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**Prey requirements and salmon consumption by Steller Sea Lions
(*Eumetopias jubatus*) in southern British Columbia and Washington State**

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ABSTRACT

This study was conducted to estimate prey requirements and salmon consumption by Steller sea lions in southern British Columbia and Washington State (between Cape Caution in central B.C. and the mouth of the Columbia River). Steller sea lion abundance in the study area has been increasing in recent decades, renewing concern over competition with fisheries and potential impact on other fishery resources. We conducted aerial surveys during the summer, fall, winter and spring to document seasonal changes in abundance and distribution. A bioenergetics model was developed to estimate prey requirements. The model integrated information on the sex- and age-structure of the population from life tables, growth and body size based on specimens collected in B.C. in the 1960s, activity budgets based on satellite telemetry, and published measurements of field metabolic rates for other otariids (fur seals and sea lions). Scat samples were collected and bone remnants analyzed to determine the prevalence of salmon in the diet, and DNA extracted from a subset of the salmon bones to determine the species of salmon consumed.

Surveys showed a marked seasonal shift in distribution. During summer, 75% of animals were on the breeding rookeries in the Scott Islands, and the remaining animals on year-round haulout sites along the outer coast of Vancouver Island and Washington. By fall, about half of breeding animals had dispersed from the Scott Islands to nearby haulouts (within 120 km of rookeries), and non-breeding animals began to appear in inside waters. By winter, a few animals continued to use the Scott Islands as a haulout, but most animals were widely distributed at year-round and winter haulout sites. Young-of-the-year were no longer distinguishable from older juveniles, but we suspect many females with dependent young had dispersed northwards out of the study area, but this was offset by an influx of animals from breeding sites off northern California and Oregon. By spring, animals were still widely distributed, and had not yet begun to return to breeding rookeries but had shifted onto year-round haulout sites. Counts were highest during the summer breeding season and lowest outside the breeding season. However, satellite telemetry indicated animals spent more time on land during summer and hauled out mainly during daylight hours, so survey corrections to account for animals at sea and missed in surveys were smaller (1.51). In contrast, animals spent less time on land outside the breeding season and haulout bouts were not as synchronized, so haulout corrections were higher (mean 2.76; range 2.51 to 2.99). As a result, estimated abundance of Steller sea lions in the study area was relatively stable throughout the year (range 21,500 to 26,900; CVs 8-11%). The bioenergetics model indicated that most energy was required for maintenance (metabolism while resting on land and foraging at sea). Net daily energy requirements were estimated to be 3-4 times Klieber's (1975) basal metabolic rates (CV 13-15%), and assimilation efficiency was estimated at 78-81% from captive studies. Assuming the diet in the study area was similar to Steller sea lions in neighbouring waters in Alaska (4.7-6.3 MJ·gm⁻¹, Winship and Trites 2003), this translated to prey requirements of 18 kg of prey per capita per day (CV 16-20%) or 161,000 tonnes per annum for the study population (CV 22-25%). Daily food requirements of young-of-the-year, provided by their lactating mothers, increased from 4 kg at birth to 15 kg by their first spring, at which point some began to forage independently, although many continued to suckle into their 2nd and 3rd year. Adult females required 15 kg of prey per day, which increased to 16 kg for pregnant females, and perhaps as high as 30 kg for lactating females by spring to meet the increasing requirements of their growing offspring. Adult males required an average of 28 kg, but intake varied seasonally from 15 kg during summer when they fasted or reduced food intake, to 32-33 kg outside the breeding season as they were fattening. Scat samples indicated that salmon consumption was widespread, with salmon occurring in 24% of samples. Salmon were consumed at most of the

sites sampled, and in all months of the year, but were most prevalent in the diet during summer (26% of samples) and fall (37%), and least prevalent during winter (17%) and spring (14%). Sea lions preyed primarily upon adult-size salmon. We estimated that salmon comprised 10% of the overall diet, ranging from 7% in spring to 15% in fall (CV 4-14%). Annual salmon consumption was estimated at 17,200 tonnes (CV ~25-34%¹), of which 84% was taken in B.C. and the remaining 16% in Washington and mouth of the Columbia River. DNA was successfully extracted from 95% of a subset of 367 salmon samples analyzed, which indicated that Steller sea lions preyed upon all 5 species of Pacific Salmon as well as steelhead. The limited number of DNA samples analyzed to date did not allow us to partition consumption among salmon species, but we provide a preliminary description of seasonal and geographic patterns.

Steller sea lions in the study area are thriving; populations have been increasing for the past 5 decades and the rate of increase appears to be accelerating, and animals grow bigger and live longer than their counterparts in western Alaska. The species has emerged as an important predator in coastal waters. The estimated annual consumption of salmon by Steller sea lions in the study area (17,200 tonnes; CV ~25-34%¹) is now of similar magnitude to salmon landings by the commercial fishery in the B.C. and Washington State over the last decade (mean 18,500 tonnes; range 5,500 to 29,400 tonnes).

¹The final Monte Carlo simulations incorporating all parameters and large sample-sizes have not yet been completed, and these preliminary CV's are based on simulations with key parameters and small sample sizes.

RÉSUMÉ

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1. INTRODUCTION

Steller sea lions (*Eumetopias jubatus*) breed along the North Pacific Rim from the Kuril Islands and Kamchatka Peninsula, west through the Aleutian and Pribilof Islands into the Gulf of Alaska, and south along the continental shelf as far as central California. Three stocks are recognized based on genetic differences (Bickham et al. 1996; Baker et al. 2005) and phylogeographic patterns (Loughlin 1997). The Asian Steller Population breeds in Russia west of the Commander Islands; the Western Steller Population (WSP) breeds in the Commander and Aleutian Islands and Gulf of Alaska west of Cape Suckling (144°W) (Burkanov and Loughlin 2005); and the Eastern Steller Population (ESP) breeds along the west coast of North America in SE Alaska, British Columbia, Oregon and north-central California.

Most attention in recent years has focused on the WSP, which has declined by about 80% since the 1970s (Merrick et al. 1987; Loughlin et al. 1992; Trites and Larkin 1996; Loughlin 1998), and been listed as endangered under the U.S. Endangered Species Act (NMFS 2008). The listing required the designation of critical habitat, which has important implications for fisheries (Ferrero et al. 1994, Fritz et al. 1995; NMFS 1998, 2000, 2001), resulting in a major research effort to determine causes for the decline in the WSP (Dalton 2005; NMFS 2008). While the proximate reason for the declines continues to be debated (Fritz and Hinkley 2005; NMFS 2008; Atkinson et al. 2008), it appears to be related to nutritional stress (Calkins et al. 1999; Trites and Donnelly 2003). Prey availability or quality may have changed as a result of an oceanic regime shift (Alverson 1992; Springer 1998, 2004; Hare and Mantua 2000; Benson and Trites 2002; Trites et al. 2006a), or affected by the expansion of commercial fisheries (Fritz et al. 1995; Atkinson et al. 2009). Top down processes, particularly predation by killer whales, may be a factor in impeding recovery, especially for populations that are depleted or spend more time foraging (Barrett-Lennard et al. 1995; Heise et al. 2003; Williams et al. 2004; Frid et al. 2006, Maniscalco et al. 2007).

The Eastern Steller Population (ESP), was, until recently, much smaller than the WSP and received less attention. Historically, Steller sea lions were considered to be a nuisance along the west coast of North America, and predator control programs reduced abundance and maintained it at low levels in California, Oregon, Washington and British Columbia (Rowley 1929; Bonnot and Ripley 1948; Pearson and Verts 1970; Scheffer 1950; Kenyon and Scheffer 1959). However, populations in SE Alaska were small and not subject to significant kills, and Steller sea lions established a rookery just north of the border on Forrester Island in the 1950s which flourished as control programs reduced breeding populations south of the Alaska and British Columbia border. Since being protected in the early 1970s, Steller sea lions in BC and SE Alaska which account for about 80% of pup production in the ESP, have been increasing (Olesiuk 2003, 2008, WP10a; Pitcher et al. 2007). Steller sea lion breeding populations have also increased off Oregon and northern California (Brown and Riemer 1997; Brown et al. 2002; Pitcher et al. 2007). The species doesn't breed in Washington, but numbers of non-breeding animals on haulout sites has increased (Pitcher et al. 2007). Steller sea lions in B.C. and SE Alaska appear to have fully recovered from control programs, but continue to increase (Olesiuk, WP10a). The breeding population in B.C. and SE Alaska is now more than twice the peak historic levels that occurred prior to the first large-scale kills in the early 1900s. Steller sea lions currently breed at 10 sites in B.C. and SE Alaska, compared with 4 when the first sea lion assessments were conducted in the early 1900s (Newcombe and Newcombe 1914). However, there is no evidence that the rate of population growth is slowing, and it appears to have accelerated in recent years (Olesiuk WP10a).

Although it is not possible to project future population trends, the increases that have occurred over the last 5 decades cannot continue indefinitely. At some point the population will ultimately be limited by prey resources and stabilize at, or perhaps fluctuate around carrying capacity. Given the potential for Steller sea lions becoming food limited, we require a better understanding of their prey requirements and the extent to which they overlap with fisheries (Fisheries and Oceans Canada 2010).

While sea lions are ultimately limited by prey availability, it is unclear whether sea lions limit their prey populations. In view of the recent growth of Steller sea lion abundance, this is obviously an increasingly important concern for fishery management. Unfortunately, the early assessments leading up to the control programs focused on the basic natural history of the species and status of Steller sea lion populations, and did not attempt to quantify feeding habits or estimate the impact on salmon and other prey (Newcombe and Newcombe 1914; Newcombe et al. 1918). Moreover, there was essentially no monitoring or evaluation of the effectiveness of control programs. The first large kills in B.C. were aimed at protecting the Rivers Inlet sockeye fishery, and targeted Steller sea lion breeding sites on the Sea Otter Group (Bigg 1985). Annual kills during the breeding season in the 1920s and 1930s had eradicated pup production on those rookeries by the late 1930s, but there is no evidence of a subsequent increase in sockeye catches in Rivers Inlet, and the Owikeeno sockeye stock continues to be severely depressed (McKinell et al. 2001). Predator control in the 1950s and 1960s targeted the major rookeries on the Scott Islands off the northwest end of Vancouver Island. Spalding (1964) subsequently examined salmon catches off Scott Islands, and saw no evidence of increase in catch corresponding with the decline in sea lion numbers. Similar predator control and bounty programs conducted in the early 1900's along the Washington and Oregon coasts severely reduced Steller sea lion numbers (Scheffer and Macy 1944; Scheffer 1950; Kenyon and Scheffer 1959; Pearson and Verts 1970).

Developing an ecosystem approach to management of our oceans and resources will require a better understanding of the role of apex predators such as Steller sea lions. Most of the research on Steller sea lions in B.C. and Washington to date has focused on assessing and monitoring population status (Pitcher et al. 2007; Olesiuk 2008; Olesiuk et al. 2008; Olesiuk, WP10a). There has also been some work on fishery and prey interactions, but these have focused on localized problem areas involving nuisance animals (Stansell 2003, 2004, 2005, 2006; Brown et al. 2007, 2008; Scordino 2009). In this study, we conducted a broader assessment of the prey requirements and salmon consumption by Steller sea lions in coastal waters of southern B.C. and Washington State (Cape Caution to the mouth of the Columbia River). Aerial surveys were flown during summer, fall, winter and spring to document seasonal changes in sea lion abundance and distribution, and satellite telemetry and time-depth recorder data were used to develop survey correction factors to account for animals that were at sea and missed during surveys. We developed a Steller sea lion bioenergetics model that integrated information on population size, population sex- and age-structure, morphometric data, published estimates of field metabolic rates for other otariids, captive studies on energy assimilation, and activity budgets based on satellite telemetry. Scat samples were collected and bone fragments analyzed to determine prevalence of salmon in the diet, and genetic analyses conducted to determine the species of salmon consumed. In addition to providing the first estimates of salmon predation levels, we anticipate that this study will provide a framework for assessing sea lion interactions with other prey and in other regions. Monte Carlo simulations were conducted to assess the uncertainty and assess potential biases in the consumption estimates, and sensitivity analyses conducted to identify important information gaps.

2. METHODS

2.1 Study Area and Sea Lion Biology

The study area encompassed the coastal waters of southern British Columbia and Washington State from Cape Caution south to and including the lower Columbia River (Figure 1). The area coincides with the Southern Transboundary Area of Pacific Salmon Commission², who provided seed funding to initiate this study. The study area supports a significant number of Steller sea lions: about 30% of the Eastern Steller Population (ESP) and 16% of world population (Burkanov and Loughlin 2005; Pitcher et al. 2007; Allen and Angliss 2009; Olesiuk, WP10a). The area is accessible by road, from small airports, and widely serviced by harbour facilities, making it practical to fly surveys economically and safely using small, single-engine aircraft, and to collect scat samples with small boats from all but the most remote or exposed sites.

Steller sea lions occur in the study area throughout the year, and utilize three distinct types of haulout sites: 1) breeding rookeries; 2) year-round haulout sites; and 3) winter haulout sites (Figure 1). Breeding sites tend to be the furthest from land and generally most exposed to ocean swells. The vast majority (>98%) of births and most breeding activity occurs on rookeries. Pitcher et al. (2007) defined a rookery as locations where 50 or more births occurred, and we adopted the same definition for this assessment. Rookeries in the study area are situated on Maggot Island off Beresford Island, Sartine Island and Triangle Island, collectively referred to as the Scott Islands.

Some non-breeding haulout sites appear to be used continuously throughout the year, and are referred to as year-round haulouts. Year-round haulout sites tend to be situated along the outer, exposed coast, but unlike rookeries are often close to land masses (Figure 1). The presence of animals in all months, particularly during the June-July breeding season, is characteristic of these sites. Steller sea lions also utilize many additional sites intermittently on a seasonal basis, referred to as winter haulouts. These can be located in exposed locations, as well as in sheltered inlets and channels and sometimes even up rivers (Figure 1). Sites in exposed locations are generally not directly exposed to ocean swells, but rather are sheltered to some extent by the surrounding topography. The main period of occupancy is outside the breeding season, but a few animals can also be present sporadically during May-August. Occupancy can be continuous or intermittent during winter months. Counts of any rafting or swimming animals observed during the surveys were added to the adjacent haulout site counts or tallied as miscellaneous with respect to location.

During the summer breeding season, breeding animals congregate on rookeries to give birth and mate. Animals tend to return to natal sites where they were born, but there is some exchange among rookeries (Raum-Suryan et al. 2002). The chronology of breeding seems to be fairly synchronized throughout the range (Bigg 1985; Pitcher et al. 2002), and has been described by a number of researchers (Gentry 1970; Sandegren 1970; Edie 1977; Withrow 1982; Higgins 1984; Gisiner 1985; Merrick 1985; Smith 1988). Dominant males establish territories in late May, which they defend until late June or early July. Females begin arriving in early June, and give birth to a single pup within a few days of arrival. Females spend about a week ashore with newborn pups, and then make a series of foraging trips lasting just under a day, punctuated by periods of just under a day on land tending pups (Milette and Trites 2003;

²A proposal to conduct a companion study in northern B.C. was concurrently submitted to the Northern Endowment Fund, but was not funded.

Rehberg et al. 2009). Pups cannot swim at birth and are confined to land for the first month of life (Sandegren 1970). During the breeding season, most non-breeding animals (juveniles, barren females and non-territorial males), which make up about 40% of the total population (or 55% of non-pups) are occupy year-round haulouts. In August, mothers with pups begin to disperse from rookeries. Outside the breeding season, animals of all ages are widely dispersed at year-round and winter haulout sites. Pups travel with their mothers and continue to nurse through the first spring. Many are probably weaned and begin to increase the frequency and depth of dives in late spring as they approach their first birthday, but some may continue to suckle until their 2nd and or sometimes even 3rd spring (Raum-Suryan et al. 2004; Pitcher et al. 2005; Trites et al. 2006b; Rehberg and Burns 2008).

Non-breeding animals, including females with older pups, may disperse many hundreds of kilometers from natal breeding sites. Animals branded as pups on rookeries in northern California and Oregon are commonly seen in the study area, and pups branded on rookeries in SE Alaska are occasionally sighted in the study area (Scordino 2006; Gearin, unpublished data; Jeffries, unpublished data; Olesiuk, unpublished data). Pups have not been branded on rookeries in B.C., but non-pups captured and tagged at a winter haulout in the Strait of Georgia subsequently ranged as far south as Crescent City, California and as far north as Prince William Sound, Alaska (see Section 2.2.2). Thus, Steller sea lions within the study area comprise an open population subject to immigration and emigration.

Historically, Steller sea lions in B.C. and Washington were subject to predator control programs that reduced their abundance (Scheffer 1950; Bigg 1984, 1985; Olesiuk WP10a). However, sea lion surveys in the study area indicate that abundance has been increasing since populations were protected in the early 1970s. These increases are evident in both pups and total numbers on the Scott Island rookeries, and in numbers of animals at non-breeding haulout sites in both BC and WA, both in summer and winter (Figure 2).

Although the focus of our study was Steller sea lions, they co-exist with California sea lions. California sea lions on the west coast breed on the Channel Islands off California (Caretta et al. 2009) and few are found north of California during the summer breeding season. During the non-breeding season, California sea lions disperse widely from breeding sites, with many subadult and adult males traveling northwards (Mate 1973, 1975). Historically, the species was rare in the study area, but began to appear regularly in the mid-1960s, and numbers increased dramatically during the 1970s and early 1980s. Since then, counts in BC have been highly variable, and show no consistent trend (Olesiuk 2004). California sea lions intermingle with Steller sea lions, mainly on winter haulout sites, but occasionally on year-round haulout sites. As a result, we counted both species during aerial surveys, and sometimes we couldn't be sure what species had deposited scat samples. In order to assess the relative role of California sea lions and the extent to which they may have confounded diet analyses, we also made preliminary estimates of their predation levels. The data were far less extensive and analyses less focused on California sea lions, thus the crude estimates for this species should be regarded as provisional.

2.2 Data Sources:

Our assessment incorporated several diverse types of data: 1) aerial surveys were conducted to determine abundance and distribution; 2) satellite telemetry and archival tags were deployed to monitor haulout patterns and activity levels; 3) morphometric data from specimens were used to describe growth and body composition; 4) energetics data from captive study and free-ranging otariids were used to estimate metabolic rates; and 5) scat collections were made to determine prevalence of salmon in the diet. In many cases these data sources were used for various components of the assessment. For example, survey data were used to estimate abundance, but also used to determine seasonal shifts in distribution so diet data could be stratified by season and site and weighted by the relative abundance of animals for each strata. Similarly, telemetry data were used to monitor haulout patterns and develop survey correction factors to account for the proportion of animals at sea and missed during surveys, and also to establish activity budgets for the bioenergetics model. So as to avoid duplication, we begin with a general overview of the data sources, and then later provide details on how these data were interpreted and analyzed to parameterize the model.

2.2.1 Aerial Surveys:

Aerial surveys were conducted from small fixed-wing aircraft flown at an altitude of 150-200 meters and airspeed of 125 km·hr⁻¹. During surveys, we attempted to check all known haulout sites, and opportunistically scanned the shoreline for new sites, but coverage of the coastline was far from complete. Surveys were conducted during daylight hours, with most counts made within the optimal (summer) survey window of between 10:00 and 18:00 local time (Withrow 1982). Survey procedures and evaluation have been described elsewhere in greater detail (Pitcher et al. 2007; Olesiuk et al. 2008; Olesiuk WP10a).

We conducted surveys during the summer breeding season, fall, winter and spring. For the purposes of this study, summer was defined as June-August so as to correspond with the breeding season. Fall included the months of September-November, winter included December-February, and spring included March-April. Several other sea lion investigators have used these same nominal seasons (e.g Winship and Trites 2003). Summer surveys that included the breeding sites were timed to coincide with the end of the pupping season, which provided an estimate of annual pup production.

Visual counts were made of swimming animals and small groups (<5-10) of animals on land. Larger groups were generally photographed with a high-resolution (>10 mega-pixel) single-lens reflex camera (Nikon D100 or D200) equipped with a Nikor AF-S 80-200 mm f2.8 lens. Images were counted in either PhotoShop CS2 using the Reindeer Graphics Image Processing Tool Kit or in PhotoShop CS5 using the built in Count Tool. Separate layers were created for pup counts, non-pup counts, and demarcation lines and notes. Counts of animals on land and any animals seen in the water adjacent to haulout sites or opportunistically while flying between haulout sites, were tallied separately.

2.2.2 Sea Lion Captures and Instrument Deployments:

During 2005-2007, we deployed satellite transmitters and time-depth recorders on Steller sea lions as part of a study to develop capture and handling techniques. Animals were

captured in a floating trap (Jeffries et al. 2004) anchored at Norris Rocks off Hornby Island (49° 29.0' N, 124° 38.9' W) in the central Strait of Georgia. The capture site is a major winter haulout where both Steller and Californian sea lions congregate during December-March to feed mainly on pre-spawning herring (Olesiuk, unpublished data).

A total of 25 sea lions were instrumented (Table 1). The trap was non-selective, and the tagged animals represented a broad spectrum of sex- and age-classes including yearlings that were still nursing, adult females some of which were pregnant and/or lactating, and full-grown adult males. However, the sample was biased toward males (Table 2), probably reflecting the sex composition of animals utilizing the haulout site. Instruments were deployed during winter and, except for yearlings, most of the tags (95%) continued to transmit into spring, and about half (47%) transmitted into summer. Tags deployed on 3 yearlings had a higher rate of attrition, all failing to transmit after 1-3 months (although archival TDR records were sometimes longer). We observed an adult female, perhaps the mother, chewing on the antenna of one yearling, and subsequently observed it and another yearling with transmitters missing antennas.

Animals were fitted with head-mounted Wildlife Computer SPLASH model (or in 6 cases SPOT4 model) transmitters. They provided information on location, as well as timeline data indicating the proportion of each hour registering dry and, in the case of the SPLASH tags, binned data on time-at-depth, time-at-temperature, and diving depths and durations. The latter data were summarized into four 6-hour bins (00:00 to <06:00, 06:00 to <12:00, 12:00 to <18:00 and 18:00 to <24:00 PST). Only the haulout timelines (HTL) and time-at-depth (TAD) records were utilized in this study, and we refer to these bins as low-resolution data. The HTL and TAD records were buffered for transmission over a 7-day period, and were 96% (range 89-100%) and 85% (range 77-92%) complete over the deployment period (with most missing records being near the end of the deployment period before the buffer was transmitted).

Sea lions were also fitted with time-depth recorders (TDRs), either integrated into the SPLASH tags and/or stand alone Wildlife Computers Mk9 units. The archival tags recorded depth and conductivity, indicating whether the animal was submerged in water or exposed to air, at 10 second intervals, and we refer to the archival records as high-resolution data. The archival tags had to be recovered to access the data, so were packaged in syntactic foam with a VHF transmitter to facilitate recovery. The stand alone TDRs were equipped with electronic release mechanisms or corrodible zinc links, and typically provided shorter records than the satellite transmitters (mean = 48.0 days, range = 4-164 days for TDRs versus mean = 112.5 days; range = 13-182 days for PTTs). Moreover, not all instruments were recovered and one tag failed to record, so TDR records were only available for a subset of 21 of the 25 (84%) of the instrumented animals (duplicate Spash and Mk9 TDRs were recovered for 3 of these animals).

Although all animals were captured, tagged and released at the same site, the tagged animals subsequently undertook extensive movements (Figure 3). Initially, many animals remained in the vicinity of the capture site, and during January-March the majority of animal locations (60-67%) were within 100 km of Norris Rocks (Figure 4). However, many animals made excursions or moved out of the Strait of Georgia during January-March, and most animals departed in April-May, and by June-July they spent little time in the Strait of Georgia (0-3%). By summer, animals were widely dispersed along the west and north coast of Vancouver Island (22-33% of locations), Washington and Oregon (22-30%), northern BC (14-21%) and SE Alaska (36-39%). Of the 9 animals tracked into the summer breeding season, two were in Alaska, one on the northern B.C. coast, one in Haida Gwaii (Queen Charlotte Islands), one on the Scott Islands, one at the mouth of the Columbia River, and three in Oregon.

Prior to analyses, biologically implausible locations were deleted using the travel-speed filter developed by McConnell et al. (1992) as modified by Austin et al. (2003). We assumed any records with swimming speeds exceeding $2\text{m}\cdot\text{sec}^{-1}$ were implausible, leaving 17,994 of 20,949 (86%) locations as being biologically plausible. Of these, 49% were standard quality (LQ=1, 2 or 3) and the remaining 51% secondary quality (LQ=0, A or B). The filtered telemetry data were imported into ArcMap 9.3 for GIS analysis. We linked the ARGOS locations with the low-resolution timelines and the high-resolution TDR records based on their common time stamp. This allowed us to directly compare the low- and high resolution data, which was useful for developing and evaluating behavioral indices (see Section 2.4.1).

2.2.3 Demographic and Morphometric Data:

The most extensive demographic and morphometric data for Steller sea lions were from specimens collected in Alaska (Calkins and Pitcher 1982). Animals were shot at haulout sites mainly in the Gulf of Alaska and Bering Sea. A total of 250 animals were collected during 1975-1978, which was just prior to the major declines in the Western Steller Population. A second sample of 178 animals, mostly reproductive females, was collected during 1985-1986 to investigate the reasons for the decline in the WSP. In both cases, animals were measured, weighed, reproductive tracts examined, and aged from teeth (see Calkins and Pitcher 1982 and Calkins and Goodwin 1988 for details). These collections provide the basis for much of what we know about the life history of Steller sea lions, and have been used to develop life tables and assess population dynamics (Calkins and Pitcher 1982; York 1994; Trites and Larkin 1996; Holmes and York 2003; Holmes et al. 2007), to describe body growth (Calkins et al. 1998; Winship 2000; Winship et al. 2001), develop condition indices (Pitcher et al. 2000), and estimate reproductive rates (Pitcher et al. 1998).

Comparable collections have not been made from the Eastern Steller Population, but some of the animals killed in control programs in B.C. during 1956-1966 were sampled (Pike, unpublished MS; Spalding 1964). Ages and standard lengths were available for 243 females aged ≥ 1 year, mainly post-partum animals killed on rookeries, with weights available for 49 of these (and lengths and weights but not ages for an additional 3 females). Ages and standard lengths were available for 101 males aged ≥ 1 year, and weights available for 23 of these (and lengths and weights but not ages for an additional 14 males). Given the biases in the way the animals were collected, these data were not suitable for assessing survival or reproductive rates. However, we used the data to fit growth curves (length on age) and subsequently applied the allometric relationships between length and weight fitted to the Alaskan data (Winship 2000; Winship et al. 2001) to estimate mass at age for the B.C. animals. Pike (unpublished data) also measured weighed 149 newborn pups (71 females and 68 males), which we used to estimate birth weight.

Calkins and Pitcher's (1982) life tables were developed for the WSP when it was thought to have been relatively stable, and are thus not directly applicable to the ESP which has been increasing for the past 50 years (Olesiuk WP10a). Comparisons of the age-structure of the WSP prior to and following the sharp declines in the 1980s indicate they were driven mainly by decreases in survival, particularly among juveniles (York 1994; Holmes and York 2003), suggesting that survival rates may be an important determinant of population status. Pendleton et al. (2006) recently estimated survival rates based on resights of animals that had been branded as pups on rookeries (i.e. known-aged animals). They found that pups branded at Forrester Island (increasing population) exhibited significantly better survival (both juvenile and adult) than had been estimated for Marmot Island in the Gulf of Alaska during the 1970s based

on specimen collections (York 1994) and during 1988-1991 based on brand resights (Pendleton et al. 2006), supporting the notion that changes in survival are an important determinant of population status. We thus incorporated Pendleton et al.'s (2006) improved survivorship schedule into the life tables for our study population (Figure 4b).

2.2.4 Captive Studies & Field Energetic Measurements

Some parameters are difficult or impossible to measure in the wild, such as energy assimilation efficiency. We thus utilized information from captive studies conducted at the Vancouver Aquarium by the University of British Columbia, and at the Alaska SeaLife Center in Seward Alaska. These studies provided detailed measurements of physiological parameters such as urinary and fecal energy losses, and heat increment associated with feeding, and how they vary with quality of diet.

Several studies have documented the gross feeding rates of captive Steller sea lions (Kastelein et al. 1990; Allen 2009). However, activity budgets, which account for a major portion of energetic requirements (see Section 3.3.1), may differ greatly between free-living and captive animals, and as would be expected captive feeding rates are typically lower than estimates made in the wild based on labeled water or gut contents (Winship et al. 2006), so we did not consider the captive feeding data as being representative of animals in the wild.

Steller sea lions are the largest species of otariid, and listed as threatened or endangered over much of their range, which has restricted some types of research. In particular, field metabolic rates have not been measured for Steller sea lions that are actively foraging. We thus examined the literature for other otariids (e.g. Arnould et al. 1996; Costa and Williams 2000; Hurley and Costa 2001; Costa and Gales 2000, 2003). Although the literature is more extensive for phocids, they seem to be energetically quite different (Innes et al. 1987) so we avoided using data from them insofar as possible.

2.2.5 Scat Collections

Scat samples have been widely used to describe diet of pinnipeds, and a number of state, federal and academic agencies had collected Steller sea lion scat samples in the study area (Table 3). Few of the data have been published, but we obtained access to and incorporated data from all of the samples that, to our knowledge, have been collected in the study area. Although our focus was on Steller sea lions, we included some samples that had been collected at sites where Steller sea lions intermingle with California sea lions, making it difficult to distinguish diet between the two species. We did not utilize samples that had been collected at any sites occupied exclusively by California sea lions.

In addition to utilizing the 6,825 scat samples that had already been collected, we made 10 additional collections from Steller sites in B.C. totaling 515 samples using PSC funding (Table 3). These targeted seasonal and geographic gaps in sampling coverage of existing samples, and were mainly collected at more remote sites outside the breeding season.

2.3 Abundance and Distribution

While survey counts are useful for assessing change in *relative* abundance and distribution, *absolute* abundance is always underestimated as some animals will be dispersed at sea and missed. We developed survey correction factors to adjust counts for animals at sea

based on haulout patterns. The high-resolution TDR records allowed us to identify precisely when haulout bouts were initiated and terminated. Examination of the TDR records indicated there were occasionally brief periods when instruments registered dry as animals surfaced between dives, or were milling at the surface. We thus defined a haulout bout as being initiated at the beginning of any period in which the TDR registered dry for more than 60 seconds. Once hauled out, animals typically remained dry for extended periods, but there were occasionally brief wet periods. These short wet periods may have been caused by contact with wet animals or tidal pools, or brief excursions into the water. We thus defined a haulout bout as being terminated at the beginning of a wet period that exceeded 15 minutes, or any wet period in which the animal dove to a depth >5m.

The low-resolution hourly timelines (HTL) did not allow such a detailed analysis, but provided data for a larger number of animals over a longer period. In interpreting the timelines, we assumed any hours registering dry for less than 10% of the readings represented periods that the animal was at sea and surfacing intermittently, and that animals were hauled out for the proportion of time indicated for any hours registering dry for more than 10% of readings. This interpretation of the timelines was assessed using the subset of animals and time for which both TDR and HTL data were available. A regression of the proportion of each day spent hauled out as indicated by the satellite timelines, $Pr(HO)_{STL}$, on the proportion of each day spent hauled out as indicated by the time-depth recorders, $Pr(HO)_{TDR}$, indicated the satellite data provided a good index the time spent hauled out (Figure 5), but that a small adjustment was required to correct for bias:

$$[1] \quad Pr(HO)_{STL} = 0.997 \cdot Pr(HO)_{TDR} - 0.01454 \quad (R^2=0.994; F_{1,652}=104,312; P<0.0001)$$

The inverse of the regression used to obtain estimates of $Pr(HO)_{jk}$, the proportion of time the k th animal was hauled out during the j th hour.

The proportion of animals hauled during a survey was subsequently estimated as:

$$[2] \quad p = \sum_{i=1}^n C_{ij} / \sum_{i=1}^n [C_{ij} \cdot (\overline{Pr(HO)})_j]^{-1}$$

where C_{ij} represents the count for the i th of n sites made in the j th hour, and $\overline{Pr(HO)}_j$ the mean proportion of tagged animals hauled out during the j th hour. The satellite timelines indicated that the proportion of time animals spent hauled out varied significantly with season ($F_{2,48}=14.75$; $P<0.0001$), and among sex- and age-classes ($F_{3,48}=7.35$; $P=0.0004$) and significant interaction between season and sex- and age-class ($F_{5,43}=4.54$; $P=0.0021$). The seasonal difference was due to animals spending more time hauled out during the summer breeding season, but when summer was eliminated there was no difference in the time hauled out during winter and spring ($F_{1,40}=1.59$; $P=0.2149$). Yearlings stood out as spending more time hauled out, but when yearling were eliminated there were no differences among juveniles, adult females and adult males ($F_{2,39}=1.22$; $P=0.3056$) or any seasonal interactions ($F_{4,39}=0.50$; $P=0.7385$). Survey correction factors were thus calculated separately for the breeding and non-breeding seasons. For the winter survey, the correction was calculated separately for yearlings and for all other sex- and age-classes and subsequently weighted according to the proportion of yearlings (0.188) in the population during winter based on life tables (Olesiuk WP10a).

Abundance estimates calculated in this manner are subject to two sources of variability: 1) variability in the proportion of tagged animals hauled out during surveys; and 2) variability in survey counts as animals move among sites and potentially in and out of the survey area. The variance in the proportion hauled out, $Var(p)$, was estimated based on the variability of the hourly averages (by season) among the tagged animals (i.e. the variance was calculated by averaging over animals as opposed to averaging over days, as we were interested in the proportion of animals in the population that would be hauled out within a given hour as opposed to the proportion of time any individual animal would be hauled out). The variance of the CF, $Var(CF)$, was calculated using the delta method as per Mood et al (1974) cited in Huber (1995),:

$$[3] \text{ Var}(CF) = \text{Var} (1/p) \approx \text{Var} (p) / p^4$$

Since sites were generally only counted once during surveys, we lacked true replicates to calculate the variability of survey counts. Instead, we used site counts from the 2006, 2008 and 2010 breeding season surveys to estimate the variability of counts by site. Since the population was increasing over this period (see Results), the counts were adjusted to 2008 levels based on the observed rate of increase over the period (See Figure 8 in Olesiuk WP10a). The weighted overall variance was calculated over all sites using the procedure developed for harbour seal site counts (Ann York, pers. comm. cited in Withrow et al. 1995).

Assuming that the variances of the correction factor (derived from the satellite timelines) and site counts (based on aerial surveys) were independent of one another, the overall variance of the abundance estimate, $Var(N_{it})$, was estimated as:

$$[4] \text{ Var}(N_{it}) = 1/p_{it}^2 \cdot \text{Var}(SC_{it}) + SC_{it}^2 \cdot \text{Var}(1/p_{it}) - \text{Var}(1/p_{it}) \cdot \text{Var}(SC_{it})$$

where the parameters are as previously defined (Goodman 1960).

In addition to missing swimming animals, it is possible that animals on land were missed at haulout sites of which we were not aware. The survey flights flew fairly direct between known haulout sites, and there are many inlets and islands particularly along the Vancouver Island coastline, that were not completely covered. During summer, we regularly fly harbour seal surveys in which we search the entire shoreline, and would have noted any sea lion haulouts. However, this type of survey coverage is lacking during the non-breeding season when Steller sea lions are most dispersed and more flexible in their utilization of haulout sites. We assessed the bias by plotting high quality ARGOS locations (LQ = 1,2, or 3) that were transmitted during haulout bouts to determine if animals were hauling out at unknown haulout sites.

2.4 Bioenergetics Model:

A bioenergetics model was constructed to estimate the prey and food requirements of Steller sea lions. In its simplest form, the bioenergetic model consists of 3 main components:

$$[5] \text{ GER} = (PR + MR) / AE$$

where *GER* denotes the gross energy requirements, *MR* denotes maintenance requirements utilized on an ongoing basis for normal life processes such as resting and swimming, and *PR* denotes the production energy an animal expends for growth, pregnancy and lactation. Combined, *MR* and *PR* represent the net energy requirements. However, not all energy consumed is available for maintenance and production, as some energy is lost in urine and feces, and some expended as heat during the processes required to extract and convert the metabolizable energy to useful form. Net energy requirements were thus divided by the assimilation efficiency, *AE*, to estimate gross energy requirements. The model is very similar to the model develop for Steller sea lions by Winship (2000) and Winship et al. (2002), and our model can be considered a refinement and adaptation to the Eastern Steller Population.

Maintenance and production energy will obviously vary with sex and age depending on the animal's size, how active it is, how fast it is growing, and whether it is mature and reproducing. Energy requirements will also vary seasonally depending on growth patterns, seasonal changes in activity levels, reproductive cycles, etc. Assimilation efficiency is generally related to quality of diet, and can vary seasonally depending on diet composition. The gross energy requirements of an individual of sex *i* and age *j* in the *k*th season was estimated:

$$[6] \text{ GER}_{ijk} = (PR_{ijk} + MR_{ijk}) / AE_k$$

This represents the energy *required* by animals in a given season, which may differ from the amount of energy actually *ingested* in a given season as animals are not always in a steady-state. Energy ingestion rates may temporarily exceed requirements as animals add to their energy reserves, or temporarily fall short of requirements as animals draw on their energy reserves. These temporary fluctuations can be important for species like Steller sea lions in which seasonal energy expenditures for reproduction may be amortized over longer periods. In particular, males tend to fast or reduce food intake during the summer breeding season, and replenish fat reserves during the non-breeding season (Schusterman and Gentry 1971; Olesiuk and Bigg 1987; Kastelein et al. 1990; Allen 2009). In estimating gross energy consumption, *GEC_{ijk}*, we thus allowed for seasonal changes in energy reserves, Δ_{ijk} , in the model:

$$[7] \text{ GEC}_{ijk} = \Delta_{ijk} + (PR_{ijk} + MR_{ijk}) / AE_k$$

where Δ_{ijk} can be either negative or positive, constrained such that $\sum \Delta_{ijk}$ summed over all *k* is equal to zero for each sex and age-class. Any net change in body mass over the year is considered to be growth (see Section 2.4.2). The parameter Δ_{ijk} has little effect on the overall annual *GER* (except for the energy lost due to the inefficiency when utilizing energy reserves), but merely affects how the *GEC* is distributed over the year to meet those requirements. This is important if seasonal changes in diet are correlated with seasonal in energy requirements (e.g. prey species will tend to be more important in the annual diet if they are consumed when animals are fattening).

The gross energy requirements for each sex- and age- class were incorporated into life tables (Section 2.2.3) to estimate the *GEC_k* for the overall population in the *k*th season:

$$[8] \text{ } GEC_k = \sum \sum \sum N_{ijk} \cdot GEC_{ijk}$$

where N_{ijk} represents the number of animals of sex i (f =female; m =male) and age j ($i=1$ to 30 for females and 0 to 20 for males) in the k th season (B =breeding, F =fall, W =winter and S =spring). It was assumed that mortality and growth occurred at a constant rate through the year, such that N_{ijk} was calculated by integrating over each of the 4 seasons and computing the average. The life tables provide a weighted estimate according to the relative prevalence of sex and age-classes in the population, and allow expenditures like reproductive costs to be weighted according to fecundity rates (see Iverson et al. 2010 for other examples).

2.4.1 Maintenance Requirements:

The metabolic requirements of mature, post-absorptive, inactive mammals, referred to as basal metabolic rate, BMR , can be estimated from Kleiber's (1975) equation:

$$[9] \quad BMR = 293 \cdot M^{0.75}$$

where M is the body mass in kilograms and BMR is in kilojoules.

Metabolic rates of juveniles tend to be elevated compared to adults of equivalent mass (Kleiber 1975; Innes et al. 1987). Based on captive studies of young Steller sea lions, it was estimated that metabolic rates of juveniles declined linearly from 3.0 times adult levels at birth to 2.0 times adult levels by 1 year of age, and to adult levels by 8 years of age (Rosen and Trites 1997; Rosen, unpublished data cited in Winship et al. 2002).

Since other expenditures such as activity also scale to, or approximately to, $Mass^{0.75}$, the resting metabolic rates (RMR) and field metabolic rates of active, free-living animals (FMR) are customarily expressed as multiples of Kleiber's BMR . Following Winship (2000), we estimated the daily metabolic rate (DMR) by weighting according to the proportion of time spent resting on land and time spent actively diving at sea:

$$[10] \quad DMR = RMR_{Land} \cdot Pr(HO) + FMR_{AtSea} \cdot Pr(DIV)$$

where $Pr(HO)$ and $Pr(DIV)$ represent the proportion of time spent resting on land and actively diving at sea respectively.

Field metabolic rates have not been measured in Steller sea lions, but data for other otariids (fur seals and sea lions) indicate they tend to have high mass-specific metabolic rates compared with phocids (true seals). RMR values for otariids typically range from 1.4 to 2.9 (Mean = 2.0) times BMR , and FMR values typically range from 3.4 to 7.0 (Mean = 5.4) times BMR (Figure 6). The foraging behaviour of Steller sea lions generally falls within the same range as reported for other sea lions (Table 4), so we adopted the average values for Steller sea lions. For the sensitivity analysis, we allowed RMR and FMR to vary uniformly over the range.

The proportion of time spent at sea was estimated from the satellite telemetry data. Although the tags transmitted information on the number and duration of dives, these data were

binned, precluding accurate estimates the amount of time spent diving. Since we defined dives as any excursions to depths >5m, we instead used the amount of time spent at depths >5m, as indicated by the time-of-depth bins, as an index of time spent actively diving. Of course, animals that are actively diving spend additional time at depths <5m as they surface, so TAD at >5m serves only as an index of diving behaviour. We thus used the high-resolution TDR records to calibrate the TAD index. Inspection of the TDR records indicated that surfacings between dives were usually short (93% of surfacings lasted <5 minutes and 97% were <15 minutes), but there were occasionally extended surface periods without any dives meeting the 5m threshold. We thus defined a diving bout as being initiated at the beginning of the first dive, and ending at the beginning of any surface period lasting more than 15 minutes. Regression analyses indicated that the total time spent diving as indicated by TDR records was highly correlated (Figure 7) with the time spent at depths >5 m as indicated by the TAD records:

$$[11] \quad TAD = 0.610 \cdot TDR + 0.0236 \quad (r^2=0.905; F_{1,2235}=21,215; P<0.0001)$$

and we used the inverse regression to estimate the at-sea time actively spent diving.

The satellite data thus provided estimates of the proportion of time spent resting on land (equation [1]) and spent actively diving at sea (equation [11]), and these two categories collectively accounted for 87% (range 77-97%) of the daily activity budget of animals (not including yearlings, which spent more time milling at the surface). The remaining 13% of the time consisted of extended periods at or near the surface (depth <5m). This behaviour was difficult to interpret as it could represent a variety of activities (Steller sea lions sometimes mill at the surface or form rafts and sleep in the water) during which *MR* may be similar to *RMR* levels, or animals might be making shallow dives or traveling near the surface, in which case *MR* could be similar to *FMR* levels. Given the uncertainty, we assumed *MR* during extended surface periods was intermediate to *RMR* and *FMR*, and allowed this parameter to vary between those limits in our sensitivity analyses.

2.4.2 Growth:

The energetic cost associated with body growth, *DGR*, are a function of size of the daily growth increment, *DGI_{ijk}*, the composition (fat versus lean tissue) of the mass added, and the efficiency of converting energy to body mass:

$$[12] \quad DGR_{ijk} = DGI_{ijk} \cdot EDG_{ijk} \cdot EEG$$

where *DGR_{ijk}* represents the gross energetic costs associated with body growth, *DGI_{ijk}* the daily growth increment, and *EDG_{ijk}* the energetic density of the growth increment. The latter was estimated as:

$$[13] \quad Pr(lipid) \cdot ED_{LIP} + [1-Pr(lipid) \cdot (1-Pr(water))] \cdot ED_{PRO}$$

where *Pr(lipid)* is the proportion of new body mass that is lipid, *ED_{LIP}* is the energetic density of lipid (39.3 kJ g⁻¹; Schmidt-Nielsen 1990), *Pr(water)* is the proportion of lean tissue that is water, and *ED_{PRO}* is the energetic density of protein (18.0 kJ g⁻¹; Schmidt-Nielsen 1990). The *DGI*'s were estimated from the Richard's growth curves describing change in body mass with age (Section 3.2). It was assumed growth occurred throughout the year. The efficiency of growth, *EEG*, has not been measured, and it is unclear to what extent any inefficiencies in converting ingested energy is included in the heat increment associated with feeding (Section 2.4.4). We

assumed a value of 0.90. As will be shown, growth accounted for a very small component of the overall energy budget, and sensitivity analyses indicated that even large departures from the assumed value have little effect on overall energy requirements (Section 3.5).

The growth term in our model was quite different from that used by Winship (2000), who considered seasonal fluctuations in body mass (i.e. deviations from the growth curves) as seasonal spurts in body growth. We interpreted such seasonal fluctuations, which often exceeded the annual growth increment, as transient changes in body condition, Δ_{ijk} , which we distinguished from the longer-term increases in body mass as animals grew with age.

Changes in the composition of the growth increment with age were estimated from body fat measurements made on live animals (labeled water injections) or carcasses. Pitcher et al. (2000) provided the most extensive description of changes in body condition with age based on various indices on scalp (skin with blubber attached), but the two were not separated. Using a small sample of subadult and adult males collected in B.C., for which the skin and blubber was separated and weighed (Olesiuk and Bigg 1987), we developed a regression between percent scalp mass and percent blubber mass:

$$[14] \quad \% \text{Blubber} = 1.248 \cdot \% \text{Scalp} - 0.143 \quad (F_{1,12}=148.8; R^2=0.925; P<0.0001)$$

and used the regression (Figure 8) to convert Pitcher et al.'s (2000) scalp weights to body fat measurements.

$$[14b] \quad \% \text{Blubber} = 4.617 \cdot X + 10.26 \quad (R^2=0.486; F_{1,155}=146.6; P<0.001)$$

where X is the Minimum(3.5-Age,0).

The regression predicted that body fat declines from about 24% at age 1 to about 10% by age 3.5 years (Figure 9). The former figure conforms with measurements of body composition in young animals (Figure 10) and the latter figure generally conforms with measurements of body composition of adults. Davis et al. (1996) reported that adult females sampled on various rookeries, when they are likely at their seasonal minimum (Allen 2009), had fat content ranging from 7.3 to 8.6% (Mean 8.3%; SE=4.08). Olesiuk and Bigg (1987) found the blubber layer of subadult and adult males ranged from an average of 5.9% when sampled in April at the seasonal minimum to 16.4% when sampled at peak condition in April, with an overall average of 11.2%.

The concurrent changes in body size and composition with age implies indicated that fat content increased 10-fold in pups during the first year of life, and growth was comprised of 29% fat and 71% lean tissue. Although animals continued to grow rapidly, body fat declined and 18% of the mass added by females between age 1 and 3.5 was fat, and about 13% was fat in males. Any mass added after age 3.5 is assumed to be 10% fat based on adult body composition.

2.4.3 Pregnancy and Lactation:

Reproductive females require energy for pregnancy and lactation prior to parturition, and for nursing pups following parturition. For pregnancy, the energy invested in the fetus was estimated from foetal growth rates (Winship 2000). Birth mass was assumed to be 18 kg and the placenta an additional 2 kg, which agrees with observed mass loss at parturition of ~20 kg (Allen 2009). We assumed the energy density of the fetus and placenta was the same as newborn pups (Section 2.5.2). The efficiency at which energy is assimilated into foetal tissue is poorly known but appears to be low. Following Winship et al. (2000), we adopted a value of 0.20 and allowed for a wide range of uncertainty (0.10 to 0.70) in the sensitivity analyses. As will be shown, pregnancy represented a very small component of the overall energy budget, so these crude assumptions had little effect on overall prey requirements. Pregnant female with fetuses tend to be larger than non-pregnant females of equivalent age (Winship 2000), such that their metabolic rates were higher, so we did not include a separate estimate for metabolism of the fetus.

It appears that lactation in Steller sea lions is protracted and in most cases extends to late spring/early summer as pups approach their first birthday. In many cases, juvenile Steller sea lions may continue to nurse into their 2nd or even 3rd years (Pitcher et al. 2004), but it appears that regardless of age, weaning occurs just prior to the birth season (Trites et al. 2006). It is unclear, however, to what extent nursing pups and juveniles forage independently, although it appears that the diving frequency and focus of pups increases in spring as they approach their first birthday (Rehberg and Burns 2008). Given these uncertainties, we did not directly estimate the costs associated with lactation *per se*, but instead estimated the energetic requirements of young animals that may have been meeting those requirements, in whole or in part, from the energy ingested through milk. This has little effect on the energy budget for the population, as it makes little difference whether the energy needs of young animals is being acquired by the young animals or by their mothers. Indeed, the only difference would be the extra energy required by females to convert their energy stores to milk. For the purposes of estimating prey requirements by age-class, we assumed young-of-the-year were weaned at the end of spring.

Pinnipeds appear to be very efficient at transferring energy to pups during lactation. The gross efficiency of lactation in phocids, for which lactation is often more protracted and can be more readily measured than in otariids,, ranges from about 60-70% (Costa et al. 1986; Oftedal et al. 1987; Reilly et al. 1996). This represents the proportion of total energy expended by the mother, including milk production as well as her own metabolism, that is assimilated by the pup. Since most of the energy not transferred in milk would be for metabolism, this implies that net efficiency of mobilizing and converting body energy stores into milk is high. We assumed a net efficiency of 90% (range 80-100%) for lactating females. We assumed the same net efficiency for animals mobilizing body energy stores when Δ_{jkl} was negative.

2.4.4 Assimilation Efficiency

Not all energy contained in prey is available to animals. Some energy is lost in urine (UEL) and feces (FEL). Overall digestive (DE) efficiency tends to increase with quality (% fat) of the diet, and can be described by a logistic equation:

$$[15] \quad DE = 1 - (FEL + UEL) = A / 1 + e^{-k(EDD_r - EDD_0)}$$

where EDD_i is the energetic density of the diet and EDD_o a reference energetic density of 2.10 (SE 0.089) with $A = 0.951$ (SE 0.0039) and $k=1.86$ (SE 0.016) (Rosen and Trites 2002; Winship and Trites 2003).

The remaining energy is referred to as metabolizable energy, a portion of which is expended as what is commonly referred to as the heat increment associated with feeding (HIF). This is energy lost as heat associated with the physiological processes of extracting and assimilating energy from prey. The heat increment rises after feeding, and persists for a number of hours, and is integrated over its duration. The heat can be considered waste, but it also contributes to thermoregulatory costs. The magnitude of the heat increment varies as a function of prey quality:

$$[16] \quad HIF_i = a \cdot EDD_i + b$$

where EDD_i is as previously defined, with $a = -0.013$ (SE 0.0023) and $b = 0.229$ (SE=0.0173) (D. Rosen, pers. comm.; Rosen and Trites 1999, 2000; cited in Winship and Trites 2003). For example, the equation indicates that HIF ranges from about 11% for very high-lipid prey like eulachon to 13% for a high-lipid prey like salmonids, and to 17% for low lipid prey like gadids.

2.4.5 Daily Prey Requirements:

Given estimates of maintenance energy requirements (Section 2.4.1), production energy requirements (Sections 2.4.2 and 2.4.3) and assimilation efficiency (Section 2.4.4), the daily food requirements (DFR) can be estimated as:

$$[17] \quad DFR = GEC / EDD$$

where GEC was previously defined as the gross energy consumption and EDD as the energetic density of the diet. We calculated GEC_{ijk} for each sex- and age-class in each of the 4 seasons. The energetic density of the diet, which appears to be inversely related to population status, was assumed to equivalent to the diet in SE Alaska where the population is increasing at a similar rate (Olesiuk WP10a), and scat samples have been collected throughout the year to assess diet composition (Winship and Trites 2003).

2.5 Life History & Population Dynamics:

Life tables that incorporated the higher survival rates estimated for the Eastern Steller Population based on brand resights predicted a population growth rate of 3.0%, which was similar to the 3.8% average rate observed over the period the resights were made (Pendleton et al. 2006; Olesiuk WP10a). Thus, it appears that the declines in the Western Steller Population in the 1980s and the recent growth of the ESP were both largely driven by changes in female survival rates. We thus assumed the acceleration in population growth rate observed in the ESP in recent years was attributable to a further improvement in survival, and simulations with life tables indicated that a 1.5% increase applied to Pendleton et al.'s (2006) survivorship schedule would account for the observed rate of population growth of 4.3% (Olesiuk WP10a). For sensitivity analyses, we also explored how changes in fecundity would affect the sex- and age-composition of the population and energetic requirements.

Interestingly, there is no evidence of differences in survival rates of males in the WSP before and during the declines or the increasing ESP. We thus used the average survival rates reported by Pendelton et al. (2006) to age 9 years and by Calkins and Pitcher (1982) for the oldest age-classes.

2.6 Diet Composition:

Steller sea lions inhabit some of the most remote locations of the study area, and often forage at night (see Figure 17). Direct observations of feeding behaviour, while useful in localized areas such as rivers and estuaries (Gearin et al. 1986; Olesiuk et al. 1996; Scordino 2009) are not practical over the large geographic range of the study area. The species is protected throughout its range, so stomach samples are not available to assess diet.

Steller sea lions haul out on a regular basis throughout the year, and often defecate on land. Scat analyses thus provides a practical alternative for assessing diet. This benign technique allows large numbers of samples to be collected for assessing seasonal changes and geographic differences in diet. We utilized scat samples that had already been collected by various agencies (Table 3), and collected 537 additional scat samples. This provided a total of 171 collections from 39 sea lion sites throughout the study area, including all 3 of the rookeries on the Scott Islands, 12 of the 15 year-round haulout sites, and 24 winter haulout sites. Collections were made in all months of the year, but the greatest number of samples were collected during the summer breeding season when conditions for boat operations in remote and offshore areas were most favourable. A total of 6,978 scat samples were collected and processed within the study area, of which 6,418 (92.0%) contained identifiable prey.

Prey in scat samples were identified using the all structures technique (Olesiuk et al. 1996; Lance et al. 2001). In all cases, prey identifications were made by specialists with expertise in bone analyses and access to reference collections of skeletal material.

2.6.1 Importance of Salmon

The focus of this study was on salmon predation. More general assessments of feeding habits and the importance of other prey types will be reported elsewhere.

We stratified scat samples by site and by season to allow for geographic and seasonal differences in diet. A weighted estimate of the overall importance of salmon in the diet was obtained by:

$$[19] \quad Pr(SAL) = \sum \sum \sum (DFR_k \cdot N_{jk}) \cdot Pr(SAL)_{jk}$$

where N_{jk} represents the estimated abundance of animals at the j th site in the k th season, DFR_k represents the mean per capita daily food requirement in the k th season, and $Pr(SAL)_{jk}$ the proportion of the diet comprised of salmon at the j th site in the k th season.

The proportion of the diet comprised of salmon was estimated using split-sample frequency of occurrence (SSFO) (Olesiuk et al. 1990; Olesiuk 1993):

$$[20] \quad Pr(SAL)_{jk} = \sum (O_{sjk} / \sum O_{pjk}) / N_{jk}$$

where O_{sijk} is a binary variable indicating whether salmon were present or absent (0=absent and 1=present) in the i th sample from the j th site in the k th season, and O_{pijk} a binary variable indicating whether the p th prey of all other prey types was present in the i th sample from the j th site in the k th season, and N_{jk} the total number of samples collected at the j th site in the k th season.

The SSFO technique was developed for situations where it is not possible to enumerate the number of individuals of each prey species consumed, precluding the use of biomass reconstruction (BR) methods. Steller sea lion scats are noteworthy in this regard, as the bone fragments recovered and identified from scats in the wild appear to represent an extremely small fraction of what was actually consumed. Although our experience with stomach samples and foraging observations indicate that sea lions generally consume the entire salmon carcass, and multiple salmon would need to be consumed to meet prey requirements, only ~2% of the scat samples contained salmon otoliths. Most salmon identifications were based on vertebrae, gill raker arches and teeth which are far more numerous than otoliths and thus more likely to be recovered, but difficult to enumerate for BR analysis.

The overall importance of a particular prey type in the diet will be determined by the frequency with which it is consumed, and the amount eaten when it occurs in the diet. At the population level, the frequency of consumption often conveys much of the information about the relative importance of a particular prey (i.e. a prey type may comprise a small part of the overall diet by virtue that it is only consumed by a small number of animals at a few sites, or a prey type may comprise a large part of the overall diet by virtue of it being consumed by large numbers of animals at many sites), and SSFO is based on the frequency of occurrence. However, the overall importance of a particular prey type is also determined by the amount eaten when it occurs in the diet consumed (i.e. a prey item may comprise a small part of the overall diet because it was an incidental prey consumed in small quantities, or a focal prey that forms the bulk of what was consumed). Since SSFO is based solely on presence or absence, it does not capture information of the relative amounts of different prey types consumed together, and assumes that each prey was consumed in equal amounts. While this is not likely to be true, sensitivity analyses can be conducted to assess violations of the assumption by assuming that, for example, salmon was an incidental prey consumed in negligible quantities whenever other prey species were also consumed, or that salmon comprised the entire meal and that any other prey species consumed at the same time were incidental prey consumed in negligible quantities.

The performance of SSFO has been assessed using diet data for northern fur seals. The northern fur seal was a good candidate in that large numbers of stomachs ($n=18,404$) were collected, and both the volume (biomass) and frequency of occurrence of prey were recorded (Perez and Bigg 1986). The results show that SSFO generally had good agreement between the importance of prey as indicated by volumetric and SSFO analyses (Figure 11). Most salmon were taken by fur seals off WA and BC, and for this region volumetric analyses indicated salmon comprised 4.4% of the fish diet, whereas SSFO estimated it comprised 4.1% of the fish diet (the salmon estimates were 1.2% and 1.4% respectively when averaged over the entire NE Pacific). More recently, a series of captive feeding trials were conducted with harbour seals to evaluate various diet indices, allowing the relative importance of various prey predicted by each index to be compared to the relative amounts of prey actually fed to the seals. The SSFO estimates appeared to correspond quite closely with the biomass actually fed to seals, including both juvenile and adult size salmon (Figure 12).

2.6.2 Species Composition of Salmon:

In most cases (~99%), salmon were not represented by otoliths, and the bone fragments used to identify salmon could only be keyed to family level. We thus attempted to extract and amplify DNA from salmon bone fragments.

Salmon bones from each scat were transferred to microtubes or to a Qiagen DNEasy collection tray. A 4 or 5 mm steel ball was added, and the samples were frozen overnight at -80°C. Bones were then pulverized with a mixer mill set at 30 Hz for 2 minutes. DNA was extracted using Qiagen DNEasy 96 Tissue kits. Semi-nested primers were used to amplify the 16S mitochondrial gene marker, and nested sets of primers were used for amplifying the major histocompatibility complex (MHC) class II B2 gene. The PCR products were visualized using denaturing gradient gel electrophoresis (DGGE), and bands were compared to known standards from each species. Results from both markers were combined to establish species identification. The reader is referred to Tolitt et al. (2009) for further details.

2.7 Sensitivity Analyses:

In addition to estimating salmon consumption, one of our objectives was to assess the level of precision and potential biases associated with the estimate, and to identify the main sources of uncertainty. The model incorporated a total of 000 parameters (Table 00), some of which had multiple values (e.g. Pr(HO) had 72 values: 3 series of 24 hourly estimates, one for all animals in the summer and for yearlings and older animals outside the breeding season).

Given the large number of parameters and potential for interactions, it was not feasible to directly calculate the variance associated with the prey consumption estimate. Instead, we conducted Monte Carlo simulations by sampling the parameters from distributions that reflected their underlying uncertainty (Shelton et al. 1997; Winship et al. 2003). Where parameters had been statistically estimated, we generally assumed the estimates were unbiased and errors normally distributed:

[21] ~Normal (0, SE)

where SE is the standard error. One exception was in estimating the uncertainty in body mass with age. We had initially attempted to fit growth curves to estimate variability in body mass based on the SE associated with each parameter. However, the parameters were highly correlated, so it didn't make sense to sample them independently. Given the paucity of weight data for specimens collected in B.C., we calculated the variability of weight by sex and age-class using data for the WSP (Calkins and Pitcher 1982), and re-scaled those SE's to account for the larger body size of sea lions in the study area (see Section 3.2).

For some parameters where we had no information beyond what we considered to be a reasonable range, values were drawn from a uniform distribution over the potential range:

[22] ~Uniform (minimum, maximum)

Finally, some of the analyses necessitated subjective decisions that may have biased the results. For example, in estimating diet, we used all available samples, including some dating back to the 1980s and 1990s, and some that had been collected at sites where Steller and California sea lions intermingled such that we could not be sure the samples represented

exclusively Steller sea lions. We examined the effects of what might be referred to as “process error” by using a binomial weighting factor:

[23] $\sim \text{Binomial}(0,1)$

such that questionable samples were either included in or excluded from the analyses to assess their effect.

We ran simulations on subsets of the model to determine the most important sources of uncertainty in the abundance, bioenergetics, and diet composition estimates. For the final salmon consumption estimates, we allowed all parameters to vary to provide a sense of the cumulative effects of all the sources of uncertainty. Marginal sensitivities for key parameters were also calculated by holding the key parameter fixed at its estimate, and resampling all other parameters to determine the extent to which the overall uncertainty was reduced. We believe the Monte Carlo simulations provide reasonably realistic estimate of precision, but it is much more difficult to assess the degree of bias, and we discuss some of these in Section 4. [Note: Monte Carlo simulations are somewhat tedious and time-consuming to run, so the final simulations will not be run until the model has been reviewed and any necessary revisions to parameters incorporated].

3. RESULTS

3.1 Abundance and Distribution:

Aerial surveys were conducted on 21 days during July 2008 to January 2010. The WA portion of the study area generally required one day to survey, and the BC portion two days to survey, but coverage was sometimes incomplete due to weather conditions or logistical constraints. At least one count, and sometimes 2-3 replicate counts were available for all major sites in each season (Table 5). Where replicate counts were available for sites within the same season, the average count was used and the CV calculated as a measure of variability. In a few cases where regions with few sea lions or minor sites were missed during surveys, we extrapolated numbers based on survey data from previous years within the season or in the adjacent season for that year. The extrapolated counts never comprised more than 1% of the total count in any given season, so were not likely to have had much effect on the overall abundance estimates.

3.1.1 Seasonal Shifts in Distribution

There was a marked seasonal shift in distribution of animals (Figure 13). During the summer breeding season, the population was highly aggregated and 75% of counted animals (45% of non-pups and all but a few pups) were at breeding sites on the Scott Islands. The majority of non-breeding animals (91%) were distributed at 15 major year-round haulout sites (10 in BC, 4 in WA, and one at the mouth of the Columbia River) (Figures 13 and 14). Many of these were traditional haulout sites that have been utilized by Steller sea lions for many decades (Scheffer 1950; Bigg 1985), although the number of year-round sites has grown in recent years as the population has expanded. The Strait of Georgia, San Juan Islands and Puget Sound were not surveyed in summer, but based on the lack of sea lion sightings during harbour seal surveys flown in August 2008, which covered the entire shoreline including all reefs and islets, it was assumed few if any sea lions were present in these areas.

Animals began to disperse from breeding sites in late summer or early fall. By the time fall surveys were conducted at the end of September, the Scott Islands pup counts had declined by 67%, and non-pup counts by 70% compared with the surveys conducted 3 months earlier. The decline probably reflects a combination of dispersal, as well as a decrease in the proportion of time spent hauled out by both females and young-of-the-year (see Section 3.1.2), such that a greater proportion of animals were at sea and missed in surveys conducted outside the summer breeding season. The decrease in numbers of sea lions on breeding sites was somewhat offset by an increase on nearby haulout sites. Numbers on haulout sites within a swimming distance of 120 km increased by about 40% and there were almost as many pups on the nearby haulouts (44% of total pup count) as remained on the rookery (53% of pup count). A few pups (3% of total pup count) were also seen at more distant haulout sites up to 270 km from the Scott Islands rookery.

Winter surveys were conducted in December-February, by which time relatively few animals (10% of total count) remained on rookeries. However, rookeries continued to be used as a haulout site, mainly by subadult and adult males, including significant numbers of California sea lions. Sea lions had become widely distributed at both year-round (43% of count) and winter (47%) haulouts. Appreciable numbers (15% of total count) had moved into the protected inside waters of Strait of Georgia and Puget Sound. Unfortunately, young-of-the-year had grown in size and had moulted or were moulting, and were therefore difficult to reliably discern from older juveniles, but they appeared to be widely distributed at sites many hundreds of kilometers from the nearest rookery. The large aggregations of pups seen at haulouts near rookeries in fall were no longer present, and it was our sense that many had dispersed out of the study area. Olesiuk (WP10a) conducted winter surveys in northern B.C., and observed appreciable numbers of young-of-the-year on haulouts along the central and northern mainland coast, but accurate counts couldn't be made as young-of-the-year could not be reliably discerned from older juveniles.

Spring surveys were conducted in mid-April in B.C. and late-April in Washington. Rookery counts were still low (7% of total count), indicating that breeding animals had not yet begun to arrive. Numbers had declined on winter haulout sites (14% of total count) and increased on year-round haulouts (79% of total count).

As had been noted by Bigg (1985), despite the pronounced shift in distribution from rookeries in summer to winter haulouts in winter, the proportion of animals utilizing year-round haulouts showed no consistent seasonal trend (Figure 14). However, it does not appear that breeding animals simply moved from breeding sites to winter sites. The dispersal pattern of pups indicates that most breeding animals with dependent young moved onto, at least initially, year-round haulout sites near the rookery. At the same time, the first animals that began to appear on winter sites and in inside waters appeared to be predominately subadult and adult males. It thus appears that breeding animals displace non-breeding animals from the year-round haulout at the end of the breeding season. Although we've observed and captured Steller sea lions of both sexes and all ages in inside waters (Section 2.2.2), many of the winter sites in inside waters appear to support a disproportionately large numbers of subadult and adult males.

California sea lions were present in very low numbers during the summer breeding season, with only 53 counted during on winter haulouts along the outer coast in the July-August surveys (including harbour seal surveys). However, large numbers (3,548 counted) of California sea lions had arrived in the study area by the time the first fall surveys were conducted in 30 September to 05 October (Figure 15). Based on a series of surveys conducted along the

Washington coast in mid- and late-October, it appeared that numbers had continued to build through the month, with numbers on the Washington coast increasing from 561 on 1 October to 1,248 by 18-19 October and to 2,932 by 29 October coinciding with their post breeding season dispersal from breeding rookeries in the Channel Islands in California and possibly from rookeries in Mexico. California sea lions continued to be present in fairly high numbers throughout winter and spring. Most California sea lions occurred at winter haulout sites shared with Steller sea lions, but small numbers also utilized other minor haulouts, mostly on marina floats, logbooms and navigation buoys. As was the case for Steller sea lions, numbers of California sea lions occupying haulout sites in inside waters peaked during winter (Figure 16).

3.1.2 Survey Correction Factors

We made no effort to count animals that were dispersed at sea during surveys, and only relatively small numbers of animals (4%) were counted in the water, usually adjacent to haul out sites, but occasionally seen feeding or rafting in other areas. The proportion of animals in the water tended to be lowest in summer (2%), and higher outside the summer breeding season (mean 6%; range 2.6-8.1%). While this pattern parallels the proportion of animal predicted to be at sea during surveys (see Figure 25), the counts of animals in the water represents a very small fraction (Mean 5.0%; range 1.5 to 16.0%) of the number predicted to be at sea during surveys.

Satellite telemetry timelines were used to estimate the proportion of animals that would have been hauled out during surveys. An ANOVA indicated the proportion of time spent hauled out varied with sex- and age-class ($F_{3,48}=7.35$; $P=0.0004$) and season ($F_{2,48}=14.75$; $P<0.0001$), with a significant interaction between season and sex- and age-class ($F_{5,43}=4.54$; $P=0.0021$). The season effect was attributable a marked difference between the breeding season, during which animals spent more time hauled out, compared with the two seasons outside the breeding season, during which animals spent less time hauled out. An ANOVA indicated no significant difference between winter and spring once summer had been excluded ($F_{1,40}=1.59$; $P=0.2149$). The sex- and age-class effect was due to yearlings, which stood as spending more time hauled out during winter than other sex- and age-classes. An ANOVA indicated there was no significant difference between juveniles, adult females and adult males ($F_{2,39}=1.22$; $P=0.3056$) or any seasonal interaction ($F_{4,39}=0.50$; $P=0.7385$) once yearlings were excluded. We thus calculated survey correction factors (CF's) separately for summer surveys and for winter/spring surveys separately. For winter surveys we calculated CF's separately for yearlings and all other sex- and age-classes combined, and weighted them according to the proportion of yearlings in the population as indicated by life tables (Section 3.2). No telemetry data were available for fall, so we assumed the winter and spring patterns were indicative of the non-breeding season and applied the winter/spring corrections to the fall surveys. A small number of satellite transmitters deployed on Steller sea lions during fall and winter in other regions supports the assumption that animals spend a higher proportion of time at sea after the summer breeding season (Merrick 1995; Swain 1996).

In addition to a change in the proportion of time spent hauled out, there was also a distinct seasonal change in diurnal haulout patterns. During the summer breeding season, animals tended to initiate haulout bouts in the morning, and terminate them in the afternoon or evening, such that peak numbers of animals were hauled out during daylight hours when surveys were conducted (Figure 17). All the tagged animals that were tracked into summer showed a propensity to haul out during daylight hours, and the pattern was similar for animals

spending the majority of time on year-round haulouts and on rookeries (Figure 17), so variability was low.

During winter and spring, animals tended to initiate and terminate haulout bouts at just about anytime, but in contrast to summer appeared to be less likely to haul out in the morning. As a result, haulout bouts were not as synchronized, and a lower proportion of animals were hauled out during daylight hours when we conducted surveys (Figure 17b). Since this had important implications in estimating survey correction factors, we examined the data to determine the robustness of this pattern. Because all the animals had been tagged at Norris Rocks and many animals subsequently remained in the vicinity of the capture site for several months (Figure 4), we were concerned that the patterns may have been unduly influenced by our biased sex- and age-structure of tagged animals, or behavioural patterns at the capture site, rather than being representative of the entire study area. The seasonal change in haulout behaviour appeared to begin in May (Figure 19). Except for yearlings, the juveniles, adult females and adult males all exhibited similar diurnal patterns (Figure 20a). Moreover, the patterns persisted when the data were partitioned by geographic region (Figure 20b). We conclude that the haulout patterns observed outside the breeding season were broadly representative of sea lions of both sexes and all ages (except yearling) throughout the study area.

For surveys conducted during the summer breeding season, it was estimated that an average of 68.4% (range 61.1% to 69.2% for individual counts) of non-pups were ashore and counted when counts were made, and the correction factors for summer surveys ranged from 1.40 to 1.49 (Mean = 1.46). These figures are similar to the 67.1% hauled out during the 10:00 to 18:00 PDT survey window, indicating that the timing of surveys was not critical. Given the consistency of the haulout patterns among the tagged animals and high proportion hauled out during the daylight survey window, the CF's for non-pups were relatively precise (SE = 0.105 to 0.124). Since pups are confined to land for the first month or so of life, and surveys were timed to coincide with the end of the pupping season, it was assumed all pups were on land during surveys. However, based on a comparison of 35mm oblique photos with vertical medium-format images, Olesiuk et al. (2008) concluded that 4% of pups were missed in the 35m photos, presumably because they were obscured in photos taken at oblique angles. We thus applied a correction of 1.05 (95% Confidence Interval 1.018-1.075) to pup counts to adjust for this bias.

For surveys conducted in fall and winter, it was estimated that an average of 36.5% (range 33.5 to 39.9%) of animals were hauled out during surveys, which corresponded to an average correction factor of 2.76 (range 2.51 to 2.99). There was much more variability in the proportion hauled, and for some site counts as few as 23.5% or as many as 44.8% of animals would have been hauled out. In retrospect, some of the BC surveys were conducted too early in the morning (starting at about 08:00 PST) when a high proportion of animals would have been at sea.

For the two surveys conducted in spring, it was estimated that an average of 32.0% (range 31.9 to 32.0%) of animals were hauled out at the time of the count, corresponding to an average correction factor of 3.13 (range 3.13 to 3.14). The corrections were slightly higher than in fall and winter because young-of-the-year started to spend a greater amount of time in the water.

It is also possible some hauled out animals were overlooked during surveys. During surveys, we checked all known sites (and made corrections for any known sites that were missed) and conducted opportunistic reconnaissance as we flew between sites or along the

coast. However, we did not search inlets or circumnavigate islands, and any new or unknown haulout sites could have been missed. To assess the potential bias, we examined the haulout sites used by the satellite tagged animals. We received a total of 2,074 quality (LQ=1, 2 or 3) locations from tagged animals during haulout bouts within the study area. The vast majority (97.4%) of the locations were from known haulout sites. The tagged animals traveled widely within the study area, utilizing 38 haulout sites, including all the rookeries and year-round sites, and many of the major winter haulout sites (Figure 21). Indeed, the sites utilized by the tagged animals collectively accounted for an average of 90.7% (range 82.3% to 96.9%) of animals counted during aerial surveys, indicating the tagged animals provided a fairly good indication of where animals were hauling out. The remaining 2.6% of locations were in areas where there were no known haulout sites. Seventeen (31.5%) of the locations were from two tagged animals that hauled out on Jimmy Judd Island in the Discovery Passage area of BC. We had not been aware of this haulout, but have since included it in surveys and have seen up to 60 Steller sea lions at the site. Twenty-one (38.9%) of the locations were from two other animals that hauled out on an offshore weather buoy on Halibut Bank in the Strait of Georgia. We had not been aware of animals hauling out on the buoy, and have never seen animals on it the few times it has been checked. The remaining locations from unknown sites were from single animals widely scattered throughout the study area, indicating that animals may occasionally haul out away from traditional haulout sites. The fact that the tagged animals used most of the known haulout sites in the study area, and rarely used haulouts that we were unaware (2.6% of haul out locations), implying there was a low likelihood of missing appreciable numbers of hauled out animals during surveys.

3.1.3 Abundance Estimates:

Despite the dramatic seasonal shift in distribution, overall abundance of Steller sea lions in the study area was relatively stable (Figure 22). Abundance estimates averaged 24,300 over the year, ranging from a low of 21,500 during summer to a high of 26,900 during spring. Abundance in BC averaged 20,300 (83.8% of the total), ranging from a low of 19,200 (89.5% of total) during the summer breeding season to a peak of 22,200 (86.7% of the total) in the fall. Abundance in WA averaged 3,900 (16.2% of the total), ranging from a low of 2,300 during the summer breeding season (10.5% of the total) to a peak of 7,100 (26.4% of the total) in spring.

The total number of Steller pups counted in the study area in September-October was only 45.4% of the number counted on the Scott Islands 3 months earlier. Most of the decline in pup numbers can be attributed to mortality (survival through the first year is only 60.6%; Section 3.2), and because pups began to spend more time in the water (young-of-the-year were only hauled out 61.0% of daylight hours hauled out in winter; Section 3.1.2), although there may also have been some dispersal of pups and breeding animals northwards out of the study area.

There were two sources of uncertainty in the abundance estimates: the variability in survey counts and the variability in the correction factors used to extrapolate abundance. Steller sea lions are typically very easy to count accurately from photographs, and there is probably negligible counting error (Olesiuk et al. 2008). However, numbers can fluctuate as animals arrive and leave to forage or move to or from other sites. The CV for “replicate” counts ranged from 4.0% in summer to 8.3% in winter. No replicates were available for spring, so we assumed the average for fall and winter (non-breeding seasons). The variability in counts represented 30-40% of the total variability in the abundance estimates. The remaining 60-70% of imprecision was due to the large correction factors applied to account for animals at sea, especially during winter.

Abundance estimates for California sea lions have also been extrapolated from pup production, and there are no correction factors to adjust survey counts. The single TDR record we obtained for a California sea lion indicated behavioural patterns were similar to Steller sea lions, but of course little can be inferred from a single animal. Since the California sea lions generally occupied the same haulout sites as Steller sea lions (Section 3.1.1), and seemed to be consuming the same prey (Section 3.4.1; Gearin, unpublished data), we made crude abundance estimates for California sea lions assuming their haulout patterns were similar to Steller sea lions. Given the lack of behavioural data, we did not calculate confidence limits, and the estimates should be regarded as provisional.

The provisional estimates for California sea lions in British Columbia and Washington indicated that abundance varied dramatically, ranging from a low of 80 during the summer breeding season, to perhaps as many as 11,000 to 17,000 in the fall. It was particularly difficult to estimate abundance during fall, which appeared to be a dynamic period. The entire study area was surveyed 30 September to 05 October 2008, yielding an abundance estimate of about 11,000 (9,600 in BC and 1,500 in WA). Subsequent surveys in WA on 18-19 October and 30 October 2008, indicated that abundance of California sea lions increased to about 3,200 and 7,500 respectively. These may have been animals moving south from BC, but since the surveys were during the peak of the northward migration (Mate 1975) were more likely animals moving northwards from California and Oregon. Averaged over the year, abundance of California sea lions in the study area was roughly 6,000, or about 25% that of Steller sea lions.

3.2 Population Sex- and Age- and Size-Structure:

Life tables for the Eastern Steller Population, including the study area, are given in Tables 6. Survival rates were increased by 1.4% over those estimated by Pendelton et al. (2006) to give a finite rate of population growth of 4.4% as observed in the study area in recent years (Olesiuk WP10a). Life tables indicated that Steller sea lions in the study area had better life expectancy than the WSP (Table 7). The reproductive potential of females (i.e. expected number of pups produced over her lifetime) was also higher than in the WSP, not so much because of higher fecundity, but mainly because the prospects of surviving to reproduce was better. The study population was estimated to be comprised of 56% juveniles, 33% adult females, and 11% adult males. Despite the differences in survival rates, the sex- and age-structure of the ESP was remarkably similar to the WSP (Table 7). The ESP was skewed toward young animals because it was increasing, such that the initial size of cohorts was increasing over time, whereas the WSP was skewed toward younger animals because of poorer survival (the WSP was assumed to be stationary so the initial size of cohorts was not changing over time).

From an energetics perspective, the biomass of a population is a more meaningful than the number of animals, and this requires information on how mass changes with age. Unfortunately, too few of the specimens collected in B.C. were weighed to fit growth curves of mass on age. However, there were sufficient numbers of specimens measured to fit growth curves of length on age, and we used these to evaluate differences between the ESP and WSP.

Newborn pups (with umbilicus attached) collected on BC rookeries had average masses of 22.3 kg ($n=28$; $SE=0.45$) for males and 21.3 kg for females ($n=24$; $SE=0.44$). As has been reported in other regions (Merrick et al. 1995), males were significantly heavier than female pups (ANOVA; $F_{2,000}=$; $P<0.001$). The values for BC are very similar to the 21.9 kg ($n=28$ SE

=0.37) reported for males and 19.6 kg (n=25; SE=0.342) for females on Forrester Island reported by Davis et al. (1996), and similar to the overall mean for ESP and WSP rookeries of 22.4 (n=53; SE=0.28) and 19.5 kg (n=49; SE=0.26) kg.

There is relatively little information on growth rates of pups over the first year while they are still nursing, but growth appears to be rapid and highly variable. Following Winship and Trites (2002) we interpolated body mass between birth and one year of age 1 as indicated by growth curves. Winship and Trites (2002) assumed the growth *increment* over the first year was constant (linear interpolation), whereas we assumed the growth *rate* was constant (exponential interpolation).

Previous analyses for WSP females aged ≥ 1 year indicated they grew faster and attained larger size in the 1970s (stable population) than in the 1980s (declining population) (Calkins et al. 2000). Winship (2000) and Winship and Trites (2001) were apparently unaware of this difference, and combined specimens collected in the 1970s and 1980s in fitting their growth curves. We adopted their methods, but recognized the temporal change and fit separate growth curves for the 1970s and 1980s (Figure 23). The females aged >1 year that were collected in BC in the 1960s (increasing population) appeared larger than WSP females collected in the both the 1970s 1980s, with 73% of the BC length measurements falling above Winship's (2000) combined growth curve and 75% falling above the WSP growth curve we fitted to the 1970s data. We thus used the growth curve for B.C., which indicated that animals in the study area attained an asymptotic length about 10cm greater than predicted by Winship (2000) (Table 8).

In contrast, for males aged ≥ 1 year, there appears to be no evidence they attained larger size in the 1970s than the 1980s (Figure 23). However, fitting separate growth curves for each period revealed significant differences in the shape parameter, M , indicating that males approached their asymptotic mass more rapidly in the 1970s than the 1980s. A growth curve fitted to the B.C. male data gave an even greater M , indicating they approached asymptotic body mass faster than the Alaskan animals in either period.

Although we could not fit mass on age growth curves for the B.C. animals, they appear to fall along the length-weight curves fitted to WSP animals by Winship (2000) (Figure 24). We thus used his allometric equations to estimate body size for animals in the study area, which indicated that the 10cm (4.4%) greater asymptotic length for females translated into a 33.1 kg (13.2%) greater asymptotic body mass.

Integrating the mass at age estimates into the life tables indicated that the mean mass (integrated over the year) was 43 kg for young-of-the year, 166 kg for older juveniles, 256 kg for adult females, and 556 kg for adult males. The overall mean per capita mass was 216 kg. Based on the seasonal abundance estimates, total biomass of Steller sea lions in the study area varied seasonally between 4,600 and 5,800 tonnes.

3.3 Bioenergetics Model and Prey Requirements:

3.3.1 Maintenance Energy Requirements

Maintenance energy requirements vary depending on the age and size of the animals and their activity levels. Since animals are either hauled out on land or at sea, the seasonal and sex- and age-specific differences in time spent at sea mirror the differences described in

Section 3.1.2 for the time spent ashore (Figure 25). Animals spent less time at sea during the summer breeding season, and spent consistently more time at sea during winter and spring (and presumably fall). Given these patterns (Figure 25), and typical RMR and FMR values (Figure 6), it was estimated that the net DMR for fully mature animals varied seasonally from 2.9-3.4 times Kleiber's (1970) BMR in summer (males were slightly lower due to reduced activity levels) to 3.9 times BMR for both sexes during winter.

There was considerable uncertainty associated with the adult DMR estimate, with CVs ranging from 13.4% for females to 14.5% for males. In both cases, most of the variability was associated with uncertainty in RMR and especially FMR multipliers (see Figure 6), which for an average activity budget had a CV of 12.8%. The greater uncertainty for males was due to greater variability in body mass and smaller samples sizes (CV ~3% for adult females and ~8% for adult males), especially for the largest males. However, the overall influence of the latter variability was somewhat tempered by relative paucity of older males in the population due to reduced longevity. The uncertainty associated with activity levels was fairly consistent throughout the year. Animals spent less time diving during summer so variability in activity budgets had less influence on the overall CV, but that was largely offset by the fact that there was greater uncertainty in the activity budgets in summer (due to smaller sample sizes, as only about half the tags continued to function into summer).

Immature animals differed from adults in two respects: they had elevated MR relative to adults of equivalent mass (Section 2.4.1), and they spent more time hauled out and less time diving (Figure 25). Interestingly, these two differences somewhat offset one another. Although captive studies indicated that young-of-the-year had MR that were elevated 3X over those of adults of equivalent mass, our model indicated that DMR of young-of-the-year in the wild ranged from 2.0-2.3X adult levels through their first summer, fall and winter, because they spent more time resting on shore than adults. Juveniles DMR peaked briefly at 2.7X adult levels in their first spring when they began spending more time actively diving, although this may have been an artifact of assuming MR remained elevated 3X over the entire first year of life. The DMRs of juveniles subsequently ranged from 1.9X adult levels in the second summer and converged on adult levels by 8 years of age.

3.3.2 Growth and Reproduction

The energetic costs associated with growth were modest. Even for young-of-the-year, who grew rapidly during the first year and deposited appreciable lipid reserves, growth represented less than 10% of the DER. Interestingly, although males grew faster than females during the first year, growth accounted for a smaller proportion of their overall energy requirements (9% in females versus 7% in males) as males also had higher RMR and FMR due to their larger body size. The uncertainty associated with growth was high in the first year, both due to variability in growth rates (which we approximated from the variability in mass at age 1 year) and variability in body composition (Rea et al. 2000). Given the variability in young animals observed in both the wild (Rea et al. 2000; Winship 2000) and in captivity (Allen 2009), it was not possible to discern any seasonal patterns, which we assumed were insignificant compared with the overall variability of body growth.

The costs associated with growth subsequently declined from about 3% of DER at age 1 year to 2% at age 2 and to about 0.5% at age 8 years as animals approached their asymptotic mass and most of the growth was lean body tissue. Although growth costs were negligible in adult males, there were seasonal changes in body mass due to fattening during the non-

breeding season and fasting or reducing food intake during the breeding season (Figure 26). Due to the combined effects of reduced activity levels and depletion of body energy reserves, DER of males during summer was 46% of DER of males outside the breeding season. Although this had very little effect on the overall prey requirements, it did effect the seasonal feeding levels. Adult females also had somewhat lower DER requirements during summer due to reduced activity levels (summer DER was 89% of DER outside the breeding season), but the small seasonal fluctuations in body mass (Allen 2009)(Figure 26) were inconsequential in the overall energy budget. At the population level, growth requirements accounted for 6.7% of total DER, which was fairly high because the increasing population was skewed to young, growing animals.

Reproductive females require additional energy for pregnancy and lactation. Although there is great uncertainty regarding the efficiency of fetal growth (Winship et al. 2000), the investment in fetal growth was nevertheless negligible. To put it in perspective, pregnant females gained about 20 kg or 7% of asymptotic body mass, and the fetus was comprised of only 2% body fat. In comparison, the weight gain in adult males as a result of seasonal fattening is about 37%, and the weight gain comprised of 47% fat (Olesiuk and Bigg 1987). Pregnant females did have higher metabolic rates than non-pregnant females, with the increase ranging from 1.7% in winter to 5.1% in spring and 6.6% during the summer prior to parturition, but this was almost all due to their higher DMR due to the weight gains associated with pregnancy.

The cost of lactation was much higher than pregnancy. As noted earlier, the costs of lactation *per se* were not estimated due to uncertainty as to when young are weaned, but we can infer the costs from the energy required by dependent offspring. Based on the development of diving behaviour (Rehberg and Burns 2008) and observations of nursing behaviour (Trites et al. 2006), it appears that most pups continue to nurse to the end of their first spring, and probably obtain all or most of their nourishment through milk over this period. This being the case, and assuming net efficiency of lactation is 90%, the overall energy requirements of a full-grown female nursing a young-of-the-year would increase from 31% in summer following parturition, to 53% in fall, to 65% during winter, to 101% by spring. In other words, a lactating female's energy requirements would have doubled by spring if she were to continue to meet the needs of her growing offspring. However, this is probably somewhat high, as the increase in energy requirements of young-of-the-year in spring is partly due to increased diving activity (Figure 25), suggesting they begin to supplement milk intake with independent foraging (Rehberg and Burns 2008). It is unlikely that costs of lactation are much higher, even if females continued to nurse juveniles through their second year. The energy requirements of juveniles in their second year are actually about the same as young-of-the-year in spring (mean 97%, seasonal range 76% to 113%) because their MR are not as elevated, and they are not growing as rapidly, and the tissue being deposited has lower fat content.

3.3.4 Assimilation Efficiency

Estimated assimilation efficiency varied slightly with season from 78% in spring to 81% in summer. Changes in urinary and fecal losses (range 5-6%) with diet quality accounted for about a third of the seasonal variability, and variability in the heat increment (range 15-17%) the remaining third. Because of the narrow range of variability, uncertainty regarding assimilation contributed little to the overall uncertainty in energy requirements.

3.3.5 Prey Requirements

Converting energy requirements to prey requirements requires knowledge of diet composition and prey quality. The general feeding habits of Steller sea lions in the study area have not been described. However, based on the prey observed in scat samples in our study that occurred with salmon, it appears sea lions feed on the same general prey types as in SE Alaska, where seasonal changes in diet composition and prey quality has been described (Winship and Trites 2003). We therefore assumed that sea lions in the study area had a similar diet to those in SE Alaska (increasing population), which had a higher-quality diet than other regions of Alaska where populations were not increasing.

It was estimated that Steller sea lions would need to consume an average of 17.9 kg of prey per day to meet their energy needs. Per capita daily prey requirements ranged from 14.1 kg in spring when activity levels were lowest, males had reduced intake, and diet quality was presumed to be highest, to 20.5 kg in spring when animals spent more time at sea, males were fattening, females were in advanced stages of pregnancy, and diet quality was presumed to be lowest.

Prey requirements varied with sex and age, but not as much as might be expected. Adult females required an average of about 15.3 kg per day (15.0 kg for non-pregnant and 15.5 kg for pregnant females), which represents about 5.3% of body weight each day. Adult males required an average of 27.8 kg of prey per day, but intake ranged seasonally from 14.7 kg in summer when they were less active and burning energy reserves, to 31.9 to 32.7 kg as they fattened during the non-breeding season. This represents an average of 4.1% of body mass per day, which is lower than adult females because requirements did not scale linearly with mass but to $\text{Mass}^{0.75}$.

Young-of-the-year prey requirements increased from 4.3 kg per day in their first summer to 15.4 kg by spring. In terms of body mass, this represented 17-23% of body mass per day, but these requirements were consumed by and provided through their mothers. The first spring is probably a critical time for young-of-the-year, as prey requirements are still elevated (22% of body mass), and their mothers are facing escalating lactation costs, and may also be in late stages of pregnancy. By the second year, prey requirements averaged 14.9 kg (range 10.4 to 19.2 kg), representing 13-14% of body mass per day. Many juveniles are likely still supplementing these needs with nourishment from their mothers (Pitcher et al. 2004; Trites et al. 2008). Prey requirements of juveniles subsequently converge to adult levels by 8 years of age.

Combining the per capita prey requirements with the abundance estimates (Section 3.1.3), the Steller sea lion population in the study area was estimated to consume 161,000 tonnes of prey per annum (CV 22-25%), of which 84% was consumed in B.C. and 16% in Washington.

Although the focus of our study was Steller sea lions, we also surveyed and collected scat samples for California sea lions, as they co-occurred at the same haulout sites. The California sea lions in the study area are predominately subadult and adult males, and we made rough provisional estimates of their prey requirements by assuming their metabolic rates were similar to those of male Steller sea lions. We scaled the metabolic rates based on $\text{Mass}^{0.75}$. Weights were obtained from 572 California sea lions live-captured and weighed in a trap near Seattle, Washington (Gearin, unpublished data). Body mass averaged 216 kg (range 68 to 471 kg) (Figure 27). Assuming the subadult and adult California sea lions had similar metabolic rates, diets and fattening cycles (Schusterman and Genrty 1970), the re-scaled average daily

prey requirements of California sea lions were estimated to range from be 13 kg in fall to 15 kg in winter.

3.4 Salmon Predation

3.4.1 *Prevalence of Salmon in the Diet*

A total of 197 scat collections were made from 40 Steller sea lion sites distributed throughout the study area, including all 3 of the rookeries on the Scott Islands, 12 of the 15 year-round haulout sites, and 25 winter haulouts (Figure 28). A total of 7,340 samples were collected and processed, of which 6,893 (94.0%) contained identifiable prey. A disproportionate number of samples were collected during the summer breeding season when conditions were most favourable (3,987 samples), compared with other months (936 to 1,265 samples) (Figure 29b). The collections represented just over half (52%) of the population when stratified by site and season. On a seasonal basis, sampling coverage ranged from 90% in summer when animals were most aggregated and sites easiest to access (i.e. 90% of the animals counted during summer surveys were on sites from which scat samples had been collected during summer), to 29% in winter when animals were widely dispersed and collections most challenging.

Salmon was common in the diet, occurring in 1,683 (24.4%) of samples with identifiable prey. Salmon occurred in all months of the year and at most (89%) of collection sites. However, prevalence of salmon varied both with season (Figure 30) and by site (Figure 31). Salmon were most prevalent during summer (26% of samples) and fall (37%), and least prevalent during winter (17%) and spring (14%). Prevalence in most collections was fairly low (0-30% of samples), suggesting that salmon was not the focal prey but consumed opportunistically along with other prey. However, there were a few (3%) collections in which salmon were present in most (70-100%) of the samples, and in a few cases we suspect that sea lions congregated at certain sites specifically to forage on salmon. Salmon were the only prey identified in 9% of samples that contained salmon, but were typically consumed along with other prey (Figure 32). Scat samples containing salmon typically contained 2-5 prey species (including salmon) and occasionally >10 prey species.

Salmon was nearly ubiquitous in the diet, occurring in 1,683 (24.4%) of samples with identifiable prey. Salmon occurred in all months of the year and at most (89%) of the collection sites. However, prevalence of salmon varied both with season (Figure 30) and by site (Figure 31). Salmon were most prevalent during summer (26% of samples) and fall (37%), and least prevalent during winter (17%) and spring (14%). Prevalence in most collections was fairly low (0-30% of samples), suggesting that salmon was not the focal prey but consumed opportunistically along with other prey. However, there were a few (3%) collections in which salmon were present in most (70-100%) samples, and in a few cases we suspect that sea lions congregated at certain sites specifically to forage on salmon. Salmon were the only prey identified in 9% of samples that contained salmon, but were typically consumed along with other prey (Figure 32). Scat samples containing salmon typically contained 2-5 prey species (including salmon) and occasionally >10 prey species.

Using SSFO to partition diet among the various prey consumed, we estimated that the proportion of salmon in the overall diet ranged from a low of 7.4% in spring to a peak of 15.7% in fall (Figure 33). Monte Carlo simulations indicated the CV varied seasonally from a low of 4% during summer when the population was most aggregated and sampling coverage best, to a

high of 14% in winter when animals were most dispersed and sampling coverage was poorest. The main source of variability was the uncertainty in the relative biomass of salmon consumed when other prey were consumed in the same meal. The variability in survey counts used to weight the estimate also contributed to the overall uncertainty, especially outside the summer breeding season when sampling coverage was poorest and survey counts more variable. The CV accounts for imprecision in the estimate (i.e. variability in the relative proportion of salmon in samples around the mean), but it does not capture potential biases (i.e. if salmon tended to comprise a smaller or larger proportion of the diet than other species consumed at the same time), which we discuss in Section 4.

Weighting the seasonal diet estimates by the total prey required by the study population, it was estimated that salmon comprised 10.6% of the overall annual diet. We tested whether this estimate may have been biased by inclusion of older samples that had been collected in the 1980s and 1990s, but restricting the analysis to samples collected in the last decade had little effect on the estimate (10.0%). We also tested whether the estimate may have been confounded by including scat samples at sites where Steller sea lions intermingled with California sea lions, but excluding any sites where there was potential for confusion also had little effect on the estimate (9.7%). Indeed, the contribution of salmon to the diet of California sea lions at the mixed species sites (12.1%) was similar to that of Steller sea lions outside the breeding season (10.6%).

Salmon skeletal elements identified in scat samples were not measured, but we usually subjectively noted the size of salmon consumed. For identifications made by WDF&W and ODF&W, size was generally noted as being adult-sized (>35cm) or juvenile-sized (<20cm). For scat samples analyzed by Pacific Identifications, salmon bones were subjectively allocated to a range of size categories (Figure 34). Following Trites and Calkins (2008), we considered the smallest category (<16cm) as being juveniles, and all larger categories as being adults. Given the very subjective nature of these size allocations and the inconsistency in methodology, caution should be exercised in interpreting the size data, but we nevertheless consider them useful as a general indicator of the size of salmon being consumed. The data indicate that most of the salmon consumed by Steller sea lions were adult-sized, with juveniles representing 1-2% of salmon in summer, fall, and winter, and increasing to 8% of salmon consumed in spring (Figure 30).

During summer, most of the salmon predation occurred near the Scott Island rookeries, which were occupied by large numbers of animals and where salmon tended to be a larger proportion of the diet (13% on Maggot Island, 20% on Sartine Island; and 14% on Triangle Island) compared to the overall summer weighted average of 7.4% at non-breeding haulouts. Most of the remaining salmon were taken at year-round haulouts along the west coast of Vancouver Island, and to a lesser degree along the outer Washington coast (Figure 35). Overall, salmon was estimated to comprise 12% (CV = 4%) of the summer diet.

During fall, sampling coverage was less complete, and there were several important sampling gaps. Appreciable numbers of animals still occupied the Scott Islands rookeries, and most of the breeding animals that had dispersed were at major haulout sites within 120km of the rookeries (Figure 14). Unfortunately, scat collections were not made at either the rookeries or the nearby haulout sites during fall. Salmon was a fairly important prey item at sites along the west and south coast of Vancouver Island, ranging from 20% to 26% of the diet at Barrier Islands, Wouwer Island, Folger Island, Sombrio Point, and Race Rocks. The latter sites were also occupied by large numbers of California sea lions, and many or most of the scat samples could have been from that species. [Note: This only includes the DFO Folger samples, as the

NMFS data arrived too late]. Salmon appeared to be somewhat less important in the diet at sites along the coast of Washington and mouth of the Columbia River. Overall, salmon was estimated to comprise 15.7% (CV = 6%) of the fall diet.

During winter, animals were more widely distributed and sampling coverage was less complete. Salmon appeared to be more prevalent in the diet on the outer coast, and less prevalent in inside waters (Figure 35). Overall, salmon was estimated to comprise 9.3% of the winter diet (CV = 14%). During spring, the prevalence of salmon continued to be low at inside water haulouts, and had declined from winter levels on the outer coast. Salmon constituted more than 10% of the diet at only one site, Perez Rocks (27%) on the central west coast of Vancouver Island. Overall, salmon was estimated to comprise 7.4% of the spring diet (CV = 9%).

Combining these seasonal diet estimates with the estimates of seasonal abundance (Section 3.1.3) and prey requirements (Section 3.3.5), total annual consumption of salmon was estimated to be 17,200 tonnes, of which, approximately 14,500 tonnes (84%) was consumed in B.C. and 2,700 tonnes (16%) in Washington and mouth of the Columbia River. The estimate is subject to the combined uncertainties in abundance, prey requirements and proportion of salmon in the diet. A final CV has not been calculated, but accounting for the major sources of uncertainty suggests it is likely on the order of 25-34%. Applying the same analyses for California sea lions, we provisionally estimate they consume on the order of 3,900 tonnes of salmon annually (72% in B.C. and 28% in Washington), or a little more than 20% of the salmon consumed by Steller sea lions.

3.4.2 Species of Salmon Consumed

Genetic analysis to determine species of salmon are still in progress, and we only report preliminary results here. Of the 337 samples processed to date, useable DNA was successfully extracted from 320 (95%) of the samples. In most cases at least one species of salmon could be identified, and 17% of the samples contained two species of salmon and 1% contained 3 species of salmon. In most cases (81%) the exact species of salmon could be identified, but in 19% there was some ambiguity and the identification could only be narrowed to one of two species of salmon. In particular, there were 53 instances in which the salmon consumed could have been pink or sockeye, which was a high proportion of the total number of samples potentially containing sockeye (19 positive sockeye identifications and 50 instances the species was either pink or sockeye salmon). We expect these ambiguities will be resolved once the DNA has been sequenced.

The samples that have been analyzed to date represent a somewhat ad hoc subset of the total scat database, and were not considered adequate for partitioning total salmon consumption by salmon species. However, the data do provide much improved information on the species of salmon consumed than has been available from analysis of bone fragments or other methods. Steller sea lions prey upon all 5 species of Pacific salmon as well as steelhead (Figure 36), and there appeared to be seasonal and geographic differences in the species consumed (Figure 37).

During summer, about half the salmon taken by sea lions on the Scott Islands were pink or sockeye, but there was considerable uncertainty between these two species (Figure 37a). Coho and chinook make up most of the other half. Pink and/or sockeye were also predominant during summer along the west coast of Vancouver Island, but considerable numbers of chum,

coho and chinook salmon were also taken. Off Washington, sea lions took mainly coho, and some chinook and steelhead, especially at the mouth of the Columbia River, whereas relatively few sockeye and pink salmon were consumed.

During fall, DNA has been analyzed for only one site off Vancouver Island, where sea lions were taking mainly coho and some chinook, with no sockeye detected. Coho also dominated off Washington, but sea lions also took considerable numbers of chinook and steelhead, again mainly at the mouth of the Columbia River.

During winter, DNA has been analyzed for only a few samples. At the two sites sampled off northern Vancouver Island (Scott Islands and Ashby Point), sea lions were taking chum, pink and/or possibly sockeye, and chinook. DNA in only 6 samples at one site (Cape Alava) off Washington have been analyzed, and they contained a mixture of steelhead, coho and chinook.

During spring, mainly chum and chinook were taken off the west coast of Vancouver Island and off Washington, and some steelhead off the mouth of the Columbia River.

4. DISCUSSION

By any measure, Steller sea lions in the study area and neighbouring waters in SE Alaska and off Washington are thriving. Local breeding populations have been growing for 5 decades, over which period pup production has increased 5-fold, and there is no sign the growth rate is slowing. The species is currently breeding at all 4 rookeries known to have existed before predator control programs were initiated in 1913, and in recent years have established 6 new breeding sites in B.C. and SE Alaska. Females in the study area attain larger body size, have greater life expectancies, and higher reproductive potential than their counterparts in western Alaska where populations have declined.

Our analyses and model indicates that Steller sea lions have emerged as an important predator in coastal waters of B.C. and Washington. Although there is considerable uncertainty associated with our estimates of annual salmon consumption (17,200 tonnes; CV ~25-34%), Steller sea lions in the study area appear to now take about as much salmon than the commercial fishery, which landed an average of 18,600 tonnes (range 5,500 to 29,400 tonnes) range in southern B.C. and Washington State during 1999-2008 (North Pacific Anadromous Fish Commission yearbook statistics; www.npafc.org). Given this finding, it is worth scrutinizing our methodology to assess whether there may be serious biases or large uncertainties that could have caused us to exaggerate the salmon consumption by Steller sea lions.

Salmon predation by sea lions was highest in summer and fall, and we are relatively confident in our abundance estimates for that period. During the summer breeding season, abundance was estimated using two methods. Traditionally, population size has been estimated from pup production by applying multipliers of the ratio of non-pups to pups as indicated by life tables. In this study, we also developed survey correction factors to adjust non-pup counts for animals that were at-sea and missed during surveys. The major sources of uncertainty inherent to each approach (pup multipliers and haulout patterns) are quite independent of each other, yet the two methods provided similar abundance estimates. The diurnal haulout patterns during summer were similar to those described in numerous other

studies (Gentry 1970; Sandegren 1970; Edie 1977; Withrow 1982; Higgins 1984), and the corresponding survey correction factors were relatively small as most animals appear to be hauled out during daylight hours during the summer breeding season. Thus, we are relatively confident in our summer abundance estimate.

During fall, our survey counts were lower, but our corrections for animals at-sea were greater, and the estimated abundance of sea lions in the study area increased slightly (but not significantly). This appears to be reasonable, as pups would still be traveling with their mothers, and it appears that many were still on rookeries, while some had dispersed to neighbouring haulout sites. It is unlikely that many had yet moved beyond the boundaries of the study area. Moreover, there was likely an influx of Steller sea lions from the California and Oregon coast. Steller sea lions appear to be displaced northwards by California sea lions migrating from breeding sites off California (Mate 1975), and we saw a large influx of California sea lions during our fall surveys. Moreover, recent brand resight data indicates that many animals branded as pups on rookeries in California and Oregon winter off southern Vancouver Island (Scordino 2008). Thus, it is unlikely there was a significant decline in abundance during fall, and the drop in our count was more likely due to animals spending more time at sea. This is also supported by the little telemetry data that has been collected for Steller sea lions outside the breeding season in other regions (Merrick 1995; Swain 1996).

By winter and spring, mothers with young-of-the year, which were no longer reliably distinguishable from older juveniles, appeared to be widely distributed and many may have dispersed beyond the study area (Olesiuk WP10a), and our correction factors to account for animals at-sea and missed were large. It would be useful to conduct broader-scale surveys outside the breeding season to document the overall distribution patterns, which would assist in interpreting more localized counts.

Our estimates of the energy requirements of Steller sea lions in the study area were nearly identical to those estimated for Steller sea lions in SE Alaska (Winship et al. 2002). Some of the similarity can be attributed to the fact the models used in each study were quite similar. However, we adapted the bioenergetics model to an increasing Steller sea lion population, and used different parameters for life tables and growth curves to estimate sex- and age-composition and body mass. Our activity budgets were based on new satellite telemetry data, and our RMR and FMR estimates were markedly different than those used by Winship et al. (2002). Based on metabolic rates measured for other otariids in the wild (Arnould et al. 1996; Trillmich 1996; Costa et al 1989a, 1989b, 2000; Costa and Gales 2003) we assumed that RMR for animals resting on land was about 2X BMR and that FMR for animals at sea was about 5.4X BMR. These were considerably higher than the values used by Winship et al. (2002) (1.2X BMR for RMR and 4.0X BMR for at-sea FMR). This is one area where our energy requirements may have been inflated, but given that otariids tend to have higher metabolic rates than phocids of equivalent mass (Innes et al. 1987), we don't think the lower values utilized by Winship et al. (2002) are supported by the literature. Nevertheless, both our models allowed for a wide range of uncertainty, which is reflected in the large CVs. Indeed, we allowed for RMR values ranging from 1.4-2.9X BMR and for at-sea FMR values ranging from 3.4-7.4X BMR with equal probability (i.e. drawn from a uniform distribution over the potential range) in our sensitivity analyses.

Measuring the metabolic rates of actively foraging animals is obviously not a trivial task, and all of the published FMR measurements have been made indirectly based on water turnover rates (Costa et al. 1900). This technique involves a number of underlying assumptions about RQ values, and also assumes that animals do not ingest seawater and obtain water only

through prey. There is thus potential for systematic biases across all the FMR estimates. Only two studies have attempted to validate the technique. Boyd et al. (1995) found that FMR gave slightly higher metabolic rates than direct respirometry and heart rate measures for California sea lions swimming in a flume, but the differences were small (Mean = 36.4 and 35.4% respectively) but not statistically different. Sparling et al. (2008) found there was little difference between daily energy requirements and estimated metabolic rates based on turnover rates in wild grey seals held temporarily (Mean = 0.7%), although there was considerable variability among individual animals (Standard Deviation = 17%; Range -39% to +44%).

While one needs to use caution in extrapolating metabolic measurements made in swim flumes to free-diving animals in the wild, captive experiments do allow for more direct measurements of swimming costs. Rosen and Trites (2002) estimated that the minimum cost of transport for juveniles Steller sea lions was about 5X their maintenance metabolic requirements (which were elevated in their juvenile animals) at swimming speeds of 1.8-2.1 m·sec⁻¹. We do not know the average swimming speeds of animals in the wild, but based on rates of descent and ascent of dives, the vertical component alone was typically 1.2-1.4 m·sec⁻¹. Considering that we only applied the FMR value of 5.4X BMR to the proportion of at-sea time actively spent diving, the FMR value seems reasonable.

In converting energy to prey requirements, we assumed that the overall quality of diet of Steller sea lions in the study area was the same as that in SE Alaska. This seems reasonable, as Steller sea lions in the two areas appear to prey on the same general array of prey (Trites and Olesiuk, unpublished data; Trites et al. 2006). Moreover, population growth rate has been shown to be directly correlated with the energetic density of the diet (get reference), and the two populations have been increasing at about the same rate. The diet in SE Alaska is higher quality than in other regions of Alaska, and thus provided a lower estimate of prey requirements than had we used the quality from any other area. Since there is an inverse relationship between prey requirements and diet quality, our assumed diet needs to be evaluated with studies of the general feeding habits and other prey types.

While we do not believe captive feeding rates can be validly applied to wild animals, they do provide ancillary information on prey requirements of Steller sea lions. Kastelein et al. (1990) and Allen (2009) both reported that long-term feeding rates for captive adult female and male Steller sea lions were about 60-70% of those estimated in this study for wild animals in our study area. Allen (2009) calculated that about 30% of the difference between feeding rates observed in captivity and predicated in the wild (Winship et al. 2003) could be attributed to differences in the energetic density of the diet, and we believe that activity levels account for much if not all of the remaining difference.

The importance of salmon in the diet was estimated using scat analysis, which involves a number of assumptions and is prone to a number of biases. Compared with other pinnipeds, Steller sea lion scats are noteworthy in that the undigested prey remnants recovered are meager and often in poor condition. Observations of feeding animals and stomach contents indicate that sea lions typically consume the entire salmon including the head. Nevertheless, only ~2% of the scat samples with adult-sized salmon contained salmon otoliths, suggesting the vast majority were completely digested or digested beyond recognition. We suspect this may be related to the presence of pebbles and rocks in the stomachs that may assist in digestion (Fiscus 1961; Spalding 1964). Prey remnants in scats from captive animals seem to be in better condition. Cottrell and Trites (1996) reported recovery rates of 10% for salmon otoliths in captive animals. The meager remains found in wild sea lions scats precludes the use of biomass reconstruction techniques. For example, had we assumed that 10% of otoliths were

recovered (which appears to be a gross overestimate for scats collected from wild animals), the vast majority of our samples would have been scored as zero due to the absence of otoliths.

One potential bias in scat analysis, especially for Steller sea lions, is that prey will not be represented because all of the hard parts have been completely digested, or they were feeding on prey that lack hard parts. By using a wide array of skeletal structures, which are more numerous than otoliths, we believe it is possible to identify most of the prey that were consumed. Indeed, the number and diversity of prey species identified in scat samples using the all-structures technique compares favorably with the number and diversity found in stomach samples (Fiscus 1961; Spalding 1964; Pitcher 1982). We recently validated prey identifications based on bone fragments using DNA (Tollit et al. 2009), which indicated that overall diet composition using both genetics and hard-parts did not differ significantly from hard-part identification alone, suggesting that past scat-based diet studies have not missed major dietary components.

Split-sample frequency of occurrence provides estimates of the relative biomass of prey based on how often the prey species is consumed (frequency of occurrence) and makes assumptions about the relative amount consumed when they are eaten. While SSFO seems to provide reasonably accurate estimates based on comparison with volumetric indices and validation with captive seal studies, there are potential biases in applying it to wild animals. Incidental prey that tend to be consumed in low volumes will be overestimated, and focal prey that tend to be consumed in large volumes will be underestimated. We allowed for this uncertainty in the sensitivity analyses by letting the relative contribution of salmon to vary between 0% and 100% of the total volume of the prey consumed whenever salmon occurred along with other prey. This introduced considerable uncertainty associated with the diet estimates (CV = 4-14%).

Although salmon were not generally a focal prey species and were often consumed along with other prey, we can make reasonable inferences regarding their *minimum* importance in the diet. Salmon occurred in 24% of samples, and were the only prey species present in 9% of those samples, suggesting that about 2% of animals had fed exclusively on salmon. Salmon comprised only a portion of the diet of the remaining 22% of animals that had consumed them. In most cases at least one salmon was consumed, and genetic analysis indicated that at least two species of salmon were consumed in about 17% of cases and 3 species in 1% of cases (genetics did not indicate how many individuals of each species were consumed). Given that most of the salmon consumed were adult-size and probably weighed an average of 3-6 kg (Olesiuk et al. 1990; North Pacific Anadromous Fish Commission yearbook statistics at www.npafc.org), these minimum estimates of the number of salmon would have comprised at least 20-40% of the average daily prey requirements (18kg). With 2% of animals obtaining all of their daily prey requirements and 22% of animals obtaining at least 20-40% of their daily requirements from salmon, salmon likely comprised at least 6-11% of the diet. It is thus unlikely that our estimate of 10.6% of the overall diet grossly exaggerates the actual importance of salmon.

While our study indicates sea lions are an important coastal predator and consume significant amounts of salmon, further studies are required to appreciate the overall role of this apex predator. Salmon comprise only 10% of the overall diet, and the remainder is comprised of a wide variety of other species, some of which may potentially be prey, or predators, or competitors with salmon. In addition to salmon, a number of other prey species consumed by sea lions are also fished commercially and as such sea lions compete with humans that harvest these same species. We have illustrated an approach for estimating the consumption for one

prey type, which we hope will provide the impetus for similar assessments on other prey types in other regions as well as additional consideration of sea lions consumption needs in fishery and ecosystem management decisions.

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Table 1. Summary of instrument deployments on 25 Steller sea lions and 2 California sea lions during 2004-2006. All animals were captured and released in January-February at Norris Rocks off Hornby Island in the central Strait of Georgia. Duration of TDR and PTT records are given in days.

Animal ID	Date	Sex	Weight (kg)	Length (cm)	Category	TDR (days)	PTT (days)	ARGOS locns
GG2004	05-Feb-04	M	173	204	Juvenile		-	-
YY2004	05-Feb-04	M	-	284	Adult		-	-
OO2004	06-Feb-04	M	250	-	Adult		-	-
BB2004	06-Feb-04	M	87	-	Yearling		-	-
RR2004	05-Mar-04	M	-	-	Adult ¹		-	-
PP2004	04-Mar-04	M	-	-	Adult ¹		-	-
YY2005	26-Jan-05	F	278	227	Adult		11.2	67
OO2005	28-Jan-05	M	163	207	Juvenile		72.1	366
PP2005	28-Jan-05	F	115	171	Juv/Year		71.3	392
GG2005	28-Jan-05	M	233	222	Adult		48.4	298
BB2005	26-Jan-05	M	101	162	Yearling		14.1	80
RR2005	28-Jan-05	M	221	214	Juvenile		89.4	464
YB2005	09-Feb-05	M	213	219	Juvenile		96.5	850
OY2005	10-Feb-05	F	222	217	Adult		128.0	1238
YR2005	09-Feb-05	M	269	242	Adult		196.1	1205
PR2005	09-Feb-05	M	166	207	Juvenile		124.5	833
YG2005	09-Feb-05	M	241	231	Adult		185.1	1154
OG2005	10-Feb-05	M	195	208	Juvenile		115.0	882
OO2006	11-Jan-06	M	479	278	Adult		112.4	956
PP2006	11-Jan-06	F	200	203	Adult		159.1	1123
GG2006	23-Jan-06	M	385	247	Adult		58.1	409
RR2006	11-Jan-06	M	216	209	Juvenile		107.7	926
OY2006	25-Jan-06	F	140	188	Juvenile		168.4	1384
YG2006	25-Jan-06	M	298	242	Adult		221.4	1615
YY2006	24-Jan-06	F	187	211	Adult		233.9	1406
OR2006	25-Jan-06	F	155	197	Juvenile		140.3	1120
YP2006	08-Feb-06	F	332	233	Adult		139.2	1226

¹California sea lion

Table 2. Summary of sex- and age-distribution of instrumented Steller sea lions compared to the estimated sex- and age-composition of the study population as indicated by life tables (see Section 3.2).

Age-Group	Number Tagged	Percent of Tagged Sample	Percent of Population
Yearlings	3 [†]	12%	20%
Juveniles	9	36%	36%
Adults Females	5	20%	33%
Adult Males	8	32%	11%
Total	25	100%	100%

[†]Includes one over-size yearling classified as a yearling as it was seen nursing after release.

Table 3. Summary of Steller sea lion scat collections used to estimate the prevalence of salmon in the diet in the study area.

Agency	Number of Samples	Collection Area	Collection Period
DFO	1,856	Southern Vancouver Island	Mainly non- breeding season, 1979-1987
DFO-WDF&W	19	Belle Chain, BC	Spring, 2008
NMFS	1,777	Outer Washington Coast	Year-round, 1993-2007
ODF&G	321	Columbia River So. Jetty	Year-round 2004-2007
UBC	1,398	North and West coast Vancouver Island including Scott Islands	Summer breeding season, 2000-2009
UBC-DFO	1,264	NW Vancouver Island including Scott Islands	Summer breeding season, 1997-2008
WDF&W	210	Split Rock and San Juan Islands	Year-round, 2002-2008
PSC	515	Remote sites in BC outside breeding season	Non-breeding season, 2009-2010
Total	7,360		

Table 4. Comparison of dive behavior and energetics for nine species of otariids with Steller sea lions in this study (modified from Costa and Gales 2003). The At-Sea FMR of Steller sea lions is assumed to be 11.9-23.4 Watts·kg⁻¹ based on the range observed in other otariids, which have similar diving characteristics.

Species	Body Mass (kg)	Dive Depth (meters)	Dive Duration (minutes)	# Dives per Hour	Dive Time at Sea (%)	At-Sea FMR (Watts·kg ⁻¹)	Source
Galapagos fur seal	27	26	<2	5.6	24	12.3	Gentry et al. (1986); Trillmich and Kooyman (2001).
Antarctic fur seal (Cape Sheriff)	33.7	19	0.9	6.1	9.8	23.4	Arnould et al. (1998)
Antarctic fur seal (Bird Island)	36.8	12.7	1.1	13	20.4	16.4	Costa et al. (2000);
New Zealand fur seal	36.4	53	2.2	-	-	-	Mattlin et al. (1998)
Australian fur seal	77.7	58	2.9	8.3	40.7	-	Arnould and Hindell (2000);
Northern fur seal	35.7	68	2.2	1.5	26.0	11.9-19.9	Gentry et al. (1986); Costa and Gentry (1986);
Australian sea lion	69.3	61	3.3	10.7	57.9	20.3	Costa and Gales (2003)
New Zealand sea lion	114.1	121	3.4	7.6	43.5	22.6	Costa and Gales (2000)
California sea lion	81.5	31-98	1.5-2.8	8.4	33.0	17.8	Feldkamp et al. (1989); Costa et al. (1990) ¹
Southern sea lion	126	61	3.1	11-19	52.7	-	Werner et al. (1995)
Steller sea lion	-	15-28	1.2-1.6	10-15-10.8	-	-	Merrick and Loughlin (1997)
Steller sea lion (this study)	205.2	44.3	2.6	9.5	40.6	(11.9-23.4)	This Study

Table 6a. Life table for female Steller sea lions in the study area. Parameters are Age (x) in years, finite annual survival rates ($SV_{f(x)}$), annual fecundity rates $FEC_{f(x)}$, proportion of females that are mature $Mat_{f(x)}$, number of females alive at midpoint between birth pulses ($L_{f(x)}$), life expectancy at age x , ($P_{f(x)}$), reproductive value at age x , $RV_{(x)}$, and proportion of age-class in the population ($Pf_{(x)}$). [Need to add growth and metabolic parameters in final version]

Age (x)	$SV_{f(x)}$	$FEC_{f(x)}$	$Mat_{f(x)}$	$L_{f(x)}$	$T_{f(x)}$	$RV_{(x)}$	$Pf_{(x)}$
0	0.683	0.000	0.000	970.0	8.7	3.661	970.0
1	0.802	0.000	0.000	657.8	11.3	5.399	630.5
2	0.884	0.000	0.000	526.0	12.9	6.752	483.2
3	0.884	0.000	0.000	463.9	13.5	7.656	408.4
4	0.946	0.214	0.320	409.1	14.2	8.681	345.3
5	0.946	0.382	0.570	386.5	14.0	8.962	312.6
6	0.946	0.556	0.830	365.1	13.7	9.082	283.1
7	0.946	0.670	1.000	345.0	13.5	9.025	256.3
8	0.946	0.670	1.000	325.9	13.2	8.843	232.1
9	0.946	0.670	1.000	307.9	12.9	8.652	210.1
10	0.946	0.670	1.000	290.9	12.6	8.449	190.3
11	0.946	0.670	1.000	274.8	12.3	8.234	172.3
12	0.946	0.670	1.000	259.6	11.9	8.006	156.0
13	0.946	0.670	1.000	245.2	11.6	7.766	141.3
14	0.946	0.670	1.000	231.7	11.2	7.511	127.9
15	0.946	0.670	1.000	218.9	10.8	7.241	115.8
16	0.946	0.670	1.000	206.8	10.4	6.955	104.9
17	0.946	0.670	1.000	195.4	9.9	6.653	95.0
18	0.946	0.670	1.000	184.6	9.5	6.333	86.0
19	0.946	0.670	1.000	174.4	8.9	5.995	77.9
20	0.946	0.670	1.000	164.7	8.4	5.636	70.5
21	0.946	0.670	1.000	155.6	7.8	5.257	63.8
22	0.946	0.670	1.000	147.0	7.2	4.855	57.8
23	0.946	0.670	1.000	138.9	6.6	4.430	52.3
24	0.946	0.670	1.000	131.2	5.9	3.980	47.4
25	0.946	0.670	1.000	124.0	5.2	3.504	42.9
26	0.946	0.670	1.000	117.1	4.5	3.000	38.9
27	0.946	0.670	1.000	110.6	3.7	2.466	35.2
28	0.946	0.670	1.000	104.5	2.8	1.901	31.9
29	0.946	0.670	1.000	98.7	1.9	1.303	28.8
30	0.000	0.000	1.000	49.4	1.0	0.000	12.1

Table 6b. Life table for male Steller sea lions in the study area. Parameters are Age (x) in years, finite annual survival rates ($SV_{m(x)}$), proportion of males that are mature $Mat_{m(x)}$, number of males alive at midpoint between birth pulses ($L_{m(x)}$), life expectancy at age x , ($T_{m(x)}$), and proportion of age-class in the population ($P_{m(x)}$). [Need to add growth and metabolic parameters in final version]

Age	$SV_{m(x)}$	$Mat_{m(x)}$	$L_{m(x)}$	$T_{m(x)}$	$P_{m(x)}$
0	0.536	0.00	1030.0	3.4	1030.0
1	0.680	0.00	545.2	4.5	522.5
2	0.791	0.00	368.2	5.2	338.2
3	0.791	0.25	290.1	5.4	255.4
4	0.884	1.00	228.6	5.5	192.9
5	0.884	1.00	201.7	5.1	163.1
6	0.884	1.00	178.0	4.7	138.0
7	0.884	1.00	157.0	4.2	116.7
8	0.884	1.00	138.5	3.6	98.7
9	0.750	1.00	122.2	2.9	83.4
10	0.700	1.00	91.2	2.6	59.7
11	0.650	1.00	63.5	2.3	39.8
12	0.600	1.00	40.9	2.0	24.6
13	0.500	1.00	24.3	1.8	14.0
14	0.400	1.00	12.0	1.5	6.6
15	0.300	1.00	4.7	1.4	2.5
16	0.200	1.00	1.4	1.2	0.7
17	0.200	1.00	0.3	1.2	0.1
18	0.000	1.00	0.0	1.0	0.0
19	0.000	1.00	0.0	0.0	0.0
20	0.000	1.00	0.0	0.0	0.0

Table 7. Life history and population parameters for the study area population compared to a stationary population in western Alaska during the 1970s.

Parameter	Study Population	Calkins & Pitcher (1982)	York (1995)
Mean Age – Females (years)	7.2	7.1	5.7
Mean Age – Males (years)	2.7	3.1	3.1
Life Expectancy – Females (years)	8.7	6.4	6.2
Life Exp – Males (years)	3.4	3.4	3.4
Reproductive Value (# offspring)	3.66	2.06	2.04
% Juveniles	55.6%	54.0%	52.9%
% Adult Females	33.2%	32.9%	33.1%
% Adult Males	11.2%	13.7%	14.0%
Population Growth Rate	4.34%	-0.03%	-0.09%
Pup Multiplier	4.491	4.877	4.790

Table 8. Growth parameters (\pm SE) for Richards growth curves of length on age for female and male specimens collected in western Alaska during the 1970s, western Alaska during the 1980s, and British Columbia during 1959-1968. Parameters are A (asymptotic length in meters), m (dimensionless shape parameter), S_0 (initial length in meters), and T (growth rate). Data from Calkins and Pitcher (1982) and Pike (unpublished MS) and analyses modeled after Winship (2000).

Population	Status	a	m	S_0	T
Females					
AK 1970s	Stable	2.31 (2.23 to 2.35)	-2.87 (-3.64 to -2.09)	-	-13.90 (-23.42 to -4.38)
AK 1980s	Decreasing	2.42 (2.30 to 2.54)	-4.369 (-5.86 to -2.87)	-	-60.077 (-126.78 to 6.63)
BC 1960s	Increasing	2.43 (2.39 to 2.47)	-1.791 (-2.84 to -0.74)	110.3 (103.6 to 117.0)	-6.730 (-17.57 to 4.11)
Males					
AK1970s	Stable	2.88 (2.71 to 3.05)	2.813 (-1.91 to 7.53)	1459.0 (1323.1 - 1594.8)	23.788 (13.4 to 34.2)
AK 1980s	Decreasing	3.16 (2.97 to 3.26)	5.063 (-0.01 to - 10.14)	1530.1 (1408.6 - 1651.5)	27.18 (21.8 to 32.5)
BC 1960s	Increasing	3.02 (2.93 to 3.10)	1.95 (0.24-3.67)	118.4 (111.0 125.7)	11.1 (8.52 to 13.43)

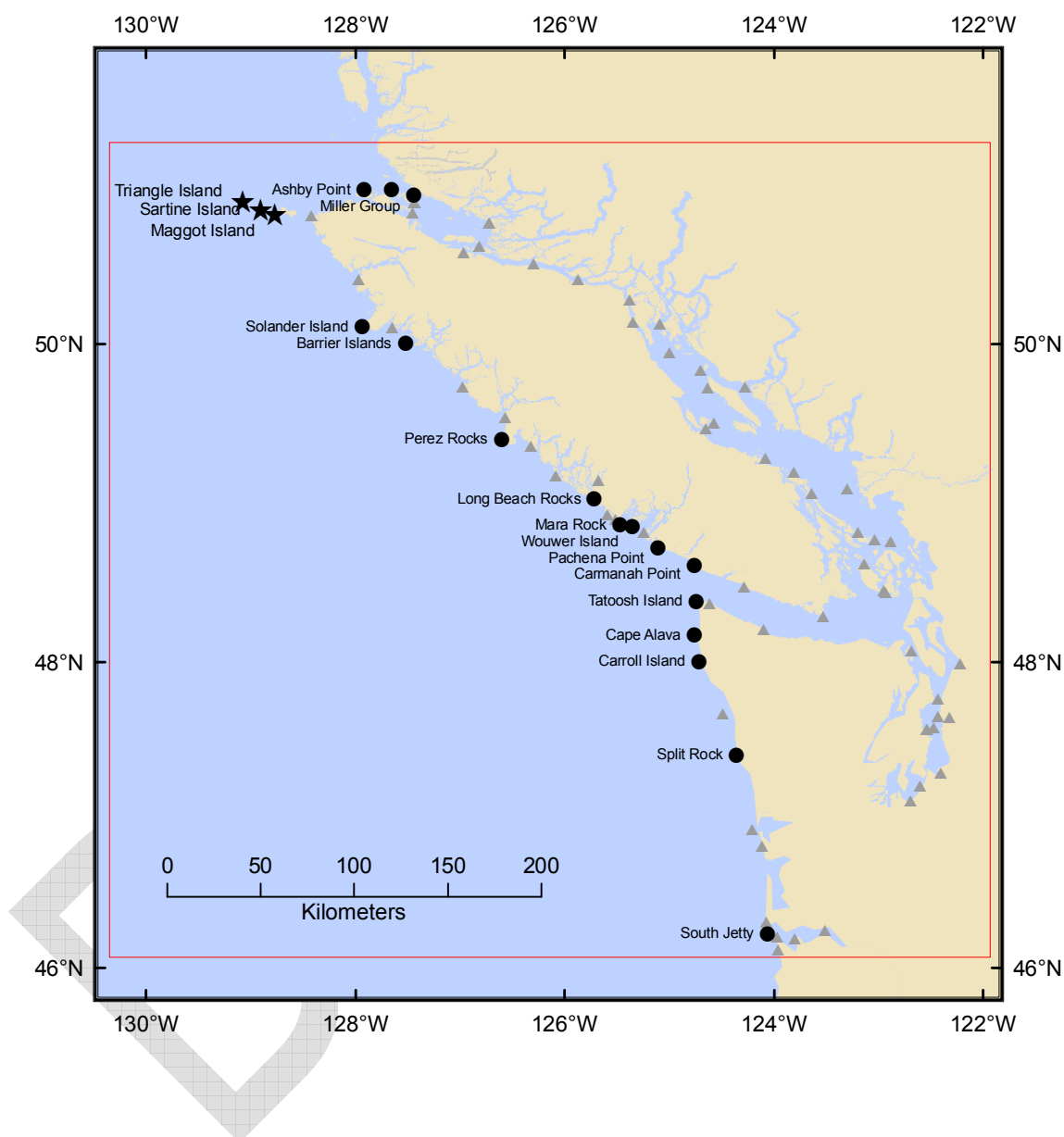


Figure 1. Map showing extent of the study area (red box) and location of breeding sites (★), year-round haulout sites (●), and winter haulout sites (▲). (WA sites need to be revised).

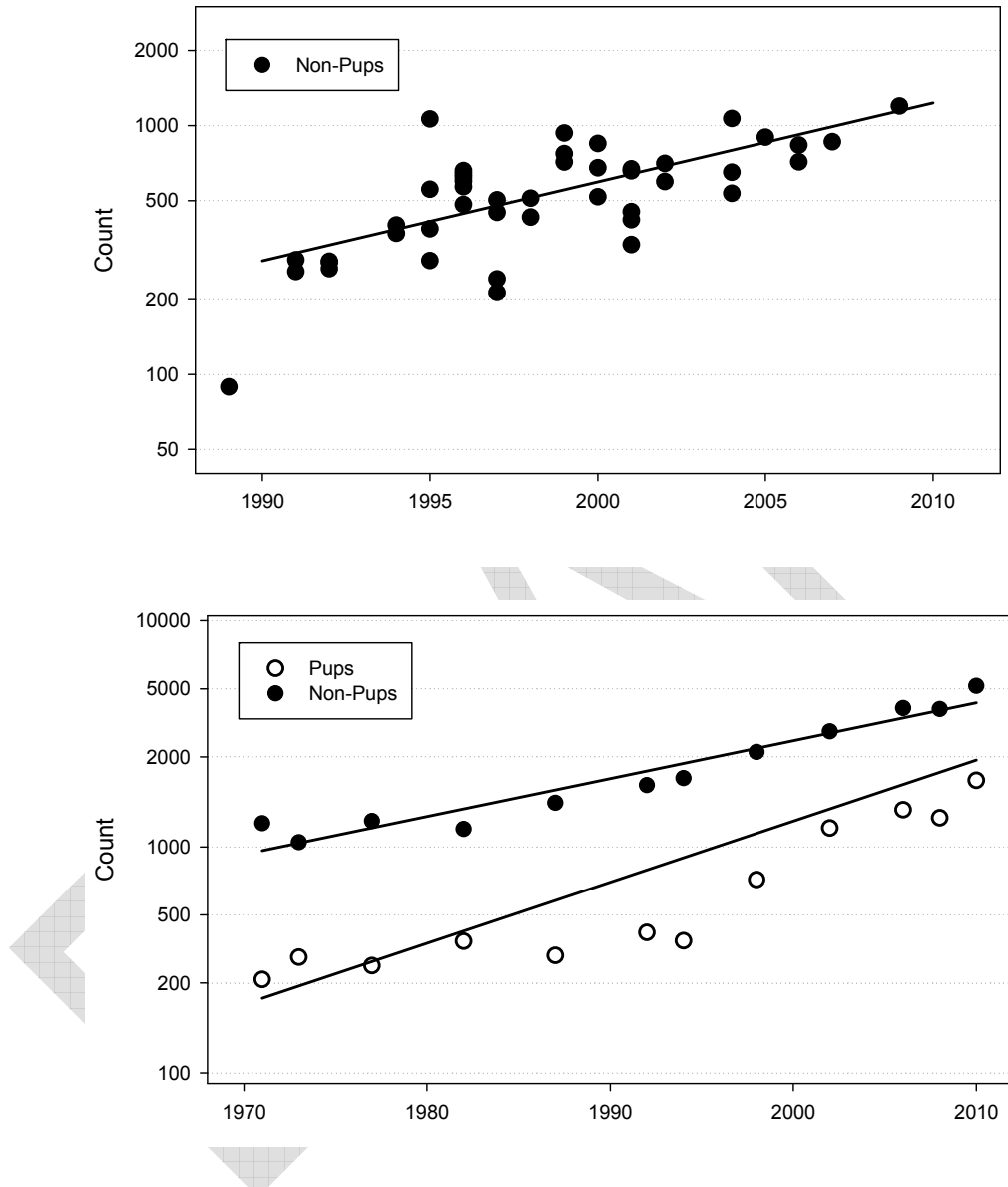


Figure 2. Trends in abundance of Steller sea lions in Washington (top panel) and British Columbia (bottom panel) based on aerial surveys conducted during the summer breeding season (WDFW and DFO unpublished survey data).

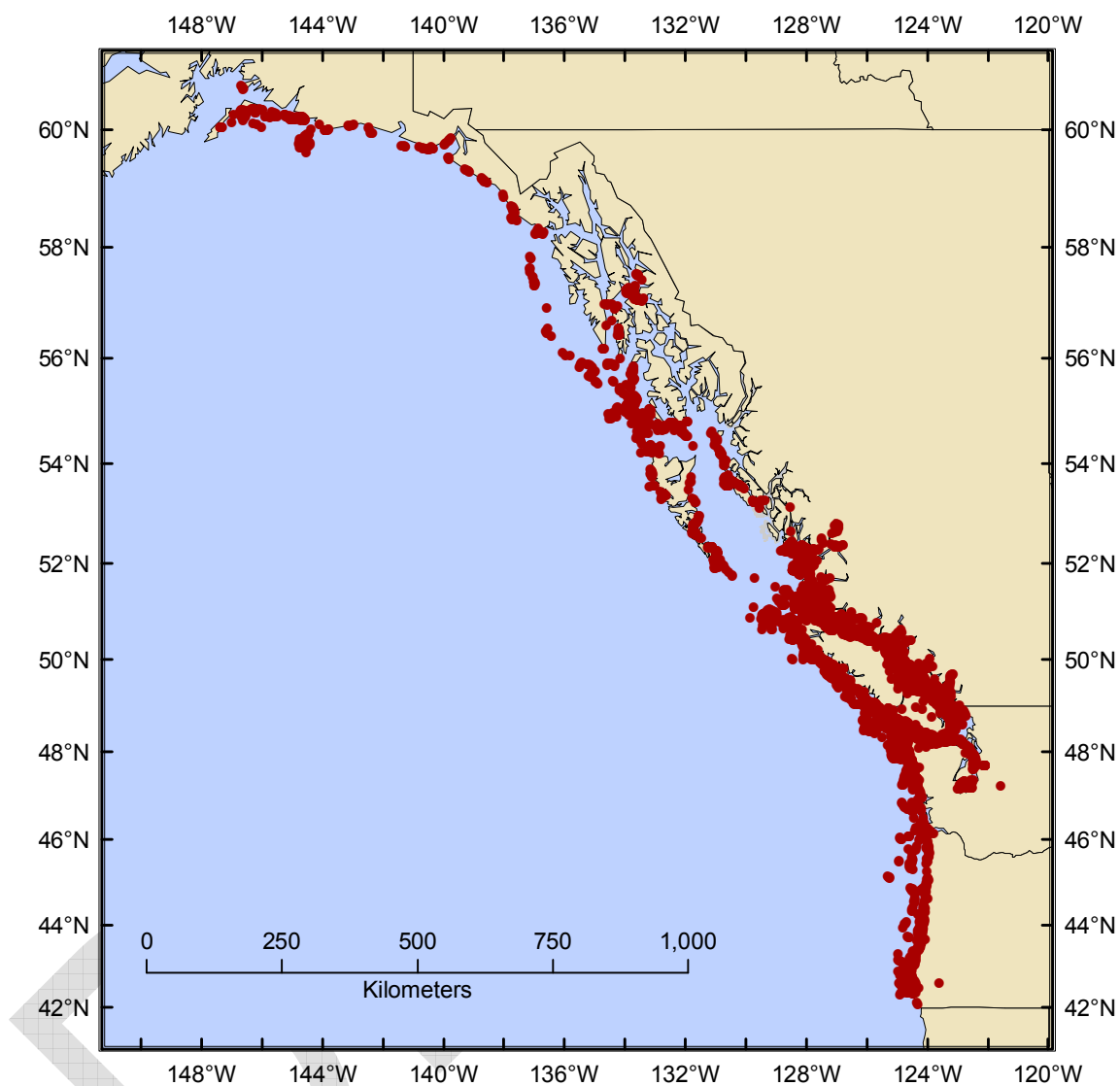


Figure 3. Overview map showing extent of movements of animals captured, satellite-tagged and released at Norris Rocks in the central Strait of Georgia. (Add symbol showing where Norris Rocks is located).

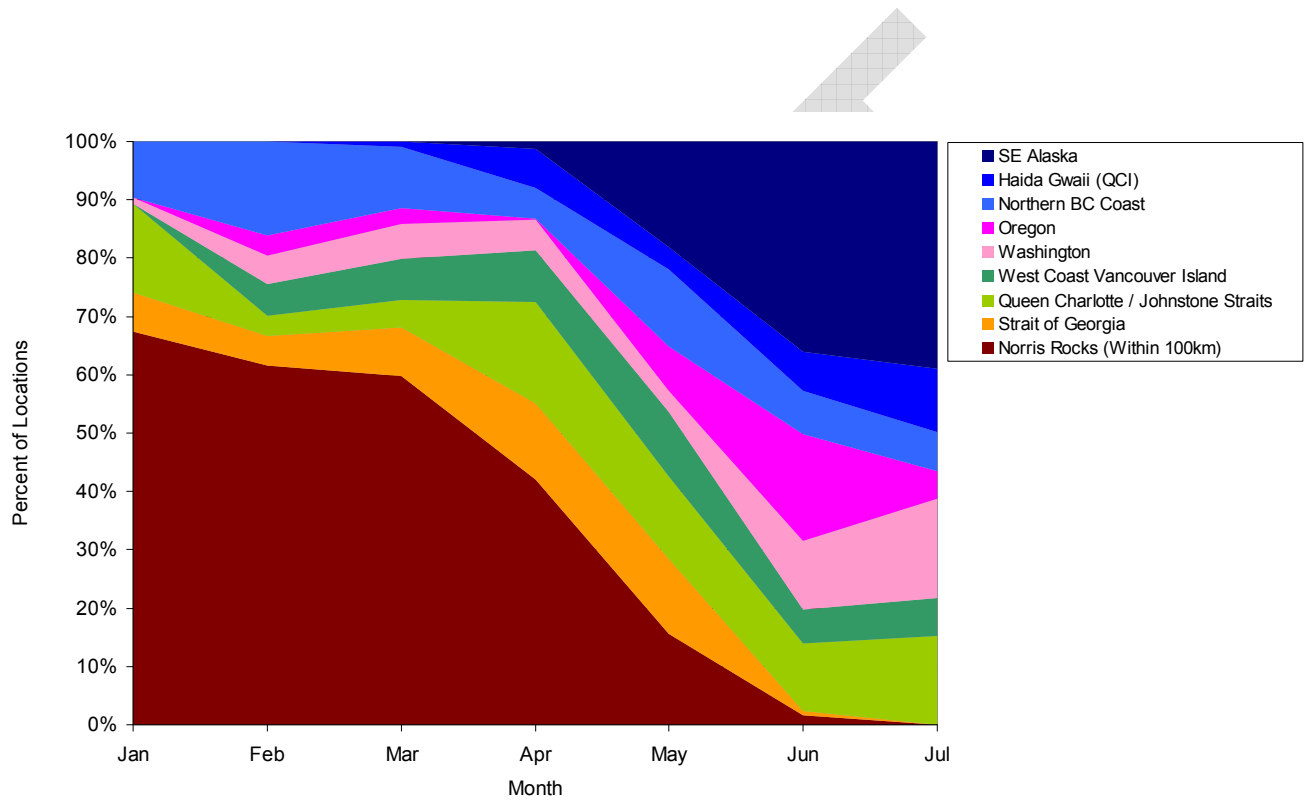


Figure 4. Geographic distribution of satellite locations over the study period.

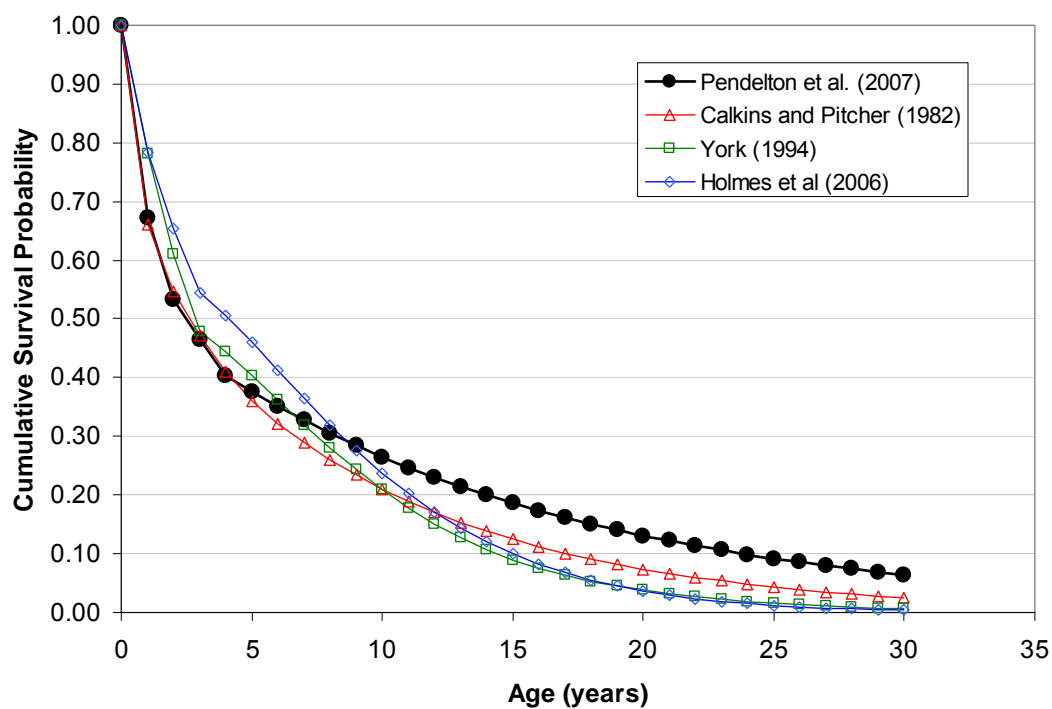


Figure 4b. Survival rates for the Eastern Steller Sea Lion Population based on resights during 1995-2003 of pups that had branded on Forrester Island during 1994-1995 (solid black line) (Pendleton et al. 2007) compared to survival rates for the Western Steller Sea Lion Population based on specimen collections made in the 1970s (thin coloured lines) (Calkins and Pitcher 1982; York 1994; Holmes et al. 2006).

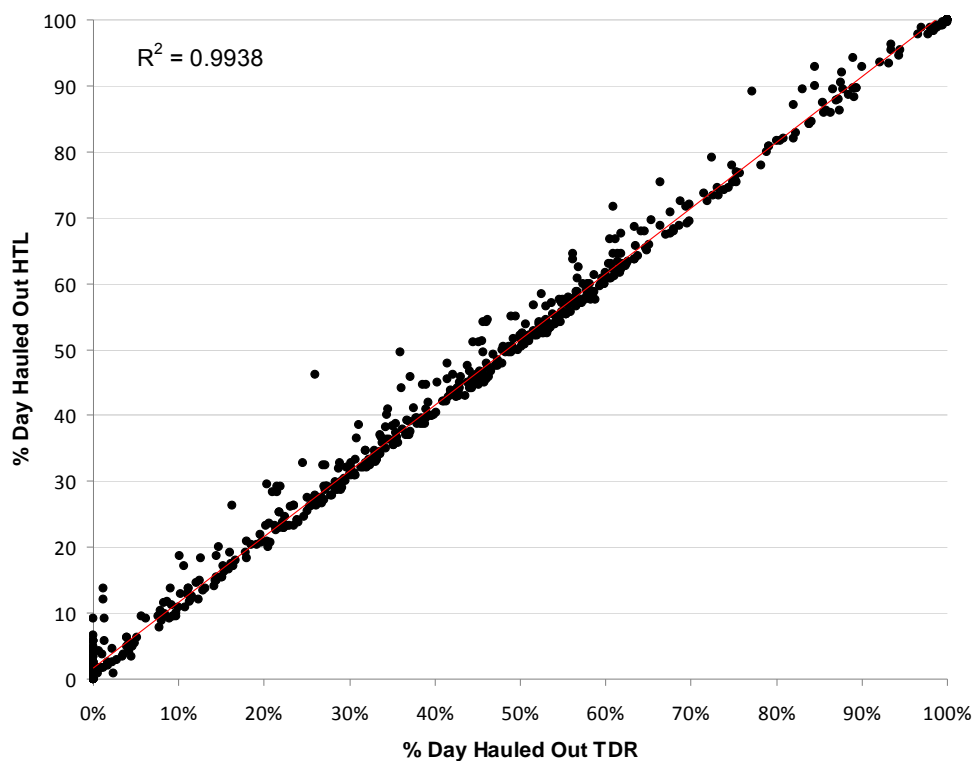


Figure 5. Comparison of the proportion of the day spent hauled out as indicated by the fine-scale time-depth recorder data (TDR) and the hourly timelines transmitted by satellite (HTL).

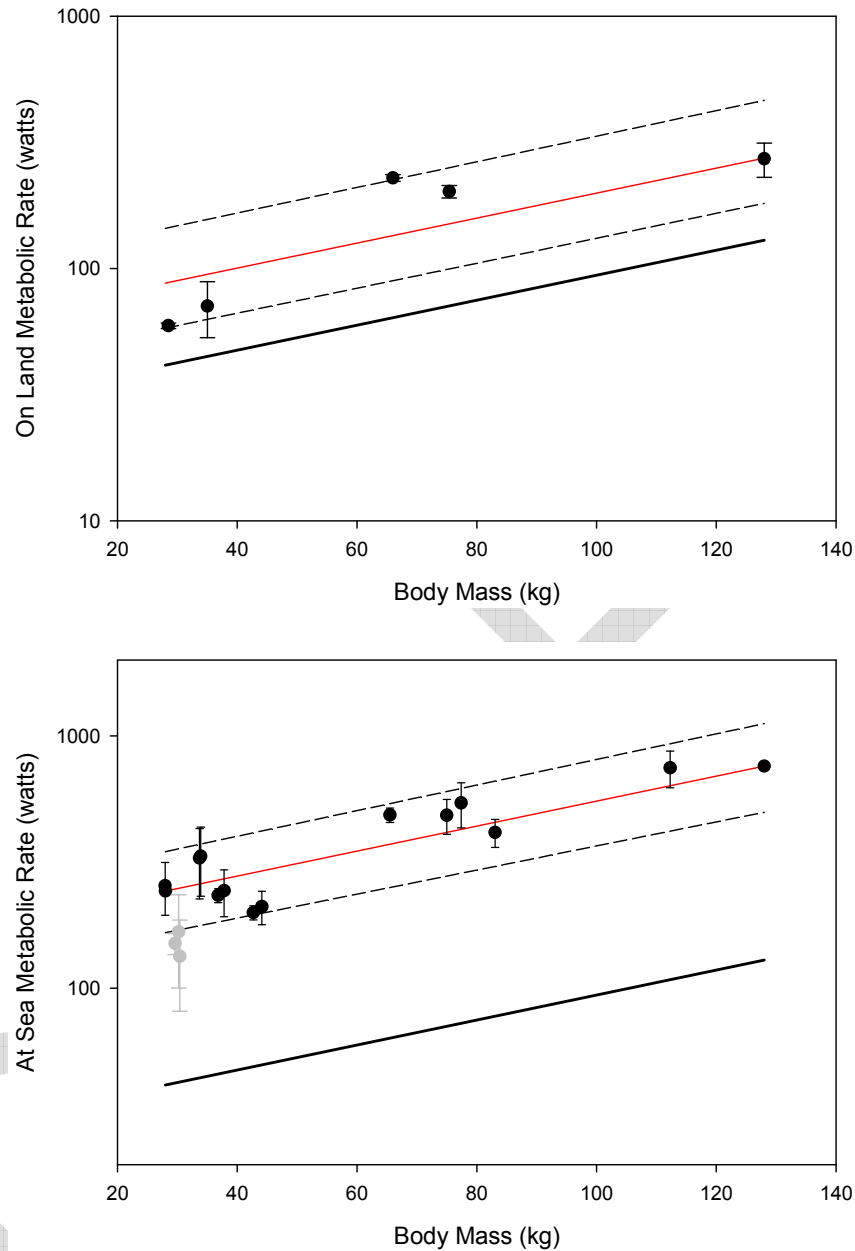


Figure 6. Field metabolic rates for otariids (fur seals and sea lions) measured for animals resting on land (top panel) and for animals on foraging trips at sea (bottom panel). The solid line represents Kleiber's (1975) BMR. Vertical bars represent standard errors where reported. The red lines show the mean and dashed lines denote the range of values. The mean was 2.0 with a range of 1.4 to 2.9 times BMR for RMR (top panel), and the mean was 5.1 with a range of 3.5 to 6.4 times BMR for FMR. Data are from Antarctic fur seals (Arnould et al. 1996; Costa et al. 1989a, 2000), Antarctic and Northern fur seals (Costa and Trillmich 1998), Australian sea lions (Costa et al. 1989b), California sea lions (Feldkamp 1987; Costa et al. 1990; Ponganis et al. 1991), New Zealand sea lions (Costa and Gales 2003).

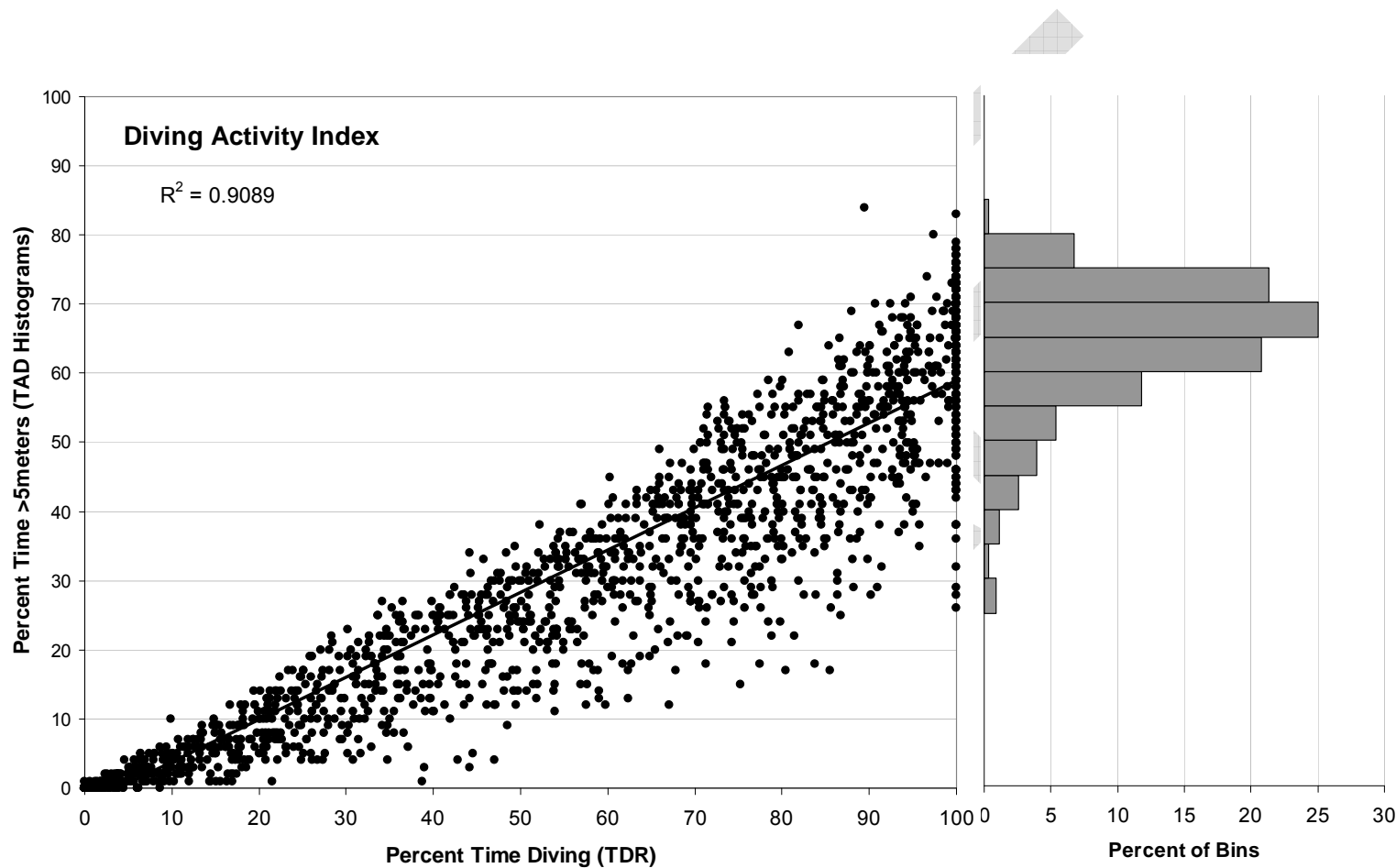


Figure 7. Relationship between the percent of time spent diving as indicated by fine scale (10 second interval) TDR records and the percent time at depths >5m as indicated by satellite the 6-hour time-at-depth bins. The linear trend on the left panel represents the regression line. The histogram on the right shows the frequency distribution of 6-hour bins in which TDRs indicated the animal was diving for the entire period (i.e. the same data at the 100% level of the plot).

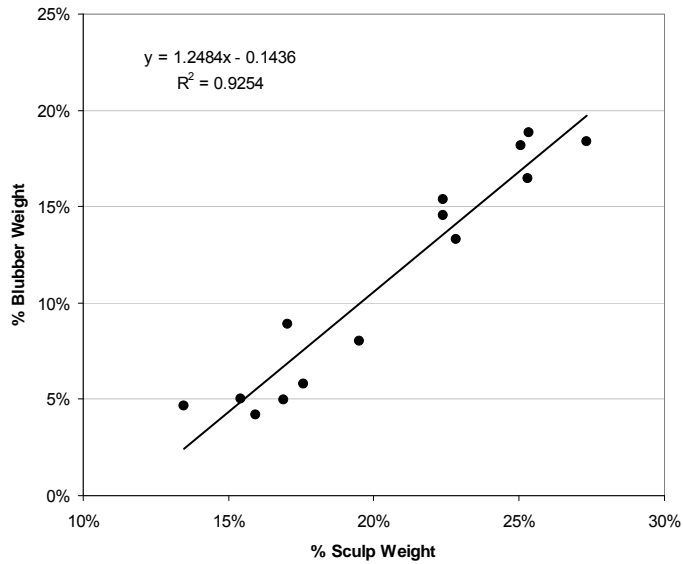


Figure 8. Relationship between sculp (blubber with skin attached) weight and blubber weight in subadult and adult male Steller sea lions collected in B.C. (from Olesiuk and Bigg 1987).

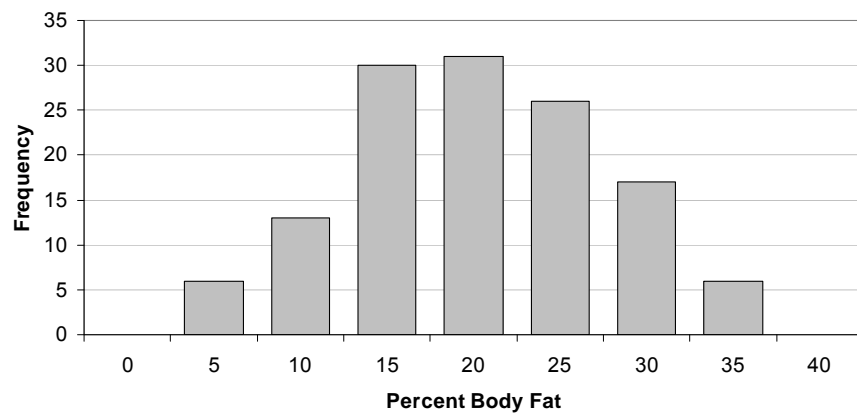


Figure 10. Percent body fat of juvenile Steller sea lions aged 5-29 months as determined by labeled water (from Rea et al. 2000).

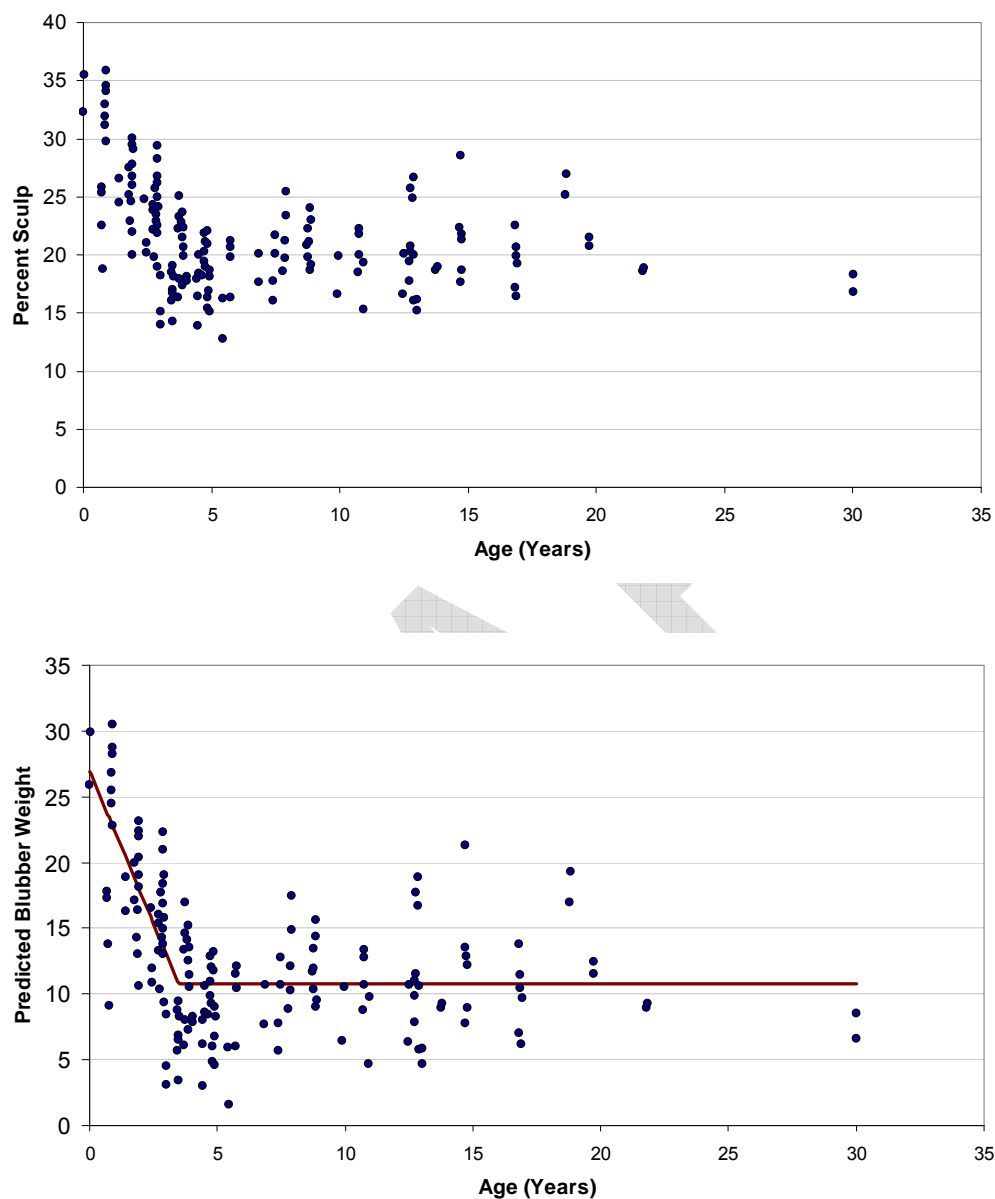


Figure 9. Relationship between scalp weight and age (top panel) and blubber mass (bottom panel) for Steller sea lions collected in the Western Steller Population. Data from Pitcher et al. (2000), and blubber mass was predicted from scalp mass based on the relationship in Figure 9.

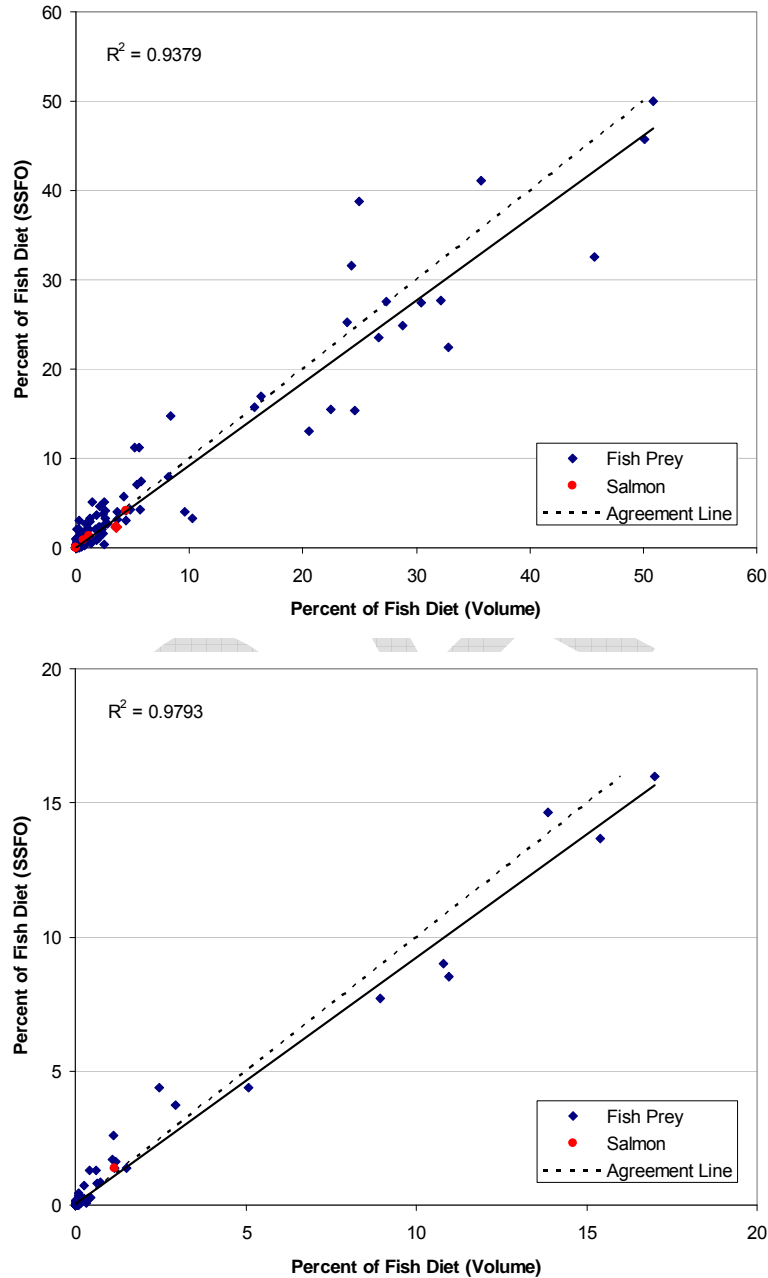


Figure 11. Comparison of the importance of fish prey in the diet of northern fur seals using volumetric analysis and split-sample frequency of occurrence. Top panel shows results by NPFSC region, and bottom panel shows results for the entire NE Pacific Ocean. Dashed lines denote the 1:1 agreement and solid lines denote linear regression lines. The importance of salmon is highlighted in red.

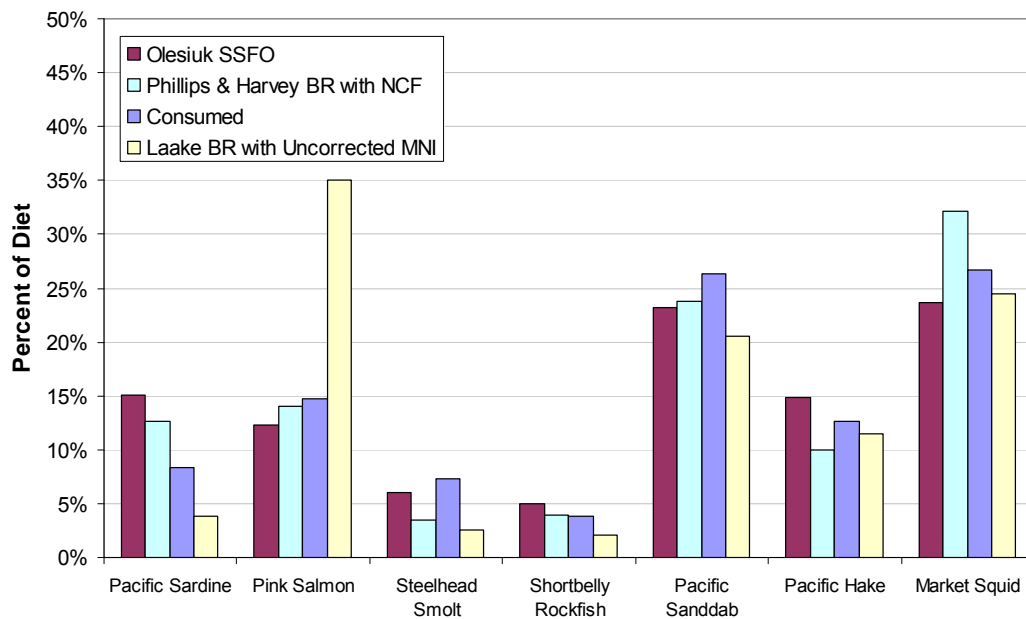


Figure 12. Comparison of accuracy of split-sample frequency of occurrence (SSFO) and biomass reconstruction with numeric correction factor (BR with NCI) at estimating biomass of various prey fed to captive harbour seals (from Phillips and Harvey 2009 with corrections based on Olesiuk et al. 1993). For comparison, the yellow bars indicate the results for biomass reconstruction using the minimum number of individual prey items (MNI) consumed (after Laake et al. 2002).

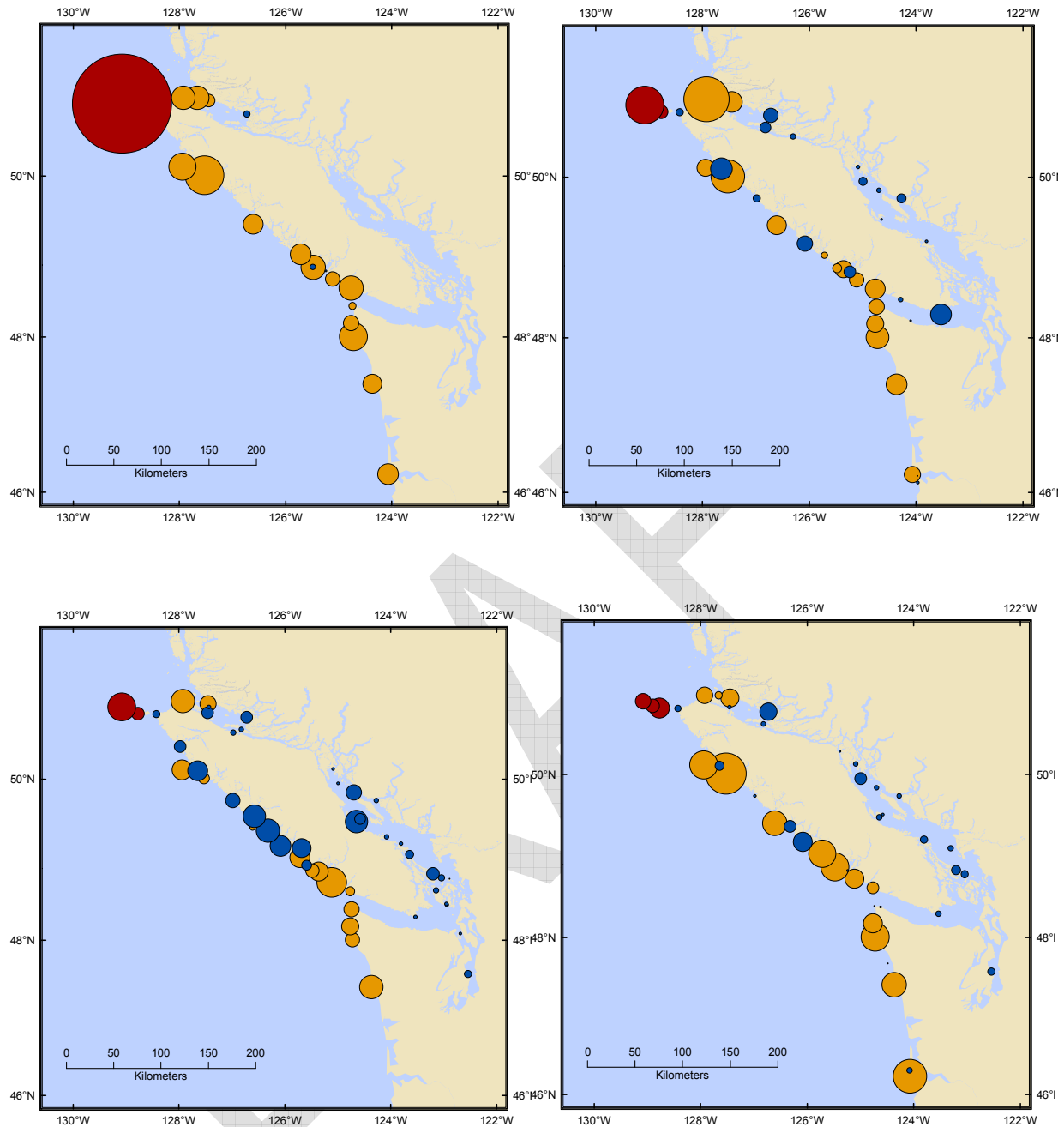


Figure 13. Maps showing seasonal changes in distribution of Steller sea lions counted during the summer (top left), fall (top right), winter (bottom left) and spring (bottom right) surveys. Symbol sizes are drawn proportional to the average site counts. Red symbols denote rookeries, orange symbols year-round haulout sites, and blue symbols winter haulout sites and swimming animals.

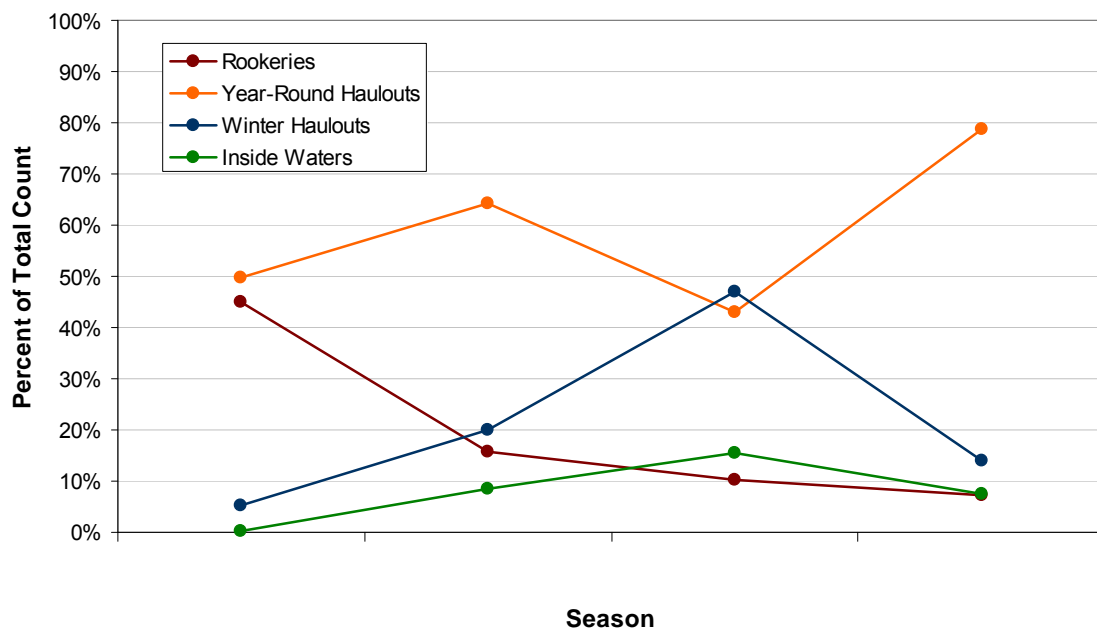


Figure 14. Seasonal shift in the proportion of animals counted on rookeries, year-round haulout sites, and winter haulout sites during summer, fall, winter and spring surveys.

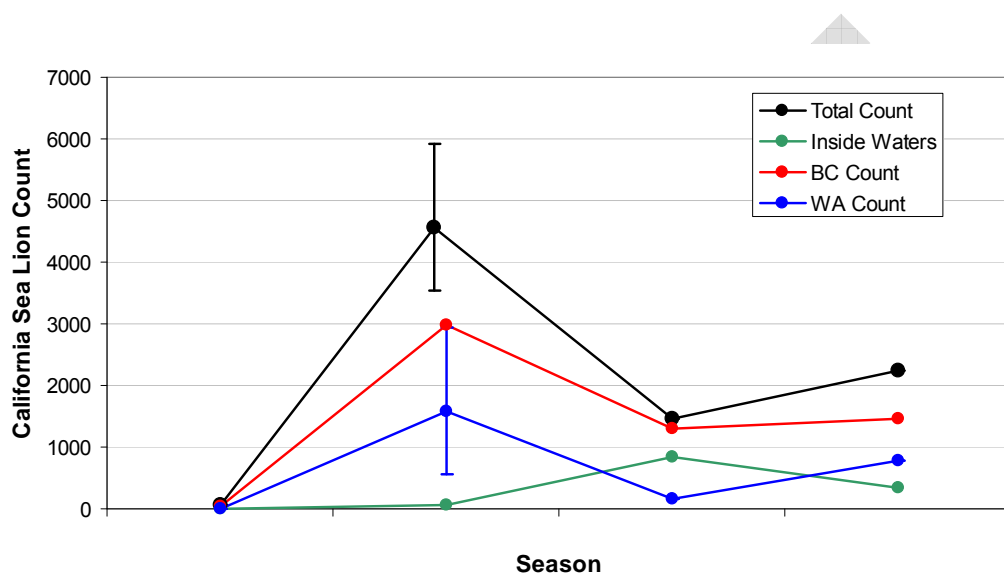


Figure 15. Seasonal trends in California sea lion counts in the study area (black line), B.C. (red line), and Washington (blue line). The vertical bars for the fall count show the range based on replicate counts made in Washington while numbers were building. The green line shows the proportion of California sea lions occupying sites in inland waters.

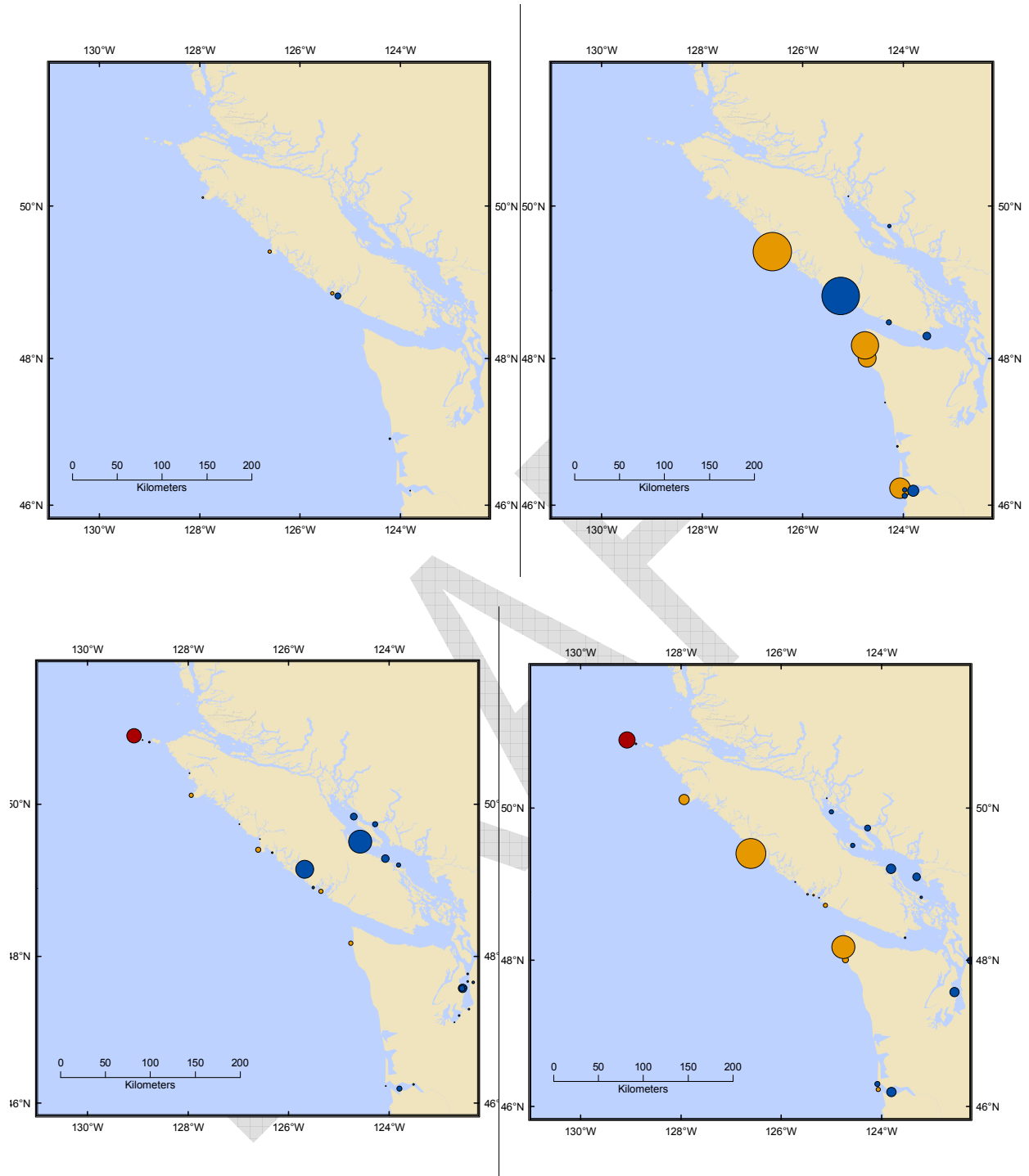


Figure 16. Maps showing seasonal changes in distribution of California sea lions counted during the summer (top left), fall (top right), winter (bottom left) and spring (bottom right) surveys. Symbol sizes are drawn proportional to the average site counts. Red symbols denote rookeries, orange symbols year-round haulout sites, and blue symbols winter haulout sites and swimming animals.

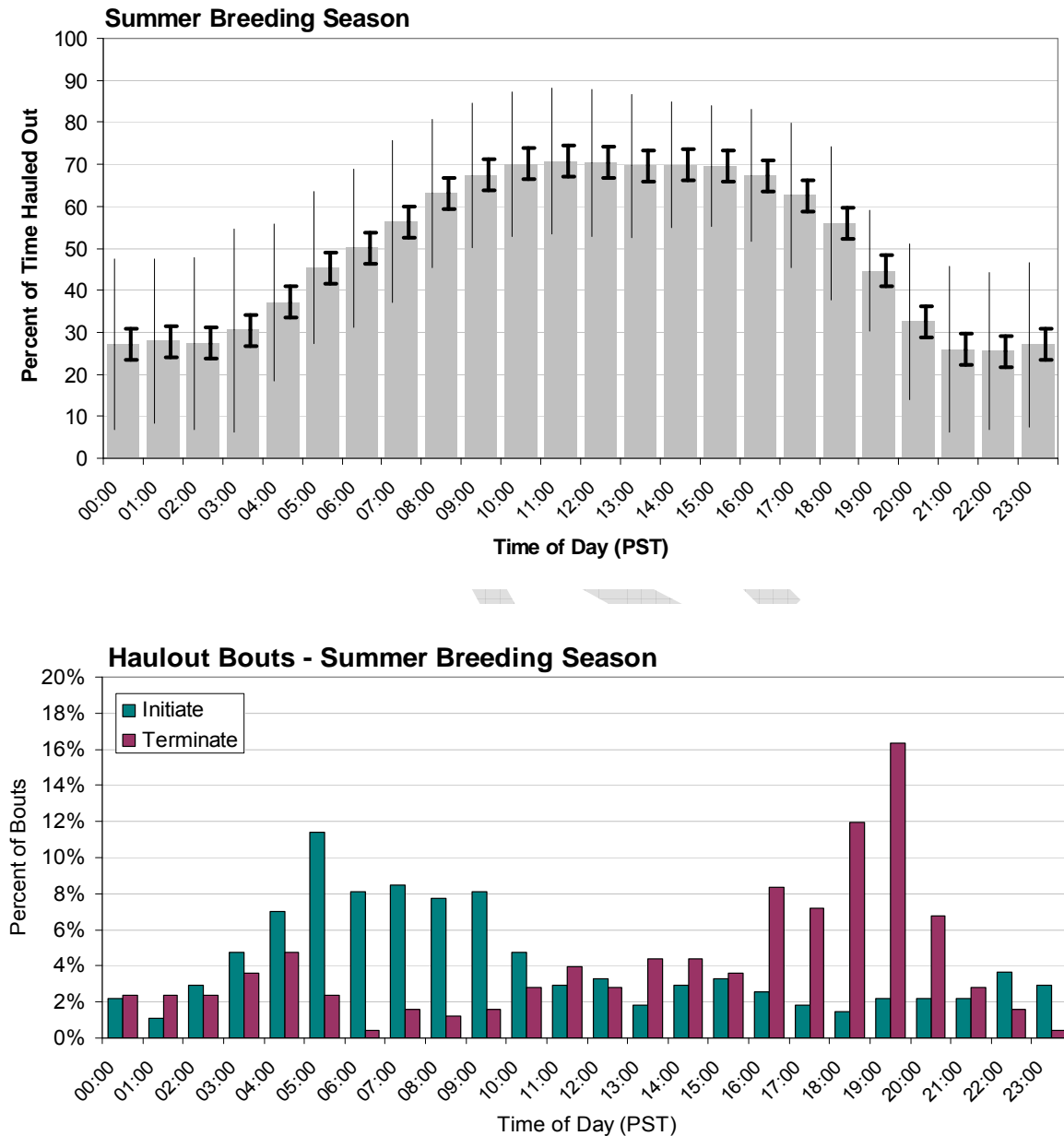


Figure 17a. Diurnal haulout patterns of Steller sea lions during the summer breeding season as indicated by the hourly haulout timelines transmitted by satellite (yearlings excluded). The top panel shows the proportion of animals hauled out by hour. Thin vertical lines are standard deviations showing variability among individual animals, and bold capped lines denote the standard errors for the population mean. The bottom panel shows the distribution of times at which animals initiated and terminated haulout bouts.

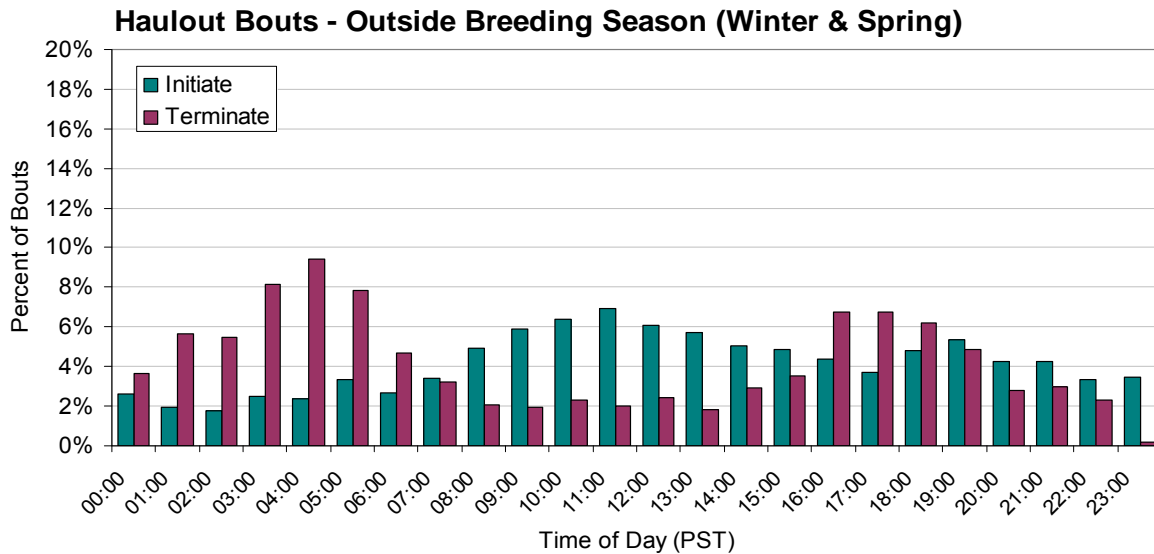
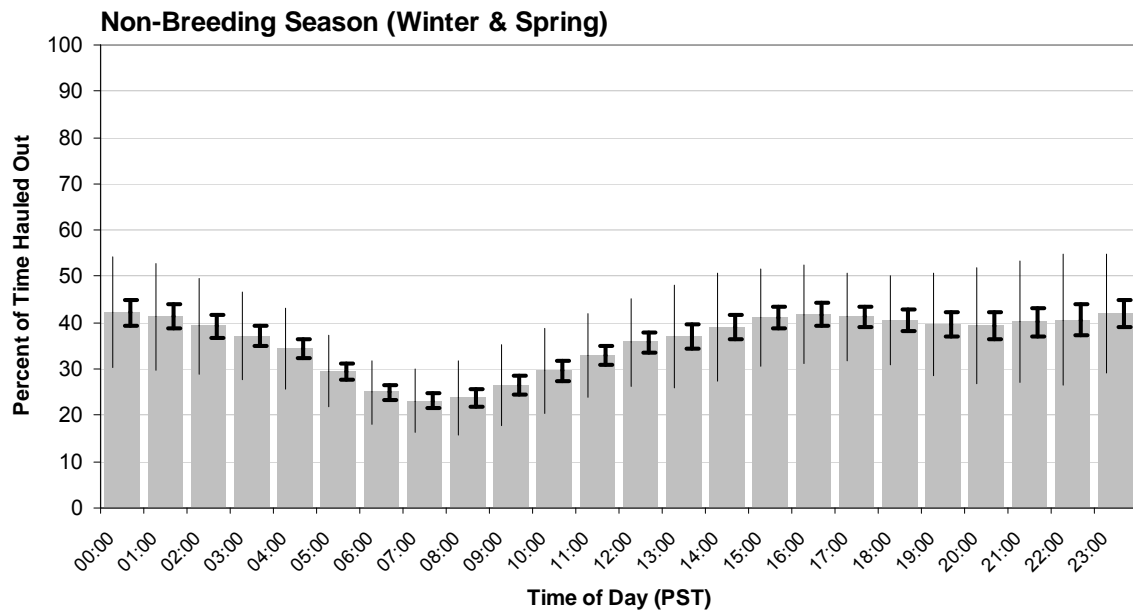


Figure 17b. Diurnal haulout patterns of Steller sea lions outside the summer breeding season (winter and spring) as indicated by the hourly haulout timelines transmitted by satellite (yearlings excluded). The top panel shows the proportion of animals hauled out by hour. Thin vertical lines are standard deviations showing variability among individual animals, and bold capped lines denote the standard errors for the population mean. The bottom panel shows the distribution of times at which animals initiated and terminated haulout bouts.

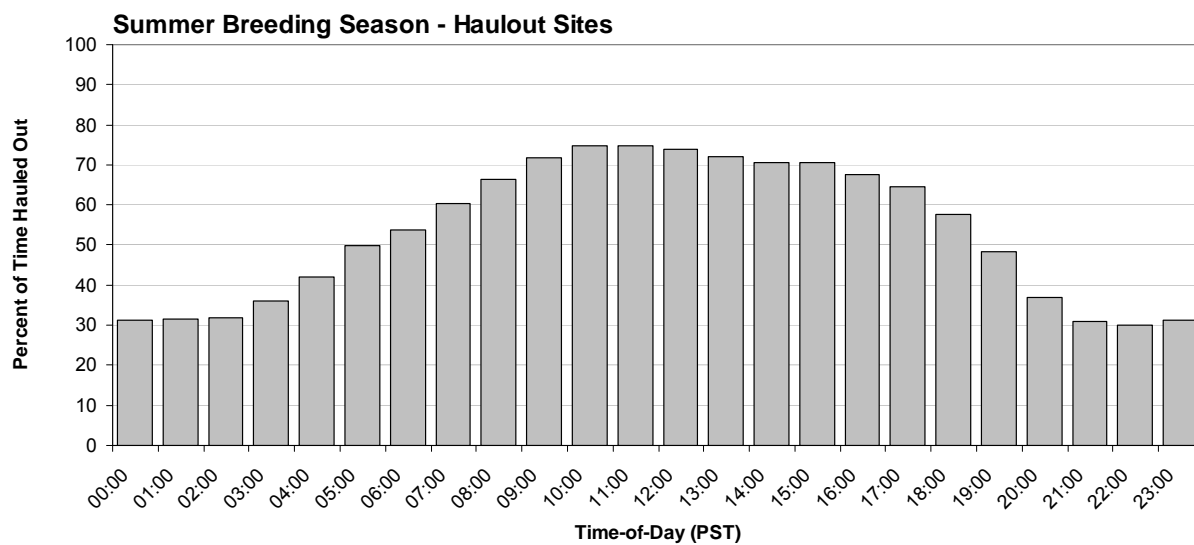


Figure 18. Diurnal haulout patterns of Steller sea lions during the summer breeding season that were spending the majority of time on breeding rookeries (top) and year-round haulout sites (bottom).

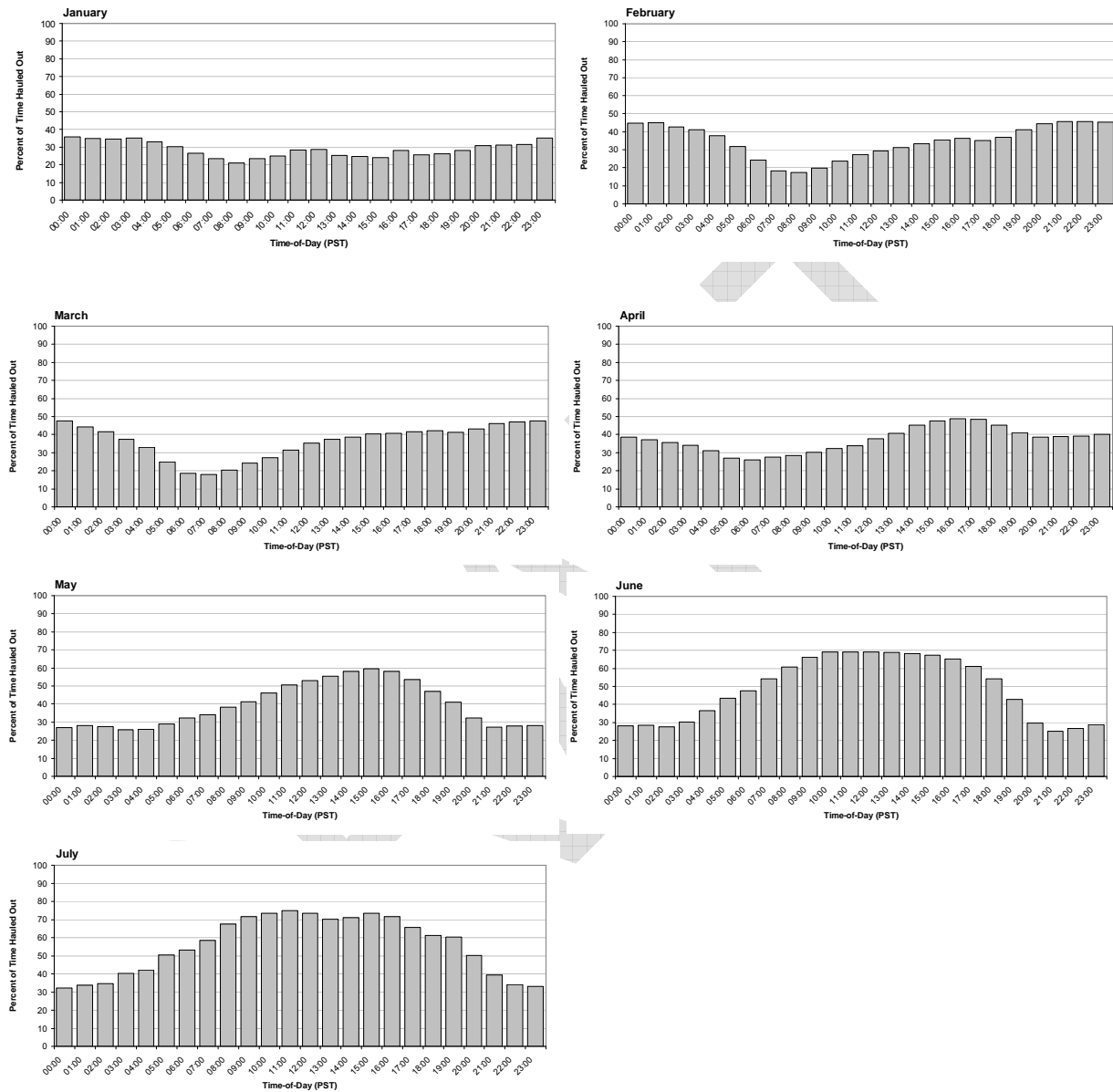


Figure 19a. Diurnal haulout patterns of Steller sea lions by month showing the seasonal change in timing of haulout patterns.

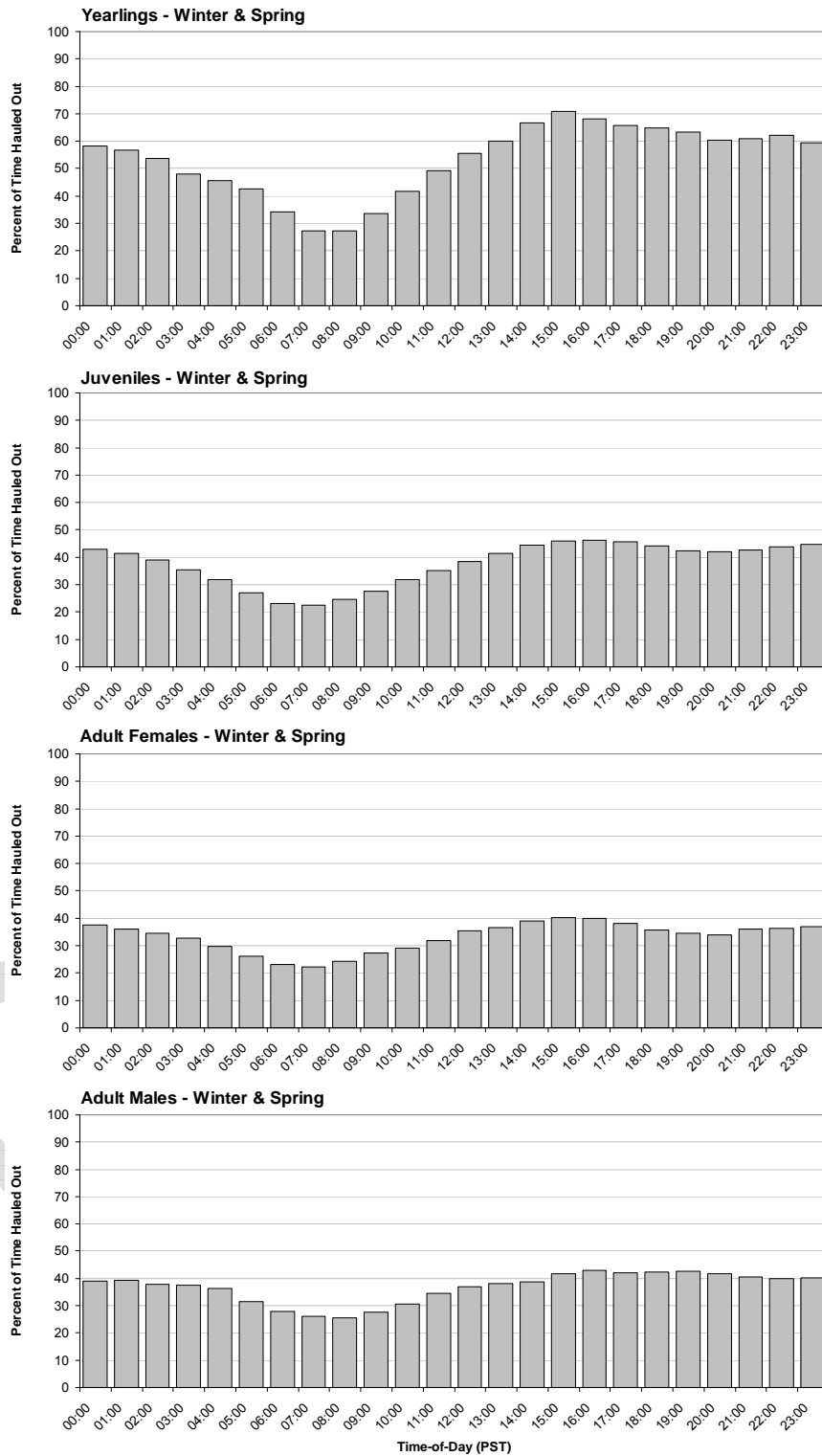


Figure 20a. Diurnal haulout patterns of Steller sea lions outside the breeding season (winter and spring) by sex- and age-group: yearlings (top), juveniles (second from top), adult females (second from bottom), and adult males (bottom).

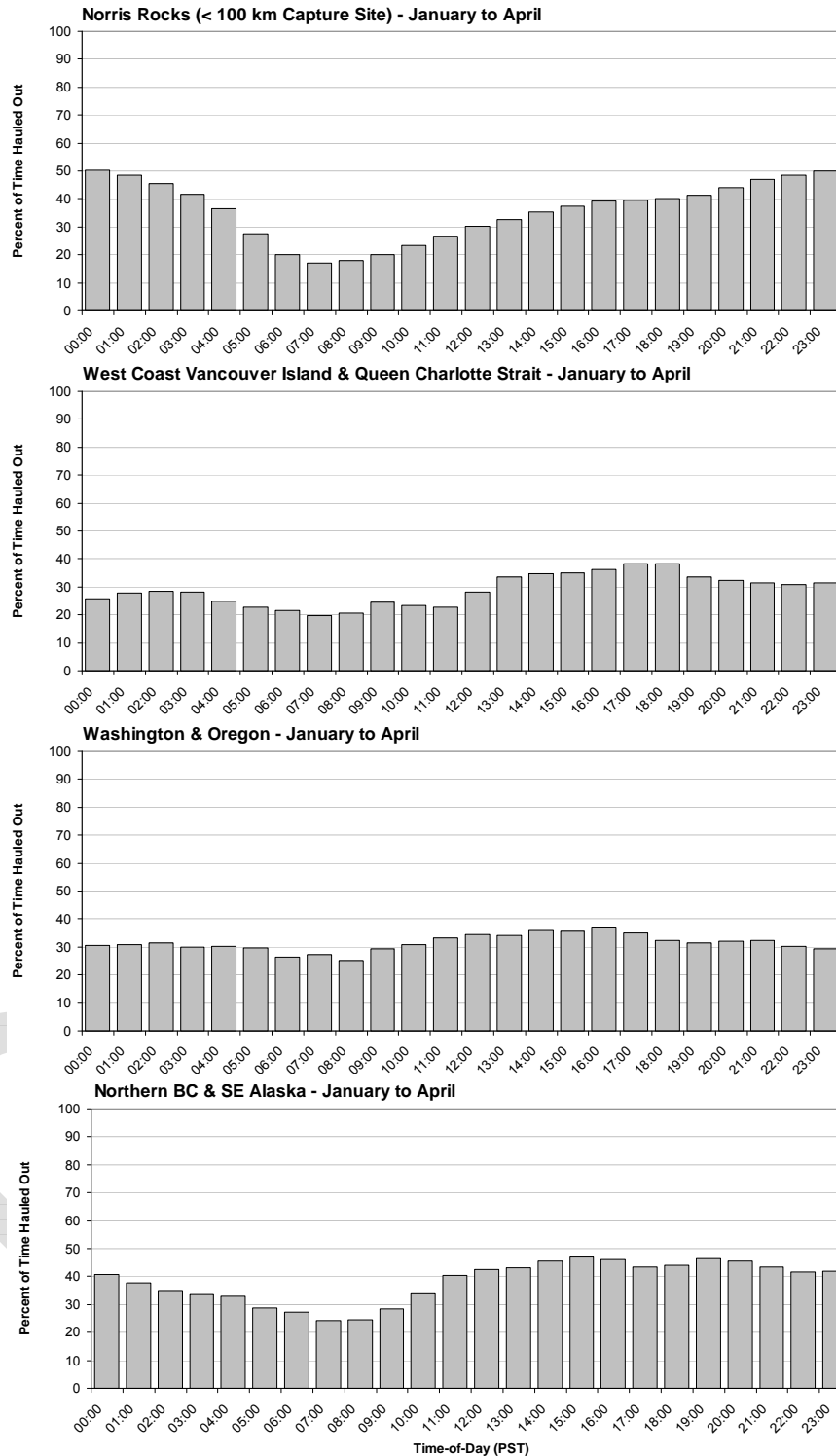


Figure 20b. Diurnal haulout patterns for Steller sea lions outside the breeding season (winter and spring) by geographic area: Norris Rocks (within 100 km of the capture site) (top); west coast of Vancouver Island and Queen Charlotte Strait (second from top) yearlings (top), Oregon and Washington (second from bottom) and northern B.C. and SE Alaska (bottom).

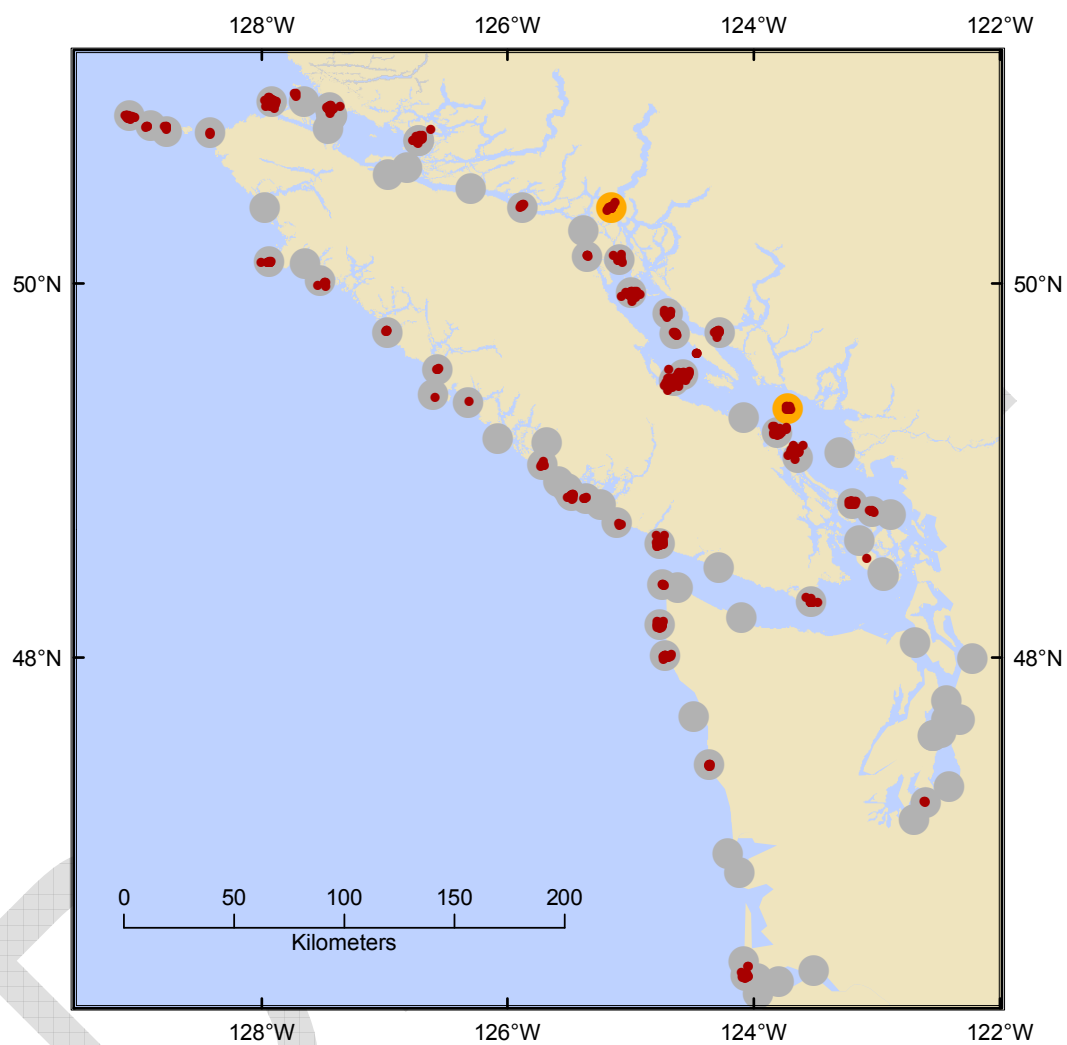


Figure 21. Map showing utilization of haulout sites in the study area by satellite-tagged Steller sea lions based on high-quality (LQ=1, 2, or 3) locations received during haulout bouts (small red circles). The large grey circles show the location of known sea lion haulout sites, and the large orange circles show locations of two new haulout sites not known to exist prior to the tagging study.

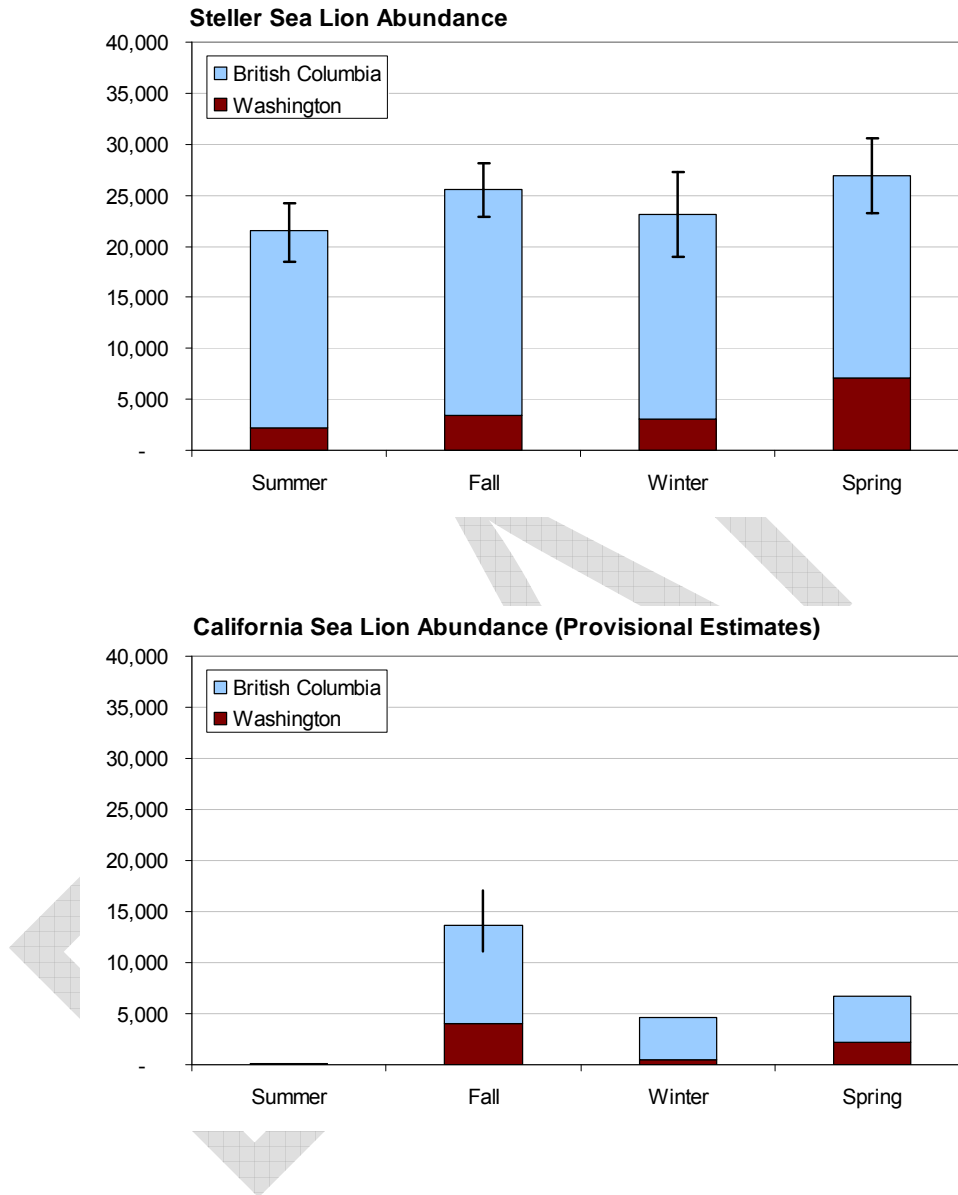


Figure 22. Estimated abundance of Steller sea lions (top panel) in the study area by season. Capped vertical bars represent calculated CVs (see text). The bottom panel shows provisional abundance estimates for California sea lions assuming they follow the same haulout patterns. The vertical line for the fall estimate represents the range based on 3 replicate counts on the Washington coast in October.

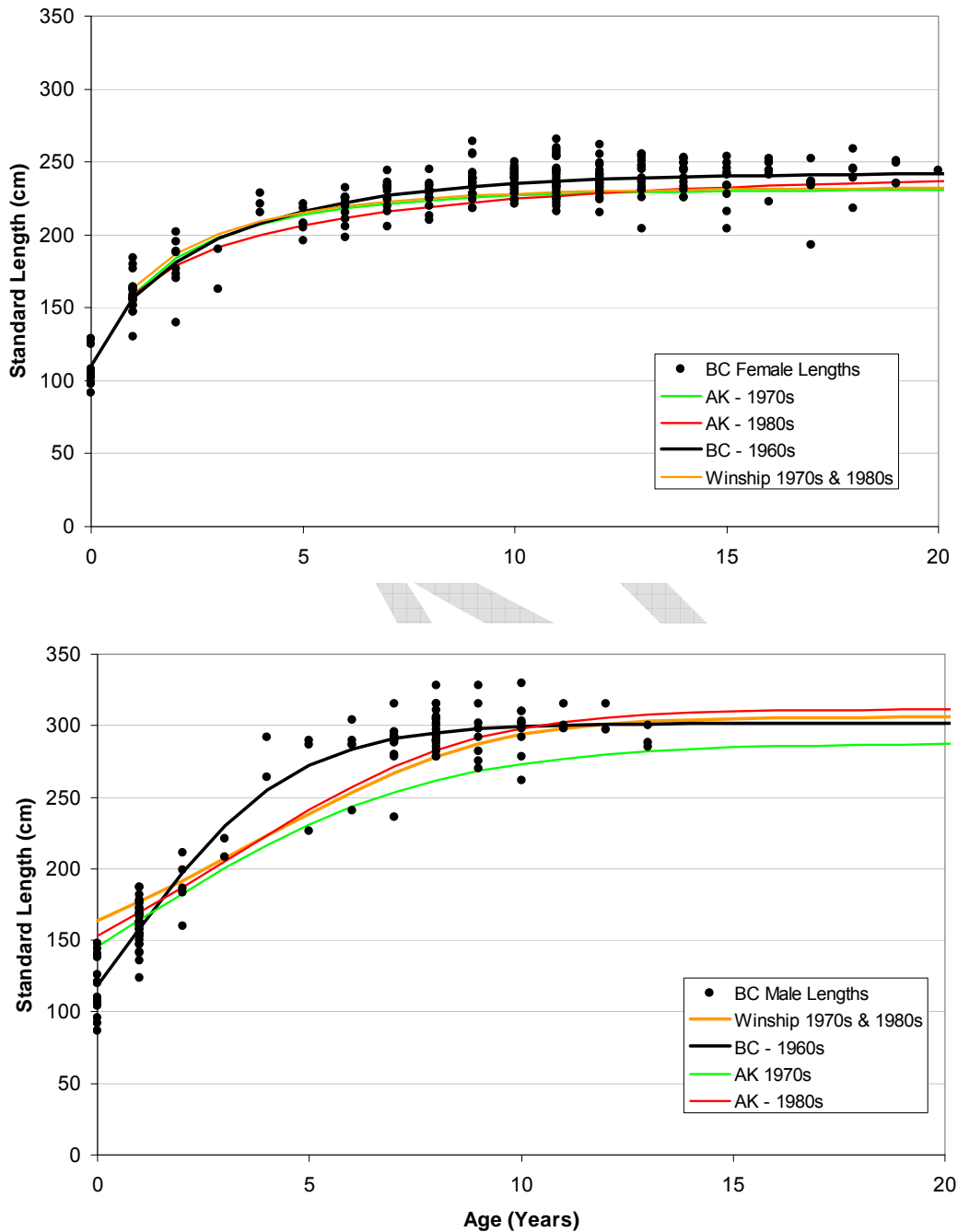


Figure 23. Growth curves for Steller sea lion females (top panel) and males (bottom panel) based on specimens collected in B.C. during 1959-1968. Comparison with growth curves for Alaska (coloured lines), the B.C. females appear to attain larger size, and the B.C. males appear to attain size more rapidly than in Alaska, so growth curves were fit to the B.C. data to estimate length at age for animals in the study area (solid black lines).

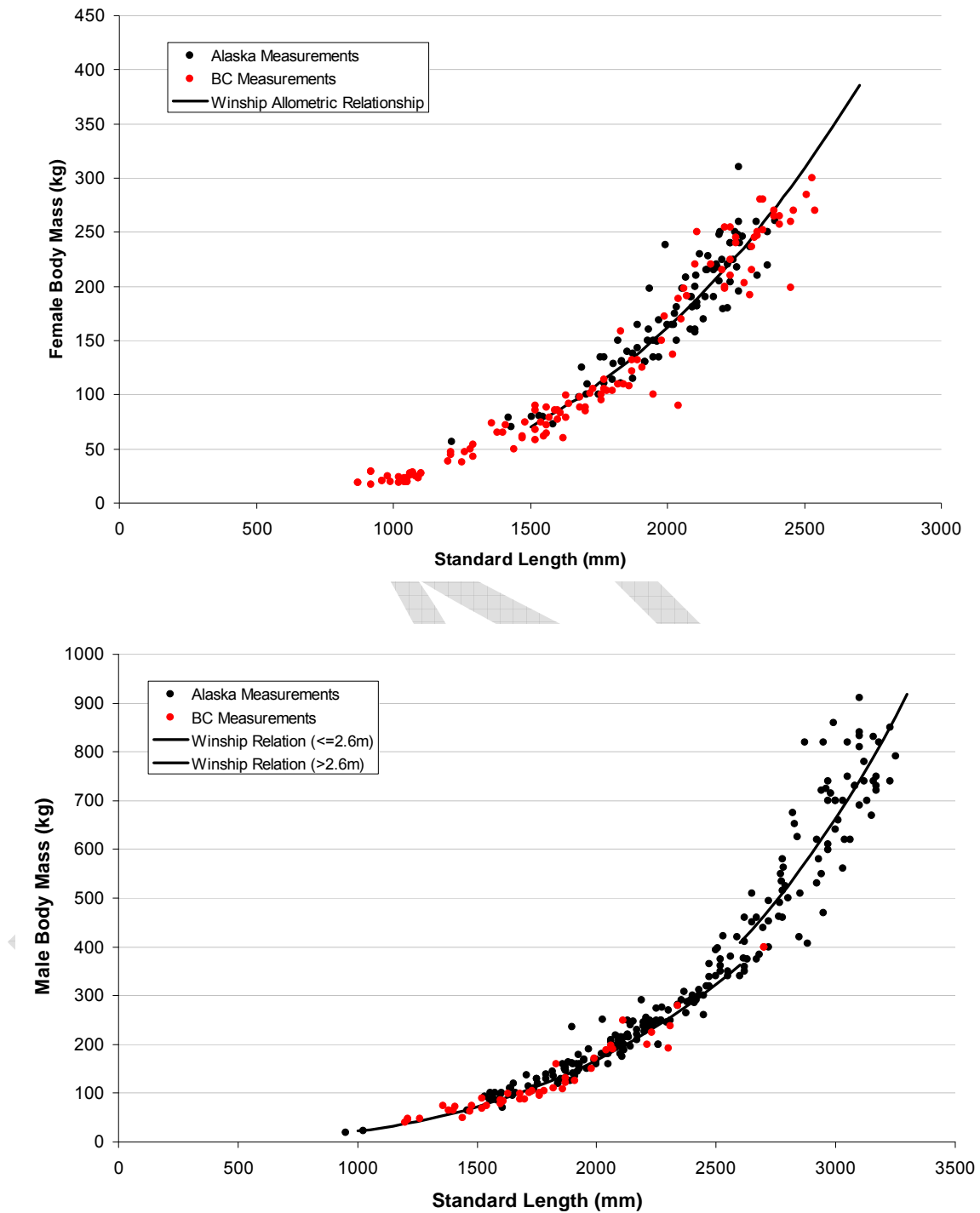


Figure 24. Allometric relationships between body mass and length for Steller sea lion females (top panel) and males (bottom pane) fit to Alaska specimens (Winship 2000). The black symbols show the Alaskan data used to fit the relationships, and the red symbols show measurements for animals collected in B.C. during 1959-1968 showing they are the same shape as Alaskan sea lions.

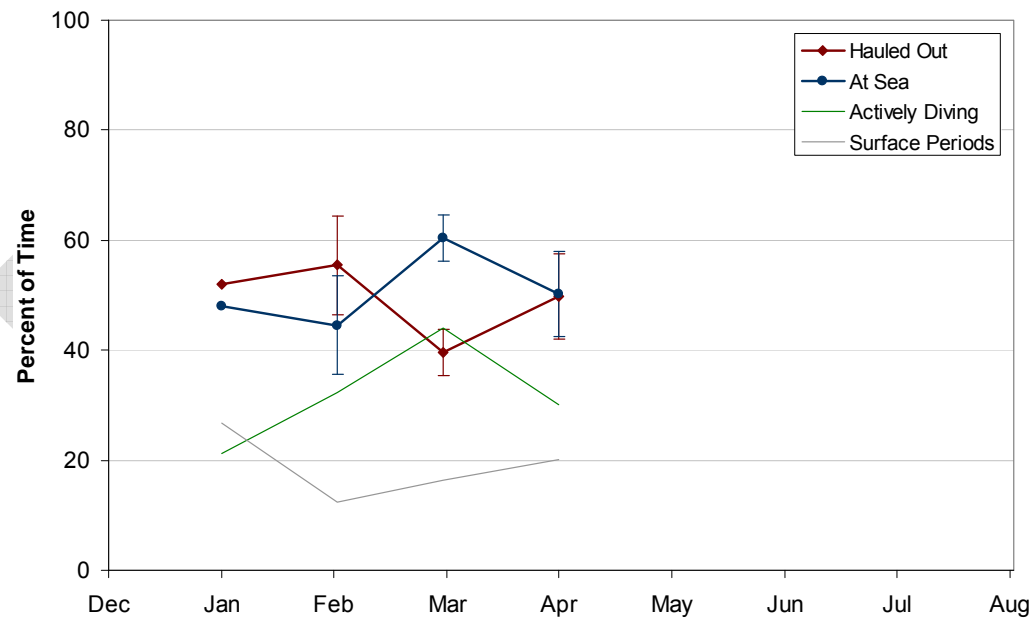
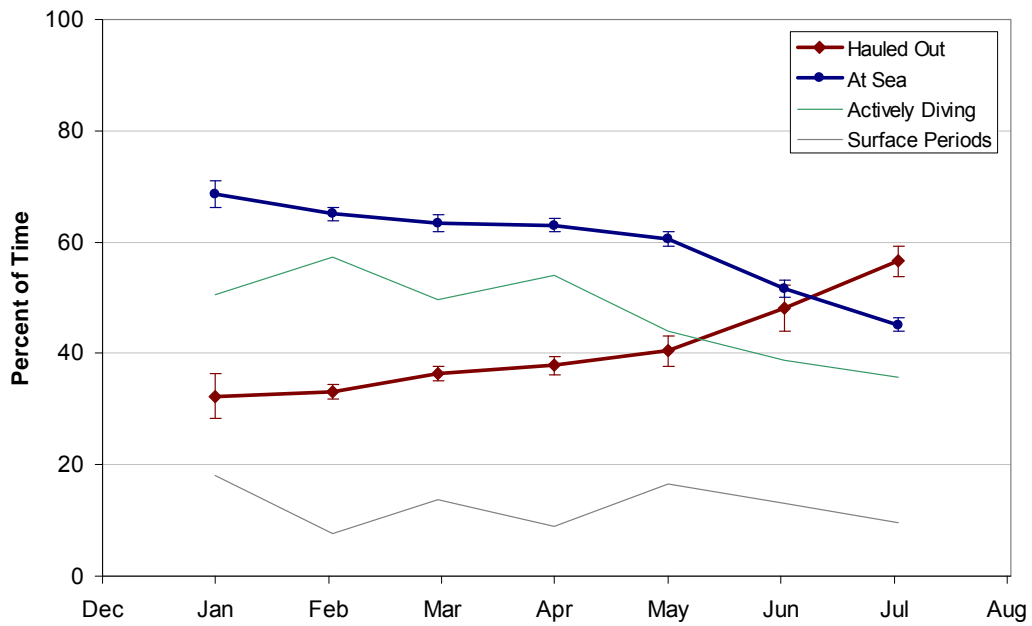


Figure 25. Monthly activity budgets for Steller sea lions showing the proportion of time spent hauled out (bold red) and at-sea (bold red). The thin green line shows the proportion of time at-sea spent actively diving, and the thin grey line the proportion of time spent for extended periods (>15minutes) at the surface.

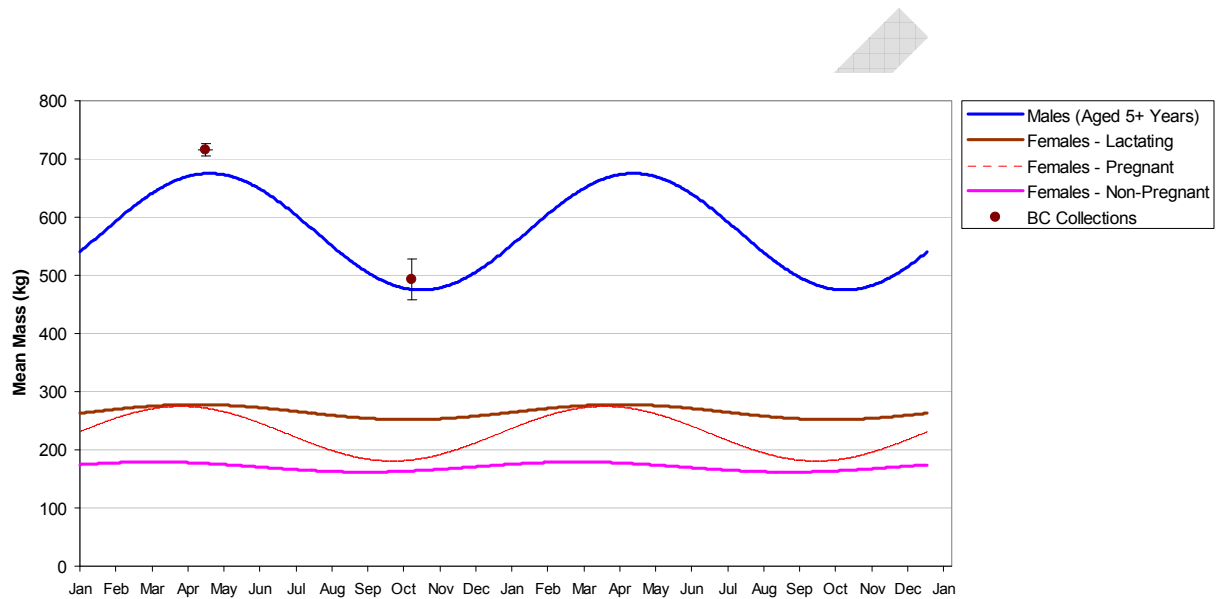


Figure 26. Seasonal weight fluctuations in captive Steller sea lion males (blue), lactating females (brown), and non-pregnant females (pink). The dashed red line shows the fitted season fluctuations for pregnant females, but these are driven by the sudden weight loss at parturition. Trends were fitted using sine functions (see Allen 2009 for details). The red symbols denote the timing and mean weight (\pm SE) of adult male specimens collected in B.C. to assess seasonal changes in condition (see Olesiuk and Bigg 1987 for details).

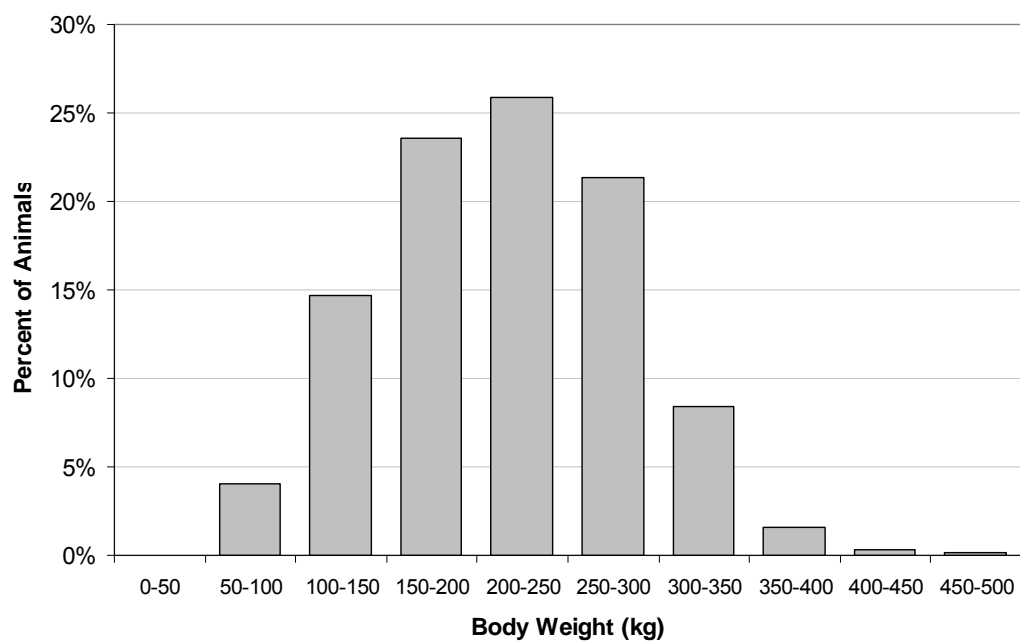


Figure 27. Frequency distribution of the weight of 572 California sea lions live-captured and weighed at a trap in Puget Sound at Shilshole Bay near Seattle Washington (Gearin, unpublished data).

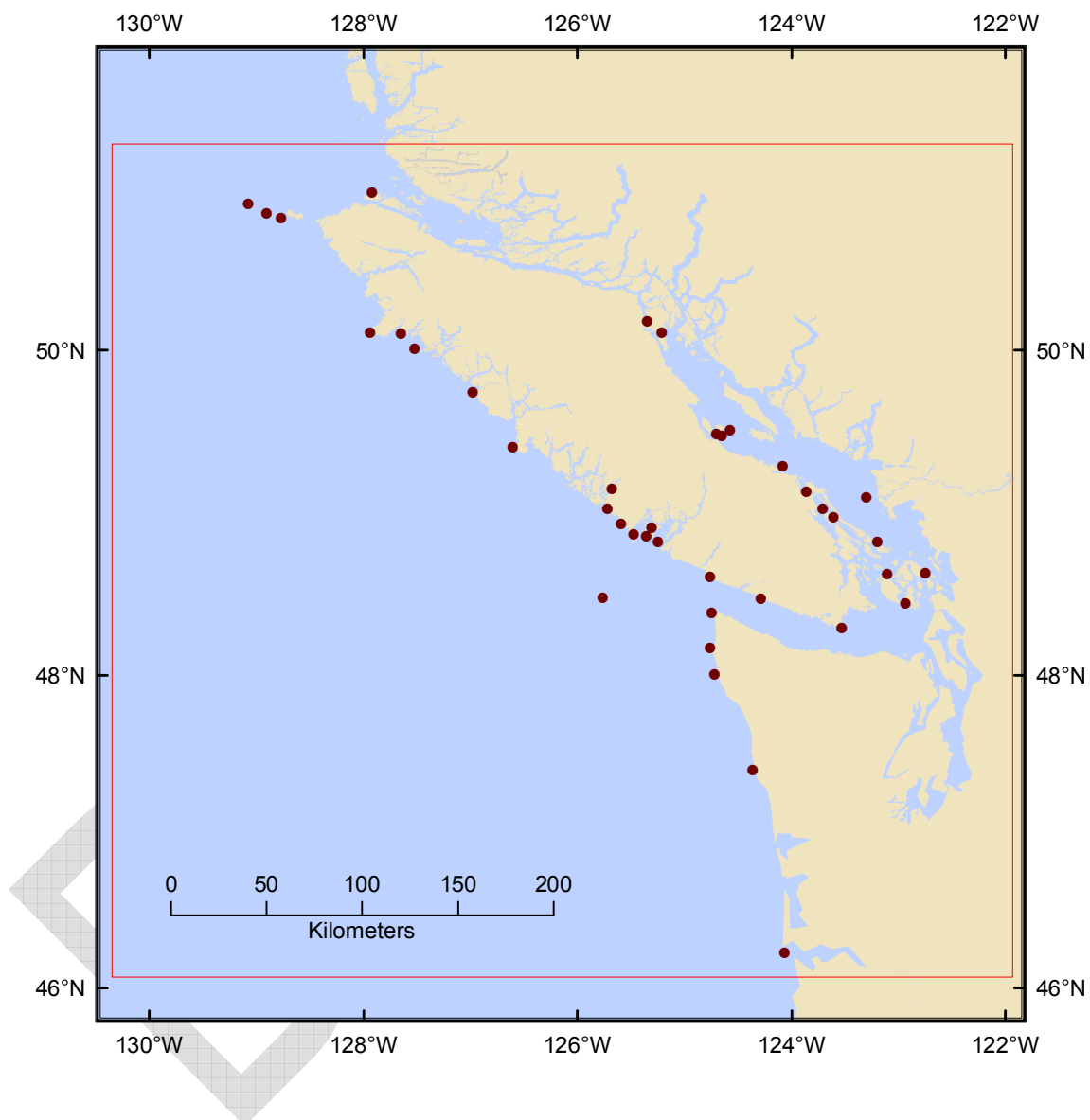


Figure 28. Map showing the study area (red box) and sites where sea lion scats have been collected (red dots). [Note: need to fix one of the San Juan sites – lon is off by 2 degrees so it shows as out in the ocean].

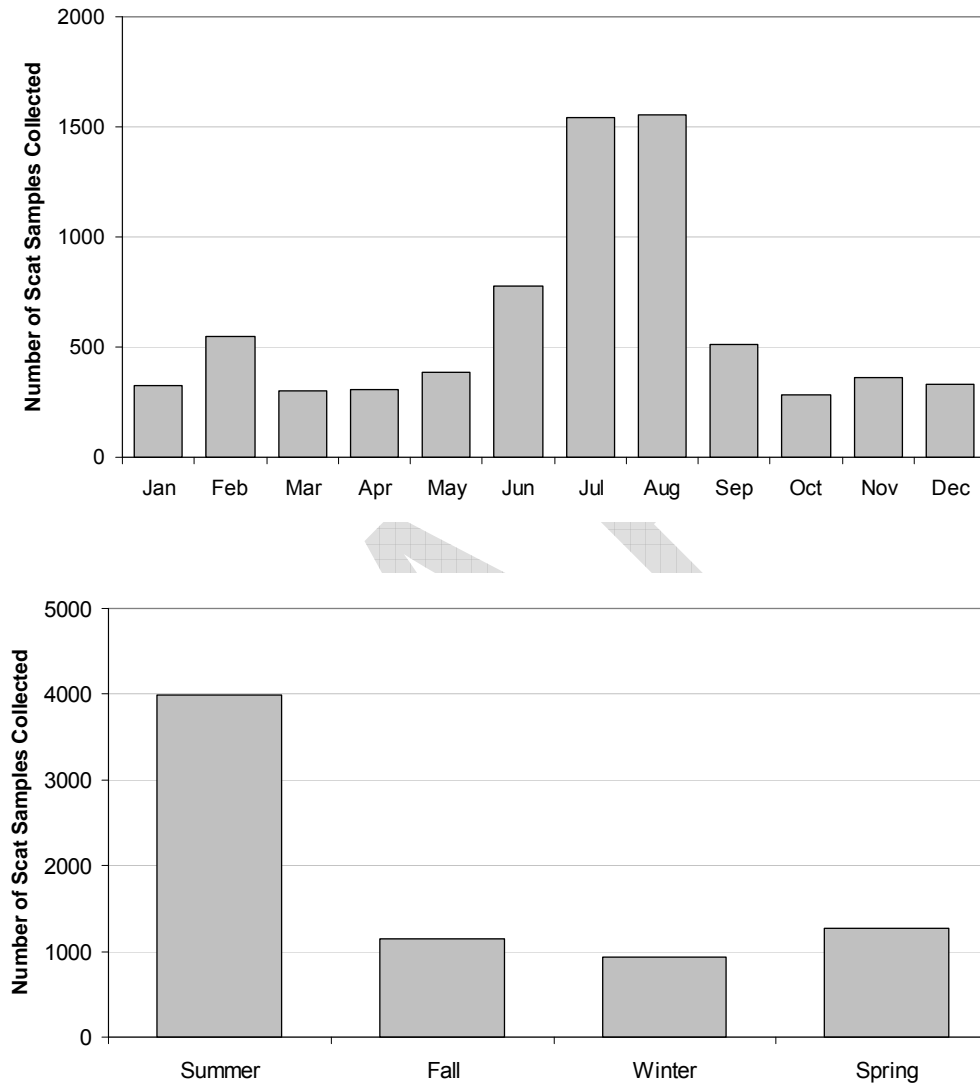


Figure 29. Histograms showing the number of Steller sea lion scat samples collected in the study area by month (top) and by season (bottom).

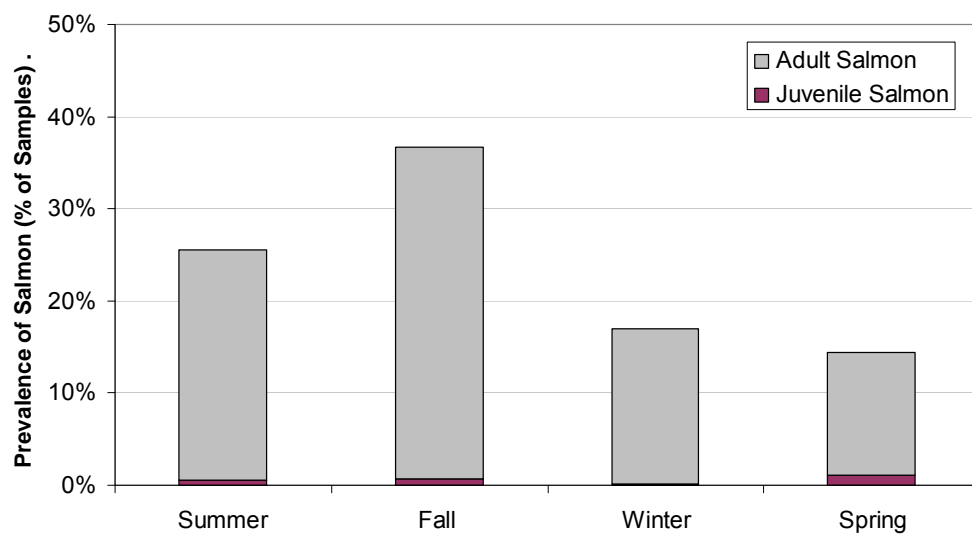


Figure 30. Prevalence of salmon in Steller sea lion scat samples by month. Adult-size salmon are shown in grey, and juvenile-size salmon in red.

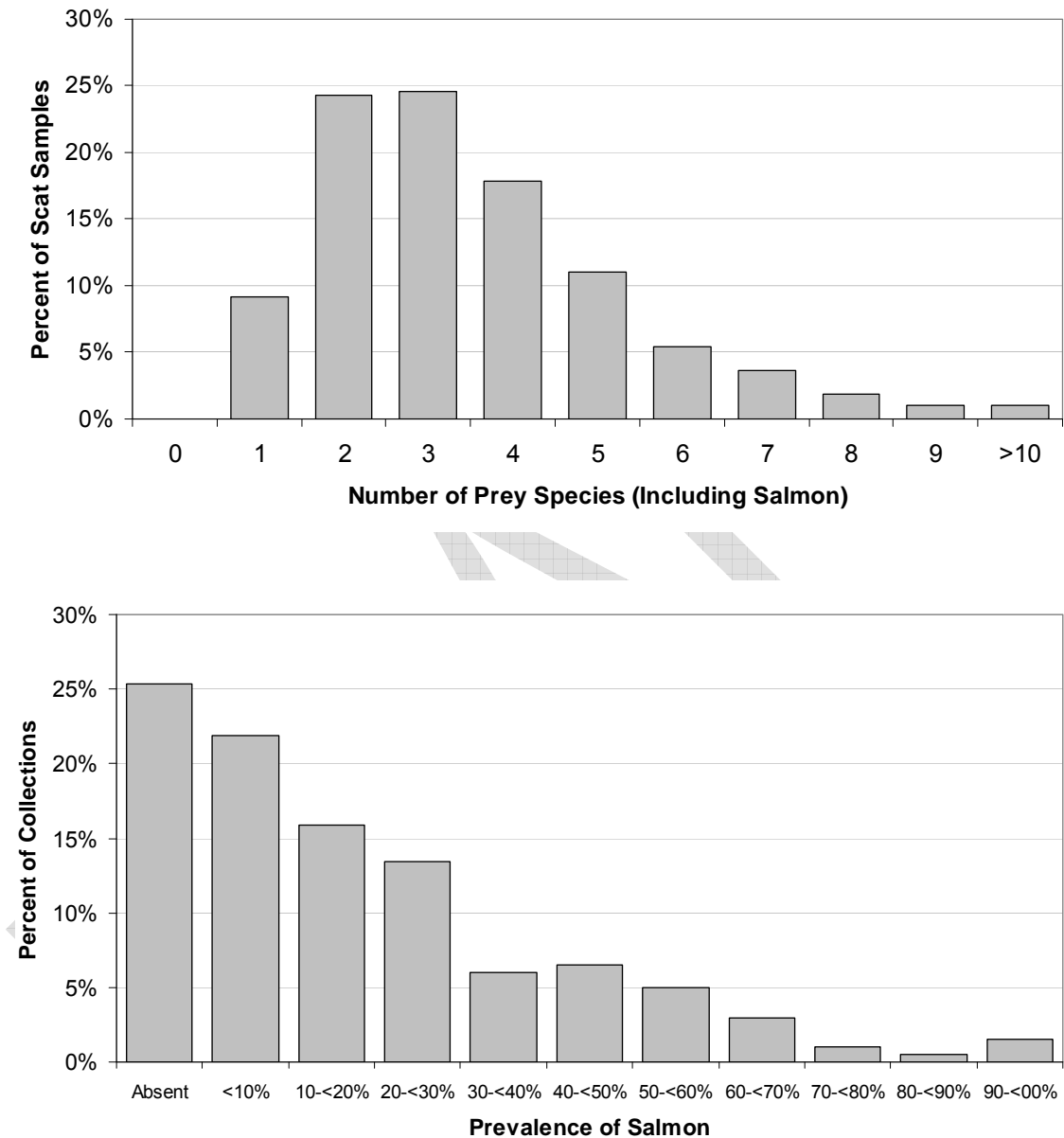


Figure 32. Frequency distribution of the number of prey species (including salmon) identified in Steller sea lion scat samples (top panel) and the proportion of samples in collections that contained salmon remains (bottom panel). In most cases, salmon occurred in relatively few (0-30%) of the samples and were generally consumed along with other prey, indicating they were not likely a focal prey species. However, in a few collections salmon occurred in most samples (70-100%) and in some cases they were the only prey consumed, indicating they were occasionally a focal prey at a few locations.

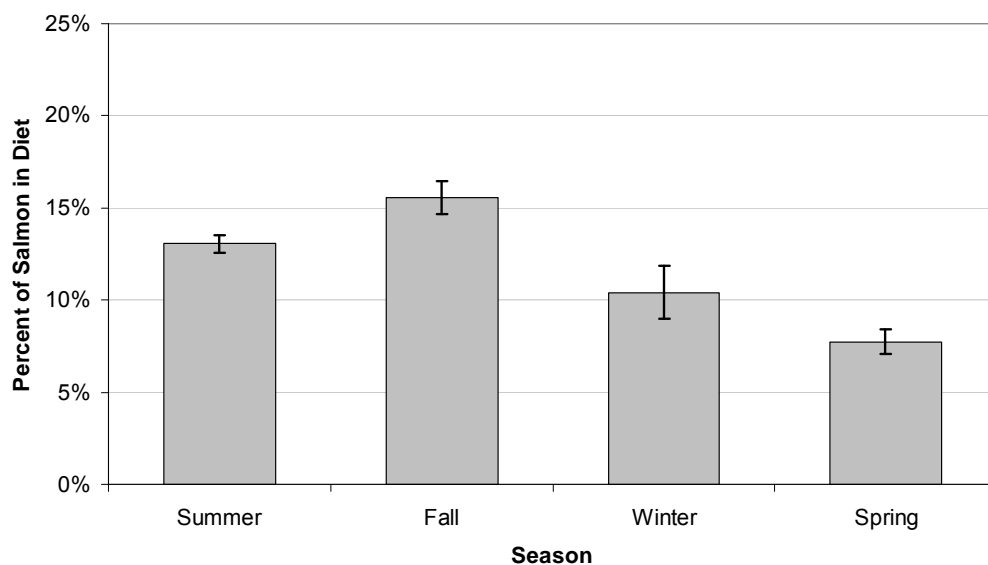


Figure 32. Proportion of overall Steller sea lion diet comprised of salmon by season. Vertical bars represent CVs that account for variability in the survey counts used to weight the scat collections by site and season, and the uncertainty in the proportion of each meal that was comprised of salmon when other prey had also been consumed. The CV does not capture potential biases introduced by assuming that all prey species consumed in meals with multiple prey had been consumed in equal volumes.

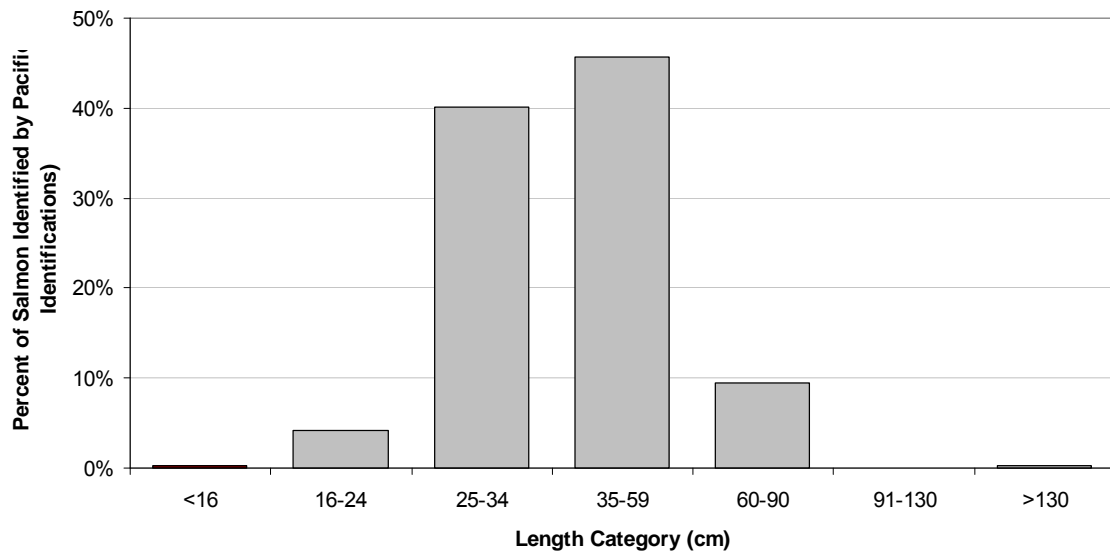


Figure 34. Size distribution of salmon in Steller sea lion scats that were identified by Pacific Identifications and subjectively categorized by size. In cases where the size may have fallen in either of two adjacent size categories, the item was tallied as half an occurrence in each of the potential size categories. Note that size was estimated subjectively and these estimates have not been tested or calibrated. The smallest size category (<16cm) were considered juvenile-sized salmon.

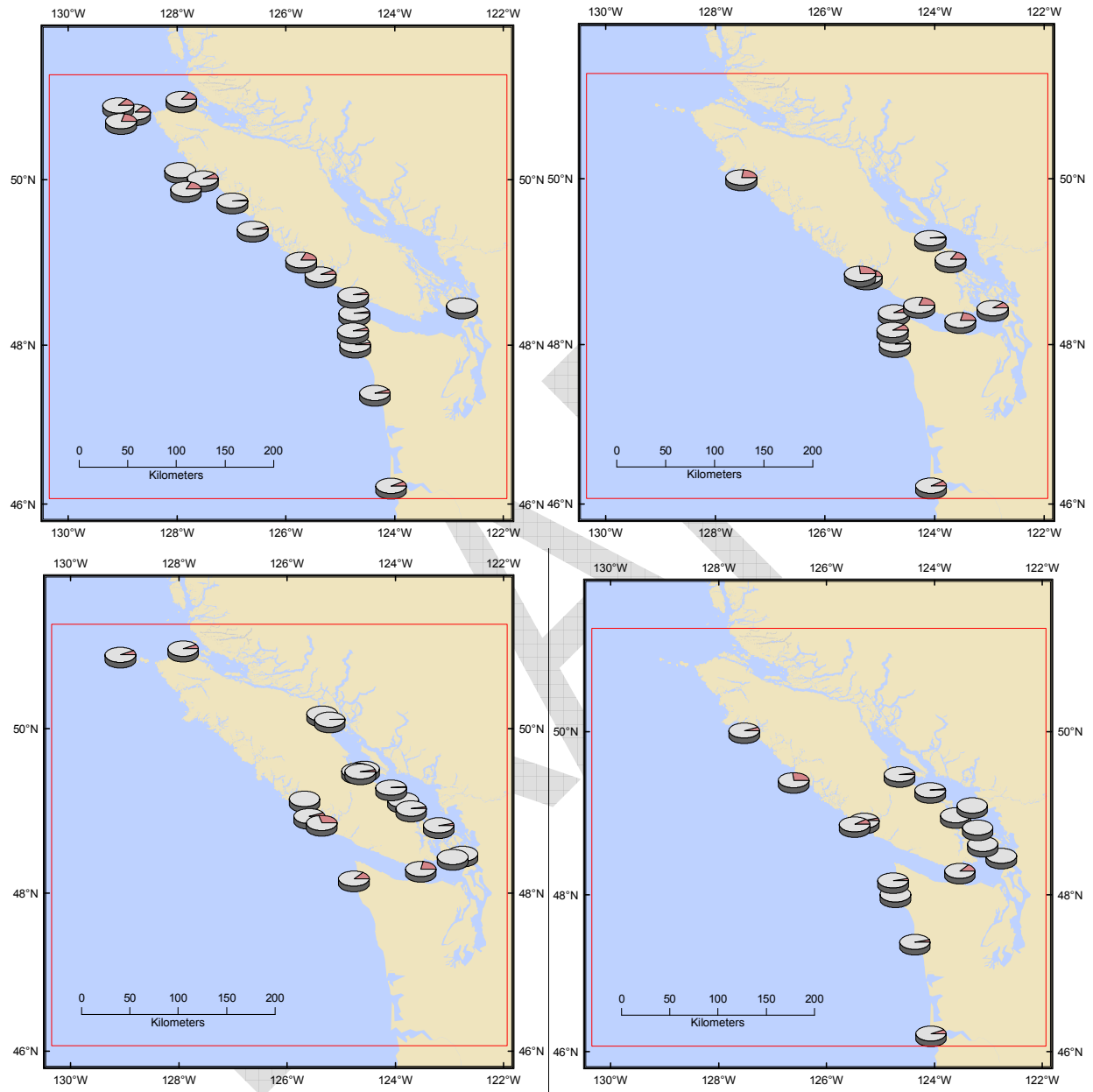


Figure 35. Proportion of salmon (red) in the overall diet of Steller sea lions (grey) by site in the summer breeding season (upper left), fall (upper right), winter (lower left) and spring (lower right). Red box denotes study area.

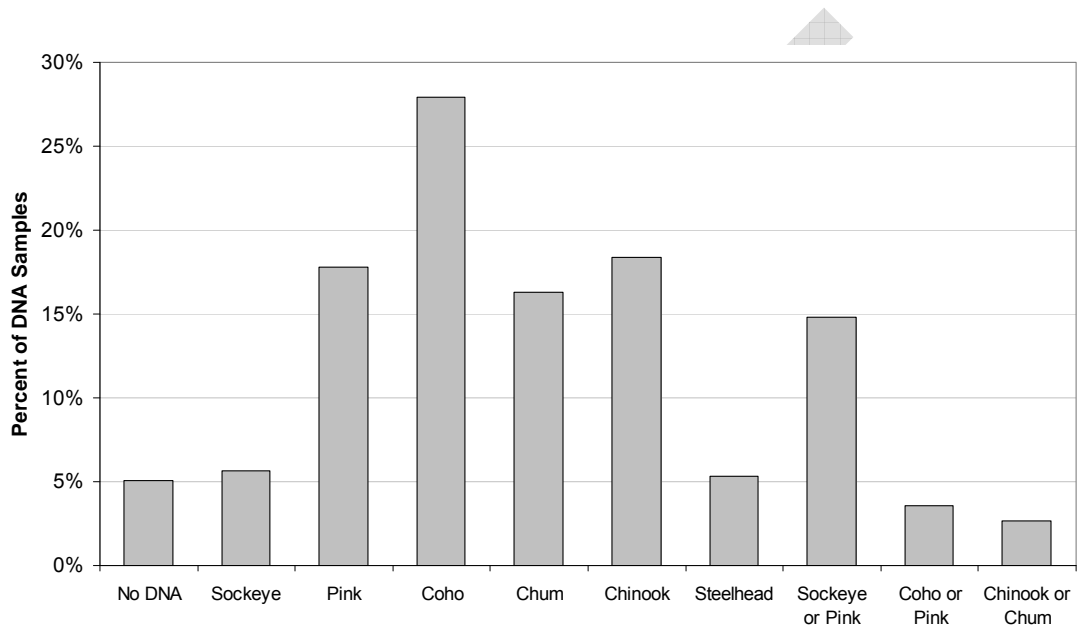
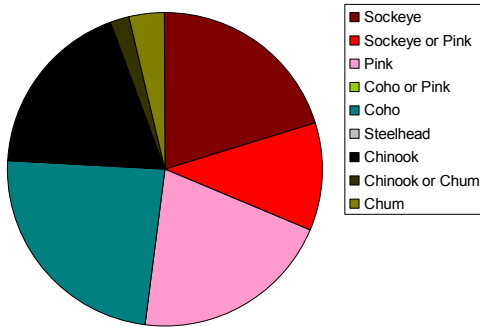
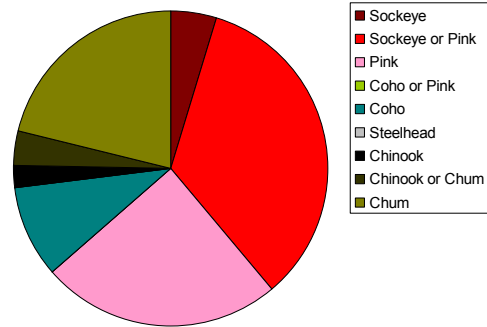


Figure 36. Species of salmon identified from DNA extracted from a subset of 320 Steller sea lion scat samples from the study area. In some cases, multiple loci were required to positively identify species, but some loci were not as robust and more prone to “drop-outs”, so there are a number of instances (3 far right bars) where the species could only be narrowed down to one of two possible species.

Summer - Scott Islands (n=54)



Summer - West Coast Vancouver Island (n=85)



Summer - Washington & Columbia River (n=53)

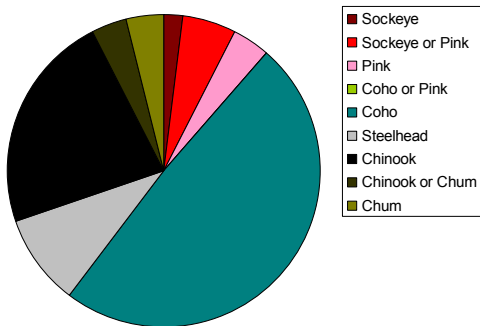
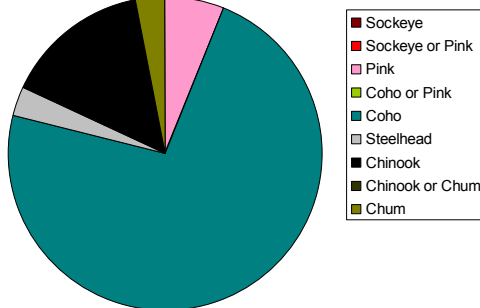


Figure 37a. Species of salmon consumed by Steller sea lions during summer at the Scott Islands (top left), northwest coast of Vancouver Island (top right), and Washington coast and Columbia River (lower left).

Fall - West Coast Vancouver Island (Barrier)(n=33)



Fall - Washington & Columbia River (n=20)

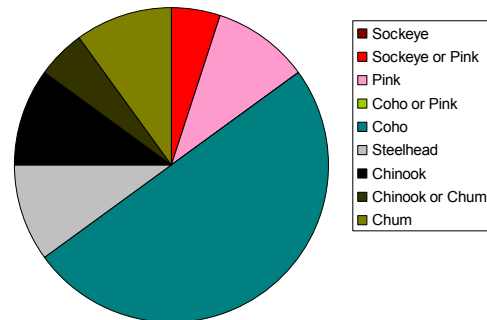
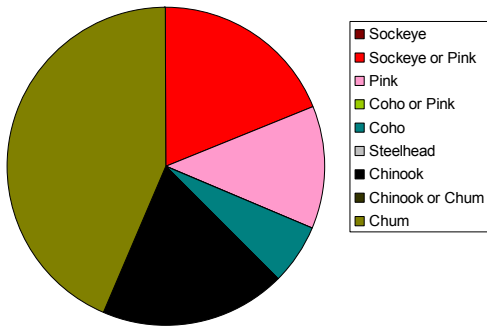


Figure 37b. Species of salmon consumed by Steller sea lions during fall on Barrier Islands off the west coast of Vancouver Island (left) and the Washington coast and Columbia River (right).

Winter - West Coast Vancouver Island (n=16)



Winter - Washington (Cape Alava) (n=6)

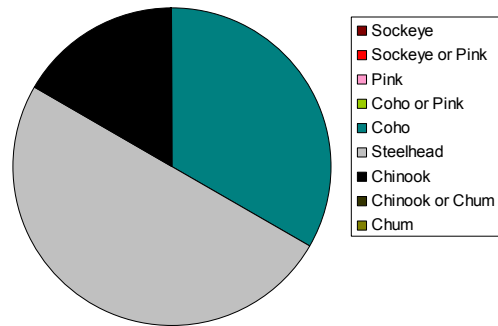
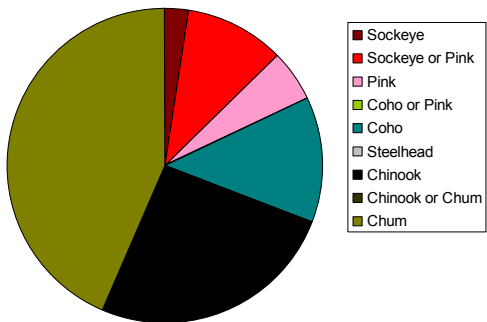


Figure 37c. Species of salmon consumed by Steller sea lions during fall based on very small numbers of samples off the west coast of Vancouver Island (left) and Cape Alava on the Washington coast (right).

Spring - West Coast Vancouver Island (n=39)



Spring - Washington & Columbia River (n=34)

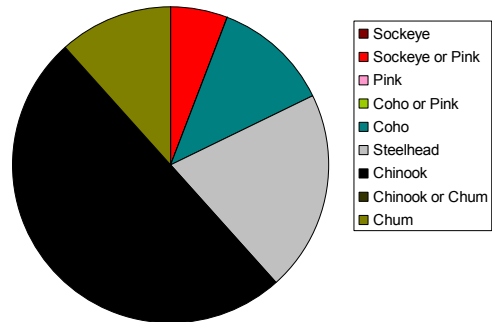


Figure 37d. Species of salmon consumed by Steller sea lions during spring off the west coast of Vancouver Island (left) and the Washington coast and Columbia River (right).