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The diet of free-ranging male Steller sea lions (*Eumetopias jubatus*) in the eastern Bering Sea: a retrospective analysis based on stomach contents of an endangered pinniped

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Abstract

This study illuminates historical diet and foraging locations of endangered western U.S. stock Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)). Prey were identified from stomachs of 22 males collected in the eastern Bering Sea from the ice edge in March, 1985, and nearshore St. Paul Island in September-October, 1985 and 1986. Percent frequency of occurrence (PFO) and number (PN) were highest for walleye pollock (*Gadus chalcogrammus* (Pallas, 1814); PFO 69, PN 15, mean length 17 cm), Pacific herring (*Clupea pallasii* Valenciennes, 1847; PFO 62, PN 16, mean length 26 cm), shorthorn sculpin (*Myoxocephalus scorpius* (Linnaeus, 1758); PFO 54, PN 30) and Pacific giant octopus (*Enteroctopus dofleini* (Wulker, 1910); PFO 39, PN 8, mean wt 31 kg) in spring; and northern rock sole (*Lepidopsetta polyxystra* Orr & Matarese, 2000; PFO 78, PN 47, mean length 35cm), Pacific cod (*Gadus microcephalus* Tilesius, 1810; PFO 56, PN 12, mean length 62 cm), walleye pollock (PFO 44, PN 7, mean length 49 cm) and red Irish lord (*Hemilepidotus hemilepidotus* (Tilesius, 1811); PFO 11, PN 9) in fall. Species of Cryptacanthidae, Liparidae and Zoarcidae were highly represented and exclusive to spring collections. Predictable seasonal concentrations and movements of mature prey along frontal boundaries of the continental shelf and ice edge may be critical to male Steller sea lion fitness during the non-breeding season.

Keywords: Steller sea lion, *Eumetopias jubatus*, diet, stomachs, male, western stock, Bering Sea, ice, Pribilof Islands

Introduction

Population declines among marine apex predators are frequently associated with anthropogenic or environmentally influenced fluctuations in the abundance or availability of their prey (Melin et al. 2008). The temporal and spatial evaluation of diet and foraging habitat is therefore central to characterizing trophic interactions and to developing conservation policies for both predator and prey. The western U.S. stock of Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) (SSLs) was listed as endangered under the U.S. Federal Endangered Species Act in 1997 and diet and prey resources remain focal areas of research to define the mechanism(s) driving their population decline (NMFS 2008). The diet of adult female western stock SSLs based on prey remains in scats (feces) is well known (Sinclair and Zeppelin 2002; Sinclair et al. 2013; Tollit et al. 2017). However, the diet of adult male SSLs in the wild is virtually unknown and remains a considerable limitation to understanding fluctuation in population patterns of this endangered population segment. Therefore, this recent recovery of high-quality and intact prey remains from stomachs of free-ranging adult male sea lions and the hand-written field records associated with the samples, adds a precious portal into the greater marine trophic interactions of this endangered pinniped.

Our current understanding of the regional and seasonal diet patterns of western U.S. stock SSLs is based on a 20-year time series (1990-2009) of prey identified from the scats of adult females (Sinclair et al. 2013). Scats are collected annually from SSL summer breeding rookeries and winter haulouts along the Aleutian Islands chain. Adult territorial males do not eat during summer and are largely absent from winter haulouts when scats are collected along the Aleutian Island chain, therefore nothing is known about their diet or distribution during the non-breeding season (fall through spring). It has long been thought that some adult and sub-adult males move

north into the Bering Sea in the fall and conjectured that they return south in the winter ahead of the advancing ice edge (Kenyon and Rice 1961). There have been few documented winter observations in Bering Sea U.S. waters (Barabash-Nikiforov 1938; Tikhomirov 1964; Calkins 1998) and even fewer opportunities to quantify the diet of males during this time (Wilke and Kenyon 1952; Fiscus and Baines 1966; Frost and Lowry 1986; Calkins 1998). This study is the first to document the importance of ice to Steller sea lion males as a long-term seasonal haulout over areas of known overwintering forage.

In the early 1980s, a newly established U.S.-Russia cooperative research program provided opportunity for joint studies of the distribution and life history of pinnipeds. Field research took place in the eastern and western Bering Sea and along the Aleutian and Commander Islands. The pivotal diet study that resulted from this effort was based on stomachs from 32 mostly adult male SSLs collected in March 1981 (Calkins 1998). Individuals were randomly shot from a large group gathered on the ice edge over the north central Bering Sea continental shelf. No females or pups were observed among the group. The Calkins (1998) study was the first, directed large-scale effort to collect SSLs in U.S. pelagic waters and the first to confirm the ice-associated distribution of adult male Steller sea lions in the eastern Bering Sea.

In March 1985, a second and final U.S.-Russia cooperative vessel survey for pinnipeds in the eastern Bering Sea was conducted. As in 1981, a single concentrated group of male SSLs was found hauled out on the ice after weeks of survey effort in both open pelagic and ice-bound waters. The group was located along the ice edge over the northern Middle Shelf Domain (between the 50 and 100m isobaths) in the southeastern Bering Sea, just southeastward of those collected in the 1981 survey. Eleven of the 13 individuals randomly selected from this group were adults (age 8+ yrs). Stomach contents were collected, but not evaluated at the time. We

analyze them here along with the stomach contents from 9 males shot in subsistence collections over the southern Middle Shelf Domain off the north shore of St. Paul Island in September and October of 1985 and 1986 (Figure 1).

Field researchers surmised that the SSLs collected from the ice in 1985 originated from rookeries in the western Aleutian Islands, today designated as an endangered Distinct Population Segment (DPS) (O’Corry-Crowe et al. 2006; NMFS 2008) or the western U.S. stock of SSLs. The 1985-1986 St. Paul Island collections are presumed to be from the nearby and now nearly extinct Walrus Island rookery which is also considered part of the western stock population. These historic collections provide a temporal window into adult and sub-adult male diet and the distribution of their prey during seasons and in locations from which we otherwise have little information, and highlight the potential consequences of rapidly changing climate conditions and ice reduction to the reproductive success of this DPS.

Materials and Methods

Field collections

We evaluate prey remains and field collection records from two separate historical collections of SSLs from the northern and southern Middle Shelf Domains (between the 50 and 100m isobaths) of the southeastern Bering Sea. On 30-31 March 1985, 13 SSLs were randomly shot from an all-male group located on the ice over the northern Middle Shelf Domain (59°N latitude, 172°W longitude) by the Russian research vessel *Zakharova* (Fig. 1). Animals were delivered to the ship and stomachs were removed and frozen whole then later sorted in a land-based laboratory. Eleven of the 13 were from adult males (age 8+ yrs) one was a juvenile (age 1-4 yrs) and one was of undetermined age. No females or young-of-the-year were present in the sample or among the remaining animals observed on the ice. Field researchers surmised that the collected animals were from the western Aleutian Islands now described as the endangered western U.S. stock of SSLs (NMFS 2008).

The second set of data were collected on October 2, 1985 and Sept 22 – October 10, 1986. Five juvenile (1-4 yrs) and 4 sub-adult (age 5-7 yrs) male SSLs were shot over the southern Middle Shelf Domain (57°N 170°W) by Aleut subsistence hunters near the northern tip of St. Paul Island in the Pribilof Island group (Fig. 1). Stomachs were recovered and processed when the animals washed ashore within one to two days of being shot. Fourteen juvenile-adult males and four juvenile-adult aged females were also collected at this time, but the stomachs from only two females contained prey remains. One stomach from a juvenile female contained unmeasured remains from a cottid fish (*Gymnocanthus* sp. cf. *G. galeatus* Bean, 1881) and a Pacific giant octopus (*Enteroctopus dofleini* (Wulker, 1910)) and the second from an adult female contained the remains of two northern rock sole (*Lepidopsetta polyxystra* Orr &

Matarese, 2000) . These samples are not included in analyses here, but are mentioned as a contrast to collections over the northern shelf on the ice edge during spring where no females were present. Field researchers surmised that the recovered SSLs in the St. Paul sample originated from the nearby, nearly extinct rookery on Walrus Island, approximately 15 km east of St. Paul Island. Animals from Walrus Island occasionally haul-out on St. Paul Island and are considered part of the western stock.

Laboratory analysis

In each of the three collection years, samples were processed for stomach contents analysis in similar fashion. Stomachs were thoroughly rinsed onto a 1 mm mesh sieve or, in the case of St. Paul samples, a series of nested brass or stainless steel sieves (2.36 mm, 1.4 mm, 1.0 mm, 0.71 mm) to separate skeletal parts from fleshy material. Whole fish were only found in the spring samples and these were identified, sexed and measured (standard length, SL) then discarded. Skeletal parts (fish bones, fish ear bones - 'otoliths' and cephalopod mouthparts - 'beaks') were stored in isopropyl alcohol and crab remains and mollusks were stored in 10% buffered formalin. St. Paul otoliths and bones were stored dry and beaks and crustacean remains were stored in isopropyl alcohol. Skeletal parts were later identified to species by comparison with prey reference collections of fishes and cephalopods from the eastern Bering Sea. Identifications and measurements were confirmed by at least two researchers. Otoliths, bones and octopus beaks were measured to the nearest 0.1 mm with an ocular micrometer or Vernier calipers. Quality categories were not assigned to hard parts however, broken or slightly compromised samples were measured only if their original size was clearly indicated in which case, both 'actual' and 'estimated' measurements were recorded. Estimated otolith lengths (OL) were recorded only occasionally in the spring samples but, regularly in the fall samples and these

were used for prey length calculations when available. The difference between ‘actual’ and ‘estimated’ measurements averaged less than 0.5mm. Severely eroded otoliths or those missing more than an estimated 2 mm of their length were not measured. Otolith length (mm) was regressed to fork length (FL, cm) or standard length (SL, cm) of fish where regression equations were available. For all regression applications, only one otolith, either the left or right, was measured from each fish and only the upper or lower beak measurements were used for octopus. All available parts beyond otoliths (e.g. dentary, vomer) were also used in identifying and measuring prey. The pigment lower-wing-length (PLWL, mm) and pigment upper-lateral-wall length (PULWL, mm) were regressed to the live weight (kg) of *E. dofleini*. The greatest carapace width (CW, mm) of snow crabs (*Chionoecetus opilio* (O. Fabricius, 1788)) was measured directly.

Body size was evaluated for most of the primary prey species including Pacific cod (*Gadus macrocephalus* Tilesius, 1810), walleye pollock (*Gadus chalcogrammus* (Pallas, 1814)) red Irish lord (*Hemilepidotus* (Tilesius, 1811)), northern rock sole, Pacific herring (*Clupea pallasii* Valenciennes, 1847), wattled eelpout (*Lycodes palearis* Gilbert, 1896) and Pacific giant octopus. The specific regression equations that were applied and their source are cited as footnotes in Table 1. Body size estimates were also made for less frequently occurring species when length regression equations or size at maturity data were available. Following Orchard (2001) the regression equation developed for red Irish lord was applied to the two other closely related members of the Cottidae, yellow Irish lord (*Hemilepidotus jordani* Bean, 1881) and butterfly sculpin (*Hemilepidotus papilio* (Bean, 1880)). The regression equation for southern rock sole (*Lepidopsetta bilineata* (Ayres, 1855)) was applied to the closely related northern rock sole. Most all of the individual fish used to develop the regression equation were based on

collections made in high abundance areas of the more recently described northern rock sole in the eastern Bering Sea (Orr and Matarese 2000). The length of Pacific herring was averaged from a combination of the fork length (FL) of intact fish measured (then discarded) at sea together with the OL to SL regression equation for remains returned to the shore-based laboratory.

Data analysis

The number of stomachs containing individual prey species is recorded as prey frequency of occurrence (FO). An individual FO value is expressed as a percentage of the total number of stomachs containing prey as percent prey frequency of occurrence (PFO). The total count of all individuals within each prey species, across all stomach samples is termed prey number (N). The number of individuals within each prey species is expressed as a percentage of the total number of individuals counted across all species as percent number (PN). The base calculation for prey frequency follows the precedent set by the longest time series of western stock SSL diet studies based on scat (Sinclair and Zeppelin 2002; Sinclair et al. 2013) as does a threshold of $\geq 5\%$ prey frequency of occurrence for ranking prey as 'primary'. A threshold of importance of $\geq 5\%$ was also set for prey number (a measure unavailable in scat based SSL studies) in this study for the sake of consistency with PFO calculations. Simple rank values of FO and N are tabled along with PFO and PN, since percentage values can misrepresent the importance of a prey item when sample sizes are small. Base calculations and mean prey body sizes are tabled for the benefit of those wishing to recalculate recorded values in different format or for different applications (Table 1). No live animals were directly handled or harmed in our retrospective re-identification and analyses of prey remains that were collected 31 years prior to this study. Original raw data

files are available from the Alaska Fisheries Science Center Metadata Library
(<https://inport.nmfs.noaa.gov>).

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Results

Prey species

Prey species that ranked $\geq 5\%$ in both PFO and PN in spring samples from the northern middle shelf ice edge were walleye pollock, Pacific herring, shorthorn sculpin (*Myoxocephalus scorpius* (Linnaeus, 1758)), Pacific giant octopus, wattled eelpout and snow crab. In fall samples over the southern middle shelf, northern rock sole, Pacific cod, walleye Pollock and red Irish lord ranked $\geq 5\%$ in both PFO and PN. Prey rank by occurrence parallels rank by number in both collections in this study with two exceptions: in spring samples the variegated snailfish (*Liparis gibbus* Bean, 1881) ranked higher in PFO than wattled eelpout but, missed the $\geq 5\%$ PN cutoff by one individual fish, and in fall samples just one of the nine SSLs collected ate all (9% total prey N) of the red Irish lord (Table 1).

SSL diet between the two regions was most similar at the family level, and less so in terms of the species consumed. The Cottidae and Gadidae occurred most frequently and in highest numbers in each sample area but, the representative species were either different (shorthorn sculpin vs. red Irish lord) or occurred at markedly different levels (Fig. 2). For example, the gadids walleye pollock and Pacific cod were consumed in both collection areas, but cod was more prevalent than pollock over the southern shelf while pollock was much more highly represented than cod in the north and occurred at smaller body sizes than pollock in the south. The two species that dominated the prey profile and were unique to each area were Pacific herring in spring collections on the northern shelf and northern rock sole in fall collections on the southern shelf (Table 1). The giant wrymouth (*Cryptacanthodes giganteus* (Kittlitz, 1858)) was unique in occurrence to the north and Pacific salmon (*Oncorhynchus* spp. Suckley, 1861) and skate (*Raja* spp. Linnaeus, 1758) were unique to fall collections over the southern middle shelf

but, ranked below the threshold of $\geq 5\%$ when both PFO and PN were considered together (Table 1).

Prey size

In spring samples, otoliths from 36 walleye pollock were regressed to a mean length of 17 cm (range 10-50 cm FL). Two Pacific cod otoliths were measured and regressed to an estimated 62 and 103 cm FL and beaks from 13 Pacific giant octopus were regressed to a mean wt of 31 kg (range 23-50 kg). A mean TL of 24 cm (range 21-26 cm FL) and 33 cm was found for 4 measureable yellow Irish lord and 2 butterfly sculpin respectively. Eight of the 13 wattled eelpout were measureable and had a mean FL of 47 cm (range 45-50 cm). Herring remains in the form of whole fish, otoliths and bones were distributed across the samples collected in spring. Thirty-one of the 45 herring identified were from intact mature-sized fish recovered from the stomach of just one SSL of unknown age. 'Mature status' was noted in field laboratory records for both male and female herring from this single sample including '11 females with roe and 7 males with mature testes'. The mean length of 26 cm for Pacific herring reported here is based on a combination of the direct measurement of five of the intact fish (FL 26-30 cm) made prior to being discarded at sea, and the OL to SL regression for an additional 5 fish (SL 21-24 cm) whose otoliths were retained and measured in the laboratory (Table 1, Fig. 3). The 14 measured snow crab were intact immature individuals (NPFMC 2009) that averaged 25 mm with a range of 16-32 mm in greatest carapace width. Immature snow crab may have been unintentionally ingested in pursuit of other prey; however, it should be noted that they were also prominent in stomach contents from the 1981 U.S./Russian collections of SSLs off the Bering Sea ice edge (Calkins 1998).

In fall samples from the southern middle shelf, northern rock sole had a mean fork length of 35 cm based on measurement of otoliths from 37 fish and an estimated range of 28-43 cm FL. Three walleye pollock otoliths were measured predicting a mean FL of 49 cm and range of 48-51 cm FL. Otoliths from 10 Pacific cod were measured with a projected mean of 62 cm FL and range of 26-91 cm FL. The total length regression estimates for 9 measured red Irish lord ranged 28-38 cm with a mean of 33 cm. Beaks from 3 Pacific octopus were available for measurement and these had a mean regression estimate of 41 kg and a range of 37-45 kg (Table 1, Fig. 3).

Prey size with SSL age

Sample sizes precluded quantitative analysis of the relationship between SSL age and prey size, however there was no apparent qualitative relationship. Adult males (8+ years of age) did not on average consume larger prey than juveniles or sub-adult males (1-7 years of age). In fact, the predominantly adult male sample collected on the northern shelf during spring consumed more juvenile-sized walleye pollock than the juvenile and sub-adult SSLs collected off St. Paul Island during fall. Twenty-eight of the 36 walleye pollock eaten by SSLs collected on the spring ice over the northern middle shelf were large age-0 fish (10-13 cm FL) and 22 of these were split between one juvenile and one adult stomach. The remaining age-0 pollock were spread throughout the sample always occurring in stomachs that contained the remains of larger pollock, primarily age-7 or greater, but also at least one fish each estimated to be 2-6 years of age. We suggest this is not an artifact of cannibalism (secondary consumption) so much as an indication of the distribution of pollock ages available to SSLs in this area and at this time of year.

Discussion

The prey identified in stomachs from male SSLs in this study add to a list of well over one hundred species identified across the range of the western U.S. stock (Sinclair and Zeppelin 2002; Sinclair et al. 2013; Tollit et al. 2017). As in earlier studies, based on scats from primarily adult female SSLs, the measurable remains of primary prey species are mostly from adult sized, mature individuals (Zeppelin et al. 2004; Tollit et al. 2017). This extensive list of species narrows to a relatively small number of prey families that share the singular behavioral characteristic of forming age-related seasonal aggregations or movements along, onto, in or near the bottom of the continental shelf and slope (Sinclair and Zeppelin 2002; Sinclair et al. 2013) (Figure 2). The timing of such aggregations matches the timing of consumption by SSLs. There is a notable absence of pelagic species (or of species eaten during the pelagic phase of their distribution, e.g. Pacific herring) suggesting that males were not foraging pelagically during the time of this study nor during the 1981 (Calkins 1998) collections despite being within close foraging distance of open water.

Stomach contents from both study areas support the general concept of SSL specialization on prey that seasonally occupy demersal and semi-demersal habitats as adults. With the exception of an extensive age-range of walleye pollock (age-0 to age-7+) and immature crab on the northern shelf (which may not have been directly targeted) the prey consumed by SSLs in both sample areas of this study were mature (Fig. 3). Most of the described prey seasonally migrate as adults onto and off of the continental shelf and slope (cod, octopus), or between frontal regions (domains) of the continental shelf to and from site-specific feeding and spawning grounds (herring, northern rock sole). For example, the semi-demersal fish families Gadidae and Cottidae dominated the prey base in both of the contrasting collection areas in this

study and bottom-dwelling adult giant Pacific octopus ranked highly in each area. Herring and northern rock sole were the dominant species that were unique to each area and both were in seasonal demersal/semi-demersal stages during the time period they were eaten by SSLs in this study. Additional species that were also area-specific included burrowing (wrymouth) and cryptic (skates) sediment dwellers to the north and south, respectively.

Satellite telemetry records support the conclusion that both male and female SSLs of the western stock are mostly localized foragers that capitalize on nearshore movements of their primarily demersal and semi-demersal prey. With few exceptions, the majority of recorded locations 'at-sea', regardless of season or SSL age or sex, occur over the continental shelf within the 200m isobath (Fadely et al. 2005; Lander et al. 2013). The predictability in timing and location of these seasonal nearshore prey movements allow SSLs to efficiently forage within relatively short distances from haul-out areas, a factor that may be critical to their reproductive success. Earlier studies have highlighted the relevance of short-foraging trips to juveniles and to adult female SSLs with accompanying young or pups left onshore (Sinclair and Zeppelin 2002; Raum-Suryan et al. 2004; Fadely et al. 2005). We subscribe similar importance to specific haul-out locations that provide close proximity to predictable abundances of prey to adult male SSLs, in order that they might rebuild fat reserves during the non-breeding season.

The foraging platform of Bering Sea ice and herring as the dominant prey of male SSLs along the spring ice edge provide the best example of SSL foraging strategy. Typically an epipelagic species, mature herring transit seasonally between pelagic offshore waters to coastal regions of the southeastern Bering Sea shelf to spawn (late April-June). In their pre-spawning state, herring aggregate near bottom in a historical overwintering area under or along the ice edge front where SSLs were collected in this study (Barton and Wespestad 1980; Tojo et al. 2007).

Calkins (1998) also found an abundance of herring in stomach contents of SSLs collected on the ice in 1981 over the north central shelf area of the defined herring overwintering grounds. The gravid females and mature male herring described from field notes in this collection and the persistent location of herring overwintering grounds (Tojo et al. 2007) suggest that specific locations along the annual ice front serve less as a platform for hauling out, and more as a distinctive bio-physical boundary region that may be sought out by non-breeding male SSLs as a reliable source of rich prey concentrations. The ice may well be key to their successful foraging during winter and spring.

The Bering Sea ‘ice-edge’ joins a list of documented shelf frontal boundaries important in the concentration of prey and successful foraging of SSLs (Sinclair and Zeppelin 2002; Fadely et al. 2005; Sinclair et al. 2005; Sinclair et al. 2013). Field notes from the U.S.-Russia surveys in 1985 (this study) and 1981 (Calkins 1998) both describe discreet, tightly packed groups of all male sea lions on the ice at single locations in late March and early April. Researchers had actively searched for weeks over open pelagic water and along the ice edge before finding SSLs. By comparison, they observed phocid seals widely distributed along the ice front throughout both cruises. We know that the Bering Sea ice edge in spring is highly productive (Niebauer et al. 1990) and while levels of productivity vary along the edge of the ice front, certain areas remain inter-annually consistent points of enhanced productivity (Sambrotto et al. 2016). We suggest that SSLs target these areas and that they provide predictable forage to both growing juvenile and adult males building and storing critical food reserves during the non-breeding season. Considering the observed reduction of the extent and duration of sea ice over the Bering Sea shelf (Stabeno et al. 2001; Hunt et al. 2002) and the projected impact on the eastern Bering

Sea ecosystem due to climate change (Niebauer et al. 1990; Niebauer 1998) the potential loss of sea ice is of particular concern for the reproductive success of male SSLs.

Fish and cephalopods tend to occupy different levels in the water column and different locations on/off shelf with age. Therefore, the more that is known regarding prey size the more can be interpreted regarding SSL foraging behavior and bio-energetic requirements, the distribution of prey and the physical oceanographic features that concentrate prey distributions (Sinclair et al. 1994; Sinclair and Zeppelin 2002; Tollit et al. 2017). Northern rock sole, for instance, is one of the most abundant flatfishes distributed on the eastern Bering Sea continental shelf (Orr and Matarese 2000) and the southeastern Bering Sea shelf is the center of their abundance (Alton and Sample 1976). Their population numbers were expanding rapidly during the time SSLs were collected over the southern middle shelf near St. Paul Island. Adult northern rock sole are benthic and are predictably distributed year-round with strong site fidelity between separate winter spawning locations on the outer shelf and summer/fall feeding distributions on the middle shelf (Wilderbuer and Nichol 2006; Hollowed et al. 2013). Given the dominant ranking of adult (Stark and Somerton 2002) northern rock sole in this study they were likely still concentrated in feeding congregations over the southern middle shelf during the time St. Paul Island samples were collected in the fall of 1985 and 1986.

The bio-physical environment of the southeastern Bering Sea is divided into seven distinct habitats (domains) including the northern Middle Shelf Domain and the Pribilof Island Domain over the southern middle shelf where SSLs were collected in this study (Schumacher et al. 2003; Sullivan et al. 2008) (Fig. 1). Physical and biological characteristics such as temperature, mixing, currents, and timing of the spring bloom differ among domains (Macklin and Hunt 2004) and these differences influence the life history patterns and seasonal distribution

of SSL prey and in turn SSL foraging ecology. Throughout the fall, during the period of collection of the St. Paul samples, the Middle Shelf Domain is typically stratified with temperature differences between the upper and lower layers of the water column as great as 8°C (Hunt et al. 2002; Schumacher et al. 2003). Temperature extremes create boundaries of layered densities between depths and these concentrate plankton, planktivores and increasing trophic levels of micro-nekton and larger fishes and squids that feed on them. Some fish species are also restricted in their mobility through the density layers depending upon life stage (e.g. juvenile pollock) and thus provide energy efficient bundles of forage for upper trophic level predators that are less restricted in their mobility (e.g. adult pollock, SSLs). In spring, when samples were collected from the ice, the intensity and timing of the phytoplankton bloom is largely dependent upon the maintenance of this temperature differential and the timing of ice retreat (Hunt et al. 2002). Productivity levels fluctuate along the length of the Bering Sea ice edge depending upon inter-annual variability in temperature and timing of ice and retreat. However, specific areas retain their highly stratified composition and remain consistent in production which in turn draws and concentrates upper level trophic organisms with some measure of predictability (Sambrotto et al. 2016). Predictably high levels of productivity essentially create a consistent hotspot, such as the herring overwintering region (Tojo et al. 2007), which we suggest is anticipated by SSL males and dictates selection of specific winter-to-spring haul-out sites.

The limitation and potential biases of methodologies used to describe the diet of marine mammals are well described (Perrin et al. 1973; Jobling and Breiby 1986; Tollit et al. 2006; Bowen and Iverson 2012). Most center on the variable effects of digestion on fish otoliths and the retention of cephalopod beaks – patterns that vary with the method of analysis, sample storage and the physical characteristics of both predator and prey species. Currently, stomachs

from free-ranging animals remain the best sample source in marine mammal foraging ecology, and even small samples of full stomachs continue to provide the most extensive information on prey consumption compared to large samples of any other method of diet analysis (Perrin et al. 1973; Jobling and Breiby 1986; Tollit et al. 2017). However, the ethics and logistics of killing animals for ecological studies have led to the long-standing emphasis on scat-based analyses and scats are a reliable sample source if collected in large enough volume and particularly if additional methods of analyses are used (Tollit et al. 2006; Casper et al. 2007; Sinclair et al. 2010). Recent advances have been made in the development of more refined research techniques to evaluate diet and ecology of SSLs including stable isotopes in SSL tissue and whiskers (Kurle and Sinclair 2003; Rea et al. 2015) prey stable isotope (Kurle et al. 2011) and DNA analyses (Tollit et al. 2009, 2017). These studies have confirmed the presence of prey types that were thought to be important to SSLs but, were absent or underrepresented in scat studies due to lack of retention of hard parts (e.g. spewing of large *E. dofleini* beaks, specifically) (Sinclair and Zeppelin 2002; Sinclair et al. 2013; Tollit et al. 2017). All studies, including this one support previous conclusions regarding SSL diet based on identification of prey hard part remains in SSL scat.

Altogether these studies confirm our understanding of the foraging behavior of SSLs and the seasonal age-based distribution of SSL prey, thereby furthering our capacity to identify and implement measures to protect critical foraging habitat. The similarities in prey type between a small sample of stomachs from free-ranging males in the Bering Sea and large samples of scats from adult female SSLs along the Aleutian Island chain (Fig. 2) add credence to the conclusion that both sexes are selecting prey that aggregate seasonally along frontal fixtures on bottom or near-bottom over the continental shelf and along its frontal boundaries. This finding is

particularly encouraging from the standpoint that our general understanding of SSL diet and foraging behavior based on scats is well-founded.

We propose that similarly to adult females, both adult and juvenile males depend upon predictable stable physical structures that concentrate prey assemblages over the continental shelf and slope. Further, we suggest that the ice edge specifically represents habitat that is critical to successful foraging during a significant portion of male SSL life cycle. A renewed look at SSL foraging behavior and value of wintering on the ice, together with our current understanding of the potential restructuring of the Bering Sea ice community composition with climate change is timely. Such studies will lend guidance to identifying the variable effects of climate change and selecting the best ecosystem management practices for this endangered pinniped.

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Fig. 1. Locations of 22 male Steller sea lions (*Eumetopias jubatus*) collected at sea from the ice (A) in March 1985 and north of St. Paul Island in September and October of 1985 and 1986 (B) over the Middle Shelf Domain of the eastern Bering Sea. Modified with permission from Macklin and Hunt (2004).

Fig. 2. Prey groups occurring in $\geq 5\%$ frequency in stomachs from mostly adult male Steller sea lions (*Eumetopias jubatus*) collected in 1985 and 1986 during spring and fall in the eastern Bering Sea in this study; and in scats from mostly adult female Steller sea lions collected in 1990-2009 during all seasons across the Aleutian Islands and Gulf of Alaska (Sinclair et al. 2013).

Fig. 3. The size of prey in stomachs from 22 male Steller sea lions (*Eumetopias jubatus*) collected over the Middle Shelf Domain off the spring ice in 1985 and north of St. Paul Island in September and October, 1985 and 1986. Size estimates were based on direct measure of whole prey or regression between prey hard parts and body size, depending upon prey condition.

100x85mm (300 x 300 DPI)

Western Stock Steller Sea Lion Primary Prey Groups

99x84mm (300 x 300 DPI)

100x85mm (300 x 300 DPI)

Table 1. Prey species frequency (FO), percent frequency (PFO), number (*N*) and percent *N* (PN) in stomachs from male Steller sea lions (*Eumetopias jubatus*) collected in the eastern Bering Sea over the Middle Shelf Domain on the ice (*n* = 13) in spring 1985 and off St. Paul Island (*n* = 9) in fall during 1985 and 1986.

	Spring prey (total <i>N</i> = 280)						Fall prey (total <i>N</i> = 148)					
	FO	PFO	<i>N</i>	PN	Mean length (cm)	Mean weight (kg)	FO	PFO	<i>N</i>	PN	Mean length (cm)	Mean weight (kg)
Rajidae												
Skate (<i>Raja</i> sp.)	0	0	0	0			1	11	1	1		
Salmonidae												
Pacific salmon (<i>Oncorhynchus</i> sp.)	0	0	0	0			2	22	2	1		
Clupeidae												
Pacific herring (<i>Clupea pallasii</i>)	8	62	46	16	26 ^a		0	0	0	0		
Gadidae												
Pacific cod (<i>Gadus macrocephalus</i>)	3	23	3	1	83 ^b		5	56	17	12	62 ^b	
Walleye pollock (<i>Gadus chalcogrammus</i>)	9	69	43	15	17 ^c		4	44	11	7	49 ^c	
Unidentified Gadidae	1	8	2	1			3	33	8	5		
Cottidae												
Shorthorn sculpin (<i>Myoxocephalus scorpius</i>)	7	54	85	30			0	0	0	0		
<i>Myoxocephalus</i> sp. cf. <i>M. scorpius</i>	1	8	1	<1			0	0	0	0		
Butterfly sculpin (<i>Hemilepidotus papilio</i>)	3	23	12	4	33 ^d		0	0	0	0		
Red Irish Lord (<i>Hemilepidotus hemilepidotus</i>)	0	0	0	0			1	11	13	9	33 ^d	
Yellow Irish Lord (<i>Hemilepidotus jordani</i>)	1	8	5	2	24 ^d		0	0	0	0		
<i>Hemilepidotus</i> sp.	0	0	0	0			1	11	2	1		
Liparidae												
Variegated snailfish (<i>Liparis gibbus</i>)	4	31	12	4			0	0	0	0		
Zoarcidae												
Wattled eelpout (<i>Lycodes palearis</i>)	3	23	13	5	47 ^h		0	0	0	0		
Cryptacanthidae												
Giant wrymouth (<i>Cryptacanthodes giganteus</i>)	3	23	10	4			0	0	0	0		
Pleuronectidae												
Northern rock sole (<i>Lepidopsetta polyxystra</i>)	0	0	0	0			7	78	70	47	35 ^e	
Pacific halibut (<i>Hippoglossus stenolepis</i>)	0	0	0	0			1	11	1	1		
Flathead sole (<i>Hippoglossoides elassodon</i>)	1	8	1	<1			0	0	0	0		
Unidentified Pleuronectidae	1	8	1	<1			2	22	12	8		
Unidentified teleosts	0	0	0	0			2	22	2	1		
Octopoda												
Pacific giant octopus (<i>Enteroctopus dofleini</i>)	5	39	21	8		31 ^f	2	22	3	2		41 ^f
Crustaceans												
Snow crab (<i>Chionoecetes opilio</i>)	1	8	14	5	25 ^g		0	0	0	0		
Unidentified crustaceans	3	23	4	1			3	33	3	2		
Bivalve molluscs												
Unidentified clam siphons	2	15	3	1			0	0	0	0		
Gastropod mollusc	1	8	1	<1			0	0	0	0		
Tunicata												
<i>Boltenia ovifera</i>	2	15	3	1			0	0	0	0		

- ^a Pacific herring fork length (FL) of five whole fish measured directly, 26–30 cm. Remaining 5 length estimates derived from otolith length (OL) in mm to standard length (SL) in cm regression: $SL = 5.24 \cdot OL - 1.85$ (Harvey et al. 2000). SL and FL values were combined for mean.
- ^b Pacific cod fork length (FL) in cm derived from otolith length (OL) in mm regression: $FL = 4.51 \cdot OL - 2.50$ (Harvey et al. 2000).
- ^c Walleye pollock fork length (FL) in cm derived from otolith length (OL) in mm regression: $FL = 0.50x^2 + 15.74x + 13.3$, where x is OL (Zeppelin et al. 2004).
- ^d Red Irish Lord, *H. jordani*, *H. papilio* total length (TL) in cm derived from dentary measurement #2 in mm regression: $TL = 28.78 + 50.70x$, where x is dentary measurement #2 (Orchard 2001).
- ^e Northern rock sole fork length (FL) in cm derived from otolith length (OL) in mm regression: $FL = 6.16 \cdot OL - 6.97$ (Harvey et al. 2000).
- ^f Robinson and Hardwick (1983) upper beak $\ln w = (\ln PULWL) \cdot 0.274 + 2.674$ and lower beak $\ln w = (\ln PLWL) \cdot 0.265 + 2.969$, where w is live weight in kg, PULWL is pigment upper lateral wall length in mm, and PLWL is pigment lower wing length in mm.
- ^g Snow crab greatest carapace width (mm) used as the best measure of size at maturity (NPFMC 2009).
- ^h Wattle eelpout fork length (FL) in cm derived from otolith length (OL) in mm regression: $FL = 5.22 \cdot OL + 12.42$ (Harvey et al. 2000).

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