THE TIMING OF MOULTING IN WILD AND CAPTIVE

STELLER SEA LIONS (*EUMETOPIAS JUBATUS*)

by

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ABSTRACT

I documented the timing and progression of the moult by sex and age class in a wild population of Steller sea lions (*Eumetopias jubatus*) on Lowrie Island, Alaska (Jul-Nov 2001) and from captive animals at the Vancouver Aquarium Marine Science Centre (1993-2000). In the wild, juveniles (ages 1-2 years) were the first to moult followed by adult females, bulls and pups. The mean date when juveniles started their moult was 21 Jun which was significantly different from the mean start date of 07 Aug for adult females, and differed from the mean start date for pups of 01 Sep (one month later). Mean completion dates were also about one month apart (19 Sept for juveniles, 26 Oct for adult females and 17 Nov for pups). Duration of the moult was about 45 days for each age group (pups and adult females). However, duration of the moult for captive sea lions was longer (averaging 83.5 days) and differed among years and within age classes. Patterns of hair loss in the wild (*i.e.*, the progression of the moult over the body surface) differed among (i) pups, (ii) juveniles and early moulting adult females, and (iii) bulls and later moulting adult females. Differences in the timing and progression of the moult may be related to physiological changes and interactions of hormones associated with body condition and the reproductive cycle.

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CHAPTER I: STELLER SEA LIONS AND EPIDERMAL COVERINGS

The epidermis helps to reduce desiccation and assists with respiration and osmoregulation among amphibious (and lower aquatic) vertebrates. In warm blooded vertebrates, the epidermis may provide cryptic colouration, mating advertisement or thermoregulation, and extensions of it may serve in specialised functions such as flying or swimming (Ebling and Hale 1970; Ling 1970). Epidermal glands can also aid in moisture maintenance and thermoregulation (Ebling and Hale 1970; Ling 1965). The function of the epidermis is more seasonally related to life-history events in birds (to attract mates) and mammals (to serve as camouflage) than in amphibians (Ling 1972). Seasonal renewal of the epidermis in birds and many mammals is coordinated with other energy-expensive life cycle events such as reproduction and migration (Ling 1972).

Hair is a mammalian characteristic that is thought to have evolved after the establishment of internal thermoregulation from keratinised, spiny sensory thickenings anchored in an amphibian-like epidermis (Ling 1970; Smith 1958). In mammals, one function of an epidermal covering is to provide a partition between the fluctuating environment and internal homeostatic environment (Young 1957). Hair may also play a role in thermoregulation, defence (*e.g.* porcupine, hedgehog) and sensory perception. The plasticity in the form and function of hair can be observed between species of closely derived ancestry (Ling 1972).

Periodic regeneration of the mammalian integument (hair, and in some cases, the entire epidermis) is important given the overall functionality of hair. The generalized mammalian hair cycle begins below the surface of the skin with mitotic activity near the anchoring base of the follicle. The mitotic activity leads to an expansion of the bulb down into the dermis and a darkening in

pigmentation (Bullough and Laurence 1958). As the new hair grows upward, the old hair becomes loose and eventually falls out of the shared follicle. Once the new hair is fully-grown, the bulb migrates up to the epidermis and becomes dormant until the next cycle begins.

The mammalian hair replacement cycle varies by species. In some, there may be a sloughing of the entire epidermal layer. In others, hairs may be replaced one at a time. Mitotic activity of the epidermis is likely controlled by photoperiod and the endocrine system, and influenced by temperature and reproductive hormones (Ebling and Hale 1970; Ling 1984). In mice, high energy production (glucose and oxygen) is required to support high mitotic activity (Bullough and Laurence 1958). Thus moulting is an energetically expensive activity that must be coordinated with other energetically demanding activities, such as reproduction.

Pinniped Adaptations in Pelage

The potential for heat loss in water is approximately 27 times greater than in air. In pinnipeds, this thermoregulatory difference is partially alleviated by the presence of hair on the skin (Ling 1970). Northern fur seals (*Callorhinus ursinus*), for example, have dense coats of under hairs that trap air and aid in thermoregulation while in water; while northern elephant seals (*Mirounga angustirostris*) appear to sit at the other end with a sparse pelage. Cetaceans have adapted a hairless skin with a substantial insulating blubber layer.

Pinnipeds all lack erector muscles that cause hair to stand erect in response to environmental changes such as decreasing temperature (which would aid in thermoregulation on land). However, the absence of erector muscles enables the hairs to lie flat over one another when wet, creating a smooth surface (Ling 1970).   The smooth surface may then increase

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hydrodynamic fluidity and assist with propulsion in the water. Another function of hair in pinnipeds may be to act as mechanical protection from abrasion on rocks and hard surfaces when they haul out on land or ice (Ling 1970; Ling 1984). All pinnipeds are constrained on land when pups are born, and most are constrained to breed on land. The time spent on land may lead to increased wear on the pelage leading to the need to periodically renew their hair. The pelage may further function to provide an abrasive surface while hauled out on ice and slippery land surfaces.

Steller Sea Lion Pelage

Steller sea lions (*Eumetopias jubatus*) belong to the family *Otariidae* and regenerate their hair coat annually. Adult pelage consists of hollow guard hairs with as many as three under hairs in a shared follicle/shaft, which is typical of most mammals (Scheffer 1964; Vania 1972). The chocolate-brown pelage of pups lacks under hairs (Scheffer 1964) and is darker in colour than the tawny adult pelage. Steller sea lions do not undergo a catastrophic moult, with a sloughing of the entire epidermal layer, similar to elephant seals. Instead, each new hair replaces and pushes out the old hair from the shared follicle. The replacement of the pelage is believed, from captive observation at the Vancouver Aquarium Marine Science Centre, to start at one end of the body and spread progressively towards the other. Therefore, the moulting period is defined as the time when new hair is first visible on the surface until all old hair has been shed.

A major function of hair for Steller sea lions may be to act as mechanical protection from abrasion on rocks and hard surfaces when they haul out. Unlike some pinnipeds that migrate for up to 10 months of the year, Steller sea lions regularly haul out every one to two days year round (Calkins and Pitcher 1982; Milette and Trites 2003; Trites and Porter 2002). The regular hauling out might

increase the wear and damage to the pelage. Therefore pelage requires periodic replacement of worn and damaged hairs.

Steller Sea Lion Biology & Seasonal Cycle

Steller sea lions are polygynous and sexually dimorphic. Males become sexually mature between 5 to 7 years of age, but may not become successful breeding bulls until 9 to 10 years of age (Pitcher and Calkins 1981; Thorsteinson and Lensink 1962). Bulls have a thick neck, triangular-shaped head, and may be more than double the size of females. Territorial bulls haul out on rookeries (sites traditionally used to give birth and mate) from approximately mid-May through mid-July in their Alaskan range (Gisiner 1985). Pregnant females begin hauling out on rookeries in early June, giving birth within days to a single pup. Females constantly attend to their pups for the first ten days on average, thereafter alternating between about one day at sea and one day on shore during early lactation. However, during later lactation they increase the amounts of time at sea, to an average of two days while spending less than a day onshore (Milette and Trites 2003; Sandegren 1970; Trites and Porter 2002). Lactation may last up to three years, but weaning usually occurs during the first year (Calkins and Pitcher 1982).

Breeding occurs on land approximately ten days after females give birth (Gentry 1970), but the embryo does not implant in the uterus until October (Calkins and Pitcher 1982), coinciding with the presumed start of the moulting period. Moulting occurs after the pupping period between July and December but the exact timing is not well defined (Vania 1972).
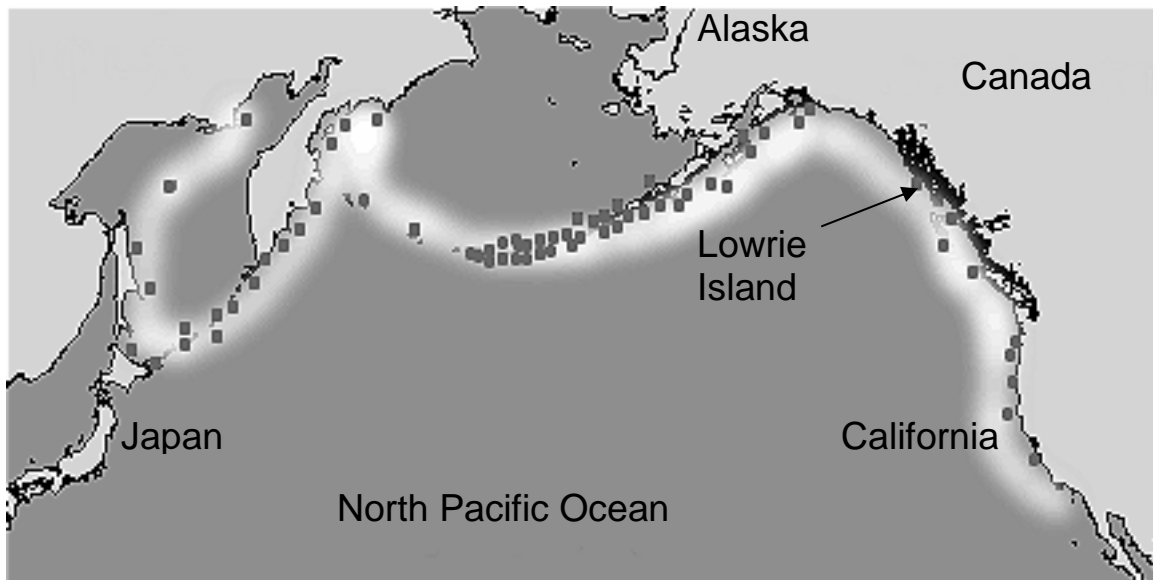
Figure 1.1. Range of Steller sea lions. Squares indicate rookery locations. Lowrie Island is the largest rookery in their range.

Steller sea lions range throughout the Pacific Rim from California to Alaska and Japan (Figure 1.1). From the 1970's to the 1990's their range-wide population size decreased by about 80%. As a result the U.S. population was declared endangered in 1997 west of 144° Longitude – the line that separates two genetically distinct populations (Bickham et al. 1996; Loughlin et al. 1992; National Marine Fisheries Service 1992; Trites and Larkin 1996). A number of studies are underway to determine possible reasons for their continued decline.

Importance of a Moulting Study on Steller Sea Lions

The regeneration of hair can be energetically expensive (Bullough and Laurence 1958). Phocid females and beluga whales (*Delphinapterus leucas*) may conserve energy during the moult by either hauling out onto land or moving into warmer water (Boily 1995) since optimal conditions for mitosis includes higher temperatures (Feltz and Fay 1966). Furthermore, it might be beneficial to conserve energy by minimising thermal conductance during the moult, by

moving to warmer temperatures. Some phocids, such as the harbour seal, haul out in greater numbers during their moult than other times during the year and it is at this time that population surveys are conducted (Calambokidis et al. 1987; Stewart and Yochem 1984; Thompson et al. 1989). However, it is not known whether greater numbers of Steller sea lions and other otariids haul out during the moult, nor if the Steller sea lion moult is energetically expensive.

The timing and progression of the moult for Steller sea lions probably varies by sex and age class (Calkins and Pitcher 1982; Vania 1972) given the differences in moulting phenology that have been documented in other species of pinnipeds. In northern fur seals, the initiation of the moult becomes progressively later as males and females age (Scheffer and Johnson 1963). In harbour seals (*Phoca vitulina*), yearlings are the first to moult, followed by subadults (males and females), adult females, and lastly adult males (Daniel et al. 2003; Thompson and Rothery 1987). Furthermore, larger numbers of all sex and age classes of harbour seals haul out during the earlier stages of their moult, a behaviour that might be due to the higher energetic cost associated with hair growth. If the maximal numbers of animals in each sex and age class occurs at different times, it confounds population based surveys. Interpretation of studies using population based surveys need to understand and incorporate underlying assumptions.

A goal of my study was to document the timing of the moult, a little known phase of the Steller sea lion seasonal cycle. Documenting the discrete timing of the moult would help to complete our understanding of their life history. Many of the studies that investigate causes surrounding the decline of Steller sea lions use electronic instruments glued to the hair on the back of sea lions to collect transmitter data. Knowing when the different sex and age classes

moult and how it relates to maximal numbers of animals hauled out may help to optimise the deployment of these instruments.

My thesis documents the progression of moulting for Steller sea lions in the wild (Chapter 2) and in captivity (Chapter 3). Emphasis is placed on determining and documenting when moulting starts and ends for different sex and age classes of wild Steller sea lions. I predict that differences exist in the timing of the Steller sea lion moult. Based on the timing of the moult by sex and age class found in other pinniped species, I hypothesise that juveniles will moult prior to the adults. I further predict that moult stage might influence numbers of individuals hauled out on land. Based on the haul out behaviour of other pinnipeds, and assuming that the moult is also energetically expensive for Steller sea lions, I hypothesise that more animals would haul out onto land during the earlier stages of the moult.

CHAPTER II: TIMING OF MOULTING IN WILD STELLER SEA LIONS

Introduction

Steller sea lions, like other pinnipeds, shed their hair annually. However, relatively little is known about the timing and progression of their moulting. They are known to regularly haul out onto land throughout the breeding and non-breeding seasons, and are believed to moult after the June-July pupping period in their Alaskan range (Vania 1972). Whether or not they haul out in greater numbers while moulting, as has been shown for phocids, is not known (Calambokidis et al. 1987; Stewart and Yochem 1984; Thompson et al. 1989).

Regenerating hair can be energetically expensive. European badgers, *Meles meles* (Stewart and Macdonald 1997) consume greater amounts of food while they moult due to the cost associated with producing protein at the cellular level (Bullough and Laurence 1958). Male harp seals (*Phoca groenlandica*) lose mass and expend little activity during the moulting period, indicative of high energy expenditure (Chabot and Stenson 2002). The energetic costs for moulting Steller sea lions are not known but are presumed to be high.

Temperature and thermal conductance are important factors influencing both the timing and the costs associated with the moult whereby some species alter behaviours to offset the costs of these molecular processes. The speed of one of the basic underlying molecular processes of moulting, mitosis, is temperature dependent. Elevated temperatures applied to cultured pinniped epidermal cells increases their mitotic rates (Feltz and Fay 1966) and may act to expedite the moulting period. Another factor that affects aquatic animals during their moult is thermal conductance (heat flow) to the environment from the body. The northern elephant seal (*Mirounga angustirostris*) and harbour seal, (*Phoca vitulina*) haul out for extended periods while they moult, presumably

because air temperatures are higher on land relative to water (Ling 1970). The temperature difference reduces energy expenditure associated with maintaining high epidermal temperatures for mitosis and minimises thermal conductance. Among cetaceans, studies have indicated that beluga whales (*Delphinapterus leucas*) may also conserve energy while they moult their epidermis by moving into warmer water (Boily 1995; Watts et al. 1991). Furthermore, thermal conductance of northern fur seal pups decreased after their first moult presumably compensated by for their new pelage and thicker blubber layer (Donohue et al. 2000).

Some species of pinnipeds, such as elephant seals undergo a catastrophic, rapid shedding of the entire epidermal layer. Others shed individual hairs, whereby new hair pushes out its shared follicle (Sokolov 1960). For these species, the pattern of hair replacement generally progresses over the body, usually beginning at one or both ends and then spreading across the remaining surface. The moult for the Steller sea lion is progressive (Vania 1972), but the topography of the progression has not been documented.

The timing of the moult for Steller sea lions probably varies by sex and age class (Calkins and Pitcher 1982; Vania 1972). Differences in moulting phenology have been documented in other pinnipeds, including harbour seals (Daniel et al. 2003; Thompson and Rothery 1987) and northern fur seals (Scheffer and Johnson 1963). Different moult timings by sex and age class may have implications for population monitoring (Daniel et al. 2003; Harkonen et al. 1999). Population surveys for pinnipeds are conducted, usually from the air, during periods when they are visibly hauled out on land or from numbers of pups counted directly on the rookeries. The estimated abundance of one or more classes of sea lions based on surveys could be over- or under-estimated if animals preferentially haul out during specific or critical moult times.

A foremost goal of my study was to document the timing of the moult for Steller sea lions, to establish a timeframe for a little known but critical event of their annual cycle. A better understanding of sea lion behaviour during this time period might provide some insight into behavioural aspects surrounding their decline, because we know very little during the fall and winter months about Steller sea lions. Another purpose of my study was to establish the progression over the body in order to determine optimal timing to glue electronic devices to the hair of Steller sea lions. Electronic instruments help to collect scientific data on behaviour, ecology and physiology that contribute to solving the puzzle of their decline.

In this study, I documented the timing of moulting in a population of wild Steller sea lions in the eastern Gulf of Alaska to determine (i) progression of moult over the body, (ii) timing of moult for the population, by sex and age classes, (iii) duration of moult for individuals and (iv) the influence of moult stage on population counts.

Methods

Study Site

Steller sea lions were observed on Lowrie Island, Alaska (54.86° latitude, 133.54° longitude, Figure 1.1) from July – November, 2001 by myself and a field assistant. Lowrie Island is part of the Forrester Island complex of rookeries, which is currently the largest breeding aggregation in the world for Steller sea lions with nearly 3000 pups born annually in recent years (Calkins et al. 1999). It consists of a rocky outcropping and cobble haulout substrate.   Sites were surveyed on or within 30m from the main island and divided the island into north and south halves.

Data Variables

Moult stage was visually determined by discerning old and new hair with 10x40 binoculars. Moult stages included (i) not yet moulting, (ii) moulting and (iii) completely moulted. I defined the moult as the time when animals were visibly shedding their old hair and the presence of new hair was evident. Old and new hair was easily differentiated since new hair was lighter in colour than old hair (Figure 2.1). Hair colour of older animals was generally lighter than that of younger individuals. For example, pups born with a dark-brown coat moult into a lighter, intermediary coat during their first year. Yearlings in turn moult into the adult coat, which is light tan or beige.

Figure 2.1. Example of moulting Steller sea lions. Pups have dark chocolate coloured coats (far right). Yearling (middle) with darker old hair and lighter new hair. Adult female (far left) with a patch of lighter new hair on foreflipper.

We documented moult stage directly in the field, and later in the lab from digital photographs using a Nikon D1 camera with 300mm zoom lens and doubler.

Animals were divided into the following sex and age classes: adult females, pups of the year, juveniles, territorial males and subadult males (as defined by Trites and Porter, 2002). Lowrie Island is predominantly populated by adult females and pups with some juveniles (juveniles and pups might be attended by their mother, or alone while their mother feeds). The few observed territorial bulls were easily identifiable because of their distinct mane with thick and coarse hair, lighter colour and distinctive head shape. Subadult males were also easily differentiated from adult females. However we could not use physical characteristics to differentiate juveniles by sex at the distances observed.

Moult Progression

I divided the body into six regions to achieve easy and consistent moult stage descriptions (Figure 2.2). The *head* was defined as the area anterior to the ears (A), while the *neck* extended from the ears to the anterior insertion of the foreflippers (B). *Foreflippers* consisted of the upper haired portion to the insertion point with the torso (C), and *hindflippers* started at the tail back towards the end of the haired region on the appendages (D). The *torso* was the region between the foreflippers and the hindflippers (E). Finally, the *ventrum* (not shown in Figure 2.2) was the belly region, distinguished by the imaginary line between the posterior insertion point of the foreflipper and hindflipper appendages. These body regions were used both in the field and later in the lab from photographs. We determined moult stage for each discrete area of the body and used four categories in the field, based on the decimal value of the proportion of new
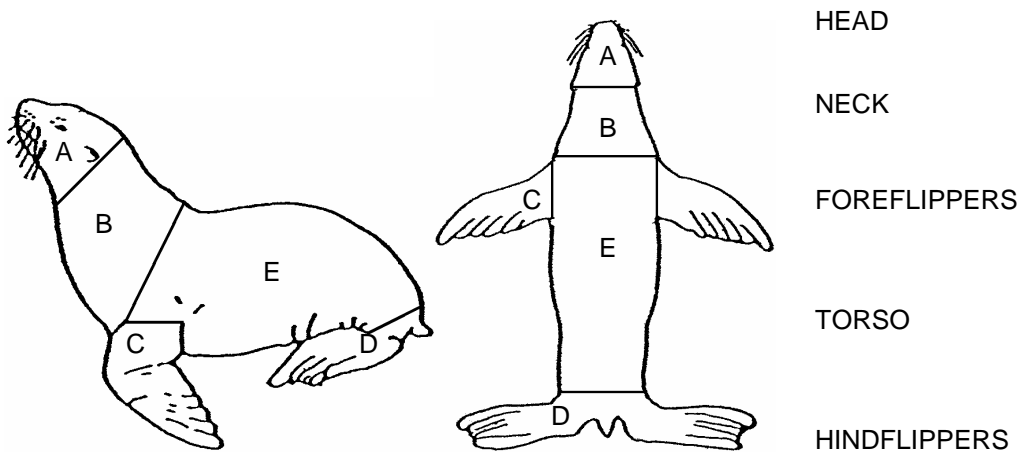
Figure 2.2. Discrete body areas assigned to each individual Steller sea lion.

to old hair. Categories were broadly encompassing and included: $x = 0.0$, $0.0 < x < 0.5$, $0.5 < x < 1.0$, and $x = 1.0$. The progression of moult was qualitatively described in the pattern of the spread of the new hair across these body regions over time for each sex and age class.

Timing of Moult - Population

Scan surveys were used to quantify the moult process for the population as a whole. A complete survey consisted of a visit to all areas on the island where sea lions were hauled out. Two sequential days were required to survey the entire island at the start of the field season, due to the number of animals present. However, later in the season when overall sea lion numbers decreased, we surveyed the entire island in a single day. We conducted 52 complete surveys between July and November 2001. Data were not included for incomplete surveys. The start and end survey points on the island were

alternated each day relative to the north-south island orientation. Group location on the island was similar day to day, but changed seasonally. If we started at the south end on Day 1, we began surveys from the north end of the island on Day 2. It was not possible to survey all animals present in a group when there were large numbers of animals present. Later in the season, when fewer animals and fewer groups were present, effort was made to ascertain a sample size of at least 30 individuals. Surveys systematically started on the right side of a group of animals, and moved left. We obtained moult stage for as many sides of an individual's body as possible, spending a maximum time period of 15-30 minutes per individual.

In the field, we categorised each animal for sex, age, and moult stage by body region. The stages of moult for each body region we obtained in the field were summed to calculate a single stage of moult for each animal for the analyses. In order to assign an individual to a single moult stage we had to view all the body areas for one side (except the ventrum, Figure 2.2). I assumed that the pattern of moult on the left and right sides of each animal was symmetrical. Thus moult stages were extrapolated for an animal that presented either its left or right side. Data could not be collected from the ventral surface because it was rare to ever observe the belly of a Steller sea lion in the wild. However captive studies indicate (Chapter 3) that the ventrum region moults after other areas.

In the laboratory, I entered data into an Excel spreadsheet and double checked each entry per individual against photographs for correct moult stage to minimize error from data transcription. All moult stages were summed to provide a single value per individual per day. Animals were considered to be moulting if new hair was noted on any single area (*e.g.* head only). Sea lions were categorised as completely moulted if all old hair was gone. I determined the proportion of animals in each moult stage for each survey date and fit a

weighted binomial model with a logit function. I conducted all statistical analyses in SPLUS. All dates were set in days from the first date that moulting was observed in the study population, 27 July 2001. I estimated the start date of moulting for each sex and age class from the binomial model where the probability of animals not moulting was 0.99. Similarly, I found the mean date when moulting ended from a weighted binomial model where the probability of the proportion of animals finished moulting was 0.99. Small sample sizes for bulls and sub-adult males meant that I used only juveniles, adult females and pups in the analysis.

Duration of Moult – Individual

I used focal sampling for individually recognisable sea lions that consisted of branded animals or repeatedly recognisable animals (*i.e.* those with distinctive scars and fungal patches). Fungal patches have been used reliably in previous studies and do not change within a single season (Milette 1999), making it possible to reliably track a single individual throughout its moult. We identified focal animals in the field from digital photographs taken during the scan surveys. Resighting of focal animals was conducted prior to each scan survey.

Moult duration was the time between when new hair was first observed on an animal until all old hair had been shed. I determined durations for all focal adult females and pups. Moult duration and start and end dates between pups and adult females were statistically compared using standard two sample t-tests. I used data from individuals where both start and end times were observed. I also compared the timing of moulting between pups and adult females using a Kaplan-Meier survival probability. Survival analysis allowed for inclusion (using censoring) of those animals whose end times may not have been directly observed since probabilities are estimated day to day based on the number of

individuals in a moult stage for that particular day. I calculated the probabilities that pups or adult females would be moulting for each day following the date when the first animal of either age class was observed moulting. Similarly, I calculated the probability of animals moulting and moving into the next moult stage (completely moulted) by date following the day when the moult was first observed.

Relationship to Number of Sea Lions Counted

I fit a binomial regression to determine whether moult stage had any effect on the overall counts of Steller sea lions on shore. I used data only for the days when a total count was available. I used a number of hierarchal models and compared using a general linear model of the form: stage ~ age + date + count, link=logit.

Results

Timing of Moult – Population

Juveniles were the first to start to moult, followed by adult females, then pups and bulls (Figure 2.3). A total of 52 complete daily surveys were conducted. The mean moult start date was 21 Jun (20 – 24 Jun, 95% CI) for juveniles, 07 Aug (26 Jul – 10 Aug,) for adult females, and was 01 Sep (26 Aug – 2 Sep) for pups (Table 2.1). Mean moult completion dates were 19 Sep (15-19 Sep) for juveniles, 26 Oct (19 – 29 Oct) for adult females and 17 Nov (12 – 18 Nov) for pups.

Table 2.1. Mean dates for the start and end of moulting for juveniles, adult females (AF) and pups estimated from a logistic regression.

		Start	End
Juvs	Mean	21-Jun-01	19-Sep-01
	95% CI	*20 - 24 Jun*	*15 - 19 Sep*
AF	Mean	7-Aug-01	26-Oct-01
	95% CI	*26 Jul - 10 Aug*	*19 - 29 Oct*
Pups	Mean	1-Sep-01	17-Nov-01
	95% CI	*26 Aug - 2 Sep*	*12 - 18 Nov*
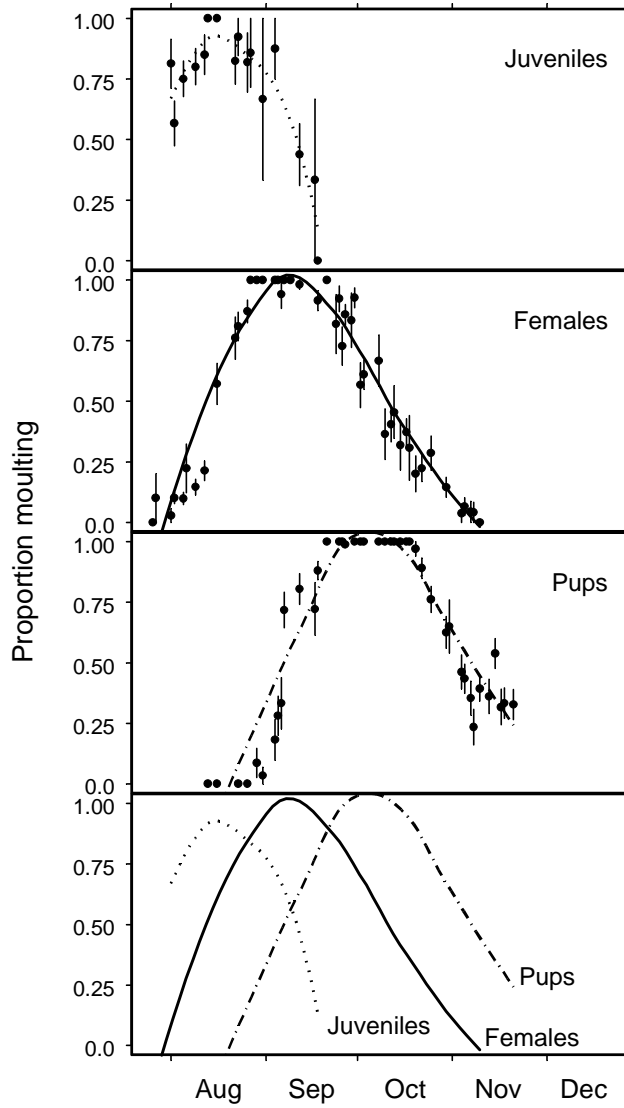
Figure 2.3. Loess curve fitted to proportion of (a) moulting juveniles, (b) adult females, and (c) pups showing (d) comparative difference in timing of moult. The error bars represent SE. Tick marks on the x-axis show the first day of each month.

Duration of Moult – Individual

The duration of the moult averaged 45.7 days (± 3.7 days, 95% CI, n=29) for focal adult females and 45.0 days (± 4.4 days, n=30) for focal pups. They did not differ significantly from each other (Table 2.2). However, the start of the moult of the two focal groups did differ significantly as illustrated by the separate lines based on a Kaplan Meier survival probability analysis (Figure 2.4). The Kaplan Meier probability analysis, conducted from the focal observations, shows the probability of the population moving from one moult stage to another. The steepest portion of the line in Figure 2.4 indicates the greatest rate of change in the population from one moult stage to another. For adult females a large shift from not moulting to moulting occurred about 30 days following the start of their moult (25 August). In contrast, the proportion of pups switching to moulting was more constant. Completion of the moult was relatively rapid for both pups and adult females, as indicted by the steep rate of declines shown in the probability of finishing the moult in Figure 2.4. Adult females experienced the greatest change around day 80 (15 October), while the transition for pups was relatively quick overall.

Table 2.2 Mean duration of moulting (in days) and mean start and end dates for focal adult females (AF) and pups. Comparisons between pups and adult female mean dates were made with standard two sample t-tests.

		AF	Pup	t	p	df
Mean Days		45.7	45.0	-0.22	0.828	57
	SE	1.83	2.14			
Mean Start		27-Aug-01	26-Sep-01	9.4	<0.001	57
	SE	2.29	2.27			
Mean End		12-Oct-01	10-Nov-01	11.9	<0.001	52
	SE	2.00	1.51			
	n	29	30			
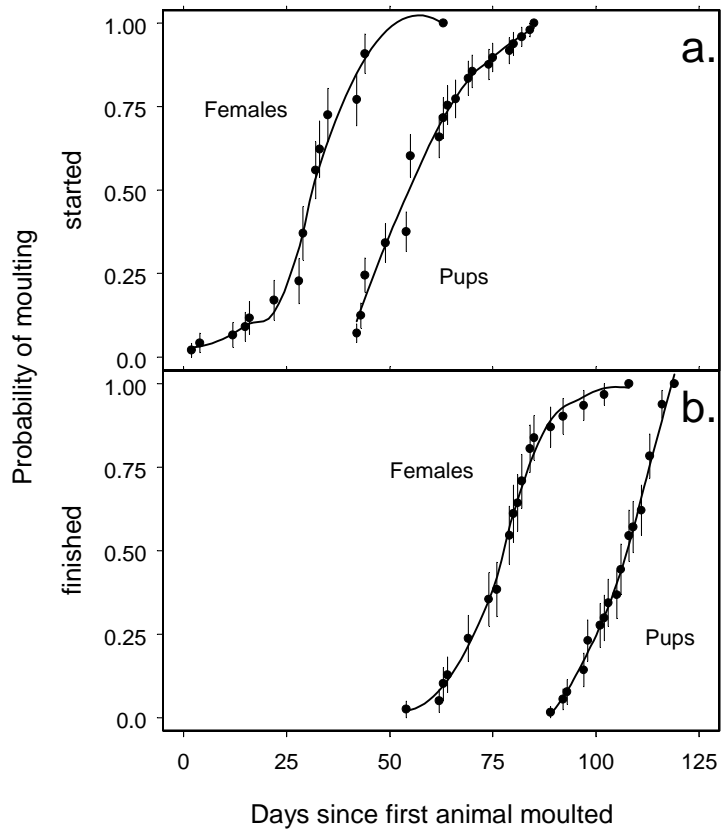
Figure 2.4. The probabilities (with SE) that the adult female and pup populations would **a.** start the moult or **b.** have completed their moult following the date that the first moulting animal was noted (which was an adult female observed on 27 July 2001). Probabilities are based on a Kaplan Meier Survival probability analyses. Loess fitted curves.

Relationship to Number of Sea Lions Counted

In general, there was an overall decline in the number of Steller sea lions counted on Lowrie Island during the study period (Figure 2.5). The greatest rate of decline appeared to occur immediately after the adult females started moulting (between the not moulting stage and the moulting stage) well before the end of their moult. Date was the most reliable predictor for the stages of moult (Table 2.3). Contrary to predictions, count did not contribute significantly to moult stage, nor were sex and age reliable predictors.

Table 2.3. Summary of model fit for moult stage (not moulting or completely moulted) and population counts, including generalized linear model regression coefficients.

Stage	glm regression coefficients			sequential terms (first to last)		
	coefficient	SE	t	df	dev. resid.	Pr (Chi)
Not moulting						
intercept	21.35	26.50	0.81			
sex/age	-6.15	5.13	-1.20	9	0.92	0.34
date	-0.42	0.43	-0.97	8	6.29	**0.01**
count	-0.002	0.01	-0.41	7	0.18	0.67
Completely moulted						
intercept	-11.39	10.72	-1.06			
sex/age	2.92	1.47	1.99	23	0.39	0.53
date	0.10	0.09	1.22	22	8.89	**0.003**
count	0.00	0.00	0.03	21	0.00	0.98

Note deviance in null model for not moulting sequential ANOVA: 8.048 and for done moulting ANOVA: 10.6607. Model: glm (stage~age+date+count, link=logit)
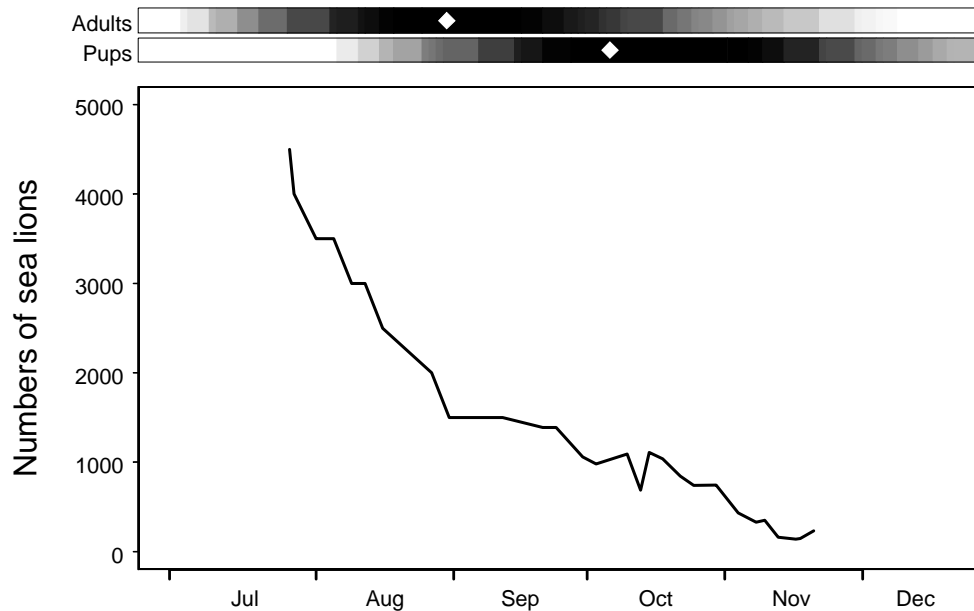
Figure 2.5. Number of Steller sea lions (in all sex and age classes) counted on Lowrie Island, July – August, 2001. The two grey scale bars above the graph represent the proportion of adult females (Adults) and pups moulting (white = none moulting, black = all moulting). The white diamond represents a peak in the proportion moulting. The proportion moulting beyond the end of observation (November 24) were extrapolated from Figure 2.3.

Moult Progression

For all sex and age classes, the general moult started on one or two areas of the body and spread over the rest of the body in a regular fashion. Scarred areas of the body, if present, were among the first regions to moult.

Adult females appeared to have two distinct patterns of moulting that were distinguished by whether they were early or late moulters. Females that

were late to start moulting tended to begin losing hair on their shoulders, continuing down towards their foreflippers and ventral region (Figure 2.6). New hair then appeared on their hindflippers and progressed over the dorsal midline and up from the ventrum and sides. The last places to moult were the neck, followed by the head. The second pattern of moult (for those who started early) was similar to the late moulting females except that new hair initially appeared concurrently near the eyes and on the snout and foreflippers.

Bulls appeared to moult in a similar fashion to later moulting adult females, although too few sightings were made to draw firm conclusions. However, juvenile moult patterns appeared to resemble that of earlier moulting females, with new hair appearing near the eyes and snout. The last areas to moult were their necks and the sides of their torsos.

Pups began moulting on their hindflippers with new hair shortly appearing on the tops of their heads (Figure 2.6). Pups that had been branded also appeared to experience early hair loss, with new hair first observed on the hindflipper region near the tail. Moult on the hindflippers moved up the sides and dorsal midline towards the head. The moult also progressed up across the ventral region while it moved simultaneously down the side of the head. It then progressed across the neck towards the dorsal midline. The last regions to moult were on the sides immediately above the foreflippers. A characteristic "shawl" often connected the two sides, just prior to this stage (Figures 2.1 and 2.6).

a. Adult Females
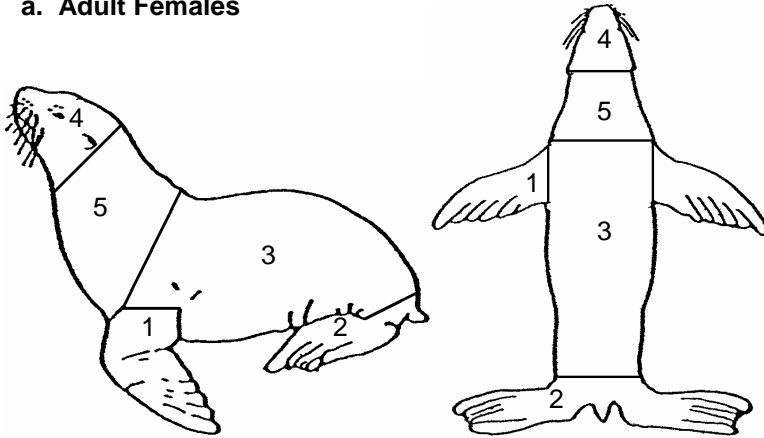
b. Pups
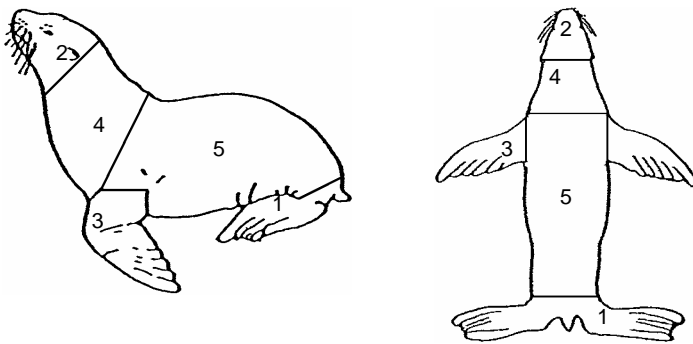
Figure 2.6. Progression of moult for (a) adult females and (b) pups of the year. Numbers indicate the progression of moult over time.

Discussion

Timing of Steller Sea Lion Moult

The timing of the Steller sea lion moult differed by sex and age class. Juveniles were the first to moult in early July, followed by adult females at the end of July, and by pups and bulls in early September. The duration of visible moult for individuals within all age classes was about 6.5 weeks, although the duration of the staggered moult for the population as a whole was about 21 weeks (Jul – Nov).

Among pinnipeds in general, the time from the first mitotic event until the old hair is pushed out ranges from 6 weeks for harbour seals to 14 weeks for northern fur seals. It takes about two weeks of this time for a hair to be fully visible once it reaches the surface of the epidermis until it forces the old follicle out of the shared shaft (Ling 1984). Thus the duration of the physiological moult of Steller sea lion is at about 8.5 weeks.

Shedding is the final stage of the hair cycle (Ling 1970; Ling 1984). Among Steller sea lions, I observed three distinct patterns of progression of hair loss: early-moulting adult females (and juveniles), later-moulting adult females (and bulls), and pups of the year.

The progression of the moult over the body surface of Steller sea lions appears to have three distinct patterns that are specific to age and sex class (*i.e.*, pups, juveniles, bulls and adult females). In the case of adult females, there appear to be two distinct patterns depending on whether the female moults early or late in the season. Moult patterns have been documented in only one other pinniped species, the New Zealand sea lion (McConkey et al. 2002), where the pattern resembled that of the early moulting adult females in this study. As with

the Steller sea lion, male New Zealand sea lions started moulting on the face and flippers, followed by the mane (neck), the ventral midline and the sides.

The timing of the moult has been documented in a diverse range of species, revealing a general tendency for juveniles to moult before older animals. Examples where juveniles moult prior to other age classes have been documented in pied flycatchers (*Ficedula hypoleuca*) (Siikamaki et al. 1994), European badgers (Stewart and Macdonald 1997), and harbour seals (Daniel et al. 2003; Thompson and Rothery 1987). Among otariids, juvenile New Zealand sea lions (*Phocarctos hookeri*) moulted prior to subadults and adults (McConkey et al. 2002), and yearling northern fur seals moulted first, followed by adult males then females (Scheffer and Johnson 1963). The Steller sea lion moult followed these general patterns.

What Drives the Steller Sea Lion Moult?

The proximate mechanism for the mammalian moult is thought to be controlled by environmental stimuli – photoperiod and temperature – which trigger a hormonal response that results in hair growth. Other factors such as body condition and reproductive hormones probably also influence when different sex and age classes moult. Poor nutrition, that might lead to poor body condition, has been documented to affect the quality of pelage and delay the timing of hair regeneration in a number of mammals and birds (Ling 1970; Siikamaki et al. 1994; Stewart and Macdonald 1997).

There are four major categories within which the costs associated with the Steller sea lion moult, for all sex and age classes could be classified. They are direct, indirect, potential conflictions, and mediating effects. Direct energetic costs include those that directly sequester energy from an animal's budget, such as growth of the hair and hormonal action. Indirect costs include those events

that require direct energy input but that might divert energy allocated towards the moult, such as thermoregulation. Limiting or potentially conflicting costs might affect the sea lion moult can be behavioural or physiological in nature and could influence the moult such that their requirements may take precedence over expediting the moult, such as fasting limitations that might affect haul out time and elevated skin temperatures that help the moult. Mediating effects of the moult include those occurrences that might act to support or depress the moult, such as body condition and the external environment, temperature.

Two of the biochemical responses that might directly affect the juvenile moult are a pair of antagonistic sets of hormones: thyroid (stimulating) and cortisol (inhibiting) (Ebling and Hale 1970; Ketterson and Nolan 1992; Mohn 1958; Nolan et al. 1992; Payne 1972; Riviere et al. 1977). Thyroid hormones (such as thyroxine – T_4, triiodothyronine – T_3, and reverse T_3 – rT_3) stimulate oxidative metabolism and mobilise energy stores. Cortisol is a glucocorticoid (a stress hormone) that stimulates gluconeogenisis, increasing blood sugar levels. In the male European badger, thyroid hormones stimulated their moult, particularly when testosterone was suppressed (Maurel et al. 1987). Among pinnipeds the timing of the moult for young (sexually immature) animals appears to correlate with antagonistic thyroxine-cortisol hormonal concentrations (John et al. 1987; Riviere et al. 1977). Conversely, frequent sampling in captive harbour seals lead to no apparent correlation between the concentrations of thyroid hormone and the moult (Renouf and Brotea 1991). Instead they hypothesised that the changes in hormone concentration were correlated to the timing and quantity of food intake.

The adult female Steller sea lion moult occurs after the pupping and breeding periods. A mediating effect associated with the timing of their moult might include lowered body condition, a result of energy allocated to parturition

and early lactation. Another indirect cost that might influence their timing includes delayed implantation and the oncoming winter season. In most pinnipeds, mating occurs after the pupping period and but before most females depart the rookeries with their pups. After mating, the embryo undergoes developmental diapause. It is not known what signals the embryo to implant, but it usually occurs in the later fall, before winter. Hormonal influences associated with implantation could further indirectly affect the adult female moult.

The moult of adult female Steller sea lions could be indirectly affected by reproductive hormones such as estrogen, progesterone and prolactin. Levels of estrogen (an inhibitor of hair growth) are at high concentrations following parturition in a number of pinniped species (Boyd 1991). Stewart and Macdonald (1997) suggest that lactation may reduce body condition and stimulate the production of prolactin. Levels of prolactin are elevated during lactation for most pinnipeds (Boyd 1991) and might indicate increased energy expenditures that could suppress the moult. However, progesterone concentrations (a hair growth stimulator) tend to be high later in the season after the blastocyst implants (Boyd 1991; Ling 1984), coinciding with the moult period. Unfortunately little is known about prolactin or progesterone in Steller sea lions.

The timing of the moult and the two observed patterns of moult progression might also be related to whether adult females were accompanied by nursing pups of the year or juveniles, or had not reproduced. Nursing females have greater food requirements than those without pups (Winship et al. 2002) and may therefore be in poorer body condition. In addition to the indirect energetic cost (relative to the moult) associated with a suckling pup, females with nursing pups are likely to spend more time on the rookery during the early pupping period (May – June), with less foraging opportunities relative to females

with nursing juveniles and females without offspring. Females both accompanied by juveniles and without offspring can leave the rookery for extended periods of time to forage. The increased time spent foraging might be beneficial to these females resulting in relatively good body condition that expedites the moult. Thus females that have either not reproduced or were supporting a nursing juvenile may have moulted earlier than those with pups. Such a phenomenon appears to account for the moult of Columbian ground squirrels (Neuhaus 2000) and yellow bellied marmots, *Marmota flaviventris* (Armitage and Salsbury 1993), where non-breeding females moulted before those that were reproductively active.

Weather conditions, a mediating effect, were not recorded at the Steller sea lion study site, but the early moulting adult females and juveniles may have been exposed to slightly warmer ambient temperatures that may have been more conducive to moulting. In general, July and August are warmer months in Southeast Alaska with little wind and swell, and September frequently has cooler temperatures and increasing swell and rain. When ambient temperatures are high, such as during July and August when juveniles and adult females moult, animals may shunt excess heat towards the head and flippers (Hart and Irving 1959). These areas could in turn be the first to moult if increased surface temperatures speed the mitotic process (Ebling and Hale 1970; Feltz and Fay 1966).

The onset of the moult among the adult female population appears to be initially gradual as indicated by the gradual slope of the change in the probability of the female population moving into the active moult stage (Figure 2.4). The population then rapidly shifts into the active moulting stage near day 25 and maintains a relatively constant rate of initiation of moulting through day 40. The rapid shift observed at day 25 may be due to the effect of thyroxine,

which is believed to promote or initiate hair growth in rats (Mohn 1958) and harbour seals (Riviere et al. 1977), and was shown to peak in gray seals (*Halichoerus grypus*) at the point of rapid hair shedding (Boily 1996). The onset and apparent synchrony of the moult might also be related to the immanent departure of mothers with their pups from the rookery. It is not known if the initial stages of the moult are more energetically expensive, but has been hypothesised for harbour seals (Daniel et al. 2003). If the early stage of the moult are also more energetically expensive for sea lions, it might also be beneficial for adult females to quickly proceed through this stage.

The moult of male sea lions may be directly affected primarily by the reproductive hormone testosterone and also by their body condition. The male European badger moult was inhibited by the presence of testosterone which coincided with poor body condition (Maurel et al. 1987; Stewart and Macdonald 1997). It may also be the case for male harbour seals that breed aquatically and lose body mass during the mating season due to the energy allocated to finding females and securing reproductive encounters (Walker and Bowen 1993), acting to potentially conflict with the moult. The combination of testosterone and poor body condition after breeding may be why male harbour seals are last to moult. Elevated levels of testosterone in bull Steller sea lions also coincide with the mating season (Harmon et al. 1999) during which they defend territories and lose weight and body mass (Winship et al. 2001). Thus, the poor body condition of bulls after the period of territoriality may mediate a later timing of moult.

Pups, along with bulls, were the last to moult. The timing of the pup moult might be indirectly affected by energy allocated to growth and development of thermoregulation for an aquatic life. Pups also are affected by their mothers' behaviour, because they will follow her when she leaves the rookery to go to another haulout site. In this case, the mothers' behaviour creates

a potentially conflicting or limiting effect on the pups' moult. Among some pinniped species, such as harbour seals, pups moult their natal pelage *in utero*, emerging with an adult coat, and can enter the water within minutes of birth. Species, such as Weddell seals, that do not shed their pup coat *in utero* do not usually enter the water until they have completed their moult about 2 to 4 weeks after birth (Ling 1974). However, Steller sea lion pups undergo their postnatal moult 4 months after birth and regularly enter the water for brief periods after spending their first month on shore, increasing the potential thermal cost associated with their moult.

Metabolic measurements from northern fur seals indicate that post-moult pups had lower metabolisms when in water compared to pre-moult pups (Donohue et al. 2000). If a similar phenomenon applies to Steller sea lion pups, the timing of their moult might reflect their transition from a relatively sedentary period on shore to an aquatic, thermally more stressful existence. It is also possible that the timing of moult reflects body condition given that some of the last pups to moult appeared to be in poorer body condition.

The estimated end of the moult for the focal animals was earlier than the estimated moult from the scan surveys. Given that the focal animals were branded it is possible that they were born earlier, on average, than the scan-sampled animals observed to moult last. These same scan-sampled pups were frequently observed during November begging and trying to sneak suckles from other females, and their hips and ribs visibly showed relative to other individuals who had completed their moult and were usually observed with their mothers and appeared fat and healthy.

Effects of Moult on Population Counts

There did not appear to be a relationship between overall numbers of animals on shore and the stage of moult of different sex and age classes (Figure 2.5). However, counts at the rookery may not reflect overall numbers of sea lions hauled out throughout the region. The dramatic decline in overall numbers of sea lions counted at the rookery occurred after the adult females began their moult, rather than after the moult was completed as might be expected for a species restricted to land for thermoregulatory reasons (such as harbour seals). Large numbers of females appeared to leave the rookery for other areas while they were well into their moult (when rapid shedding of old hair may occur). A further look at the relationship between the presence of females with pups (Figure 2.7) showed females tended to outnumber pups when densities were high (*i.e.*, early in the season) and were outnumbered later in the season as numbers dropped and females spent longer at sea.
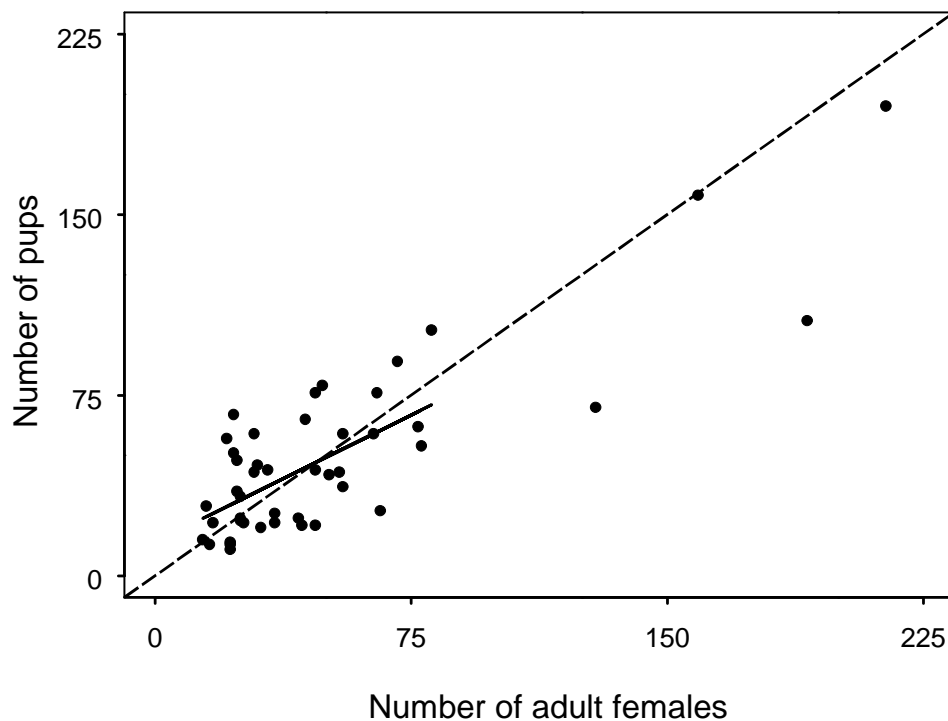
Figure 2.7. Regression of the number of females with number of pups counted. (r=0.40, d.f.=22.9, p<0.001). Regression line was fit to adult counts less than 100 individuals. The broken line represents a 1:1 ratio.

The departure of females prior to the completion of their moult might signify that the later stages of moult are not as energetically expensive as the earlier stages. Mediating effects of poor weather and less food availability might outweigh the direct costs of hair growth during the later moult resulting in females leaving the rookery. Energetic requirements for nursing increase as the pup grows and might result in females increasing the length of their foraging trips (Milette and Trites 2003). In the winter months the proportion of time spent away from the rookery increased (Trites and Porter 2002). It is also possible that

the energetic gain of traveling to protected inland locations to feed outweighs the direct energetic cost of completing the moult on the rookery.

The greatest numbers of juveniles (ages 1-3 y) were observed during early August just before the overall numbers of sea lions declined. Traditionally, counts of pups and non-pups have been made during the pupping period (the end of June, beginning of July) when highest numbers of adult females, pups and bulls are believed to be on shore. Most of these rookery surveys focus on counts of pups and reproductive females, but few juveniles are observed. Numbers of moulting juveniles at the rookery appeared to increase after the peak of pupping. Thus August might be an opportune time to observe juveniles given the central role they are believed to play in the decline of sea lion populations in the Gulf of Alaska and the Aleutian Islands. Condition indices might be developed for juveniles during this time of year to compare among regions during this energetically expensive period of their life cycles.

Potential Biases

A fundamental assumption of this moulting study was that the animals observed on shore represented the population as a whole. While there is no information to suggest otherwise, it could be argued that the focal animals were more likely to haul out and be seen because they were better fed and were in better body condition than other animals. Animals that are more likely to haul out on land may have moulted faster than individuals that were absent, if hauling out on land has some benefit that expedites the moult.

Another factor that could have influenced the timing and progression of the moult was the presence of parasites such as sea lice (*e.g.*, *Proechinophthirus fluctus, Antarctophthirus callorhni*). Sea lice could have confounded the estimated start date for the pup moult because many of the pup rumps (region above the

tail) were bald – likely due to lice. On a bald surface new hair is easy to recognise. Emergent new hairs may be visible on a bald surface up to 2 weeks prior to the shedding of old hair, as was the case for the pups. However, this was not the case for adult females.

A further cautionary note is that the dates of the moult observed at Lowrie Island may not be the same throughout the range of Steller sea lions. The timing of the moult may also vary if it is indirectly affected by the timing of pupping. The timing of pupping has been shown to vary by time and space with the mean earliest pups born 4 Jun on Forrester (Lowrie) and the latest mean pups born 21 Jun at Año Nuevo Island (Pitcher et al. 2001). However, regional differences are likely to be small. Differences in body condition could also vary by region and might influence the moult. If body condition affects the timing of the moult, and animals in the western range are physiologically stressed, as has been hypothesised to occur in this population (Trites and Donnelly 2003), it could result in higher concentrations of glucocorticoids that may also inhibit moulting (Ebling and Hale 1970; John et al. 1987; Mohn 1958). Such changes have been noted in the timing of the moult for harbour seals in the Gulf of Alaska, although reasons for this shift are not known (ADFG, unpublished data).

Optimal Instrument Attachment

Researchers use radio tracking instruments affixed to sea lion fur to examine movement across time and space (two and three dimensional) that might provide insight into behaviour, physiology and foraging ecology. The life of an instrument glued to the fur will theoretically be one year from moult to moult; therefore, it is important to maximise the time the instrument is attached to the fur. The maximal use of an electronic instrument will require an optimal time frame for attachment. The optimal timing to glue electronic instruments to

Steller sea lion fur is a function of the timing and progression of the moult and the time when the greatest numbers for different sex and age classes would be present.

The first factor affecting the optimisation of instrument attachment is the timing and progression of the moult, which should serve as the earliest time for attachment. Instruments have fallen off prematurely in the past due to being glued to old hair before it had completely shed. Instruments should be glued to hair that has reached its maximum length, but this point is difficult to ascertain in the field. In the wild, instruments are typically glued to sea lion fur on the dorsum behind the head and neck. The moult of this area differs for all sex and age classes such that the optimal time to attach electronic instruments also varies by month and year.

Adult females generally completed their moult by the first to second week of October. New hair appeared on the dorsal midline as early as the middle of September. Earliest attachment of instruments to adult females should therefore occur at the end of the first week of October to allow their hair to reach its maximum length. Juveniles can safely be assumed to have completed their moult by the middle of September and this time would be the earliest recommended to affix devices to them, given that their backs moult prior to other areas of the body. Pups are the last to moult and have greater variation in their completion times. The earliest pup moult was completed in the middle of November. However, the presence of a "shawl" moult stage (Figure 2.1) might preclude early attachment of instruments to pups. At best, the end of November to early December is probably the best time to capture and glue devices to pups that are in good health and have finished their moult.

The second factor to consider for optimal instrument attachment is the time when the greatest numbers of individuals for each sex and age class are

available or easily accessible. Knowing when sea lions congregate reduces the time spent looking for more individuals, increasing cost-effectiveness. The time when the largest numbers of animals are concentrated is not the same for each sex and age class and might be at a different time in relation to the moulting period. The largest congregation of females and bulls occurs during the pupping period, before the moult. However some females remain beyond their moult in September to look after their pups. Thus a larger proportion of the remaining females will have completed their moult, and would make instrument attachment more cost efficient.

Numbers of pups remain relatively high on the rookery during the pupping and nursing periods, but numbers of individuals decline as the moult progresses. Pups follow their mothers to haulout sites within during late fall, near the end of their moult, making this an optimal time for access to many individuals that have completed their moult. The numbers of juveniles observed at the rookery were the greatest during the earlier stages of the moult (August), which was not a good time for instrument attachment. Another time period with increased concentrations of juveniles and sub adult sea lions is during the fall and winter months when moulting individuals congregate at inshore haulouts.

There is no single optimal time for all sex and age classes for instrument attachment. Instead, the targeted sex and age class should be first optimised to when all old hair is shed in the targeted body region, then thereafter with the next time they occur in greater concentrations (not necessarily the peak). By focusing on secondary peaks in abundance, there might be a risk of accessing fewer individuals, but this cost is not as great as the probability of having fewer individuals that have completed the moult, curtailing the problem of instruments falling off prematurely.

Future Research – Is the Steller Sea Lion Moult Energetically Expensive?

An area for further study is evaluating the energetic cost of the Steller sea lion moult. This evaluation could be done by examining behavioural adaptations and physiological compensations that deal with the energetic costs associated with the moult as have been observed in other species of pinnipeds. There is evidence of high energetic costs associated with the moult in land mammals (Neuhaus 2000; Perez-Barberia and Nores 1996; Stewart and Macdonald 1997) and possibly amphibious mammals.

Semi-aquatic mammals that have little fat stores, such as beaver and muskrat, prolong their moult to span an entire year, unlike animals of similar ancestry that moult twice a year (Ling 1970). The extended moult is likely due to balance of energy allocated to other events within their seasonal cycle and the direct cost of hair replacement. The timing of the moult for these species contends with other costly events of their seasonal cycle, including mating, implantation and hibernation. In an amphibious species such as the beaver or muskrat a role of the pelage may act greatly towards thermoregulation in air. The role of the pelage in water is less defined (Ling 1970). The timing of the moult for them might be better balanced to span the entire year and maintain the function of thermoregulation rather than be devoted to a brief and energetically costly time period.

Behavioural adaptation in response to mediating effects associated with the moult may explain the need for phocids to haul out on land and for belugas to move to warmer estuaries during the moulting period (Boily 1995). Harbour seals and belugas could moult in cooler water, but would require higher energy input to maintain elevated epidermal temperatures. Physiological adaptation may include altering energy expenditure, as indicated by a change in metabolic rate. Seasonal study of the metabolism in harbour seals found a lowered resting

metabolic rate during the moult, possibly due to lowered activity levels (Rosen and Renouf 1998). The gray seal, for example, can lower its metabolic rate during the moult to compensate for less energy input (Boily 1996).

The northern and southern elephant seal share the same genus but have adapted different energy-saving strategies that incorporate both physiological and behavioural adaptations during the moult (Boyd et al. 1993). The elephant seals may be affected by different geographic and environmental factors. Northern elephant seals living along the California coastline are less active and have lower metabolic rates while moulting compared to southern elephant seals in the Antarctic that have a higher metabolic rate and may need to be more active.

To explore behavioural and physiological adaptations among moulting Steller sea lions, a measure of field metabolic rate would be required in addition to determining activity patterns of known individual sea lions during the moulting period. The body condition of individuals of different sex and age classes could be followed throughout their entire seasonal cycle. For example, the effect of reproduction and lactation on the timing of the moult of adult females would provide further insight on how sea lions balance energetic costs of events within their seasonal cycle. The body condition and metabolic rate of reproducing (females with pups vs. juveniles) and non reproducing females could be followed and compared to see if females nursing pups delay their moult relative to other females.

Another fruitful area for further research is to examine the progression of the moult by measuring surface temperature or heat flux across the Steller sea lion body using thermisters and thermal cameras. If increased temperatures are necessary for mitosis and the production of hair, then the early stages of the moult may be detected non-invasively. A thermal camera might detect these

"hot spots" and could be used to examine the early moult (not seen by eye) in a wild population of sea lions or other moulting pinnipeds.

Additionally, it would be advantageous to document "hot spots" on the body for different sex and age classes, in particular to see if they relate to the different patterns of moult progression observed in Steller sea lions. A pup's ability to thermoregulate may differ from that of an adult, and an interesting study might examine both the progression of "hot spots" and metabolic rate to examine if they are associated with the moult. In most mammalian species, the metabolic rate in juveniles is significantly higher than in adults due to the high cost of body growth (Brody 1945). Both metabolism and heat flux in northern fur seal pups decreased significantly after their moult was completed, likely a result of a more efficient pelage and thicker blubber layer (Donohue et al. 2000). Such physiological changes might also exist in Steller sea lion pups and might influence their moult topography.

Summary

I determined the timing and progression of the moult for wild Steller sea lions (*Eumetopias jubatus*) on Lowrie Island, Alaska. On average, the moult started on 21 Jun for juveniles, 7 Aug for adult females, and on 26 Oct for pups that were born in June. Mean completion dates also differed significantly (19 Sep for juveniles, 26 Oct for adult females and 17 Nov for pups). The mean duration of the moult was similar for adult females (45.7 days) and pups (45.0 days). However, the pattern and progression of hair loss over the body surface differed for 1) pups, 2) juveniles and early moulting adult females, and 3) bulls and later moulting adult females. Differences in the timing and patterns (progression) of the moult might be influenced by body condition and physiological changes associated with age and reproductive state. Numbers of individuals hauled out

does not appear to be influenced by the moult, and may be affected by other aspects of their seasonal cycle that might take precedence over the physiological cost of the moult. The timing and pattern of the moult have implications on research study designs that rely on attaching electronic devices to sea lion fur.

CHAPTER III: TIMING OF MOULT IN CAPTIVE ANIMALS

Introduction

Steller sea lions have been raised at the Vancouver Aquarium Marine Science Centre (Vancouver, BC, Canada) since 1993 to study their nutritional and physiological requirements. Five pups were brought to the Aquarium in 1993, one in 1994, four in 1997, and five in 2000. All animals (except 1) were obtained from the Scott Islands rookery complex (50.12 °N latitude, 128.06 °W longitude) at the northern end of Vancouver Island, British Columbia. Data from captive studies can provide a general baseline comparison for what might be observed in the wild and can help formulate questions and hypotheses for further study. The added benefit of using captive animals is that their physical conditions and nutritional supplements are known, unlike most individuals that might be observed in the wild.

The following presents observations of moulting among captive Steller sea lions held at the Vancouver Aquarium. The data are contrasted with observations from the wild to gain further insight into the mechanisms that might influence the timing and duration of moulting.

Methods

The onset and progression of the moult were documented at the Vancouver Aquarium Marine Science Centre, (Vancouver, BC) since 1993. Animals were monitored for initial signs of new hair during weekly health checks. Subsequently, areas where new hair appeared were shaded on data forms containing two Steller sea lion profiles (one viewed from the side and the other from above – Figure 2.2 composite). Observations were made by researchers who worked with the sea lions on a daily basis and were able to readily detect the onset of moulting.

A total of 56 complete moult records were made on 15 individuals (10 females and 5 males) representing 9 age classes (Appendix 2). A moult record consisted of the moult progression for an individual during one season. For this study, I sorted the 56 records to include only data that encompassed an individual's complete moult (with both start and end dates). In some cases the first date of recorded moult was not the actual start date and those data were omitted.

The duration of the moult was defined as the time from when the first signs of new hair were observed until the last old hair was shed for each individual. I calculated the mean duration of the moult for completed moult records across all ages and years. I made comparisons between age classes and years using standard two sample t-tests.

I investigated the progression of the moult for captive Steller sea lions for the year 2001 with analysis methodology similar to that applied to wild animals (Chapter 2). Detailed records with shorter intervals between observations were kept for animals in 2001 compared to other years. Only these data were used for determining the progression of the captive moult. I assigned moult stage for each body area as in Chapter 1 (Figure 2.2).

Results

A total of 33 moulting records were used in the analyses that had a complete start- and end-moult time. These records represented 14 individuals (9 females and 5 males) and 7 age classes (one individual was omitted due to incomplete records. Duration of moult differed among years and within age classes (Table 3.1), with a mean duration of 83.5 days (4.6, SE) for all combined years and ages. Mean moult duration was 82.1 (4.9 SE) days for females (n=20) and 85.7 (9.1 SE) days for males (n=13, Table 3.1).

Duration of the moult differed among years (Table 3.2). Before 2000 (n=15) the average moult duration was 64.9 (3.5 SE) days, while in 2000 (n=9) the average moult duration increased to 93.3 (7.8 SE) days. Moult duration increased again in 2001 (n=9) to 104.7 (8.2 SE) days. Duration also differed by age class (Figure 3.1). In 2001, the mean duration was 85.6 (4.9 SE) days for animals under age 3 y (n=5), and was 128.5 (5.1 SE) days for those animals 3+ y (n=4, Table 3.2).

Table 3.1. Summary statistics for the mean duration of moulting (in number of days) for captive animals at the Vancouver Aquarium, 1993 – 2001.

	Mean	SE	n	Variance	SD
all animals all years	83.5	4.6	33	685.1	26.2
age 0 (all years)	79.4	5.6	11	348.1	18.7
ages 1&2 (all years)	72.7	5.5	11	330.4	18.2
ages 3+ (all years)	98.5	10.1	11	1121.3	33.5
female (all years)	82.1	4.9	20	469.9	21.7
male (all years)	85.7	9.1	13	1074.4	32.8

Table 3.2 Mean duration of moulting (in number of days) for captive animals at the Vancouver Aquarium, 2000 – 2001.

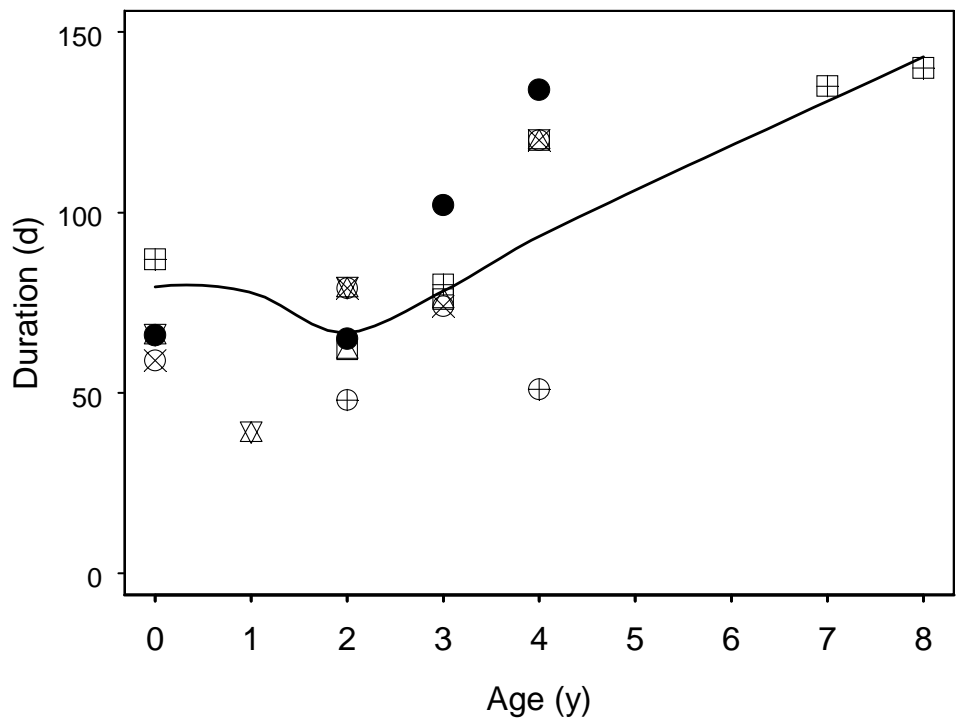|	Mean	SE	n	Variance	SD
year 2001 (all ages)	104.7	8.2	9	608.8	24.7
year 2000 (all ages)	93.3	7.8	9	550.0	23.5
before 2000 (all ages)	64.9	3.5	15	184.2	13.6
ages 3+ in 2001	128.5	5.1	4	102.3	10.1
ages1&2 (year 2001)	85.6	4.9	5	118.3	10.9

Figure 3.1. Moult duration (in number of days) by age of captive Steller sea lions. Symbols represent 6 individual animals. Loess fitted curve.

Animals under the age of 3+ y were all pups (n=5) in 2000 and became yearlings in 2001 (Table 3.3). The mean start date of moulting for this cohort was 24 Aug (4.2 SE) in 2000, and 5 Aug (2.0 SE) the following year. Mean end dates were 22 Nov (11.0 SE) for the pups in 2000 and 29 Oct (6.1 SE) for the yearlings in 2001. In contrast, the mean start date for sea lions aged 3+ y (n=4) was 28 Jul (21.8 SE) in 2000 and 7 Aug (3.4 SE) in 2001; while their respective mean end dates were 2 Nov (34.9 SE) in 2000 and 14 Dec (8.1 SE) in 2001 (Table 3.3).

Moult progression varied more among the captive Steller sea lions than in the wild. Generally, animals began moulting on their rumps, followed by the foreflipper/shoulder region and the neck. New hair then appeared on the head, followed by the ventrum and finally the sides and dorsum. While there was some variability to this progression, the area that seemed to finish moulting the fastest appeared to be the ventral region, which went quickly from no new hair being present to being completely moulted prior to other areas moulting.

Table 3.3. Mean date that moulting started and ended for captive Steller sea lions by age class in consecutive years, 2000 and 2001.

		Mean	SE	t	df	P
Start	Pups 2000	24-Aug-00	4.2	-74.31	6	<0.001
	yearlings 2001	5-Aug-01	2.0			
	age 3+ 2000	28-Jul-00	21.8	-16.99	3	<0.001
	age 3+ 2001	7-Aug-01	3.4			
End	Pups 2000	22-Nov-00	11.0	-27.05	6	<0.001
	yearlings 2001	29-Oct-01	6.1			
	age 3+ 2000	2-Nov-00	34.9	-11.36	3	<0.001
	age 3+ 2001	14-Dec-01	8.1			

Discussion

The duration of moult for captive Steller sea lions for all years combined was 83.5 days. Before 2000, mean moult duration was 64.9 days, while after 2000 mean moult duration was 93.3 days. The moult duration for captive animals was significantly longer than the moult duration observed in the wild animals. Why the two groups of animals should differ is not obvious. One possibility is that it reflects observational error. However, a more likely explanation is that the moult of captive animals was affected by the conditions of captivity (*e.g.*, water quality, food, temperatures, etc.).

Captive Moult Duration

It is not clear why the timing of moult differed so much across years in captive animals. One possibility is that more attention was given to moult start dates in 2000 and 2001 due to the simultaneous wild study counterpart (Chapter 2). The majority of the records removed from the analyses were from the first years of observations and the quality of observations also increased with time, with more detailed sketches in the later years. The increase in quality could also be due to increased recognition of the moult. Earlier years of observations often had questions associated with them, suggesting that the observers were not as familiar with differentiating old and new hair. Differentiation between old and new hair is easily made when the pelage is uniformly wet or dry, but is difficult if wet and dry hair are interspersed. Observations made in later years were taken after animals were hosed with water and the pelage was uniform in colour and texture. It is also possible that the onset of the first moulting animals was overlooked in past years, since the moult start date is the same for all animals, while the degree of the moult progression differs among individuals for the first

moult date indicated on the data sheets (*i.e.* some animals are more advanced in the amount of new hair present than others).

While the difference in the moult duration might be partially explained by the increased attention to detail by observers, it seems to be too great an increase to be explained by observational error alone. Another possibility is that a change in latitude might result in a difference in photoperiod exposure and may have influenced the timing of moulting in captivity. Breeding aggregations of Steller sea lions exhibit synchronous pupping, but the start of pupping varies between sites (Pitcher et al. 2001). Relative to the Forrester Island breeding complex, animals located both north and south are born later. The apparent cline in timing of pupping might be mirrored by a similar cline in the timing of moult. If so, animals taken from south of Forrester at the Scott Islands and brought further south to Vancouver might be expected to begin moulting later than those observed at Forrester. There may also be some effect on hormones that altered timing of moult during their first year in captivity in Vancouver. All told, these factors should have resulted in the captive animals moulting later than their wild counterparts on Lowrie Island, which was not the case.

Wild and Captive Moult Duration Comparison

I found that the durations of moult for both pups and adult females were similar in the wild. However, their timing differed from that observed in captivity. In studies of other captive pinnipeds, moult duration and timing has deviated greatly from what is expected in the wild, albeit all based on small sample sizes. Harbour seal moult durations (Ashwell-Erickson et al. 1986) were longer (by two to three times) in captivity than what has been observed in the wild (ADFG, Tugidak Island unpublished data). Similarly, captive gray seals started moulting 2 months earlier than their wild counterparts (Boily 1996).

A likely explanation that may account for the disparity in the moult durations of captive and wild pinnipeds may be related to differing environmental conditions and the physiological effects of captivity. Something as simple as a difference in diet could affect the timing of moult. In the Gulf of Alaska for example, ecosystem changes altered the diet of harbour seals, which in turn affected the timing of reproductive events, such as the timing of pupping (Jemison 1997). Dietary shifts had further cascading effects on other aspects of the harbour seal life cycle, including the moulting period (Daniel et al. 2003). Differences in diet between captive and wild sea lions may therefore explain some of the differences in moulting times or durations.

A second possible explanation is that the different physical conditions of the wild and captive Steller sea lion environments (*e.g.*, temperature, water pH, salinity) influenced the timing of moult through basic physiological processes. Chlorinated water may affect the hair of the animals, and has been shown to negatively affect the epidermis of bottlenose dolphins (Harrison and Thurley 1974).

Nutritional supplements and changes in activity levels may also have affected the sea lion moult, as could reproductive status. Preventing sea lions from conceiving could feasibly trigger the production of prolactin or some other potential moult mechanism. The physiological response to not reproducing is an interesting possibility given that the moult durations of sea lions in the 3+ y classes were slightly longer than those of younger animals over the same years. The animals in the captive study aged 3+ y were not reproducing and were not going through changes similar to their wild counterparts.

In general, the moult duration for captive animals decreased until age 3, then increased until age 8 (Figure 3.1). The change in the moult duration in the captive animals contrasts with observations from the wild with no difference in

the moult duration of pups and adult females (Chapter 2). Differences in nutritional intake and energy expenditures seem to be the most likely explanation for these observed differences.

Summary

Moult duration was determined for captive Steller sea lions and contrasted to the moult duration found in wild animals. The mean moult duration for all captive animals was 83.5 days with all combined years and ages (n=33). Mean moult duration did not significantly differ between males and females. Differences were found by age class and by year. Before 2000 the average moult duration was 64.9 days, which increased significantly to 93.3 days in 2000 and 104.7 days in 2001. The increase may not be attributed to an increase in age alone, as the pups of the year also had longer moult durations. In 2001, the mean duration was 85.6 days for animals under age 3 y, and was 128.5 days for those animals 3+ y. These results differ significantly from the mean moult durations of wild Steller sea lions in Southeast Alaska. Possible explanations for the difference in moult duration between wild and captive animals might be directly related to the physical characteristics of their environments. Animals in captivity might also extend their moult because they do not have the same reproductive events that might regulate hormonal changes, changes that affect events such as the moult.

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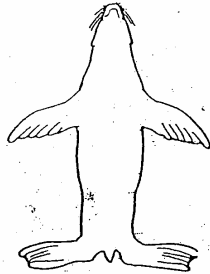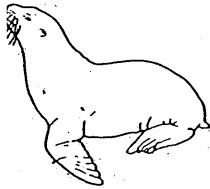Young, J.Z. 1957. Life of Mammals. Clarendon Press, Oxford.

APPENDIX

Appendix 1. Data forms for Steller sea lion moulting study (Chapter 2).

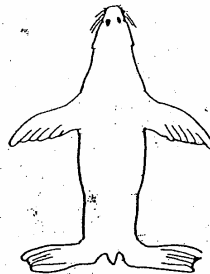STELLER SEA LION MOULTING DATA FORM (PUP)
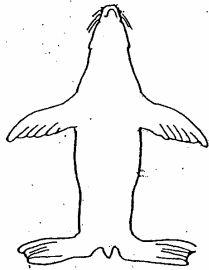
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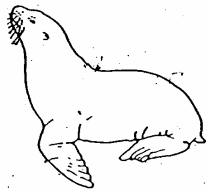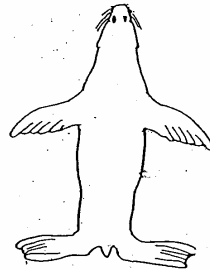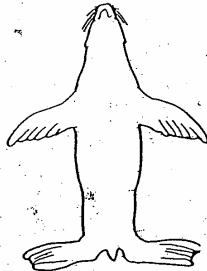
Comments

ventrum (v)   dorsum (d)

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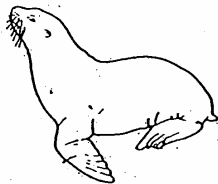
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Appendix 2. Captive moult observations used in Chapter 3.

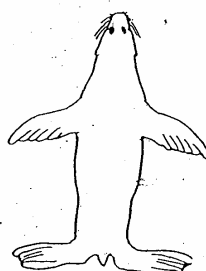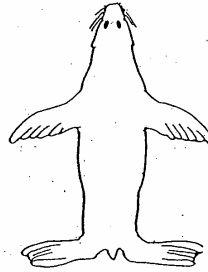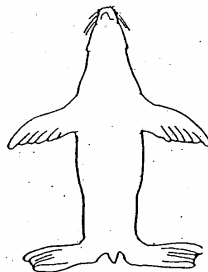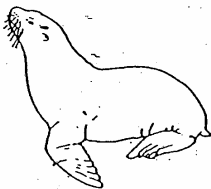| Sea lion	Year	Age (years)	Sex	Start Moult	End Moult	Duration (days)	Duration (weeks)
Adak	1993	0	m	5-Nov-93	14-Jan-94	70	10.0
Adak	1994	1	m				
Adak	1995	2	m		20-Nov-95		
Adak	1996	3	m		22-Oct-96		
Boni	2000	0	f	31-Aug-00	27-Dec-00	118	16.9
Boni	2001	1	f	10-Aug-01	2-Nov-01	84	12.0
Eden	2000	0	f	15-Aug-00	26-Oct-00	72	10.3
Eden	2001	1	f	2-Aug-01	11-Oct-01	70	10.0
Hazy	1997	0	f		28-Nov-97		
Hazy	1998	1	f	14-Aug-98	22-Sep-98	39	5.6
Hazy	1999	2	f	16-Jul-99	16-Sep-99	62	8.9
Hazy	2000	3	f	9-Jul-00	23-Sep-00	76	10.9
Hazy	2001	4	f	2-Aug-01	30-Nov-01	120	17.1
Kiska	1993	0	f	13-Oct-93	24-Dec-93	72	10.3
Kiska	1995	2	f		24-Oct-95		
Kiska	1996	3	f		15-Oct-96		
Kiska	1997	4	f		1-Nov-97		
Kodiak	1997	0	m	7-Oct-97	12-Dec-97	66	9.4
Kodiak	1998	1	m	4-Sep-98			
Kodiak	1999	2	m	29-Jun-99	2-Sep-99	65	9.3
Kodiak	2000	3	m	3-Jul-00	13-Oct-00	102	14.6
Kodiak	2001	4	m	16-Aug-01	28-Dec-01	134	19.1
Nuka	2000	0	f	21-Aug-00	8-Dec-00	109	15.6
Nuka	2001	1	f	10-Aug-01	17-Nov-01	99	14.1
Sade	1994	0	f				
Sade	1995	1	f		20-Nov-95		
Sade	1996	2	f		7-Oct-96		
Sitka	1997	0	f	7-Oct-97	5-Dec-97	59	8.4
Sitka	1998	1	f		15-Sep-98		
Sitka	1999	2	f	29-Jun-99	16-Sep-99	79	11.3
Sitka	2000	3	f	9-Jul-00	21-Sep-00	74	10.6
Sitka	2001	4	f	2-Aug-01	30-Nov-01	120	17.1
Sugar	1993	0	f		11-Nov-93		

Sea lion	Year	Age (years)	Sex	Start Moult	End Moult	Duration (days)	Duration (weeks)
Sugar	1995	2	f	3-Oct-95	20-Nov-95	48	6.9
Sugar	1996	3	f		7-Oct-96		
Sugar	1997	4	f	11-Sep-97	1-Nov-97	51	7.3
Tag	1993	0	m	5-Nov-93	31-Jan-94	87	12.4
Tag	1994	1	m				
Tag	1995	2	m		20-Nov-95		
Tag	1996	3	m	6-Sep-96	25-Nov-96	80	11.4
Tag	1997	4	m	8-Sep-97			
Tag	1998	5	m				
Tag	2000	7	m	2-Oct-00	14-Feb-01	135	19.3
Tag	2001	8	m	10-Aug-01	28-Dec-01	140	20.0
Tasu	2000	0	f	6-Sep-00	16-Nov-00	71	10.1
Tasu	2001	1	f	2-Aug-01	2-Nov-01	92	13.1
Timber	1997	0	m	7-Oct-97	12-Dec-97	66	9.4
Timber	1998	1	m	14-Aug-98	22-Sep-98	39	5.6
Timber	1999	2	m	29-Jun-99	16-Sep-99	79	11.3
Woody	1993	0	m				
Woody	1994	1	m	23-Sep-94			
Woody	1995	2	m		1-Nov-95		
Woody	1996	3	m				
Woody	1997	4	m	11-Sep-97	1-Nov-97	51	7.3
Yasha	2000	0	f	17-Aug-00	8-Nov-00	83	11.9
Yasha	2001	1	f	2-Aug-01	24-Oct-01	83	11.9