) using nonlinear least squares estimation.

An analysis of covariance (ANCOVA) test was run to determine any significant differences between male and female fetuses for each fetal measurement. Fetal growth was described using linear regression analysis to examine standard length, curvilinear length, axillary girth, the cube root of mass, and the four skull measurements as a function of the day of the year the mother was harvested (Stewart *et al.* 1989, Garlich-Miller & Stewart 1999, Chabot & Stenson 2000, Yunker *et al.* 2005). Day 1 and day 366 represent January 1st in consecutive years (Garlich-Miller & Stewart 1999, Chabot & Stenson 2000, Yunker *et al.* 2005). The day of implantation was approximated by the x-intercept of the linear regression of each measure against day of the year (Stewart *et al.* 1989). Those estimates were then averaged to produce a mean implantation date.

Each seal was categorized as reproductively immature, nonpregnant, or pregnant to compare morphometric measurements by reproductive status. Seals were considered immature if their ovaries showed no signs of prior ovulations and the uterus and uterine horns were noticeably small and had not previously expanded or experienced involution subsequent to a prior pregnancy. Females with ovaries that contained at least one corpus luteum or corpus albicantium were considered sexually mature. Nonpregnant seals were sexually mature seals that were not pregnant at the time of harvest. When analyzing the ovarian measurements, pregnant seal ovaries were further categorized as pregnant-active (ovary on the pregnant side of the reproductive tract) or pregnant-inactive (ovary on the nonpregnant side of the reproductive tract). For immature and nonpregnant animals the mean mass and volume of the right and left ovary were recorded. Lactating animals (n=2) were excluded from this analysis due to a small sample size and unique reproductive state that did not fit into any of the aforementioned reproductive categories. Standard length and body mass data were approximately normally distributed and mean measurements were compared among reproductive statuses using analysis of variance (ANOVA) and post-hoc Tukey-Kramer multiple comparison tests. Ovary mass and volume data were not normally distributed and did not have constant variance. These data were log-transformed to meet normality and constant variance assumptions and the mean measurements were then compared among reproductive statuses using ANOVAs and post-hoc Tukey-Kramer multiple comparison tests. The significance level for all tests was $P \leq 0.05$.

1.4 Results

1.4.1 Postnatal Growth

The age of animals used in the postnatal growth analysis ranged over 0 – 21 yr. Growth was asymptotic in both standard length and body mass. The von Bertalanffy growth model fit the data well (Fig. 1.2; Table 1.1). Seals reached 90% of asymptotic length (132.9 cm) at age 3.3 yr. Mass increased at a slower rate and did not reach 90% of asymptotic growth (74.0 kg) until 7.9

yr. The largest seal collected in this study was pregnant at the time of capture and was 13 yr old, weighed 104.4 kg and measured 150 cm in length. The largest nonpregnant seal was 8 yr old, weighed 80.8 kg, and measured 159 cm in length. Body mass was much more variable than length, likely explained by weight gain and loss associated with pregnancy. The sole 15 yr old seal in the dataset showed an abnormally low body mass (48.6 kg) for its age. This particular seal was lactating at the time of capture and had given birth approximately 2 wk earlier. Such a low body mass was likely the result of the extensive fat resources that a mother seal provides to its pup.

First-year growth was examined using seals under 1 yr of age, with ages ranging from 0 to 10 mo. Growth over the first year showed a strong linear trend for both standard length (R^2 = 0.85, n=15) and body mass (R^2 = 0.63, n=15) (Fig. 1.3). However, body mass showed greater variability and did not increase as sharply over the first year as was seen for standard length. Initial growth over the first few months for both standard length and body mass was rapid, followed by a decrease in the rate of growth of both length and mass. One 9 mo old seal had an abnormally high body mass (41.8 kg), which resulted in an elevated mean value and a large standard deviation for 9 mo old seals. It is possible that this seal was aged incorrectly, but its standard length (111 cm) aligned closely with the values for the other 9 mo seals in the study.

1.4.2 Fetal Growth

Of the 27 fetuses, 16 were male and 11 were female. Data from male and female fetuses were combined due to no significant difference between sexes for standard and curvilinear length, axillary girth, body mass and all four skull measurements (Table 1.2). All measurements were plotted as a function of day of the year (Figs. 1.4 and 1.5). Standard length (R^2 = 0.95, n = 27), curvilinear length (R^2 = 0.92, n = 25), axillary girth (R^2 = 0.92, n = 24), the cube root of body mass ($R^2 = 0.88$, n = 27), skull length ($R^2 = 0.76$, n = 26), CBL ($R^2 = 0.92$, n = 27), skull width ($R^2 = 0.95$, n = 27), and zygomatic width ($R^2 = 0.93$, n = 26) all showed a strong linear relationship with day of the year. The x-intercept of the linear least-squares regression provided estimates of the implantation date for each measure. Those dates ranged from September 22nd to October 17th, with a mean of September 30th ± 8 d (SD). Estimated implantation dates for each measurement and predicted growth rates are presented in Table 1.2.

1.4.3 Sexual Maturity

Forty of the 85 female seals were determined to be sexually mature. Of those sexually mature seals, 27 were pregnant at the time of collection. Seal reproductive status had a statistically significant effect on both body mass and standard length (ANOVA, F = 82.85, P = <0.001; F = 36.71, P = <0.001). Mean values of standard length and body mass by reproductive status are presented in Table 1.3. Sexually immature seals were significantly lighter and shorter than both pregnant and nonpregnant animals (Table 1.3). Pregnant and nonpregnant seals showed no significant difference in body mass or standard length (Table 1.3).

Ovary mass and volume also differed significantly based on the reproductive status of the individual (ANOVA, F = 123.9, P = <0.001; F = 115.5, P = <0.001). Ovary mass and volume were log-transformed for statistical analysis, and then back-transformed. The geometric mean values by reproductive status are presented in Table 1.3. Ovaries of immature animals were significantly lighter and had a smaller volume compared to those of sexually mature animals (Table 1.3). The ovary on the active side of the reproductive tract was significantly heavier and had a significantly greater volume than the ovary on the inactive side of the reproductive tract (Table 1.3). There were no significant differences between the ovary mass and volume of the ovary on the inactive side of the reproductive tract and the ovaries of nonpregnant animals

(Table 1.3). Interestingly, there was also no significant difference between the ovary mass and volume of nonpregnant animals and the ovary on the active side of the reproductive tract (Table 1.3).

The examination of the total number of corpora (corpora lutea and corpora albacantia) in relation to age, standard length, and body mass revealed thresholds at which harbor seals become mature (Fig. 1.6). Animals did not mature until a minimum age of 3 yr (n = 81), a standard length of 122 cm (n = 67), and a weight of 48 kg (n = 64). The average age (with 95% confidence limits) of sexual maturity was estimated at 4.2 ± 0.7 yr using the technique described by DeMaster (1978), although the sample size (n = 82) limited the strength of this calculation.

1.5 Discussion

1.5.1 Sampling Biases and Limitations

The data used in this study come from harvested animals and therefore do not represent a truly random sample. There is the possible bias of hunter selection and the availability of the seals to be harvested. For example, older age classes of adult seals were poorly represented in our data. Important life history events for harbor seals such as reproductive maturity and the majority of growth, typically occur within the first 5 yr of life, minimizing the effect of this bias on our data analyses

1.5.2 Postnatal Growth

Standard length for harbor seals in the GOA has experienced a downward trend since the 1960s. The asymptotic value of 147.7 ± 2.6 (SD) cm for standard length in this study is slightly smaller than that reported for the GOA previously by Bishop (1967) (155 cm) and McLaren (1993) (150.2 cm). McLaren’s (1993) value is an estimate from the combination of data from

Bishop (1967), Pitcher (1977), and Pitcher and Calkins (1979). However, our maximum reported standard length and body mass for a nonpregnant female (159 cm and 80.8 kg) were slightly larger than those found previously (151 cm (n= 141) and 76.2 kg (n=140)) for the GOA (Bishop 1967). Our asymptotic standard length is also slightly smaller than the 150 cm found for harbor seals in British Columbia (Bigg 1966). Harbor seals in the Kattegat-Skagerrak area in the northeast Atlantic (Härkönen & Heide-Jørgensen 1990), at a similar latitude to the GOA, showed an asymptotic length (146.0 ± 1.2 (SE) cm) similar to the seals in our study. However, our asymptotic body mass (82.2 ± 4.8 kg) is considerably heavier than that found for seals in the Kattegat-Skagerrak area (66.7 ± 2.4 (SE) kg) (Härkönen & Heide-Jørgensen 1990), British Columbia (65 kg) (Bigg 1966), and in the GOA previously (68 kg) (Bishop 1967). Our asymptotic value for body mass of female harbor seals in the GOA aligns more closely with seals from Svalbard, Norway (83.2 ± 2.7 (SE) kg) (Lydersen & Kovacs 2005). Lydersen and Kovacs (2005) concluded that harbor seals in Svalbard carry more blubber than other populations further south, hence giving them a higher asymptotic body mass. The high asymptotic body mass found for our seals may also be an indication of increased blubber levels. Body mass, however, showed considerably more variation than did standard length. This is not surprising, as blubber levels, and consequently body mass, fluctuates greatly throughout the year due to reproduction, molting, and seasonality of prey (Härkönen & Heide-Jørgensen 1990). Lydersen and Kovacs (2005) used measurements from seals collected during the same period of the year (June-September). Our samples were collected throughout the year with a majority of the samples collected in November – March when pregnancy occurs, and therefore a higher asymptotic body mass may be a result of sampling time, and not a true indication of increased body mass for seals in the

GOA. Length is a more static measure, as it is a reflection of skeletal growth, and therefore we see less variation among similarly aged animals, making it a more accurate measure of growth.

Growth over the first year appears to be divided into two phases. Over the first 1 to 2 months the pup suckles from the mother, during which time the pup exhibits rapid growth. Harbor seal pups have been found to approximately double their birth mass during the suckling period (Bishop 1967, Bigg 1969b). After the pup is weaned, the growth rate of standard length and body mass decreases as the pup is now nutritionally independent from the mother and must hunt on its own. This pattern has been documented in previous studies for harbor seals and other pinnipeds (Bishop 1967, Pitcher & Calkins 1979, Chambellant *et al.* 2003). Our dataset included just one 0, 1, and 3 mo-old seal and no 2 mo-old seals, making it difficult to definitively talk about the change in growth rate pre and post-weaning.

1.5.3 Fetal Growth

The reproductive cycle of most pinnipeds is characterized by a period of embryonic diapause (Boyd 1991, Atkinson 1997). The timing and duration of this diapause varies between and within species (Bigg 1966, Bishop 1967, Bigg & Fisher 1974, Garlich-Miller & Stewart 1999, Chabot & Stenson 2000). Data in this study indicate implantation for harbor seals in the GOA ranges from late September to early October. From the x-intercept of the linear least-squares regression of each fetal measurement, we estimated the implantation date for harbor seals in the GOA to be between September 22nd and October 17th, with a mean of September 30th ± 8 d (SD). Implantation date for harbor seals has previously been estimated at early to mid-September near Tugidak Island in the 1960s (Bishop 1967) and early October for the GOA in the 1970s (Pitcher & Calkins 1979). Our estimate of September 30th aligns more closely with the latter (Pitcher & Calkins 1979) and indicates that implantation date for harbor seals in the GOA is later than that found for seals in the 1960s (Bishop 1967). This later implantation date would likely result in a later mean pupping date. Seals at Tugidak Island and Aialik Bay were observed to give birth earlier in the mid-1960s and mid-1990s (early June) compared to the mid to late 1970s (late June) (Jemison & Kelly 2001, Hoover-Miller *et al.* 2011). If a nine month active gestation period is assumed, a mean implantation date of September 30th would result in a late June birthing peak for our study animals.

As we combined data for the entire GOA in our analyses, we cannot rule out the possibility of regional differences. Limited sample sizes did not allow us to examine the sub-regions separately, yet little variability in our data may indicate similar fetal growth rates and implantation date for harbor seals throughout the GOA. Also, the size of the blastocyst is not zero at the time of implantation, which may have resulted in a slight underestimation of implantation date, but this effect is likely to be minimal considering that the size of the newly implanted blastocyst is extremely small (<0.1 g) (Pitcher & Calkins 1979).

The cause(s) of the termination of embryonic diapause and the subsequent initiation of implantation is not fully understood in pinnipeds. Some of the suggested controls include photoperiod (Temte 1994), environmental conditions such as water temperature (Sergeant 1973), and maternal body condition (Boyd 1984, Stewart *et al.* 1989). In regards to implantation, Temte (1991, 1994) found that harbor seals respond to a specific photoperiod, and consequently there is a latitudinal variation in the timing of pupping due to this response. However, populations north of 50°N latitude show no significant latitudinal effects like populations further south, indicating populations such as those in the GOA are controlled by more complex factors than just photoperiod (Temte *et al.* 1991). Boyd (1991) suggested that, for harbor seals in the North Pacific, food supply plays a significant role in the determination of implantation. In other pinnipeds, maternal condition affects the timing of implantation (Boyd 1984, Stewart *et al.* 1989). Implantation in northwest Atlantic harp seals (*Phoca groenlandica*) occurs after the seal attains a specific level of body fat (Stewart *et al.* 1989). Theoretically, implantation should occur when the conditions are right to supply the mother with the needed resources and energy to support a growing fetus and a suckling pup (Boyd 1984). Therefore, changes in implantation can provide insight into changes in environmental conditions. For example, an earlier implantation date could indicate improved prey availability. Improved prey availability could lead to replenishment of fat levels in a reduced amount of time, shortening the length of embryonic diapause (Reijnders *et al.* 2010). Conversely, a later implantation date, as found in our study, could indicate reduced or poorer prey availability. Reduced prey availability leads to poorer maternal body condition, which results in later implantation and later birth (Reijnders *et al.* 2010).

In the present study, the rate of increase for fetal mass (0.09 $g^{1/3}$ d^{-1}) was similar to that found for northwest Atlantic harp seals (0.10 $g^{1/3}$ d^{-1}) (Stewart *et al.* 1989) and Atlantic walruses (*Odobenus rosmarus rosmarus*) (0.12 $g^{1/3}$ d^{-1}) (Garlich-Miller & Stewart 1999). Taken together, these results indicate that fetal growth in mass is fairly consistent across different species of pinnipeds. Of the eight fetal measurements used in this study, standard body length had the highest correlation coefficient and exhibited the least variance. Standard length is a reflection of skeletal growth, and therefore does not fluctuate as significantly as body mass and axillary girth.

1.5.4 Reproductive Maturity

We identified thresholds that harbor seals in the GOA must exceed to reach sexual maturity. These thresholds were 3 yr of age, 122 cm standard length, and 48 kg body mass. Using morphometric measurements to predict the actual age of harbor seals is confounded by substantial variability in length of immature seals and slow growth rates of adult seals. However, these threshold points can be useful for distinguishing immature from mature seals (Blundell & Pendleton 2008).

Comparing size at sexual maturity for harbor seals in the GOA, it appears that seals from this study are slightly larger than seals collected in the 1960s. The mean size at sexual maturity in the 1960s was 126 cm standard length and 50.3 kg body mass based on all 3 and 4 yr old animals (when sexual maturity was determined to occur) (Bishop 1967). Calculating the mean of 3 and 4 yr old animals in this study resulted in values of 131 cm and 55.6 kg for standard length and body mass, respectively.

It is thought that pinnipeds, along with other mammals, must reach a certain critical mass before they can become sexually mature (Laws 1956, Laws 1977, Boyd 1991). Moreover, it appears that body mass is a more definitive determinant of sexual maturity than standard length. With the exception of two seals in our dataset, all seals heavier than 48 kg were sexually mature. Thus, we estimated 48 kg to be the minimum maternal size a harbor seal in the GOA must obtain before they can become sexually mature. Admittedly, this value is a rough estimate, which may show some regional differences within the GOA. Nonetheless, it may serve as a baseline against which to compare future changes over time and climate condition.

The average age (with 95% confidence limits) of sexual maturity for seals in this study was estimated at 4.2 ± 0.7 yr and was similar to that for harbor seals in the GOA in the 1970s (4.96 ± 0.43 yr) (Pitcher & Calkins 1979), but greater than that calculated for seals in British Columbia in the 1960s (3.3 yr) (Bigg 1969b). Harbor seals in the GOA are smaller in length, have a later implantation date, and are larger at sexual maturity compared to harbor seals in the 1960s (Bishop 1967). Bishop's (1967) study was conducted before the major declines of harbor seal populations in Alaska, and may represent near carrying capacity abundance. As density decreases and the per-capita prey resources available increase, it would be predicted that growth would be faster and sexual maturity achieved earlier (Stearns 1992). The later age at maturity and smaller size of animals in this study may indicate that environmental conditions are not at optimal levels and are limiting growth and maturation.

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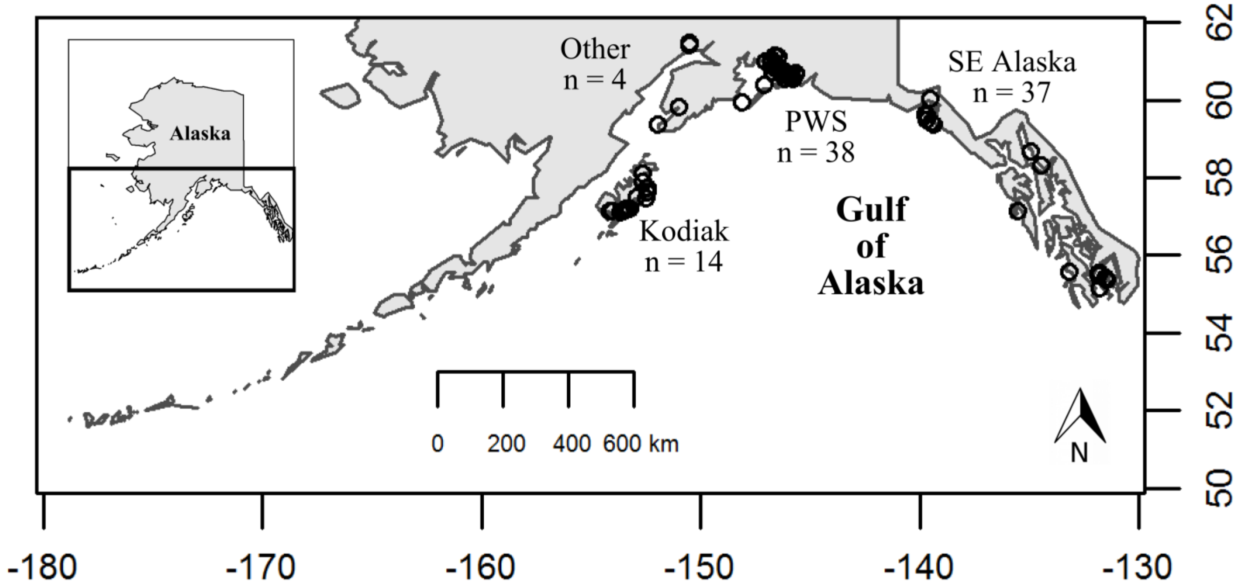

Figure 1.1. Locations of subsistence-harvested harbor seals used in this study. Female harbor seals were harvested by Alaska Native subsistence hunters from 1998 to 2005 as part of the Alaska Native Harbor Seal Commission's Biosampling Program. Eighty-five reproductive tracts and 27 fetuses were collected from Southeast Alaska (n=37), Prince William Sound (PWS) (n=38), Kodiak (n=14), and the Kenai Peninsula area (n=4). Eight fetuses from Prince William Sound were not associated with a reproductive tract.

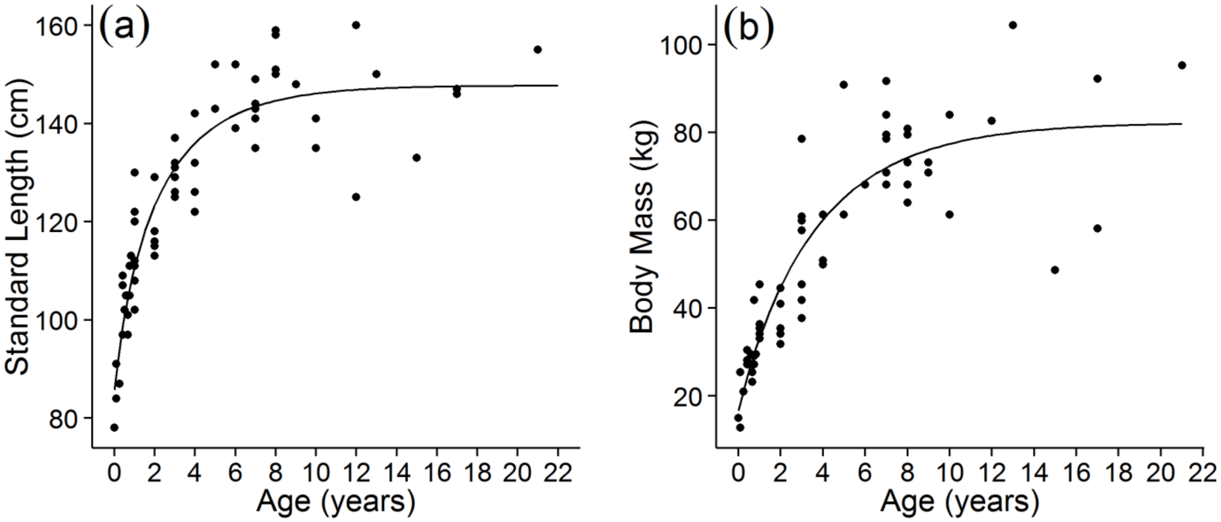

Figure 1.2. Von Bertalanffy growth curves fitted to (a) standard body length (n=65) and (b) body mass (n=63). Female harbor seals were harvested in the Gulf of Alaska from 1998 to 2005. (See Table 1.1 for parameter values).

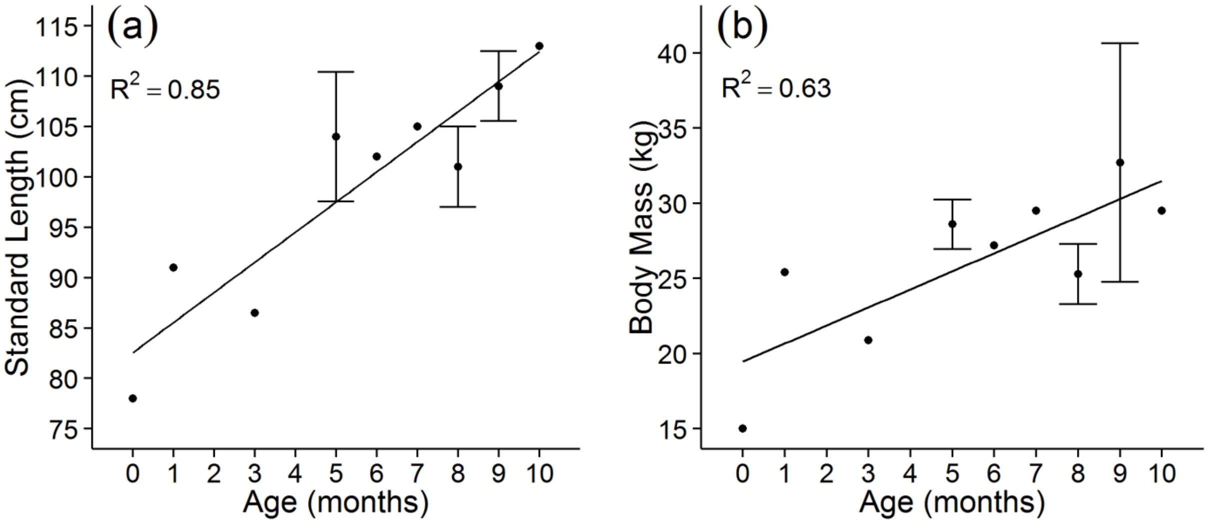

Figure 1.3. First year growth (±SD) in (a) standard length (n=15) and (b) body mass (n=15). Female harbor seals were harvested in the Gulf of Alaska from 1998 to 2005.

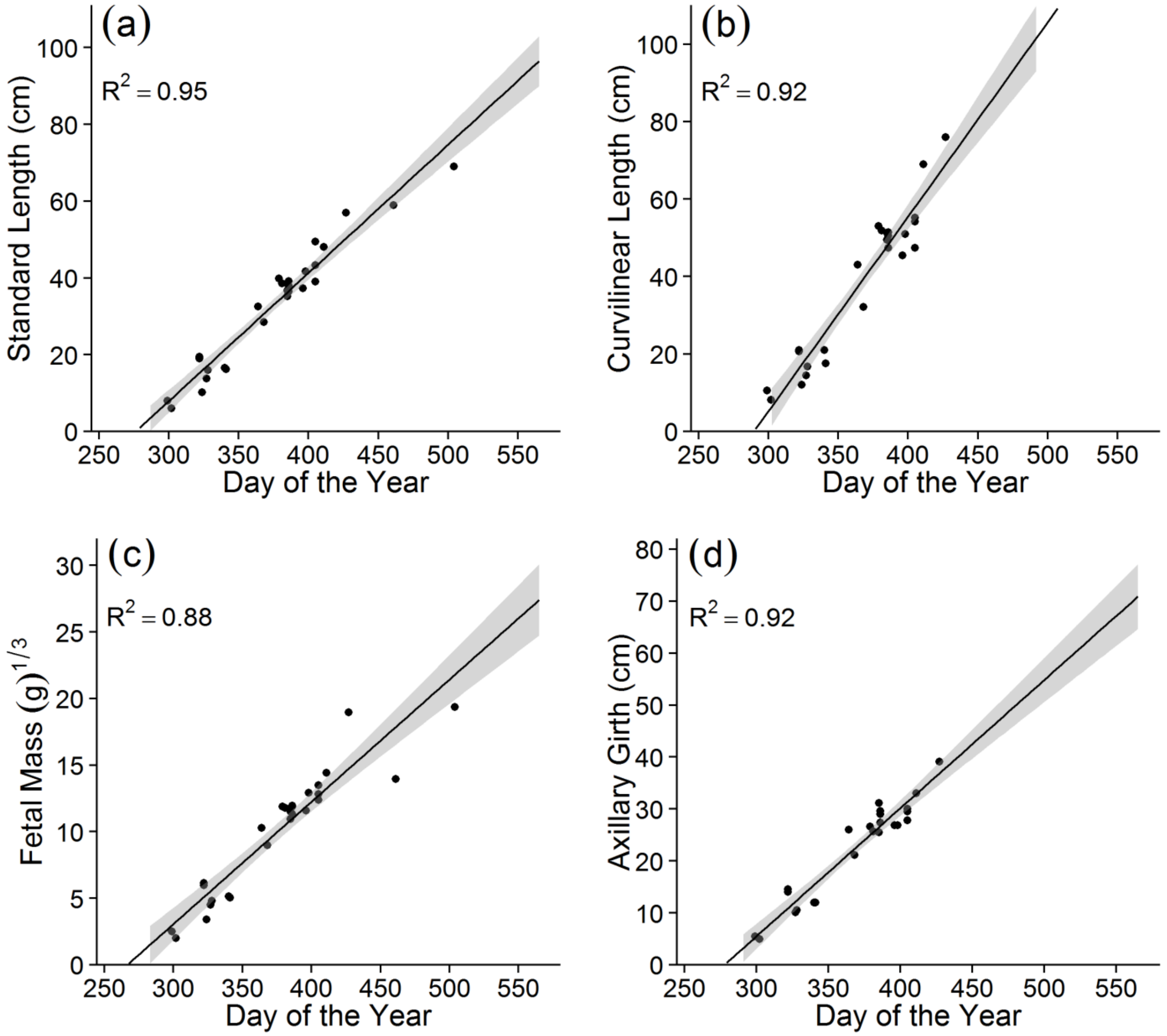

Figure 1.4. Harbor seal fetal body growth. Growth in (a) standard length (n=27), (b) curvilinear length (n=25), (c) fetal mass$^{1/3}$ (n=27), and (d) axillary girth (n=24). Day 1 and day 366 represent January 1st in consecutive years. Gray shaded areas indicate 95% confidence limits.

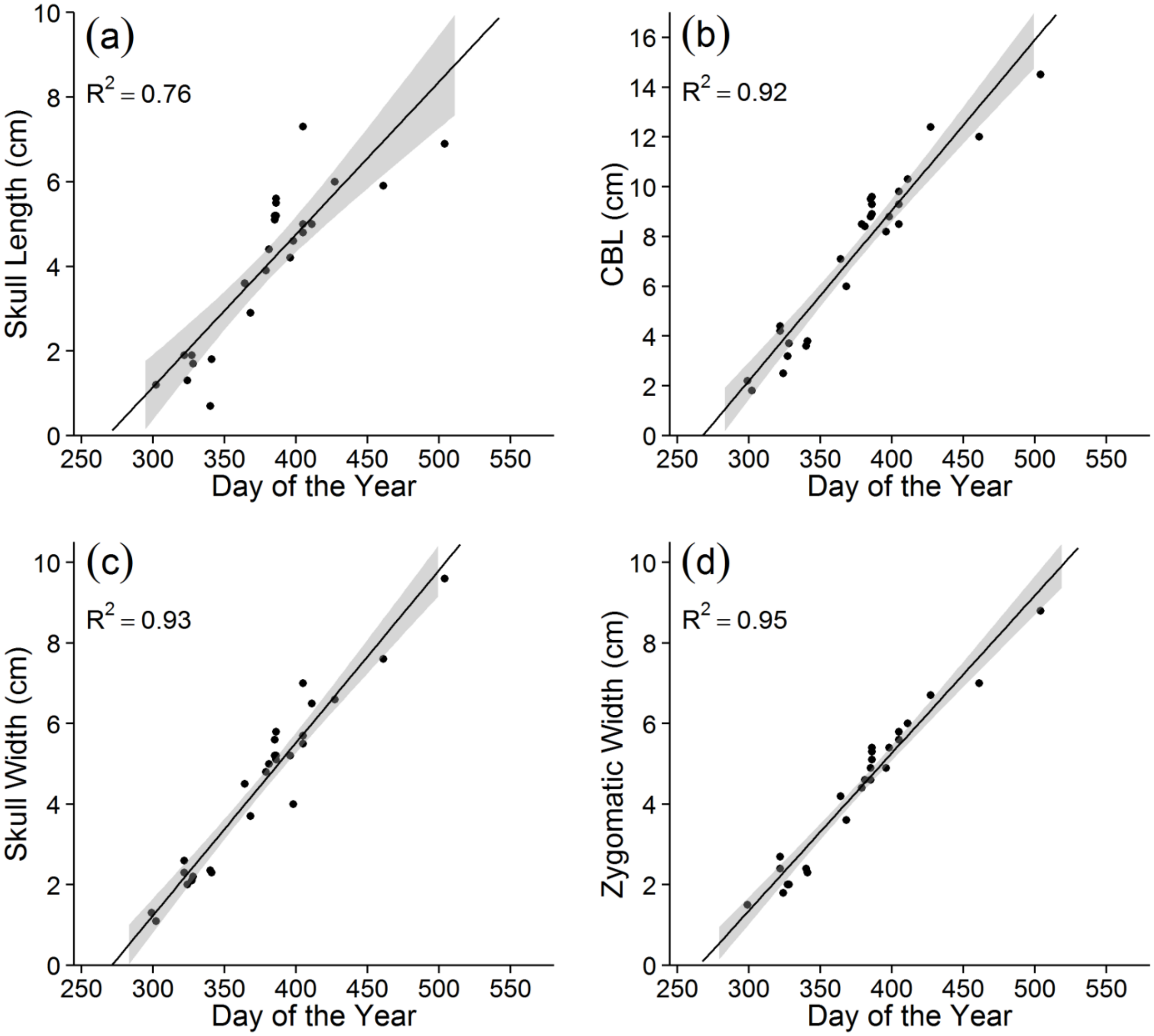

Figure 1.5. Harbor seal fetal skull growth. Growth in (a) skull length (n=26), (b) condylobasal length (CBL) (n=27), (c) skull width (n=27), and (d) zygomatic width (n=26). Day 1 and day 366 represent January 1st in consecutive years. Gray shaded areas indicate 95% confidence limits.

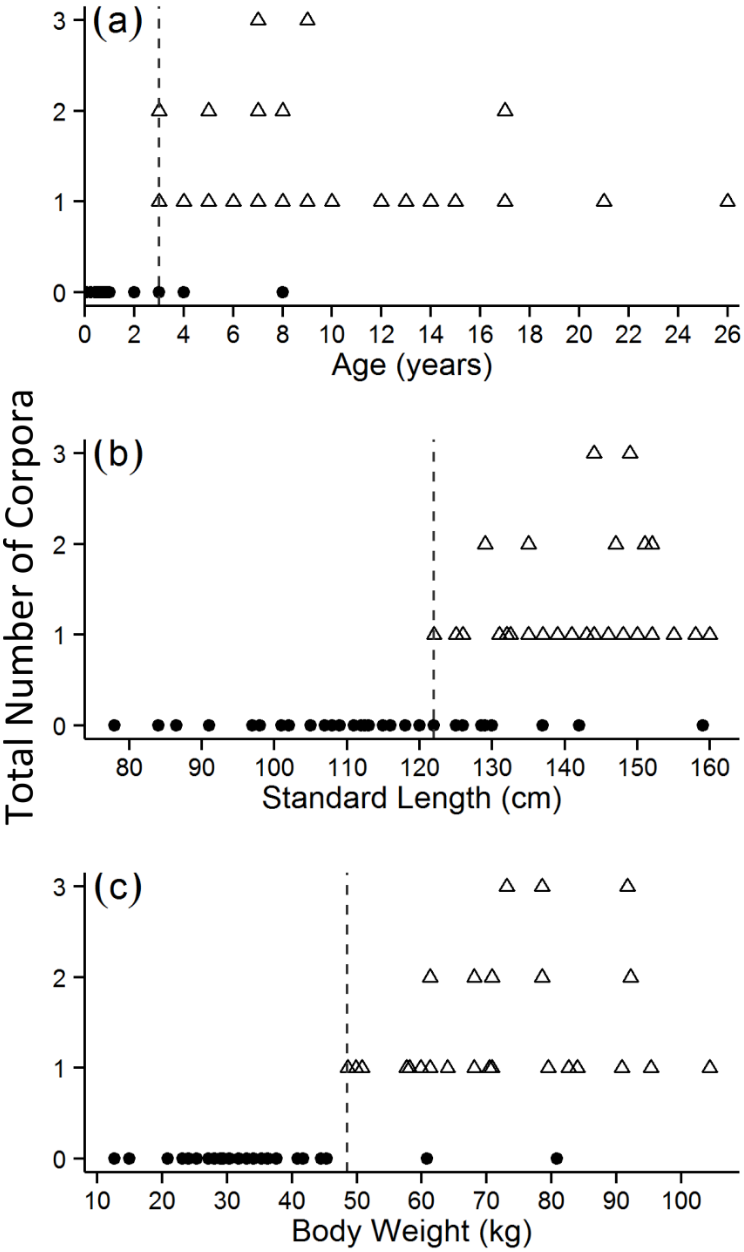

Figure 1.6. Total number of corpora in the ovaries of immature and mature harbor seals. Total number of corpora lutea and corpora albicantia in the right and left ovaries combined versus (a) age (n=81), (b) standard length (n=67), and (c) body mass (n=64). Filled circles represent immature animals and hollow triangles represent mature animals. The dotted line in each plot represents the threshold each animal crosses to become sexually mature.

Table 1.1. Parameter estimates (±SE) of von Bertalanffy growth functions for standard length and body mass. Measurements came from harvested female harbor seals from the Gulf of Alaska between 1998 and 2005. L_∞ and M_∞ represent the asymptotic length and body mass respectively, a represents the rate of approach to the horizontal asymptote, and b represents the curvilinearity of that approach. Model (Eq. 1.1): $L_x\ (or\ M_x) =\ L_\infty(or\ M_\infty)[1 - e^{-a(x-x_0)}]^b$.

Growth parameter	n	L_∞ or M_∞	a	b
Standard Length (cm)	65	147.7 ± 2.6	0.32 ± 0.08	0.32 ± 0.05
Body Mass (kg)	63	82.2 ± 4.8	0.25 ± 0.08	0.83 ± 0.17

Table 1.2. ANCOVA results and estimated implantation dates and growth rates for fetal measurements. ANCOVA results indicate no significant differences ($\alpha = 0.05$) in growth for male and female harbor seal fetuses in the Gulf of Alaska for all measurements. The estimated implantation dates and growth rates were derived from the linear regression of each measurement against day of the year for male and female fetuses combined.

Measurement	ANCOVA – Slopes (p, F)	ANCOVA- Intercepts (p, F)	Estimated Implantation Date	Growth Rate Per Day
Standard Length	0.94, 0.006	0.63, 0.23	October 3rd	0.33 cm
Curvilinear Length	0.32, 1.0	0.50, 0.57	October 17th	0.50 cm
Fetal Mass$^{1/3}$	0.28, 1.2	0.90, 0.015	September 25th	0.09 g$^{1/3}$
Axillary Girth	0.62, 0.26	0.62, 0.26	October 5th	0.25 cm
Skull Length	0.61, 0.26	0.86, 0.032	September 25th	0.036 cm
Condylobasal Length	0.86, 0.032	0.36, 0.87	September 25th	0.069 cm
Skull Width	0.61, 0.27	0.84, 0.043	September 28th	0.043 cm
Zygomatic Width	0.98, 0.001	0.81, 0.062	September 22nd	0.039 cm

Table 1.3. Mean values for body mass (kg), standard length (cm), ovary mass (g), and ovary volume (cm^3) by reproductive status. Nonpregnant animals were mature but not pregnant at the time of harvest. Measurements came from harvested female harbor seals from the Gulf of Alaska from 1998 to 2005. The “Pregnant Active” and “Pregnant Inactive” reproductive statuses represent the ovary on the pregnant and nonpregnant side of the reproductive tract, respectively. Data for ovary mass and volume were log-transformed for statistical analysis, and means presented here are the back-transformed geometric means.

Reproductive Status		Body Mass (kg)			Standard Length (cm)			Ovary Mass (g)			Ovary Volume (cm³)		
		Mean	*CI*	*n*	*Mean*	*CI*	*n*	*Mean*	*CI*	*n*	*Mean*	*CI*	*n*
Immature		33.7^{a}	29.6, 37.8	35	111.9^{a}	106.5, 117.3	36	0.99^{a}	0.86, 1.1	45	1.2^{a}	0.97, 1.4	45
Nonpregnant		66.2^{b}	58.6, 73.8	8	143.5^{b}	138, 149	8	4.0^{b,c}	3.1, 5.3	10	6.4^{b,c}	4.7, 8.8	10
Pregnant	*Inactive*	76.8^{b}	71, 82.6	21	140.6^{b}	136.1, 145.1	22	3.4^{b}	3.2, 4.0	24	6.0^{b}	9.3, 11.9	25
	Active							5.9^{c}	5.2, 6.6	24	10.5^{c}	5.0, 7.1	25

Values not sharing a common letter are significantly different at $P \leq 0.05$ by Tukey –Kramer multiple comparisons test.

Chapter 2:

Growth and sexual maturation in male northern sea otters (*Enhydra lutris kenyoni*) from Gustavus, Alaska[1]

2.1 Abstract

Northern sea otters (*Enhydra lutris kenyoni*) are experiencing rapid population growth and expansion in Southeast Alaska. Fluctuations in population density can produce profound changes in ecological constraints, influencing growth and sexual maturity of animals in a population and can transform the ecology of newly populated ecosystems. Using morphometric measurements and reproductive tracts collected from 40 sea otters by an Alaska Native subsistence hunter, we evaluated growth rates and the age at sexual maturity of male sea otters near Gustavus, Alaska. All size measurements increased markedly between ages 0 and 2 yr and began to decrease at 2 to 4 yr and approach a horizontal asymptote. The youngest sea otter classified as mature was 2 yr old and all animals ≥ 4 yr old were mature. At puberty, mean seminiferous tubule diameter, baculum length, and testes mass increased abruptly 104, 42, and 189 percent, respectively, at 130 cm body length. Mean seminiferous tubule diameter increased markedly to 140 µm at 14 cm baculum length. Male sea otters near Gustavus, Alaska reach sexual maturity at age 3-4 yr, after attaining a standard body length of 130 cm, a mean seminiferous tubule diameter of 140 µm, and a baculum length of 14 cm.

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[1] Hutchinson, E.A., and S. Atkinson. (2014). Growth and sexual maturation in male northern sea otters (*Enhydra lutris kenyoni*) from Gustavus, Alaska. In preparation for Marine Mammal Science.

2.2 Introduction

Northern sea otters *(Enhydra lutris kenyoni)* are widely distributed in coastal waters of the North Pacific, from the Aleutian Islands in the west, throughout the Gulf of Alaska (GOA), and south into British Columbia and Washington. Within Alaska there are three separate stocks: Southwest, Southcentral, and Southeast. The Southeast stock ranges from Dixon Entrance in the south to Cape Yakataga in the north (Gorbics & Bodkin 2001). Sea otters in Alaska were hunted extensively by Russian fur traders starting in the late 1700s, and by the late 1800s were extirpated from Southeast Alaska (Kenyon 1969, Jameson *et al.* 1982). From 1965 to 1969 the Alaska Department of Fish and Game (ADF&G), with the assistance of other state and federal agencies, reintroduced 412 sea otters from Prince William Sound and Amchitka Island to six sites in Southeast Alaska, including Cape Spencer, Yakobi Island, Khaz Bay, Biorka Island, the Maurelle Islands, and the Barrier Islands (Jameson *et al.* 1982, Riedman & Estes 1990, Esslinger & Bodkin 2009). The reintroduction was successful, and since the late 1900s sea otters have rapidly recolonized portions of Southeast Alaska (Estes 1990, Estes *et al.* 1996, Bodkin *et al.* 2006, Doroff *et al.* 2011).

The Southeast Alaska stock has doubled in size since 2003 (USFWS 2014). Southern Southeast Alaska, from the Kuiu and Kupreanof Islands south to the Canadian border, and northern Southeast Alaska, from the Admiralty and Baranof Islands north to Glacier Bay (excluding Glacier Bay National Park and Preserve) were surveyed separately by the U.S. Fish and Wildlife Service (USFWS) in 2010 and 2011, respectively. These surveys produced population estimates of 12,873 and 2,717 sea otters for southern and northern Southeast Alaska (USFWS 2014). Glacier Bay National Park and Preserve (GBNPP) was surveyed independently by the U.S. Geological Survey (USGS) in 2012, producing a population estimate of 8,508 sea otters (USFWS 2014). Southern Southeast Alaska has increased at an average annual rate of 12% per year over the last 7 years, while northern Southeast Alaska, excluding GBNPP, has shown only a 4% average annual rate of increase over the last 9 years (USFWS 2014). Conversely, GBNPP increased by an average annual rate of 50% between 1998 and 2004, and 20% over the last 6 years (Bodkin *et al.* 2006, Bodkin *et al.* 2007, USFWS 2014). When colonizing new areas, sea otter population growth can be as high as 20% per year (Estes 1990). Such high rates of increase in GBNPP in the late 1990s/early 2000s are thought to be the result of significant immigration of sea otters from portions of Icy Strait and Cross Sound starting in the mid-1990s (Bodkin *et al.* 1998, Bodkin *et al.* 2002, Bodkin *et al.* 2006). The USGS began conducting surveys for sea otters in Glacier Bay, Cross Sound, and Icy Strait in 1994, following initial reports of sea otters in Glacier Bay in 1993 (Bodkin *et al.* 2002). Sea otters in Icy Strait and Cross Sound declined at a rate of -7 % per year between 1994 and 2004 (Bodkin *et al.* 2007). The current rate of 20% increase per year over the last six years appears to indicate that immigration into the park has declined in recent years.

Sea otters are top marine carnivores that consume a variety of benthic invertebrates, the majority of which are ecologically, commercially, or culturally significant. They are a keystone species that exert strong influence on community structure in nearshore ecosystems (Paine 1969, Estes & Palmisano 1974, Estes 1990, Estes & Duggins 1995, Jessup *et al.* 2004). To meet metabolic demands sea otters must consume up to 25% of their body mass per day (Estes *et al.* 2003). Following the sea otter extirpation in Southeast Alaska, profitable dive fisheries were established for species including clams, sea urchins, sea cucumbers, and crabs. Sea otters are now re-expanding into regions they previously occupied (Esslinger & Bodkin 2009). When sea otters populate new regions, they are known to quickly remove large, calorically rich species that are easy to capture (Lowry & Pearse 1973, Estes & Palmisano 1974, Laidre & Jameson 2006). These same characteristics render those invertebrates appealing to commercial and subsistence fishermen. High rates of prey consumption by sea otters can lead to closure of formerly profitable fisheries (Lowry & Pearse 1973, Fanshawe *et al.* 2003, Larson *et al.* 2013). The pace and extent of the return of sea otters to Southeast Alaska has caused concern about loss of fishery productivity (Johnson 1982). Rapid expansion of sea otters in Southeast Alaska and increasing frequencies of resource conflicts are therefore important issues for scientists, fishery managers, and commercial, recreation, and subsistence fishermen alike. However, increasing populations of sea otters are favorable for tourism, Alaska Native subsistence hunters that harvest sea otters for their fur, and Alaska Native crafters who work with sea otter pelts. These conflicting interests highlight the need to study and understand sea otter biology in Alaska.

Fluctuations in population size are known to cause changes in life history parameters such as growth and age at sexual maturity in mammals (Bowen *et al.* 1981, Jorgenson *et al.* 1993, Hammill & Gosselin 1995, Ostfeld & Canham 1995, Bonenfant *et al.* 2002). As population density increases, the per-capita prey availability typically declines and organisms must make trade-offs between survival, growth, and reproduction (Stearns 1989). Life history theory predicts that growth should be slower and sexual maturity achieved later as resources become limiting (Stearns 1992). As population density increases, and prey resources are more constraining, the body mass of individuals typically declines and animals reduce the amount of energy allocated to reproduction, increasing the age of first reproduction and reducing reproductive success (Scheffer 1955, Fowler 1990, Wauters & Lens 1995, Festa-Bianchet & Jorgenson 1998, Williams *et al.* 2013). The energy organisms allocate to growth and reproduction can therefore be a reflection of the population status, resource availability and environmental stability (Wilbur *et al.* 1974, Stearns 1976, Stearns & Koella 1986, Reiter & Le Boeuf 1991). For example, slow growth and delayed sexual maturity may indicate scarcity of food resources due to high population density and/or poor environmental conditions (Bengtson & Laws 1985, Trippel 1995). Conversely, a population with rapid growth and an early age at sexual maturity may indicate abundant nutrient resources and good environmental conditions and/or densities below carrying capacity (Bengtson & Laws 1985). Understanding growth and reproduction is vital for resource management, but is also a mechanism for understanding ecosystem-level changes.

Female sea otter reproduction is fairly well studied in Alaska (Sinha *et al.* 1966, Sinha & Conaway 1968, Bodkin *et al.* 1993, Jameson & Johnson 1993, Eberhardt & Schneider 1994, Monson & DeGange 1995, von Biela *et al.* 2008, von Biela *et al.* 2009), but few studies have examined male reproduction (Kenyon 1969, Schneider 1978, Garshelis *et al.* 1984, Riedman & Estes 1990). From what is known, spermatogenesis in male sea otters occurs throughout the year and old animals show no indication of diminished sperm production (Kenyon 1969). In Alaska, sea otter mating and pupping occurs at all times of the year (Kenyon 1969, Riedman & Estes 1990). However, in Prince William Sound there is a peak in mating in late fall/early winter and a peak in pupping in late spring/early summer (Kenyon 1969, Garshelis *et al.* 1984). When not breeding, sea otters are sexually segregated (Kenyon 1969, Garshelis *et al.* 1984, Riedman & Estes 1990). Males in Alaska are generally located in more exposed areas where there is strong wave action and stormy weather, while females are located in more protected areas where they can safely raise their pups (Schneider 1978, Garshelis *et al.* 1984). Males are usually the first to colonize new habitat, and are generally at the edges of the range of expanding populations (Garshelis *et al.* 1984, Riedman & Estes 1990). Juvenile males leave natal areas and migrate to adult male areas immediately following weaning at around 6 months (Garshelis *et al.* 1984). Sexual maturity for male sea otters is thought to occur around 5 years of age in California (Green 1978) and 5 to 6 years in Alaska (Schneider 1978). However, male size and age are important determinants of mating success (Garshelis *et al.* 1984). Large males are better able to defend territories within female areas to mate successfully (Garshelis *et al.* 1984). Therefore, males may not successfully mate until years after reaching sexual maturity.

In conjunction with the large increase in sea otter abundance in Southeast Alaska, subsistence hunting of sea otters has steadily increased over recent years. In 2008, only 668 sea otters were harvested in all of Southeast Alaska. In 2012 Alaska Native harvesters in coastal communities throughout the state harvested a total of 1,281 sea otters, 952 of which came from Southeast Alaska. At the time of this study, harvests from January – October, 2013 totaled 1,380 animals, including 1,008 harvested in Southeast Alaska (USFWS tagging statistics). Subsistence harvests provide a valuable opportunity to work with Native Alaskan hunters to collect measurements and fresh biological tissue samples (biosamples), from harvested animals.

This study investigates growth and sexual maturity of male sea otters using morphometric measurements and macro- and microscopic analysis of reproductive organs from a rapidly expanding group of sea otters adjacent to GBNPP. Specific objectives were to determine (1) age and size at sexual maturity and (2) morphometric changes based on age and reproductive state for male sea otters. This research compliments and expands on previous work to create a clearer and more detailed understanding of the reproductive strategies of sea otters in Southeast Alaska, specifically those otters at the forefront of the population expansion.

2.3 Materials and Methods

2.3.1 Study Area and Animals

Forty-one male and eight female sea otters were collected by an Alaska Native subsistence hunter in the waters adjacent to Gustavus, Alaska between March and September, 2013 (Fig. 2.1). In the field, the hunter measured standard length and axillary girth of each sea otter to the nearest 0.64 cm (0.25 in) using a flexible vinyl measuring tape. Standard length was measured from the tip of the nose to the tip of the tail along a flat surface with the sea otter on its back. Axillary girth was measured around the body of the otter at the axilla. The hunter collected reproductive samples from 40 of the 41 male sea otters harvested. Both testes and the baculum were removed from each sea otter, placed in a Ziplock bag, and delivered to Juneau, Alaska, within 24 hr of the conclusion of the hunting trip. Also, a premolar or incisor tooth was removed from the skull by the hunter in the field or else the skull was brought to the laboratory and a premolar tooth was removed for age analysis. Samples were refrigerated at -1.1 – 4.4°C until analysis.

2.3.2 Laboratory Analyses

Samples were analyzed fresh in the laboratory within 3 d of the hunting trip for all but one trip. The final trip had extended transit time and longer processing times due to a large number of samples, and consequently samples were not analyzed completely until 7 d after the conclusion of the hunting trip. Samples were refrigerated at approximately 1.7°C during that week. The baculum and both testes, with the epididymides attached, were trimmed of excess tissue and then weighed to the nearest 0.1 g. The length, width and depth of each testis were measured to the nearest 0.1 mm using dial calipers. We were unable to locate the right testis of one sea otter, either because it was small or missing. Testes measurements are absent for that individual due to no histological samples obtained from the left testis. The length of each baculum was measured to the nearest 0.1 cm using a flexible vinyl measuring tape. The diameter was measured to the nearest 0.1 mm at the base, middle, and head of the baculum using dial calipers. Individual ages were determined from the extracted premolar or incisor. Teeth were prepared, analyzed, and aged based on growth layers in the cementum at Matson's Tooth Aging Laboratory (Milltown, MT, USA). Each tooth was assigned a certainty code by Matson's Laboratory, signifying a reliability index. The highest, or "*A*", certainty code indicates that the cementum characteristics of the tooth very nearly match those for the standardized cementum aging model for the species and tooth type. For a "*B*" certainty code, there is histological evidence to support the result, and the correct age is expected to be within a range given. All the teeth in this study were aged with either an *A* or *B* certainty code. Ages are missing from nine sea otters due to a lack of collection or tooth breakage.

Testes were stored frozen after the gross morphological analysis, and then thawed and fixed in 10% formalin for histological analysis. The testes were sent to Histology Consultation Services, INC. (Everson, WA) for processing. Tissues were dehydrated, embedded in paraffin, sliced using a microtome, and then placed on a glass slide and stained using a standard hemotoxylin and eosin (H&E) stain for microscopic examination. Ten round seminiferous tubules were randomly identified for each right testis. For one individual the left testis was measured due to damage to the right testis during freezing to the extent that 10 round seminiferous tubules could not be located. The seminiferous tubule cross section diameter (STD) was measured twice for each tubule at 90° angles to one another across the tubule based on the opening of the stroma (O'Hara *et al.* 2002). Every seminiferous tubule was characterized by the complexity of its epithelium, the presence/extent of a lumen, and the presence or absence of spermatozoa. The presence or absence of spermatozoa was also noted for the epididymis.

2.3.3 Data Analysis

Changes with age in standard length, axillary girth, mean STD, mean testes length, width, mass, and volume, baculum length and mass, and baculum head, middle, and base diameters were described using Gompertz growth curves (Gompertz 1825, Ricker 1979), of the form:

$$S_t = A_\infty (e^{-ke^{-bt}}), \tag{2.1}$$

where S_t is the size at time t, A_∞ is the asymptotic maximum size, k is a growth rate constant, b is the time at which the absolute growth rate begins to decrease, t is the age in years, and e is a mathematical constant that is the base of the natural logarithm (2.71828). Growth models were fit in R, version 3.0.2 (R Core Team 2013) using nonlinear least squares estimation.

Each sea otter was characterized as reproductively immature, pubertal, or mature based on the characterization and diameters of the seminiferous tubules. Immature animals had closed tubules with no obvious lumen, a simple epithelium that consisted of a single layer of prospermatogonia along the basement membrane, no spermatozoa present in the testis or the epididymis, and STDs that were markedly small in size. Mature animals had open tubules with pronounced lumens, complex epithelia, spermatozoa present in the testis and the epididymis, and large STDs. Pubertal animals' seminiferous tubules were complex, but were not fully open and they lacked spermatozoa in the epididymis (Fig. 2.2). Mean morphometric and reproductive measurements were calculated for each reproductive category (immature, pubertal, and mature) and were compared using ANOVAs and post-hoc Tukey-Kramer multiple comparison tests. For both standard length and axillary girth the sample size of pubertal animals (n=2) was too small to conduct statistical analyses. Consequently, Welch's two sample t-tests were conducted for those measurements to test for differences in standard length and axillary girth of mature and immature animals. The significance level for all tests was $P \leq 0.05$.

2.4 Results

Eighty-four percent of all sea otters harvested by the subsistence hunter were males. The age of male sea otters used in this study ranged from 0 to 14 yr. One yr old animals were absent from the sample. All six sea otters aged 0 yr by the analysis of cementum layers in their teeth were assigned an age of 0.5 yr for growth curve analysis based on their large standard lengths. In Alaska, newborn sea otters are between 40 – 60 cm (Kenyon 1969), and all of the 0 yr old animals in this study were greater than 100 cm in length. The mean of the left and right testis was calculated due to no significant difference between testes for length (Student's *t*-test; paired t (76) = -0.17, P = 0.86), width (Student's *t*-test; paired t (76) = -0.015, P = 0.99), depth (Student's *t*-test; paired t (76) = 0.15, P = 0.88), or mass (Student's *t*-test; paired t (76) = -0.13, P = 0.89). Growth with age in standard length, axillary girth, mean STD, baculum length, mass, and diameter, and mean testes length, width, volume, and mass were all asymptotic. The changes in these measurements with age were described well by the Gompertz growth curves. Parameters for the models, including asymptotic size are presented in Table 2.1. The maximum recorded standard length and axillary girth were 160 cm and 78.7 cm, respectively, and were from the same individual from which the age was unknown. The standard length and axillary girth for one individual were not included in the analyses because the standard length value was unrealistically low, and when verified with the subsistence hunter it was determined that none of the tanned hides from that day's hunt were near the size recorded. The measurement was considered compromised by a recording error and deleted from further analysis.

All measurements showed a large increase in size between 0 and 2 yr, which was most pronounced in baculum length and mass, STD, and all four testes measurements (Figs. 2.4, 2.6, and 2.7a). Growth rate for all measurements began to decrease around 2 to 3 yr of age and approached a horizontal asymptote, with the exception of baculum mass, which did not decrease until age 3 to 4 yr (Figs. 2.3 – 2.7).

Mean STD, baculum length, and mean testes mass were plotted as a function of sea otter standard length and all showed an abrupt increase in size at 130 cm body length (Figs. 2.7a and 2.8). Mean STD was also plotted versus baculum length and mean testes length, and showed a marked increase to 140 µm at 14 cm baculum length and 45 mm mean testes length (Fig. 2.7). At puberty mean STD, baculum length, and mean testes mass increased abruptly 104, 42, and 189 percent, respectively, at 130 cm body length (Table 2.2, Figs. 2.7a and 2.8).

Of the 40 sea otters in this study, 8 were determined to be immature, 27 mature, 3 pubertal, and 2 unknown. Of the 2 unknown animals, one did not have any reproductive parts collected and the other did not have any testes measurements, and therefore sexual maturity could not be assessed. The mean STD was 169.3 ± 12.8 µm (SD) for mature sea otters and 72.9 ± 18.3 µm for immature animals. Three sea otters were determined to be going through puberty at the time they were harvested based on a lack of spermatozoa in the epididymides, seminiferous tubules that were not fully open, and smaller STD's than mature animals (Fig. 2.2). Their mean STD was 149.0 ± 3.9 µm. All morphometric and reproductive measurements varied significantly among reproductive categories (Table 2.2). For all reproductive measurements (baculum length, baculum mid diameter, baculum mass, mean testes length, mean testes volume, mean testes mass, and mean STD), immature animals were significantly smaller than both mature and pubertal animals (Table 2.2). However, pubertal animals were not significantly different from mature animals for any reproductive measure, with the exception of mean testes mass (Table 2.2). Animals going through puberty had a significantly smaller testes mass than mature animals. Mature animals had significantly greater standard lengths and axillary girths compared to immature animals (Table 2.2).

The youngest sea otter classified as mature was 2 yr old and all animals 4 yr and older were mature (Percent mature: 2 yr = 33, 3 yr = 83, 4+ yr = 100). The single 2 yr old animal classified as mature had a B confidence level for its tooth age estimate, and had an age range of 2 to 3 yr. Its morphometric measurements aligned closely with the other 3 yr old sea otters in the study. We estimate that sexual maturity in male sea otters from Gustavus, Alaska occurs between 3 and 4 yr of age.

2.5 Discussion

The group of sea otters adjacent to GBNPP appears to be a male dominated group. The Native subsistence hunter we worked with to obtain the samples for this research harvested 49 sea otters just outside of GBNPP between March and September, 2013 near Gustavus, Alaska and of those 49, 41 were male and only 8 were female. As the hunter indicated that he harvested opportunistically and was not targeting specific animals, the ratio of 84% males may be representative of the sex ratio in that region.

In this study, six animals were aged at 0 yr old. Sea otters can breed throughout the year, and consequently there is no accurate way to determine exactly the age of 0 yr-old animals. Pups in Alaska are typically weaned after 6 mo, at which point males would migrate to a male area

(Garshelis *et al.* 1984). Due to sexual segregation, one would not expect to have male animals less than 6 mo of age in a male area unless they were with a female that was in the region. Additionally, newborn sea otters in Alaska are typically between 40 and 60 cm standard length (Kenyon 1969), and the smallest 0 yr old animal in our study was greater than 100 cm. Consequently, we concluded that the 0 yr old animals in this study were at least 6 mo of age. The sea otters in this study were collected between March and September, with the majority of 0 yr old animals harvested in September. Fifteen percent of the sea otters harvested in June and July combined were 0 yr old, while in September it was 25%. These data could indicate an increase in births in March (6 months prior to September). In Prince William Sound, births peak in May (Garshelis *et al.* 1984). If this is the case for the Glacier Bay region, then it would be expected that the number of age 0 animals would increase around November. Unfortunately no samples for this study were collected during November, but future research could provide insight into the birthing cycle of sea otters in the region.

Growth in standard length of male sea otters in this study was greater than previous studies in Alaska. Male sea otter growth in the Aleutian Archipelago attained asymptotic standard length at 118.7 ± 2.7 cm (SE) between 1967-71 and 131.5 ± 1.3 cm between 1992-97 (Laidre *et al.* 2006). Our asymptotic standard length (148.2 ± 2.9 cm) was greater than both of those time periods. During the 1967-71 period, the sea otter population in the Aleutian Archipelago was near carrying capacity, while during the 1992-97 period the population was in a large decline, attributed to increased killer whale predation (Laidre *et al.* 2006). Standard length continued to increase through 2004 when the population size was extremely low, although sample size was very small (n=2) (Laidre *et al.* 2006). Laidre et al. (2006) concluded that the depressed population was afforded greater per capita food resources, allowing the animals in the population to attain greater sizes in both length and mass in a shorter amount of time. Consistent with this, adult sea otters from a dense population (Amchitka Island) exhibited smaller sizes than those from a sparse population (Shumagin/Unimak/Adak Islands area) (Kenyon 1969). However, Kenyon (1969) measured the mean standard length of adult animals, instead of the asymptotic length as measured in this study and the Laidre *et al.* (2006) study. He defined adult animals by observations of dentition, sagittal crest development, and baculum size in males. Without specific definitions of those criteria, a direct comparison with our data was difficult, but taking the mean of all sea otters 4 yr and older (age at which all animals were mature) in our study produced a mean standard length of 147.2 ± 7.5 cm (SD). This value is greater than the mean standard lengths for both the Amchitka (135.0 ± 4.3 cm) and Shumagin/Unimak/Adak (140.8 ± 0.5 cm) populations (Kenyon 1969).

Growth in mean testicular mass for sea otters in our study slowed at 2 to 3 yr of age and the Gompertz growth model produced an asymptotic size of 26.0 ± 1.2 g. For male sea otters near Amchitka Island in western Alaska, if the testicular mass was greater than 14 g, spermatozoa was present indicating that reproduction was possible (Kenyon 1969). Our results lack data from 1 yr old animals, making it difficult to compare directly to those results. However, all animals 2 yr and older had spermatozoa present and had testes greater than 17.5 g. All immature animals had testicular masses less than 8 g, with the exception of one individual. That individual (#8) was classified as immature by a lack of spermatozoa in both its testes and epididymides, and by the small and non-complex nature of the seminiferous tubules. However, all the body and reproductive morphometric measurements were of a size that would indicate the animal should be mature (standard length = 148.6 cm, axillary girth = 73 cm, baculum length = 16.4 cm, baculum mass = 66.6 g, mean testes length = 49.6 mm), except for mean testes mass

(16.75 g) which fell in between the values for immature and mature animals. Unfortunately, the age of this animal is unknown due to lack of tooth collection. The large size of the animal and its baculum, but small testes and undeveloped seminiferous tubules suggest the animal is reproductively sterile or extremely slow maturing for some unknown reason.

The growth of the baculum is stimulated at the onset of sexual maturity by male hormones (Wright 1950). Its development is rapid, and it is therefore thought to be a useful measurement to distinguish sexually immature and mature animals (Green 1978). Our data showed a clear distinction between immature and mature animals. If individual #8 that was mentioned earlier is excluded, the baculum length for immature animals ranged from 8.5 – 11.3 cm (n= 7), while for mature animals it ranged from 14.7 – 17.9 cm (n= 27). The baculum length of animals going through puberty (15.1 – 16.1 cm) (n= 3) overlapped with mature animals, but not with immature animals. These data suggest that the maturity status of a male sea otter can be evaluated by examining the length of its baculum. Animals with bacula lengths less than 14 cm would be considered immature.

Aging mammals from the layers of cementum in the teeth is a well-established technique (Fancy 1980, Bodkin *et al.* 1997), but is subject to the skill and judgment of the reader and the condition of the tooth. The reader assigns a confidence level to each tooth, indicating how certain they are of the estimated age. All of our teeth had a confidence level of either an A or B. Those teeth with a B confidence level also provided a range of usually 2 yr, but up to 3 yr. For seven teeth aged with B confidence, the animals were 5 yr or older, which is beyond the age at which sexual maturity was estimated to occur and after which the majority of growth had taken place. However, there were six animals with B confidence estimates that were in the 0-3 yr old range, which is extremely important for evaluating sexual maturity. One of the animals determined to be going through puberty was estimated to be 2 yr old, but had an age range of 1-2 yr. However, all of its reproductive and morphometric measurements aligned with the other 2 yr old animal, which had an A confidence level age estimate. The one 2 yr old animal that we determined to be mature had a B confidence level and an age range estimate of 2-3 yr. All of its morphometric and reproductive measurements were higher than the other two 2 yr old otters and aligned more closely with the other 3 yr old animals in our study. The data strongly suggests that animal was 3 yr old.

We estimated sexual maturity to occur at 3 to 4 yr of age for the sea otters in our study. This is lower than previous estimates for sea otters in Alaska (5-6 yr) (Schneider 1978) and California (5 yr) (Green 1978). Maturation has been shown to occur at younger ages at lower population density, when growth rate increases in response to greater food resources (Bowering 1989, Jørgensen 1990, Pistorius *et al.* 2001). The population status and the ecology of the Glacier Bay region support the finding of a lower age at sexual maturity. Population levels are not at carrying capacity and Glacier Bay and the surrounding areas have a rich supply of benthic organisms for sea otters to consume (Bodkin *et al.* 2006). Increased body size and lower age of sexual maturity of sea otters near Gustavus, Alaska is consistent with the assessment of Bodkin *et al.* (2006) that resources are abundant and are not limiting maturation rates of male sea otters near Glacier Bay.

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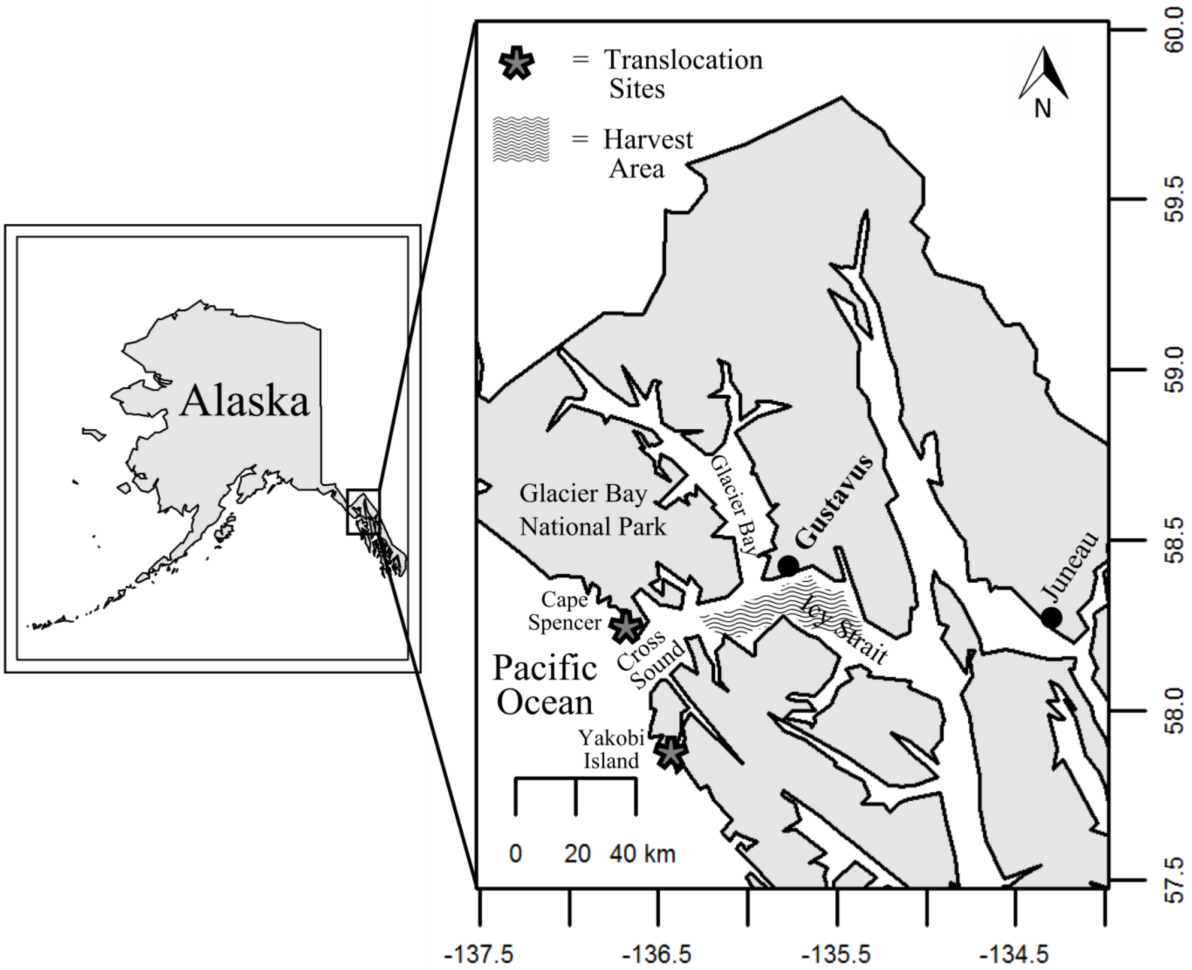

Figure 2.1. Map of the sea otter harvest area near Gustavus, Alaska. Forty male northern sea otters were harvested from March to September 2013. The gray shaded area represents the harvest area. The two stars represent the sea otter translocation sites closest to the study area. The translocation sites are two of the six sites in Southeast Alaska where ADF&G translocated sea otters in 1965 – 1969 after their extirpation from the area in the late 1800s.

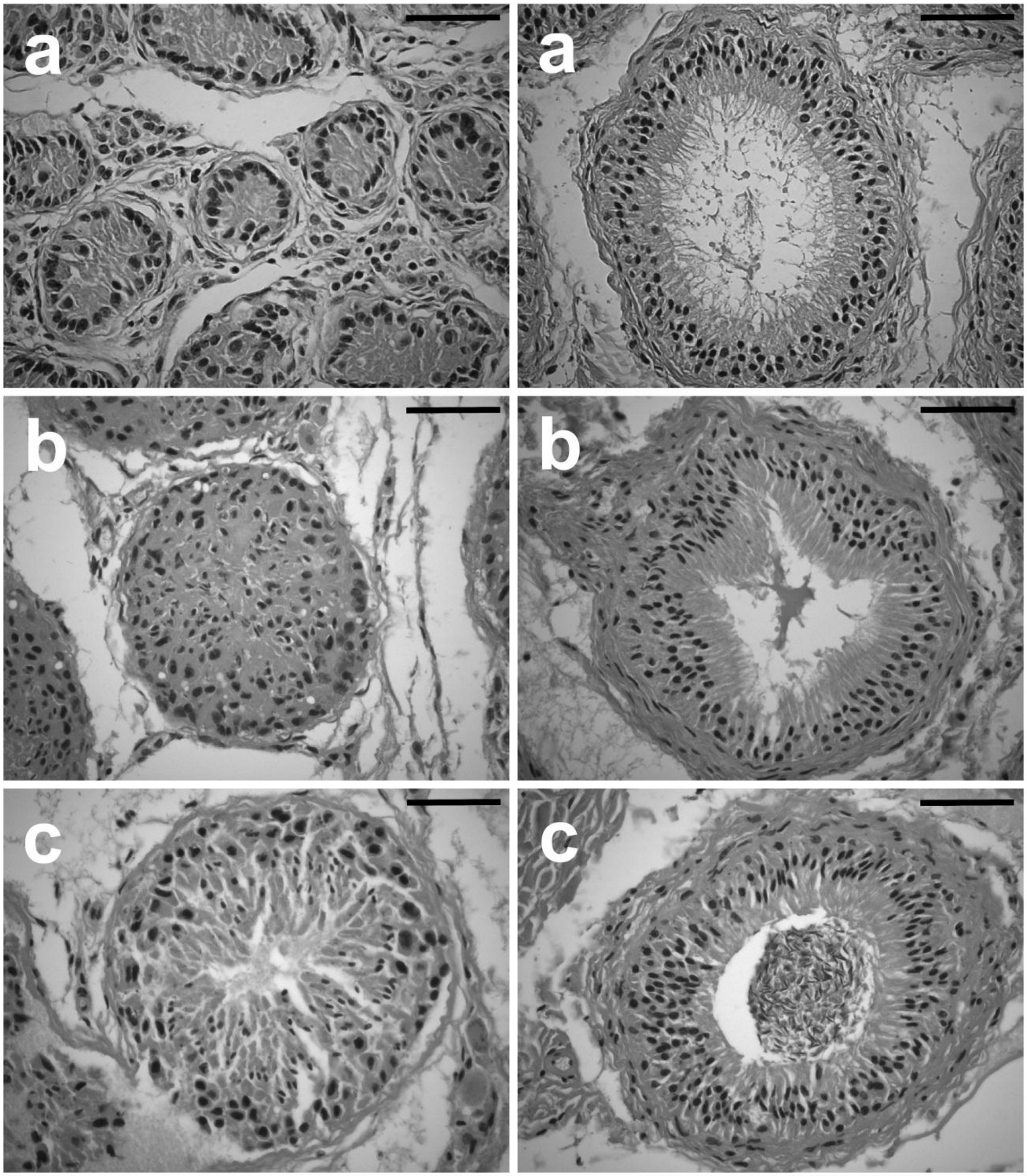

Figure 2.2. Representative seminiferous tubules of (a) immature, (b) pubertal, and (c) mature sea otters at 40x magnification. The left and right columns are seminiferous tubules from the testis and the epididymis, respectively. The black bars = 50 µm.

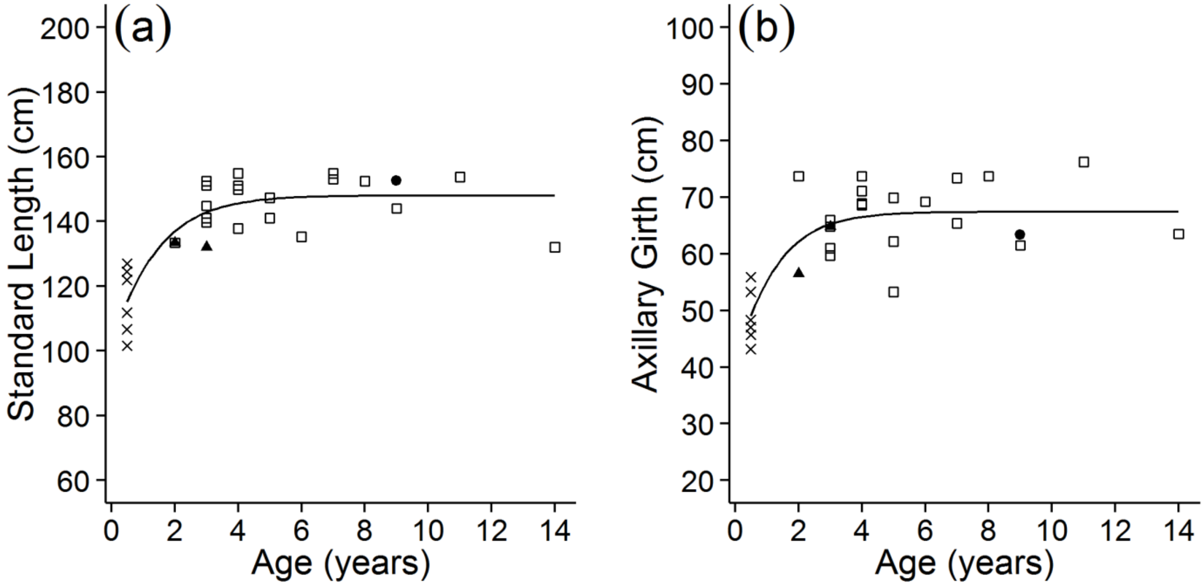

Figure 2.3. Gompertz growth curves fitted to (a) standard body length (n=29) and (b) axillary girth (n=29). See Table 2.1 for parameter values. Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals respectively. Eleven animals were not included due to missing ages (9) or standard length and axillary girth (2).

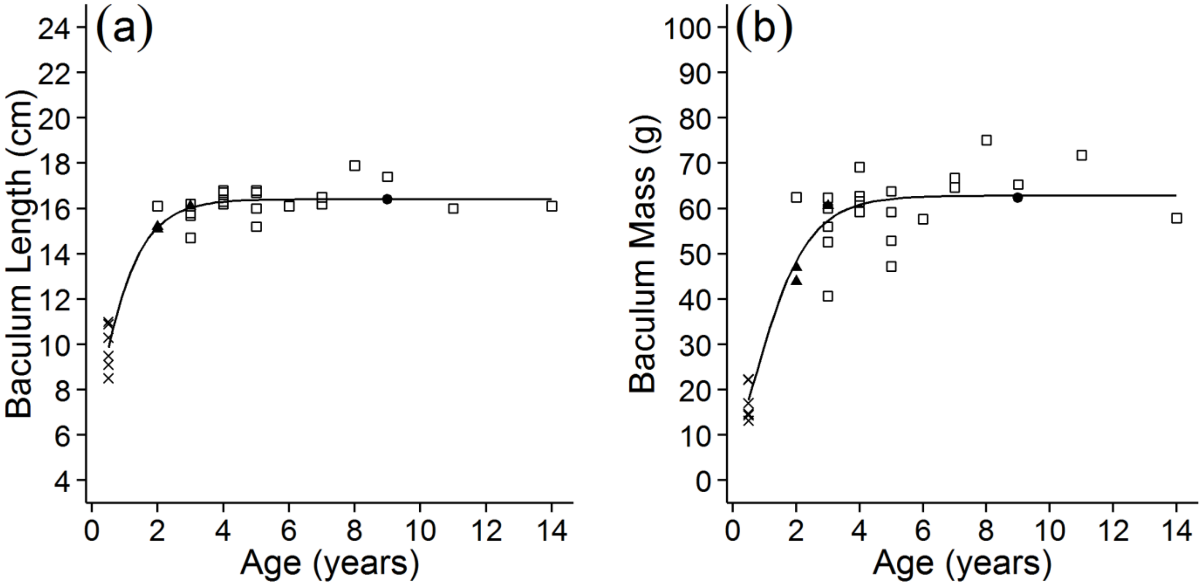

Figure 2.4. Gompertz growth curves fitted to (a) baculum length (n=31) and (b) baculum mass (n=31). See Table 2.1 for parameter values. Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals, respectively. Nine animals were not included due to missing ages.

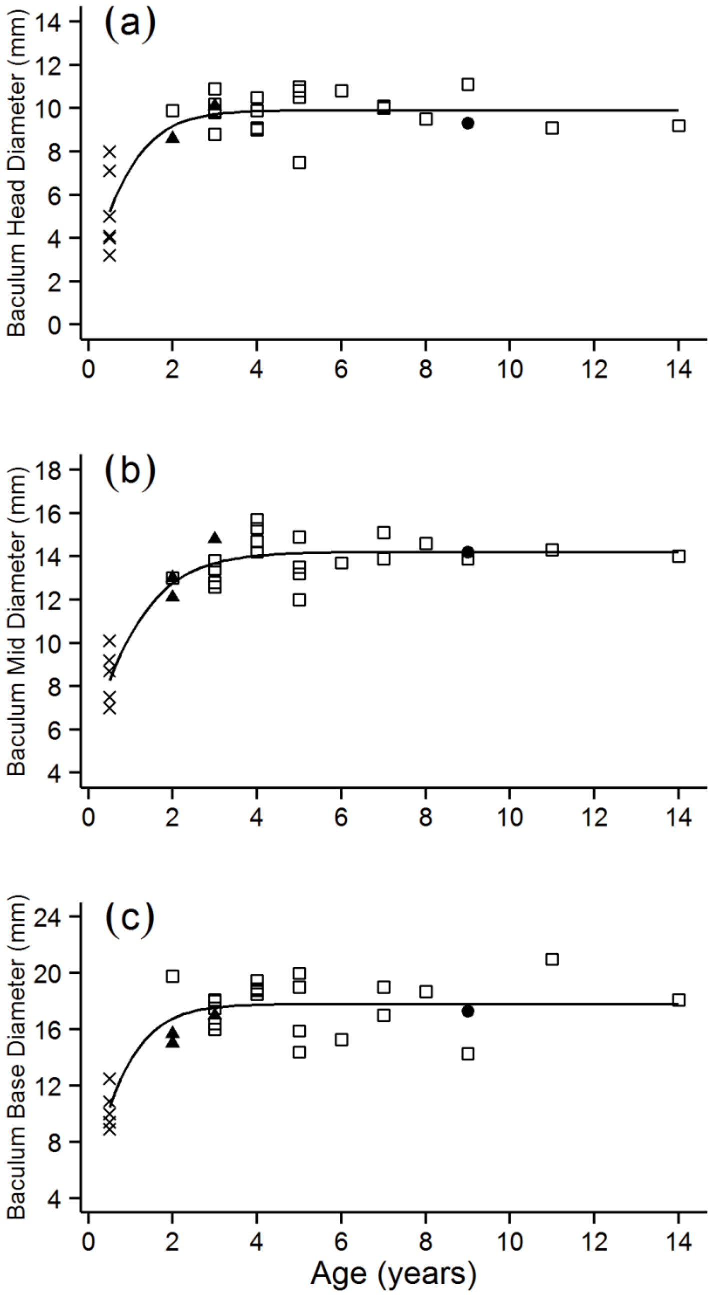

Figure 2.5. Gompertz growth curves fitted to baculum diameter (n=31) at the (a) head, (b) middle, and (c) base. See Table 2.1 for parameter values. Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals respectively. Nine animals were not included due to missing ages.

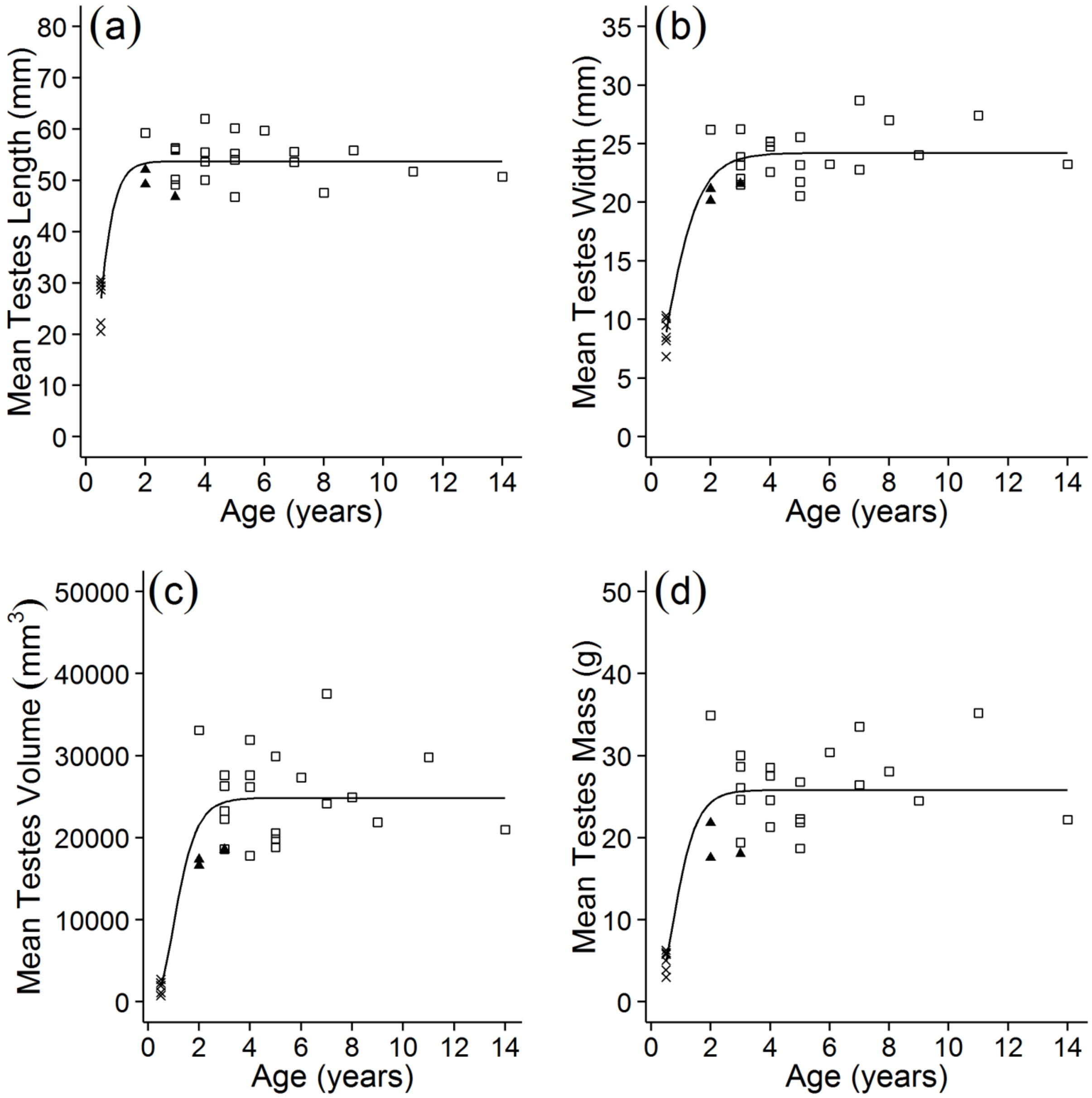

Figure 2.6. Gompertz growth curves fitted to mean testes (a) length, (b) width, (c) volume, and (d) mass versus age (n=30). See Table 2.1 for parameter values. Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals respectively. Ten animals were not included due to missing ages (9) or testes measurements (1).

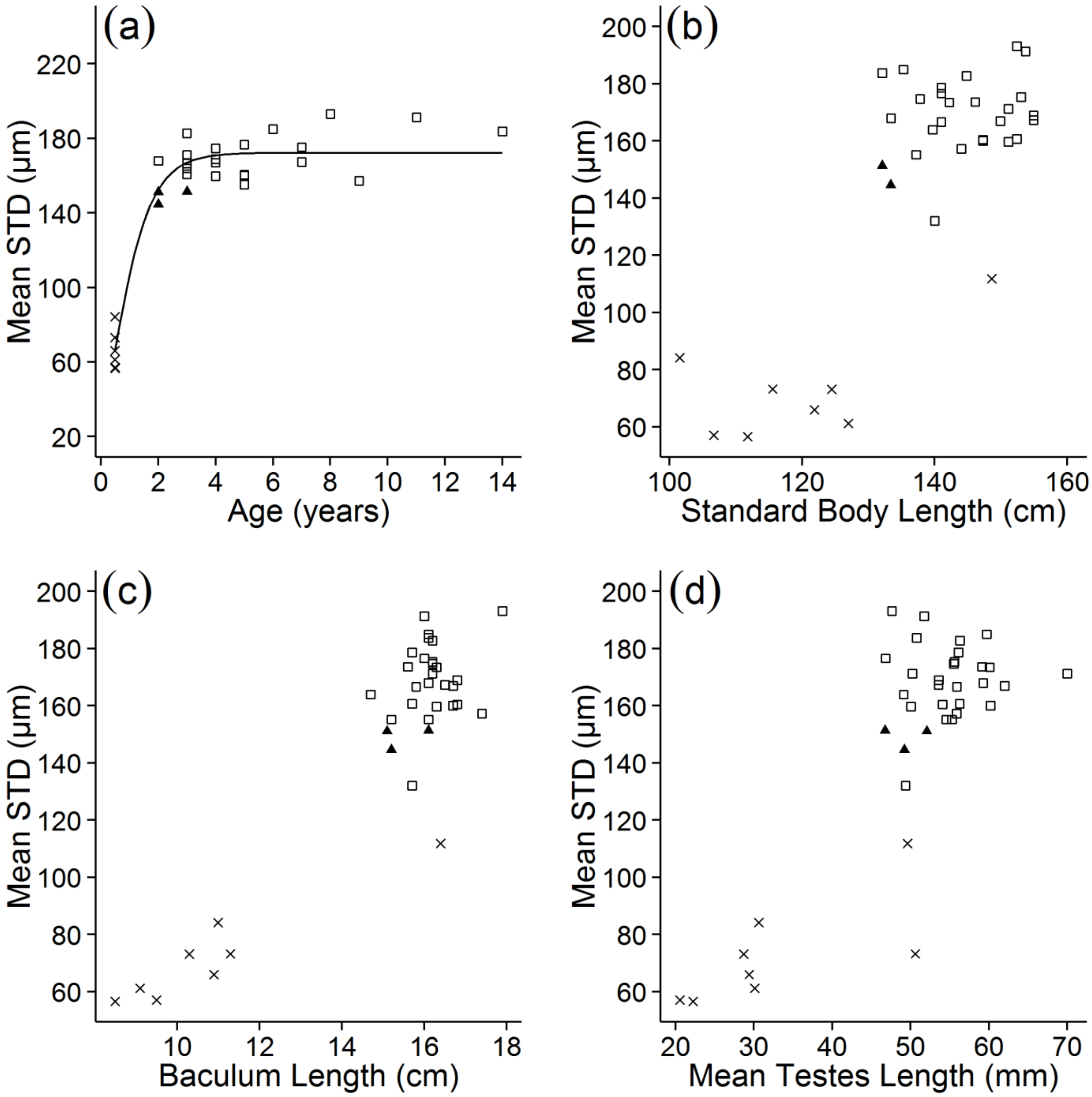

Figure 2.7. Mean seminiferous tubule diameter (STD) versus (a) age (n=30), (b) standard body length (n=36), (c) baculum length (n=38), and (d) mean testes length (n=38). A Gompertz growth model was fit to STD versus age (See Table 2.1 for parameters). Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals, respectively. Some specimens were not included owing to missing ages (9), standard length (2), mean testes length (1), or STD (2).

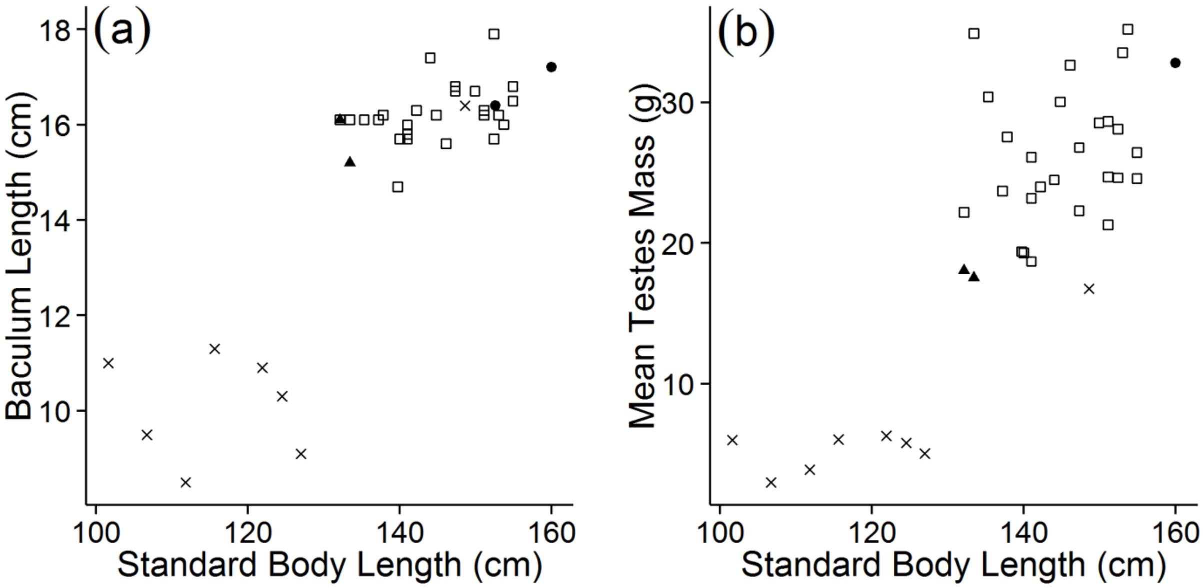

Figure 2.8. Sea otter (a) baculum length (n=38) and (b) mean testes mass (n=37) versus standard body length. Open squares, x's, filled triangles, and filled circles represent mature, immature, pubertal, and unknown animals, respectively. Three animals were not included owing to missing standard body length (2) animals or mean testes mass (1).

Table 2.1. Parameter estimates (±SE) for Gompertz growth functions. A_∞ represents the asymptotic size, k represents a growth rate constant, b represents the time at which the absolute growth rate begins to decrease, and e is a mathematical constant that is the base of the natural logarithm (2.71828). Model (Eq. 2.1): $S_t = A_\infty(e^{-ke^{-bt}})$.

Growth Parameter	n[*]	A_∞	k	b
Standard Body Length (cm)	29	148.0 (2.67)	0.37 (0.062)	0.78 (0.28)
Axillary Girth (cm)	29	67.4 (1.81)	0.50 (0.13)	0.91 (0.45)
Baculum Length (cm)	31	16.4 (0.19)	0.95 (0.12)	1.25 (0.23)
Baculum Mass (g)	31	62.8 (1.99)	2.14 (0.38)	1.05 (0.20)
Baculum Head Diameter (mm)	31	9.9 (0.29)	1.30 (0.45)	1.42 (0.65)
Baculum Middle Diameter (mm)	31	14.2 (0.26)	0.93 (0.14)	1.08 (0.26)
Baculum Base Diameter (mm)	31	17.8 (0.44)	1.10 (0.41)	1.46 (0.71)
Mean Testes Length (mm)	30	53.7 (0.98)	3.21 (8.06)	3.08 (5.04)
Mean Testes Width (mm)	30	24.2 (0.53)	2.17 (0.50)	1.56 (0.41)
Mean Testes Volume (mm^3)	30	24840 (1223)	6.72 (4.36)	1.93 (0.74)
Mean Testes Mass (g)	30	25.8 (1.10)	4.92 (3.62)	2.20 (1.36)
Mean STD (µm)	30	172.2 (3.03)	1.89 (0.28)	1.37 (0.25)

[*] Sample sizes do not equal 40 animals due to missing ages (9) and growth parameters (2).

Table 2.2. ANOVA results, mean, standard deviation (SD), range, and sample size (n) for body size and reproductive measurements for immature, pubertal, and mature sea otters.

Reproductive Maturity		Standard Length (cm)	Axillary Girth (cm)	Baculum Length (cm)	Baculum Middle Diameter (mm)	Baculum Mass (g)	Mean Testes Length (mm)	Mean Testes Mass (g)	Mean Testes Volume (mm^{3})	Mean STD (µm)
ANOVA Results (P, F)		0.0014*, -4.8	0.0024*, -4.2	<0.001, 58.2	<0.001, 30.4	<0.001, 37.2	<0.001, 34.4	<0.001, 59.3	<0.001, 52.6	<0.001, 152.1
Immature	*Mean*	119.7^{a}	52.8^{a}	10.9^{a}	9.5^{a}	23.9^{a}	32.7^{a}	6.6^{a}	3846.7^{a}	72.9^{a}
	SD	14.6	9.4	2.4	2.6	17.6	11.3	4.3	4363.7	18.3
	Range	101.6 - 148.6	43.2 - 73.0	8.5 - 16.4	7.0 - 14.1	13.2 - 66.6	20.56 – 50.6	3.0 – 16.8	761.7 – 1.4E4	56.6 – 111.8
	n	8	8	8	8	8	8	8	8	8
Pubertal	*Mean*	132.8^{b}	60.7^{b}	15.5^{b}	13.3^{b}	50.5^{b}	49.3^{b}	19.1^{b}	17507.9^{b}	149.0^{b}
	SD	0.9	5.9	0.6	1.4	8.9	2.7	2.3	996.5	3.9
	Range	132.1 - 133.4	56.5 - 64.8	15.1 - 16.1	12.1 - 14.8	43.9 - 60.6	46.8 - 52.1	17.6 - 21.8	1.6E4 - 1.9E4	144.5 - 151.3
	n	2	2	3	3	3	3	3	3	3
Mature	*Mean*	145.2^{b}	67.7^{b}	16.2^{b}	14.0^{b}	59.6^{b}	55.1^{b}	26.1^{c}	24814.6^{b}	169.3^{b}
	SD	7.0	5.7	0.6	0.9	7.3	5.0	4.6	5452.1	12.8
	Range	132.1 - 154.9	53.3 - 76.2	14.7 - 17.9	12.0 - 15.7	40.7 - 75.1	46.8 - 70.0	18.7 - 35.2	1.4E4 - 3.8E4	132.1 - 193.1
	n	26	26	27	27	27	27	27	27	27

[*] Sample size for pubertal animals was too small so a Welch's two sample t-test was conducted for immature and mature animals. The t-statistic and P-value are provided.

Values not sharing a common letter are significantly different at $P \leq 0.05$ by Tukey –Kramer multiple comparisons test.

General Conclusion

Marine mammals provide significant subsistence and economic resources to the people of Alaska. Native Alaskans rely on marine mammals for food, clothing, and handicrafts to sustain their cultural and traditional ways of life. Alaskan residents and business owners benefit from the thousands of tourists who travel great distances each year to observe marine mammals in the wild. Protecting these species and understanding their biology is of high priority and concern. Harbor seals and sea otters are two marine mammal species that have experienced extreme population fluctuations over recent decades in Alaska (Estes 1990, Frost *et al.* 1999, Estes *et al.* 2005, Jemison *et al.* 2006, Mathews & Pendleton 2006, Small *et al.* 2008, Esslinger & Bodkin 2009, Womble *et al.* 2010, Doroff *et al.* 2011, Hoover-Miller *et al.* 2011). Researching the growth and reproductive biology of these species is important for management of human activities to promote their restoration, understanding ecosystem-level changes over time and space, and ensuring food and economic security of those who rely on these species.

In Chapter 1, harbor seal growth and sexual maturity were examined using samples collected by the Alaska Native Harbor Seal Commission's Biosampling Program. Harbor seals in the Gulf of Alaska (GOA) are slightly smaller in length, have a later implantation date, and are larger at sexual maturity compared to harbor seals in the 1960s. However, small sample sizes from sub-regions in the GOA only allowed for analysis of growth and reproduction for the GOA region pooled as a whole, and localized perturbations could still be occurring. It would be beneficial to obtain additional samples from various areas of the GOA and analyze reproduction and growth by sub-region. Subsistence hunting of marine mammals is prohibited in Glacier Bay National Park and Preserve (GBNPP), and consequently no samples for this research came from that region. Additional research on this group of harbor seals is important as it, along with the western GOA and Aleutian Island population, are still declining precipitously in Alaska.

The cues of implantation for pinnipeds in Alaska are complex and not well understood. Whatever the cause of implantation, knowing the window in which implantation occurs is extremely valuable. During that period harbor seals are making a physiologically critical decision, and are especially vulnerable to disturbance. The cues for implantation are not fully understood, so therefore how anthropogenic actions influence them are not understood as well. Knowing the window of time for implantation, in the case of harbor seals in the GOA from late September to early October, in which harbor seals are especially vulnerable, is important so human actions can be managed to protect populations of harbor seals.

In Chapter 2, I examined the growth and sexual maturity of male sea otters outside Gustavus, Alaska. Generally, studying female reproduction is thought to be more valuable than that for males, as it can produce estimates of reproductive rates that are then used in population modelling. A great deal of research has been dedicated to the understanding of female sea otter reproduction (Sinha *et al.* 1966, Sinha & Conaway 1968, Siniff & Ralls 1991, Bodkin *et al.* 1993, Jameson & Johnson 1993, Eberhardt & Schneider 1994, Monson & DeGange 1995, Larson *et al.* 2003, von Biela *et al.* 2009), while extremely little has been published on male reproduction (Kenyon 1969, Green 1978, Riedman & Estes 1990). Information on male growth and sexual maturity, however, can provide insight into the population status and conditions of the ecosystem. I found that male sea otters outside GBNPP exhibited rapid growth rates and matured at an early age. This can indicate that the ecosystem has plentiful resources, whether it is due to high productivity or a high standing stock resulting from the absence of sea otters over many decades, and can support high numbers of sea otters.

The rapid increase of sea otters in the Glacier Bay region has management implications, in the form of conflicts between sea otters, Alaska Natives, and commercial fishermen for benthic resources. Sea otters exert a strong top-down control of ecosystems in which they inhabit (Estes & Palmisano 1974, Estes 1990). They have the ability to alter the structure and diversity of nearshore marine ecosystems (Estes & Duggins 1995, Reisewitz *et al.* 2006). As has occurred in other regions where sea otters are recolonizing areas from which they have been absent for an extended period of time, there is likely going to be a reduction in the size and density of various benthic invertebrates (Kvitek & Oliver 1992, Fanshawe *et al.* 2003, Bodkin *et al.* 2007). This will have repercussions on the structure and function of the ecosystem and will affect the other seabird, marine mammal, and fish species in the region. Sea otter predation on benthic invertebrates is also known to cause increases in canopy forming macroalgae species that consequently increase the diversity of nearshore marine taxa (Estes & Palmisano 1974, Estes & Duggins 1995, Reisewitz *et al.* 2006). Understanding the growth and reproduction of sea otters in Alaska can aid in monitoring sea otter populations and in predicting any direct and indirect effects of sea otter re-colonization on the ecosystems and the developing resource conflicts between Alaska Native subsistence hunters of both sea otters and benthic invertebrates, commercial fishermen of those benthic invertebrates, and the tourism industry that benefits from the presence of sea otters.

All of the samples used in this research were gathered with the assistance of Native Alaska subsistence hunters. Formal and informal biosampling programs are excellent tools for collecting data on wild marine mammal populations that are otherwise difficult to collect biological samples from. The research is mutually beneficial to both the scientific and Native Alaskan communities and can foster relationships that have the ability to produce more comprehensive understandings of wild populations. Native Alaskans are concerned about the food safety and sustainable use of the marine mammals that they rely on, and encourage and support research on the individual and population health of marine mammal species in Alaska. The Alaskan Native Harbor Seal Commission’s Biosampling Program, which supplied the samples for this research was suspended in 2006 due to lack of funding. Formally implemented biosampling programs are excellent tools for marine mammal monitoring and should be highly considered for funding opportunities. A less structured partnership with subsistence hunters, such as the one formed here with an Alaskan Native sea otter subsistence hunter is another excellent way to study marine mammals. It can be achieved with limited funding if both parties are willing to communicate and there is a level of trust and mutual understanding of what is trying to be accomplished. Initiating a biosampling partnership takes time and a period of protocol refinement to standardize the methods and logistics, but, when successful, provides high quality data and samples from marine mammals over an extended time period. In the future, as anthropogenic influences continue to increase, enhanced biosampling programs will be an invaluable tool for continued monitoring of marine mammals in Alaska.

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