Chapter 23
Behavioral Insights into the Decline and Natural History of Steller Sea Lions

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Abstract Two competing hypotheses were proposed to explain why Steller sea lions had declined in the Gulf of Alaska, Bering Sea and Aleutian Islands. One of the theories was that young sea lions were starving because fisheries had reduced the abundance of groundfish—the overfishing hypothesis. The other was that these low-fat species of fish had increased in abundance as the sea lion population declined following the 1976–1977 oceanic regime shift, and were compromising sea lion reproductive and survival rates—the junk-food hypothesis. Behavioral ecologists tested these hypotheses by comparing sea lion behaviors in the declining region (Gulf of Alaska and Aleutian Islands) with sea lion behaviors in an increasing region (Southeast Alaska) to determine whether the populations exhibited behavioral differences consistent with food shortages. These studies involved comparing dive depths, dive durations, time spent foraging, and time spent nursing by regions and seasons. Research also focused on weaning—a critical life-history stage—to determine when and how it occurs. Collectively, these observations and measures of behavioral responses revealed that most dependent young begin supplementing their milk diet with fish between April and May, and wean just before the start of the upcoming June breeding season. However, the proportion of young sea lions that wean at 1, 2 or 3 years of age appears to vary by year due to regional and temporal differences in the quantity and quality of prey available to them once weaned. None of the behavioral studies of adult and juvenile Steller sea lions supported the overfishing hypothesis—but were, instead, consistent with the junk-food hypothesis. It appears that lactating females that consume large amounts of low-energy fish (such as walleye pollock and Pacific cod) have a high probability of miscarriage, and will keep their dependent young for an extra one or two years—thereby causing birth rates and population size to decline. In contrast, lactating females that consume larger amounts of fattier fish (such as sand lance and Pacific herring) can successfully wean a pup every year. Plasticity in age at weaning appears to be an

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evolutionary adaptation to natural shifts in community prey structure in the North Pacific Ocean—and is an adaptation that successfully slows population declines of Steller sea lions until the ocean shifts to an alternative state containing greater proportions of energy-rich fish that allows sea lion numbers to increase again.

Keywords *Eumetopias jubatus* · Life history · Population decline · Endangered · Maternal strategies · Phenology · Weaning · Abortions · Breeding · Junk food · Overfishing · Regime shifts

23.1 Introduction

In 1980, biologists reported seeing fewer Steller sea lions than expected at breeding sites in the Aleutian Islands (Braham et al. 1980). Subsequent surveys confirmed the sea lion population was in steep decline (Merrick et al. 1987; Trites and Larkin 1996)—which in turn led the United States to list Steller sea lions as *threatened* and later as *endangered* (NMFS 1992). In 1995, the North American population of Steller sea lions was split into two populations—an Eastern (*threatened*) and Western (*endangered*) population (Fig. 23.1; NMFS 1995). The dividing line at 144° W longitude (east of Prince William Sound) corresponded to a break in the genetic and breeding-site distributions of Steller sea lions, as well as a difference in population trajectories (Fig. 23.2; Bickham et al. 1998; Trites and Larkin 1996).

Since the two Steller sea lion populations were listed, the Eastern population (ranging from southeast Alaska to California) has increased at a rate of ~5% per year (Fig. 23.2)—and was delisted (NMFS 2013). Animals permanently emigrating from the Western population also augmented sea lion numbers in Southeast Alaska (Jemison et al. 2013, 2018; O'Corry-Crowe et al. 2014; Hastings et al. 2020). In contrast, the Western population has remained *endangered.* It has continued to decline in the Aleutian Islands, but has increased in the Gulf of Alaska. Overall, the Western population numbers ~20% of its peak 1970s' abundance (Fig. 23.2).

Once Steller sea lions were listed under the US Endangered Species Act, the US government restricted fisheries and initiated an unprecedented research effort in Alaska to uncover the underlying cause of the population decline (Mansfield and Haas 2006; NMFS 2008; Cheever and Riley 2019). Much of the initial scientific research focused on overfishing and fisheries-related mortality—the leading theory to explain the decline of Steller sea lions in the Gulf of Alaska and Aleutian Islands (Trites and Larkin 1992; Springer 1992; Atkinson et al. 2008; Hui et al. 2015; Conn et al. 2014). Major fisheries targeting species that dominated sea lion diets (i.e., walleye pollock, Pacific cod, and Atka mackerel) had expanded as Steller sea lions declined (Alverson 1992). Fisheries were therefore thought to have reduced the abundance and accessibility of prey, and impeded the ability of sea lions to meet their daily energy needs (Trites and Donnelly 2003).

Steller sea lions in the declining population were hypothesized to be nutritionally stressed (Trites and Donnelly 2003). Put more simply, adults were presumed to be no

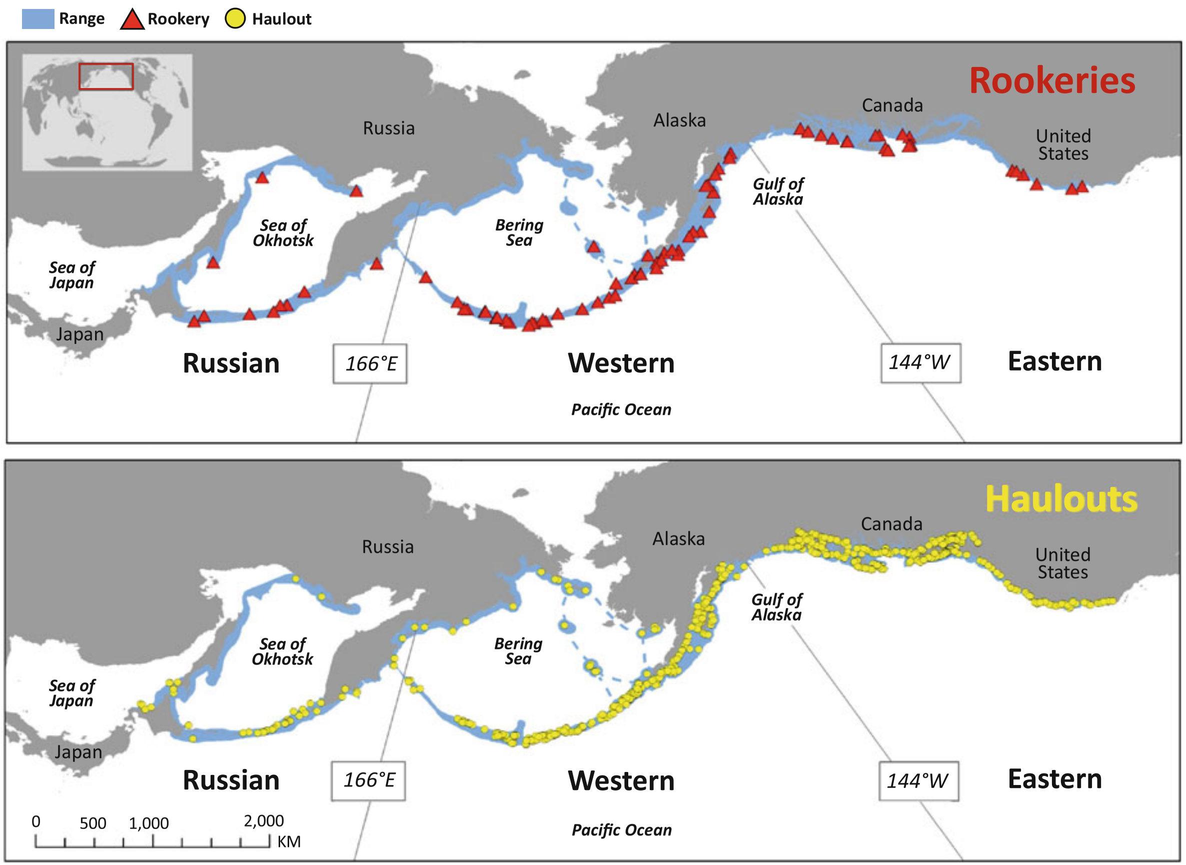

Fig. 23.1 Locations of rookeries and haulouts used by the Russian, Western and Eastern populations of Steller sea lions in 2020. The shaded range reflects the tendency for Steller sea lions to stay within ~30 km of haulouts and rookeries, and to feed over shelf areas. Dashed lines indicate presumed inter-site movements.

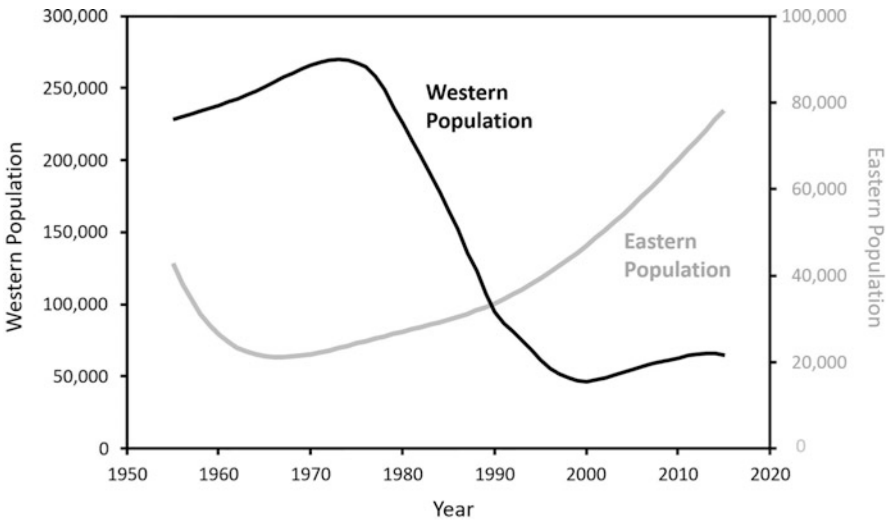

Fig. 23.2 Estimated numbers of Steller sea lions in the Western (Gulf of Alaska, Bering Sea and Aleutian Islands) and Eastern populations (California to Southeast Alaska) from 1956 to 2018. Numbers were reconstructed from census counts of pups and non-pups as per Trites and Larkin (1996). Note the three-fold difference in scales used to plot the two population trajectories

longer getting enough to eat, and their young were thought to be starving after weaning. Some speculated that fisheries were out-competing sea lions by removing too many cod, pollock, and Atka mackerel—the over-fishing hypothesis (Atkinson et al. 2008). However, others speculated that rather than not finding enough of these fish, the sea lions were eating too many of them—the junk-food or nutri-lite hypothesis (Rosen and Trites 2000; Alverson 1992). Stock assessments indicated that these species of commercially caught groundfish had increased as the sea lion population declined (Alverson 1992; Bakkala et al. 1987; Bulatov 2014; Merrick 1997). The sea lions were therefore presumed to be consuming greater numbers of fish that had less lipid and fewer calories compared to the forage fishes such as sand lance and smelts that were a greater portion of sea lion diets prior to the population decline (Merrick et al. 1997; Alverson 1992; Winship and Trites 2003).

Much of the research undertaken to test whether young were starving and whether sea lions were generally having difficulty obtaining prey fell under the umbrella of behavioral ecology. The behavioral studies involved tracking the movements and diving behaviors of sea lions in the increasing and decreasing populations. It also involved documenting diets and watching and recording the attendance

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Fig. 23.1 (continued) Note that the range of the Russian population once extended further south to the Toyama Gulf in Japan, and along the Asian coast of the Sea of Japan to the Korean Peninsula (Map produced by S. Agbayani and A.W. Trites based on Loughlin et al. 1992; Trites and Larkin 1996; Burkanov and Loughlin 2005; Olesiuk 2018; Gregr and Trites 2008; Jemison et al. 2018; Hui et al. 2015)

Fig. 23.3 An observation blind used by Milette and Trites (2003) to record perinatal periods and duration of foraging trips of Steller sea lions breeding on Lowrie Island (Forester Island complex) in Southeast Alaska (Photo by A.W. Trites)

patterns of sea lions at their breeding (rookery) and resting (haulout) sites from blinds (Fig. 23.3) and through remotely operated cameras. Interactions between mothers and their dependent young were particularly noteworthy to determine the weaning process and the perilous time of year when young sea lions might be dying. Collectively, behavioral studies yielded critical pieces of new information about the life history of Steller sea lions. They also revealed much about the plasticity of sea lion behavior and the ability of Steller sea lions to adapt to changes in their environment. More importantly, behavioral observations provided significant insights needed to resolve why Steller sea lions had declined.

23.2 Natural History

Georg Wilhelm Steller was the first to describe Steller sea lions (Steller 1751). During June 1742, while shipwrecked on Bering Island, Steller noted that the sea lions were polygamous (with each male having 2–4 females), and that females gave birth on land to a single pup at the beginning of June (Fig. 23.4). Pups, he said, bleated like sheep, and the females bellowed like cows. He also observed that bulls ate little or nothing during June and July—and that they generally preyed on fish. However, Steller reported little about sea lions beyond the breeding season, other than they only used certain areas during winter and summer that were “rocky and near precipices”.

Today, the range of Steller sea lions is known to cross the Pacific Rim from California through Alaska and Russia, down to northern Japan (Fig. 23.1). They

Fig. 23.4 A Steller sea lion bull in July with pups, a harem of adult females—and a dependent juvenile (upper right corner) (Photo by A.W. Trites)

have been grouped into three populations or stocks—Russian, Western and Eastern (Baker et al. 2005). Despite their huge range, Steller sea lions only breed at about 100 sites (rookeries, Figs. 23.1 and 23.5) and rest at over 600 other sites (winter and year-round haulouts, Figs. 23.1 and 23.6) (Loughlin et al. 1992; Trites and Larkin 1996; Burkanov and Loughlin 2005; Olesiuk 2018). As noted by Georg Steller, the terrestrial sites used by Steller sea lions tend to be on relatively steep barren rocks and wave-cut outcrops associated with sheer drop offs (Ban and Trites 2007). Most of their terrestrial sites have been continuously used for centuries (Lyman 1988; Steller 1751) and tend to be exposed to ocean swells, with limited protection (Bigg 1985). While some haulouts are on steep cobblestone beaches, most are characteristically on solid stone from which the sea lions can quickly enter deep waters. The consistency with which they have repeatedly used so few sites over centuries (Lyman 1988) suggests that Steller sea lions have a fairly narrow set of criteria for haulout selection throughout their range—from California to Japan.

Indigenous hunters likely played a significant role over the past 10,000 years in shaping the distribution and natural history of Steller sea lions and other hunted species (Maschner et al. 2014; Suraci et al. 2019; Gaynor et al. 2019). Hunting may, for example, explain the tendency for rookeries and haulouts to be far from land in areas with challenging topographies and currents for people to navigate (Lyman 1989). However, reduced consumption of Steller sea lions by Indigenous people in recent times combined with the legal protection of sea lions from disturbance and commercial hunting may be leading to new rookeries and haulouts being established in the growing Eastern population that are more easily accessed by people (Fig. 23.1; Pitcher et al. 2007; Olesiuk 2011; Cammen et al. 2019).

It was almost 200 years after Georg Steller first reported his observations that a second paper was published on Steller sea lions. In it, Scheffer (1945) provided information on the timing of births, and reported the weights and measurements of

Fig. 23.5 A Steller sea lion rookery in Southeast Alaska in June showing typical substrate and the distribution of pups and adult females across the territories of four bulls (Photo by A.W. Trites)

11 young sea lions shot at a small sea lion rookery. He also described how mothers attempted to carry their young to safety by biting onto the skin fold of the neck or rump of their pups. He further noted how the young followed their mothers into the water.

A more complete account of the timing of births, reproductive behaviors, and the attendance patterns of bulls and adult female Steller sea lions was obtained in the 1960s and 1970s (Orr and Poulter 1967; Mathisen et al. 1962; Sandegren 1976; Gentry 1974). However, none of the behavioral observations documented weaning

Fig. 23.6 A Steller sea lion haulout in British Columbia in August showing typical substrate and the presence of mostly mature and immature females, as well as a few bulls and dependent juveniles. The two pups (near the water edge, left side) would have swum over 100 km from the closest rookery with their mothers (Photo by A.W. Trites)

behavior or provided baseline measurements that could be used to determine why the Western population of Steller sea lions was declining.

Variations in attendance patterns of pinnipeds (e.g., time spent at sea, and time spent nursing) are generally accepted to reflect variation in the availability of prey near breeding areas (Trillmich and Ono 1991; Hood and Ono 1997). For example, when the availability of prey declined during the 1982–83 El Niño, sea lions and fur seals from California to South America spent more time at sea searching for prey—and less time on land nursing their pups—because prey were difficult to obtain (Trillmich and Ono 1991). The perinatal period (time between giving birth and making the first feeding trip) was also shortened; and pups were underweight, and died at higher rates. These measures of maternal behavior were therefore considered useful proxies for inferring whether prey availability was reduced or adequate to support Steller sea lions (Hood and Ono 1997).

The challenge in using behavioral studies to resolve whether there was a prey shortage is that there were no baseline of historical behavioral data for comparison. Normal nursing times and normal foraging times were unknown for Steller sea lions. As a result, the control population for comparison with the declining Western population became the increasing Eastern population of Steller sea lions in Southeast Alaska, where sea lions were presumed to have more prey available to them. As such, sea lions in the declining population were predicted to compensate for reduced prey by making longer feeding trips and spend less time nursing their pups compared with sea lions in the increasing population. Results, however, proved counterintuitive.

23.3 Breeding Behavior

Steller sea lions are the largest of the five species of sea lions, and are the fourth largest pinniped (after elephant seals and walrus). At birth, male pups are about 4% longer and 10% heavier than females—with male pups measuring 0.98 m and weighing 22 kg, and females averaging 0.94 m and 20 kg (Winship et al. 2001; Brandon et al. 2005). However, when fully grown and holding a territory (Figs. 23.4 and 23.7), males are 2.5 times heavier than adult females (~700 kg vs ~275 kg), but just 1.3 times longer (3.0 m males vs 2.3 m female). Breeding males will average ~ 700 kg at their peak body weight, although weights as heavy as 910 kg have been recorded in the wild (Fig. 23.7) (Winship et al. 2001) and some captive raised Steller sea lions have exceeded 1000 kg.

Aerial photographs taken in 2008 suggest that adult sea lions in the Eastern population were shorter than in the Western population (Sweeney et al. 2015). This difference in body size may reflect an inherent morphological difference between the two sea lion populations (Sweeney et al. 2015). However, it may also reflect relative differences in the quantity and quality of prey available to the two populations. Reduced food availability could have stunted body growth in the increasing region—while better feeding conditions augmented body growth in the declining population further north.

Steller sea lions grow quickly. By the time females have turned 4 years old, many are sexually mature and have attained ~90% of their asymptotic lengths (Winship et al. 2001). Most will ovulate for the first time between the ages of 3 and 5 years old (range 2–8 years), and will, on average, give birth for the first time when they are 5 years old (Pitcher and Calkins 1981; Perlov 1971). Female body mass, however, does not reach 90% of its asymptotic mass until the females are 13 years old. In contrast, males attain 90% of their final body length when much younger—at ~8 years old (Winship et al. 2001)—which coincides with the start of the male growth spurt in body mass. Similar to females, males become sexually mature between 3–8 years old (Pitcher and Calkins 1981; Perlov 1971). However, most males lack the social and physical maturity to defend a territory until they are 9 years or older (Fig. 23.7). Average age of ~90% of territorial bulls is 9–13 years old (range 6–15 years) (Thorsteinson and Lensink 1962).

Males have a much shorter life expectancy than females. About 40% of male pups die on average during their first year (range 27–60%), compared with an average death rate of 30% for female pups (range 29–44%) (Hastings et al. 2011; Pendleton et al. 2016; Maniscalco et al. 2015). Death rates can vary considerably between years and breeding sites. Of the sea lions that survive to their first birthdays, average age at death (life expectancy) is 4 years old for males (range 2–9 years) and 10 years old for females (range 2.5–13 years; calculated from life tables in: Pendleton et al. 2006;

Fig. 23.7 A scarred Steller sea lion bull weighing over 700 kg among young females (Photo by A.W. Trites)

Hastings et al. 2011; Maniscalco et al. 2015). The longest Steller sea lions might live (i.e., longevity—defined as the oldest age attained by $<1\%$ of the population) is about 16 years old for males and 23 years old for females.

Large body size provides males with an advantage over other bulls while breeding, but carries a metabolic cost outside of the breeding season. Thus, territorial bulls lose mass through the breeding season and into the fall before fattening up again from November to March (Winship et al. 2001). Females also experience seasonal growth and fattening between November and March, and grow little during the breeding season (May–July) (Winship et al. 2001).

Acquiring a territory is a prolonged process. Most bulls begin their tenure a year earlier by becoming a post-season territorial male (i.e., by establishing a territory on unused periphery areas of the rookery after copulation activity has ended). They will hold their empty territory until they can safely move onto the territory abandoned by a breeding bull (Gisiner 1985).

Most males that arrive at the start of the breeding season to reclaim past territories are considered dear-enemies of each other—having gotten to know each other through past interactions. New males that try to fight their way onto a rookery to establish a breeding territory have low success (<15% obtain a territory) compared to the post-season territorial males (Gisiner 1985). Bulls typically hold a territory for ~2 years (range 1–8 years) (Gisiner 1985; Parker and Maniscalco 2014).

Most combative challenges between competing bulls start as chest-to-chest pushing matches—much like sumo wrestlers—but can escalate into bloody fights. Fighting involves hard bites and shaking around the neck, shoulders, face, and edges of the front flippers (Fig. 23.7) (Gentry 1970; Gisiner 1985). The weaker of the two will either be pushed out or will take a submission posture while backing away and fleeing. These fights usually occur only with males that cross territorial boundaries or with unknown bulls approaching from the sea. For the most part, bulls engage in little fighting and spend most of their time making territorial displays towards neighboring territorial males (i.e., by rushing towards the territory boundary and falling forward on their bellies with head raised and mouth open towards the neighboring male) (Fig. 23.8) (Gentry 1970). However, territorial bulls have noticeably fewer boundary displays with bulls they know than with unfamiliar neighbors (Gisiner 1985).

The breeding season begins in early May with the arrival of bulls that held territories in past years (Gisiner 1985; Thorsteinson and Lensink 1962; Pitcher and Calkins 1981). They will wait for the first pregnant females to arrive a couple of weeks later. An average bull will maintain a territory for ~6 weeks (range 3–10 weeks) without eating (Gentry 1970)—and most will begin leaving their territories around mid-July when mating is complete and post-season males begin securing peripheral territories (Gisiner 1985; Parker and Maniscalco 2014).

The average territorial bull copulates ~7 times in a breeding season (range 0–38 times) (Gisiner 1985). However, as many as two-thirds of territorial bulls are thought to not copulate successfully in their first year (Parker and Maniscalco 2014). Those that are most successful tend to have used the rookery for 3 or more previous years, and have held territories that were near the water edge and center of the rookery with favored access to and from the water (Gisiner 1985; Parker and Maniscalco 2014). Another successful strategy for maximizing reproductive success is to occupy peripheral territories where fewer births occur, but a longer tenure (7–8 years) can be had (Parker and Maniscalco 2014). Lifetime reproductive success is thereby a combination of tenure duration and territory location.

Within a week of arriving on shore (starting in mid-May), females will give birth to a single pup (Fig. 23.9). Those first to arrive and give birth appear to be ~10–13 years of age, with progressively younger and older females giving birth as the season progresses (Hastings and Jemison 2016). Pups born earlier tend to be marginally heavier than later born pups, with male pups being born about a day earlier on average than female pups (Maniscalco and Parker 2017).

Fig. 23.8 Steller sea lion bulls making territorial displays towards each other. Note the scars on the face, chest and flippers from fights that involved hard bites and shaking. Note also the difference in color and texture of dry and wet pelage (Photo by A.W. Trites)

This parabolic relationship between age of mothers and her date of parturition (Hastings and Jemison 2016) is consistent with the non-linear relationship between age of northern fur seal mothers and the size of fetuses they carry (Trites 1991). Fetuses of northern fur seals increase in size as mothers age until the females are 10–13 years, after which adult females continue to growth, but the sizes of their fetuses decline (Trites 1991). This suggests that timing of birth in Steller sea lions reflects the size of a fetus at term, with larger fetuses being delivered earlier on average than smaller fetuses. Male pups are heavier on average than female pups (Brandon et al. 2005; Merrick et al. 1995), which suggests that differences in body size may also explain the apparent difference in timing of male and female births.

Nearly all births occur between May 15 and July 15 (Pitcher et al. 2001; Kuhn et al. 2017b). Mean date of birth is earliest in Southeast Alaska (June 4) and becomes progressively later further north and further south (by as much as over 2 weeks later in California) (Pitcher et al. 2001). Almost 90% of pups are born within a ~3-week window (Pitcher et al. 2001).

As parturition approaches, most pregnant females (~80–85%) go to the rookery of their birth in the Eastern population, and a slightly smaller proportion (~75%) return to their natal rookeries in the Western population (Hastings et al. 2017; Raum-Suryan et al. 2002). Females choose a location within a bull's territory, and tend to return to the same areas in subsequent years (Hastings et al. 2017)—with some females pupping within about 6 m of where they pupped the previous year (Parker et al. 2008).

Following birth, mothers remain with their pups for an average of 8–11 days (range 3–13 days) before leaving for their first feeding trip (the perinatal period; Sandegren 1970; Hood and Ono 1997; Milette and Trites 2003; Maniscalco et al.

Fig. 23.9 A nursing Steller sea lion pup. Females have four or six functional teats, such as this female with six teats (Photo by A.W. Trites)

2006). Typically, first time mothers (i.e., primiparous females aged 3–6 years) return to sea to feed before multiparous females—due perhaps to having a smaller body size with less body reserves than multiparous females to produce milk for their pups (Maniscalco et al. 2006; Hastings and Jemison 2016).

Copulations typically occur at the end of the perinatal period before females leave their pups for the first time (Sandegren 1970; Gentry 1970). Males rarely hinder female movement across territories for more than a few minutes, and general rely on olfactory senses in most pre-copulatory interactions to detect estrus (>65%) (Gisiner 1985). In other cases, females may initiate sexual solicitation (<10%), or males may spontaneously mount females with no pre-copulatory interactions (<25% of copulations) (Gisiner 1985).

Once the egg is fertilized in June and early July, the blastocyst will remain dormant until implantation in the fall (~3–3.5 months later between late September and mid-October) (Pitcher and Calkins 1981). Based on the distribution of births (occurring as early as late May and as late as the end of June), gestation is between 8–9 months, and likely averages ~8.5 months.

Some females are seen nursing juveniles during the breeding season at their natal rookeries (~40% of mothers with juveniles), at other rookeries (~20%), and at haulouts (~40%) (Hastings et al. 2017). Some of these females returning to rookeries with juveniles in tow will give birth, and will have to choose between keeping their pup and continuing to nurse their juvenile. Females nursing juveniles at haulouts will breed with territorial males (which occurs ~1–2 weeks earlier than on rookeries; Trites, unpubl. data). Thus, females nursing juveniles during the breeding season have mating options (Hastings et al. 2017).

When pups are young (~2 weeks), females spend ~1.2 days with their pups on land and 0.8 days at sea (Milette and Trites 2003). As the pup ages, mothers spend more time at sea and less time on shore, such that by ~7 weeks old, females are spending ~0.5 days with their pups and 1.1 days at sea (Milette and Trites 2003). The increased time spent feeding is presumed to reflect the time needed to increase milk production to meet the increased energetic needs of the growing pup.

Pups will enter the water for the first time when 2–4 weeks old (Sandegren 1970), and will move with their mothers to haulouts when 2–3 months old (Fig. 23.6; Calkins and Pitcher 1982). Mothers with pups may start dispersing from the rookeries as early as the last week of June, with significant increases in numbers leaving during the last two weeks of July (Kuhn et al. 2017a; Hastings and Jemison 2016). Some females will call their pups into the water, while others will drag and carry them by the scruffs of their necks, and block their attempts to climb back onto the rookery.

Dependent pups generally stay within 500 km of where they are born, although a few as young as 5 months have been seen with their mothers at haulouts further away (Raum-Suryan et al. 2002). Juveniles (1–3 years old) disperse much further than pups (up to ~2000 km), with males being resighted further on average from their natal rookeries, and at older ages, than females (Raum-Suryan et al. 2002; Fuller 2012).

Steller sea lions rely on a thick layer of blubber to insulate themselves from the cold water. However, while on land, their fur provides some additional protection from convective heat-loss to air and wind. Steller sea lion fur is thick, short and coarse when dry—and lies flat against the skin when wet to reduce drag while swimming (Fig. 23.8). However, the main function of the fur is to protect the skin from abrasion against rocks and barnacles. As such, the hairs become damaged over time, and are replaced each year during an annual molt (Daniel 2003).

It takes ~45 days for a Steller sea lion to shed its old hair (Daniel 2003). The first age-class to molt are the juveniles (starting in June), which are followed by adult females (August), and bulls and pups (October) (Daniel 2003). The molt progresses over the body surface much like an unravelling sweater. Pups will lose their dark chocolate-colored coats—and older sea lions will attain a fresh tan to golden-brown colored coat, which darkens to chocolate brown on their flippers and underside (Fig. 23.9). However, once wet, the pup appears black while the coats of older age-classes look dim- or dark-gray (Figs. 23.4 and 23.8).

23.4 Behavioral Proxies of Environmental Conditions

Changes in the abundance of prey available to fur seals and sea lions are known to affect the duration of perinatal periods, and the time that mothers spend foraging and nursing their pups (e.g., Ono et al. 1987; Trillmich and Ono 1991; Boyd et al. 1994; McCafferty et al. 1998; Goldsworthy 2006). Dive depths and duration of dives can also be used to infer differences in the abundance and distribution of prey accessible to different populations of pinnipeds (e.g., Chilvers 2018). Collectively, these measures of maternal investment and foraging efficiency translate into differences in growth and weights of pups (e.g., Kirkman et al. 2002; Goldsworthy 2006; Jeanniard-du-Dot et al. 2017; Trillmich 1990; Trillmich and Limberger 1985; Roux 1997)—and can be used to assess the relative abundance of prey available to fur seals and sea lions.

Behavioral studies of Steller sea lions in the 1990s set out to compare the behavioral ecology of sea lions in the declining and increasing populations. Under the assumption that the Western population in the Gulf of Alaska was declining because of a shortage of prey, nursing females were predicted to have (1) short perinatal periods, (2) spend more time searching for prey, (3) have greater difficulty finding and capturing prey, and (4) spend less time nursing their pups (Milette and Trites 2003; Trites and Donnelly 2003). It was further predicted that pups in the declining population should be (5) smaller during the breeding season than pups in the increasing population (Trites and Donnelly 2003). However, none of the behavioral studies yielded results consistent with Steller sea lions in the declining population having difficulty accessing prey. Rather they indicated that the population having trouble finding food was the increasing population in Southeast Alaska.

Counter to predictions, Steller sea lions spent more time with their pups where the population was declining than in the areas where the population was growing. Mean perinatal periods (time between birth and first feeding trip) of females observed at rookeries were significantly longer where they were declining (9.9 vs 7.9 d), and the length of their foraging trips was also shorter on average (19.5 vs 24.9 h) (Milette and Trites 2003). In addition, females in the declining population spent more time with their pups between feeding trips (27.0 vs 22.6 h) (Milette and Trites 2003). Satellite-tracked lactating females were also found to make shorter feeding trips in the area of decline (Seguam Island) than in the area of growth (Forrester Island) (Andrews et al. 2002). These females from the declining population generally made single bouts of uninterrupted dives to capture prey, while those from the increasing population made multiple bouts separated by time travelling and resting (Andrews 2004). These tracked sea lions were also 5-times faster at capturing their first prey in the declining area than in the increasing area (based on stomach temperature records) and ingested it twice as fast (Andrews et al. 2002). Thus, sea lions in the declining area appeared to find and consume prey faster, and spend more time nursing their pups compared with sea lions in the increasing population.

Body weights of pups taken throughout the Steller sea lion's range also supported the conclusion that lactating Steller sea lions in the declining regions were not having difficulty obtaining prey during summer. Instead of being undersized, pups grew faster in the declining areas than in the increasing areas (0.41 vs 0.25 kg/day), and required half as much milk (Adams 2000). Pups (2–6 weeks old) were heavier on average at declining rookeries (Aleutian Islands and Gulf of Alaska) compared to pups at stable and increasing rookeries (Southeast Alaska and Oregon) (Merrick et al. 1995; Rea 1995). Older pups (7–9 months old) were also similarly heavier and in better condition in the Aleutian Islands (with 36% total body lipid) and Gulf of Alaska (30% body fat) than in Southeast Alaska (28% body fat) where the population was increasing (Rea et al. 2016). No one expected Steller sea lion pups from the increasing population to be leaner than pups from the declining population. Nor did anyone expect pups in the declining area to be heavier in the 1980s and 1990s than during 1965–1975—prior to when the population declined (Merrick et al. 1995).

The most notable change that occurred in the Gulf of Alaska, Bering Sea and Aleutian Islands pre- and post-decline was a dramatic shift in ocean climate conditions, ecosystem community structure, and sea lion diets. Prior to the decline, fat-rich forage fishes such as smelts and sand lance made up a significant portion of Steller sea lions diets in the Gulf of Alaska—to the exclusion of walleye pollock (Mathisen et al. 1962; Thorsteinson and Lensink 1962). However, pollock dominated the post-decline diet (a low-lipid fish not reported in the earlier diet studies) (Sinclair et al. 2013; Sinclair and Zeppelin 2002). This dietary shift in the Gulf of Alaska corresponded with an oceanic regime shift in 1976–1977 (Hare and Mantua 2000; Benson and Trites 2002) that altered the structure of fish communities (Anderson and Piatt 1999; Trites et al. 1999) and the relative abundances of dominate prey species available to Steller sea lions (Alverson 1992; Trites et al. 2007b; Bakkala et al. 1987; Bulatov 2014).

Regional populations of Steller sea lions in the Western population that experienced the most rapid declines consumed diets dominated by energy-poor species (Merrick et al. 1997; Winship and Trites 2003) that consisted primarily of pollock in the Gulf of Alaska, and Atka mackerel (a hexagramid) and Pacific cod in the Aleutian Islands (Sinclair et al. 2013; Tollit et al. 2017; Sinclair and Zeppelin 2002). In contrast, the growing population of sea lions in Southeast Alaska were consuming a more energy-rich and diverse diet dominated by gadids, forage fish and salmon (Trites et al. 2007a) that appears to be closer to what was once consumed by sea lions in the Gulf of Alaska prior to the population decline.

As the Western population of Steller sea lions rapidly declined through the late 1970s and 1980s (Fig. 23.2), Atka mackerel increased in the Aleutian Islands, and walleye pollock increased in the Gulf of Alaska and Bering Sea (Bakkala et al. 1987; Bulatov 2014; Merrick 1997). These two prey species appear to have been very abundant and available to lactating females during summer and fall throughout the period of sea lion decline based on the ease with which mothers seemed to capture them, the relative shortness of their feeding trips, time spent nursing pups, and increased weights of pups (from birth—9 months of age). Thus, the high abundance of pollock and Atka mackerel are consistent with the observed maternal behaviors and increased sizes of pups—and suggest that lactating females in the declining population were not food limited. Rather, they appear to have had abundant prey that allowed them to nurse bigger pups. However, the high abundance of these prey species may have placed a nutritional limitation on the ability of pups to successfully wean as shown by behavioral observations of the weaning process and the frequencies of abortions.

23.5 Weaning Behavior

Comparing the age composition of the Steller sea lion population in the 1970s and 1980s revealed significantly fewer juvenile sea lions among the animals present in the 1980s (York 1994). This relatively small number of juveniles in the 1980s led many to conclude that the decline of sea lions in the Gulf of Alaska was due to an increase in juvenile mortality (Merrick and Loughlin 1997; Alaska Sea Grant 1993; DeMaster and Atkinson 2002). One line of logic held that the missing juveniles had starved and died after weaning because fisheries had reduced prey biomass and altered the distribution of fish consumed by sea lions. It was theorized that young sea lions were food-limited because their poor diving abilities prevented them from catching prey that had become less accessible (Merrick and Loughlin 1997). However, there was no evidence that fisheries had reduced the biomass or changed the distribution of prey available to Steller sea lions. Nor were there observations of starving juveniles to support the hypothesis that young sea lions were nutritionally stressed due to consuming less prey. Research was therefore initiated to find malnourished juveniles and document the poorly understood weaning process that potentially held the key to understanding why trajectories of the Western and Eastern populations of Steller sea lions differed.

It has been generally accepted that most Steller sea lions wean during their first year, with some young staying with their mothers for as long as 3 years (Pitcher and Calkins 1981). Less certain, however, was whether Steller sea lions wean from mid-April to late-May before the start of the next breeding season (Pitcher and Calkins 1981; Raum-Suryan et al. 2004), or whether they wean much earlier between November and March (Merrick and Loughlin 1997; Loughlin et al. 2003). The extent to which immature sea lions supplemented their milk diet with fish (and when this might occur) was equally uncertain (Kuhn et al. 2017a; Raum-Suryan et al. 2004; Rehberg and Burns 2008). Nor was it understood why some sea lions should continue to suckle beyond their first year.

Attempts to document the weaning process began with field observations of Steller sea lions at a winter haulout (late January to end of March) when young were expected to transition from milk to independent foraging (Trites and Porter 2002). During this time, mothers were observed coming and going from their haulout, while dependent pups (8–10 months) and yearlings (20–22 months) played in the intertidal zone or made short independent trips. No immature sea lions were observed leaving and returning with their mothers on their feeding trips. However, some dependent young were seen playing with fish and octopus near their haulout—although none of these sea lions were weaned, and none were observed swallowing the prey in their mouths (Trites and Porter 2002).

A few pups at the winter haulout appeared to have lost their mothers and were starving (Porter and Trites 2004). Some of these pups tried to steal milk from other mothers, but were rebuffed with bites when discovered by the females. Curiously, none of the starving pups switched to eating fish that similarly sized pups had been observed to be readily capable of catching.

The tenacity of the starving pups to acquire milk rather than catch fish was similar to what occurred when bottle-raised Steller sea lions pups were weaned at the Vancouver Aquarium in the early 1990s (Trites, unpubl. data). Under the mistaken belief that wild pups weaned during winter, the captive-raised pups were cut off of milk and offered live fish during January when 8 months-old. All of the hand-raised pups were adept at catching and killing the fish they were offered, and played with them ceaselessly until only bits of flesh hung from the skeletons. However, none of these 8-month-old pups—which were no longer receiving milk—would consume any of the fish they killed.

Subsequent attempts to switch the trained pups from milk to solid food (after giving up on them eating live fish) involved putting fish into their mouths, and holding their mouths closed until they swallowed (Trites, unpubl. data). Initial attempts at force-feeding resulted in the unweaned pups coughing the fish back up. With time and patience, however, the pups accepted whole fish. This experience in trying to hand-wean Steller sea lion pups—and the subsequent lack of field observations that weaning occurs during winter (Trites and Porter 2002)—pointed to a flawed conceptual understanding of weaning and the factors that influence it. Neither weaning nor transitioning to live food occurs during winter (Jan–Mar).

Additional teams of researchers sent to observe sea lions behavior at haulouts during spring and summer (Apr–Aug) concluded that most sea lions begin supplementing their milk diet with fish between April and May, and wean before the start of the breeding season when 1 or 2 years old (Trites et al. 2006). These conclusions were drawn from the marked decline in the proportions of time that immature sea lions spent suckling (Trites et al. 2006), and are consistent with an independent study of vibrissae from known-aged immature sea lions between November and April that looked for trends in stable isotopes indicative of fish consumption (Rehberg et al. 2018).

As with their reduced time spent suckling, the depths and durations of dives of immature sea lions also change significantly towards the end of the first and second years (May and June) when pups are 11–12 months old, and yearlings are 22–-24 months old (Loughlin et al. 2003; Rehberg and Burns 2008). The diving behaviors of the dependent pups and yearlings (recorded by satellite dive-depth recorder tags) become more adult-like in May and June. Maximum daily dive depths and dive durations also increase around their first and second birthdays (Pitcher et al. 2005). Similarly, round-trip distances and durations of trips made by tracked pups and yearlings show notable changes from April to June (Raum-Suryan et al. 2004). Collectively, all of these studies of diving and movement behaviors suggest that pups and yearlings undertake a gradual process of supplementing milk with solid food 2–3 months before the oncoming breeding season when they are most likely abruptly weaned.

Mothers of dependent pups and yearlings make significantly longer foraging trips during winter than in spring and summer (Trites et al. 2006; Merrick and Loughlin 1997). These lactating females spend about 2 days away from the haulout during winter, and 1 day away during spring (Trites et al. 2006). Lactating females also make longer trips if nursing a yearling than if supporting a pup (Trites et al. 2006).

However, no difference was noted in the attendance patterns of lactating females between regions during winter and spring (i.e., between increasing and decreasing populations) (Trites et al. 2006). This suggests that lactating sea lions observed at haulouts in the 1990s did not have more difficulty capturing prey during winter, spring and summer in the area of decline compared to where sea lions were increasing.

Male and female pups and yearlings do not appear to follow the same weaning schedule (Trites et al. 2006). During the 1990s, about half of the female pups observed in Southeast Alaska weaned at 1 year, and the other half continued suckling until 2 years old. In contrast, most males weaned at 2 years—with a small number weaning at 3 years, and one male continuing to suckle at 4 years of age (Trites et al. 2006).

This difference between the age at which young males and females wean presumably reflects their different size-based nutritional needs and their likelihood of surviving and successfully reproducing when independent. Weaning (at 1 to 3 years of age; Pitcher and Calkins 1981; Trites et al. 2006) appears to occur at the start of summer when survival is likely optimal, and pregnant mothers must return to rookeries to give birth and mate. However, the proportion of young sea lions that wean at 1, 2 or 3 years old likely varies by year due to regional and temporal differences in the available quantity and quality of prey needed to ensure the survival of recently weaned individuals.

Some biologists have assumed that the limited diving abilities of pups make them nutritionally dependent on their mothers during winter (Rehberg and Burns 2008). However, this explanation for why pups do not wean earlier is unlikely given that yearlings have the diving abilities of adults, but also continue to depend on their mothers for nutrition. Dependent pups and yearlings are also all capable of catching prey as shown by field observations (Porter and Trites 2004). The fact that pups and so many yearlings remain with their mothers rather than wean implies that they obtain greater energy (and benefit) from milk than from fish to support rapid body growth and high daily energy needs (Winship et al. 2002; Trites et al. 2006).

Feeding trials and bioenergetics models show that growth of young sea lions (from birth to 2 years) can be achieved on a diet of milk (Winship et al. 2002; Rosen and Trites 2000, 2004; Rosen 2009). Similarly, older pups and yearlings can grow on a diet of high-fat fish (such as herring, sardines, and sand lance). However, young Steller sea lions can lose body mass on a diet of only low-fat fish (such as cod and pollock) because they become full before meeting their daily energy needs (Rosen and Trites 2000, 2004; Rosen 2009). Older and larger sea lions, however, have lower relative energy requirements and can do equally well on high- or low-fat fish—they simply have to eat more of the low-fat fish to compensate for the caloric difference.

Consuming fish at the expense of not having room for milk—or simply replacing milk with fish—would most likely lead to the death of a pup in the wild. The behavior of the captive-raised Steller sea lion pups when presented with fish further suggests that pups evolved the skills to hunt and kill by at least 8 months, but not to swallow because they cannot assimilate sufficient energy from a stomach full of fish to meet their daily energy requirements. This simple physiological process can explain the observations made of starving and healthy pup behaviors in the wild

(Porter and Trites 2004). It can also explain why so many sea lions stay an extra year with their mothers when milk is an option.

The community structure of the ecosystem in which Steller sea lions evolved periodically shifts between one dominated by low-energy gadids and one dominated by high-energy forage fishes (Trites et al. 1999, 2007b; Maschner et al. 2014; Benson and Trites 2002; Mantua et al. 1997; Alverson 1992; Anderson and Piatt 1999; Hare and Mantua 2000). Such an ecosystem shift is consistent with the observed shift in Steller sea lion diet from forage fishes to gadids following the 1976–1977 oceanic regime shift (Mathisen et al. 1962; Thorsteinson and Lensink 1962; Sinclair et al. 2013; Sinclair and Zeppelin 2002). However, pups weaning at 1 year of age are unlikely to survive on a gadid-dominated diet, but could do so on a diet dominated by energy-rich forage fish (Rosen and Trites 2000, 2004; Rosen 2009). Young sea lions simply do not have the stomach capacity to process enough gadids to meet their daily needs. Thus, Steller sea lions should stay an extra year with their mothers until they are large enough (approaching 2 years of age) to continue normal growth on a diet dominated by gadids. This plasticity in age of weaning displayed by Steller sea lions is likely an evolutionary adaptation to natural shifts in ocean productivity in the North Pacific.

The thought that an animal can get full before it has consumed enough to meet its daily needs (or that energy density of fish matters to apex marine predators) is accepted by seabird biologists (e.g., Romano et al. 2006; Grémillet et al. 2008; Osterblom et al. 2008; Whitfield 2008; Jodice et al. 2006), but is rejected by some marine mammalogists (e.g., Fritz and Hinckley 2005; Calkins et al. 2013). Arguments raised to dispute the notion that quality of prey matters to young sea lions range from an obfuscation of facts to failure to recognize that feeding studies purported to disprove that young animals require high-caloric food are actually consistent with this simple premise. They also fail to recognize that methodically weaning pups on a fixed schedule as done by most other pinniped species is a poor evolutionary strategy for mothers to follow if there is little likelihood of offspring surviving to pass on their mother's genes during years when low-energy prey species will dominate yearling diets.

If quality of prey and stomach capacity were inconsequential to young Steller sea lion, males should wean earlier than females—thereby allowing young males to gorge on low-energy prey species and free themselves of the 1–2 day waits for mothers to return to haulouts to nurse them. However, the opposite occurs—males tend to wean later than females. This suggest that the sporadic delivery of milk is significantly more advantageous to males than daily consumption of fish to ensure that males attain sufficient body sizes to successfully hold a territory and breed. Larger sizes at weaning likely ensure higher breeding success as adults.

Feeding trials, mathematical models, and field observations of Steller sea lions all suggest that age at weaning is a function of the energy densities of fish available to young sea lions. They further suggest that age at weaning should be later in the declining sea lion population because the average energy densities of fish available to weaning sea lions is significantly less than the energetic densities of prey available to sea lions weaning in the increasing population (Trites et al. 2007b; Winship and

Trites 2003). Such an increase in age at weaning would increase the inter-annual interval between females having subsequent pups (from 1 to 2 or 3 years)—thereby causing birth rates and the size of the population to fall.

While age at weaning can be linked to quality of prey available to weaned individuals, determining who initiates the weaning process is less obvious—as is the question of how Steller sea lions assess the likelihood that the prey base at weaning will support recently weaned individuals. Possible answers lie with the high frequency of abortions and stillbirths among Steller sea lions.

23.6 Abortions and Stillbirths

Collectively, the behavioral observations of Steller sea lions made at rookeries and summer haulouts indicate that most mature females breed each year either on rookeries following the birth of a pup, or on haulouts if they are not pregnant and are nursing a pup or yearling. First time breeders may breed on either rookeries or haulouts, and some non-pregnant females with dependent young may return to rookeries instead of haulouts to breed. Thus, females have mating choices and opportunities to ensure maximum numbers become pregnant each year.

Having sex, becoming pregnant, and carrying a fetus to term comes at a small energetic cost compared to the cost of producing milk (Winship et al. 2002). It therefore makes sense for all females to become pregnant each year and give birth 12 months later if they can successfully wean their offspring. It would also make evolutionary sense to cease pregnancies during years when the prey base is insufficient to support weaned offspring—thereby ensuring that pups and yearlings approaching weaning remain with their mothers for another year until they have grown big enough to thrive on a low-energy diet.

One means by which pregnancies might be terminated is through a hormonal process associated with lactating and consuming a high-protein low-fat diet that triggers spontaneous abortions midway through fetal development. Such a cause-and-effect scenario is consistent with observing aborted fetuses at haulouts during winters (Fig. 23.10; Marcotte 2006; Gentry 1970; Mate 1973; Calkins and Pitcher 1982), and with seasonal trends in pregnancy rates observed during the 1970s and 1980s before and during the Western population decline (Pitcher et al. 1998; Pitcher and Calkins 1981).

Examining the reproductive tracts of Steller sea lions shot in the Gulf of Alaska showed that all sexually mature females are pregnant during early gestation (Pitcher et al. 1998). However, nearly half may lose their fetus before the start of the breeding season as occurred during the start of the population decline (1980s) when only 55% of sexually mature females remained pregnant in late gestation (Pitcher and Calkins 1981). Conversely, a greater percentage (67%) remained pregnant at this stage in the 1970s prior to the population decline (Pitcher and Calkins 1981).

The decline in pregnancy rates that occurs as the fetus develops is consistent with the discovery of fetuses on Steller sea lion haulouts from December through mid-May (Fig. 23.10; Marcotte 2006; Gentry 1970; Mate 1973; Calkins and Pitcher

Fig. 23.10 An aborted Steller sea lion fetus found on a haulout during January. Photographed on snow with a 15 cm ruler for scale (Photo by A.W. Trites)

1982). The highest frequency of abortions occur from January to March during the second trimester of pregnancy when the fetus is about 2–5 months developed. Fetuses collected and tested for disease known to cause abortions in mammals have not revealed underdevelopment or pathogen-related causes (Esquible et al. 2019; Burek et al. 2005). There is no medical explanation for the high frequency of abortions among Steller sea lions.

Most of the females aborting fetuses are likely still nursing pups and yearlings. During the 1980s, pregnancy rates during late gestation were just 30% for lactating females compared with 84% for non-lactating females (Pitcher et al. 1998). It is equally noteworthy that pregnancy rates of lactating females were twice as high during late gestation in the 1970s when Steller sea lions were presumed to consume a more energy-rich diet than in the 1980s (i.e., 63% in the 1970s vs 30% pregnancy rates in the 1980s) (Pitcher et al. 1998).

The small number of lactating females that return to give birth on rookeries with a pup or yearling in tow face inevitable squabbles with juveniles pushing newborns away or attempting to suckle at the same time. Females do not appear to continue supporting both, and ultimately appear to choose juveniles over newborns.

From a strategic point of view, it makes sense that all lactating females should become pregnant, and that their pregnancies should continue if their pup or yearling dies, or conditions prove favorable for successful weaning. Under favorable conditions, females could wean a pup as frequently as once a year. However, should conditions not favor successful weaning, aborted fetuses ensure that mothers can continue putting all of their energy into their pups for a second year or longer. Thus, abortions in sea lions may be an evolutionary selected process that simultaneously maximizes reproductive potential and increases the likelihood that newborns survive and pass on a mother's genes. The high frequency of abortions among Steller sea lions is most likely an innate hormonal response associated with lactation and lipid content of prey—and not a function of female choice or body condition.

23.7 Conclusions

Behavioral ecology can help resolve conservation conflicts and aid species at risk—and has proven to be a powerful means to test whether the behaviors of the declining population of Steller sea lions were consistent with the predictions of overfishing or over-abundance of low-quality prey. However, behavioral studies require context from physiological ecology and a solid understanding of the natural history of the species at risk to attain their full power.

So much of what has been learned about the behavioral ecology of Steller sea lions has come from graduate thesis research (e.g., Sandegren 1970; Gentry 1970; Harestad 1973; Gisiner 1985; Kucey 2005; Marcotte 2006; Milette 1999; Parker 2006; Porter 1997; Smith 1988; Higgins 1984; Vazquez 2013; Scordino 2006; Fuller 2012; Merrick 1987; Daniel 2003; Brandon 2000; Keech 2008). These university-based studies represent tens of thousands of hours of observations by students and their assistants in California, Oregon, British Columbia and Alaska—and are the backbone of much that has been learned about Steller sea lion behavior. Each of the behavioral studies contributed a small piece of knowledge needed to bring the puzzling natural history of Steller sea lions into focus. Without these core behavior studies, it would not have been possible to make behavioral inferences about food availability or causes of population declines and recoveries.

Behavioral ecology has provided significant insights into the decline and natural history of Steller sea lions. It has revealed that Steller sea lions wean when about 12, 24 or 36 months old, and that they start transitioning to solid food 2–3 months before they wean. The exact age at weaning appears to depend on whether their mothers remain pregnant in the last trimester of fetal development. It is unknown, however, if late-term pregnant-females discourage their pups and yearlings from suckling, or if some other progressive change initiates the weaning process. In all likelihood, the final stage of weaning is probably abrupt, and may well occur when their pregnant mothers leave them at the haulout and return alone to their natal rookeries to give birth.

All sexually mature females appear to breed each year on rookeries and haulouts, regardless of whether they have recently given birth or are still nursing a 1- or 2-year old. Most non-lactating females carry their fetuses to term. However, up to half of lactating females may lose their fetuses during the second trimester of pregnancy. Females that miscarry will likely continue nursing their pup or yearling for another year. Rates of abortions may therefore be related to lactation and the extent to which mothers consume species that are low in fat and high in protein.

Behavioral observations revealed regional differences in feeding behaviors of Steller sea lions that were inconsistent with there being less prey available to sea lions in the declining population. Instead, maternal attendance patterns and measures of foraging success indicate that more prey were available to the declining population than to the increasing population. However, the greater abundance of prey available to the declining population was of lower average quality (i.e., energy density) than the prey available to the increasing population. Sea lions beyond the age of 1.5 years appear to have no trouble meeting their daily energy requirements by increasing daily amounts of food consumed. However, the same cannot be said for yearlings that do not yet have sufficient stomach capacity.

Low quality prey likely explains the increased rate of abortions that occurred during the decline, which in turn allowed females to keep their dependent young longer and increase the interval between having subsequent pups. This longer period of dependency would increase body size and enhance reproductive fitness, but may come at the cost of increased risk of predation on dependent young by killer whales—a significant source of death (Barrett-Lennard et al. 1995; Williams et al. 2004; Guénette et al. 2007; Matkin et al. 2007).

The plasticity observed in age of weaning of Steller sea lions is likely an evolutionary adaptation to survive the reorganization of fish communities known to follow ocean-climate regime shifts in the North Pacific Ocean (Trites et al. 2007b). Extending age at weaning is one means by which population declines would slow until the ocean shifts naturally back to a state that supports a more energy-rich prey field and greater numbers of Steller sea lions. Shifts in the abundance of walleye pollock, Pacific cod and Atka mackerel (such as followed the 1976–1977 oceanic regime shift) have occurred repeatedly over millennia—as have shifts in sea lion numbers (Trites et al. 2007b; Maschner et al. 2014). Recovery of Steller sea lions requires another regime shift to increase the energy density of prey available to pups and yearlings—and may indeed be underway in the Gulf of Alaska and Eastern Aleutians where recent increases in sea lion numbers have been observed.

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