STELLER SEA LIONS AND FISHERIES: COMPETITION AT SEA?

by

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ABSTRACT

A leading hypothesis to explain the decline of Steller sea lions (*Eumetopias jubatus)* in western Alaska is the reduction of prey abundance or change in prey distributions caused by commercial fisheries. We sought to improve on past studies that attempted to assess competition between sea lions and fisheries by estimating the local amounts of prey accessible to sea lions. We explored the relationships between sea lion population trends, fishery catches and the prey biomass accessible to sea lions around 33 rookeries from 2000-2008. We focused on three commercially important species that dominate the sea lion diet: walleye pollock, Pacific cod and Atka mackerel. We estimated available prey biomass by removing fishery catches from predicted prey biomass distributions in the Aleutian Islands, Bering Sea and Gulf of Alaska; and modelled the likelihood of sea lions foraging at different distances from rookeries (accessibility) using satellite telemetry locations of tracked animals. We combined this accessibility model with the prey distributions to estimate the prey biomass accessible to sea lions by rookery. For each rookery, we compared sea lion population change to accessible prey biomass (estimated using our accessibility model and also within 10, 20 and 50 km of each rookery). Of the 304 statistical models we constructed to compare accessible prey biomass and catch to sea lion population trends, only three relationships were significant. These three suggest that sea lion population change rates increased (became less negative) with increasing accessible pollock biomass in the Aleutian Islands and with cod biomass in the Gulf of Alaska. No relationships were found between sea lion population trends and Atka mackerel biomass. Given that the majority of the relationships we explored were insignificant, it seems unlikely that the availability of pollock, cod or Atka mackerel was limiting sea lion populations in the 2000s. Sea lion population trends appeared to be affected by some unknown factor associated with regional differences. Removing fish catches or adding catch to our predicted distributions of groundfish abundances had no measurable effect on sea lion population trends. These observations suggest that sea lion populations were largely unaffected by fishery removals during this period.

PREFACE

I, Tabitha Cheng Yee Hui, am the main contributor to this thesis in all of the required areas:

- Identification and design of research project: My supervisor, Dr. Andrew W. Trites, committee member, Edward J. Gregr, and I are the main identifiers of this research project. I am the main designer of this research project.
- Performing the research: I performed all of the research in this thesis. Prey biomass distributions were provided by Rowenna Gryba, and the Steller sea lion population model was provided by Brian Battaile. Suggestions were given by my supervisor, Dr. Andrew W. Trites, committee members, Edward J. Gregr, Dr. Brian Klinkenberg and Dr. Murdoch McAllister, and our lab's biostatistician, Ruth Joy.
- Data analyses: I performed all the data analyses in this thesis. Suggestions were given by my supervisor, Dr. Andrew W. Trites, committee member, Edward J. Gregr, and our lab's biostatistician, Ruth Joy.
- Manuscript preparation: I prepared the whole manuscript. Editing was performed by me, my supervisor, Dr. Andrew W. Trites and committee member, Edward J. Gregr.

A version of Chapter 2 will be submitted for publication. Hui, T.C.Y., Gryba, R., Gregr, E.J., Joy, R. and Trites, A.W. Steller sea lions and fisheries: Competition at sea?

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LIST OF ABBREVIATIONS

ADFG	Alaska Department of Fish and Game
AIC	Akaike's information criterion
Aleutian Island rookeries	Rookeries west of Samalga Pass
ANOVA	Analysis of Variance
Cod	Pacific cod *Gadus macrocephalus*
CPUE	Catch per unit effort
EEZ	Exclusive Economic Zone
ESA	Endangered Species Act
Gulf of Alaska rookeries	Rookeries east of Samalga Pass
LME	Linear mixed-effects
LRT	Likelihood ratio test
Mackerel	Atka mackerel *Pleurogrammus monopterygius*
MFCMA	Magnuson Fishery Conservation and Management Act
NMFS	National Marine Fisheries Service
NMML	National Marine Mammal Laboratory
NOAA	National Oceanic and Atmospheric Administration
NPGOP	North Pacific Groundfish Observer Program
NPFMC	North Pacific Fisheries Management Council
Pollock	Walleye pollock *Theragra chalcogramma*
ROMS	Regional Oceanographic Modelling System
Sea lion	Steller sea lion *Eumetopias jubatus*
TAC	Total Allowable Catch

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DEDICATION

To my parents and brother

CHAPTER 1: GENERAL INTRODUCTION

1.1 Competition between marine mammals and fisheries

Humans have developed fisheries that span entire oceans, and have the capability to overexploit the resources in any region within a very short time (Pauly et al. 1998, Pitcher 2001, Pauly et al. 2002, Berman et al. 2008). The impact that fishing may have on marine mammals and other components of marine ecosystems is a major concern (Jackson et al. 2001, Worm et al. 2006). Fisheries can cause by-catch mortalities and affect marine mammals through direct and indirect competition for the same food sources (Trites et al. 1997, Kaschner et al. 2001). They may, for example, disrupt foraging patterns or cause marine mammals to abandon a foraging area because of disturbance. Fisheries can also compete indirectly with marine mammals for prey by reducing the abundance, or changing the size structure, distribution, or community composition of prey.

There are few documented cases of commercial fisheries negatively impacting marine mammal populations, perhaps because of the inherent difficulties in establishing such cause and effect relationships. Large reductions in the Barents Sea stocks of Atlantic herring *Clupea harengus* in the 1960s, polar cod *Boreogadus saida* in the early 1970s and capelin *Mallotus villosus* in the mid-1980s coincided with observable declines in the Barents Sea harp seal *Pagophilus groenlandicus* population (Baraff & Loughlin 2000). Food limitations precipitated by the collapse of the capelin stock is presumed to have led to increased mortality of juvenile harp seals and a mass movement of harp seals into Norwegian coastal waters during the late 1980s (Baraff & Loughlin 2000). In the Mediterranean and Black Seas, signs of malnutrition in bottlenose *Tursiops truncatus*, striped *Stenella coerule* and short-beaked common *Delphinus delphis* dolphins, and harbour porpoises *Phocoena phocoena* were presumed to have been caused by overfishing of prey stocks and intensive trawling (Bearzi et al. 2006).

In the past 50 years, a number of marine mammal species such as the Chinese river dolphin *Lipotes vexillifer* and Hawaiian monk seal *Monachus schauinslandi* have fallen to low levels and have failed to recover despite extensive management efforts. It has been speculated that human fishing activities may be one of the major factors affecting recovery rates (Bowen 1985, Crespo et al. 1997). Any mention of competition between marine mammals and fisheries

tends to arouse controversy because of the complex mix of biological, economic, social, political and moral factors involved. Some fishermen believe the presence of marine mammals on their fishing grounds will result in a reduction in potential catch, whereas others see the presence or expansion of fisheries as a threat to the recovery of marine mammal populations from previous heavy exploitation (Harwood & Croxall 1988). Understanding the mechanisms and the extent to which fisheries are competing with marine mammals would facilitate management decisions regarding conservation of marine ecosystems and protection of endangered marine mammal populations.

The following outlines the history of the decline and relevant biological characteristics of the Steller sea lion *Eumetopias jubatus*, and the past and present status of fisheries in western Alaska with a primary focus on three commercially important species that dominate the sea lion diet: walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus* and Atka mackerel *Pleurogrammus monopterygius*.

1.2 Decline of the Steller sea lion

Steller sea lions (Schreber, 1776) are the largest otariid (eared seal). They are widely distributed along the coasts of the North Pacific Ocean, occurring from central California (Ano Nuevo Island) along the Pacific Rim, through the Gulf of Alaska, Bering Sea and Aleutian Islands to Russia (Kuril Islands and Sea of Okhotsk) and Japan (Loughlin et al. 1984). The population has been divided into two stocks at Cape Suckling, Prince William Sound in the Gulf of Alaska (144°W), based primarily on genetic evidence (Bickham et al. 1996, Loughlin 1997, Bickham et al. 1998) They have been called the eastern and western stocks for management purposes. Over the past 30 years, these two stocks have exhibited opposite population trends. Overall, the western stock in Alaska has declined by over 80% (Loughlin et al. 1992, Trites & Larkin 1996, Loughlin & York 2000, Sease et al. 2001), whereas the eastern stock has increased substantially, having more than doubled (increase of ~3% per year) since the late 1970s (Bigg 1988, Calkins et al. 1999, Sease et al. 2001, Pitcher et al. 2007).

The decline in western Alaska is not unique to Steller sea lions. Two other pinniped species in Alaska also declined in abundance over the same period (Gerber & Hilborn 2001): the northern fur seal *Callorhinus ursinus* (Pitcher 1990, Trites & Larkin 1992, Towell et al. 2006)

and harbour seal *Phoca vitulina* (Pitcher 1990, NMFS 1993, Small et al. 2003, Jemison et al. 2006). Many seabird and marine mammal species also declined across the North Pacific Ocean from the 1970s through the 1990s (York & Hartley 1981, NRC 1996b, Merrick 1997, Anderson & Piatt 1999, Trites et al. 1999a, Hunt et al. 2002, Springer et al. 2003, DeMaster et al. 2006). These widespread declines suggest that large-scale forces such as industrial fishing and environmental changes are likely at work, although other causes which could have exacerbated the decline have not been ruled out. Other potential causes include entanglement (Perez & Loughlin 1991), predation (Springer et al. 2003, Williams et al. 2004, Springer et al. 2008), pollution, harassment, commercial pup harvests prior to 1972, subsistence harvests and disease (Burek et al. 2005). However, while much effort has been applied to determining the most proximate factors of the decline, the indirect and interactive nature of the effects have made it difficult to attribute the decline to specific factors.

A leading hypothesis to explain the decline of sea lions is nutritional stress resulting from changes in the distribution, abundance, or quality of prey due to commercial fisheries or large-scale oceanographic changes (Alverson 1992, Merrick et al. 1995, Merrick et al. 1997, Calkins et al. 1998, Loughlin et al. 1998, Loughlin & York 2000, DeMaster & Atkinson 2002, Trites & Donnelly 2003). Major changes in ocean climate occurred during the 1976-77 regime shift (Beamish 1993, Benson & Trites 2002, Barange 2003). Formerly dominated by crabs, shrimp and pelagic (mostly forage) fishes, the Bering Sea and western Gulf of Alaska shifted to groundfish dominated ecosystems following the regime shift (Trites et al. 1999a, Barange 2003). Groundfish such as walleye pollock, Pacific cod and Atka mackerel may not provide adequate nutrition as they are not as fatty as forage fishes and are harder to digest (Rosen & Trites 2000, Trites & Donnelly 2003, Adams et al. 2008). A shift in sea lion diet from high lipid to low lipid prey may have been detrimental to sea lions, because juvenile sea lions are unable to obtain sufficient energy from low lipid prey (Alverson 1992, Anderson & Piatt 1999, Trites & Donnelly 2003, Rosen & Trites 2004, Womble et al. 2005, Trites et al. 2007b). This so called ‘junk food hypothesis’ has also been implicated in the decline of other top marine predators such as seabirds (Osterblom et al. 2008).

Another compelling hypothesis to explain the decline not only of sea lions but other small marine mammals as well is that killer whales *Orcinus orca* were forced to switch to a diet of

progressively smaller pinnipeds and marine mammals after commercial whalers severely depleted fin *Balaenoptera physalus*, sei *Balaenoptera borealis*, and sperm *Physeter macrocephalus* whales in Alaskan waters between 1949 and 1969. Termed the 'sequential megafaunal collapse' hypothesis, it is suggested that this accounts for a sequential decline of harbour seals, northern fur seals, Steller sea lions and sea otters *Enhydra lutris* that followed through the 1980s and 1990s (Estes et al. 1998, Springer et al. 2003). However, others have found little evidence to support this hypothesis (DeMaster et al. 2006, Mizroch & Rice 2006, Trites et al. 2007a, Wade et al. 2007), mainly because sea lions have always been known to be an important component of the diet of transient killer whales in Alaska (Heise et al. 2003, Herman et al. 2005), while whales have not (Jefferson et al. 1991, Ford et al. 1998, Saulitis et al. 2000, Heise et al. 2003, Ford et al. 2005, Mizroch & Rice 2006). The population trends of seals, sea lions and sea otters in British Columbia, where commercial whaling was just as intense as in Alaska, were also opposite to those in Alaska (Trites et al. 2007a), contradicting this 'sequential megafaunal collapse' hypothesis.

Although no definitive cause has been determined for the decline, competition with fisheries has been assumed to be a contributing factor because the decline coincided with a sharp increase in domestic commercial fishing in the North Pacific after the United States created its Exclusive Economic Zone (EEZ) in 1976. Sea lion populations started increasing in southeast Alaska in the 1970s, coincidental with a reduction in herring fishing and a rapid increase in herring stock size (Hebert & Pritchett 2003). Many of the species targeted by fisheries are also consumed by sea lions at the same time and in the same areas where these fisheries operate. Fishing can remove or disperse large aggregations of fish from an area (Baraff & Loughlin 2000) and can also reduce overall levels of fish biomass (NMFS 2009). Sea lions may abandon traditional foraging areas, or change their foraging patterns, as a result of such fisheries related disruptions (NMFS 2009). Fisheries are thus believed to have the potential to reduce sea lion foraging efficiency and compete with sea lions for prey by altering the abundance, composition and distribution of the available prey field, potentially leading to nutritional stress. Reduced availability of important prey species could result in a diet that is insufficient to meet the energy requirements of sea lions (Alverson 1992, Trites & Donnelly 2003). Poor nutrition caused by a

lack of quantity, quality or availability of prey can stunt growth, reduce birth rates and increase mortality through disease, predation and starvation (Rosen & Trites 2000).

Evidence for competition between commercial fisheries and Steller sea lions has previously been sought. Zeppelin et al. (2004), for example, found considerable size overlap (68% pollock and 53% mackerel) in the relative size-frequency distributions of prey selected by sea lions and those taken by commercial trawl fisheries. A high degree of overlap highlights a potential conflict between fisheries and sea lions, but any interpretation of overlap as competition requires a measure of the resource being competed for. Others have attempted to correlate time series of sea lion abundances on rookeries with removals by fisheries (e.g., Loughlin & Merrick 1989, Trites & Larkin 1992, Ferrero & Fritz 1994). However, correlations between sea lion counts and fishery catches have yielded few significant results and the relationships were both positive and negative (Loughlin & Merrick 1989, Ferrero & Fritz 1994, Sampson 1995). Moreover, correlations between catch and abundance do not give information about the underlying cause of declines in sea lion numbers. Interspecific competition is defined as a reduction in the fecundity, growth or survivorship in the individuals of one species as a result of resource exploitation by another species (in our case, humans) (Begon et al. 2006). Any evidence for competition requires demonstrating that the resources that fisheries and sea lions seek are limited across the space and time in question (Krebs & Davies 1991).

The tendency for sea lions to forage nearshore, combined with the local intensity of groundfish fishing, has led to the suggestion that localised depletions within a sea lion's foraging range may be an important mechanism for the decline of the western stock (Fritz et al. 1995, Fritz & Ferrero 1998, DeMaster et al. 2001). Localised depletion is defined as intense fishing pressure leading to disproportionately large reductions in local densities of the target fish relative to the overall harvest rate (Conners & Munro 2008). Localised depletion occurs when fish are removed faster than immigration and recruitment can replace removed individuals (Battaile & Quinn 2006). Sea lions are predators that capitalise on the precise timing of high-density, seasonal aggregations of their prey to detect or capture prey successfully (Fiscus & Baines 1966, Pitcher 1981, Sinclair et al. 1994, Sinclair & Zeppelin 2002). They may encounter reduced foraging success if the prey school structure is disrupted or marginalised and local prey resources are depleted (NMFS 2001). There is evidence that patch density and fish schooling behaviour are

affected by trawl operations, which may alter the fine-scale availability of prey to sea lions following fishing episodes (Sease et al. 2001, Shima et al. 2002). Vessel traffic may temporarily cause fish to compress into tighter, deeper schools or split schools into smaller concentrations (Freon et al. 1992). Studies of sea lions in captivity have demonstrated a predictable decrease in foraging efficiency with decreased simulated patch density (Cornick & Horning 2003, Cornick et al. 2006a).

There is some evidence for the potential for fisheries to locally deplete prey resources, though direct links with sea lion populations have not been found. Battaile and Quinn (2006) detected within-season decreases in catch per unit effort (CPUE) from the commercial pollock fishery in many areas in the Bering Sea. They concluded that this decline was invariably due to some depletion of the prey base by the fishery and perhaps some emigration from each area. Trawl fisheries in the Aleutian Islands may have reduced some local abundances of Atka mackerel by as much as 90% even though only 10% of the total stock was scheduled to be harvested (Lowe & Fritz 1997). Harvest indices for Pacific cod within a portion of sea lion critical habitat in 2001 were 5-16 times greater than the annual rate for the entire Bering Sea-Aleutian Islands stock (Fritz & Brown 2005).

Fisheries management is intended to ensure that fisheries are sustainable over large management areas and over years. Competition with sea lions (if it occurs) is more likely to occur at relatively fine temporal and spatial scales, during fishing seasons in areas where sea lions forage. The population dynamics of prey species in management areas are probably only broadly correlated with the local availability of prey to sea lions. Assessing fisheries impacts on sea lions therefore requires assessing localised prey abundance, particularly around rookeries and haulouts (Trites & Larkin 1992).

Accessibility — the likelihood of a sea lion foraging at a particular distance from its rookery or haulout — varies with distance from its terrestrial resting place. Satellite telemetry has shown that breeding female sea lions forage closer to their rookeries during summer compared to winter (Merrick et al. 1994, Merrick & Loughlin 1997), probably due to the need to regularly nurse a dependent pup every 1-4 days (Milette & Trites 2003, Davis et al. 2006). Satellite telemetry has also shown a tendency for juveniles (1-3 years old) to remain closer to

shore (Raum-Suryan et al. 2004, Fadely et al. 2005, Rehberg & Burns 2008, Rehberg et al. 2009, Winter et al. 2009). These observations suggest that prey located closer to shore are likely more important to foraging sea lions than prey located further away. Thus it is important to assess the accessibility of prey at varying distances from rookeries and haulouts, in addition to estimating the local abundance of available prey (Mathiopolous 2003, Gregr and Trites 2008).

Competition between sea lions and fisheries is a typical example of a conflict between humans and wildlife in which the wildlife component is highly valued by some sectors of society and is often legally protected—while the human component often involves the livelihoods of entire communities that may have few options for alternative employment (Matthiopoulos et al. 2008). It is thus crucial to carefully assess the potential for competition between fisheries and sea lions in a consistent, logical and scientifically sound manner using the best available data.

1.3 Steller sea lion biology

Steller sea lions are a gregarious species that congregate throughout the year at haulouts between bouts of feeding at sea. The weight of adult males averages 566 kg and females 263 kg (maximum about 1,120 kg and 350 kg respectively) (Fiscus 1961, Calkins & Pitcher 1982, Loughlin & Nelson 1986, Winship et al. 2001). Juveniles (1-3 years old) weigh 72-152 kg (Fadely et al. 2005). Newborn pups weigh 16-23 kg (Calkins & Pitcher 1982, Daniel 2003). During the breeding season in summer, adult sea lions concentrate on specific haulouts known as rookeries (Kenyon & Rice 1961, Sandegren 1970, Calkins & Pitcher 1982, Loughlin et al. 1984). Juveniles are more transient than breeding adults and are less present on rookeries during the breeding season. There are about 88 rookeries and 600 haulouts along the North Pacific rim (Coombs & Trites 2005). Up to 50 rookeries and over 250 haulouts occur along the coastline extending from Dixon Entrance in Southeast Alaska to Attu Island, the westernmost Aleutian Island (Loughlin et al. 1984, Loughlin et al. 1987, Sease et al. 2001). Most of the haulouts and rookeries are on remote and exposed rocks and islands, and are generally believed to be in close proximity to food resources. These aggregations rarely exceed a few thousand individuals (Calkins & Pitcher 1982).

In western Alaska, males come ashore in early May to establish territories for breeding on rookeries and remain until mid-July; females follow shortly thereafter (Thorsteinson &

Lensink 1962, Gentry 1970, Gisiner 1985). One pup is born to each pregnant female shortly after her arrival on the rookery. In Alaska, 60-65% of adult females give birth each year, although at least 90% implant during the preceding November (Calkins & Pitcher 1982). Pupping peaks in mid-June and is completed by mid-July (Pike & Maxwell 1958, Mathisen et al. 1962, Pitcher et al. 2002). Females mate following parturition. Gestation is approximately 8 months, following delayed implantation of approximately 4 months. Pups are dependent upon maternal energy for approximately one year but may continue to nurse occasionally for as long as two to three years (Gentry 1970, Sandegren 1970, Pitcher & Calkins 1981, Trites & Porter 2002, Trites et al. 2006b), despite pups often ingesting solid food as early as 10 months of age (Trites et al. 2006b).

Females reach sexual maturity at 3-6 years and appear to remain reproductively active well past age 20. They are typically philopatric (high natal rookery fidelity). Males reach sexual maturity at 3-7 years, but are generally not able to hold a territory until they are 9-11 years old (Thorsteinson & Lensink 1962, Gentry 1970, Pitcher & Calkins 1981). Males hold territories an average of two years. The maximum life expectancy of males and females is about 18 and 30 years respectively (Calkins & Pitcher 1982). Males store large quantities of energy in the form of increased fat and protein during the non-breeding season and then remain on the rookery and fast during the breeding season (Olesiuk & Bigg 1990, Pitcher et al. 2000). Females make regular and brief (1-4 days) foraging trips 11-14 days after giving birth and return to nurse their pups for similar periods, repeating this cycle until their pups are weaned (Loughlin et al. 1998, Rehberg et al. 2009). After the breeding season ends in July (pupping completed and males cease being territorial), adult males disperse from the rookeries, whereas adult females and their pups remain or move to haulouts (Sinclair & Zeppelin 2002).

1.3.1 Diet and foraging behaviour

Steller sea lions are generalist and opportunistic predators that eat a variety of fishes and cephalopods depending on their availability (Pitcher 1981, Shima et al. 2002, Trites et al. 2006a, Sigler et al. 2009). In addition to pollock, cod and mackerel, they also consume forage fishes (e.g., capelin *Mallotus villosus*, eulachon *Thaleichthys pacificus*, Pacific herring *Clupea harengus* and Pacific sand lance *Ammodytes hexapterus*), flatfish (e.g., arrowtooth flounder

Atheresthes stomias and rock sole *Lepidopsetta bilineata*), rockfish (*Sebastes* spp.), salmon (*Oncorhynchus* spp.), sculpins (e.g., Irish lord *Hemilepidotus hemilepidotus*), squid and octopus (Pitcher 1981, Calkins 1998). However, their diets within a specific region are typically dominated by a few species.

Prey species can be grouped into those that are consumed seasonally when they become locally abundant or aggregated when spawning (e.g., herring, cod, eulachon, capelin, salmon and Irish lords), and those that are consumed and available to sea lions more or less year-round (e.g., pollock, cephalopods, mackerel, arrowtooth flounder, rock sole and sand lance) (Pitcher 1981, Calkins 1998, Sinclair & Zeppelin 2002, Trites et al. 2007b). Some of the seasonal prey species occur most frequently in summer and fall (e.g., salmon and Irish lords) or winter and spring (e.g., herring, cod, eulachon and capelin).

Most prey consumed are less than 35 cm long (Calkins 1998, Trites & Calkins 2008, Sigler et al. 2009), although prey up to 70 cm are taken (McKenzie & Wynne 2008). Fish are either swallowed whole, or torn apart and consumed at the surface (Mathisen et al. 1962). Energetic modelling suggests that a mature male sea lion requires about 25 to 40 kg of prey per day compared to 10 to 20 kg for a mature female (Winship & Trites 2003).

Steller sea lions are central place foragers (Orians & Pearson 1979, Raum-Suryan et al. 2004) which forage primarily over the continental shelf at depths of 10-50 m, although they are known to reach depths greater than 250 m (Merrick & Loughlin 1997, Pitcher et al. 2005, Rehberg & Burns 2008). They usually forage alone or in small groups (<20), though they sometimes cooperatively forage in large groups (Sigler et al. 2009). Most dives are short (<5 minutes). They spend about half their time at sea, with about a third of this time spent diving (Pitcher et al. 2005, Rehberg & Burns 2008). The proportion of time that sea lions spend ashore varies with time of year, age and sex (lower in winter than summer, lower for juveniles than adults, breeding males remain ashore during summer) and ranges from 10 to 63% (Holmes et al. 2007). Sea lions spend more time at sea, dive deeper and have greater home ranges in winter compared with summer (Merrick 1997). Pups make shorter, shallower and fewer dives than juveniles and adults, though these differences are not apparent by the time the animals are in their second year of life, suggesting that any physiological constraints ease by the time they

become juveniles (Rehberg & Burns 2008). Sea lions can function as either benthic or epipelagic feeders (Pitcher & Calkins 1981, Sinclair & Zeppelin 2002).

1.3.2 Dispersal patterns and population trends

Dispersal distance from the natal rookery varies greatly with age. Pups generally remain within 500 km of their natal rookeries and learn to forage specifically in these waters (Raum-Suryan et al. 2002, Sinclair & Zeppelin 2002, Raum-Suryan et al. 2004). Pups first enter the water two to four weeks after birth (Sandegren 1970) and with their mothers, begin to disperse from rookeries to haulouts between two and three months of age (Calkins & Pitcher 1982, Merrick et al. 1988). Two month old pups are capable of travelling up to 120 km from their rookeries (Raum-Suryan et al. 2004). As pups are maternally dependent through most of the first year (Pitcher & Calkins 1981), their distribution probably reflects the distribution of foraging resources available to their mothers. Once weaned, pups may disperse more extensively due to competition with adults for limited resources or to assess future alternative breeding locations (Baker 1978). Juvenile males disperse much greater distances, up to 1,785 km from their rookeries. Adults tend to remain within 500 km of their natal rookeries. Males tend to utilise more haulouts and rookeries, and disperse greater distances than females (Raum-Suryan et al. 2002).

Steller sea lions may disperse great distances over the course of their lifetime, but show fairly strong site fidelity to their natal rookeries during the breeding season (Raum-Suryan et al. 2002, Parker et al. 2008). Similar to other otariids such as the northern fur seal (Kenyon & Wilke 1953, Baker et al. 1995), female sea lions are thought to return to their natal rookery to mate and raise their young. Similarities in population trends (York et al. 1996) and diet (Sinclair & Zeppelin 2002) within a region indicate strong site fidelity.

In the 1970s, before the world population of Steller sea lions started to decline, it was estimated to number about 290,000 (Merrick et al. 1987), with 90% of the animals in the western population (Loughlin et al. 1984). Today, the western U.S. stock (Aleutian Islands, Bering Sea and western Gulf of Alaska) is estimated at fewer than 40,000 individuals (Angliss & Outlaw 2006). The eastern stock was traditionally thought of as being small. However, it is now as large as or larger than the western stock (Pitcher et al. 2007). The total population of the eastern stock

in 1992 was 10,000 (Trites & Larkin 1996). In 2002, it was estimated to number between 46,000 and 58,000 animals (Pitcher et al. 2007). The Kuril Islands support the largest group of Steller sea lions in Russia. From 1955 to 1968 the sea lion population in the Kuril Islands was stable at about 15,000-20,000 individuals, but it declined steadily since then to the 5,000 counted in 1989 (Loughlin et al. 1992). As of 2005, the population of sea lions in Russia was estimated to be about 16,000 (NMFS 2008b).

The decline of sea lions began in the eastern Aleutian Islands in the 1970s (Braham et al. 1980). By the early 1980s, declines had spread east to the Gulf of Alaska and west to the central Aleutian Islands (Braham et al. 1980, Merrick et al. 1987, Trites & Larkin 1996). The western stock continued to decline through the 1990s at about 4% per year, although since 2000 the decline may have abated in the central and eastern Aleutian Islands (Sease & Gudmundson 2002). The recent (2005-2008) overall trend of the western stock of sea lions in Alaska is stable or declining slightly. This follows a four year period of population increase (at ~3% per year) between 2000 and 2004. However, the increase did not occur across the entire western stock. Abundance increased in parts of the Aleutian Islands and the Gulf of Alaska, but declines continued in the western Aleutian Islands (Figs. 1.1). Pup production in the Alaskan western stock was relatively stable between 1998 and 2007, despite overall increases in non-pup counts between 2000 and 2008 (Fritz et al. 2009).

1.3.3 Proximate causes of the decline

Although there has been much debate as to the ultimate cause of decline of Steller sea lions, nutritional stress (Calkins et al. 1998, Pitcher et al. 1998), resulting in excessive juvenile mortality (perhaps due to the inability of mothers to adequately nourish their pups during lactation, or weaned juveniles not being able to successfully forage on their own), is widely believed by many to be the proximate cause of the decline during the 1980s (Pascual & Adkinson 1994, York 1994, Merrick 1995). Extremely low sightings of branded pups during the mid-1980s are consistent with these findings (Merrick et al. 1995, Chumbley et al. 1997, Raum-Suryan et al. 2002, Pendleton et al. 2006). The condition of nursing pups during the first few months of life did not appear to have been compromised (Castellini et al. 1993, Rea et al. 1993), suggesting that the population decline was not caused by reduced survival of nursing pups nor

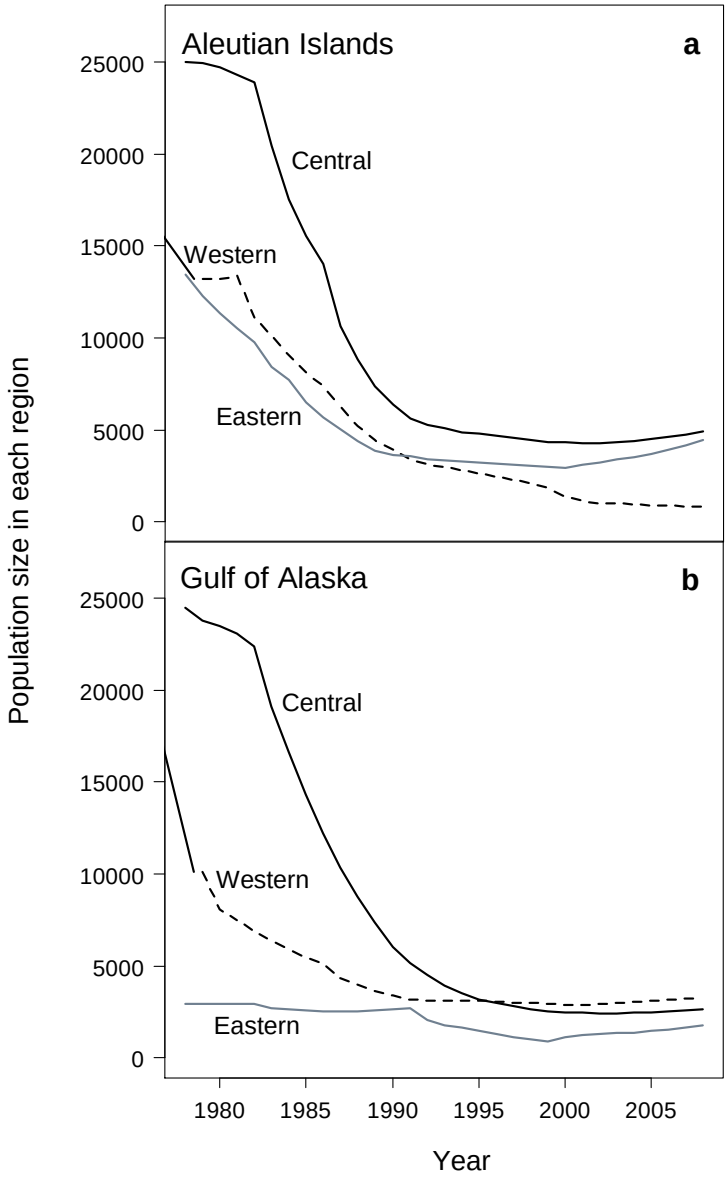

Fig. 1.1. Steller sea lion population trends from 1978-2008 in the (a) Aleutian Islands and (b) Gulf of Alaska (data from Fritz et al. 2009).

reduced condition of pregnant or lactating females. Terrestrial observational studies of foraging trip durations have not found that sea lions from the declining western stock expend greater effort foraging than those in the increasing eastern stock (Brandon 2000, Trites & Porter 2002, Milette & Trites 2003). In fact, foraging trips were shorter in the western region and females spent more time nursing their pups. Western stock females managed to deliver milk with similar energy content to eastern stock milk, pup energy intake was identical between stocks (Adams

2000), and western stock females achieved pup growth rates similar to or faster than eastern stock females (Brandon et al. 2005). Pups from the western stock were also found to be heavier (Merrick 1995, Merrick et al. 1995, Rea et al. 1998, Brandon 2000), although the time spent nursing was greater (Milette & Trites 2003). The general conclusion from these studies comparing the eastern and western stocks has been that acute nutritional stress (i.e., starvation) was not evident in adult females or pups from either stock (Trites & Donnelly 2003, Maniscalco et al. 2006).

Recent modelling work implicated reduced natality as a primary driver of the 1990s decline and current failure of the western stock to recover (Holmes et al. 2007). Pitcher et al. (1998) found high levels of prenatal mortality during the 1970s and 1980s. By the mid-1990s, the decline was associated with low fecundity (Holmes & York 2003) and recent models by Holmes et al. (2007) demonstrated that sea lion natality is currently low and decreasing.

1.4 Fisheries in western Alaska

The biological richness of the Aleutian Islands, Bering Sea and Gulf of Alaska has been exploited by humans for at least 5,000 years (NRC 1996a). Groundfish such as Pacific halibut *Hippoglossus stenolepis* and cod were first harvested in nearshore waters by Alaskan natives for subsistence. Beginning in the late 19th century, domestic fisheries began for cod, halibut and sablefish *Anoplopoma fimbria*. In the 1930s, Japanese trawl fisheries developed for pollock and flatfish (primarily yellowfin sole *Limanda aspera*). After World War II, large multinational fisheries for salmon, crabs, halibut, cod, sablefish, Greenland turbot *Reinhardtius hippoglossoides*, herring and shrimp developed off Alaska. Conflicts between foreign and domestic vessels resulted in increasing restrictions on foreign fleets. In 1976, the Magnuson Fishery Conservation and Management Act (MFCMA) instituted a fishery management system under the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS), and established the North Pacific Fisheries Management Council (NPFMC). The MFCMA promoted domestic fishing by limiting the total allowable level of foreign fishing to that portion of the optimum yield that was not expected to be harvested by domestic vessels (NRC 2003).

The current domestic fisheries target pollock, cod, mackerel, sablefish and a variety of rockfish and flatfish species. The total annual groundfish biomass has been estimated to be around 15 million tonnes in recent years (in 2009, it was 15.9 million tonnes). Despite the huge biomasses of annual catches, the removal rates of groundfish in Alaska are low and conservative compared to other fisheries in the world targeting species of similar sizes and life histories (Alverson 1992, Pauly 1996, Shima et al. 2000).

In the eastern Bering Sea, the initial target species was yellowfin sole. During this period, total catches of groundfish peaked at 674,000 tonnes in 1961. Following a decline in the abundance of yellowfin sole, other species (principally pollock) were targeted, and total catches of groundfish peaked at 2.2 million tonnes in 1972. After the MFCMA was adopted in 1976, catch restrictions and other management measures were put in place and total groundfish catches have since varied from 1-2 million tonnes. In 2005, Congress implemented a statutory cap of 2 million tonnes on total allowable catches (TACs) for Bering Sea and Aleutian Island groundfish. Catches generally total about 10% below the cap (NMFS 2009).

Catches in the Aleutian Islands have always been much smaller than in the eastern Bering Sea. Target species have also differed. Pacific Ocean perch *Sebastes alutus* was the initial target species. As perch abundance declined, the fishery diversified to other species. During the early years of exploitation, total groundfish catches peaked at 112,000 tonnes in 1965. Atka mackerel is now the largest fishery (catches totalled 57,700 tonnes in 2008) in the Aleutian Islands, followed by Pacific cod (catches totalled 31,000 tonnes in 2008). Recent groundfish catches have been about 100,000 tonnes annually, after peaking at 191,000 tonnes in 1996 (NMFS 2009).

In the Gulf of Alaska, Pacific Ocean perch was the first species targeted by large-scale commercial fisheries (in 1962), but catches were not officially reported until 1966 when a total catch of 83,000 tonnes was recorded. From the 1970s through the 1980s, the total groundfish catch rose considerably, reaching 550,000 tonnes in 1985, of which pollock accounted for over 95% (Trites et al. 1999b).

1.4.1 Walleye pollock

Pollock are semi-pelagic schooling fish broadly distributed throughout the North Pacific with the largest concentrations found in the southeastern Bering Sea. They form spawning aggregations between February and April. A significant proportion of pollock spawning in the Gulf of Alaska occurs in Shelikof Strait (Hinckley et al. 1991) and ocean currents disperse growing larvae southwest along the Aleutian Islands and north into the Bering Sea. Another large spawning assemblage occurs near Bogoslof Island in the eastern Aleutian Basin. Large aggregations of pollock are found throughout the eastern Bering Sea and around Unimak Pass and Unalaska during summer (Yanagimoto et al. 2002, Logerwell et al. 2005). Ages 0 and 1 year old pollock are primarily distributed in coastal shelf habitat along the Alaska Peninsula (Brodeur & Wilson 1996b, Shima et al. 2002). Pollock can live up to 20 years and attain a maximum length of 75 cm. Juveniles reach 12-14 cm by the end of the first year. Sexual maturity is attained at about 4 years, at a length of 45-50 cm (Shima et al. 2000). Pollock vertically migrate and are more accessible near the surface at night (Smith 1981, Schabetsberger et al. 2000). Juvenile pollock inhabit depths of 30-110 m in the daytime and move within 40 m of the surface at night (Brodeur et al. 1999, Schabetsberger et al. 2000). Adults are commonly found at depths of 50-400 m, with concentrations on the continental shelf from 100-300 m (Shima et al. 2000). Pollock occur at greater depths during winter than during summer (Brodeur & Wilson 1996b, Sigler & Csepp 2007).

Pollock consume a variety of prey, but primarily eat large zooplankton, copepods and myctophids. Adult pollock also eat fish. Groundfish predators of pollock include cod, yellowfin sole, Alaska plaice *Pleuronectes quadrituberculatus*, arrowtooth flounder and Greenland turbot. Predation on pollock is dominated by cannibalism on 0 year-old pollock by adult pollock (Sissenwine 1986, Livingston 1993). Atka mackerel cause most juvenile pollock mortality in the Aleutian Islands. Pollock fisheries are the next largest source of mortality, followed by marine mammals and birds. Within the marine mammal group, northern fur seals are the largest consumers of pollock (Livingston 1993). Fish, pinnipeds and the fishery are the primary removers of pollock >25 cm. Juvenile sea lions may prefer pollock <30 cm in length. Most pollock taken by the fishery are >40 cm (Livingston 1993).

Pollock became the dominant species in the North Pacific in the mid-1970s. Their numbers peaked in the early 1980s, and have declined in relative abundance since then (Figs. 1.2) (Mueter & Norcross 2002). The 2009 bottom trawl survey biomass estimate for pollock in the eastern Bering Sea was 2.28 million tonnes, down 25% from the 2008 estimate, and the lowest point in the 1982-2009 time series (NMFS 2009).

The commercial fishery for pollock in the Gulf of Alaska started as a foreign fishery in the early 1970s. Catches increased rapidly during the late 1970s and early 1980s (Fig. 1.2a). From 1954 to 1963, pollock harvests were low in the eastern Bering Sea until directed foreign fisheries began in 1964. Catches increased rapidly during the late 1960s and reached a peak in 1970-1975 when they ranged from 1.3 to 1.9 million tonnes annually. Following the peak catch of 1.9 million tonnes in 1972, bilateral agreements with Japan and Russia resulted in reductions. Since the establishment of the EEZ in 1976, the annual average eastern Bering Sea pollock catch has been 1.2 million tonnes and has ranged from 0.8 million tonnes in 2009 to nearly 1.5 million tonnes from 2003-2006 (Fig. 1.2b). Pollock is now the principal fishery in Alaska (NMFS 2009).

Pre-spawning aggregations of pollock are the focus of the “A season” which opens on January 20 and extends into early or mid-April. This fishery produces highly valued roe which can comprise over 4% of the catch in weight. Since the closure of the Bogoslof management area to directed pollock fishing in 1992, the “A season” pollock fishery on the eastern Bering Sea shelf has been concentrated primarily north and west of Unimak Island. The “B season” opens on June 1 and extends through late October. The pollock fishery focuses primarily on pollock aged 4-7 years. All pollock fishing vessels are bottom or pelagic trawlers (Edward Richardson, pers. comm.).

In 1999, the Aleutian Islands region was closed to directed pollock fishing due to concerns for Steller sea lion recovery. The Aleutian Islands directed fishery was reopened in 2005, but the areas surrounding rookeries and haulouts remain closed, limiting fishing to two small areas with commercial concentrations of pollock within easy delivery distance to Adak Island (NMFS 2009).

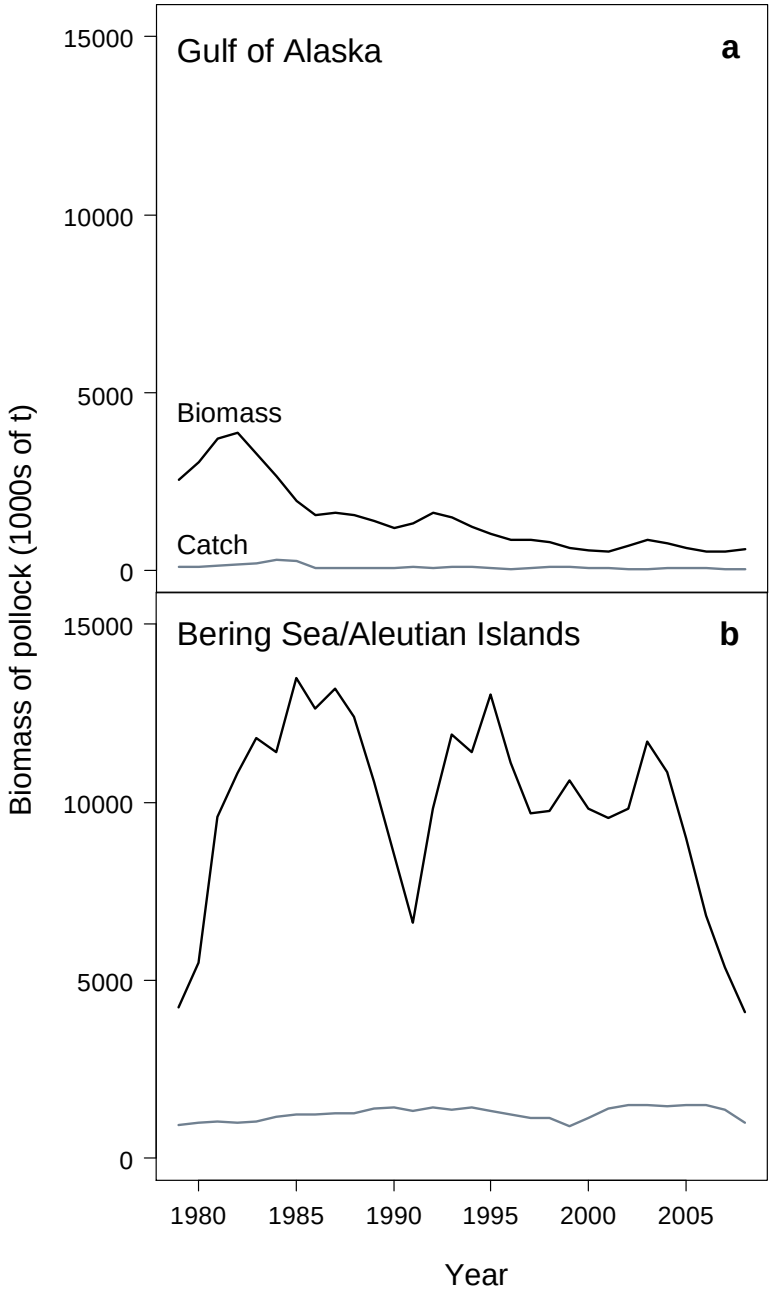

Fig. 1.2. Walleye pollock biomass (age 3+ years) and catch trends from 1979-2008 in the (a) Gulf of Alaska and (b) eastern Bering Sea/Aleutian Islands fisheries management areas (data from NMFS 2009).

1.4.2 Pacific cod

Pacific cod are distributed widely in the Aleutian Islands, eastern Bering Sea and Gulf of Alaska, though their center of abundance is in the Bering Sea. The annual cycle of cod migration begins in late September, when fish move off the Bering Sea shelf and seaward to the shelf break. Major winter spawning aggregations occur near Unimak Pass along the outer shelf edge, Pribilof Islands along the shelf edge and near the Shumagin Island group in the western Gulf of Alaska. Following the spawning season, cod move further inshore in concert with seasonal warming of the inner shelf. By summer, they move back to the outer shelf (Shimada & Kimura 1994). Juveniles grow to 44-75 cm over 2-3 years with adult males reaching 49 cm and females reaching 55 cm in length. Juveniles occur mostly over the inner continental shelf at depths of 60-150 m. Adults occur in depths from the shoreline to 500 m, although occurrence in depths greater than 300 m is rare. Cod move to shallower depths (50-100 m) after spawning in the spring (NMFS 2009).

Juvenile cod feed mostly on invertebrates such as shrimp. Adult cod are piscivorous, consuming mainly ages 0 and 1 pollock and also Atka mackerel. Cod is the most consistent groundfish predator on herring (Livingston 1993). Adult cod are cannibalistic on juveniles. Predators of cod include halibut, salmon sharks *Lamna ditropis*, northern fur seals, harbour porpoises, various whale species and tufted puffins *Fratercula cirrhata*. Following the highest bottom trawl survey biomass estimate in the eastern Bering Sea (BS/AI?) in 1994, Pacific cod biomass estimates declined steadily through 1998. The estimates remained around 600,000 tonnes from 2002 through 2005, however, they dropped steadily from 2005 through 2008 (Fig. 1.3b). The 2009 survey biomass estimate was 421,000 tonnes, up 4% from 403,000 tonnes in 2008 (NMFS 2009).

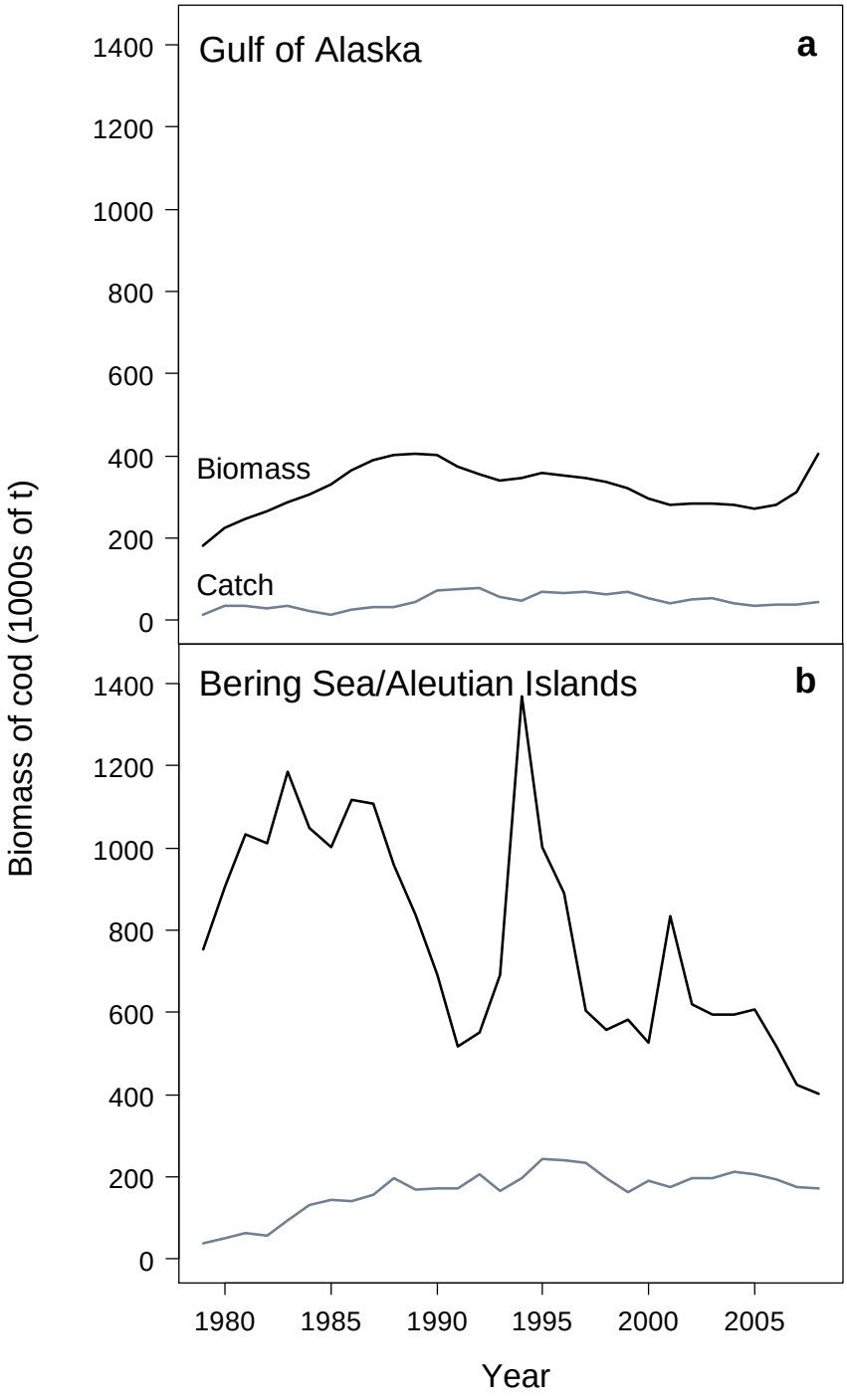

Fig. 1.3. Pacific cod biomass (age 3+ years) and catch trends from 1979-2008 in the (a) Gulf of Alaska and (b) eastern Bering Sea/Aleutian Islands fisheries management areas (data from NMFS 2009).

Beginning in 1964, the Japanese trawl fishery for pollock in the Bering Sea expanded and cod became an important bycatch species and an occasional target species when high concentrations were detected during pollock fishing operations. By the time the MFCMA went into effect in 1976, foreign catches of cod had consistently been in the 30,000-70,000 tonne range for a full decade. Cod catches in the late 1980s remained at well over 100,000 tonnes (Fig. 1.3). Presently, the cod stock is exploited by a multiple-gear fishery, including trawl, longline, pot and jig components. Trawlers take the largest share of the catch. During the two decades prior to passage of the MFCMA in 1976, the fishery for cod in the Gulf of Alaska was small, averaging around 3,000 tonnes per year. By 1976, catches had increased to 6,800 tonnes (Fig. 1.3). Pacific cod is now the third-most valuable commercial fish species in the U.S.; the value of the 2006 harvest was estimated at $197 million (NMFS 2009).

Seasons for the Pacific cod fishery are defined for hook-and-line gear (A season - January 1 to June 10, B season - June 10 to December 31), trawl gear (A season - January 20 to April 1, B season - April 1 to June 10, C season - June 10 to November 1), pot gear (A season - January 1 to June 10, B season - September 1 to December 31) and jig gear (A season - January 1 to April 30, B season - April 30 to August 31, C season - August 31 to December 31).

Approximately 40% of the cod catch is taken by trawling in the southeastern portion of the Bering Sea during the winter “A season” (NMFS 2009). The trawl fishery has historically been concentrated in an area of the continental shelf north of Unimak Island, where cod form dense spawning aggregations during the winter (Conners & Munro 2008). In the commercial fisheries, cod are first recruited at about 40 cm or age 3 years.

1.4.3 Atka mackerel

Atka mackerel are widely distributed along the continental shelf across the North Pacific Ocean from Asia to North America. In Alaska, their center of abundance is in the Aleutian Islands. Atka mackerel are substrate-spawning fish with male parental care. Single or multiple clumps of adhesive eggs are laid on rocky substrates in individual male territories within nesting colonies where males brood eggs for a protracted period. Nesting colonies are widespread across the continental shelf of the Aleutian Islands down to bottom depths of 144 m (Lauth et al. 2007b). In early June, a fraction of the adult males end schooling and diurnal behaviour and

begin aggregating and establishing territories on rocky substrate in nesting colonies (Lauth et al. 2007a). The spawning phase begins in late July, peaks in early September, and ends in mid-October (Lauth et al. 2007a).

Atka mackerel mature at 3-4 years and adults range in size from 28-33 cm. The 2000, 2002 and 2004 bottom trawl surveys and the fishery catch data revealed a strong east-west gradient in mackerel size, with the smallest fish in the west and progressively larger fish to the east. Most of the fish were from 36-47 cm long. They are found at depths up to 575 m, but concentrate at depths from 90-130 m. They display strong diel behaviour, with vertical movements away from the bottom occurring almost exclusively during daylight hours, presumably for feeding and little to no movement at night (Nichol & Somerton 2002).

Adult Atka mackerel in the Aleutian Islands consume a variety of prey, but principally calanoid copepods (40%) and euphausiids (25%), followed by squids (10%) and juvenile pollock (6%) (Yang 1999). They are consumed by a variety of piscivores, including groundfish (e.g., Pacific cod and arrowtooth flounder). Approximately 20% of the mackerel mortality rate is due to the fishery and 62% due to predation. Of the 62% of mortality due to predation, a little less than half was due to cod predation and one quarter due to sea lion predation. This translates to 100,000-120,000 tonnes/year of mackerel consumed by predatory fish (of which approximately 60,000 tonnes are consumed by cod) and 40,000-80,000 tonnes/year consumed by sea lions (NMFS 2009).

Atka mackerel biomass in the Aleutian Islands increased significantly after the mid-1980s, though the abundance of mackerel is currently decreasing (Fig. 1.4). Annual catches of mackerel in the Aleutian Islands increased during the 1970s, reaching a peak of over 24,000 tonnes in 1978. A mackerel population existed in the Gulf of Alaska primarily in the Kodiak, Chirikof and Shumagin areas, and supported a large foreign fishery through the early 1980s. By the mid-1980s, this fishery and presumably the population had all but disappeared. There has not been a directed fishery for Atka mackerel in the Gulf of Alaska since 1996.

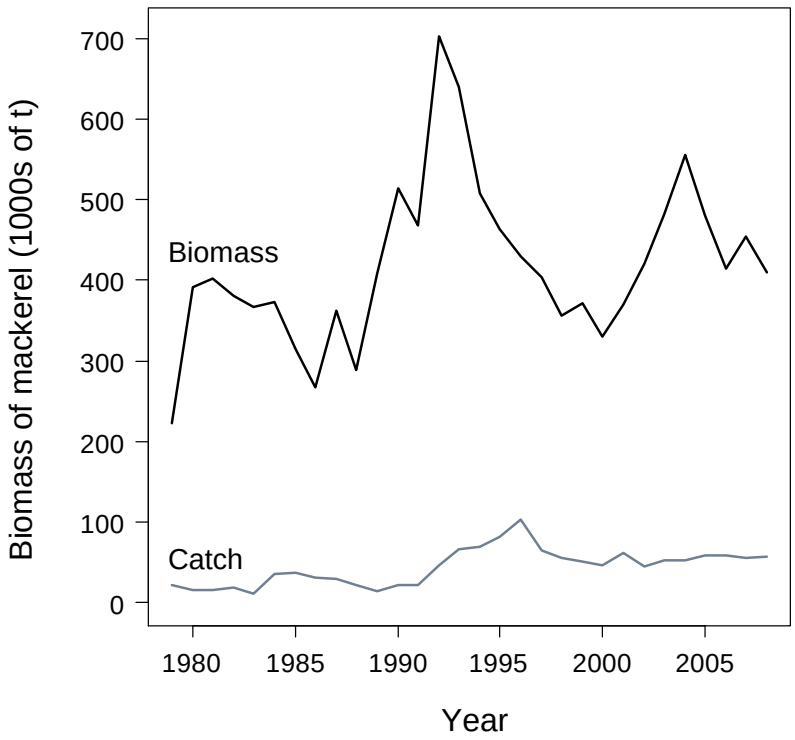

Fig. 1.4. Atka mackerel biomass (age 3+ years) and catch trends from 1979-2008 in the Aleutian Islands (data from NMFS 2009).

In June 1998, fishery regulations were amended to temporally and spatially disperse and reduce the level of mackerel fishing within sea lion critical habitat in the Aleutian Islands. Temporal dispersion was accomplished by dividing the Atka mackerel total allowable catch (TAC) into two equal seasonal allowances: an "A season" beginning January 20 and ending April 15, and a "B season" from September 1 to November 1. The mackerel fishery is prohibited from fishing inside sea lion critical habitat east of 178°W, while up to 60% of the TAC can be taken within critical habitat west of 178°W.

1.4.4 Fisheries management

Sea lions prey upon a number of commercially valuable, federally managed species of groundfish. The groundfish fisheries contribute over 40% of total U.S. landings annually, generating over $1 billion in annual revenues and supporting the seasonal employment of more than 12,000 workers on boats and in shore-based processing plants in Alaska (Berman 2007). Hence, there is considerable interest academically, and from conservation and management perspectives, in understanding the causes of decline in this iconic species. As the western stock

of sea lions continues to decline in some areas, fisheries managers may place additional controls on commercial fisheries as protective measures.

The U.S. Marine Mammal Protection Act of 1972 addressed the diminished status of many marine mammal populations and introduced mechanisms to limit their mortality by commercial fisheries operating inside the 3-200 nautical miles EEZ. In 1973, the U.S. Endangered Species Act (ESA) established rules to protect species considered to be threatened with or in danger of extinction. NMFS listed the Steller sea lion as a threatened species under the ESA in 1990 and established 3 nautical miles no transit zones around rookeries. In 1992, the agency further restricted trawl fishing within either 10 or 20 nautical miles (18.5 or 37 km) of rookeries. In 1993, NMFS designated ESA critical habitat within 20 nautical miles of 39 rookeries and 83 haulouts, and inside three foraging areas: Seguam Pass, Bogoslof and Shelikof. In 1997, the newly defined western stock of Steller sea lions was listed as endangered under the ESA in the region between Prince William Sound and the far western Aleutian Islands. In 2000, there was a court-ordered closure of Steller sea lion critical habitat to trawl fisheries and NMFS proposed a set of conservation measures to avoid jeopardy and mitigate adverse modifications of critical habitat. In 2002, NMFS implemented a set of regulations to change the spatial and temporal patterns of the pollock, cod and mackerel fisheries throughout the range of the western stock in U.S. waters. This suite of fishery conservation measures was intended to reduce fishing in nearshore critical habitat, reduce competition for prey and disperse fisheries spatially and temporally to avoid localised depletions of prey. The 2002 measures specifically identified those areas within 0-10 nautical miles of listed haulouts and rookeries as more important for foraging sea lions than waters from 10-20 nautical miles offshore.

1.5 Thesis aims and objectives

Competition between fisheries and a marine mammal species implies that marine mammals are limited by food availability and that their vital rates should change in response to changes in prey availability (Plaganyi & Butterworth 2005). The goal of my thesis was to determine whether a relationship could be detected between Steller sea lion population trends at 33 major rookeries in the Aleutian Islands, Bering Sea and western Gulf of Alaska and 1) prey availability or 2) the amount of commercial catch. I sought to improve on past studies of

potential competition between sea lions and commercial fisheries by creating localised estimates of prey biomass available that account for the accessibility of prey to sea lions and their foraging behaviour. I focused on three commercially important sea lion prey species that dominate the sea lion diet: walleye pollock, Pacific cod and Atka mackerel. Specifically, I tested whether there was a relationship between: (1) the biomass of pollock, cod or mackerel accessible (with and without fishery removals) to sea lions in summer, and the regional rates of sea lion population change at the 33 rookeries, and (2) the total localised biomass of pollock, cod or mackerel removed annually by fisheries and the annual rates of sea lion population change.

1.6 Thesis structure

My thesis is structured to ease publication of the manuscript chapter (Chapter 2). There is therefore some necessary redundancy between the three chapters. Chapter 1 provides an overview of the research topic and objectives, and descriptions of the species and fisheries involved. Chapter 2 is written as a self-contained manuscript with details on the methods, results and discussion of the main findings. Chapter 3 reviews and summarises the research conducted, with a discussion of the strengths and weaknesses of the research, potential applications of the research findings and comments on future research priorities. There are also 8 appendices that provide additional details about the models, data and methodologies that I used.

CHAPTER 2: STELLER SEA LIONS AND FISHERIES: COMPETITION AT SEA? [1]

2.1 Introduction

Steller sea lions *Eumetopias jubatus* declined by more than 80% in western Alaska between the 1970s and late 1990s (Merrick et al. 1987, Loughlin et al. 1992, Trites & Larkin 1996, Calkins et al. 1999), leading to the species being listed as threatened in 1990 under the U.S. Endangered Species Act. The western (west of 144°W longitude) stock of sea lions was subsequently listed as endangered in 1997 due to continued declines in the region (NMFS 2008b). One of the leading hypotheses to explain this decline is that large-scale fisheries in the Aleutian Islands, Bering Sea and Gulf of Alaska could have modified the abundance, composition and distribution of prey to the detriment of Steller sea lions (Braham et al. 1980, Alverson 1992, Trites & Donnelly 2003).

Commercial fishing is assumed to be a contributing factor in the decline of Steller sea lions because the expansion of groundfish fisheries for walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus* and Atka mackerel *Pleurogrammus monopterygius* roughly coincided with the period of decline (Braham et al. 1980, Merrick et al. 1987, Loughlin & Merrick 1989, Megrey & Westpestad 1990, Alverson 1991, Springer 1992, Hanna 2000). Fisheries for these species target some of the same sizes and age classes of fish eaten by sea lions (Lowry 1982, 1986, Alverson 1991, Zeppelin et al. 2004). There has thus been the potential for these groundfish fisheries to decrease sea lion foraging efficiency and compete with sea lions for prey by altering the abundance, composition and distribution of the available prey field. Reduced availability of important prey species could result in a diet that is insufficient to meet the energy requirements of sea lions (Alverson 1992, Trites & Donnelly 2003).

Evidence for the effects of commercial fisheries on Steller sea lion populations has previously been sought. Studies by Loughlin and Merrick (1989), Trites and Larkin (1992), Ferrero and Fritz (1994), Sampson (1995), Trites et al. (1999b), Dillingham et al. (2006), Hennen (2006) and Calkins (2008) have identified some correlations between catch rates and declines in

[1] A version of this chapter will be submitted for publication. Hui, T.C.Y., Gryba, R., Gregr, E.J., Joy, R. and Trites, A.W. Steller sea lions and fisheries: Competition at sea?

sea lion abundance. However, the correlations have tended to be inconsistent with the overall patterns of sea lion declines, and have been specific to particular time periods, geographic regions, prey species and gear types. For example, Sampson (1995) found that large winter catches of pollock occurred near sea lion rookeries that suffered severe declines in the early 1980s. However, very little pollock was caught in the regions surrounding rookeries that suffered declines in the late 1980s. Trites et al. (1999b) found that catches of halibut *Hippoglossus stenolepis*, pollock and cod were negatively correlated with sea lion abundance from the Alaskan peninsula through the Aleutian Islands (i.e., higher catches were associated with fewer sea lions), while higher catches of crab and shrimp occurred with higher numbers of sea lions. In contrast, Dillingham et al. (2006) observed a positive relationship between sea lion population trends and trawl fishing effort (i.e., more fishing – more sea lions), but a negative relationship with longline fishing effort. These results are equivocal regarding the impacts of fishing activities on sea lions. Moreover, correlations between catch and abundance do not give information about the underlying cause of declines in sea lion numbers. Determining whether fisheries have negatively affected sea lions through reductions in prey abundance requires determining the effects of fisheries on the quantity of prey available to sea lions.

Fisheries may not only reduce the overall levels of prey biomass, they can also remove or disperse large aggregations of fish from an area (Baraff & Loughlin 2000, Sease et al. 2001, Shima et al. 2002). These removals can cause localised depletion — intense fishing pressure leading to disproportionately large reductions in local densities of the target fish relative to the overall harvest rate (Conners & Munro 2008). Localised depletion occurs when fish are removed faster than immigration and recruitment can replace removed individuals (Battaile & Quinn 2006). Localised depletions can negatively impact sea lions by reducing foraging efficiency, leading to deterioration in physical condition and population declines.

Assessing fisheries impacts on sea lions requires assessing localised prey abundance, particularly around rookeries and haulouts (Trites & Larkin 1992). Unfortunately, the broad-scale estimates of total prey abundance, which have been used in many studies on potential competition between sea lions and fisheries (e.g., Cornick et al. 2006b, Guenette et al. 2006), may have little to do with the prey available to foraging sea lions. Not all prey may be available to sea lions due to spatial and temporal differences in habitat and the distribution of prey.

Competition between sea lions and fisheries (if it occurs) is therefore more likely to occur and be detected on a local level than at the broad scale.

Accessibility — the likelihood of a sea lion foraging at a particular distance from its rookery or haulout — varies with distance from its terrestrial resting place. Satellite telemetry has shown that breeding female sea lions forage closer to their rookeries during summer compared to winter (Merrick et al. 1994, Merrick & Loughlin 1997), probably due to the need to regularly nurse a dependent pup every 1-4 days (Milette & Trites 2003, Davis et al. 2006). Satellite telemetry has also shown a tendency for juveniles (1-3 years old) to remain closer to shore (Raum-Suryan et al. 2004, Fadely et al. 2005, Rehberg & Burns 2008, Rehberg et al. 2009, Winter et al. 2009). These observations suggest that prey located closer to shore are likely more important to foraging sea lions than prey located further away. Thus it is important to assess the accessibility of prey at varying distances from rookeries and haulouts, in addition to estimating the local abundance of available prey.

Steller sea lions continued to decline through the past decade (2000-2009) at a number of breeding sites (particularly in the Aleutian Islands), though the rate of decline was not as severe as during the 1980s and 1990s. Continued interactions with fisheries are believed by some to be causing the declines of populations in some regions while limiting recovery at other sites. We sought to improve on past studies that attempted to assess potential competition between sea lions and commercial fisheries by estimating the fine-scale local abundance of prey accessible to sea lions. We focused on three commercially important fish species that dominated the diet of the declining sea lion populations: walleye pollock, Pacific cod and Atka mackerel.

Competition between fisheries and sea lions implies that sea lion populations are limited by the food available and hence, it should be possible to demonstrate a response of some vital population parameter to a change in prey availability. We therefore sought to determine whether there was a relationship between the availability of prey, the amounts of fish commercially caught, and the differing rates of sea lion population change at 33 major rookeries (breeding sites) from the declining western stock in Alaska. We focused on the summer breeding season (June-July), a critical period for breeding females, pups and recently weaned juveniles. Specifically, we tested whether there was a relationship between: (1) the biomass of pollock, cod or mackerel accessible to sea lions in summer with and without fishery removals accounted for

and the regional rates of sea lion population change at the 33 rookeries, and (2) the total localised biomass of pollock, cod or mackerel removed annually by fisheries and the annual rates of sea lion population change.

2.2 Methods

The relationships between sea lion population trends, fishery catches, and the biomass of prey accessible to sea lions at individual rookeries from 2000-2008 were explored using three primary sources of data: (1) aerial and ground census counts of sea lions made at rookeries by the U.S. National Marine Fisheries Service (NMFS), (2) fisheries catch of pollock, cod and mackerel obtained from the North Pacific Groundfish Observer Program (NPGOP-NMFS), and (3) available prey (pollock, cod and mackerel) predicted from spatial models (Gryba et al. 2011) based on bottom trawl fish survey data (NMFS). Data were compiled and synthesised using ArcGIS 9.2 (ESRI, Redlands, CA) and IDRISI Kilimanjaro. All analyses were performed at a 9 x 9 km^2 resolution for the Aleutian Islands, Bering Sea and Gulf of Alaska using the Alaska Albers projection (NAD27). All statistical analyses were performed using R 2.8.1 (R Development Core Team 2009) and the nlme library from Pinheiro and Bates (2000).

2.2.1 Sea lion population sizes and trends

We assessed population trends at each of the 33 major sea lion rookeries from the declining western stock of Steller sea lions (Fig. 2.1) – 15 west of Samalga Pass (hereafter referred to as Aleutian Island rookeries) and 18 east of Samalga Pass (hereafter referred to as Gulf of Alaska rookeries). We grouped the Aleutian Island rookeries into those east and west of Amchitka Pass and grouped the Gulf of Alaska rookeries into those east and west of Unimak Pass (Fig. 2.1). The sea lions at Sea Lion Rock (Amak) were grouped with the western Gulf of Alaska rookeries because of their location north of the Alaskan Peninsula in the Bering Sea (Fig. 2.1). The sea lions from this rookery thus forage in habitat that is more similar to that of the other western Gulf of Alaska rookeries in the Gulf of Alaska and Bering Sea. We chose Amchitka, Samalga and Unimak Passes as regional breaks between the rookeries because of the known biological and oceanographic differences between these regions (Call & Loughlin 2005, Hunt & Stabeno 2005, Ladd et al. 2005, Logerwell et al. 2005, Sinclair et al. 2005, Trites et al. 2007b).

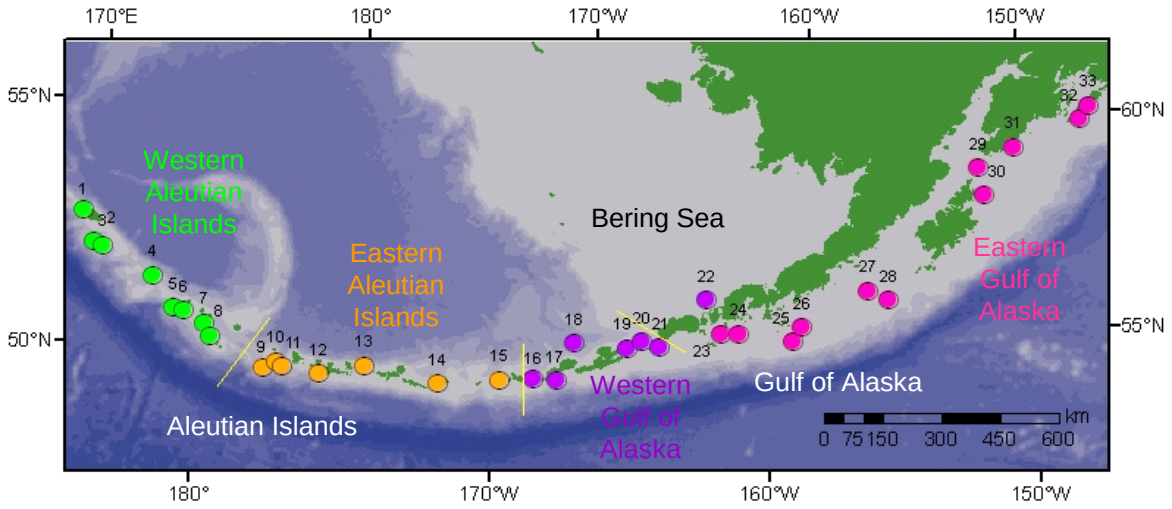

Fig. 2.1. The locations of the 33 Steller sea lion rookeries studied: (1) Attu Cape Wrangell (2) Agattu Gillon Point (3) Agattu Cape Sabak (4) Buldir (5) Kiska Cape St Stephen (6) Kiska Lief Cove (7) Ayugadak (8) Amchitka Column Rock (9) Ulak Hasgox Point (10) Tag (11) Gramp Rock (12) Adak Lake Point (13) Kasatochi North Point (14) Seguam Saddle Ridge (15) Yunaska (16) Adugak (17) Ogchul (18) Bogoslof Fire Island (19) Akutan Cape Morgan (20) Akun Billings Head (21) Ugamak Round (22) Sea Lion Rock Amak (23) Clubbing Rocks North (24) Pinnacle Rock (25) Chernabura (26) Atkins (27) Chowiet (28) Chirikof (29) Sugarloaf (30) Marmot (31) Outer Pye (32) Wooded Fish (33) Seal Rocks. Rookeries were grouped into 4 regions (western Aleutian Islands – green, eastern Aleutian Islands – orange, western Gulf of Alaska – purple, eastern Gulf of Alaska – pink).

Sea lions at the 33 selected rookeries were counted approximately every two years during the breeding season (June-July), and had different rates of population declines and increases. Annual population estimates of pups (<1 year old) and non-pups (>1 year old) from 2000-2008 were obtained from Winship and Trites (2006) and Battaile and Trites (unpublished manuscript) who modelled population trajectories using Leslie matrix methods from raw counts available from the National Marine Mammal Laboratory (NMML-NMFS) Steller sea lion databases (http://www.afsc.noaa.gov/nmml/alaska/sslhome/databases). We used their quantitative population models to estimate population sizes in years where counts were not available (pups: 2000, 2006-2008; non-pups: 2001, 2003, 2005) and to smooth out yearly noise in the count data that likely reflected observation error (Appendix 1).

2.2.2 Prey biomass distributions

Predicted prey biomass distributions were obtained from Gryba et al. (2011) (e.g., Figs. 2.2). These biomass distributions were derived from NMFS bottom trawl survey data using

Generalised Least Square models to determine the relationships between survey catch per unit effort (CPUE for pollock, cod and mackerel) and bathymetry, modelled oceanographic data, and remotely sensed data of the areas sampled at a 9 x 9 km^2 resolution throughout the Aleutian Islands, Bering Sea and Gulf of Alaska (Appendix 2). Biomass predictions were available for pollock, cod and mackerel in the Aleutian Islands for 2000, 2002 and 2004; and for pollock and cod in the Gulf of Alaska and Bering Sea for 2001 and 2003 (e.g., Figs. 2.2). The biomasses predicted were standing biomass of age 1+ year-old pollock, cod and mackerel in June and July (the period during which the trawl surveys were conducted). Biomass predictions were limited to depths less than 600 m, the maximum depth of the trawl surveys and near the maximum observed haul taken by fisheries. We assumed that biomass in areas deeper than 600 m was negligible as pollock, cod and mackerel are not known to reach depths greater than 600 m (Shima et al. 2000, Nichol & Somerton 2002, NMFS 2009). CPUE was interpolated using ordinary kriging for the few locations (grid cells) within the NMFS survey areas (Aleutian Islands, Bering Sea and Gulf of Alaska) that had missing oceanographic data. We then averaged the June and July CPUE distributions for each year to obtain an overall summer CPUE distribution, and predicted biomass by distributing the total NMFS biomass estimates of pollock, cod and mackerel for the summer of each year throughout the respective fisheries survey areas in proportion to the CPUE within each grid cell (Appendix 2).

2.2.3 Fisheries Catch

NPGOP-NMFS places trained observers on commercial fishing boats to monitor the quantity and composition of commercial catches. The level of observer coverage depends mainly on the boat's length and fishing gear type. Trawl, longline and pot vessels longer than 38.1 m are required to have observers on board 100% of the time. Vessels between 18.3 m and 38.1 m in length are required to have observers on board at least 30% of the time and vessels under 18.3 m in length are not required to have observers on board. Although this means that information on catches taken by vessels under 38.1 m in length is limited, the majority of pollock, cod and mackerel is caught by vessels longer than 38.1 m (NMFS 2008a, Appendix 3). Measures of fishing intensity recorded for pollock, cod and mackerel caught from 2000-2004 included the estimated biomass caught in each haul, CPUE and the location of each haul.

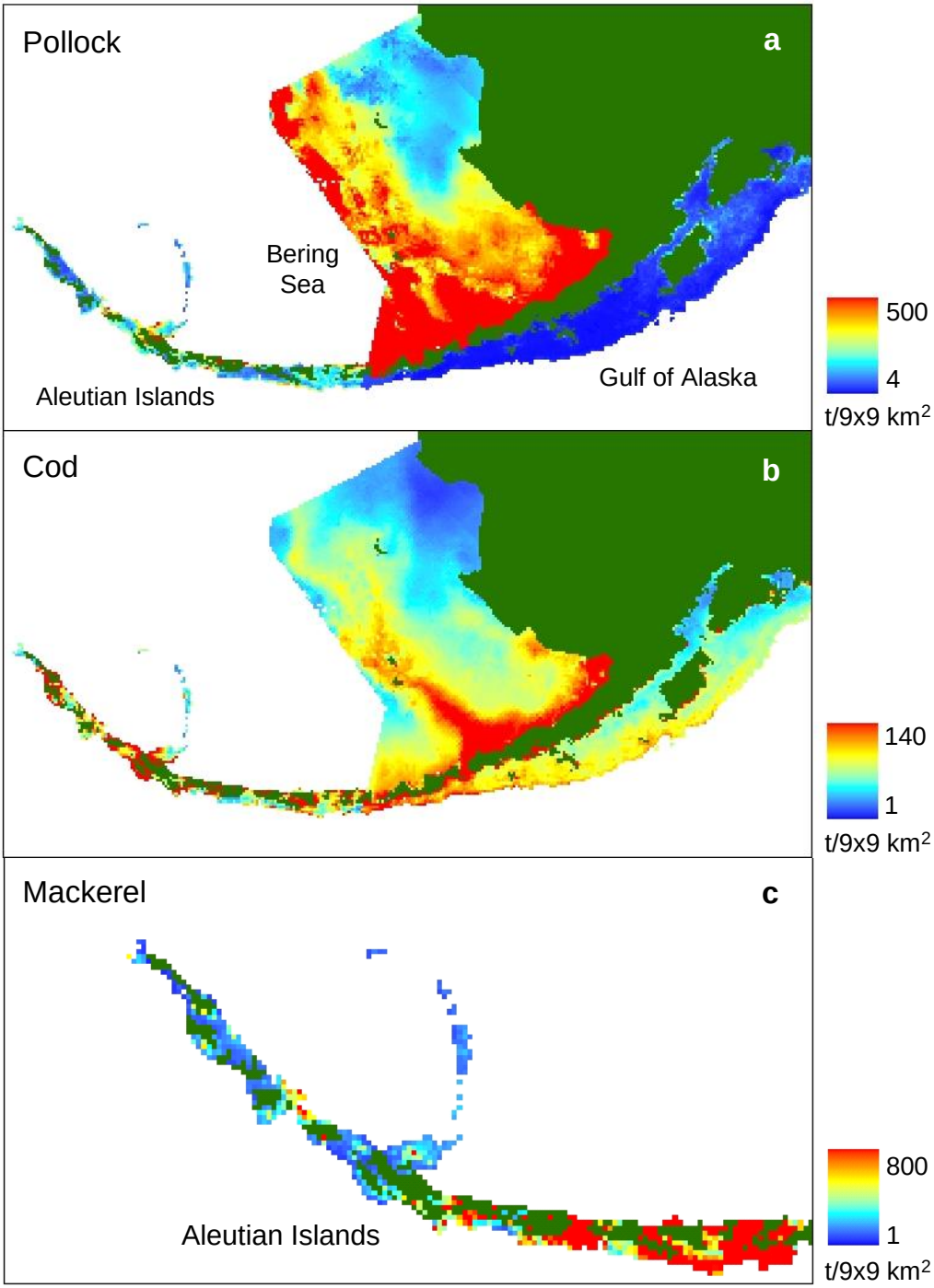

Fig. 2.2. Predicted biomass distributions (t/9x9 km2 grid cell) of (a) walleye pollock available in the Aleutian Islands (2000), Bering Sea (2001) and Gulf of Alaska (2001), (b) Pacific cod available in the Aleutian Islands (2002), Bering Sea (2003) and Gulf of Alaska (2003) and (c) Atka mackerel available in the Aleutian Islands (2004) (modified from Gryba et al. 2011).

2.2.4 Fisheries reduced prey biomass distributions

We used three methods to remove fisheries catches from the predicted distributions of prey biomass to examine the potential for fisheries to cause localised depletions of sea lion prey. First, we deducted the biomasses of pollock, cod and mackerel caught in June and July of each year from the summer (average of June and July) prey biomass distributions based on the assumption that the distribution of prey biomass was not significantly different between June and July (Method 1). Second, we assumed that the distribution of prey biomass in July was the same as in June, and removed the biomasses of pollock, cod and mackerel caught in June and July of each year from the June prey biomass distributions (Method 2, e.g., Fig. 2.3). Methods 1 and 2 assumed fishing removals caused a local reduction in fish abundance in the immediate vicinity of fishing and that this reduction remained geographically stable over June and July. Thus, Method 1 is an average of the June and July distributions, while Method 2 assumes that the distribution of fish in July was what remained following fishing in June.

For Method 3, we assumed that catches at any one location drew biomass proportionately from all locations within the same fisheries survey area — and therefore deducted the biomasses of pollock, cod and mackerel caught in June and July of each year from the respective trawl survey biomass estimates (Appendix 2, Table A2.1), and distributed these fisheries-reduced prey biomasses throughout the respective fisheries survey areas (Aleutian Islands, Eastern Bering Sea or Gulf of Alaska) in proportion to the predicted July CPUE value at each location (Method 3). Method 3 assumed that fishing reduced the overall biomass of prey available, but had little effect on the local availability of prey (Method 3). All three methods of removing catch were intended to predict the biomass distributions of pollock, cod and mackerel at the end of summer (end of July) after accounting for the total amount of fisheries removals in summer (June and July).

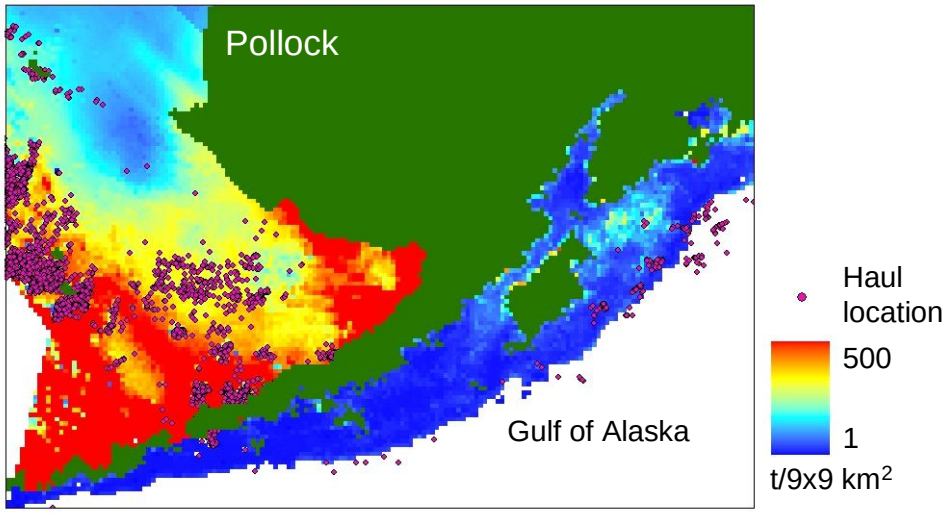

Fig. 2.3. Predicted biomass of walleye pollock (t/9x9 km2 grid cell) in June 2001. Purple points indicate haul locations from commercial fishing vessels in June and July 2001. The biomass of pollock removed at each of these haul locations was subtracted from the predicted biomass available at the same locations (fisheries reduced prey biomass distribution Method 2).

2.2.5 Accessibility model

Accessibility of prey to Steller sea lions varies with distance from a sea lion's terrestrial resting place. Satellite telemetry has shown that sea lions tend to forage closer to their rookeries in summer than in winter (Merrick & Loughlin 1997, Loughlin et al. 2003, Raum-Suryan et al. 2004). At-sea locations of sea lions as determined from satellite telemetry were used to predict the likelihood of sea lions occurring at different distances from their haulouts and rookeries assuming that the animals captured and tagged are representative of an average sea lion, and that the movements of tracked animals are not affected by the tags.

At-sea distributions of telemetry locations for individual sea lions were obtained from NMFS and the Alaska Department of Fish and Game (ADFG). They included the numbers of locations recorded per sea lion at 1 nautical mile intervals from the nearest rookery or haulout shoreline (straight line distance 'as the crow flies'), as well as the cumulative proportions of locations with cumulative distance from shore (at 1 nautical mile intervals). The tagged sea lions (n=116 pups and juveniles) were tracked from 2000-2005 in the Aleutian Islands and Gulf of Alaska primarily during spring and summer, with a few tracked in the fall of 2001. The tags typically transmitted data for 1-3 months (Brian Fadely, NMML-NMFS, personal

communication) and yielded 2-523 locations per sea lion (124 ± 44 locations, mean ± s.e., n=116 sea lions). The data were filtered for quality and estimated to be within 150 to 1,000 m of the true location of the animal. We inspected the frequency distribution of the data and retained only those records from animals that were located at sea 30 times or more for further analysis. The foraging locations of sea lions seen only a few times at sea were considered insufficient to accurately represent the at-sea distribution of animals. We also screened the remaining records for outliers.

The tracked sea lions ranged in age from 3-28 months (13 ± 5 months, mean ± s.e.). Sea lions have been observed making independent trips away from their resting sites at 7-9 months old (Trites & Porter 2002), and tend to reduce suckling behaviour in late spring and early summer around their first birthday, suggesting that a large portion of sea lions wean around this time (Marcotte 2006; Trites et al. 2006). We therefore grouped the telemetry records into two age categories: <10 months of age and >10 months of age. For each sea lion, we calculated the proportion of locations in 1 nautical mile intervals from the nearest rookery or haulout shoreline. From these individual proportions, we calculated an average proportion of locations in each distance interval of the sea lions in each age group, and tested for possible differences between sexes and regions (Aleutian Islands versus Gulf of Alaska).

We inspected the retained sea lion telemetry records and fitted models to the average proportions of locations in each 1 nautical mile distance interval by age group, region and sex. We transformed the data where necessary to look for similarities in trends between distance intervals. The fitted models allowed us to calculate a continuous distribution of accessibility values (average proportions of locations) with distance from the nearest rookery or haulout shoreline.

2.2.6 Combining prey accessibility with available prey biomass

The tendency for sea lions to forage close to their rookeries in summer suggests that prey closer to rookeries are more important and more accessible than prey further away. This implies that the prey biomass available to sea lions at a rookery should be scaled to reflect differences in accessibility between locations as a function of distance from their terrestrial resting places.

We selected the fitted model which best described the observed distance of sea lions from shore and applied this accessibility model to each of the 33 study rookeries across 9 x 9 km^2

grids using a distance function (Eastman 2001) to calculate the straight line distance from the center of each location (grid cell) to each rookery (Appendix 4). The rookery (starting) grid cells were assigned a value of 2.25 km — the estimated mean distance of an 'average' sea lion in the starting grid cells from the rookeries (center points of starting grid cells) (Appendix 4). We thereby determined the likelihood that a sea lion would forage in any given grid cell as a function of its distance from the nearest rookery (calculated using the selected accessibility model equation). To calculate the likelihood of a sea lion occurring within each grid cell, we divided the relative accessibility value of each grid cell by the sum of all accessibility values within the foraging arena of each rookery. Land barriers were excluded from the analysis (grid cells containing mostly land were given an accessibility value of 0). Thus the final accessibility values for the grid cells in each rookery's foraging arena summed to 1.

We multiplied the accessibility values within each rookery's foraging arena by the predicted prey biomass at the same locations. This gave prey resources closer to the rookeries more importance (higher accessibility) to sea lions than prey located further away. Combining the prey biomass distributions with the accessibility model allowed the biomass of pollock, cod and mackerel accessible to the sea lions from each rookery to be estimated. We then summed the biomass of pollock, cod and mackerel contained within the grid cells accessible to the sea lions at each rookery from 2000-2004 (2000, 2002 and 2004 in the Aleutian Islands; 2001 and 2003 in the Gulf of Alaska).

We compared the total biomass of pollock, cod and mackerel within 10, 20 and 50 km of each rookery with the biomass we predicted to be accessible to sea lions (from our accessibility model) from 2000-2004 (2000, 2002 and 2004 in the Aleutian Islands; 2001 and 2003 in the Gulf of Alaska). Thus we considered the possibility that accessibility of prey declined with distance from shore, as well as the possibility that all prey within 10, 20 and 50 km of shore was available and equally accessible to the sea lions (i.e., accessibility value of each grid cell within the selected ringed distances was 1). Beyond these selected distances, the likelihood of sea lion foraging was assumed to be 0. These ringed distances approximated the reported mean straight line foraging distances of adult females and juveniles from rookeries and haulouts in summer (Appendix 5) and were within the spatial extents of the prey biomass distributions.

2.2.7 Statistical analyses

Spatial autocorrelation

Rookeries that are close to each other tend to have similar population sizes and trends over time (Call & Loughlin 2005, Sinclair et al. 2005, Trites et al. 2007b) and are also likely to have similar accessible prey biomasses. To reduce spatial autocorrelation between rookeries and prevent the total biomass of prey accessible to the rookeries from exceeding the predicted biomass available at the same locations, we grouped rookeries that were within 50 km of each other (Appendix 5) into clusters. We also analysed semivariograms of the differences in average annual rates of sea lion population change from 2000-2008 and the distances between rookeries to determine whether our groupings of rookeries and the 50 km distance rule selected were reasonable (sufficient for reducing potential spatial autocorrelation) (see Appendix 6 for additional explanation). Thus we assumed that sea lions at these rookery clusters shared a common prey base.

We used a weighted average to calculate the prey biomass accessible to the sea lions in each rookery cluster,

(1) $$\frac{N_A \, fish_A}{N_A + N_B} + \frac{N_B \, fish_B}{N_A + N_B}$$

for a cluster consisting of rookeries *A* and *B*, where N_A and N_B are the population size estimates of pups or non-pups at rookeries *A* and *B* respectively, and $fish_A$ and $fish_B$ are the biomasses of pollock, cod or mackerel accessible to rookeries *A* and *B* respectively.

Relationships between prey biomass and sea lion population change

We used linear mixed-effects (LME) models to determine whether there was a relationship between the annual rate of sea lion population change and the biomass of pollock, cod or mackerel accessible to each rookery (or rookery cluster) and the region in which a rookery is located (eastern or western Aleutian Islands; or eastern or western Gulf of Alaska). LME models allowed us to characterise the variation within rookeries relative to the mean of all rookeries while considering the correlation between repeated measurements within the same rookery. The fixed effects explored included the biomass of pollock, cod or mackerel accessible to each rookery (or rookery cluster) and the region in which a rookery is located. Repeated

measurements on each rookery across years were treated as a random effect for all models. The models fitted were of the general form:

(2) $$r_{i,j,k} = \beta_0 + \beta_{region} region_k + \beta_{fish} fish_{i,j,k} + \beta_{fish:region} fish_{i,j,k} : region_k + b_{j,k} + \varepsilon_{i,j,k}$$

where $r_{i,j,k}$ is the annual rate of sea lion population change (pups or non-pups) in the ith year (2000, 2002 or 2004 in the Aleutian Islands; 2001 or 2003 in the Gulf of Alaska) at the jth rookery (or rookery cluster) in the kth region (eastern or western Aleutian Islands; or eastern or western Gulf of Alaska),

β_0 is the regression intercept,

β_{region} is the regression coefficient for regional effects

$region_k$ is the region specific intercept used to test for differences between regions

β_{fish} is the regression coefficient for accessible prey biomass (pollock, cod or mackerel),

$fish_{i,j,k}$ is the biomass of pollock, cod or mackerel accessible in the ith year to the jth rookery (or rookery cluster) in the kth region,

$\beta_{fish:region}$ is the regression coefficient for the interaction between accessible prey biomass and region,

$b_{j,k}$ is the random effect associated with the jth rookery (or rookery cluster) in the kth region, assumed to be independent from the other rookeries,

and $\varepsilon_{i,j,k}$ is the independent, homogenously distributed within-rookery error associated with the jth rookery (or rookery cluster) in the kth region in the ith year, assumed to be independent of the random effects.

The annual rate of sea lion population change $r_{i,j,k}$ was calculated as

(3) $$\ln\left(\frac{N_{i+1,j,k}}{N_{i,j,k}}\right)$$

where $N_{i,j,k}$ is the population size estimate of non-pups or pups (which do not subsist on fish, but are an indication of numbers of lactating females) in the ith year at the jth rookery (or rookery cluster) in the kth region. The annual rate of sea lion population change at rookery clusters was calculated as

$$(4) \qquad \ln\left(\frac{N_{A,i+1,j,k} + N_{B,i+1,j,k}}{N_{A,i,j,k} + N_{B,i,j,k}}\right)$$

for a cluster consisting of rookeries *A* and *B*, where $N_{A,i,j,k}$ and $N_{B,i,j,k}$ are the population size estimates of pups or non-pups at rookeries *A* and *B* respectively in the ith year at the jth rookery cluster in the kth region. Annual rates of sea lion population change were log transformed to normalise the data and homogenise the distribution of the variances (within-rookery errors).

Region was included as a fixed effect in the models because much of the variability in Steller sea lion population trends and accessible prey biomasses between rookeries can be attributed to regional differences in oceanography (Call & Loughlin 2005, Hunt & Stabeno 2005, Trites et al. 2007b) and diet (Sinclair & Zeppelin 2002). As variability in population change was greater among rookeries in the western Aleutian Islands than in the eastern Aleutian Islands (heterogeneity of variances), we chose a model that incorporated regional variances as a measure of within-rookery errors. We fit separate models for the (1) Aleutian Island and Gulf of Alaska rookeries, (2) pup and non-pup population changes, (3) each of the three prey species, (4) each of the three predicted distributions of prey, and (5) for each of the chosen distances and the accessibility model. All 160 models were run using the maximum likelihood method and the intercept was allowed to vary for each rookery or rookery cluster during model optimisation.

For each analysis, the best model in terms of fixed effect factors (simplest model with the fewest number of parameters which could explain most of the variation in sea lion population change) was determined using likelihood ratio tests (LRTs) and Akaike's information criterion (AIC). An Analysis of Variance (ANOVA) performed on two nested models (the simpler model nested within the more complex model) produced a LRT that compared the likelihoods of the models in explaining the relationship between the independent and dependent variables. AIC was calculated from the number of parameters and the likelihood function of the model. It not only

assessed model goodness of fit, but also included a penalty that increased as a function of the number of estimated parameters. This penalty discouraged model overfitting.

We investigated more general or long-term relationships between sea lion population trends and accessible prey biomasses by comparing the average annual rate of sea lion population change (pups or non-pups) from 2000-2008 with the average biomass of pollock, cod or mackerel accessible to each rookery (or rookery cluster) across all years (2000, 2002 and 2004 in the Aleutian Islands; 2001 and 2003 in the Gulf of Alaska) using the multiple regression model:

(5) $$\lambda_{j,k} = \beta_0 + \beta_{region} region_k + \beta_{fish} fish_{j,k} + \beta_{fish:region} fish_{j,k} : region_k + \varepsilon_{j,k}$$

where $\lambda_{j,k}$ is the average annual rate of sea lion population change (pups or non-pups) from 2000-2008, calculated from linear regressions of log transformed population estimates from Winship and Trites (2006) and Battaile and Trites (unpublished manuscript), at the jth rookery (or rookery cluster; average annual rates of change at rookery clusters were calculated from the total estimated population size of each cluster's constituent rookeries) in the kth region (eastern or western Aleutian Islands; or eastern or western Gulf of Alaska),

β_0 is the regression intercept,

β_{region} is the regression coefficient for regional effects

$region_k$ is the region specific intercept used to test for differences between regions

β_{fish} is the regression coefficient for average accessible prey biomass (pollock, cod or mackerel),

$fish_{j,k}$ is the average biomass of pollock, cod or mackerel accessible across all years (2000, 2002 and 2004 in the Aleutian Islands; 2001 and 2003 in the Gulf of Alaska) to the jth rookery (or rookery cluster) in the kth region,

$\beta_{fish:region}$ is the regression coefficient for the interaction between average accessible prey biomass and region,

and $\varepsilon_{j,k}$ is the independent, homogenously distributed error associated with the jth rookery (or rookery cluster) in the kth region.

Separate models were fitted for (1) pup and non-pup population change, (2) each of the three prey species, (3) each of the three types of prey distributions, and (4) for each of the chosen distances and the accessibility model (total of 96 models). Again, the simplest model with the fewest number of parameters which could explain most of the variation in the average annual rate of sea lion population change was determined using LRTs and AIC. F tests were used to determine the significance of the regression coefficients. All results are reported as mean ± standard error; significance tests were conducted at the $\alpha = 0.05$ level.

We conducted post hoc power analyses to determine the statistical power of our models to detect non-significant relationships between accessible prey biomass, fishing and sea lion numbers (i.e., that we did not make Type II errors). We calculated the power of our models using the F distribution, as recommended by Murphy and Myors (2004), and set the desired minimum effect size that we wanted to detect equal to 1% of the variance in sea lion population change. Thus we tested the hypothesis that changes in prey biomass could account for less than 1% of the variance in sea lion population change. We chose this small effect size because relatively small effects of prey biomass on sea lion population change are of interest to the scientific community. Choosing a smaller effect size such as 0 did not seem reasonable given that prey biomass is bound to have some effect on sea lion numbers—the question is whether it is small enough to be negligible.

Relationship between fisheries catch and sea lion population change

We wanted to test whether there was a relationship between the annual biomass of pollock, cod and mackerel caught by fisheries, and the annual rates of sea lion population change. However, the prey biomass distributions were only available for June and July in alternating years between the Aleutian Islands and Gulf of Alaska, unlike the catch data that were available year round every year in both the Aleutian Islands and Gulf of Alaska. Analysing catch distributions outside the Steller sea lion's breeding season may be important as substantial fishing for pollock, cod and mackerel occurs in fall and winter (Appendix 7). Analysing catch data also gives an indication of prey availability in high biomass areas where fishing and

probably sea lion foraging are most intense. We therefore compared the total biomass of pollock, cod or mackerel removed annually by fisheries to the annual rates of sea lion population change.

The biomass of pollock, cod and mackerel caught by fisheries within 10, 20, 50 and 100 km of each rookery was summed annually for each rookery from 2000-2004 (e.g., Fig. 2.4). The 100 km distance was included as Steller sea lions travel further than 50 km in winter (Appendix 5). We used the same rookery clusters and associated formulas to minimise spatial autocorrelation. Fisheries catch was then compared to sea lion population change using LME and multiple regression models similar to Models 2 and 5 above, except that we used the biomass of pollock, cod or mackerel caught annually by fisheries in place of accessible prey biomass in the model equations. We analysed catch relationships with sea lion population change in all four regions (eastern and western Aleutian Islands; eastern and western Gulf of Alaska) together as catch data were available in all regions every year from 2000-2004. Separate models were fitted for (1) pup and non-pup population change, (2) each of the three prey species and (3) selected distances (24 yearly LME and 24 long-term average multiple regression models). The biomass of Atka mackerel caught was only considered for the Aleutian Island rookeries as there has not been a directed fishery for mackerel in the Gulf of Alaska since 1996. We conducted post hoc power analyses for all these catch models using the same method and criteria described above for the prey biomass models.

2.3 Results

2.3.1 Sea lion population trends and fishery catches

The decline of the western stock of Steller sea lions from 2000-2008 was largely due to the continued declines among sea lions using the Aleutian Island rookeries (Fig. 2.5a). Mean annual rates of change for all rookeries combined in the Aleutian Islands were -1.7% for non-pups and -1.9% for pups. In contrast, sea lions in the Gulf of Alaska increased at an overall annual rate of 2.4% for non-pups and 2.8% for pups. Rookery sizes tended to be smaller in the Aleutian Islands than in the Gulf of Alaska, averaging 215 pups and 366 non-pups in the Aleutians, and 326 pups and 588 non-pups in the Gulf.

Examination of the semivariograms of the differences in average annual rates of sea lion population change from 2000-2008 and the distances between rookeries revealed that there was a

gradual increase in similarity in population trends as the distances between rookeries decreased (Appendix 6). Population trends at rookeries in the Gulf of Alaska tended to become more similar with one another as the distances between rookeries decreased, indicating the possibility

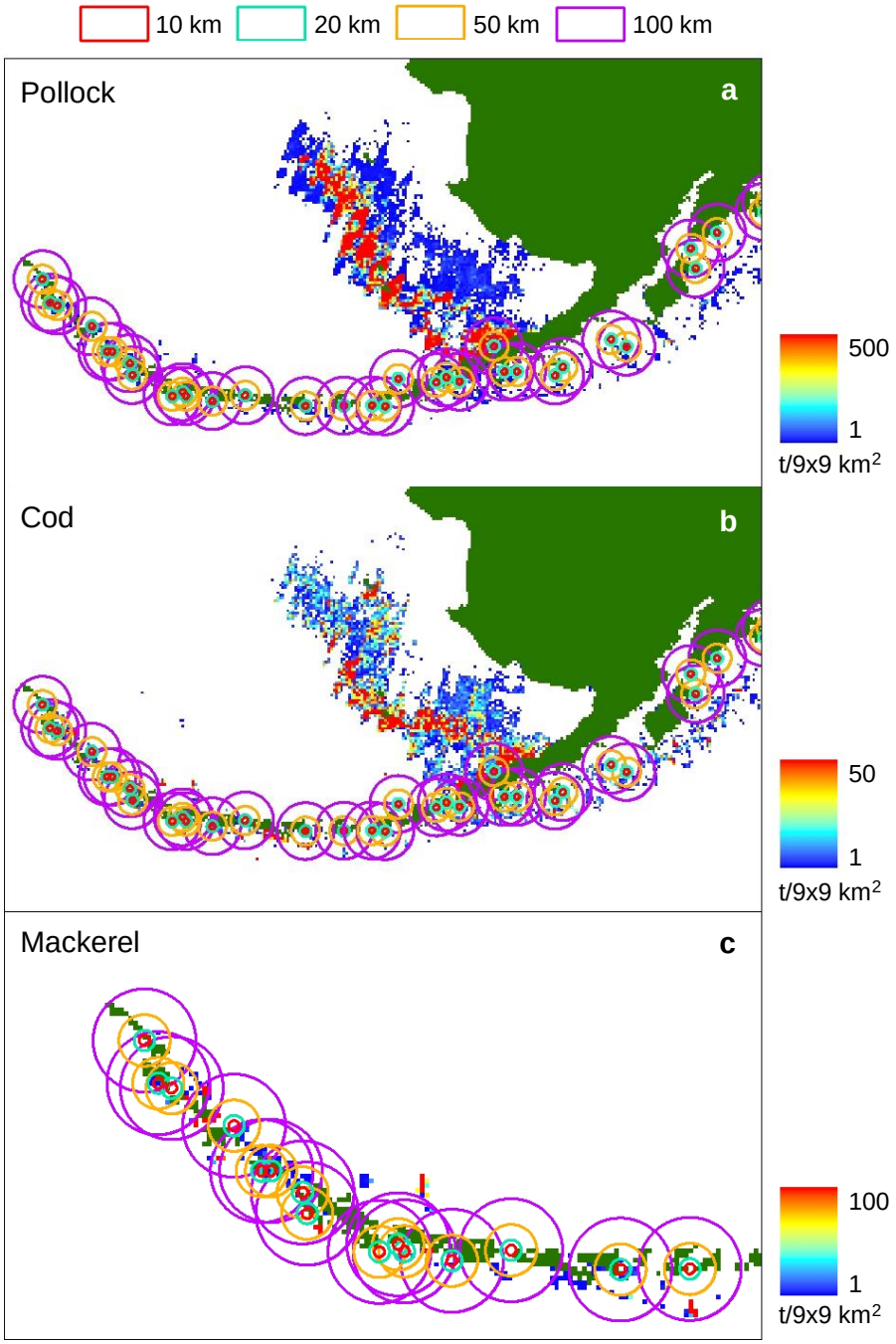

Fig. 2.4. Annual biomass (t/9x9 km2) of (a) walleye pollock (2003), (b) Pacific cod (2002) and (c) Atka mackerel (2004) caught. Total amounts removed within 10, 20, 50 and 100 km of each rookery (red, cyan, orange and purple rings respectively) were calculated by summing the total biomass of catches within each of the respective rings.

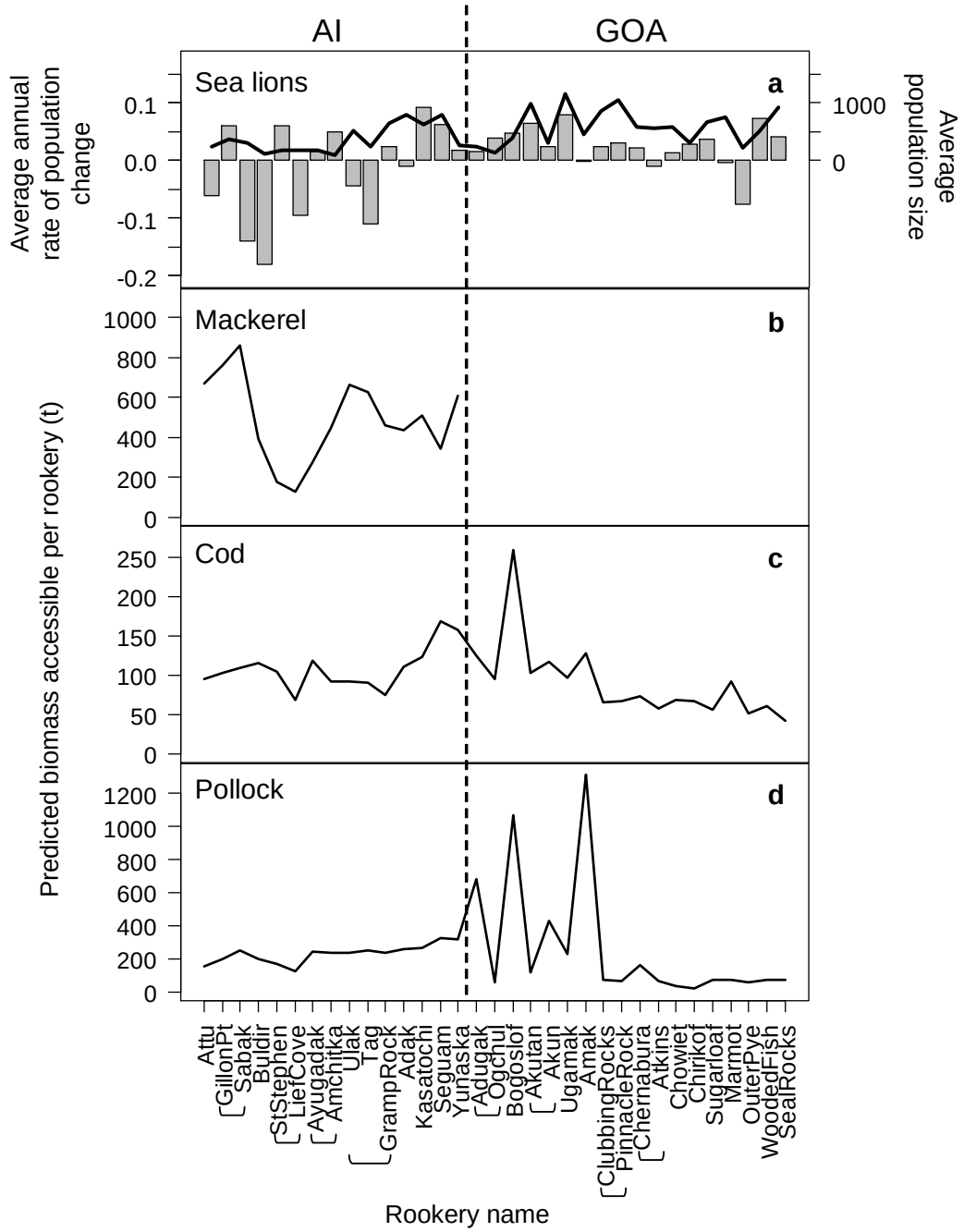

Fig. 2.5. Comparisons between the average numbers of non-pup Steller sea lions, annual rate of sea lion population change and predicted amounts of groundfish accessible to sea lions at each of the respective rookeries. (a) Average non-pup population change and population size from 2000-2008, (b) average biomass of Atka mackerel accessible (tons), (c) average biomass of Pacific cod accessible (tons) and (d) average biomass of walleye pollock accessible (tons), estimated using our accessibility model. Biomasses are averages for 2000/2002/2004 in the Aleutian Islands (AI) and 2001/2003 in the Gulf of Alaska (GOA). No data on mackerel were available in the Bering Sea and Gulf of Alaska due to the small amount of mackerel present in those regions. Brackets around rookery names indicate rookeries which were clustered together.

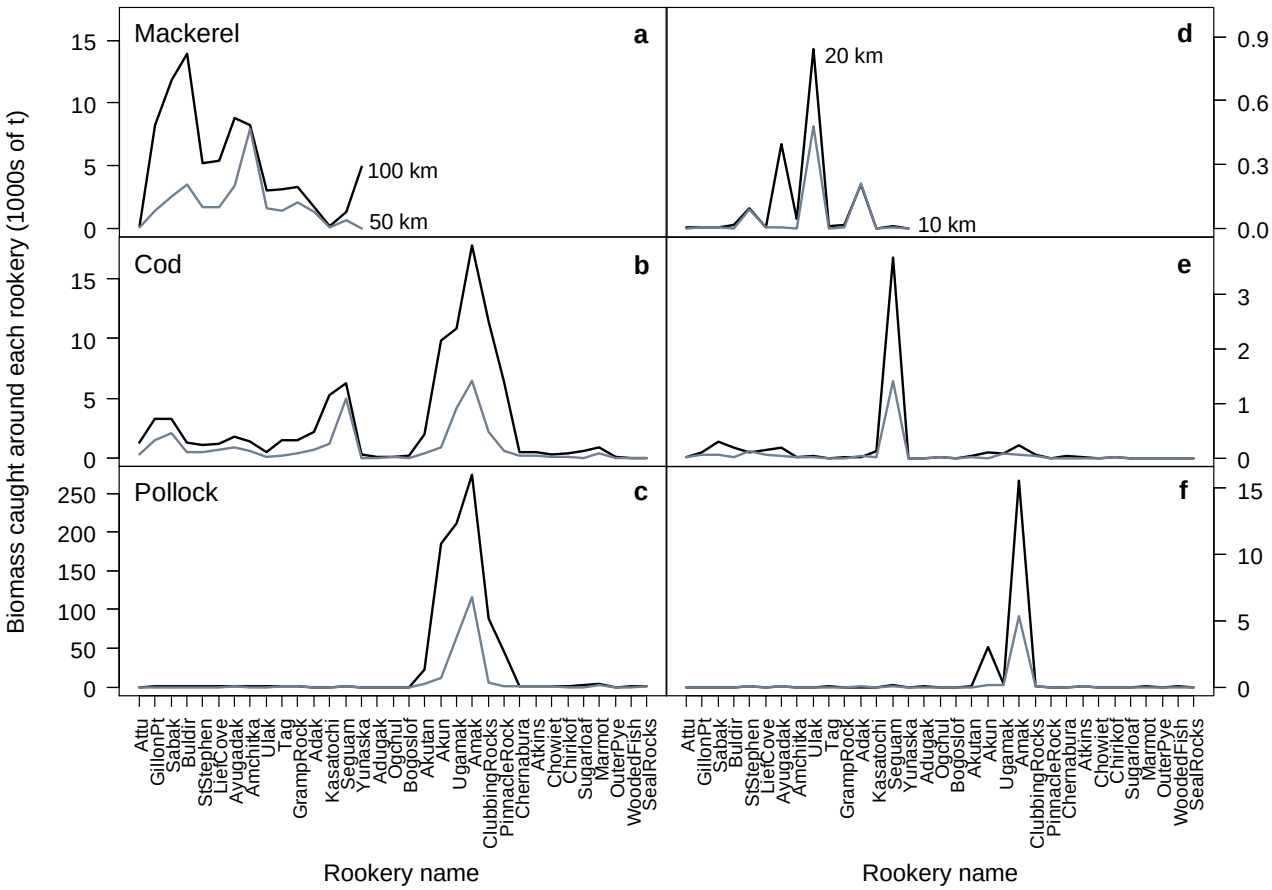

Fig. 2.6. Average annual biomass (1000s of tons) of Atka mackerel (a,d), Pacific cod (b,e) and walleye pollock (c,f) commercially caught within 10 and 20 (d, e, f) and 50 and 100 (a, b, c) km of the rookeries from 2000-2004. No data on mackerel were available in the Bering Sea and Gulf of Alaska which have not had a directed fishery for mackerel since 1996.

of spatial autocorrelation (Appendix 6). In contrast, population trends at the Aleutian Island rookeries were more variable, with no apparent relationship between population trends and the distances between rookeries (Appendix 6). From these observations, we concluded that grouping rookeries within 50 km of each other into clusters was sufficient to reduce the potential for spatial autocorrelation between rookeries. Grouping the rookeries within 50 km of each other into the same cluster resulted in 16 single rookeries and 8 rookery clusters (Agattu Gillon Point and Agattu Cape Sabak; Kiska Cape St Stephen and Kiska Lief Cove; Ayugadak and Amchitka Column Rock; Ulak Hasgox Point, Tag and Gramp Rock; Adugak and Ogchul; Akutan Cape Morgan and Akun Billings Head; Clubbing Rocks North and Pinnacle Rock; and Chernabura and Atkins) (Fig. 2.5d). Accessible prey biomasses and rates of population change were calculated by rookery or rookery clusters.

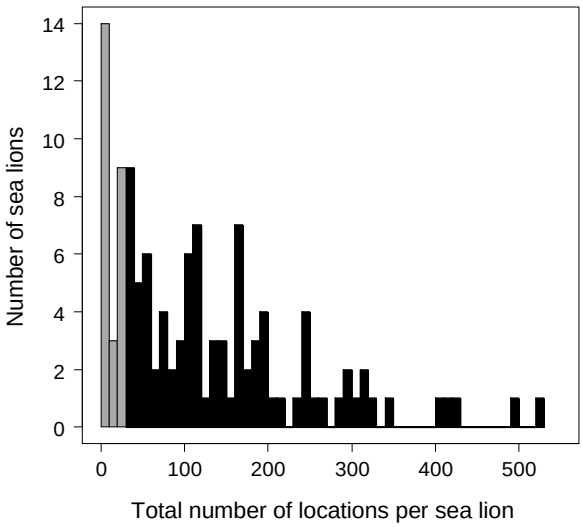

Fig. 2.7. Frequency distribution of the number of satellite telemetry locations recorded per Steller sea lion (n=116 animals). Only the records of those sea lions for which there were more than 30 recorded locations (black bars, n=90) were retained for further analysis.

Annual catches of pollock and cod within 50 and 100 km of the rookeries were highest in the Bering Sea (Figs. 2.6b-c). There was relatively little catch within 20 km of the rookeries (Figs. 2.6d-f). Region was the only significant factor influencing sea lion population trends ($F_{3,20}$ = 6.74, P = 0.0025, power = 0.96), with the lowest (more negative) rates of population change in the western Aleutian Islands and population change rates increasing (becoming more positive) toward the eastern Gulf of Alaska. No significant relationships were found between catch and sea lion population change (n = 48 catch models fitted).

2.3.2 Distributions of sea lions and prey

Sea lions tracked by satellite with fewer than 30 recorded at-sea locations (n = 26) were considered insufficient to accurately represent accessibility because the distribution of the records did not approximate the normal distribution of the mean, and were removed (Fig. 2.7). Of the remaining animals (n = 90), one had an at-sea distribution indicative of a non-resident migrant (locations stretched to 267 nautical miles) and was removed from further analysis (leaving n = 89 sea lions). Inspection of the at-sea locations for outliers identified two suspect satellite locations that were over 40 nautical miles from the previous recorded location. We removed the two suspect locations and rebalanced the remaining proportions so that the cumulative proportion of locations for each of these sea lions summed to 1.

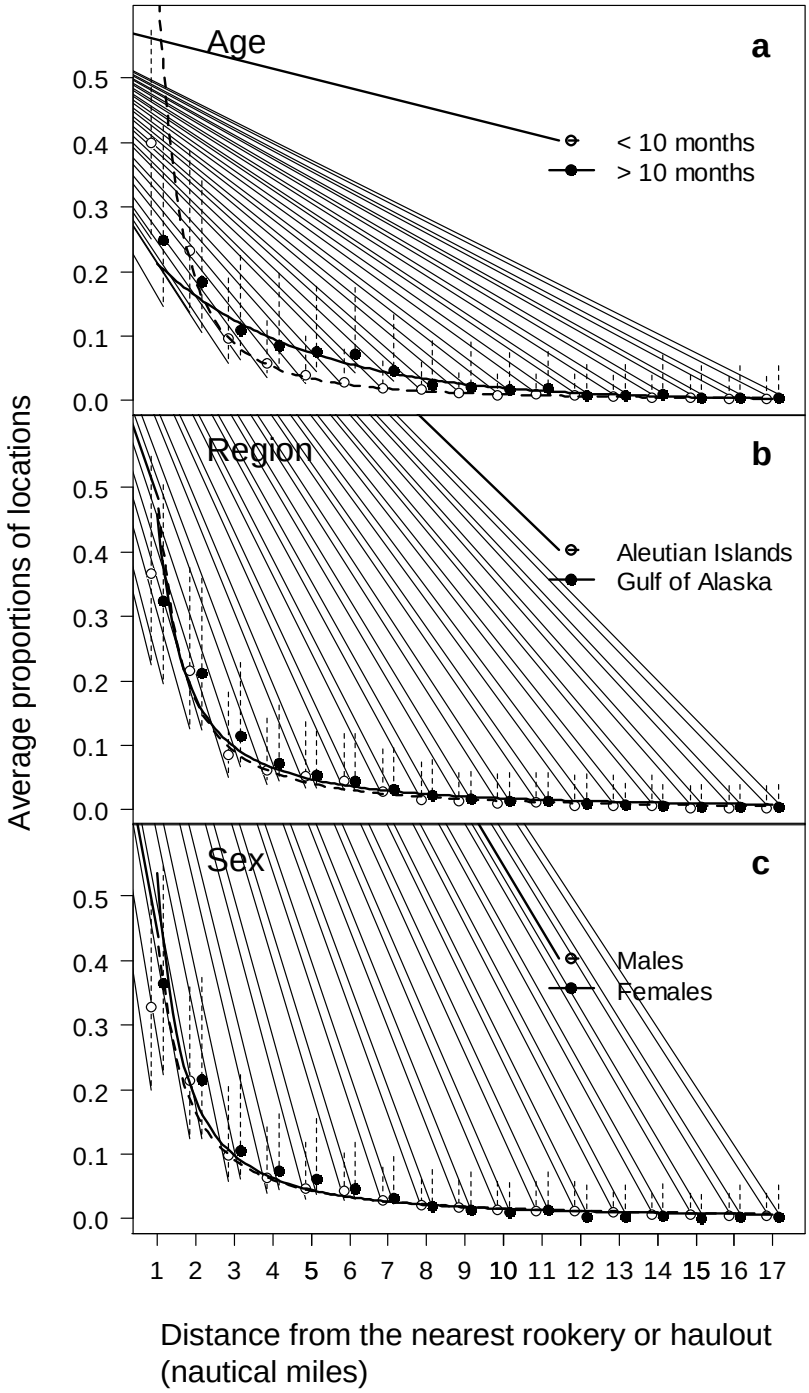

Fig. 2.8. Average proportion of locations in each distance interval (in 1 nautical mile increments) of (a) Steller sea lions older (n=33) (y>10 = 0.2756e-0.2639x) and younger (n=56) (y<10 = 0.6757x-1.8506) than 10 months of age, (b) sea lions from the Aleutian Islands (n=41) (yAI = 0.4964x-1.5478) and Gulf of Alaska (n=48) (yGOA = 0.4591x-1.4068), and (c) male (n=51) (ymale = 0.4512x-1.4515) and female (n=38) (yfemale = 0.5367x-1.) sea lions. Proportions are shown as mean ± s.e.

Plotting the average proportions of locations of sea lions older than 10 months as a function of distance from shore showed that accessibility declined exponentially. We log transformed the data to look for similarities in trends between distance intervals and detected a change point around 17 nautical miles from shore. We fit an exponential decay function to the average proportions of locations up to 17 nautical miles and found that this model gave reasonable predictions beyond 17 nautical miles when compared to the original data points (Fig. 2.8a). Attempts to fit an additional model to describe accessibility beyond 17 nautical miles did not improve the overall model predictions. The extremely low proportions of locations beyond 17 nautical miles (<0.003) indicated that the likelihood of adult female or juvenile sea lions foraging beyond 17 nautical miles in summer was extremely low.

For sea lions younger than 10 months, we found their at-sea distribution was best described by a power function (Fig. 2.8a). These younger sea lions spent smaller proportions of time at greater distances from land compared to sea lions older than 10 months (Fig. 2.8a). Power functions also provided the best fit to the data for comparisons between males and females, and between regions (Aleutian Islands versus Gulf of Alaska). The at-sea distributions of males and females were similar (Fig. 2.8b) and showed no differences between regions (Fig. 2.8c). We therefore pooled the available data (by sex and region) to mathematically describe accessibility to prey for sea lions older than 10 months (which were more likely to be representative of foraging animals; n = 33). We extended the model predictions up to 99 km (~53.46 nautical miles, 1 nautical mile = 1.852 km) in the accessibility model grids (i.e., eleven 9 x 9 km grid cells) to reflect the possibility (though extremely slight) of sea lions foraging far away from their rookeries (Appendix 8). This was also the distance at which the predicted accessibility values stabilised near 0.

In terms of prey distributions, the models predicted the highest pollock biomass areas in the Bering Sea. Pacific cod was more evenly distributed throughout the Aleutian Islands, Bering Sea and Gulf of Alaska. Atka mackerel biomass was higher in the eastern Aleutian Islands than in the west. The predicted biomass of all three prey species tended to increase with increasing distance from the rookeries towards the shelf break (e.g., Figs. 2.9). Overall, there was little difference between the predicted distributions of prey biomass (e.g., Figs. 2.9).

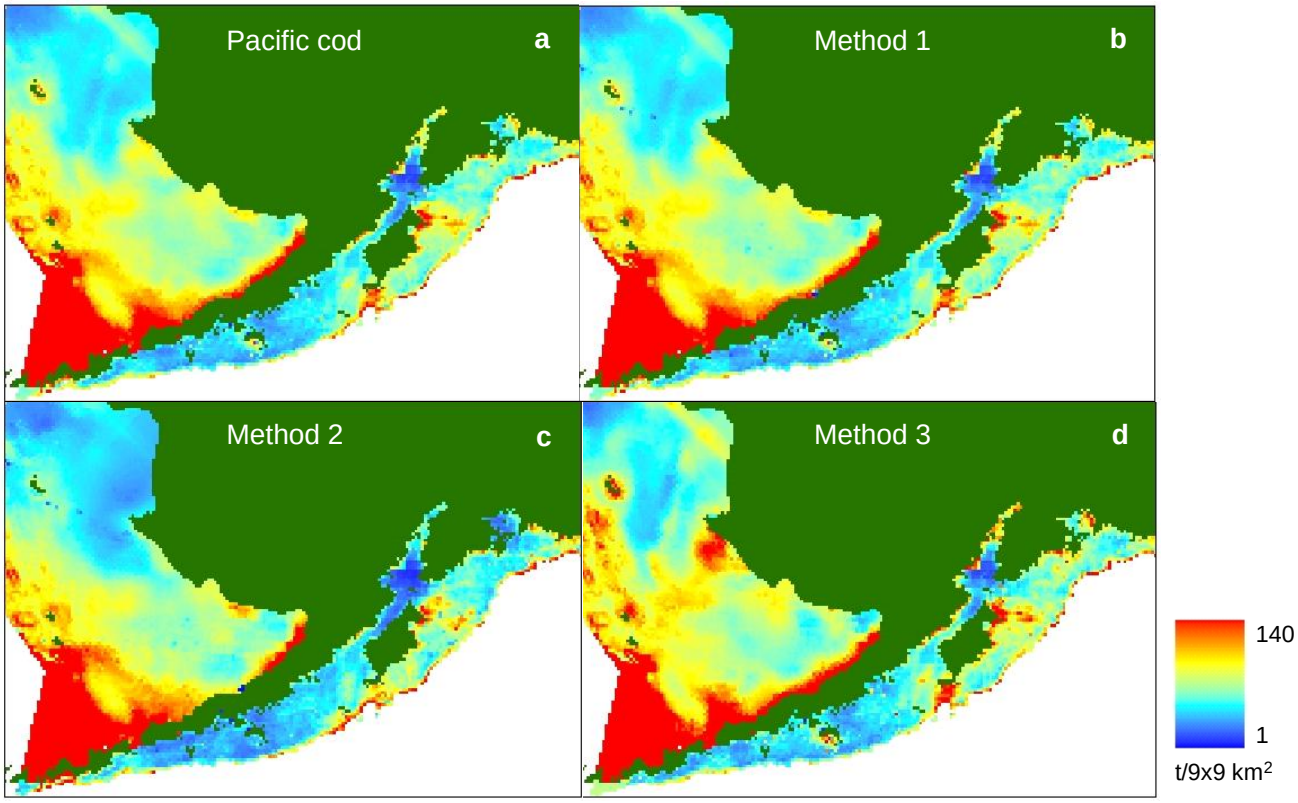

Fig. 2.9. Predicted abundance of Pacific cod (t/9x9 km2 grid cell) at the end of July 2001 before fishing (a) and after removing catches following Method 1 (b), Method 2 (c) and Method 3 (d) in the Gulf of Alaska and Bering Sea.

Comparing the total biomass of pollock, cod and mackerel within 10, 20 and 50 km of the rookeries to that predicted to be accessible to sea lions (from our accessibility model) showed that the predicted biomass available to sea lions was always lower when the accessibility model was applied (i.e., biomasses were in the hundreds of tons using the accessibility model, and in the thousands of tons without the accessibility model; see Figs. 2.5b-d and 2.10). In addition to reducing the total prey biomass accessible to sea lions at each rookery, the accessibility model also moderated the accessible biomasses among rookeries. In particular, rookeries with exceptionally high accessible biomasses within 20 and 50 km (Figs. 2.10) had moderately high biomasses as measured by the accessibility model (Figs. 2.5b-d). This is because most high biomass areas were located further away from the rookeries.

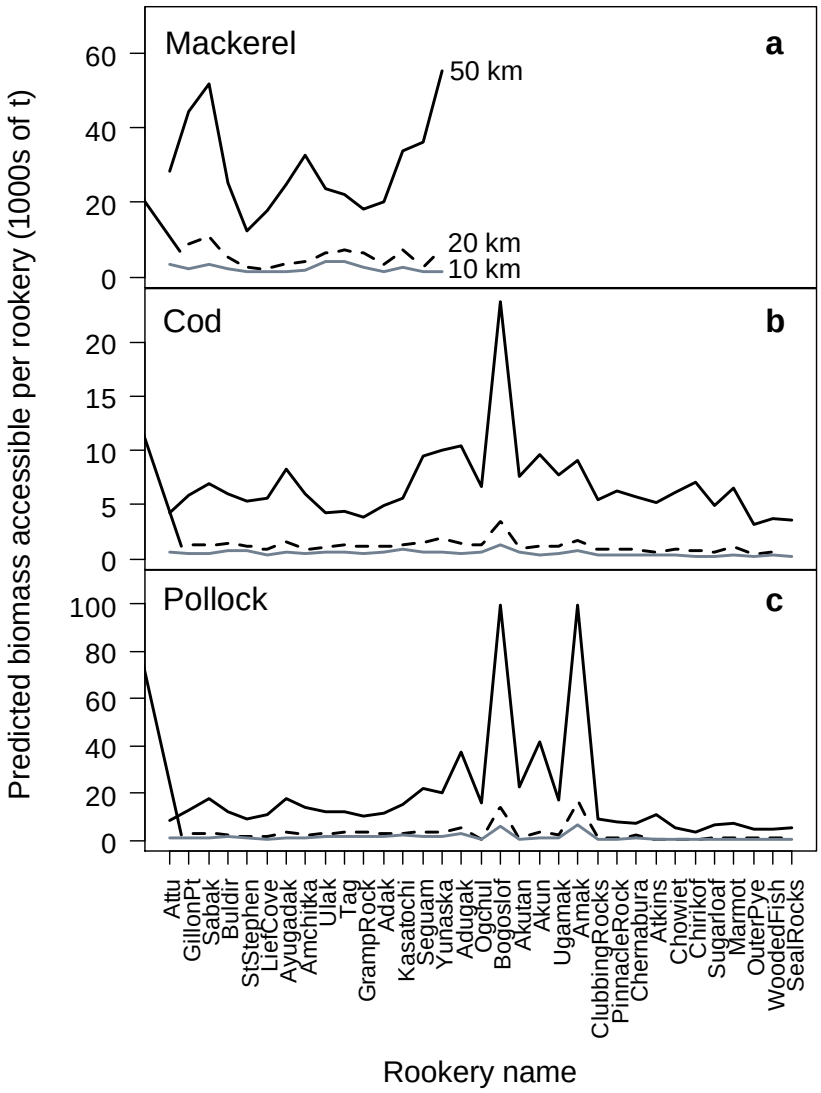

Fig. 2.10. Predicted biomass (1000s of tons) of (a) Atka mackerel, (b) Pacific cod and (c) walleye pollock accessible to Steller sea lions within 10, 20 and 50 km of the rookeries. Biomasses are averages for 2000/02/04 in the Aleutian Islands (AI) and 2001/03 in the Gulf of Alaska (GOA). No data on mackerel were available in the Bering Sea and Gulf of Alaska due to the small amount of mackerel predicted in those regions.

Of the 256 sea lion population change-prey biomass models fitted, we found 3 significant relationships. The biomass of pollock accessible using reduced Method 3 was positively associated with non-pup population change in the Aleutian Islands ($F_{1,18}$ = 4.57, P = 0.046, power = 0.52) (Fig. 2.11a). We also found a significant interaction between biomass and region ($F_{1,18}$ = 8.67, P = 0.0087, power = 0.80), with western Aleutian Island rookeries showing a greater change with pollock biomass (Fig. 2.11a). In other words, population increases were significantly associated with more pollock in the Aleutian Islands, particularly in the western Aleutians.

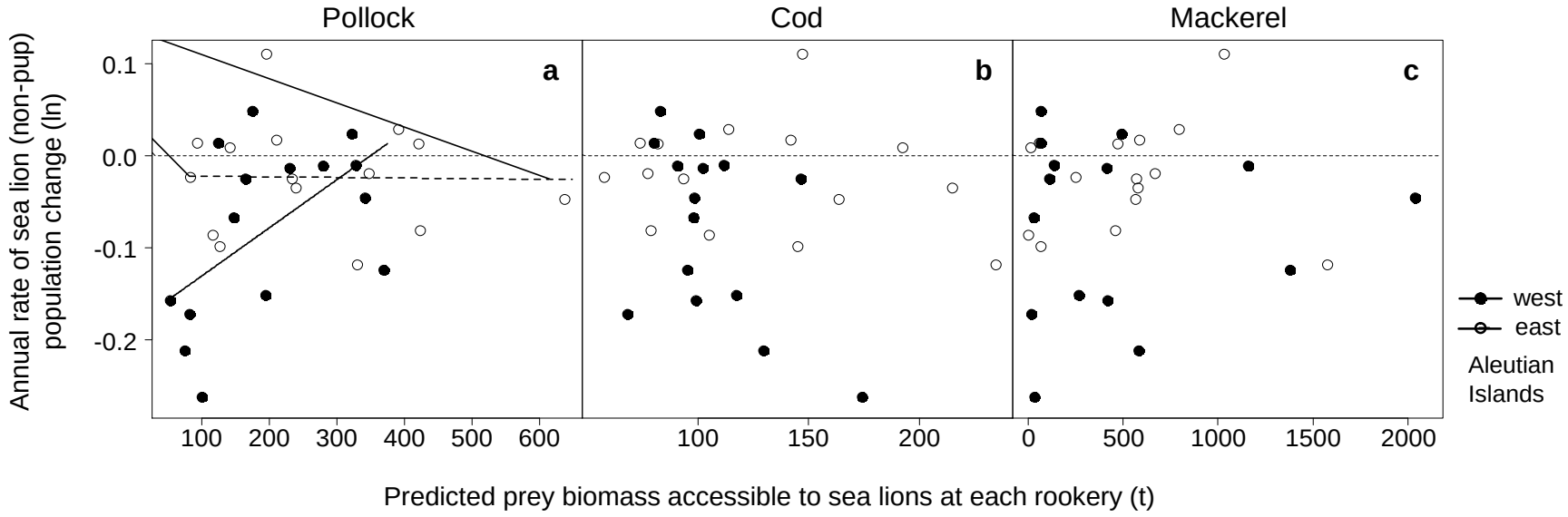

Fig. 2.11. The relationships between predicted prey biomass accessible to Steller sea lions (a, b, c) using the reduced (Method 3) and the annual rate of non-pup population change in the Aleutian Islands were significant for walleye pollock only (a), with western Aleutian rookeries (west, from rookeries 1-8, see Fig. 2.1) showing a greater change with pollock biomass than eastern Aleutian rookeries (east, from rookeries 9-15, see Fig. 2.1).

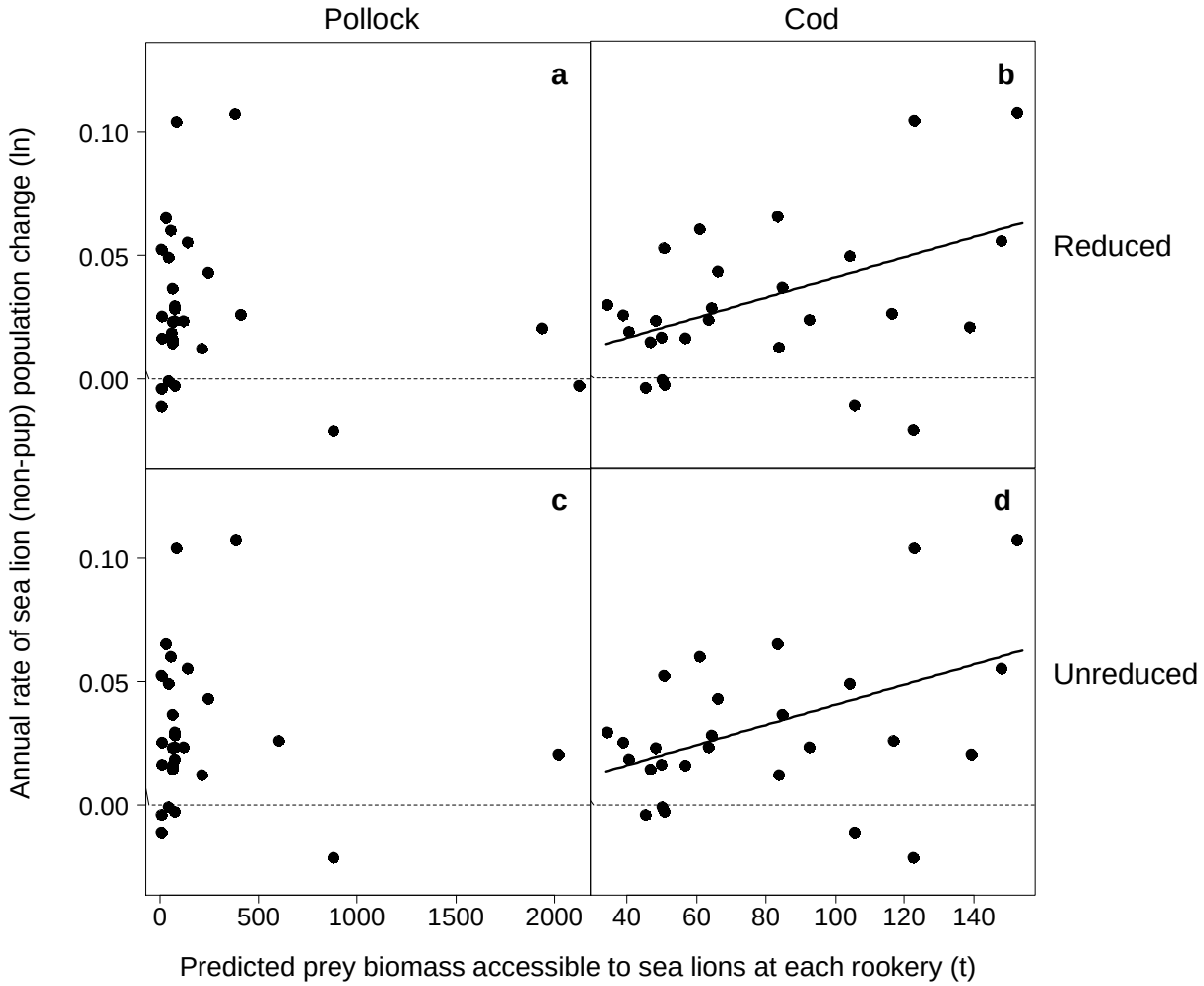

Fig. 2.12. Positive relationships between predicted prey biomass accessible to sea lions using the (a, b) reduced (Method 1) and (c, d) unreduced biomass distributions, and the annual rate of non-pup population change in the Gulf of Alaska were significantly positive for Pacific cod only. The trends with and without fishery removals accounted for were very similar due to the small amount of cod removed within the accessibility model extents of the rookeries in June and July.

We found positive relationships between the biomass of cod accessible to sea lions (both reduced Method 1 and unreduced) and the annual rate of non-pup population change in the Gulf of Alaska ($F_{1,13} = 4.85$, $P = 0.046$, power = 0.52). Removing a single outlier with more than 400 t of cod notably strengthened the relationship (reduced and unreduced: $F_{1,12} = 16.11$, $P = 0.0017$, power = 0.93) (Figs. 2.12b, d). The results with and without fishery removals were very similar due to the small amount of cod removed within the model extents in June and July (Fig. 2.12b, d).

None of the models for Atka mackerel, nor for the other prey species within 10, 20 or 50 km, were significant (power ranged from 0.56-0.82 for these models). Neither were any models that tested for effects on pups. None of the 96 multiple regression models used to examine the long term relationships between sea lion population trends and accessible prey biomasses were significant (power ranged from 0.64-0.87) for these models.

2.4 Discussion

Interspecific competition is defined as a reduction in the fecundity, growth or survivorship in the individuals of one species as a result of resource exploitation by another species (in our case, humans) (Begon et al. 2006). Determining whether competition exists between fisheries and sea lions requires demonstrating that the species being caught and eaten are limited. We sought to improve on past studies that attempted to assess potential competition between sea lions and commercial fisheries by considering the distribution of prey accessible to sea lions, and not just the prey removed by fisheries or fishing effort. We compared sea lion population trends with spatially-explicit distributions of prey to assess whether the observed rates of sea lion declines were related to the availability and accessibility of prey, or the amount of commercial catch. The analysis allowed us to detect the potential for localised depletion of prey to have occurred around individual rookeries. Including sea lion accessibility in our models gave a more realistic representation of the prey available to sea lions by taking into account their foraging behaviour (Matthiopoulos 2003; Gregr and Trites 2008).

Evidence for competition between commercial fisheries and Steller sea lions has previously been sought. By examining the relative size-frequency distributions of prey selected by sea lions and those taken by commercial trawl fisheries, Zeppelin et al. (2004) found considerable size overlap (68% pollock and 53% mackerel). A high degree of overlap creates the potential conflict between fisheries and sea lions, but any interpretation of overlap as competition requires a measure of the resource being competed for. Others have attempted to correlate time series of sea lion abundances on rookeries with removals by fisheries (e.g., Loughlin & Merrick 1989, Trites & Larkin 1992, Ferrero & Fritz 1994). However, correlations between sea lion counts and fishery catches have yielded few significant results and the relationships were both positive and negative (Loughlin & Merrick 1989, Ferrero & Fritz 1994, Sampson 1995). There

are two ways that positive and negative correlations associated with catch statistics may be interpreted. One is that the catch represents prey no longer available to sea lions. The other is that it is an index of the relative abundance of prey available to sea lions. High catches of cod for example, might mean that cod is extremely abundant or it could mean that sea lions are being out-competed. The key to sorting out these interpretations is to understand what sea lions eat, what proportion of the various stocks are caught each year and how much prey is available (Trites et al. 1999b). Competition occurs only if prey is limited. Even large harvests of prey species may have limited effect on availability to sea lions if sufficient biomass remains unharvested and accessible. To determine whether fisheries compete with sea lions for prey, we need to demonstrate that fisheries reduce the quantity of prey available to sea lions and that this reduction in prey abundance negatively affects sea lion populations.

The majority of the models we tested (i.e., 301 of the 304 regressions) found no significant relationship between sea lion population change and the catches of groundfish and the amount of accessible prey. Our models had statistical power to detect an effect as small as 0.01 if it was present (i.e., power for the models ranged from 0.52-0.96). The three common effect sizes used to assess the statistical power of regression models are 0.00, 0.01 and 0.05, which appear in the F tables. A level of 0.01 is generally accepted as a small effect size and 0.05 as a medium effect size (Murphy and Myors (2004). We decided to be conservative by using an effect size of 0.01 because the scientific community is particularly interested in detecting an effect of prey biomass or catch on sea lion population change—no matter how small. We therefore used an effect size equal to 1% of the variance in sea lion population change. The high statistical power of our tests to detect such small changes in sea lion numbers reflects the repeated measures design of our statistical models. Repeated measures analyses tend to have more power than a study that treats all observations as independent because there is less random variability between subjects. Thus the high power values associated with our statistical tests are as expected.

2.4.1 Importance of pollock and cod in the diet of sea lions

Our study took the approach of creating localised estimates of prey biomass available while accounting for the accessibility of sea lion prey and their foraging behaviour. We also examined the potential impacts of fisheries removals on prey availability by predicting four possible scenarios of fisheries removals and fish movements following fishing. However, we

only found three statistically significant relationships between prey abundance and sea lion population change out of a total of 256 models comparing the accessible prey biomass of pollock, cod and mackerel to sea lion population trends. These three significant relationships suggest that sea lion population change rates increased (became less negative) with increasing accessibility during summer of pollock in the Aleutian Islands and cod in the Gulf of Alaska. While these relationships may be spurious given the number of models we fitted, it can be argued that they make biological sense.

Pollock tend to stay in deeper waters over winter and move to shallower waters for spawning and feeding in summer when they are more accessible to sea lions (Springer 1992, Sigler & Csepp 2007, Sigler et al. 2009). The availability of pollock throughout the year may also provide a maintenance diet for sea lions when other seasonal prey resources are not available (Womble & Sigler 2006, Sigler et al. 2009). In addition, the lipid content of pollock peaks in summer (Kitts et al. 2004), providing sea lions with a relatively nutritious prey source.

Sinclair and Zeppelin (2002) found that Pacific cod was one of the four most important prey items of Steller sea lions in terms of frequency of occurrence averaged over years, seasons and sites, and was especially important in winter. Pitcher (1981) and Calkins (1998) also found that Pacific cod was an important winter prey item in the Gulf of Alaska and Bering Sea, respectively. The increase in sea lion numbers with cod biomass in summer is somewhat surprising however, as cod have a relatively low energy density in summer (postspawning) compared to winter (prespawning) (Smith et al. 1990). Moreover, most cod move to the outer shelf in summer in accordance with their annual migration cycle (Shimada & Kimura 1994). Adult cod are known to prey on juvenile pollock (Livingston 1993) and cod are often caught together with pollock (NMFS 2009), so it could be argued (assuming the statistical relationship was not spurious) that the increase in sea lion numbers were in response to the concurrent increase in pollock biomass rather than cod biomass.

2.4.2 Regional differences in sea lion populations trends

The region where a rookery was located was significantly associated with sea lion population trends. The relationship between pollock biomass and sea lion population trends was influenced by the region in which the rookery was located, with western Aleutian Island

rookeries showing a greater change than eastern Aleutian Island rookeries. Population change rates tended to be greater and more negative among the western Aleutian Island rookeries compared to the eastern Aleutian Island rookeries, and also among the Aleutian Island rookeries compared to the Gulf of Alaska rookeries. These observations confirm that the observed regional biological and oceanographic differences can also influence the distribution and abundance of prey available to sea lions.

The more positive and stable population trends among the eastern Aleutian Island rookeries may be due to the availability of a greater diversity of prey species. Moving westward from the Alaska Peninsula, fish species richness drops sharply at Samalga Pass, whereas there is little decline between Samalga and Amchitka Passes. Species richness then drops again west of Amchitka Pass (Hunt & Stabeno 2005). It may be easier for sea lions with a more diverse diet to obtain sufficient prey to meet their energy requirements (Merrick et al. 1997, Rosen & Trites 2004, Trites et al. 2006b). They may also be less sensitive to changes in overall prey abundance (Merrick et al. 1997, Trites et al. 2006a). Sea lions using the eastern Aleutian Island rookeries may therefore be less dependent on any one prey species compared to those breeding further west.

The higher diversity and abundance of prey available to sea lions east of Samalga Pass may explain why sea lion population change rates tended to be more positive among the Gulf of Alaska rookeries than the Aleutian Island rookeries. Samalga Pass is an important transition point from coastal to open-ocean conditions westward along the Aleutian Islands (Ladd et al. 2005). In addition to lower species richness, productivity, abundance and growth rates of fish species are lower west of Samalga Pass, consistent with lower chlorophyll levels and reduced sea lion diet diversity (Hunt & Stabeno 2005, Logerwell et al. 2005).

2.4.3 Sea lion accessibility

Steller sea lions are central place foragers (Orians & Pearson 1979), regularly resting on land between foraging trips (Merrick & Loughlin 1997, Brandon 2000, Trites & Porter 2002, Milette & Trites 2003, Raum-Suryan et al. 2004). Their rookeries and haulouts are likely chosen, in part, for their proximity to prey resources (Ban & Trites 2007). We thus expected sea lions to concentrate most of their foraging closest to their rookeries and haulouts. We found evidence to

support this prediction, with the number and proportion of locations for each sea lion decreasing exponentially with increasing distance from the nearest rookery or haulout. Although distances were measured to the nearest rookery or haulout, which was not necessarily the rookery or haulout where the sea lion was captured and tagged, many of the sea lions relocated from their initial site of capture (Brian Fadely, pers. comm.). As most of the sea lions were captured as pups, their movements to other rookeries and haulouts were thought to be movements to sites in closer proximity to suitable foraging areas as they matured (Brian Fadely, pers. comm.). It is therefore reasonable to assume that the nearest rookery or haulout to where a sea lion was located is where the foraging trip for that sea lion originated. We also felt that it was reasonable to assume that our accessibility model (which was based on satellite telemetry locations from juvenile sea lions) was a reasonable proxy for adults as well because juveniles forage at similar distances from rookeries and haulouts as adults (Appendix 5).

The accessibility of foraging areas from a central place has been described for birds and mammals using linear equations and normal density functions. For example, the likelihood of seabirds foraging near nesting sites has been assumed to decrease linearly with distance from land (Karpouzi et al. 2007), while Gregr and Trites (2008) modelled the accessibility of a foraging area from a Steller sea lion rookery or haulout using the positive half of a normal density function. However, both these descriptions contrast with our telemetry-based model that shows accessibility decreases exponentially with increasing distance from land. The telemetry data we used suggest there is no distance within which accessibility by sea lions is more or less equal as suggested by the initial plateau of a normal curve. Our observation suggests that foraging areas closest to the rookeries may be many orders of magnitude more important than foraging areas located further away, at least during the spring and summer months when most of the telemetry locations for our accessibility model were recorded. While sea lions are known to forage further from shore in winter than in summer (Merrick & Loughlin 1997), the exponential relationship between distance and accessibility likely holds during the winter months as well, given the propensity of sea lions to haulout regularly on land to rest. Thus the distribution of sea lions during winter can probably be described by extending the summer accessibility values to reflect the greater foraging distances of sea lions in winter.

Foraging patterns have been described for a number of species such as seals (Austin et al. 2004), albatrosses (Viswanathan et al. 1996, Viswanathan et al. 1999, Edwards et al. 2007),

bumblebees (Viswanathan et al. 1999) and deer (Viswanathan et al. 1999). They tend to show that most individuals make short foraging trips that are concentrated near central places. For example, the movements of grey seal *Halichoerus grypus* from one location to the next tend to be short (~6 km) and decrease linearly in frequency with increasing movement length. Similarly, the proportion of flights made by wandering albatrosses *Diomedea exulans* decreased exponentially with increasing flight duration (Viswanathan et al. 1996, Edwards et al. 2007), as did the frequency of feeding behaviour in deer with increasing foraging time (time spent searching for food) (Viswanathan et al. 1999). Both studies assumed that time spent travelling between food items or patches were related to the distance travelled. Such observations suggest that accessibility of prey may decrease exponentially with increasing distance from the central place for other species as well.

2.4.4 Are sea lions prey limited?

Only 3 of the 304 regressions we ran comparing the accessible prey biomass and catch of pollock, cod and mackerel to sea lion population change were statistically significant. Given that the majority of the relationships we tested were insignificant, it is unlikely that the availability of pollock, cod or mackerel was limiting sea lion populations in the 2000s. Any changes in sea lion numbers from year to year in response to changes in pollock, cod or Atka mackerel availability were probably temporary, as we failed to find any significant long-term (i.e., 9 yrs) relationships between sea lion population trends and accessible prey biomass or catch. It seems that pollock, cod and mackerel biomass was high enough, relative to the number of sea lions, that there was no shortage of these three prey species. If sea lions were prey limited, it would most likely be the result of species besides pollock, cod and mackerel.

Steller sea lions are opportunistic, generalist predators and take advantage of prey with strong, predictable, nearshore migratory movements (Sinclair & Zeppelin 2002, Fadely et al. 2005, Logerwell et al. 2005, McDermott et al. 2005). Pitcher (1981) and Sinclair and Zeppelin (2002) found that sea lions ate forage fishes and salmon almost exclusively during their summer spawning season, while other fishes and cephalopods were eaten more frequently in spring and fall. When forage fishes such as herring *Clupea harengus*, sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus* are aggregated nearshore, they are likely more energetically rewarding than groundfish because they are more densely aggregated, are higher in energy density and lipid

content, and are easier to catch than groundfish (Womble & Sigler 2006). Sea lion populations may therefore be more responsive to changes in the seasonal availability of these alternative prey resources than to the biomass of groundfish.

2.4.5 Do fisheries compete with sea lions for prey?

Of the three prey species we considered, only accessible pollock and cod biomass had any statistically significant relationships with sea lion population change. The positive relationship between pollock biomass and sea lion population change was significant for only one of the prey biomass distributions (reduced pollock biomass distribution calculated using Method 3). The positive relationship between cod biomass and sea lion population trends did not change, whether or not fishery removals had been accounted for, due to the small amount of cod removed within the accessibility model extents of the rookeries in June and July. The similarity between the four types of prey biomass distributions suggests there was little effect of fishing on the prey available to sea lions. In other words, we could not detect an effect on sea lion numbers when we assumed fishing did not reduce prey biomass (unreduced distributions), or when we assumed that fishing removals caused local and geographically stable reductions in fish abundance during summer in the immediate vicinity of where fishing occurred (Methods 1 and 2). Nor could we detect any effect on sea lion numbers when we assumed that fishing reduced the overall biomass of prey available but had little effect on the local availability of prey (Method 3).

The prey biomass and catch distributions further showed that areas with relatively higher biomass tended to be further away from the rookeries around the shelf break where fishing was heaviest, but sea lion accessibility was lower. Eliminating all pollock and cod fishing within approximately 99 km (the extent of the accessibility model around each rookery) during summer is therefore unlikely to produce any significant changes in sea lion numbers. Moreover, we did not find any significant relationships between amounts of groundfish caught and sea lion population change to support the hypothesis that fisheries negatively affected sea lions.

Differences in the timing and magnitude of regional sea lion population trajectories in the 1970s, 1980s, and 1990s suggest that the overall decline of the western stock may not have been caused by a single factor, but rather by the cumulative effect of multiple factors that had different

relative spatial and temporal magnitudes (Loughlin & York 2000, Bowen et al. 2001, NRC 2003). Ecosystem models of the central and western Aleutians, and southeast Alaska suggest that killer whale predation, ocean productivity, fisheries and competition with other species likely contributed to the trends observed in sea lion numbers in both ecosystems (Guenette et al. 2006). Concurrent with the decline of sea lions and expansion of groundfish fisheries in the Aleutians in the late 1970s, there was a substantial change in ocean climate and declines in the abundance of non-fished species such as capelin, skates and benthic invertebrates (Mueter & Norcross 2002). Thus while commercial fisheries might be evoked to partially explain the interannual fluctuations in the abundance of some species (Orensanz et al. 1998), the geographic and temporal coherence of the collapse of large numbers of taxa argues for a large-scale common cause such as climate change (Orensanz et al. 1998, Anderson & Piatt 1999, Trites et al. 2007b).

The relative abundances of prey species available to sea lions have changed over time. Over the same period in the 1970s that fisheries expanded and sea lions declined, there were major changes in community structure and the abundances of several species in the north Pacific, possibly in response to changes in ocean temperature, circulation, and upwelling patterns (Alverson 1991, Beamish 1993, Anderson & Piatt 1999, Hollowed et al. 2001, Benson & Trites 2002, Trites et al. 2007b). These included an overall increase in groundfish (Hollowed et al. 2001) and salmon (Francis & Hare 1994), and decreases in forage fishes such as herring, capelin and eulachon *Thaleichthys pacificus* (Anderson & Piatt 1999). Concurrently, sea lions made a significant prey shift from a diet that consisted mostly of forage fishes pre-1970s (Mathisen et al. 1962, Thorsteinson & Lensink 1962, Fiscus & Baines 1966) to one that was dominated by groundfish post-1970s (Pitcher 1981, Alverson 1992). Groundfish have relatively lower mass energy densities compared to forage fishes and correspond to what is termed ‘junk food’ in the diet of sea lions (Rosen & Trites 2000). The decline of the western sea lion population may therefore have been due to changes in prey composition and abundance associated with a shift in ocean climate.

The 2000s were a relatively stable period for sea lion populations compared to the more severe declines pre-2000s. It is plausible that fisheries could have affected sea lions in the past or exacerbated the effects of other factors. Unfortunately, understanding the historical or long term effects of fishing on sea lions has been hampered by a lack of historical data on sea lion

populations and prey abundance prior to the 1970s. For this reason, it is important to continue monitoring sea lion populations and prey abundances even though sea lion declines in several areas appear to have abated.

Conservation measures implemented since 1990 could be positively affecting the recovery of the western sea lion population. Beginning in 1992, NMFS restricted trawl fishing within either 10 or 20 nautical miles (18.5 or 37 km) of rookeries. This may explain why there was little difference in the relationship between accessible prey biomass and sea lion population trends whether or not fishery removals had been accounted for. Hennen (2006) showed that a positive correlation existed between several metrics of historical fishing activity and sea lion population declines. This relationship was less consistent after 1991, supporting the hypothesis that management measures around some of the rookeries may have been effective in moderating the localised effects of fishing activities on sea lions. However, it is not known whether the slowdown in decline and the current stability or near stability is a result of management actions, natural changes in the ecosystem, or other factors as they all occurred at about the same time and their effects are difficult to isolate from each other (Hennen 2006).

2.4.6 Study limitations

Our study focused mainly on the sea lion's summer breeding season as this is a time when energetic demands are high for lactating females. Recently weaned juveniles are also more vulnerable at this stage as they must start foraging independently. This was also the time scale of the available datasets. We could have assumed that the prey biomass distributions would remain the same throughout the year and continued predicting the biomass of prey accessible to sea lions through the winter and spring. However, we doubt that such out-of-season predictions would be valid, due to behavioural changes and migratory movements of groundfish throughout the year. For example, pollock distributions are less predictable from month to month than from year to year (Gende & Sigler 2006). Nonetheless, it is important to assess the relationship between the availability of prey, the amounts of fish commercially caught, and the differing rates of sea lion population change in other seasons as well, because substantial fishing for pollock, cod and Atka mackerel occurs in fall and winter (Appendix 7). The colder temperatures of the winter months increase the sea lions' demands for body fat stores for insulation, resulting in greater energetic

requirements (Winship et al. 2002, Rea et al. 2007). Many prey species such as pollock (Brodeur & Wilson 1996a, Sigler & Csepp 2007) and cod (Shimada & Kimura 1994) also move to deeper waters further from land during winter. Prey limitation and the potential for fisheries to compete with sea lions may thus be more severe in fall and winter.

As there was no controlled experiment to test for the effects of fishing—cause and effect relationships could not be stated definitively. For example, it was not possible to tell whether sea lion population change increased in response to increasing accessible pollock or cod biomass, or whether the increase was due to some other variable, such as an increase in the biomass of another prey species not examined in our study. While we were able to estimate four possible scenarios of prey biomass available to sea lions (three of which had fishery removals accounted for based on different assumptions of fish movements after fishing), we were not able to test for before and after effects of fishing on sea lion populations. Only a manipulative experiment (perhaps comparing sea lion populations at rookeries with fishing restrictions enforced around them to those which are open to fishing) conducted over multiple locations and years can assess whether the relationships we observed were correlative or causal (Dillingham et al. 2006). However, experimental investigations are often impractical for large free-ranging populations such as fish or marine mammals. Consequently, biologists need to obtain the best possible answers from the limited data available (Pascual & Adkinson 1994).

Our analyses of the relationship between accessible prey biomass and sea lion population change span the time period from 2000-2004. Effects of fisheries on sea lion trajectories may lag by four or more years, given the time taken for females to reach sexual maturity (Pitcher & Calkins 1981). The time period considered in our study may have been too short for any responses in sea lion population demographics to be detected. We therefore encourage the continuation of studies on accessible prey biomass and sea lion population change as more recent survey data becomes available. The addition of more recent datasets may also increase the statistical power of this study, which was only moderate in many of the models with insignificant results.

2.4.7 Conclusions

We found little evidence to support the hypothesis that the walleye pollock, Pacific cod and Atka mackerel fisheries in the Aleutian Islands, Bering Sea and Gulf of Alaska modified the abundance and distribution of prey to the detriment of sea lions from 2000-2008. The variable trajectories of sea lion populations appeared to be unrelated to the biomass of groundfish accessible near rookeries, and trends in sea lion numbers were similar with or without fishery removals. These observations suggest that sea lions were not prey limited and that their populations were largely unaffected by fishery removals during this period. While it is conceivable for fisheries to have affected sea lions in the past, further constraining fishing activities is unlikely to produce any significant increases in sea lion numbers.

CHAPTER 3: GENERAL CONCLUSIONS

3.1 Research summary

The causes of the decline of the western stock of sea lions during the late 20th century continue to be the subject of much speculation and debate despite numerous analyses and many detailed reports (NRC 2003). There is still no commonly accepted answer to the question of why the western stock declined or is currently failing to recover (population decline arrested or reversed). Many marine mammal populations declined over the last 200 years, typically as a result of commercial harvest for fur, meat and oil or because of fishery interactions through incidental catch in fishing nets, disturbance from fishing activities, or predator control programs (e.g., Murawski 1995, Fujiwara & Caswell 2001). However, the case of the dramatic decline in the Steller sea lion population has been less straightforward. Steller sea lions have not been subject to commercial harvests since 1972 and the incidental take of sea lions by fisheries has been estimated to be small relative to the size of the population (<15 animals per year, Allen & Angliss 2010). During the period of rapid population decrease of sea lions during the late 1970s through the 1980s, there were major shifts in the abundance of many other marine species in the North Pacific attributed to climatic changes or commercial harvests of fishes (Alverson 1991, Beamish 1993, Anderson & Piatt 1999, Hollowed et al. 2001, Benson & Trites 2002, Trites et al. 2007b). The indirect and interactive nature of these possible causes and their effects on sea lions has made it difficult to attribute changes in abundance to specific factors.

Despite the uncertainty surrounding the causes of the decline of Steller sea lions, there are many who believe that industrial-scale fisheries in western Alaska modified the abundance, composition and distribution of prey to the detriment of sea lions for no other reason than the period of decline coincided with the rapid expansion of groundfish fisheries in Alaska (Alverson 1992, Trites & Donnelly 2003). Localised depletion of fish stocks is commonly thought to be the mechanism by which fisheries compete with sea lions for prey. Previous studies attempting to assess the impacts of prey availability on sea lions were either conducted at too coarse a scale to make inferences about the local availability of prey biomass (Cornick et al. 2006b, Guenette et al. 2006), or at too few rookeries to generalise about the Alaskan sea lion population (Adams et al. 2008, Winter et al. 2009). We attempted to address this issue by using relatively fine-scale

and continuous prey biomass distributions to estimate the amount of prey available to sea lions. We also considered the accessibility of foraging areas to sea lions at various distances from the rookeries and examined the potential impacts that removals by fisheries might have on the availability of sea lion prey by simulating four possible scenarios of fisheries removals and fish movements following fishing (Chapter 2).

Of the 304 regressions comparing the accessible prey biomass and catch of pollock, cod and Atka mackerel to sea lion population changes, we found three statistically significant relationships between prey abundance and sea lion population change. These three significant relationships suggest that sea lion population change rates increased (became less negative) with increasing summer accessible pollock and cod biomass in the Aleutian Islands and Gulf of Alaska respectively. Although most of the regression models fitted were statistically insignificant, moderate statistical power for many of these models prevented us from ruling out the possibility that there may be an impact of fishing on sea lions. Increasing the sample size (e.g., conducting the study on more rookeries or haulouts and increasing the number of years of prey biomass data available) will improve the statistical power of this study and increase the likelihood of correctly accepting or rejecting the possibility of fisheries having an impact on sea lions. The region in which a rookery was located was a significant factor affecting sea lion population trends, supporting the emerging understanding that there are regional biological and oceanographic differences influencing the distribution and abundance of prey available to sea lions. Regional differences probably influence the abundance of prey species other than pollock, cod and Atka mackerel; whose abundance of which may be more significant in influencing sea lion population trends.

We investigated the potential for pollock, cod and Atka mackerel fisheries to affect sea lion populations through reductions in prey biomass, but found no relationship between fisheries-reduced prey abundance and numbers of sea lions. The similarity between reduced and unreduced prey biomass distributions suggests that there was little effect of fishing on the prey available to sea lions, at least during summer. When sea lion accessibility was taken into account, there were few significant relationships between prey biomass and sea lion population trends. The application of our accessibility model to scale down available prey biomass with distance from the rookeries also showed that prey close to the rookeries was not limiting for sea

lions. This was confirmed by comparisons with total prey biomass within 10, 20 and 50 km of each rookery, which showed that prey was not limited within critical foraging distances from the rookeries. Even at the scale of fisheries management areas, the amounts of pollock, cod and Atka mackerel caught were always well below what was estimated to be available (Figs. 1.2-1.4). All these observations suggest that sufficient sea lion prey was available in the 2000s, at least in terms of pollock, cod and Atka mackerel. If groundfish was not limiting, then fisheries could not have been competing with sea lions for prey.

Previous studies have also found that commercial fishing and sea lion population trends were largely independent of each other. Calkins (2008) found negative associations between cod longline fishing and sea lion population trends from 1996-2000 and a positive association from 2000-2004. Calkins (2008) concluded that the results may indicate that management actions taken in the late 1990s or early 2000s were effective at mitigating an adverse reaction. On the other hand, the correlation from 1996-2000 may be spurious (caused by some other factor), while the correlation from 2000-2004 may reflect areas of high productivity where both fisheries and sea lions did well {Calkins (2008)}. Cornick et al. (2006b) examined the impact the pollock fishery could have on the prey available to sea lions. None of the fisheries management regimes they simulated produced an energy deficit for sea lions, and thus no evidence of competition, even after the pollock biomass estimates were halved to control for differences in pollock distribution, sea lion foraging range and other predators on pollock.

The 2000s were a relatively stable period for sea lion populations compared to the more severe declines pre-2000s (Fig. 1.1). It is plausible that fisheries affected sea lions in the past or exacerbated the effects of other factors. Unfortunately, analyses of historical trends have been complicated by the scarcity of baseline population data on the larger sea lion population that existed before 1975. Such baseline data are needed for comparison with data on the current depleted population. Since there are few avenues for augmenting this historical database (e.g., reanalysis of existing data, testing of archived tissue samples for contaminants and disease agents, reconstruction of environmental events based on isotope anomalies or annual growth patterns), the causes of the early phase of the sea lion population decline will likely remain a source of speculation and debate (NRC 2003). However, existing information can be used to

identify scenarios that could explain the historical decline, which will be valuable in understanding the prospects for recovery of the remaining population.

The implementation of conservation measures in the late 1990s and early 2000s occurred at about the same time as a reduction in the rate of decline of the western stock of sea lions. It is not known whether the slowdown in decline and the current stability or near stability is a result of management actions, natural changes in the ecosystem, or other factors as they all occurred at about the same time and their effects are difficult to isolate from each other. As the western stock of sea lions continues to decline in some areas, fisheries managers may place additional controls on commercial fisheries as protective measures. The results of our study suggest that placing additional restrictions on fishing activities will probably not result in any significant changes in sea lion numbers. However, maintaining the status quo may be a precautionary measure until all sea lion populations start recovering, or until experimental manipulations can show directly that fishing does not reduce or change the distribution of prey to the detriment of sea lions.

3.2 Strengths and weaknesses

3.2.1 Weaknesses

Our study focused mainly on the sea lion's summer breeding season when energetic demands are high for lactating females. This was also the time scale of the datasets available. We could have assumed that the prey biomass distributions would remain the same throughout the year and continued our predictions of prey biomass accessible to sea lions through the winter and spring. However, we doubt that such out-of-season predictions would be valid, due to behavioural changes and migratory movements in groundfish throughout the year. For example, pollock distributions are less predictable from month to month than year to year (Gende & Sigler 2006). Nonetheless, it is important to assess the relationship between the availability of prey, the amounts of fish commercially caught, and the differing rates of sea lion population change in other seasons as well, because a substantial amount of fishing for pollock, cod and Atka mackerel occurs in fall and winter (Appendix 7). The colder temperatures of the winter months increase the demand for body fat stores for insulation, resulting in greater food consumption by sea lions (Winship et al. 2002, Rea et al. 2007). Many prey species such as pollock (Brodeur & Wilson 1996a, Sigler & Csepp 2007) and cod (Shimada & Kimura 1994) also move to deeper

waters further from land during winter. Prey limitation and the potential for fisheries to compete with sea lions may thus be more severe in fall and winter.

As there was no controlled experiment to test for the effects of fishing—cause and effect relationships could not be stated definitively. For example, it was not possible to tell whether sea lion population change increased in response to increasing accessible pollock biomass (and decreasing pollock catch), or whether the increase was due to some other variable, such as an increase in the biomass of another prey species not examined in our study. Only a manipulative experiment conducted over multiple locations and years can assess whether the relationships we observed were correlative or causal (Dillingham et al. 2006). However, experimental investigations are often impractical for large free-ranging populations such as fish or marine mammals. Consequently, biologists need to get the best possible answers from the limited data available (Pascual & Adkinson 1994).

Our analyses of the relationship between accessible prey biomass and sea lion population change span the period 2000-2004. Effects of fisheries on sea lion trajectories may lag by four or more years, given the time for females to reach sexual maturity (Pitcher & Calkins 1981). The time period we considered may have been too short for any responses in sea lion population demographics to occur. We therefore encourage the continuation of studies on accessible prey biomass and sea lion population change as more survey data become available.

The rookeries studied consisted mostly of breeding females and pups as sexually immature sea lions are less likely to use rookeries (Burdin et al. 2009). Among otariid pinnipeds, population dynamics are most heavily influenced by the reproductive success of adult females and the survival of juveniles (York 1994, DeMaster & Atkinson 2002). Thus, the foraging behaviour of these two groups is often used to make inferences regarding prey availability (Adams et al. 2008). We studied rookeries as localised depletion is more likely to affect lactating females because they must fulfill their energy requirements on a relatively short time scale in a relatively small area (DeMaster et al. 2001). However, examining prey availability and sea lion population trends at haulouts would be important for assessing prey availability impacts on juvenile survival, especially in seasons other than summer.

3.2.2 Strengths

The resolution of our study may have been coarse compared to the foraging range of sea lions in summer, or to dedicated field studies such as the ones carried out by Winter et al. (2009) and Womble et al. (2005). Focused field studies typically provide the most detailed information, but are generally done on limited spatial and temporal scales making generalisations more difficult. On the other hand, large-scale studies such as the ones by Cornick et al. (2006b) and Guenette et al. (2006) cover many areas, but not in fine detail. Our study struck a balance between focused field studies and large-scale ecosystem modelling approaches by incorporating relatively fine-scale prey biomass distributions and sea lion population trends at individual rookeries over a broad spatial extent.

3.2.3 Conservation applications

Our research has the potential to aid in species recovery by investigating why sea lions have so far failed to recover. Our approach represents the first example of using well-resolved prey surfaces to assess fishery interactions. It is also the first time that the foraging behaviour of sea lions has been used to estimate prey availability, through incorporation of an accessibility model. This accessibility model can be used to determine which areas are most important to foraging sea lions and where fisheries management should be focused, should management be deemed necessary. Models such as those used in our study aid in the conceptualisation of complex systems such as the North Pacific and can be used to predict properties of real systems that are difficult or impossible to measure (Hall & Day 1977, Keen & Spain 1992). Our methodology may be applicable to other species that are potentially negatively impacted by fisheries such as short-beaked common dolphins *Delphinus delphis* in western Greece (Bearzi et al. 2008), or populations undergoing rapid population change across a broad geographic range, such as sea otters *Enhydra lutris* in the Aleutian archipelago (Doroff et al. 2003). Additionally, by providing a means to quantify the predator-prey-fisheries interaction, our approach may contribute to ecosystem-based management systems, which are in need of further development (Barange 2003).

3.3 Future research priorities

The effects of competition with fisheries on sea lions, if it is occurring, are dependent on the distribution of fishing effort, prey movements and dispersal patterns, sea lion foraging behaviour, and the spatial and time scales over which these processes take place. The intensity of competition will depend on the extent to which sea lions and fisheries overlap in space and time with their shared resource, and the way in which sea lions' preferences for particular prey or the fisheries' target species vary in response to variations in the population composition of these prey and the abundance of other components of the system. Future research on the effects of commercial fisheries on sea lion populations should focus on assessing the abundance and distribution in time and space of the prey species potentially competed for. It is also necessary to know how sea lions will respond to changes in the abundance and distribution of prey. We suggest extending our study to include other commercially important sea lion prey species such as arrowtooth flounder *Atheresthes stomias* and yellowfin sole *Limanda aspera* to determine whether the relationships we found between accessible pollock, cod and Atka mackerel biomass, and sea lion population trends also hold true for these other prey species. Although forage fishes such as sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus* and herring *Clupea harengus* are not commercially fished in western Alaska, they are nutritionally superior to groundfish in terms of energy density and their abundance may have a more significant influence on sea lion populations. The accessible biomass of forage fishes should therefore be quantified as well.

Our study focused mainly on the sea lion's summer breeding season as the prey biomass distributions were only available for June and July (the period during which the NMFS trawl surveys were conducted). As a substantial amount of fishing for pollock, cod and mackerel occurs in fall and winter, an assessment of the potential for fisheries to compete with sea lions for prey would not be complete without quantifying the prey available to them in other seasons. Extending our study to include other seasons would also require examining sea lion population trends at haulouts in addition to rookeries, as most sea lions forage from haulouts during the non-breeding season (Burdin et al. 2009).

As we did not conduct a controlled experiment to test for the effects of fishing, our predictions of the prey biomass accessible to sea lions and the number of sea lions present were

for a particular time period (summer). To determine the before and after effects of fishing on the prey available to sea lions, it would be necessary to quantify the prey available through time after a series of fishing episodes with known amounts of catch. Such studies have been attempted (e.g., Fritz & Brown 2005, Conners & Munro 2008), although differences in scale and the mobility of prey species make it difficult to distinguish between changes in abundance due to fishing removals and those due to fish dispersal or movement across the boundaries of the study area. Closure of selected areas around rookeries and haulouts to fishing while opening others may help differentiate between decreases in prey availability due to human or natural factors.

The resolution of our study may have been coarse compared to the foraging range of sea lions in summer. Many foraging trips made by juveniles and most trips by pups are <10 km from their rookeries or haulouts (Appendix 5). At the resolution of our study (9 x 9 km^2), we would not have been able to detect changes in the prey availability of foraging patches used by sea lions <9 km across. The ability of our methodology to detect localised changes in prey availability would be improved if the prey biomass distributions were created at a resolution to match the resolution of the sea lion telemetry data.

Other predators that exploit pollock, cod and mackerel, such as harbour seals, northern fur seals, several marine birds and predatory fishes were not accounted for in our study. Nor did we consider the prey consumption by sea lions using the 17 minor rookeries and 250 haulouts. Therefore, the prey biomass we determined to be accessible to sea lions in our study represents the maximum biomass accessible to them. It would be useful to assess the relationship between the availability of prey, the amounts of fish commercially caught, and the differing rates of population change of other species undergoing declines in western Alaska. Other pinniped species, such as harbour seals and northern fur seals, which feed on many of the same prey species as sea lions would be ideal candidates for further study as the prey biomass distributions and catch data used eto assess fisheries competition with sea lions could also be used for them.

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APPENDICES

Appendix 1 – Steller sea lion population model

From Winship and Trites (2006) and Battaile and Trites (2011)

The basic population model was an age-structured birth-pulse simulation of the adult female population with a time-step of one year. The main assumptions of this model were: (1) all female sea lions are sexually mature at 5 years and potentially give birth for the first time at 6 years of age, (2) birth rate does not vary with age, (3) juvenile (applied before sexual maturity) and adult (applied after sexual maturity) survival rates do not vary with age and (4) no females live longer than 25 years. Three primary vital statistics were calculated: adult survival, juvenile survival and fecundity. Each of these rates was estimated separately for each rookery and time period. The number of time periods considered depended on the number of inflexion points in the population dynamics of a particular rookery. The 33 rookery populations were assumed to be at their carrying capacity in 1978 with equilibrium survival and birth rates. Each rookery's population was simulated from 1978 to 2008. Final model estimates were of males and females, with about a third of each rookery's population estimated to be males.

Appendix 2 – How prey biomass distributions were created

National Marine Fisheries Service (NMFS) bottom trawl surveys

NMFS trawl surveys have been conducted since the 1980s to monitor the condition of the demersal fish and crab stocks of Alaska. Data from 1982-2009 can be accessed at http://www.afsc.noaa.gov/RACE/groundfish/survey_data. Beginning in 2000, this database also included data from the Alaska Department of Fish and Game surveys (management of fisheries within 3 nautical miles of the shoreline is under state control). The dataset was developed to describe the temporal distribution and abundance of commercially and ecologically important groundfish species, examine the changes in species composition over time and space, and describe the physical environment of groundfish habitat. The spatial extent of the trawl surveys spans the eastern Bering Sea, Gulf of Alaska and Aleutian Islands from 170°E to -130°W and 75°N to 50°S. The spatial sampling is stratified to improve accuracy. Surveys are conducted from mid-May to the end of July and move systematically from west to east. The depths for these surveys are limited to <600 m, which approximates the deepest observed trawl haul taken by fisheries. The surveys provide data on both commercial and non-commercial fish species.

Modelling of prey biomass distributions

Predicted biomass distributions of walleye pollock, Pacific cod and Atka mackerel were modelled by Gryba et al. (2011). These prey biomass distributions were derived from NMFS bottom trawl survey data using Generalised Least Square models to determine the relationships between survey catch per unit effort (CPUE) values of pollock, cod and mackerel, and bathymetry, modelled oceanographic data (from a ROMS - Regional Oceanographic Modelling System) and remotely sensed data of areas sampled at a 9 x 9 km^2 resolution throughout the Aleutian Islands, Bering Sea and Gulf of Alaska (e.g., Fig. A2.1). Remotely sensed data included sea surface temperature, sea surface height, wind and chlorophyll-*a*. The ROMS model used was provided at a 9 x 9 km^2 resolution and summarised as monthly averages of indicators such as temperature, salinity, velocity vectors in three directions at 30 different vertical levels, mixed layer depth and sea surface height anomaly. ROMS models were available from 2000-2004 (Hermann & Stabeno 1996, Hermann et al. 2002). Variables that correlated significantly with CPUE were used to predict the spatial distribution of prey biomass by applying the CPUE

equations to the fisheries survey area bound surfaces of the significant environmental variables to obtain continuous CPUE surfaces (e.g., Fig. A2.1). The NMFS trawl survey biomass estimates of pollock, cod and mackerel for the summer of each year were then distributed throughout the respective fisheries survey areas (Aleutian Islands, eastern Bering Sea or Gulf of Alaska) in proportion to the predicted CPUE value at each location (Fig. A2.1, Table A2.1). The prey biomass distributions should therefore be treated as predictions of relative biomass, rather than absolute biomass. The Gulf of Alaska and Bering Sea prey biomass distributions were combined for comparisons with Steller sea lion population trends.

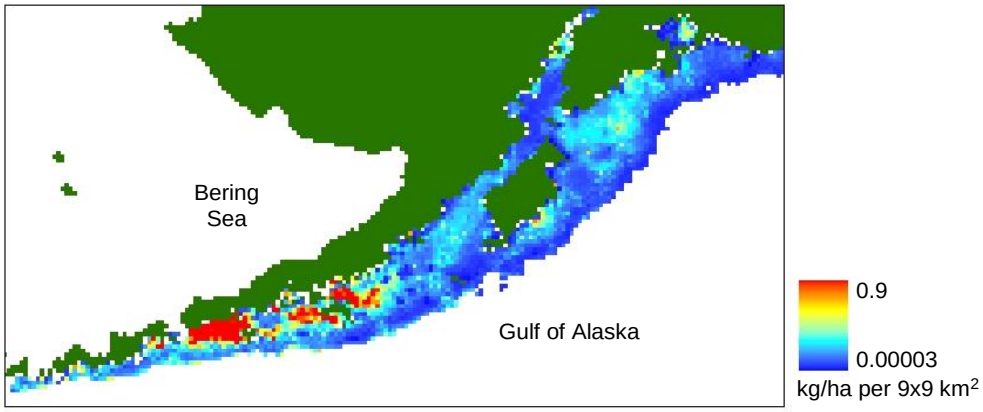


Fig. A2.1. An example of a CPUE distribution showing the predicted CPUE (kg/ha per 9x9 km^2) of walleye pollock in the Gulf of Alaska fisheries survey area (June 2003).

Table A2.1. Standing biomass (age 1+ years) in metric tonnes of walleye pollock, Pacific cod and Atka mackerel in the Aleutian Islands, Bering Sea and Gulf of Alaska fisheries survey areas as estimated by NMFS bottom trawl surveys conducted in June and July of each survey year. Missing values indicate that no survey was conducted in that survey area in that year.

	Estimated survey biomass (t)						
	Walleye pollock			**Pacific cod**			**Atka mackerel**
Survey year	Aleutian Islands	Bering Sea	Gulf of Alaska	Aleutian Islands	Bering Sea	Gulf of Alaska	Aleutian Islands
2000	128,060	5,265,000		136,075	528,466		510,857
2001		4,200,000	216,777		833,626	257,614	
2002	356,617	5,038,000		82,853	618,680		772,798
2003		8,458,000	399,690		593,876	297,402	
2004	366,110	3,886,000		114,396	596,467		886,783

Appendix 3 – Notes on observed catches

- In the Bering Sea, almost all walleye pollock is harvested by large vessels (>38.1 m in length), either by large catcher boats delivering ashore or to motherships, or large factory trawlers. In the Gulf of Alaska, smaller shore-based trawlers are more prevalent. Atka mackerel is almost exclusively a large vessel fishery. In the Gulf of Alaska, several smaller vessels fish for Pacific cod (Bill Wilson and Jeannie Heltzel, personal communications).
- From 2004 – 2008, more than 97% of Atka mackerel in the Aleutian Islands and Bering Sea was taken by catcher processors. Most of these had 100% observer coverage. There was some catch taken by smaller catcher vessels (probably 30% coverage), but this did not amount to much catch (1,000 - 2,000 t) and was probably only a couple of vessels (Todd Loomis, personal communication).
- From 1998-2004, there were approximately 22 vessels catching Atka mackerel in the Aleutian Islands and Bering Sea. Of these, four vessels were between 18.3 and 38.1 m in length. These four vessels accounted for less than 2% of the total allowable catch (NMFS 2009; Todd Loomis, personal communication).

Appendix 4 – Distances from rookery grid

105.3423	102.6157883	100.6231	99.40825	99	99.40825	100.6231	102.6158	105.3423
96.93297	93.96275858	91.78235	90.44888	90	90.44888	91.78235	93.96276	96.93297
88.63972	85.38149682	82.9759	81.49847	81	81.49847	82.9759	85.3815	88.63972
80.49845	76.89603371	74.2159	72.56032	72	72.56032	74.2159	76.89603	80.49845
72.56032	68.54195795	65.52099	63.63961	63	63.63961	65.52099	68.54196	72.56032
64.89992	60.37383539	56.921	54.74486	54	54.74486	56.921	60.37384	64.89992
57.62812	52.47856705	48.46648	45.89118	45	45.89118	48.46648	52.47857	57.62812
50.91169	45	40.24922	37.10795	36	37.10795	40.24922	45	50.91169
45	38.18376618	32.44996	28.4605	27	28.4605	32.44996	38.18377	45
40.24922	32.44996148	25.45584	20.12461	18	20.12461	25.45584	32.44996	40.24922
37.10795	28.46049894	20.12461	12.72792	9	12.72792	20.12461	28.4605	37.10795
36	27	18	9	**2.25**	9	18	27	36
37.10795	28.46049894	20.12461	12.72792	9	12.72792	20.12461	28.4605	37.10795
40.24922	32.44996148	25.45584	20.12461	18	20.12461	25.45584	32.44996	40.24922
45	38.18376618	32.44996	28.4605	27	28.4605	32.44996	38.18377	45
50.91169	45	40.24922	37.10795	36	37.10795	40.24922	45	50.91169
57.62812	52.47856705	48.46648	45.89118	45	45.89118	48.46648	52.47857	57.62812
64.89992	60.37383539	56.921	54.74486	54	54.74486	56.921	60.37384	64.89992
72.56032	68.54195795	65.52099	63.63961	63	63.63961	65.52099	68.54196	72.56032
80.49845	76.89603371	74.2159	72.56032	72	72.56032	74.2159	76.89603	80.49845
88.63972	85.38149682	82.9759	81.49847	81	81.49847	82.9759	85.3815	88.63972
96.93297	93.96275858	91.78235	90.44888	90	90.44888	91.78235	93.96276	96.93297
105.3423	102.6157883	100.6231	99.40825	99	99.40825	100.6231	102.6158	105.3423

Section of a grid showing the straight line distances (km) from the center of each location (grid cell) to each rookery (represented by the cell in bold). Each grid cell measures 9x9 km^2. Each rookery (starting) grid cell was assigned a value of 2.25 km – the estimated mean distance of an 'average' sea lion in the starting grid cells from the rookeries (center points of starting grid cells).

Appendix 5 – Mean straight line foraging distances of Steller sea lions

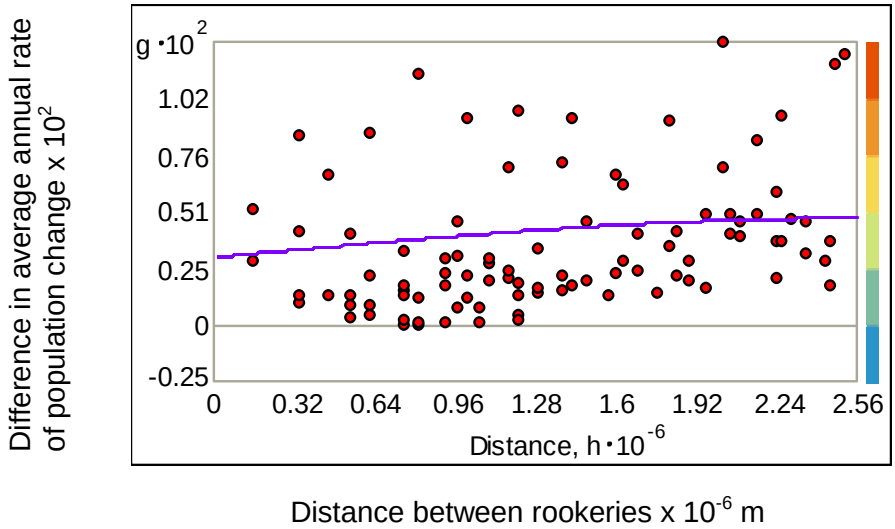
Reported mean maximum and maximum straight line foraging distances of Steller sea lions in different regions. Distances presented here are approximations (rounded to the nearest whole number) of the values published in the literature.

Age class	Mean foraging distance (km)	Maximum foraging distance (km)	Season	Study area	Reference
Adult females (>3 years)	20	>300	spring 1992	GOA	(Merrick et al. 1994)
	17 (summer) 133 (winter)		summer and winter 1990-1993	central GOA, eastern AI	(Merrick & Loughlin 1997)
	Most locations within 10, mean = 20	263	summer 1991	Russia	(Loughlin et al. 1998)
	18	55	summer 1992-1993	SEA	(Rehberg et al. 2009)
Juveniles (1-3 years)	Most locations within 15	111	year round 1998-2002	GOA, eastern AI, SEA	(Raum-Suryan et al. 2004)
	25, long range mean = 50	447	year round 1994-2000	GOA, AI, WASH	(Loughlin et al. 2003)
	Most locations within 10-20	>50	year round 2000-2002	GOA, central/eastern AI	(Fadely et al. 2005)
Pups (<1 year)	7	261	year round 1994-2000	GOA, AI, WASH	(Loughlin et al. 2003)
	5	50	year round 1998-2002	GOA, eastern AI, SEA	(Raum-Suryan et al. 2004)
	30 (winter)		winter 1990-1993	western Alaska	(Merrick & Loughlin 1997)
		>250 (pups older than 6 months)		GOA	(Merrick et al. 1994)

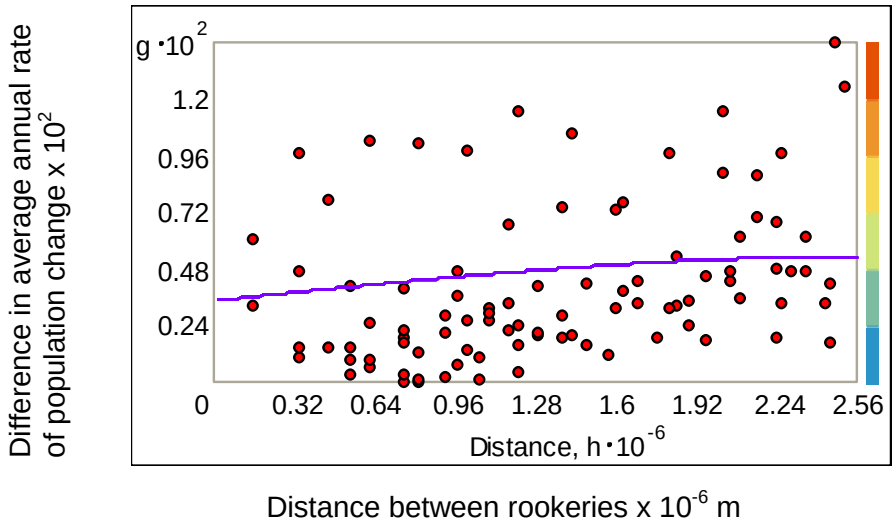
AI – Aleutian Islands, GOA – Gulf of Alaska, SEA – Southeast Alaska, WASH – Washington

Appendix 6 – Semivariograms

All rookeries

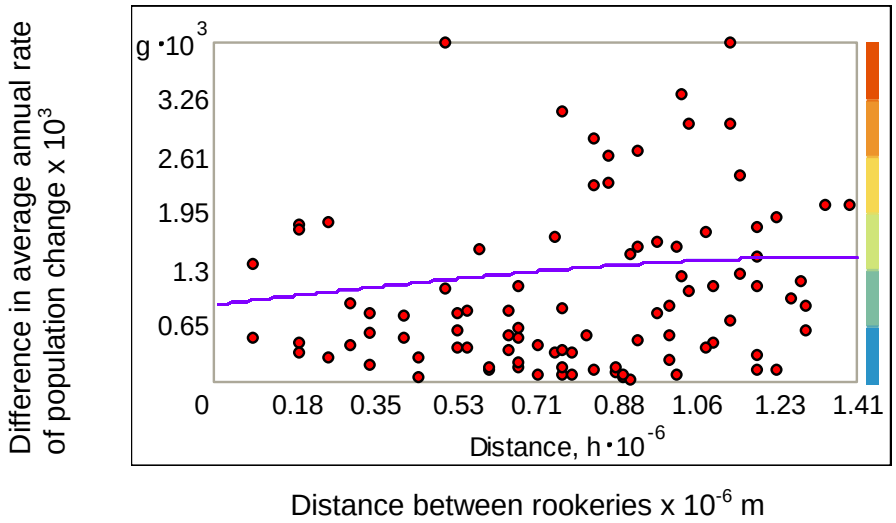


Semivariogram of the differences in average annual rates of Steller sea lion (non-pup) population change from 2000-2008 and the distances between all 33 rookeries studied. There was a gradual increase in differences in average annual rates of sea lion population change as the distances between rookeries increased.

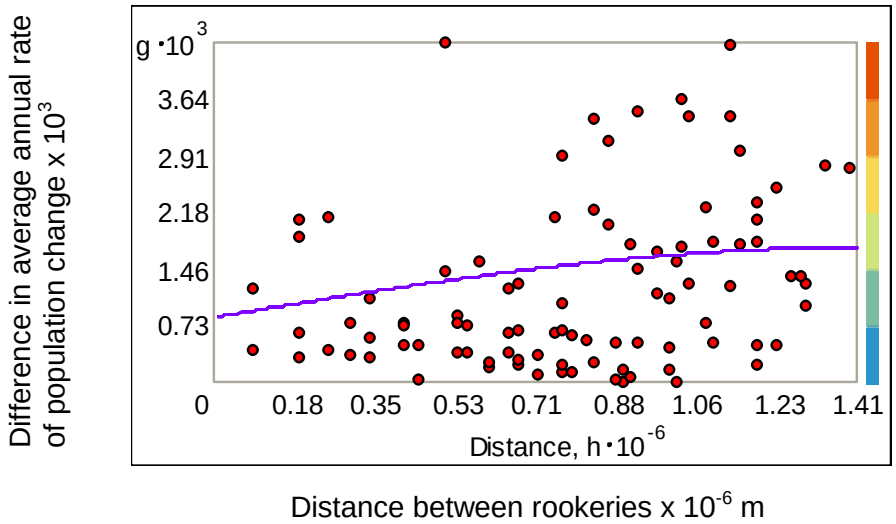


Semivariogram of the differences in average annual rates of Steller sea lion (pups) population change from 2000-2008 and the distances between all 33 rookeries studied. There was a gradual increase in differences in average annual rates of sea lion population change as the distances between rookeries increased.

Gulf of Alaska

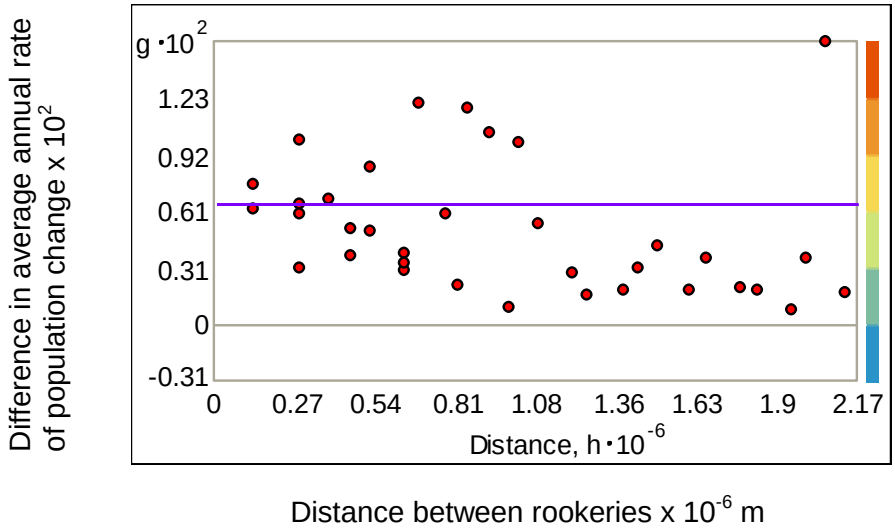


Semivariogram of the differences in average annual rates of Steller sea lion (non-pup) population change from 2000-2008 and the distances between the Gulf of Alaska rookeries. There was a gradual increase in the differences in average annual rates of sea lion population change as the distances between rookeries increased, indicating the possibility of spatial autocorrelation.

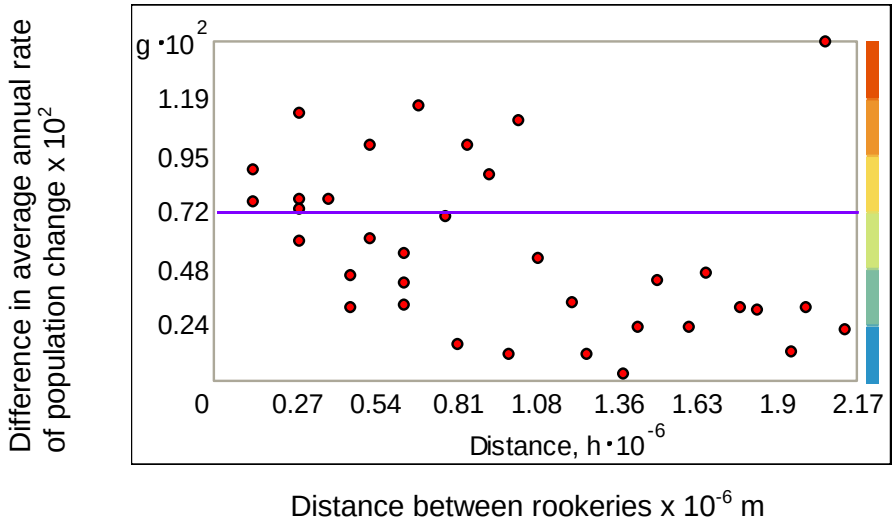


Semivariogram of the differences in average annual rates of Steller sea lion (pup) population change from 2000-2008 and the distances between the Gulf of Alaska rookeries. There was a gradual increase in the differences in average annual rates of sea lion population change as the distances between rookeries increased, indicating the possibility of spatial autocorrelation.

Aleutian Islands

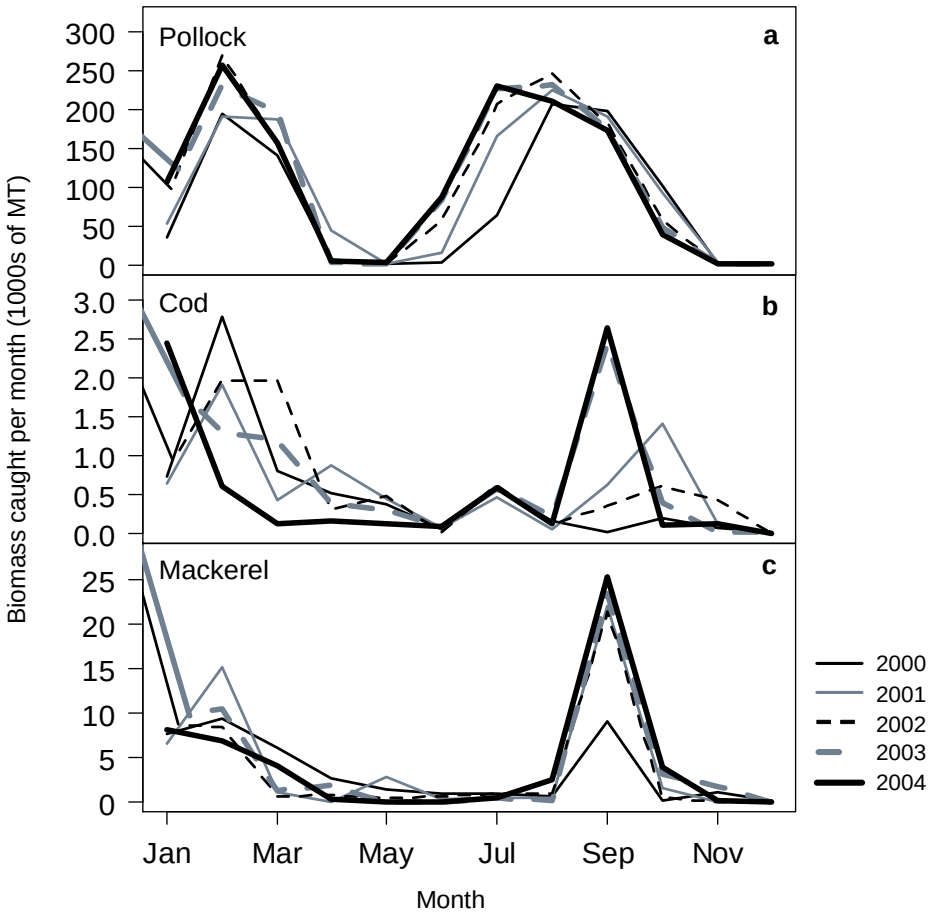


Semivariogram of the differences in average annual rates of Steller sea lion (non-pup) population change from 2000-2008 and the distances between the Aleutian Island rookeries. There was no apparent relationship between the differences in average annual rates of sea lion population change and the distances between rookeries.



Semivariogram of the differences in average annual rates of Steller sea lion (pup) population change from 2000-2008 and the distances between the Aleutian Island rookeries. There was no apparent relationship between the differences in average annual rates of sea lion population change and the distances between rookeries.

Appendix 7 – Monthly catches



Monthly catches (1000s of tons) of (a) walleye pollock in the eastern Bering Sea, (b) Pacific cod in the Gulf of Alaska and (c) Atka mackerel in the Aleutian Islands from 2000-2004.

Appendix 8 – Accessibility model

8.34E-08	1.2301E-07	1.63E-07	1.94E-07	2.06E-07	1.94E-07	1.63E-07	1.23E-07	8.34E-08
2.76E-07	4.22114E-07	5.76E-07	6.96E-07	7.42E-07	6.96E-07	5.76E-07	4.22E-07	2.76E-07
9.01E-07	1.43376E-06	2.02E-06	2.49E-06	2.68E-06	2.49E-06	2.02E-06	1.43E-06	9.01E-07
2.88E-06	4.80394E-06	7.04E-06	8.91E-06	9.65E-06	8.91E-06	7.04E-06	4.8E-06	2.88E-06
8.91E-06	1.57974E-05	2.43E-05	3.18E-05	3.48E-05	3.18E-05	2.43E-05	1.58E-05	8.91E-06
2.65E-05	5.05903E-05	8.27E-05	0.000113	0.000125	0.000113	8.27E-05	5.06E-05	2.65E-05
7.48E-05	0.000155834	0.000276	0.000398	0.000452	0.000398	0.000276	0.000156	7.48E-05
0.000195	0.000452347	0.00089	0.001393	0.001631	0.001393	0.00089	0.000452	0.000195
0.000452	0.00119479	0.002705	0.004775	0.00588	0.004775	0.002705	0.001195	0.000452
0.00089	0.002704741	0.007327	0.015663	0.021201	0.015663	0.007327	0.002705	0.00089
0.001393	0.004775426	0.015663	0.044938	0.076439	0.044938	0.015663	0.004775	0.001393
0.001631	0.005880233	0.021201	0.076439	**0.200004**	0.076439	0.021201	0.00588	0.001631
0.001393	0.004775426	0.015663	0.044938	0.076439	0.044938	0.015663	0.004775	0.001393
0.00089	0.002704741	0.007327	0.015663	0.021201	0.015663	0.007327	0.002705	0.00089
0.000452	0.00119479	0.002705	0.004775	0.00588	0.004775	0.002705	0.001195	0.000452
0.000195	0.000452347	0.00089	0.001393	0.001631	0.001393	0.00089	0.000452	0.000195
7.48E-05	0.000155834	0.000276	0.000398	0.000452	0.000398	0.000276	0.000156	7.48E-05
2.65E-05	5.05903E-05	8.27E-05	0.000113	0.000125	0.000113	8.27E-05	5.06E-05	2.65E-05
8.91E-06	1.57974E-05	2.43E-05	3.18E-05	3.48E-05	3.18E-05	2.43E-05	1.58E-05	8.91E-06
2.88E-06	4.80394E-06	7.04E-06	8.91E-06	9.65E-06	8.91E-06	7.04E-06	4.8E-06	2.88E-06
9.01E-07	1.43376E-06	2.02E-06	2.49E-06	2.68E-06	2.49E-06	2.02E-06	1.43E-06	9.01E-07
2.76E-07	4.22114E-07	5.76E-07	6.96E-07	7.42E-07	6.96E-07	5.76E-07	4.22E-07	2.76E-07
8.34E-08	1.2301E-07	1.63E-07	1.94E-07	2.06E-07	1.94E-07	1.63E-07	1.23E-07	8.34E-08

Section of a grid showing the likelihood (calculated using the selected accessibility model equation y=0.2756e-0.2639x,, where x and y are distance in nautical miles and accessibility respectively) that a sea lion would forage in any given grid cell as a function of its distance from the nearest rookery (represented by the cell in bold). Distances were obtained from the distance grid in Appendix 4.

7.9E-08	1.1655E-07	1.55E-07	1.84E-07	1.95E-07	1.84E-07	1.55E-07	1.17E-07	7.9E-08
2.62E-07	3.99945E-07	5.46E-07	6.6E-07	7.03E-07	6.6E-07	5.46E-07	4E-07	2.62E-07
8.54E-07	1.35847E-06	1.91E-06	2.36E-06	2.54E-06	2.36E-06	1.91E-06	1.36E-06	8.54E-07
2.72E-06	4.55164E-06	6.67E-06	8.44E-06	9.14E-06	8.44E-06	6.67E-06	4.55E-06	2.72E-06
8.44E-06	1.49678E-05	2.3E-05	3.01E-05	3.3E-05	3.01E-05	2.3E-05	1.5E-05	8.44E-06
2.52E-05	4.79334E-05	7.84E-05	0.000107	0.000119	0.000107	7.84E-05	4.79E-05	2.52E-05
7.09E-05	0.00014765	0.000262	0.000377	0.000429	0.000377	0.000262	0.000148	7.09E-05
0.000185	0.00042859	0.000843	0.00132	0.001545	0.00132	0.000843	0.000429	0.000185
0.000429	0.001132041	0.002563	0.004525	0.005571	0.004525	0.002563	0.001132	0.000429
0.000843	0.002562693	0.006943	0.01484	0.020088	0.01484	0.006943	0.002563	0.000843
0.00132	0.004524628	0.01484	0.042578	0.072425	0.042578	0.01484	0.004525	0.00132
0.001545	0.005571412	0.020088	0.072425	**0.1895**	0.072425	0.020088	0.005571	0.001545
0.00132	0.004524628	0.01484	0.042578	0.072425	0.042578	0.01484	0.004525	0.00132
0.000843	0.002562693	0.006943	0.01484	0.020088	0.01484	0.006943	0.002563	0.000843
0.000429	0.001132041	0.002563	0.004525	0.005571	0.004525	0.002563	0.001132	0.000429
0.000185	0.00042859	0.000843	0.00132	0.001545	0.00132	0.000843	0.000429	0.000185
7.09E-05	0.00014765	0.000262	0.000377	0.000429	0.000377	0.000262	0.000148	7.09E-05
2.52E-05	4.79334E-05	7.84E-05	0.000107	0.000119	0.000107	7.84E-05	4.79E-05	2.52E-05
8.44E-06	1.49678E-05	2.3E-05	3.01E-05	3.3E-05	3.01E-05	2.3E-05	1.5E-05	8.44E-06
2.72E-06	4.55164E-06	6.67E-06	8.44E-06	9.14E-06	8.44E-06	6.67E-06	4.55E-06	2.72E-06
8.54E-07	1.35847E-06	1.91E-06	2.36E-06	2.54E-06	2.36E-06	1.91E-06	1.36E-06	8.54E-07
2.62E-07	3.99945E-07	5.46E-07	6.6E-07	7.03E-07	6.6E-07	5.46E-07	4E-07	2.62E-07
7.9E-08	1.1655E-07	1.55E-07	1.84E-07	1.95E-07	1.84E-07	1.55E-07	1.17E-07	7.9E-08

Section of a grid showing the likelihood of a sea lion occurring within each grid cell after dividing the relative accessibility value of each grid cell by the sum of all accessibility values within the foraging arena of each rookery. Thus the final accessibility values for the grid cells in each rookery's foraging arena summed to 1.

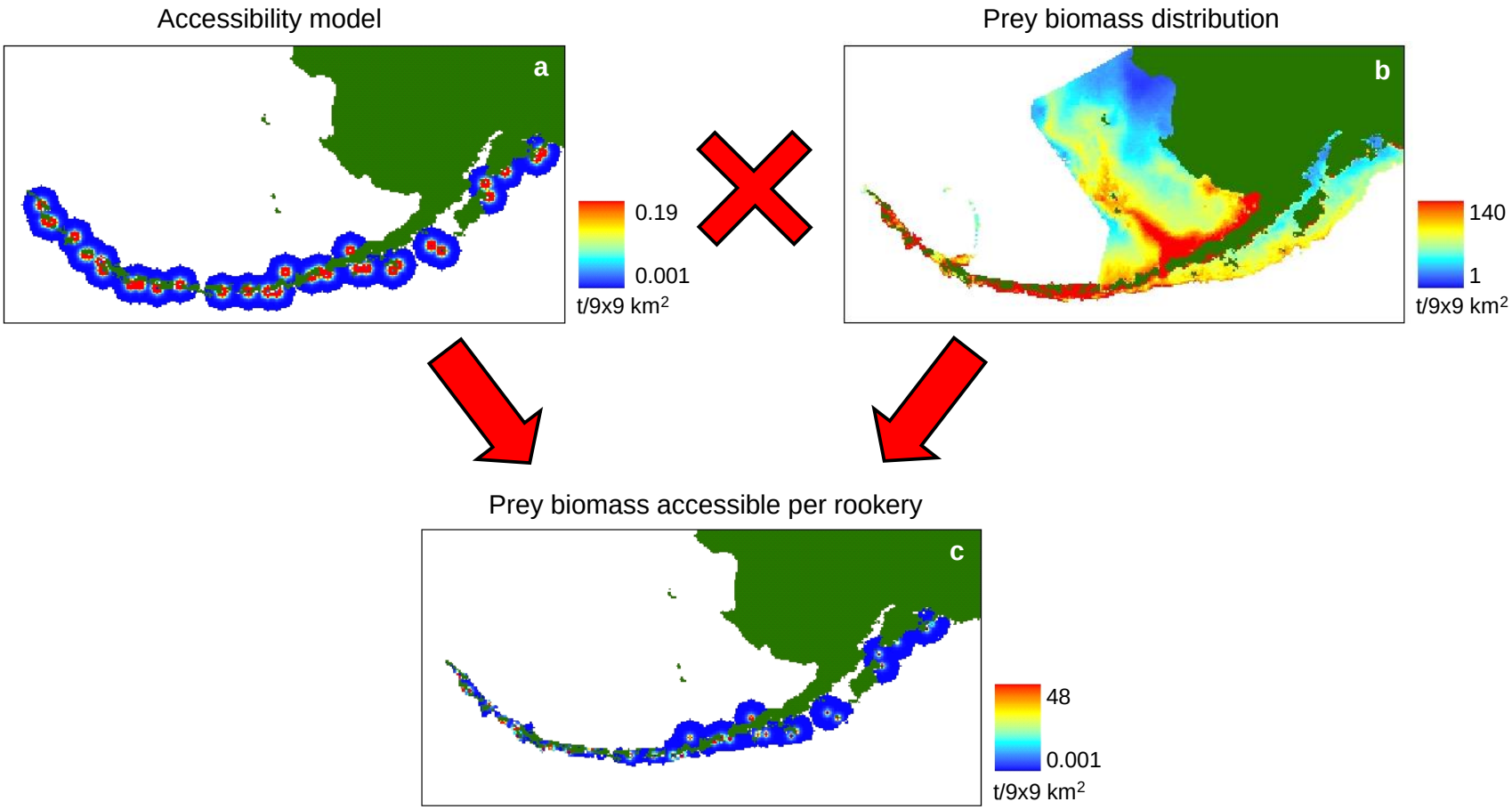


Fig. A8.1. Example of how the accessibility model was combined with the prey biomass distributions: (a) accessibility of marine foraging areas to the 33 sea lion rookeries in the Aleutian Islands, Bering Sea and Gulf of Alaska, (b) predicted biomass (t/9x9 km^2 grid cell) of Pacific cod available in the Aleutian Islands (2004), Bering Sea (2003) and Gulf of Alaska (2003) and (c) predicted biomass (t/9x9 km^2 grid cell) of Pacific cod accessible to sea lions from the 33 rookeries in 2003/04.