

**HUMAN DISTURBANCE
AND THE HAULING OUT BEHAVIOUR
OF STELLER SEA LIONS (*Eumetopias jubatus*)**

by

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Abstract

There is considerable interest in assessing and mitigating disruptive effects of humans on the behaviour of marine mammals, especially for species with uncertain or decreasing population trends. Steller sea lions (*Eumetopias jubatus*) have been under intensive study throughout their range over the past few decades in an attempt to identify the causes of a large population decline in the Gulf of Alaska and Aleutian Islands. Consequently, disturbance due to scientific research has also increased at rookeries and haulouts.

The purpose of my study was to determine if there were measurable short-term effects of human disturbance on the numbers of Steller sea lions using terrestrial sites. Numbers and composition of sea lions were documented for 2 – 3 week periods in southeast Alaska and British Columbia during summer (n = 8 sites) and winter / spring (n = 6 sites). They revealed considerable daily variation in numbers of sea lions hauled out within and among study sites that was related in part to prevailing environmental conditions. However, counts could not be corrected to account for environmental influences on the total numbers of sea lions using haulouts.

Hauling out trends were examined for pre- and post-disturbance periods across multiple sites over two seasons. Predetermined research disturbances occurred to collect scats at the haulouts, and to brand pups at the rookery. Three methods were explored to assess local population recovery that addressed both quantitative and temporal aspects of sea lions returning to the study locations. Disturbances resulted in significantly fewer sea lions using haulouts during the post-disturbance period. Variation in the numbers of animals using the haulouts increased following the disturbance, but rates of change in daily numbers did not differ significantly between periods. Six of ten disturbed sites reached full recovery (100% of the pre-disturbance mean) on average 4.3 days after the research disturbance.

To determine if individual behaviour was affected by disturbance, sea lions arriving on shore were followed to determine normal patterns of interactions and behaviour. Significant differences were noted in hauling out behaviour between animals that remained on land and those that returned to the water. Sea lions that returned to the water exhibited higher rates of behaviour and interactions with other animals during the week that followed the disturbance. Seasonal differences were also noted in the rates of behaviour and interactions

that may be indicative of certain times of the year when sea lions are more sensitive to human presence and disturbance.

Increasing levels of human–sea lion contact are expected as more and more people visit the remote coastal habitat of Steller sea lions. Future studies are needed to assess the influence of disturbance on sea lion redistribution within a critical recovery period, as well as to determine the physiological effects that sea lions experience with repeated human disturbance. Disturbance studies are an important aspect of conservation initiatives because they can help guide policies and establish restrictions to protect wild populations from human intrusion.

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This has been a dream of a project, taking me to remote, beautifully lush but not-so-tropical islands, and day after day, allowing me to watch such extraordinary animals on their own terms, in their own environment.

Chapter 1:

General Introduction: Human disturbance and the hauling out behaviour of Steller sea lions

Wildlife populations are affected to varying degrees by human disturbance (Allen *et al.*, 1984; Lewis, 1987; Andersen *et al.*, 1996; Fowler, 1999; Verhulst *et al.*, 2001; Frid, 2003). Ranging from behavioural modifications to physiological stress responses, an animal's resting, feeding and breeding patterns may all be affected by human presence (Suryan and Harvey, 1999; Gill *et al.*, 2001). Activity and development in remote areas has increased considerably in recent years raising concern about potential effects on animal populations.

Since the late 1970's, research on Steller sea lions (*Eumetopias jubatus*) has focused on a range of physiological, environmental and ecological factors to determine causes of an 85% population decline (Merrick *et al.*, 1987; Trites and Larkin, 1996). Some of this research has resulted in repeated disturbance of sea lion haulouts and rookeries. The skittish nature of Steller sea lions usually results in entire colonies being disrupted when researchers go on shore to capture animals or to collect scats for dietary analyses. This raises behavioural and physiological concerns for populations experiencing repeated or high levels of human disturbance.

Various methodologies used to evaluate the effects of disturbance on other species have often revealed species-specific responses (e.g., Salter, 1979; Born *et al.*, 1999; Suryan and Harvey, 1999; Engelhard *et al.*, 2002; Orsini, 2004). Anecdotal reports and limited knowledge of the effects of human disturbance on Steller sea lions necessitated a systematic approach to measuring sea lion response to disturbance. Understanding when and how animals use the environment is important for population conservation efforts (Reder *et al.*, 2003), and determining response to research activities and subsequent recovery is an important step in determining the vulnerability of sea lions to disturbance.

There are two main components in assessing response to disturbance. The first involves determining whether human presence causes animals to avoid disturbed areas, and the second requires long-term assessment of the physiological and distributional parameters of disturbed populations (Gill *et al.*, 1996). Due to the lack of experimental data concerning Steller sea lion response to disturbance (see Lewis, 1987 for an assessment of a rookery disturbance), I chose

to address the first aspect by determining recovery (return of animals following human presence on the haulout) at haulouts and one rookery in an attempt to provide baseline data concerning the numbers of Steller sea lions that use haulouts following research activities.

Ongoing long-term dietary studies of Steller sea lions using haulouts in southeast Alaska and British Columbia provided dates and locations of planned scat collection events. Knowing when researchers would be on shore collecting fecal samples provided a controlled disturbance, allowing me to experimentally measure the short-term effects of research activities on Steller sea lions by performing observations before, during and after scat collection. Observations were conducted at multiple locations with replicated sites in summer and winter / spring. Two control sites were included that were close to haulouts experiencing a research disturbance.

The numbers of animals on land before the disturbance were compared to assess normal or baseline haulout use, and then examined for changes occurring as a result of the research disturbance. I addressed recovery both in terms of percentage of animals that returned following human presence on the haulout, and the time it took for sea lions to return in relation to hauling out trends. I also examined the daily variability in sea lion haulout use to more fully understand the factors affecting the numbers of sea lions on shore such as tidal height, time of day and the tidal stage (high tide, low tide). Such observations not only contribute to understanding the effects of disturbance on sea lion numbers, but they also have important implications in the interpretation of population surveys.

The difference between the effects of disturbance on haulout populations (numbers of animals on shore) and individual sea lions (behaviour) is an important distinction. The first involved frequent counts to document recovery and determine if there were changes in numbers of animals on shore before and after the research disturbance. The second involved assessing individual behavioural changes by recording behaviours and interactions of sea lions that had just hauled out of the water. Pre- and post-disturbance behavioural follows of animals were compared to determine if research activities affected individual hauling out behaviour. Applying both methodologies provides greater insight into the effects that researchers have on the numbers of Steller sea lions using haulouts following human disturbance as well as the daily variability within and among sites. Documenting recovery rates may help to guide the issuing of research permits when considering the frequency of proposed fieldwork.

Overview

The goals of my thesis were to determine the factors that influence the numbers of sea lions on shore, and the short-term effects of human disturbance on the hauling out numbers and behaviour of Steller sea lions during summer and winter / spring.

My thesis has three principal chapters. Chapter 2 examines the influence of environmental and anthropogenic factors on the hourly and daily variability in numbers of sea lions hauled out at eight sites in southeast Alaska and British Columbia in summer and winter / spring. Chapter 3 considers the short-term effects of human disturbance on the numbers of Steller sea lions on land, and addresses three measures of local population recovery. Finally, Chapter 4 addresses the effects of season and disturbance on individual sea lion hauling out behaviour, specifically examining the likelihood of an animal remaining on land after hauling out, as well as subsequent behaviours and interactions with other animals.

Chapters 2, 3 and 4 were written as independent manuscripts, and contain some redundancies because they were based on the same set of behavioural observations and counts of Steller sea lions made at multiple sites over two seasons.

Field research was performed under Federal Marine Mammal permits: 358-1564 and 715-1457; and University of British Columbia Animal Care certificate: Category B, Protocol Number A02-0190.

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Chapter 2:

Single census counts may not accurately reflect numbers and trends of Steller sea lions using haulout sites

Summary

Accurate estimates of pinniped population size are needed to properly monitor and manage seals and sea lions. Most pinniped populations are counted from aerial photos taken at a single point in time. Aerial censuses of pinnipeds are usually scheduled to ensure peak numbers on land and can sometimes be corrected for tidal effects, time of day and other environmental conditions. I sought to evaluate the reliability of single counts of Steller sea lions (*Eumetopias jubatus*) made at haulouts and at a single rookery. Numbers of Steller sea lions were counted at 20-minute intervals during summer (n = 7 sites) and winter / spring (n = 6 sites) in southeast Alaska and British Columbia. Maximum generalized linear models showed that tidal height, time of day, tidal stage (high tide, low tide), season and location affected sea lion haulout numbers. However, daily and seasonal hauling out patterns appeared to be site-specific for all sets of observations. Numbers of sea lions on shore varied considerably among hours on any given day, such that there was the potential to miss as many as 49% (mean; range 20 – 86%) of the sea lions that used a haulout on any given day. Coefficients of variation for hourly counts of sea lions ranged from 16 – 48% for individual haulouts (average CV = 32%), and was much lower at the one rookery that I examined (CV = 9%). Single counts of sea lions using haulouts were highly variable and could not be corrected for environmental influences on hauling out behaviour using a single correction factor. Consideration should be given to developing site-specific correction factors that address the variety of environmental factors that affect the numbers of sea lions on land. In general, rookery counts have less variability than haulout counts and are likely to yield better indices of sea lion population sizes and trends.

Introduction

Most seals and sea lions haul out onto land or ice to rest between feeding trips, or to give birth, mate and engage in social interactions (Salter, 1979; Calambokidis *et al.*, 1987; Watts, 1996; Reder *et al.*, 2003; Orsini, 2004). Predator avoidance as well as thermoregulation may also play an important role in determining when and for how long individual animals remain out of

water (Daniel, 2003; Fernández-Juricic and Schroeder, 2003). Haulouts consist of groups of individuals that may vary by age and sex classes among locations. Overall, seals and sea lions tend to use traditional sites that are free of predators and presumably close to areas of optimum feeding.

Steller sea lions (*Eumetopias jubatus*) are quite gregarious and generally haul out of the water in large groups on rocky offshore islands along the North Pacific rim (Loughlin, 2002). Numbers of animals using any given haulout can range from fewer than fifty, to thousands of individuals. They do not migrate, but exhibit seasonal movements between breeding (rookeries) and non-breeding (haulouts) sites (Sease and York, 2003). Haulout and rookery locations are well documented, and in some cases are known to have been consistently used for centuries (Sease and Gudmundson, 2002, Ban, 2005). Adult males defend territories at rookeries during late spring / early summer (May – June) where females give birth to pups, and mating occurs. The breeding population disperses during late summer / early fall (August – November) to join the rest of the population at haulouts for the remainder of the year.

The criteria used by Steller sea lions to select terrestrial sites may be influenced by environmental or behavioural factors, or by prey availability around haulouts (Ban, 2005; Call and Loughlin, 2005). Environmental factors such as tidal heights and tidal stage, time of day, season, distance to the nearest alternative haulout, weather, risk of predation and available space on the haulout might affect a sea lion's decision to haul out (Kastelein and Weltz, 1991; Grellier *et al.*, 1996; Porter, 1997; Moulton *et al.*, 2002; Reder *et al.*, 2003). Similarly, the age and sex of a sea lion may dictate behavioural needs to haul out during certain times of the year to moult, nurse or reproduce (Bengston and Cameron, 2004). Numbers of animals hauling out at any given location might also reflect daily or seasonal movements or seasonal behavioural variation (Thompson, 1989).

Numbers of Steller sea lions that haul out vary daily and seasonally (Calkins *et al.*, 1999) however, this variation has yet to be quantified. Understanding the factors that affect numbers of sea lions that haul out could improve the precision of population estimates and trends, which are essential components of conservation plans and provide a basis for management decisions.

Current estimates of the Steller sea lion population are based largely on aerial surveys. Aircraft are flown over traditional sea lion rookeries and haulout sites at an approximate altitude of 150 – 200 m. Each site is surveyed with overlapping photographs (80 – 200 mm

zoom lenses) at 100 – 150 knots air speed. Once the surveys are completed, magnified images are projected and independent replicate counts of sea lions are made (Sease and Gudmundson, 2002).

Aerial survey analyses currently employ correction factors to estimate the total populations size (Trites and Larkin, 1996; Sease and Gudmundson, 2002). The correction factors address the proportion of animals that may be away from the haulouts and rookeries at the time of the census, as well as account for the proportion of animals that may not be visible to the surveyor due to visibility or site topography (Sease and Gudmundson, 2002). Pinniped surveys are typically flown between 1000 and 1600 h in an attempt to photograph peak numbers of animals on land. However, hauling out patterns may vary significantly among species. For example, harbour seals (*Phoca vitulina*) tend to be tidally restricted with peak numbers generally occurring at low tides (Henry and Hammill, 2001; Reeder *et al.*, 2003). Steller sea lion pups are also predictably found on land during their first few weeks of life, offering a temporal window of obligate haulout use. Such predictability in hauling out patterns reduces the error in estimating the true numbers of pinnipeds using any particular site. However, not all species or age groups may use terrestrial sites in such a predictable manner.

In this Chapter, I examine the influence of environmental and anthropogenic factors on the hourly and daily variation in numbers of Steller sea lions at haulout sites in southeast Alaska and British Columbia during summer and winter / spring. The study was conducted at one rookery and seven haulout sites, and yielded results that have bearing on the interpretation of census data used to assess the status of Steller sea lions throughout their range.

Methods

Data collection

Study sites were chosen for accessibility, ease of observing sea lions without detection, and suitability for camping within hiking distance to the sea lions. Final selection of sites involved consultation with the National Marine Fisheries Service, the Alaska Department of Fish and Game, Fisheries and Oceans Canada, Glacier Bay National Park and Pacific Rim National Park Reserve. Sea lions at all study sites formed part of the eastern genetic stock of Steller sea lions (Bickham *et al.*, 1996).

Counts of Steller sea lions on shore were conducted for 2 – 3 weeks at one rookery and six haulouts between May and August of 2003. Five of the haulouts were revisited between February and April of 2004 to repeat the observations, while the breeding site was replaced with a year round haulout (Fig. 2.1). The sites were typically exposed rocky outcrops and shores with steep intertidal areas. Systematic counts were made at 20-minute intervals, 12 hours a day during summer (0800 – 2000), and during daylight hours during winter and spring (range 7 – 12 hours per day). Sea lions were observed from fixed location blinds with the aid of binoculars and spotting scopes to avoid detection. Sea lions were classified by age and sex class (pup, juvenile, female, subadult male and adult male). Age and sex class percentages were arcsine transformed and differences in composition among non-breeding haulouts were evaluated with Chi-square tests for proportional data (Zar, 1996). An F-test was used to determine differences in variance in numbers of sea lions on land (coefficients of variation) among islands.

My study was part of a larger study designed to determine the effects of human disturbance on Steller sea lions (see Chapter 3). Hence, a predetermined disturbance occurred halfway through the observation period at each site to collect fecal samples for dietary analysis (except at Lowrie Island, where pup branding occurred). These disturbances were included as factors in the analyses of hauling out patterns. Scats were not collected at one site in the summer of 2003 (Carmanah 2, control) and at two sites during the 2004 winter / spring field season (Carmanah Point and SW Brothers Island where significant disturbances were respectively caused by a vessel approach followed by human-sea lion contact, and by eagles feeding on a dead sea lion, which both led to sporadic use of the haulout by the sea lions).

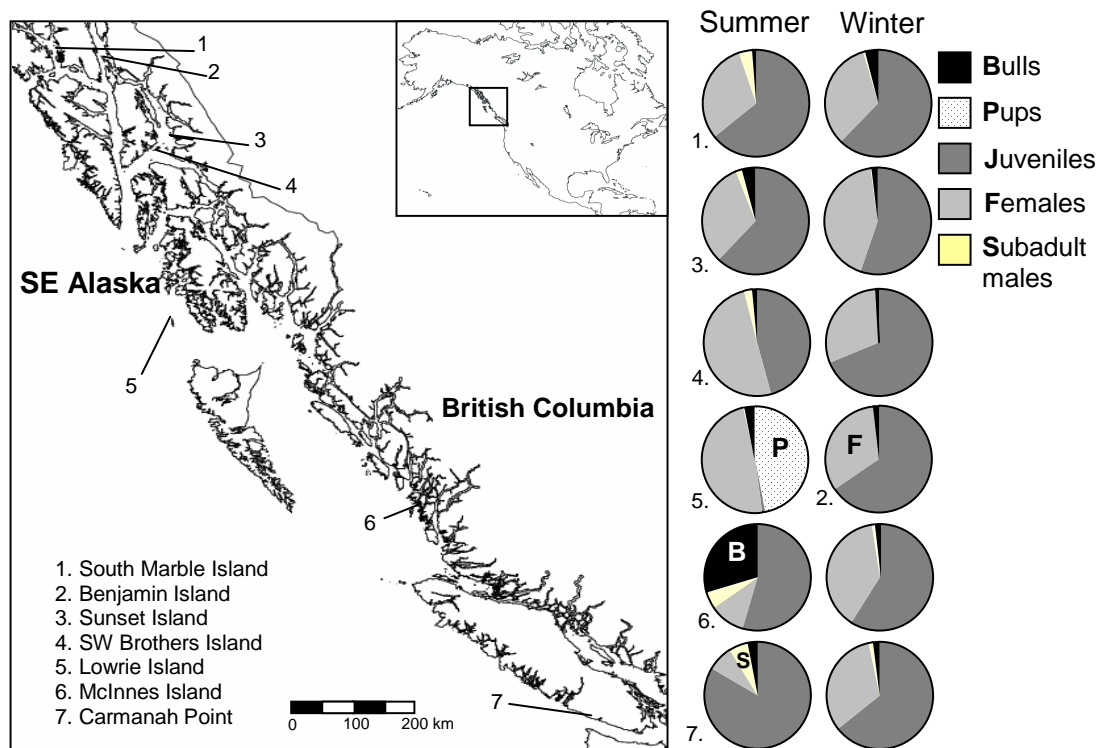


Figure 2.1. Study site locations and proportional age and sex composition of six Steller sea lion haulouts and one rookery (#5). All islands were visited between May – August 2003 and again between February – April 2004 except for Lowrie Island, which was replaced by Benjamin Island, AK in 2004. South Marble (Jun 14 – Jul 8, Feb 22 – Mar 9), Benjamin (Mar 17 – Mar 31), Sunset (May 18 – Jun 5, Feb 23 – Mar 9), SW Brothers (May 18 – Jun 5, Mar 16 – Mar 31) and Lowrie (Jun 15 – Jul 8) Islands are located in southeast Alaska, USA. McInnes Island (Jul 13 – Jul 24, Apr 7 – Apr 22) and Carmanah Point (Jul 30 – Aug 14, Apr 7 – Apr 22) are located in British Columbia, Canada.

Generalized linear models

Following analyses of population trends by Calkins *et al.* (1999) and Small *et al.* (2003), a maximum likelihood generalized linear model (S-Plus 6.2) was used to address multivariate influences of environmental and anthropogenic factors on the numbers of sea lions hauled out. This model contained an overdispersion parameter allowing for non-normal Poisson distributed data to be examined in relation to tidal height, time of day, tidal stage (high tide, low tide), the research disturbance and interactions between these variables.

Tidal stage was included in the model as a quadratic term to account for the non-linear aspect of fluctuating tidal levels. Low tide was given an integer value of 0, with subsequent changes in tide height assigned values of 1 (20 minutes before and after low tide), 2 (40 minutes before and after low tide), 3, 4, 5, etc. Quadratic tidal values were then calculated as 1, 4, 9, 16, 25, etc. Two tide variables were included in the model to measure potentially different aspects of the influence of tides on the numbers of sea lions hauled out. Tidal height directly affects the available space for animals to haulout, whereas daily variation in the height of low tide can have substantially different effects on the amount of available haulout substrate, even at the same tidal stage (i.e., low tide) (Small *et al.*, 2003). Interactions between the above variables assessed relationships between terms and were included to rule out any underlying correlation between variables.

The generalized linear model was applied to each study location and season in keeping with the methodology employed by Calkins *et al.* (1999), who estimated population trajectories for separate sites under the assumption that the trajectories differed among sites. I wanted to identify differences in covariate influence on the response variable. I therefore employed stepwise deletion and Akaike's Information Criterion (AIC) to determine the best model fit for each site, with the expectation that different combinations of covariates would be retained in the various models due to physical and locational differences in haulout sites. Main effects were not considered for elimination from the final model if they were included in a significant interaction term. As has been done in other analyses of population trends (Calkins *et al.*, 1999; Moulton *et al.*, 2002; Small *et al.*, 2003) the Chi-square goodness-of-fit test was used to assess the significance of observed differences in numbers of sea lions hauled out with each model term, and results were considered statistically significant based on $\alpha = 0.05$. Residuals were examined for correlations that might have influenced significance levels.

Results

Differences among study locations included the average number of animals hauled out, age and sex composition and the influence of environmental variables on the hauling out behaviour of the sea lion communities.

Numbers and variation of sea lions on land

There was a large range in the mean numbers of animals observed hauled out among study sites (e.g., 18 ± 0.69 SE at McInnes Island and 447 ± 1.66 at Lowrie Island before disturbances occurred). This wide range in numbers hauled out made it difficult to compare locations with regards to the strength or influence of various factors on the number of animals hauled out. Coefficients of variation (CV, used as a relative measure of variability in the number of sea lions hauling out each day) were significantly different among islands before and after research activities (CV, $F_9 = 0.314$, $p < 0.001$); (CV range 9.36% - 48.20% before and 19.05% - 85.82% after the research disturbance, excluding Carmanah Point where the post-disturbance CV exceeded 100%). Both time periods were examined separately to rule out potential variance due to disturbance.

Using daily midday counts from the days that preceded the research disturbance resulted in a CV of 35.29% over an average of 9 days, compared to a CV of 29.90% when hourly variation in numbers was accounted for (Table 2.1). Thus, the CV associated with midday counts differed by 18.03% (relative difference) when compared to counts made throughout the day (*absolute difference* 5.39% / *hourly variation* 29.90% * 100). Numbers of sea lions observed varied by an average of 49% between minimum and maximum counts (all sites and days combined) (Table 2.2). Maximum differences in numbers of sea lions ranged from 20% at Lowrie Island (breeding site) to 86% at McInnes Island during summer.

Age / sex composition

Age and sex classes of sea lions differed significantly among study sites during the summer months ($\chi^2_6 = 478.7$ for juveniles, 142.6 for females, 37.8 for subadult males, 51.7 for adult males, $p < 0.001$) (Fig. 2.1). However, only the proportion of juveniles differed significantly among islands during winter / spring ($\chi^2_5 = 45.10$, $p < 0.001$). Adult female, subadult male and adult male proportions were not significantly different among islands during the winter / spring months (χ^2_5 , $p > 0.05$).

Table 2.1. Coefficients of variation for all count data and midday counts. The estimated variation between midday counts resulted in an absolute difference of 5.39% and relative difference of 18.03% ($5.39/29.90 * 100 = 18.03\%$) if single counts were used instead of multiple counts per day. Only data from days preceding the research disturbance were included to calculate these coefficients of variation to exclude variation due to human disturbance. Numbers of counts are shown in parentheses.

Season	Location	Coefficient of variation	
		All counts	Midday counts
Summer 2003	Sunset	35.43 (n = 281)	27.81 (n = 8)
	Brothers	28.52 (304)	31.06 (8)
	Lowrie	9.36 (633)	9.29 (17)
	South Marble	28.47 (694)	42.60 (19)
	McInnes	48.20 (157)	74.08 (5)
	Carmanah Point	37.13 (320)	54.35 (11)
	Carmanah 2	27.53 (193)	25.89 (6)
Winter / Spring 2004	Sunset	43.93 (169)	38.46 (7)
	Benjamin	30.55 (205)	47.26 (7)
	South Marble	16.01 (189)	16.54 (8)
	McInnes	23.75 (282)	20.87 (9)
	All seasons	Mean (n = 11)	29.90%

Table 2.2. Maximum percent difference in daily counts $[(\max - \min) / \max] * 100$. The mean minimum and maximum daily counts were used to calculate the potential percent difference in observed numbers of sea lions on shore. This methodology was chosen to report differences ranging from 0 – 100%. Only data from days preceding the research disturbance were included (mean: 49%; range: 20 – 86%).

Season	Location	Mean daily count		
		Minimum	Maximum	% Difference
Summer 2003	Sunset	39	148	74
	Brothers	173	306	43
	Lowrie	393	493	20
	South Marble	149	324	54
	McInnes	4	29	86
	Carmanah Point	71	134	47
	Carmanah 2	68	135	50
Winter / Spring 2004	Sunset	130	238	45
	Benjamin	125	255	51
	South Marble	179	253	29
	McInnes	156	247	37

Factors that affect numbers of sea lions on land

Different combinations of tidal height, time of day, tidal stage, the research disturbance and interactions between these variables significantly influenced the numbers of animals on land at the study sites (Table 2.3). The influence of covariates on daily variation was significant and varied among sites and seasons, demonstrating the need to include covariates in statistical analyses to address daily variation in numbers of animals hauled out.

Tidal height. Tidal height significantly influenced the numbers of sea lions on shore at Sunset, South Marble, Carmanah Point and Carmanah 2 in summer — and at Sunset, SW Brothers and Benjamin Islands during winter / spring (χ^2 , $p < 0.05$, see Table 2.3 for degrees of freedom). Negative correlation coefficients indicated that increasing tidal heights corresponded with a decrease in numbers of sea lions on shore. Counts and tidal heights at Sunset Island in May and June 2003 are illustrative of the sets of observations made at haulouts (Fig. 2.2, see Chapter 3 for counts made at the other 12 sites).

Time of day. Time of day significantly influenced the numbers of sea lions on shore at McInnes Island during the summer study period (χ^2_{422} , $p = 0.011$), and at Carmanah Point during both summer (χ^2_{630} , $p = 0.017$) and winter / spring seasons (χ^2_{603} , $p < 0.001$). However, only weak trends were documented at other locations.

Research disturbance. The research disturbance significantly influenced the numbers of animals on land at nine of the 10 study locations, as well as at a nearby haulout during summer (Summer: Sunset, SW Brothers, Lowrie, South Marble, McInnes, Carmanah Point and Carmanah 2; Winter / Spring: Sunset, South Marble and McInnes: χ^2 , $p < 0.05$). In two cases, scat collection did not occur due to a severe boat harassment at Carmanah Point in April 2004, and because eagles frightened the sea lions while eating a dead animal at SW Brothers Island in March 2004. The research disturbance did not significantly influence the numbers of sea lions hauled out at Benjamin Island in March 2004 (χ^2_{489} , $p = 0.80$).

Tidal stage. Tidal stage significantly influenced the numbers of sea lions on shore during summer at Carmanah 2 (χ^2_{408} , $p < 0.001$), and during winter / spring at Sunset Island (χ^2_{394} , $p = 0.001$), and during both seasons at SW Brothers Island (summer: χ^2_{696} , $p = 0.039$, winter / spring: χ^2_{516} , $p = 0.004$) and Carmanah Point (summer: χ^2_{630} , $p < 0.001$; winter / spring: χ^2_{603} , $p = 0.012$).

Table 2.3. Factors affecting numbers of sea lions hauled out in summer (S) and winter / spring (W) months. Correlation coefficients for generalized linear models fit to the response variable of sea lion haulout count data at each study location. Stepwise deletions were performed to determine the best model fit for each study period. Insignificant covariates were included in the model if they appeared in a significant interaction term, but were deleted from the model otherwise. All models were significantly different than the null model. Significant covariates are shown in bold. There were no experimental disturbances at SW Brothers or Carmanah Point during winter / spring, and consequently BA and BA interactions were not included in these initial model equations. Carmanah 2 was not disturbed for scat collection, but was close to the Carmanah Point study location. The research disturbance factor was included in this model to account for the possibility of scat collection affecting more than one site in an area, specifically addressing the movement of animals between these two sites.

variables	Sunset		Brothers		Lowrie	South Marble		McInnes		Carmanah Point		Carmanah 2	Benjamin
	S	W	S	W	S	S	W	S	W	S	W	S	W
tidal height	-0.6	-0.67		-0.71		-0.63				-0.31		-0.82	-0.83
time				-0.96				-0.95		-0.65	-0.92		
BA	-0.6	-0.57	-0.49	na	-0.84	-0.69	-0.66	-0.17	-0.71	-0.62	Na	-0.36	
tide:time	0.11	0.35	-0.63	0.04						0.14	-0.23	0.52	
tide:BA				0.77									
BA:stage				na						0.48	Na		
	0.43			na						-0.21	Na		
dispersion parameter	0.12	0.52	0.06	1.17	0.021	0.09	0.27	0.44	0.06	1.82	1.64	0.12	0.13
df	704	394	696	516	894	959	432	422	552	630	603	408	489

Interactions between variables. The interaction between tidal height and the time of day showed that the effect of tidal height on sea lion numbers varied at different times of the day during the winter / spring study period at SW Brothers Island (χ^2_{516} , $p < 0.001$). The interaction between tidal height and the research disturbance indicated that the disturbance affected sea lions numbers differently at varying tidal heights during the summer at Carmanah Point (χ^2_{630} , $p = 0.001$). Similarly, the interaction between the research disturbance and tidal stage indicated that the effect of the disturbance differed depending on tidal stage during summer at Sunset Island and Carmanah Point (Sunset: χ^2_{704} , $p = 0.007$; Carmanah Point: χ^2_{630} , $p < 0.001$).

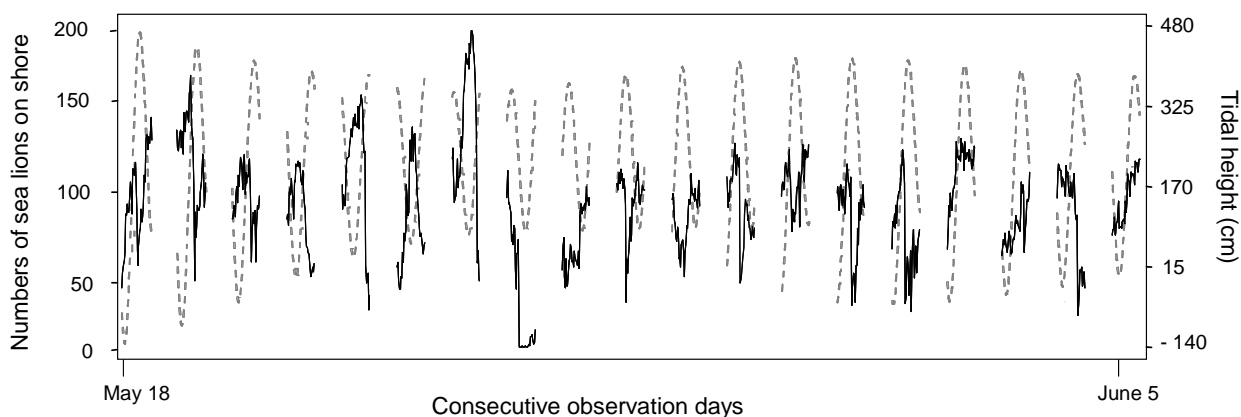


Figure 2.2. Tidal heights (lighter dashed lines) and numbers of sea lions on shore at Sunset Island from May 18 - June 5, 2003 (dark lines). These data are representative of other study sites visited, and show that numbers of sea lions on shore typically decrease as tidal height increases.

Discussion

Various environmental influences affected the hauling out behaviour of Steller sea lions. The combination and degree of influence that these factors had on the numbers of sea lions hauled out varied seasonally and by site. My study suggests that sea lions are subject to site-specific environmental effects, but that they alter their hauling out behaviour to accommodate various influences. These findings support those of other studies indicating that environmental influences have strong effects on the hauling out behaviour of pinnipeds (Calkins *et al.*, 1999; Moulton *et al.*, 2002; Small *et al.*, 2003). Data obtained with systematic counts are valuable when assessing the reliability of aerial census counts in terms of optimal conditions in which to survey. Observations from specific haulouts and rookery locations may provide guidance for estimating daily variation in the numbers of animals hauled out at any given time. Ultimately, it is important to determine if these environmental covariates have a discernible effect on estimates of population trends.

Numbers of sea lions on land

The numbers of animals hauled out differed significantly among study locations, but were assumed to reflect the natural distribution of animals at their preferred locations. Daily movements to and from haulouts accounted for some of the daily fluctuation in numbers of animals hauled out. Preference for haulout locations may be influenced by local prey abundance, shelter or occurrence along seasonal routes (Härkönen *et al.*, 1999). Individual sea lions may prefer certain locations, returning regularly to particular haulouts, while other individuals may exhibit transient behaviours and move from one haulout to another (Raum-Suryan and Pitcher, 2002). These differences in site fidelity may account for some of the residual variance that was not explained by the generalized linear regression models.

Topographic and age and sex differences among study locations may influence seasonal use of haulouts and may indicate potentially different types of haulouts. There may be inherent differences in hauling out behaviour that determine the numbers or proportions of certain age or sex classes on a haulout at any given time, and specifically over seasons (Reder *et al.*, 2003; Sease and York, 2003). Seasonal changes in the behaviour of breeding and non-breeding individuals will influence site choice, while the distance to other available haulouts might affect the degree of local movement and flux among haulouts. Seasonal changes likely did not occur within the short study periods (2 – 3 weeks). However, research disturbances that cause animals to leave the haulout and occur within a few days of aerial surveys will directly influence the results of census efforts (Chapter 3).

Environmental influences

Environmental influences on the numbers of sea lions hauled out are substantial and biologically significant (Small *et al.*, 2003). For that reason, determining influences on the numbers of sea lions on shore is extremely important for evaluating methods to assess population trends, especially in terms of conditions during population surveys. Most studies attempting to identify variables that affect pinniped hauling out trends have been done at single locations (Ono *et al.*, 1987; Grellier *et al.*, 1996; Porter, 1997; Moulton *et al.*, 2002). However, it is clear from my assessment of multiple sites that seasonal and site-specific factors affect the numbers of sea lions on land. While in practice it is nearly impossible to conduct all aerial surveys and counts at optimal times and tidal stages, it is necessary to address these

influences on numbers of observed animals. Of added importance are the various influences that these factors have among locations. My study documented changes in numbers of sea lions using the haulouts in response to tidal height, time of day, tidal stage, a research disturbance and interactions between these variables.

Time of day has typically been examined to determine circadian trends in hauling out patterns (Porter, 1997; Calkins *et al.*, 1999). This may be related to available sunlight or prey availability in the water column. However, graphical analyses of individual study sites indicated only weak trends. The numbers of animals on land seemed to follow the tidal cycles more closely than the time of day. Numbers of sea lions hauled out differed significantly at nine of ten sites that experienced a research disturbance, as did numbers at a nearby undisturbed haulout (Carmanah 2) (see Chapter 3 for further details concerning the research disturbance).

It is difficult to quantify weather variables in terms of intensity and duration, or to document subjective qualitative descriptions of conditions (i.e., intense snowfall, light rain or downpours), whereas tidal stages, time of day and human presence all have discreet measurements at distinct intervals. Other weather related factors such as temperature, wave and water state, precipitation, wind and solar radiation should be included in future analyses.

The degree to which tide influences hauling out behaviour is likely related to the physical geography of a site (Kastelein and Wetz, 1991). Tidal height significantly influenced the numbers of animals hauled out during at least one season at seven of eight study locations. The eighth location, Lowrie Island, was a breeding site. Steller sea lion rookeries appear to have limited tidal disturbance, which may enhance the safety of pups during their first few weeks of life. Correlation coefficients revealed a negative correlation among increasing tidal levels and sea lion numbers, as noted in other pinniped studies (Allen *et al.*, 1984; Porter, 1997; Henry and Hammill, 2001). My observations indicated that preferred exposed haulout areas can be a limiting factor in numbers of animals on shore. Sea lions returning from trips to sea might be restricted from hauling out due to increasing tidal levels, and other animals may be forced to leave the haulout due to submersion. Sea lion foraging behaviour may correspond to tidal stage (high tide, low tide) and the effects of incoming and outgoing water that may influence prey behaviour around the haulout (Baumgartner, 1997). Tidal variation affects the numbers of animals visible during aerial surveys, which in turn affects the evaluation of

changes in abundance and distribution of animals. My results support the general conclusions of other studies indicating that environmental variables have varying influences on the hauling out behaviour of pinnipeds (Small *et al.*, 2003).

Estimated variation

Steller sea lion hauling out behaviour is an important component of interpreting census counts and formulating population trend estimates. Correction factors calculated for the proportion of animals that may be away from land at the time of a census count attempt to account for the high mobility of sea lions. Aerial surveys typically replicate counts over subsequent days or years to calculate coefficients of variation for observed numbers of sea lions on shore (Sease and Gudmundson, 2002).

One of the most difficult aspects of calculating correction factors for animals that may be away from haulout locations is estimating their variance. Replicating counts at individual sites allows for coefficients of variation (CV) to be calculated as a measure of variability in observed numbers of sea lions hauled out. Although this measure of variation may account for some of the environmental influences that affect the numbers of sea lions hauled out, on its own it cannot pinpoint the factors that affect the numbers of sea lions on land.

Reported CV's for pinniped aerial surveys range from 2.3 – 12% for harbour seals, and up to 48 – 139% for Pacific walrus (*Odobenus rosmarus*) (Ferrero *et al.*, 2000; Jeffries *et al.*, 2003). Assessment of multiple Steller sea lion pup aerial surveys (1997, 1998) resulted in CVs ranging from 1 to 16.22% (Snyder and Pitcher, 2001). In contrast, replicated sites during the 2002 Steller sea lion population census of rookeries resulted in an extremely low coefficient of variation of 2.9% (Sease and Gudmundson, 2002).

To assess whether the use of replicated counts is consistent with the variation that was observed, I calculated the difference between CV's for midday counts (a single measure per day) and CV's for all counts made during my study period (Table 2.1). CV's calculated for midday counts resulted in an average CV of 35.29% (range 9.29 – 74.08%). Using all counts from days preceding the research disturbance resulted in an estimated average CV of 29.9% for all haulouts (range 16.0 – 48.2%). Such values indicate that a single census count might not reasonably reflect the numbers of sea lions using the haulout on the day of the survey. The

lowest CV recorded was for the rookery (CV = 9.36%) suggesting that a single count at a rookery is more reliable than one at a haulout.

Maximum differences in daily counts revealed that 49% of peak numbers of animals could potentially be missed if surveys occurred when the daily minimum number of sea lions were hauled out (Table 2.2). However, rookery counts (which have generally formed the basis for the population assessment, e.g., Trites and Larkin, 1996) would not be expected to have the same daily variation in numbers of animals on shore. Counts made at Lowrie Island (breeding site) revealed a maximum difference of 20% and a CV of 9.36%, the lowest observed values for all of the study sites. These measures indicate a level of certainty in counting the actual numbers of sea lions using a breeding site throughout the day during summer months. Aerial surveys of rookeries to estimate adults present and pups born could be fairly confident in photographing close to peak numbers of sea lions on land in good weather conditions at any given time.

Unlike harbour seals and some other pinnipeds, no single correction factor could be applied to the haulout counts of Steller sea lions to correct for time of day, tidal state or other influences. The equations that accounted for daily variability in numbers on shore were site-specific and would need further testing to determine how well they might apply to future years. These results have bearing on the use of sea lion haulout counts to monitor population abundance and trends.

Conclusions

The purpose of my study was to address factors that affect the numbers of sea lions on the haulout and the reliability of single census counts. Conservation and management plans rely on accurate trend analyses and population surveys, both of which are largely based on visibility of sea lion numbers during land and aerial counts. My results support the statement by Calkins *et al.* (1999) that there may not be an appropriate single survey window regarding date, time and tidal stage to perform aerial surveys throughout the Steller sea lion range and accurately estimate peak numbers of sea lions. Single environmental correction factors cannot be applied to all sea lion haulout locations, because the same environmental conditions may have different influences among locations. However, counts of sea lions at rookeries are considerably less

variable than haulout counts, and appear to yield more accurate estimates of population abundance and trends (Sease and Gudmundson, 2002).

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Chapter 3:

Major human disturbances cause short-term reductions in numbers of hauled out Steller sea lions

Summary

There is considerable interest in assessing and mitigating disruptive effects of humans on the behaviour of marine mammals. This is particularly true for listed species that are endangered or threatened with extinction. I sought to determine if there were measurable effects of human disturbance on Steller sea lions (*Eumetopias jubatus*) by documenting the numbers and composition of sea lions on land before and after an experimental disturbance. Haulout population trends were recorded at fourteen sites in southeast Alaska and British Columbia. Two of these sites were undisturbed (controls), two were disturbed by unforeseen factors, and ten incurred an experimental disturbance. Observations were conducted for 1 – 2 weeks before and 1 – 2 weeks after a predetermined research disturbance at six sites in summer, and four sites during winter / spring. Large daily variation in the numbers of animals on land occurred within and among study sites. Disturbances resulted in significantly fewer sea lions using haulouts during the post-disturbance period, and an increase in variation in numbers at nine of the ten disturbed sites. Rates of animals joining and leaving the haulout were not significantly different throughout the study. However, sea lion numbers did not return to pre-disturbance levels at four sites suggesting a departure of animals at the time of the disturbance. At the remaining six sites, the daily mean numbers of sea lions took 1.1 days to reach 50% of the pre-disturbance grand mean, 2.1 days to reach 75%, and 4.3 days to reach 100% recovery. Other disturbances from both natural (birds and sea lions) and unnatural events (boats and aircraft) appeared to be frequent events at these sites and typically resulted in up to 20% of the animals leaving the haulout. Responses of sea lions to different disturbances were site-specific and indicated varying degrees of sensitivity.

Introduction

Disturbance events can disrupt ecosystem, community or individual activities, and have the potential to alter normal behaviour (Suryan and Harvey, 1999; Forbes *et al.*, 2001). Recent pinniped studies have classified disturbance into two categories: anthropogenic (Salter, 1979;

Born *et al.*, 1999; Suryan and Harvey, 1999; Engelhard *et al.*, 2002; Cassini *et al.*, 2004) and non-anthropogenic (Ono *et al.*, 1987; Grellier *et al.*, 1996; Porter, 1997; Deecke *et al.*, 2002). Monitoring individual and group responses of wildlife to disruption of daily activities is a critical component of assessing the long-term viability of populations faced with human pressures (Andersen *et al.*, 1996).

Any activity that has the potential to disturb a marine mammal is considered harassment under the 1994 amendment to the U.S. Marine Mammal Protection Act (1972). Under this Act, Level A harassment addresses intentional disturbance whereas, Level B harassment considers the potential to disturb as any disruption of behavioural patterns, including, but not limited to, migration, breathing, nursing, breeding, feeding or sheltering.

Growing ecotourism ventures and technological advances have facilitated access to previously undisturbed areas. As a result, the potential for aquatic and terrestrial disturbance of pinnipeds has increased considerably worldwide. Behavioural studies have examined short-term pinniped responses to human presence, but results indicate that reactions to disturbances vary within and among regions and species (Salter, 1979; Born *et al.*, 1999; Suryan and Harvey, 1999; Henry and Hammill, 2001; Engelhard *et al.*, 2002). These studies offer differing conclusions about human effects on wildlife, inferring a need for species-specific investigations.

Steller sea lions (*Eumetopias jubatus*) have declined by over 85% in the Gulf of Alaska and Aleutian Islands since the late 1970's (Trites and Larkin, 1996; Loughlin, 1998). An equally dramatic increase has occurred in scientific research in the past few decades in an attempt to identify the causes of the decline and to monitor population status (NMFS, 2002). Some research activities have the potential to disturb large numbers of sea lions. However, it is not known whether research activities themselves have impacted Steller sea lion populations (NMFS, 2002).

Large groups of sea lions haul out of the water at preferred locations making them particularly vulnerable to repeated disturbance events. For the most part, Steller sea lions tend to avoid people and usually enter the water upon sudden human approach. Human forms of potential Steller sea lion disturbance include human approach (both scientific and recreational), vessel and aircraft movements, industrial activities, engine fumes, noise, subsistence take and illegal

activities. Non-human disturbances can involve environmental changes, storms, birds, predators, other species and other sea lions.

Varied responses to disturbance have been reported for Steller sea lions ranging from short- to long-term abandonment of haulout sites, to local populations recovering almost immediately after the disturbance has ceased (Thorsteinson *et al.*, 1961; Harestad, 1977; Lewis, 1987; Johnson *et al.*, 1989). The variation in historic response to disturbance makes it difficult to determine how sea lions will respond to future events. There is also a dearth of experimental data concerning the response of Steller sea lions to human disturbance, despite reported reactions and anecdotal reports.

Lewis (1987) examined census-related disturbance of Steller sea lions at a breeding site during summer, noting an increase in activity and female territoriality and aggression, as well as variation in the numbers of animals hauling out post-disturbance. His study documented a marked decrease in numbers of animals in the disturbed area and an increase in numbers at a nearby area where humans had not visited.

On the whole, the effects of past and present research activities on Steller sea lion populations are uncertain, as are the cumulative or synergistic effects of research activities (NMFS, 2002). A U.S. Environmental Assessment (NMFS 2002) determined that the effects of harassment associated with any given activity should be evaluated relative to the total number of animals that could be affected, and that it be evaluated by the intensity of the observed reaction of the animals, as well as by the potential short- and long-term effects of disturbance on survival and reproductive success. The apparent skittishness of Steller sea lions in the presence of humans raises behavioural and physiological concerns for populations that experience high levels of human disturbance.

The purpose of my study was to determine if there were measurable short-term effects of human disturbance on numbers of Steller sea lions using terrestrial sites. This was achieved by documenting the numbers and composition of sea lions on land before and after experimental disturbances. Behavioural responses provide a systematic assessment of disturbance effects on wildlife (Beale and Monaghan, 2004) and were recorded to provide a baseline examination of short-term responses of Steller sea lions to scientific research activities. The primary research activity involved collecting fecal samples for dietary analysis, and was monitored at select sites to determine the response of Steller sea lions to human presence on haulouts. Trends in

numbers were examined before and after the research disturbance over two seasons and across multiple sites. As well, three methods were explored to assess local population recovery.

Methods

Steller sea lion behavioural observations were conducted at five haulouts and one rookery between May and August of 2003. These sites were revisited between February and April of 2004, replacing the breeding site with a year round haulout (Fig. 3.1). Two additional undisturbed areas were used as comparisons to disturbed sites during the summer field season. Sites were chosen for the ease with which the animals could be observed from a distance without detection, and for their accessibility and suitability for camping within hiking distance to the animals. Topographic and substrate characteristics of the haulouts varied among sites. Some locations were large rocky outcrops, while others were ledges or cliffs. Only islands that were scheduled for scat collection during my study period were considered, because this experimental disturbance provided a predictable, controlled event around which to base my study. Pup branding was used as the experimental disturbance at Lowrie Island, the only breeding site included. Final selection of sites involved consultation with the National Marine Fisheries Service, the Alaska Department of Fish and Game, Fisheries and Oceans Canada, Glacier Bay National Park, and Pacific Rim National Park Reserve. All study sites were located within the designated Steller sea lion eastern genetic stock, listed as threatened in southeast Alaska in 1990 under the U.S. Endangered Species Act (U.S. Federal Register 62:2434355), and as a species of special concern in British Columbia by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2003).

Counts and behavioural scans were conducted for 1 – 2 weeks before and 1 – 2 weeks after each predetermined research disturbance. Counts were made at 20-minute intervals from 0800 – 2000 during the summer months, and during daylight hours during the winter and spring months (range 7 – 12 hours per day). Observations were made from fixed location blinds with the aid of binoculars and spotting scopes to avoid detection by the sea lions. All animals that could be seen from the blinds were included in the counts.

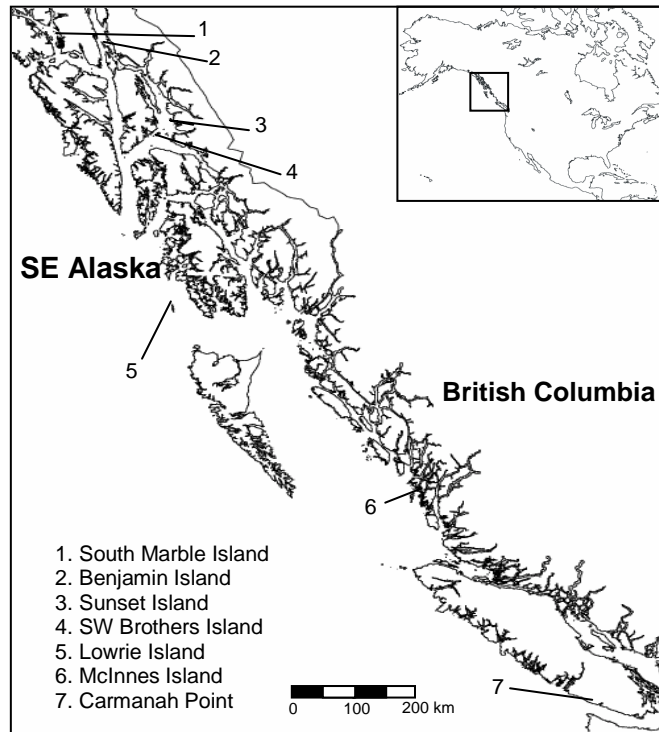


Figure 3.1. Study site locations in southeast Alaska, USA and British Columbia, Canada were visited between May – August 2003 and again between February – April 2004 (except for Lowrie Island, which was replaced by Benjamin Island in 2004).

The primary field disturbance (scat collection) began with slow arm movements and a direct approach by boat or land by research personnel to guide sea lions into the water to collect fecal samples from the haulout for dietary analysis. Human presence on the haulout was typically 2 hours. The research disturbance at Lowrie Island involved pup branding for long-term estimation of age-specific survival and fecundity rates. Researchers guided non-pups into the water while herding pups into groups on land. Individual pups at Lowrie Island were anesthetized and hot-branded with individual letter and number codes. Human presence on the rookery was about 6.5 hours.

Carmanah Point and SW Brothers Island were not disturbed for scat collection during the winter / spring 2004 field season due to unexpected disturbances caused by a vessel approach and subsequent human-sea lion contact and by eagles (*Haliaeetus leucocephalus*) feeding on a dead sea lion, respectively. Both of these events resulted in sporadic use of the haulout by the sea lions. Additional disturbance events were also recorded at all sites such as approaching

vessels, low flying aircraft or eagles flying overhead which caused sea lions to react with vocalizations, head movements and / or entering the water.

Results

Numbers of sea lions on shore varied greatly among study sites (Figs. 3.2 and 3.3). Mean numbers of sea lions on land following the experimental disturbances differed significantly from pre-disturbance levels (Wilcoxon Signed Rank, $V = 52$, $n = 10$, $p = 0.005$), decreasing at nine of ten sites. There were significant differences among age and sex composition of sea lions. The proportions of females (percent counts arcsine transformed) hauled out before and after the disturbance were significantly different at my study locations (Wilcoxon Signed Rank, $V = 51$, $n = 10$, $p = 0.007$).

Coefficients of variation of numbers of animals typically increased after the disturbance indicating a change in daily variation of sea lions using the haulout but these differences were not statistically different (Wilcoxon Signed Rank, $V = 4$, $n = 10$, $p = 0.995$) (Fig. 3.4). However, coefficients of variation differed significantly among islands before and after the disturbance (F-test, $F = 0.314$, $df = 9$, $p < 0.001$) indicating a difference in variation among sites.

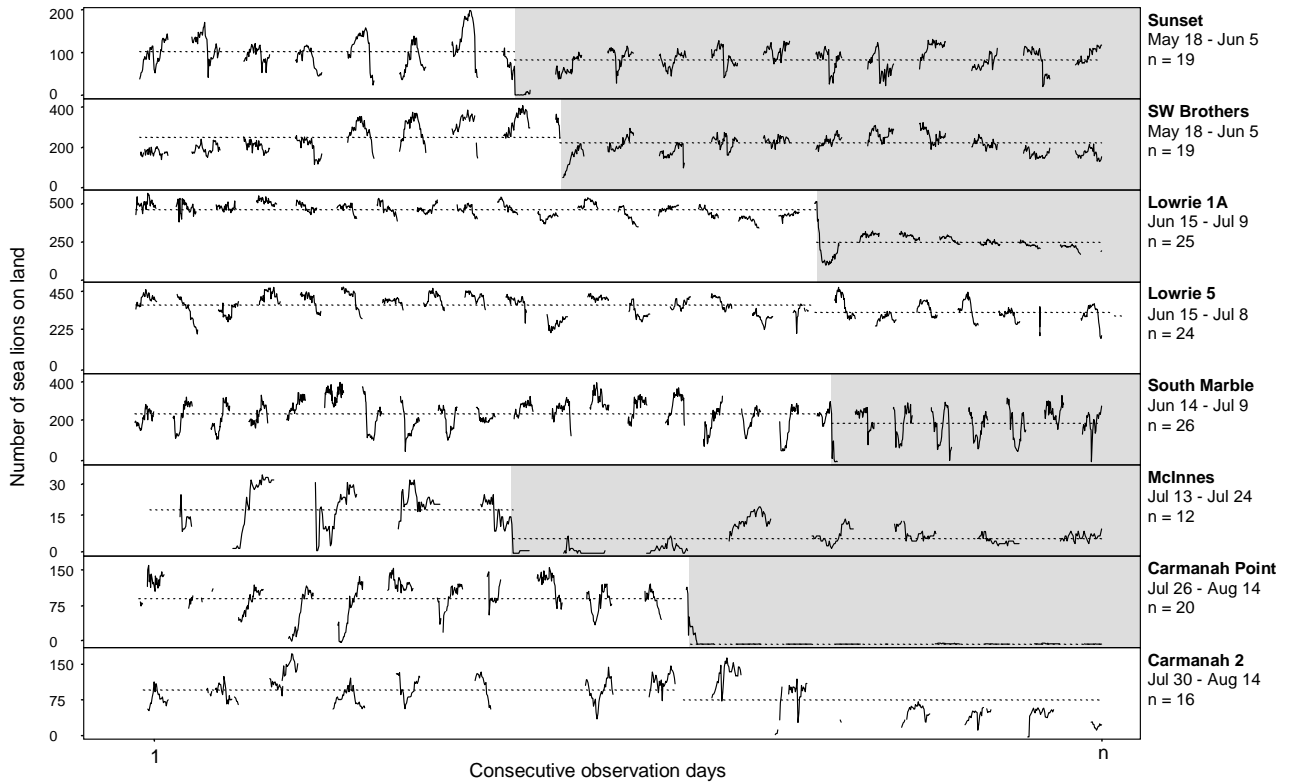


Figure 3.2. Steller sea lion counts before and after a research disturbance during summer 2003. Total numbers of sea lions on land were recorded every 20 minutes from 0800 to 2000 for 2 – 3 week periods. Shaded areas represent counts made after an experimental disturbance. Dashed lines represent the mean numbers of sea lions on land before and after an experimental disturbance. Lowrie 5 and Carmanah 2 were undisturbed control sites for Lowrie 1A and Carmanah Point, respectively. Breaks in the dashed lines for these sites reflect the disturbance event at a nearby location. In all cases the mean numbers of sea lions on land were lower following the research disturbance.

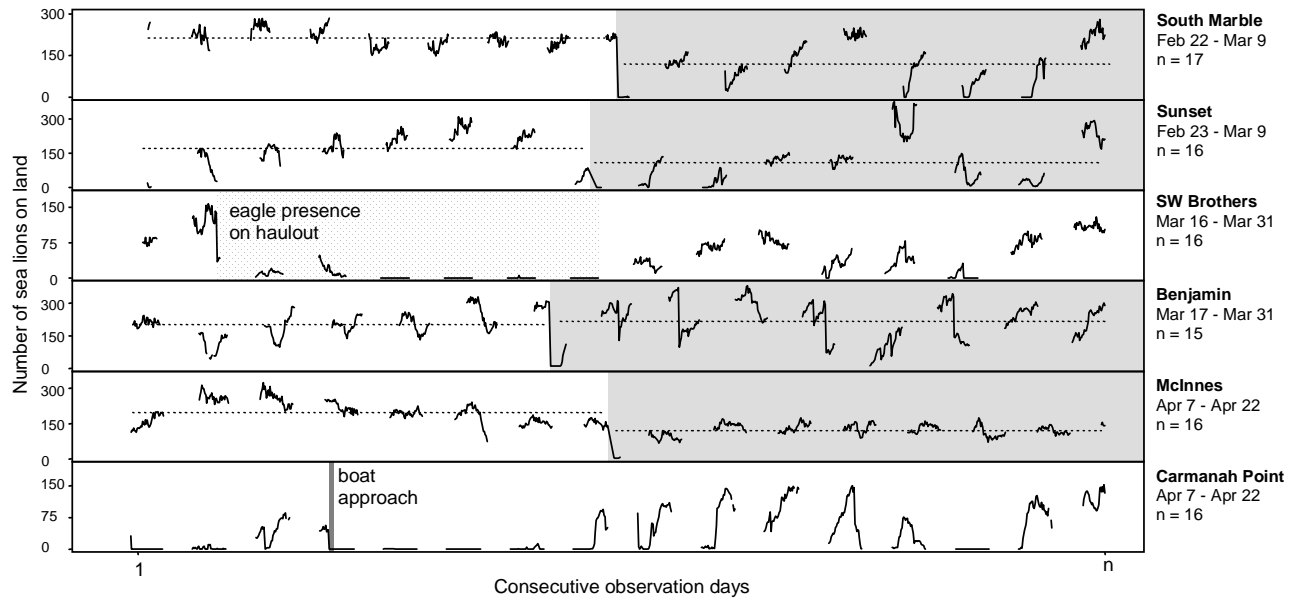


Figure 3.3. Steller sea lion counts before and after a research disturbance during winter / spring 2004. Total numbers of sea lions on land were recorded every 20 minutes during daylight hours for 2 – 3 week periods. Dark shaded areas represent counts made after an experimental disturbance. Dashed lines represent the mean numbers of sea lions on land before and after an experimental disturbance. SW Brothers and Carmanah Point were not disturbed for scat collection due to eagles feeding on a dead sea lion and a boat approach followed by human-sea lion contact, respectively.

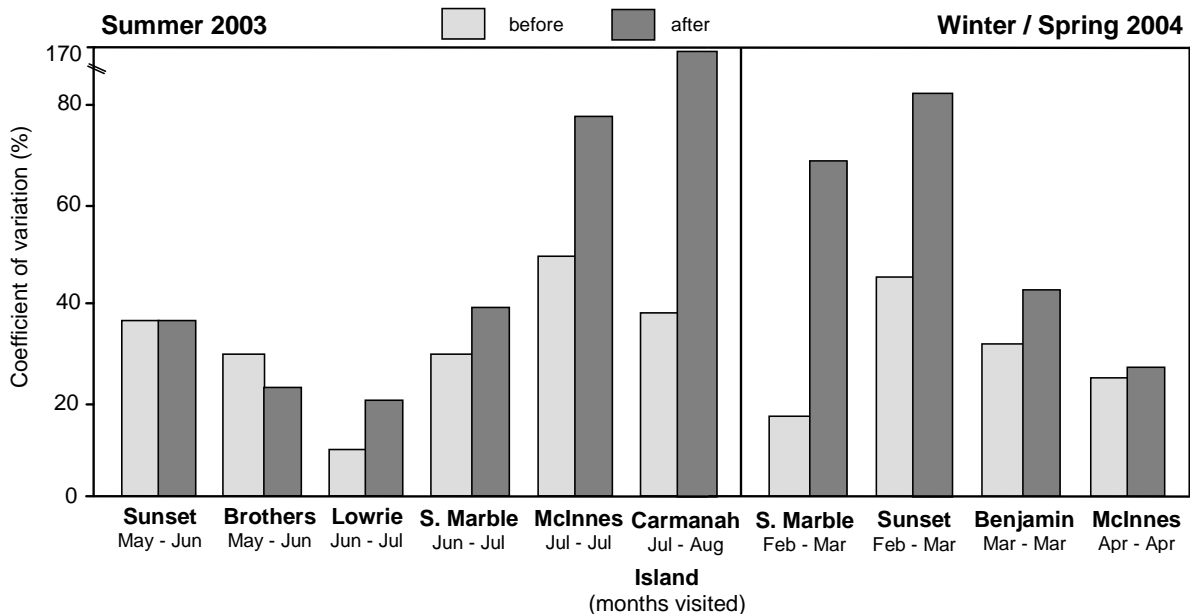


Figure 3.4. Coefficients of variation $[(SD / \text{mean}) * 100]$ calculated for daily mean numbers of sea lions hauled out before and after a research disturbance for each site. Coefficients of variation increased after the disturbance at eight of ten sites. The extreme post-disturbance coefficient of variation for Carmanah was due to the near zero post-disturbance mean.

Table 3.1. Sea lion haulout recovery. Percent recovery of sea lions hauled out during the study periods. The post-disturbance grand mean calculated as a percent of the pre-disturbance grand mean (1 – 2 weeks).

Location	Percent recovery (%)	
	Summer 2003	Winter / Spring 2004
Sunset	81	63
SW Brothers	85	—
Lowrie	48	—
South Marble	80	56
McInnes	34	61
Carmanah Point	0.37	—
Benjamin	—	107
Average % recovery	54.7 %	71.8 % = 63%

Recovery

There is little consensus within the scientific literature on how to measure local population recovery (Allen *et al.*, 1984; Born *et al.*, 1999; Kucey and Trites, 2005). Hence, I used three methods to determine local population recovery at haulout locations that addressed both quantitative and temporal factors of sea lions returning to sites following a research disturbance. The first measure reported the post-disturbance grand mean as a percentage of the pre-disturbance grand mean (mean of daily means) for each disturbed location (Table 3.1), and showed that recovery averaged 63% 1 to 2 weeks after the disturbance (summer: 55%; winter / spring: 72%). The second and third measures considered the time it took for sea lion numbers to return to 50, 75 and 100% of the pre-disturbance grand mean as point counts and daily means, respectively.

Calculating the time for a *point count* (i.e., a single observation) to reach the pre-disturbance means revealed that it took sea lions at my study locations an average of 0.7 days to reach 50% of the pre-disturbance grand mean numbers, 1.1 days to reach 75%, and 2.0 days to reach 100% recovery (Table 3.2). Three sites did not reach 100% recovery and were not included in the final calculation of recovery time.

The third analysis of hauling out trends used *daily means* as the variable of interest, and showed that on average, the daily mean number of sea lions reached 50% of the pre-disturbance grand mean after 1.1 days, obtained 75% at 2.1 days and 100% recovery at 4.3 days (Table 3.3). Again, these estimates do not include sites that did not reach certain recovery

levels within my study period (i.e., 100% daily mean recovery was not obtained in summer at Carmanah Point or at the Lowrie Island rookery, or over both seasons at the McInnes Island haulout).

Recovery time based on daily means was approximately double that of point count recovery. These measures offer different interpretations of response to the same event. Unfortunately, I could not determine from my observations whether the same sea lions returned to the haulout after the disturbance, or if recovery was due to sea lions returning after foraging trips or from other haulouts with no knowledge of the disturbance event.

Table 3.2. Point count haulout recovery. Time in days for post-disturbance counts to reach 50, 75 and 100% of the grand mean number of sea lions on land before the experimental disturbance. Long dashes indicate sites that did not reach certain levels of recovery within the study period.

Season	Location	Time to return (days)		
		to 50%	to 75%	to 100%
Summer 2003				
	Sunset	0.8	1.1	1.5
	SW Brothers	0.1	0.3	0.7
	Lowrie	0.3	—	—
	South Marble	0.3	0.3	0.3
	McInnes	2.6	2.8	2.9
	Carmanah Point	—	—	—
Winter / Spring 2004				
	Sunset	1.0	1.1	4.5
	South Marble	0.5	1.1	3.5
	Benjamin	0.1	0.4	0.4
	McInnes	0.3	1.7	—
Average (excluding sites that did not recover)				
	Summer	0.8	1.1	1.4
	Winter / Spring	0.5	1.1	2.8
All seasons average point count time to return		0.7	1.1	2.0

Table 3.3. Daily mean haulout recovery. Time in days for post-disturbance daily means to reach 50, 75 and 100% of the grand mean number of animals on land before the experimental disturbance. Daily means were calculated for each day. To calculate half days and to account for night-time recovery, the combined mean was also calculated for 1400 – 2000 and 800 – 1400 the following day. Long dashes indicate sites that did not reach certain levels of recovery within the study period.

Season	Location	Time to return (days)		
		to 50%	to 75%	to 100%
Summer 2003				
	Sunset	0.0	1.5	5.0
	SW Brothers	0.0	1.0	5.5
	Lowrie	1.0	—	—
	South Marble	0.5	0.5	6.0
	McInnes	3.0	3.0	—
	Carmanah Point	—	—	—
Winter / Spring 2004				
	Sunset	2.5	4.5	4.5
	South Marble	1.0	3.5	4.0
	Benjamin	0.5	0.5	0.5
	McInnes	1.5	—	—
Average (excluding sites that did not recover)				
	Summer	0.9	1.5	5.5
	Winter / Spring	1.4	2.8	3.0
All seasons average daily mean time to return		1.1	2.1	4.3

Movement to and from haulouts

Distance to other available haulouts may affect the degree to which local movements occur among sites. Sea lions may be more likely to move among haulouts close to one another as opposed to travelling to haulouts further away. My study locations ranged between 27 – 476 m from the closest alternative haulouts (Table 3.4), which were within sea lion daily travel distances (Raum-Suryan and Pitcher, 2002; Sease and York, 2003). However, none of my measures of recovery times correlated with distances to nearby haulouts.

Table 3.4. Study site details. Latitude and longitude of study locations and distance to the closest alternative haulout (mean: 218 m; range: 27 – 476 m).

Location	Latitude (N)	Longitude (W)	Closest alternative haulout	Distance to closest haulout (m)
South Marble	58°64	136°04	Case Point (Tlingit)	165
Benjamin	58°56	134°91	Met Point	441
Sunset	57°50	133°58	Point League	124
SW Brothers	57°27	133°87	Round Rock	39
Forrester - Lowrie	54°86	133°53	Forrester Complex	27
McInnes	52°26	128°72	Gosling Rocks	476
Carmanah Point	48°61	124°76	Whale Rock	250

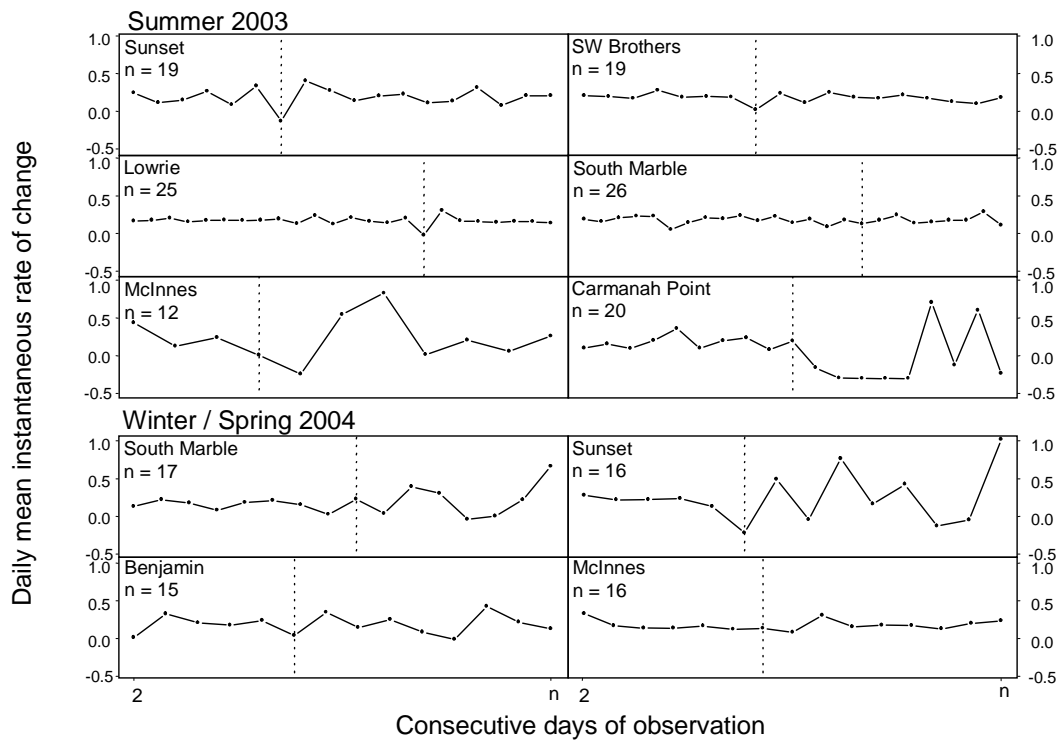


Figure 3.5. Daily mean instantaneous rate of change $\log[(\text{daily mean day 2} / \text{daily mean day 1}) + 0.5]$ before and after a research disturbance. The research disturbance is shown with a dashed vertical line. Straight lines represent a constant rate of change, whereas peaks and valleys in these lines indicate a change in the rate in numbers of animals hauling out between days. Rates of change were not significantly different before and after the disturbance, but did differ among islands.

Daily mean instantaneous rates of change were calculated for each disturbed site to address differences between daily haulout variation before and after the experimental disturbance (Fig. 3.5). Overall, instantaneous rates of change in the daily mean numbers of animals hauled out were more varied after the research disturbance, but were not statistically different (Wilcoxon signed rank – with correction due to exact sign match, $Z = 0.051$, $n = 10$, $p = 0.48$; data from the day of the disturbance were not included). However, rates of change did differ significantly among islands before and after the disturbances (F-test, $F = 0.010$, $df = 9$, $p < 0.001$) indicating that hauling out patterns differed among sites.

Non-research disturbances

Additional non-research disturbance events occurred on a daily basis and were recorded in six different categories: aircraft, birds, sea lions (entangled in fishing gear, flipper slapping and aggressive interactions), humans, boats (motorized watercraft and kayaks) and unknown disturbances. With the exception of two events (eagles feeding on a sea lion body for six days, and a boat disturbance), none of the additional recorded disturbances caused animals to stay away from the haulout longer than the research disturbances. A total of 1049 additional disturbances were recorded at my study sites (Fig. 3.6). However, only 467 caused animals to leave the haulout. These events were analysed to determine the magnitude of response to additional disturbances, evaluated as the percentage of animals to leave the haulout in response to the disturbance event (Fig. 3.7). These disturbances caused an average of 4 – 16% of the animals to leave, compared to 100% of the haulout populations that entered the water when researchers went ashore to collect scats.

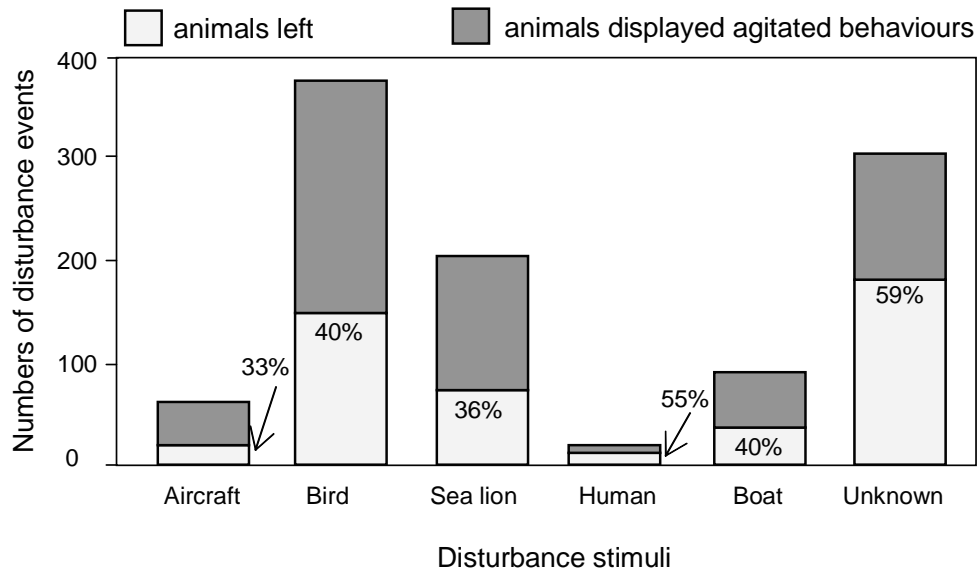


Figure 3.6. Sea lion response to additional disturbance events. White portions of the bars represent the percentage of disturbance events that caused animals to leave the haulout (n = 467). Dark portions of the bars represent the percentage of disturbance events that caused some form of agitated behaviours and changes in vocalization levels (n = 582). Data were combined for all islands over both seasons for 257 observation days. Sea lion disturbances included animals entangled in fishing gear, flipper slapping or aggressive interactions. Human events refer to non-research approach. Boats included both motorized vessels and kayaks.

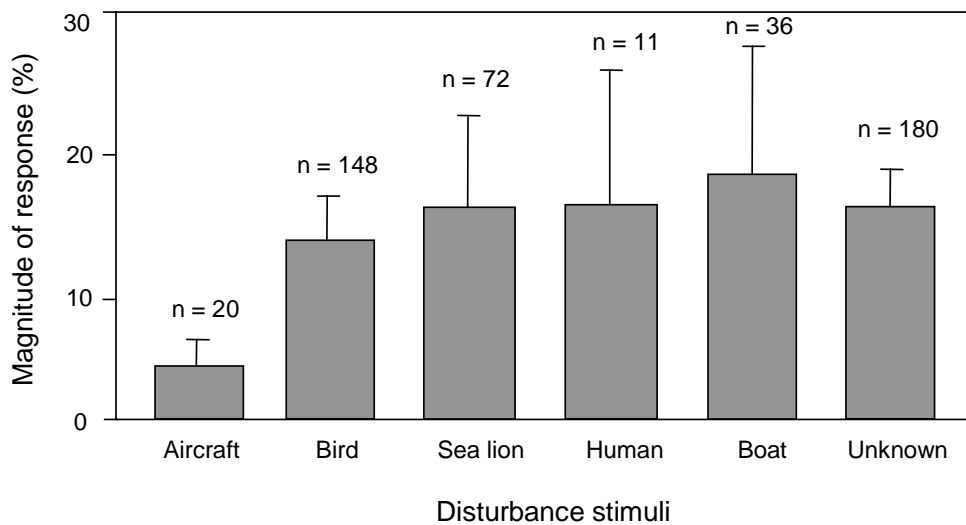


Figure 3.7. Percentage of sea lions leaving haulouts in response to additional disturbance events. Data were combined for all islands over both seasons (SE bars; n = number of events in each category). Scat collection, not shown here, resulted in all animals (100%) leaving the haulout.

Discussion

My study was designed to assess the short-term effects of a disturbance on Steller sea lions, and revealed a statistically significant drop in mean numbers of animals using the haulouts after researchers went ashore to collect scats for dietary analysis. However, I also uncovered considerable daily variation in haulout numbers and documented many sources of natural disturbances that have bearing on understanding how disturbance and recovery should be defined and assessed. My study also raises concerns about possible long-term consequences associated with disturbing Steller sea lions.

Before addressing questions concerning the response of sea lions to disturbance, it is important to recognize the limitations that were associated with my study. Most apparent was the fact that not all animals or areas were visible from my observation points, as is the case with most land and ship-based surveys. Topography and the propensity of animals to move within and among sites limited the number of animals that could be observed at any given time. However, my observation blinds were positioned to view the maximum numbers of sea lions at each site. I assumed that animals had hauled out in preferred areas at each site prior to the research disturbance, and that the numbers of animals visible from the research blinds represented typical distributions of animals on the haulout. Post-disturbance observations were made from the same locations. Redistribution of sea lions to other areas on the same or different islands was certainly possible, as was recovery during night hours.

Longer observation periods (i.e., additional days beyond my study window) would likely have resulted in full recovery being observed at additional haulout locations, depending on the criteria applied to assess recovery. However, recovery periods had not been assessed for Steller sea lions prior to my study, such that there was no precedent to better guide my study design. Tolerance and habituation levels likely varied by location, but were not evaluated. Finally, differences in age and sex composition might also have accounted for some of the site-specific responses to various disturbance stimuli, and the additional non-research disturbances might also have affected recovery levels or have had cumulative effects.

Variation in numbers of sea lions on land

The observed daily variation in the numbers of animals hauled out both within and among the study locations highlights the dynamic nature of sea lion haulouts (Chapter 2). Seasonal and

environmental variations likely affect the hauling out behaviour of Steller sea lions. Factors that affected the numbers of sea lions at my sites included tidal height, time of day, tidal stage, season and location (Chapter 2). However, I found varying degrees of environmental effects at the same site over different seasons, which may be related to tidal cycles or changes in sea lion response to environmental variables throughout the year.

Whether sea lions return to the same haulout day after day is highly relevant to the question of assessing human impact on local haulout populations (Orsini, 2004). Coefficients of variation in numbers of sea lions were larger following the disturbances, indicating that the daily variation in sea lions using each haulout increased after the research disturbance. This increase in variation may be due to an increased flight response, with animals fleeing additional disturbances with greater frequency, or it may reflect less site tenacity on the part of animals that remained or joined the haulout from other sites. However, daily mean instantaneous rates of change did not differ significantly after the research disturbance, even though there were fewer sea lions using the haulout. This indicates that the rate of animals joining and leaving the haulout remained steady over the course my study, despite the overall lower numbers. Thus, the lower mean may reflect a one time departure of some animals from the haulout at the time of the disturbance.

Steller sea lions and disturbance

Animals are able to respond to disturbances in two general ways, either by moving out of the area in search of an undisturbed environment, or by reacting to the disturbance within the affected area (Andersen *et al.*, 1996). The reactions of Steller sea lions to direct human approach in the wild are characterized at an individual level by increased vocalization, agitated head movements, movement on the haulout and fleeing into the water (Fig. 3.8).

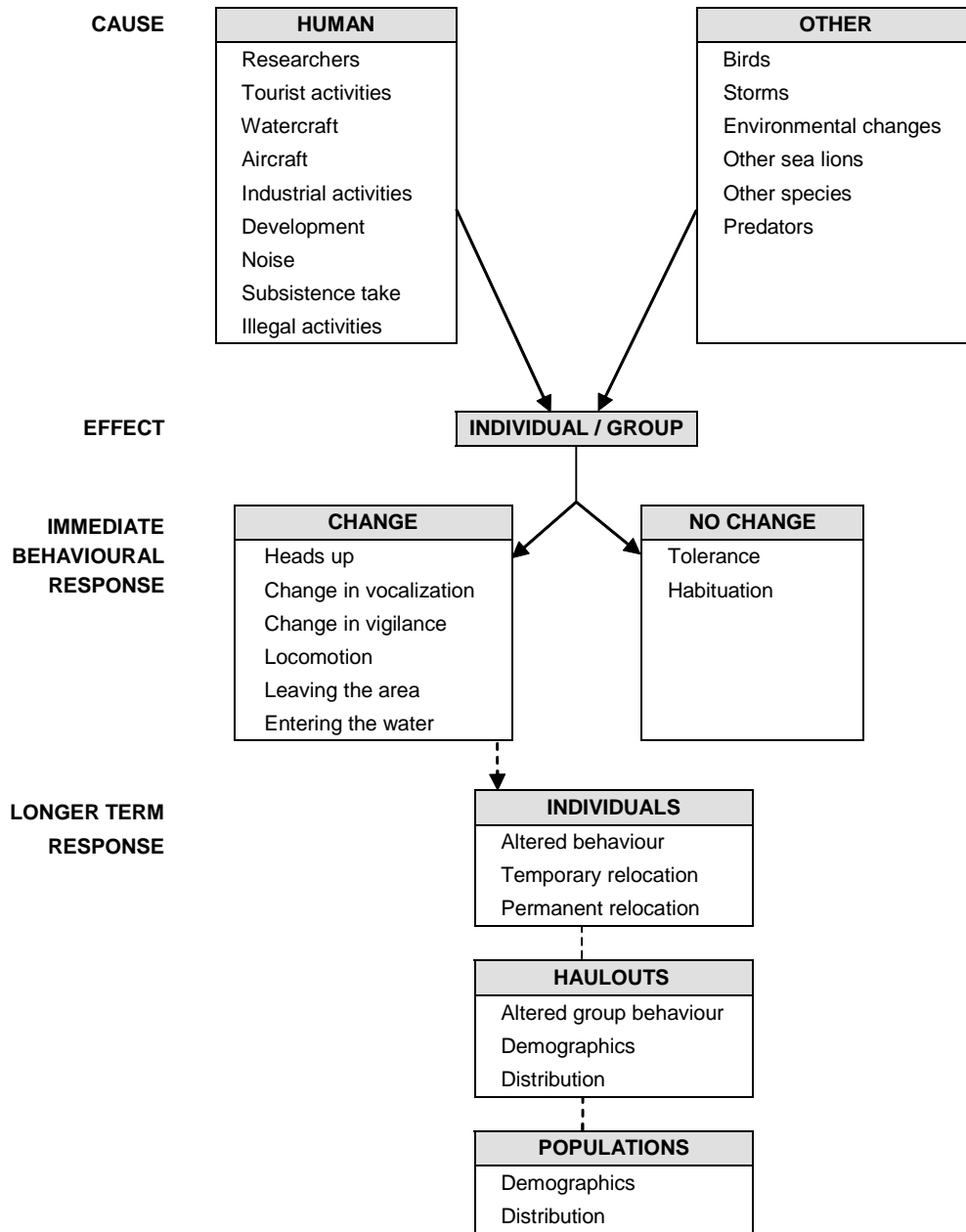


Figure 3.8. A conceptual model of individual and group level response of Steller sea lions to disturbance. Based on a model of response of wildlife to recreational activities (Knight and Cole, 1995).

Disturbance type, intensity and duration, as well as the frequency of the disturbance events may all affect how animals respond (Born *et al.*, 1999; Suryan and Harvey, 1999; Henry and Hammill, 2001). My results revealed different levels of response to disturbance by site indicating that location is an important determinant of sea lion sensitivity.

Sea lions at most of my haulout study sites reacted strongly to direct boat approaches, particularly if the boat did not slow down when nearing the haulout, or if noise and engine fumes were associated with the approach. In most cases though, with slow, parallel passes, boats were able to gain close access for sea lion viewing without many animals entering the water. The magnitude of aircraft disturbance seemed to be determined by height above the haulout, noise associated with the aircraft and weather conditions. Type of approach and human behaviour seemed to determine if an agitated response would follow anthropogenic disturbance events. Some haulout populations were particularly sensitive to avian flight, while others did not seem to react to birds landing on the haulout. Eagles and ravens (*Corvus corax*) produced the strongest reactions, whereas gulls and smaller birds were typically ignored. Sea lion response was inconsistent, because not all birds flying over the haulouts caused disturbance reactions among individuals.

Prevailing weather conditions and the magnitude of storms generally determined whether sea lions would leave the haulout or cluster tightly on land. At three winter locations, sea lions reacted on a number of occasions to intense snowfall by slowly and methodically entering the water until the haulout was completely cleared. No agitated behaviours were exhibited during these events. Presence of California sea lions (*Zalophus californianus*) and harbour seals (*Phoca vitulina*) did not create large disturbances. Humpback (*Megaptera novaeangliae*) and gray whale (*Eschrichtius robustus*) presence occasionally resulted in individuals entering the water, whereas killer whale presence (*Orcinus orca*) caused elevated activity on land with increased vocalizations and agitated movements. Not all killer whale pods swimming by haulouts elicited reactions, but I was unable to distinguish between fish eating and mammal eating pods of killer whales. Sea lions with fishing flashers or entangled in nets did not create large disturbances, but they were typically avoided by other individuals on the haulout. Disturbance responses to landslides and falling rocks have also been reported (Porter, 1997), but did not occur at my study sites.

My post-disturbance counts indicate that fewer animals use haulout locations following human presence on shore. Significant differences in the mean numbers of animals on land before and after the disturbance demonstrate the measurable short-term effect of human disturbance on Steller sea lion hauling out behaviour. Recognizing that research activities affect sea lion hauling out behaviour may be the first step in addressing the tradeoff between obtaining information needed to monitor and conserve the population, and the cost to the animals of obtaining it.

Recovery

Recovery can be used to assess a population's susceptibility to disturbance. However, there is no consensus on how local recovery of wildlife populations should be defined and measured (Allen *et al.*, 1984; Gill *et al.*, 1996; Born *et al.*, 1999; Suryan and Harvey, 1999; Boren *et al.*, 2002; Engelhard *et al.*, 2002; Beale and Monaghan, 2004; Blackmer *et al.*, 2004; Kucey and Trites, 2005). Using an assortment of measures of recovery can lead to inappropriate comparison of studies that will likely influence the interpretation of results.

I presented three methods to assess recovery using both quantitative and temporal measures. The first, percent recovery, is relatively simple and useful for those responsible for conservation and management to determine acceptable levels of recovery. However, levels depend on the period of assessment used to determine the percentage. In addition, the large daily variation in numbers of animals hauled out indicates that the count at the time of the disturbance may not accurately reflect hauling out trends. Using the number of animals on land just prior to the disturbance may be misleading due to tidal effects, time of day or other disturbance events. The two other methods I used to assess recovery to a pre-disturbance grand mean (point count and daily mean recovery) allow for the inclusion of hauling out trends in recovery measures and can provide a time period for when the haulout has returned to pre-disturbance levels and when it may be permissible to revisit the haulout without potential adverse effects (Kucey and Trites, 2005).

Based on point count and daily mean recovery measures, it appears that it took between two and four days for numbers of sea lions using my study locations to recover to pre-disturbance count levels, respectively. Of added interest are the four locations that did not return to 100% of the pre-disturbance grand mean within the study period. At the outset, the 1 – 2 week post-

disturbance observations were considered appropriate recovery periods, but full recovery was not obtained at McInnes Island over both seasons, nor at Carmanah Point and Lowrie Island in the summer. In some cases, such as the rookery at Lowrie Island, the research disturbance may have sped up natural seasonal movements, with females taking their offspring to other locations sooner than they would have otherwise. Seasonal movements may also explain the declining counts made at Carmanah 2, which was not disturbed.

Effects of disturbance

Impacts on sea lions from human disturbance could range from a potential physiological stress response, to sea lions leaving the haulout (temporarily or permanently) (Orsini, 2004). Events that have no discernable immediate or short-term effects may have the potential to cause cumulative impacts that do not become apparent until the disturbance has continued for some time (Lewis, 1987). Conversely, disturbances that cause immediate effects may not necessarily generate cumulative effects over time (Riffell *et al.*, 1996). Thresholds and lag times in response to disturbances further complicate the detection of cumulative impacts. At a population level, species with high fitness costs and few habitat choices are the ones most likely to be adversely affected by disturbance (Creel *et al.*, 2002).

Short-term effects of human intrusion include disruptions of sea lion daily activities and potential redistribution of animals within and among sites. Displacements may increase population numbers and density at alternative sites or force individuals to inhabit sub-optimal habitat (Creel *et al.*, 2002). Determining whether research disturbance results in short-term changes in spatial distribution of sea lions, or if it ultimately results in reduced use of preferred habitat is important if it has the potential to alter life-history parameters. However, the effects of repeated short-term disturbance at the population level are unknown (NMFS, 2002).

Long-term effects of human interference that significantly reduces the time that sea lions haul out, or substantially interferes with the activity pattern of hauled out sea lions, could potentially have consequences on life cycles and activities (Orsini, 2004). For rare or declining species, displacement may reduce reproductive success as well as presence in an area, in addition to reduced parental care, foraging efficiency and prey intake rates, and increased stress and vigilance levels (Andersen *et al.*, 1996; Riffell *et al.*, 1996; Gill *et al.*, 2001; Engelhard *et al.*, 2002).

To date, Steller sea lion research in Alaska and British Columbia has focused on both the eastern (increasing) and western (declining) populations. However, two decades of comparable intensive research activities have not revealed any discernible negative effects on either population. It could be argued that the long-term effects of reduced resting behaviour on long-lived species such as sea lions might affect their fitness, individual reproductive success and population size, and that it could take an additional thirty to forty years to detect (Constantine *et al.*, 2004). However, the lack of any obvious long-term effect in southeast Alaska and the apparent resilience of sea lions to human encroachment and hunting pressures they have sustained, argues in favour of the resiliency of sea lions to long-term effects of intermittent disturbances. At some sites, the short-term reductions in observed numbers of Steller sea lions may be accounted for by accelerated natural seasonal movement that would have occurred at a later date in the absence of human presence, but how this affects sea lions in the long- and short-term is not known.

Sea lions at some haulouts may become habituated to repeated exposure to disturbance stimuli, or conversely, they may exhibit increased levels of response (Frid and Dill, 2002). Habituation may vary temporally and spatially among locations depending on exposure rates and level of threat (Boren *et al.*, 2002; Blumstein *et al.*, 2003). Sea lions at haulouts that are visited repeatedly by tourists and researchers (e.g., Benjamin Island) may become habituated to human presence and consequently, their response may not be as dramatic as those sea lions using haulouts with minimal human intrusion. However, animals can still experience continued physiological stress (elevated corticosteroid levels) with frequent human approach despite an apparent habituated response to high levels of intrusion (Fowler, 1999).

Increasing frequency of human–sea lion contact are expected as more and more people visit the remote coastal habitat of Steller sea lions. Exposure to different disturbance stimuli may also affect levels of habituation. Nevertheless, it is abundantly clear that Steller sea lions have a flight response to sudden movement, noises, smells and approaches, all of which should be considered when approaching Steller sea lion haulouts and rookeries.

Future research

Determining the effects of human disturbance on wildlife is an essential component of conservation and management plans (Kerley *et al.*, 2002). Assessing and mitigating

disturbance requires knowing whether human presence causes animals to avoid areas that they would otherwise use, and whether this affects mortality, reproductive success or population size (Gill *et al.*, 1996). I addressed short-term response to disturbance by documenting the numbers of sea lions on land before and after research disturbances. The second component of assessing disturbance requires long-term monitoring of the physiological and distributional parameters of disturbed populations. The data from my study provide a baseline against which the effects of future human activity might be compared.

Future studies are needed to assess the influence of disturbance on sea lion redistribution within a critical recovery period as well as to determine the physiological effects that sea lions experience with repeated human intrusion. Results from such studies will further our understanding of group dynamics and the behavioural response of Steller sea lions when presented with major disruptions to their daily activities. Determining how human disturbance affects sea lions is needed to limit the potential adverse effects of scientific investigations, population monitoring and recreational disturbance, as well as to provide managers with the best conservation policies for local situations. Assessing the severity of the effects of disturbance also has important practical consequences for management and conservation initiatives.

Conclusions

Reductions in numbers of Steller sea lions observed on haulouts following human presence represents a measurable effect of human disturbance. Variation in numbers of animals using the study haulouts increased following the disturbance, but rates of change in daily numbers did not differ significantly between periods. Daily mean recovery from the research disturbance averaged 4.3 days (excluding sites that did not recover). The magnitude of response to other types of disturbance stimuli (i.e., non-research events) varied, but typically did not exceed a 20% response of animals leaving the haulout.

Possible long-term effects of disturbance, if any, are unknown. Nor is the biological significance and cumulative impact of short-term events known. Addressing these questions would require long-term datasets and determination of exact measurement parameters, whereas short-term responses are more readily ascertained and can be described and mitigated in terms of cause and effect.

My findings provide insight into the short-term effects that field research has on the numbers of Steller sea lions hauled out following human presence on shore and can serve as a discussion point for determining local recovery criteria of wildlife populations experiencing human disturbance. Behavioural data can help identify strategies for conservation and management plans. Specifically, disturbance studies can help shape policies and establish restrictions to protect wild populations from human intrusion.

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Chapter 4:

Disturbance does not appear to significantly affect the hauling out behaviour of individual Steller sea lions

Summary

At a population level, observations of Steller sea lions (*Eumetopias jubatus*) conducted at six haulouts and one rookery in summer and winter / spring in southeast Alaska and British Columbia showed fewer sea lions used these sites following a major human disturbance. Whether or not the disturbance altered sea lion behaviour at the individual level was addressed using focal sampling to follow individual animals (n = 3894) from the moment they came onto land, until the time they either returned to the water or lay down to rest, whichever came first. Behaviours were categorized into 11 types, and their frequency was recorded for juveniles (1 – 3 y), mature females, subadult males and bulls. Interactions with other sea lions were also recorded. In the absence of disturbance, individuals were found to take longer to settle down and displayed lower rates of behavioural interactions with other animals in winter / spring compared to summer. Bulls and subadult males were also found to be more active behaviourally than juveniles and females. In particular, subadult males that remained on land interacted with more animals per minute than did juveniles, females and bulls. However, no appreciable difference was noted in the behaviour of Steller sea lions that rested on shore during the days that followed an experimental disturbance (which occurred after approximately one week of observations when researchers went onto the haulouts to collect fecal samples and caused the haulout populations to enter the water). Only the sea lions that failed to stay on shore after hauling out showed a significant increase in rates of behaviour and interactions with other animals. Overall, disturbance did not appear to have a significant detrimental effect on the hauling out behaviour of individual Steller sea lions, unlike the effect it had on population numbers.

Introduction

Studies of Steller sea lions (*Eumetopias jubatus*) at rookeries and haulouts have increased over the past few decades in an attempt to determine the causes of a large population decline that occurred in the Gulf of Alaska and Aleutian Islands (Merrick *et al.*, 1987; Trites and Larkin,

1996; NMFS, 2002). Entire haulout populations are typically disturbed when researchers go ashore to collect scats (for dietary analyses) or to capture animals (for physiological measurements, or for attaching tracking devices). It is unknown whether these types of disturbances affect sea lions at the individual or population level (NMFS, 2002).

In general, behavioural tendencies of individual animals are typically narrower and more specific than those of populations. However, individual decisions and responses can shape group behaviour and ultimately determine how a group will act during disruptions to daily activities (Gentry, 1998). Most pinniped species haul out of the water in groups to rest, breed and engage in social interactions (Salter, 1979; Watts, 1996; Reder *et al.*, 2003), and species that congregate in large groups are most likely to be influenced by the behaviour of animals around them.

The distinction between the effects of disturbance on the population (i.e., numbers) versus the individual (i.e., behaviour) is important to recognize when evaluating the effects of disturbance. As shown in Chapter 3, a major disturbance of sea lions at a breeding (rookery) and non-breeding (haulouts) sites resulted in a short-term reduction in numbers of sea lions present. Disturbance may have a more subtle but equally important effect at the individual level. However, little is known about the influence of human disturbance and season on normal sea lion behaviour.

The purpose of this portion of my study was to document baseline hauling out behaviour and sea lion interactions, and to determine if individual behaviour was affected by human disturbance. Additionally, I documented age / sex class and seasonal differences in Steller sea lion hauling out behaviour. The principal objectives of these analyses were to examine differences in the likelihood of an animal remaining on shore after hauling out, and to address factors that affected the time it took for a sea lion to settle down on shore between summer and winter / spring months. In addition to this, I also examined factors influencing the rate of behaviours and interactions that sea lions engaged in after hauling out.

Methods

Sea lions arriving on shore at haulouts were followed to determine normal patterns of interactions and behaviour associated with the movement of animals on land. Focal animals joining the haulout were not individually identifiable, but were chosen by scanning the

shoreline and selecting the first sea lion to haul out of the water. Observations documented the age / sex class of the animal, the length of the follow session, 11 types of behaviours (i.e., locomotion, head movements, vocalizations, jaws with another animal, scratch / groom, aggressive display, initiates physical contact, bites another animal, climbs over another animal, play and nurse / suckle) and numbers of interactions that the target animal had with other sea lions. Each animal was followed until it went back into the water, did not exhibit any active behaviours for five minutes (settling down), or disappeared from view (behind another animal or blocked by topographic features). The next animal to join the haulout from the water became the next targeted animal to follow.

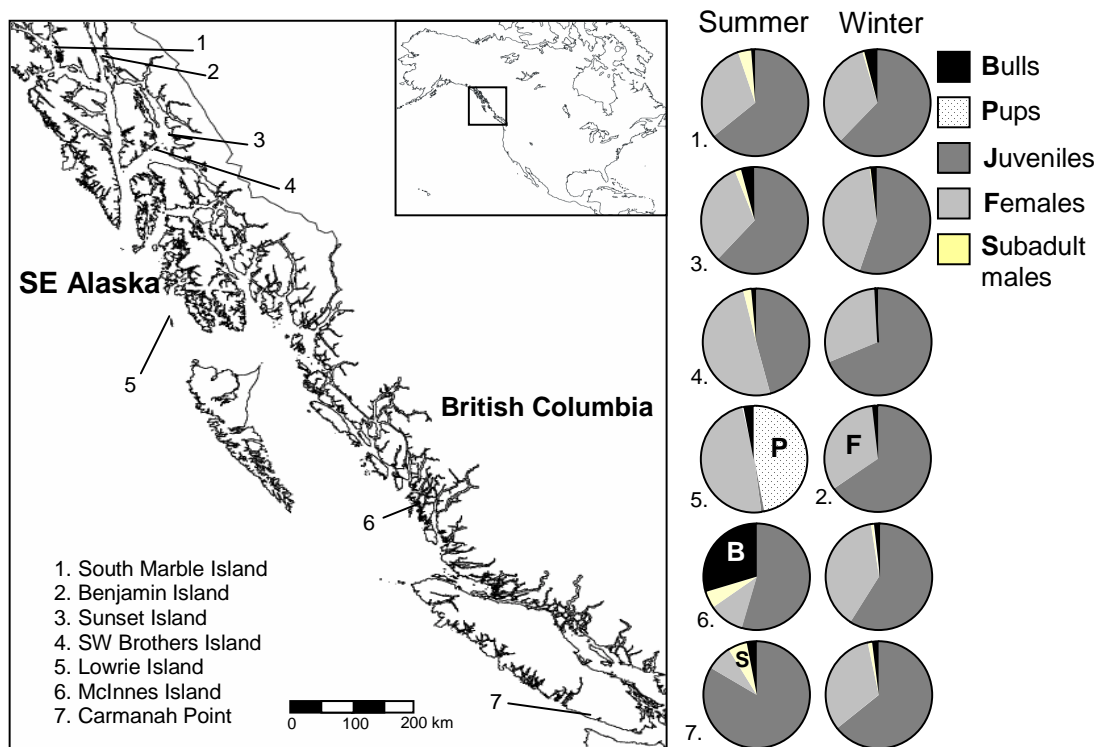


Figure 4.1. Study site locations and proportional age and sex composition of six Steller sea lion haulouts and one rookery (#5). All islands were visited between May – August 2003 and again between February – April 2004 except for Lowrie Island, which was replaced by Benjamin Island, AK in 2004. South Marle (Jun 14 – Jul 8, Feb 22 – Mar 9), Benjamin (Mar 17 – Mar 31), Sunset (May 18 – Jun 5, Feb 23 – Mar 9), SW Brothers (May 18 – Jun 5, Mar 16 – Mar 31) and Lowrie (Jun 15 – Jul 8) Islands are located in southeast Alaska, USA. McInnes Island (Apr 7 – Apr 22) and Carmanah Point (Jul 30 – Aug 14, Apr 7 – Apr 22) are located in British Columbia, Canada. Focal animals were not recorded at McInnes Island during summer.

Observations were conducted at six Steller sea lion haulouts and one rookery between May and August 2003 (n = 5 sites) and from February to April 2004 (n = 6 sites) in southeast Alaska and British Columbia (Fig. 4.1). Sea lions were followed each day between 0900 – 1200, 1300 – 1600 and 1800 – 2000 during the summer months, and between 0900 – 1100 and 1300 – 1500 during the winter / spring study period to document behaviour of individual animals once hauled out of the water before and after a research disturbance. Disturbances caused during collection of fecal samples (dietary analyses) at the haulouts and pup branding (documenting survival and reproductive rates) at the rookery, occurred at the midpoint of the study periods.

Variables of primary interest were length of the follow session, ending behaviour (e.g., going back into the water or settling down), the rate of exhibited behaviours (total number of behaviours exhibited per minute) and the rate of interactions that the follow animal had with other sea lions on the haulout.

Cox proportional hazards model

A Cox proportional hazards model determined factors that affected the length of a follow session (i.e., whether an animal settled down or went back into the water shortly after hauling out). Cox proportional hazards regression typically assesses the effect of several risk factors on the continuation of an event. I adopted this approach to examine the length of each follow session and the variables (risk factors) that might have affected the termination of a follow session. The probability of the endpoint (entering water or settling down) was treated as the ‘hazard’. After removing follow sessions that were dropped or discontinued due to animals disappearing from sight (e.g., behind another animal or rock) as well as sessions that were greater than 60 minutes in length, 3894 follows remained that ended in animals settling down (not exhibiting predetermined active behaviours for five minutes) or going back into the water.

Age / sex class, location, season, end behaviour (into the water or settling down) and the research disturbance were examined to determine their effect on observed differences in follow session lengths. Proportional hazards models are not based on any assumptions concerning the nature or shape of the underlying survival distribution and thus, the underlying hazard rate (length of a follow session) was assumed to be a function of the independent variables. This model addressed the probability of a sea lion remaining on land once hauled out.

Generalized linear models

Maximum likelihood generalized linear models, with an overdispersion parameter, were used to examine sea lion hauling out behaviour. In order to account for the varying lengths of follow sessions and the assumption that sea lion activity is highest just after hauling out, rates were calculated for the total number of behaviours combined and interactions per minute and examined separately for sea lions that settled down and those that returned to the water. Regression analyses assessed factors influencing the rate of behaviours per minute exhibited by focal animals and additionally, the rate of interactions per minute that the focal animal had with other animals after hauling out. Stepwise deletion and Akaike's Information Criterion (AIC) were employed to determine the best model fit. The Chi-square goodness-of-fit test was used to assess the significance of observed differences in the influence of covariates on the rates of behaviours and interactions between animals.

Results

A total of 3894 sea lions were followed after coming ashore over two seasons at seven different locations. Juveniles made up 69% of the focal sea lions hauling out, 20% were females, and subadult males and bulls made up 10% of the follow sessions (Fig. 4.2), consistent with most documented haulout compositions (Fig. 4.1). Sea lion rate of return to the water ranged from 60% (females) to 78% (bulls) (Fig. 4.2).

Likelihood of a sea lion remaining on land after hauling out

The Cox proportional hazards model, illustrated with Kaplan-Meier survival curves (Fig. 4.3), determined the influence of several risk factors on the continuation of behavioural follows. There were distinct behavioural differences between animals that stayed on land and those that soon returned to the water ($Z = 37.49$, $p < 0.001$). Duration of follow sessions differed significantly among age and sex classes ($Z = 2.66$, $p = 0.008$). Animals that returned to the water took between 2.22 minutes \pm 0.1 SE (juveniles) and 2.73 minutes \pm 0.38 SE (subadult males) on average. Sea lions that settled down typically did so between 12.68 minutes \pm 0.47 SE (juveniles) and 14.22 minutes \pm 2.65 SE (subadult males). Focal sea lions took longer to settle down and return to the water in winter / spring compared to summer ($Z = -5.08$, $p < 0.001$) (Fig. 4.3).

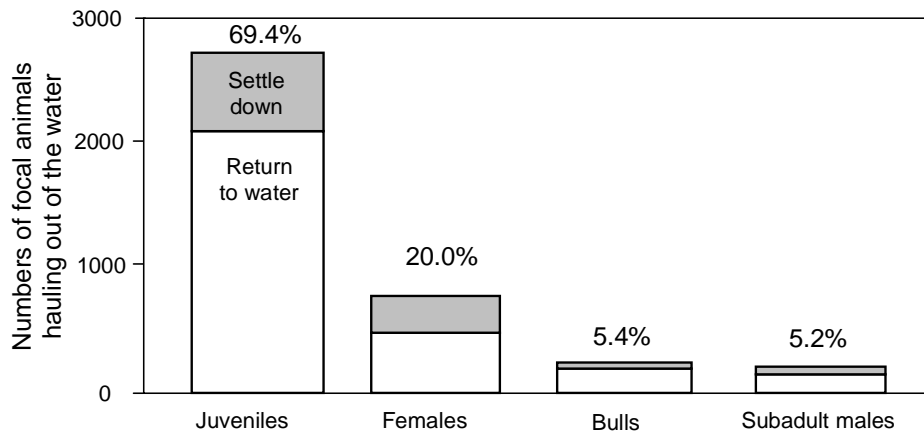


Figure 4.2. Numbers and percentages of focal animals hauling out of the water by age / sex class. Dark portions of the bars represent follow sessions ending with the sea lion settling down ($n = 1026$). White portions of the bars represent follow sessions ending with the sea lion returning to the water ($n = 2868$). Juvenile follow sessions ended with the animal returning to the water 77% of the time, females 60%, bulls 78% and subadult male follow sessions ended in animals returning to the water 74% of the time. Data were combined for all islands over both seasons ($n = 3894$).

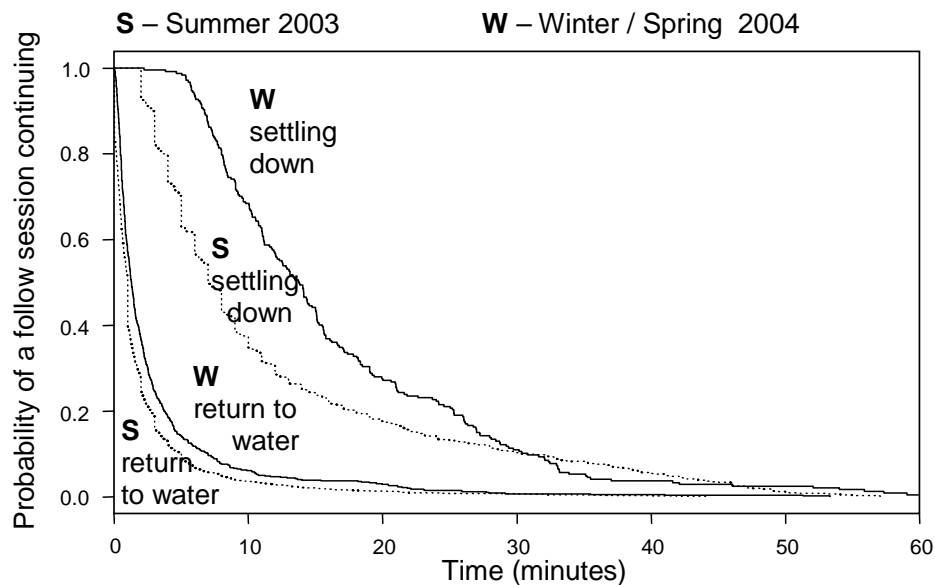


Figure 4.3. Kaplan-Meier survival curves illustrate the probability that an animal hauling out on land will remain engaged in active behaviours. Behaviours of 3894 Steller sea lions were recorded at seven locations over two seasons as they hauled out onto land until they either returned to the water or stopped moving and settled down. All follow sessions had 100% probability of continuing at time = 0. Season and ultimate ending behaviour (settling down or returning to the water) significantly influenced the length of the follow. Each step down on the survival curve indicates the time at which a follow session ended.

Final Cox proportional hazards model covariates were end behaviour (water or settling down), age / sex class (female, juvenile, subadult male and adult male), season (summer, winter / spring) and location (Cox proportional hazards, $df = 3893$, $R^2 = 0.37$). However, there was no difference in model fit with the addition or deletion of the research disturbance as a covariate, suggesting that the disturbance did not affect the likelihood of an individual staying on land or returning to the water following human presence on the haulout. This model was significantly different from the null model (Likelihood ratio test, $G_{12} = 1791$, $p < 0.001$).

Hauling out behaviour

Maximum likelihood generalized linear models examined factors affecting rates of behaviours observed during individual animal follows (Table 4.1). As expected, the longer the follow session, the greater the number of documented behaviours exhibited by a focal animal. Follow sessions that ended with animals returning to the water were much shorter (2.28 minutes \pm 0.13 SE, $n = 2868$) than those that remained on land (13.13 minutes \pm 0.61 SE, $n = 1026$). Due to the high activity of sea lions within the first few minutes of hauling out, and the short duration of the follow sessions that ended with animals returning to the water, rates of behaviours and interactions for animals settling down and those returning to the water were examined separately.

Table 4.1. Correlation coefficients, covariates and interaction terms from maximum generalized linear models examining factors influencing the rates of total number of behaviours combined and sea lion interactions per minute. Stepwise deletion determined best model fit. Significant covariates are shown in bold. Correlation coefficient ranges are given for covariates with multiple categories.

*Location excluded from the Interactions generalized linear model to obtain linear convergence.

Covariates	Correlation coefficients			
	Behaviours per minute		Interactions per minute	
	Settle down	Water	Settle down	Water
Sex (juvenile, female, SAM, bull)	- 0.28 to 0.19	- 0.17 to 0.16	- 0.48 to 0.61	- 0.68 to 0.36
Season (summer, winter / spring)	- 0.29	- 0.13	0.75	0.86
Location	- 0.73 to 0.51	- 0.88 to - 0.74	*	*
Disturbance (before, after)	0.013	- 0.44	0.02	0.01
	Season:Location	Season:Location Location:Disturbance	Sex:Season	Sex:Season Sex:Disturbance
df	1025	2867	1025	2867

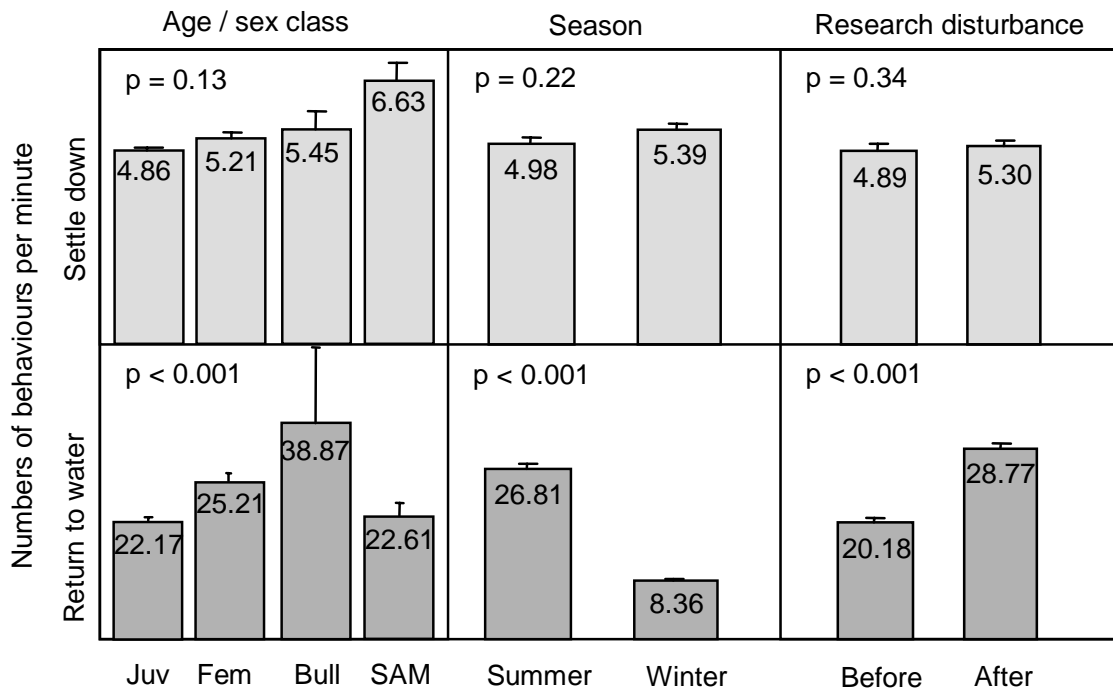


Figure 4.4. Numbers of behaviours per minute for sea lions that settled down (light bars, $n = 1026$) and returned to the water (dark bars, $n = 2868$). Rates of behaviours per minute \pm SE for age / sex class (juveniles, females, bulls and subadult males), season and before and after the research disturbance. Significance values were calculated in generalized linear models.

Of the animals that settled down, subadult males exhibited the highest rate of behaviours per minute (6.63 ± 0.29 SE, $n = 52$) and juveniles the lowest (4.86 ± 0.07 SE, $n = 620$), but were not significantly different (χ^2_{1025} , $p = 0.13$) (Fig. 4.4). Focal animal rates of behaviours differed significantly among locations (χ^2_{1025} , $p < 0.001$). Rates of behaviours amongst animals that settled down did not differ significantly between seasons (χ^2_{1025} , $p = 0.22$), or following the research disturbance (χ^2_{1025} , $p = 0.34$) (Fig. 4.4).

Rates of observed behaviours of animals returning to the water differed significantly among age / sex classes (χ^2_{2867} , $p < 0.001$). Bulls returning to the water exhibited the highest rate of behaviours per minute (38.87 ± 6.21 SE, $n = 164$), and juveniles the lowest (22.15 ± 0.75 SE, $n = 2084$). Rates of documented behaviours for animals returning to the water differed significantly among locations and seasons (higher in summer) (χ^2_{2867} , $p < 0.001$), as well as before and after the research disturbance (higher after the disturbance) (χ^2_{2867} , $p < 0.001$) (Fig. 4.4).

Rates of sea lion interactions

Rates of interactions between focal animals and other sea lions were examined separately for sea lions that remained on land and for those that returned to water (Table 4.1). Haulout location, although considered an important factor in promoting or inhibiting social interactions, was excluded from this analysis in order to obtain linear convergence in the model. Of the sea lions that remained on land, subadult males had the highest rate of interactions per minute (0.54 ± 0.07 SE, $n = 52$) and adult males and juveniles had the lowest (bulls: 0.41 ± 0.07 SE, $n = 47$; juveniles: 0.41 ± 0.02 SE, $n = 620$) (χ^2_{1025} , $p = 0.22$) (Fig. 4.5). Rates of interactions differed significantly between seasons (higher in summer compared to winter / spring) (χ^2_{1025} , $p < 0.001$). Rates of interactions among animals that remained on land were slightly but not statistically lower after the research disturbance (χ^2_{1025} , $p = 0.13$). Of the animals that returned to the water, rates of interactions differed significantly among age / sex class, season (higher in summer) and before and after the research disturbance (higher after the disturbance) (χ^2_{2867} , $p < 0.001$) (Fig. 4.5).

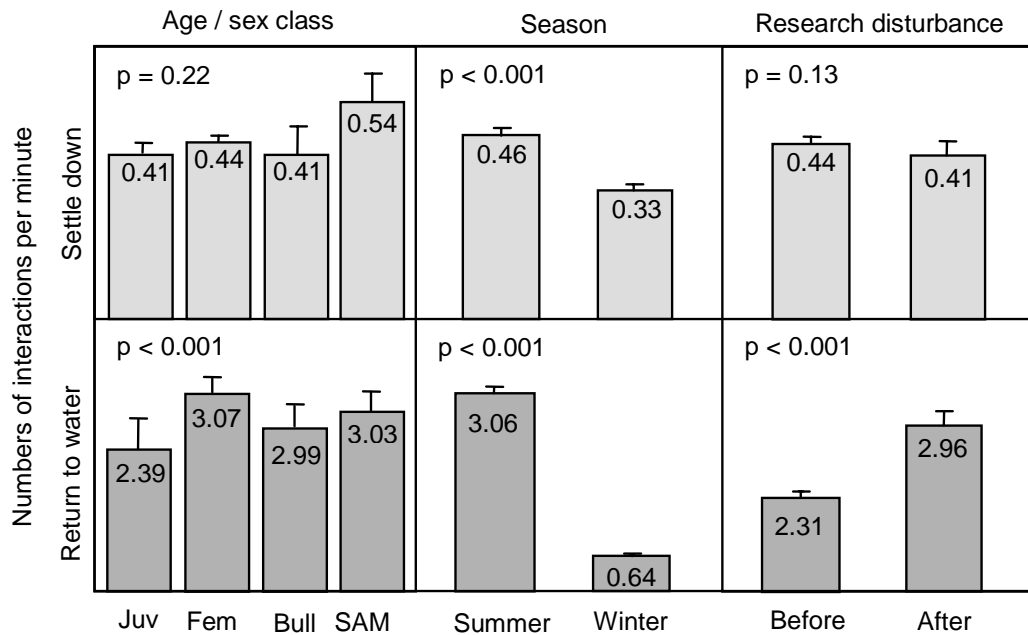


Figure 4.5. Numbers of sea lion interactions per minute for animals that settled down (light bars, $n = 1026$) and returned to the water (dark bars, $n = 2868$). Rates of interactions per minute \pm SE for age / sex class (juveniles, females, bulls and subadult males), season and before and after the research disturbance. Significance values were calculated in generalized linear models.

Discussion

Determining the effects of human disturbance on individual sea lion behaviour first required establishing what was normal or baseline behaviour. Observations of 3894 sea lions revealed significant seasonal differences in the behaviours between animals that remained on land and those that returned to the water. Animals that returned to the water showed a decrease in rates of total numbers of behaviours and interactions in winter / spring compared to summer, and an increase following the research disturbance. Seasonal considerations that might have affected sea lion hauling out behaviour include reproductive status, prey availability and corresponding sea lion foraging efforts, travel distances between haulout and rookery locations, and weather affecting conditions on the haulout and in the water. Steller sea lion behavioural observations at seven different locations over two seasons revealed that individual sea lions take longer to settle down in winter / spring than in summer. While observed rates of behaviour were similar for animals remaining on land, there were substantially different rates among age / sex classes for animals returning to the water.

Pinniped terrestrial behaviour

There is considerable variation in terrestrial behaviour among pinnipeds. Movement on land is the most noticeable difference between phocids (true seals), that propel themselves with their forelimbs in undulating motions, and the otariids (sea lions and fur seals) and odobenids (walrus) that walk using fore and hindlimbs (Berta, 2002). Differences in locomotion affect the types of behaviours that species are capable of on land. Social interactions, dominance hierarchies and group aggregation sizes also vary among species (Bowen, 2002). Similarly, differences in mating systems ranging from extreme polygyny to lekking (Berta, 2002) influence seasonal movements and use of haulouts, and would likely result in varied responses to human disturbance.

It is not clear to what extent my results apply to other species of otariids or to pinnipeds in general. In terms of Steller sea lions, there is a short-term effect of disturbance at a local population level, whereby mean numbers of sea lions using haulouts drop following a major disturbance and do not recover for 2 – 4 days (Chapter 3). At the individual level, rates of behaviours increased amongst animals that returned to the water following a disturbance, but showed no appreciable difference amongst those that elected to stay on land.

Hauling out

The likelihood of a sea lion remaining on land after hauling out was not affected by the experimental disturbance. Instead, the likelihood was influenced by season, which may be indicative of behavioural shifts related to foraging efforts, travel distances, weather or the onset of breeding cycles, all of which may have varying effects on a sea lion's need to haul out and rest (Henry and Hammill, 2001). Harsh weather conditions and limited prey availability may impose behavioural limitations on individuals in the winter (Stillman and Goss-Custard, 2002).

Observations revealed that sea lions took longer to settle down in the winter / spring than they did in the summer (Fig. 4.3). During winter / spring, proportionally fewer animals returned to the water (with an average of 2.5 sea lions returning to the water for every 1 that settled down) as opposed to the summer (2.9:1). This seasonal difference, albeit small, might be related to the fact that sea lions typically spend longer at sea during the winter / spring months (Merrick and Loughlin, 1997; Sease and York, 2003) and may behave differently on shore after their winter trips. A greater proportion of sea lions may also remain on land in winter in response to lower temperatures, harsh weather conditions or fatigue due to greater physical exertions. The seasonal variability in hauling out behaviour may further be indicative of certain times of the year when sea lions are more in need of rest and are therefore more sensitive to human presence and disturbance.

Sea lions intending to stay on land may take their time to find a resting spot, whereas animals not intending to rest may haul out to quickly assess available space and haulout composition before returning to the water. Alternatively, if the location that a sea lion has chosen is full or crowded, there may not be room to remain hauled out. Topography and density of animals on the haulout may also play a large role in determining hauling out behaviour and may explain why there were significant differences in time it took sea lions to settle down at many of the study sites. Study sites varied in size, slope, height, tidal range and rock face features, all of which might have influenced the length of time that it took for follow animals to find resting spots.

Behavioural differences

Of the observed focal animals that remained on land, subadult males had higher rates of behaviour and interactions than did juveniles, bulls and adult females (Fig. 4.4). Such age and

sex class behavioural differences may be related to the social, physical or reproductive status of individual animals and their varying energetic expenditures (Härkönen *et al.*, 1999). Site choice, the amount of time spent on land, and the frequency of hauling out also likely varies among age and sex classes (Suryan and Harvey, 1999).

From spring to the summer breeding season, sea lions redistribute themselves within and among sites according to their reproductive state. Adult males (bulls) begin to establish territories in early summer and actively defend them, allowing some sea lions (females) to remain in the area while keeping others out (typically subadult and other adult males). While this is most common on rookeries, similar behaviours were observed at haulout sites.

Disturbance that displaces adult male sea lions from their territories, especially during the breeding season, increases the likelihood of aggressive interactions occurring among males (NMFS, 2002). Territoriality or aggressiveness may also be responsible for the higher rates of behaviours and interactions observed for bulls and subadult males (Figs. 4.4 and 4.5). Adult males may also provide a stabilizing influence in the summer months that shortens the time it takes other sea lions to settle down after hauling out (Fig. 4.3). Unfortunately, I was not able to differentiate between the effects of density or site topography, either aiding or restricting contact with other animals. However, behavioural indices can provide insight into locations or age classes that may be more vulnerable during certain times of the year.

Effects of disturbance

Generally, higher rates of behaviours and interactions (except for rates of behaviour for animals settling down) observed during summer compared to winter / spring may provide insight into potentially sensitive times of year for sea lions at my study locations. Conservation measures should consider incorporating seasonality when addressing potential effects of human presence in areas of sea lion habitat.

Overall, individual sea lion follows revealed that season, age and sex class, location and the research disturbance played important roles in sea lion hauling out behaviour. Sea lions returning to the water exhibited significantly higher rates of behaviours and interactions following the research disturbance. Determining whether the change in rates of observed behaviours significantly affects the daily activities of Steller sea lions is the next logical step in assessing the effect of disturbance on individual sea lion hauling out behaviour. Even though

sea lion behaviours were affected by human presence, no significant behavioural changes were noted post-disturbance amongst sea lions remaining on land after hauling out. However, those that returned to the water displayed higher rates of behavioural interactions. Whether a sea lion remains on land after hauling out is likely related to environmental conditions and the numbers and density of sea lions already hauled out in a given area (Chapters 2 and 3).

Behavioural follows are time intensive and may not reveal biologically significant changes in patterns of behaviour unless predetermined indicators were identified prior to the onset of the study. It is not known if there are differences in response to events among sea lion age and sex classes, or if all animals observed during the post-disturbance period were present at the site at the time of the disturbance. However, changes in distribution and numbers of animals using the haulout can be assessed in terms of pre- and post-disturbance counts and the influence of environmental variables on numbers of sea lions on land. It may therefore be more appropriate to assess the effects of disturbance in terms of local population recovery (counts and distribution) as opposed to individual behavioural tendencies.

In conclusion, behavioural observations, conducted at six haulout locations and one rookery in southeast Alaska and British Columbia, documented 3894 sea lions hauling out of the water and their subsequent behaviours. This study yielded results indicating that season is an important determinant in Steller sea lion hauling out behaviour and that rates of behaviours and interactions between sea lions differed before and after an experimental disturbance. However, there were no indications of disturbance having a detrimental effect on individual sea lion hauling out behaviour.

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Chapter 5:

Concluding Chapter

The goal of my study was to determine if there were measurable effects of human disturbance on Steller sea lions. To do so, I documented the numbers and composition of sea lions on land before and after a predetermined experimental disturbance. I addressed the various influences of environmental factors on the numbers of sea lions on land to determine the effect that they might have on observed numbers of sea lions. Additionally, to determine if individual behaviour was affected by disturbance, I documented sea lions arriving on shore and their subsequent behaviours to determine normal patterns of interactions and behaviour associated with the movement of animals on land.

Factors that influence haulout numbers

Overall, my study revealed that sea lions appeared to be subject to site-specific environmental pressures, but accommodate these varying influences by altering their hauling out behaviour. Additionally, my study determined that there is a measurable short-term effect of human disturbance on Steller sea lion haul out numbers at both rookery and haulout locations.

Chapter 2 investigated factors influencing the numbers of Steller sea lions on shore at eight locations over two seasons. Numbers of sea lions on shore were compared with tidal height, time of day, tidal stage and the research disturbance. The combination and degree of influence that these factors had on the numbers of sea lions varied seasonally and by site.

My analyses suggest that there is no optimum time of day to count maximum numbers of sea lions, as numbers on shore vary considerably throughout the day. Maximum differences in daily counts revealed that 49% of the peak number of sea lions hauled out could be missed if the survey occurred during times of reduced haulout use. Additionally, using single measures as opposed to multiple counts per day, resulted in a relative difference of 18% estimated variability of numbers of animals on land (absolute value 5.39%). This difference in estimated variability may have implications on estimates of population trends and abundance. Observations from specific haulouts and rookery locations may provide guidelines for estimating daily variation in the numbers of animals hauled out over the course of days and weeks.

Population level effects of disturbance

Chapter 3 documented the short-term effects of research related disturbance on numbers of Steller sea lions using haulouts. Counts and observations made for 1 – 2 weeks before and after a research disturbance were used to determine local population recovery at nine Steller sea lion haulouts and one rookery. My results revealed a site-specific response to disturbance indicating that location is an important determinant of sea lion sensitivity.

Significantly fewer animals used the sites following human presence on shore. I measured recovery both as a percentage and in terms of time. Based on pre-disturbance grand means, the study sites recovered to 63% of pre-disturbance levels during my study periods. Before this study began, 1 – 2 weeks of post-disturbance observations were thought to be sufficient to record full (100%) haulout recovery. However, full percent recovery was only attained at one site (Benjamin Island). If study periods were extended, haulout recovery would likely have been attained at additional sites. To address the temporal nature of recovery, I used two methods for measuring local population recovery. Point count and daily mean recovery to pre-disturbance grand means allowed for determination of 50, 75 and 100% levels of recovery. However, only sites that attained these levels were included in the calculation. Six of the ten sites had daily means that reached the pre-disturbance grand mean with an average recovery time of 4.3 days for these sites.

Coefficients of variation in numbers of sea lions were larger following the disturbances, indicating that the daily variation in sea lions using each haulout increased after the research disturbance. However, daily mean instantaneous rates of change did not differ significantly after the research disturbance, even though fewer sea lions were using the haulout. This indicates that the rate (but not numbers) of animals joining and leaving the haulout remained steady over the course my study period. Overall, reduced numbers of Steller sea lions using haulout sites following human presence represents a measurable short-term effect of human disturbance.

Non-research disturbances were recorded at every study location with varying degrees of response. Disturbance events involving boats, aircraft, birds and other sea lions occasionally caused animals to flee to the water. However, with the exception of two events (a vessel disturbance and eagles feeding on a dead sea lion), none of the additional disturbances caused animals to stay away from the haulout longer than the research disturbance.

Individual level effects of disturbance

Chapter 4 investigated the effects of disturbance and season on individual sea lion hauling out behaviour. Using 3894 individual sea lion follow sessions, I addressed the likelihood of a Steller sea lion remaining on land after hauling out in relation to age / sex class, location and season. Seasonal considerations that might affect sea lion hauling out behaviour include reproductive status of the animal, prey availability and corresponding sea lion foraging efforts, travel distances between haulout and rookery locations and weather affecting conditions in the water and on the haulout.

The likelihood of a sea lion remaining on land after hauling out was most significantly influenced by season and ending behaviours (going back into the water or settling down). Animals took longer to settle down in winter / spring months, which might reflect harsher weather conditions, extreme tidal fluctuations or a redistribution of sea lions within their social order as the breeding season approaches. Rates of behaviour differed significantly among locations. For animals that returned to the water, exhibited rates of behaviours differed significantly among age / sex classes, season, location and the research disturbance. Topography and density of animals on the haulout may play a large role in determining hauling out behaviour. These behavioural observations may provide some insight into potentially sensitive times of year for sea lions when rates of behaviour may change at our study locations.

Strengths and weaknesses

Studies addressing the response of wild populations to any sort of disruption of normal activities are strengthened by examining response at multiple locations. Over two seasons I was able to document sea lion recovery following human presence on six sea lion haulouts and one rookery. Systematic count methodology (20-minute intervals) allowed for detailed analyses of environmental factors influencing the numbers of sea lions on shore as well as addressing three measures of recovery following a research disturbance. My results demonstrate that the numbers of sea lions on land are affected by seasonal and site-specific elements, emphasizing the importance of studying wild populations at multiple sites and during different times of the year.

To further address the issue of recovery from human disturbance I would recommend longer periods of observation, and the inclusion of additional control sites. Although I included two

control sites, they proved to be under varying environmental pressures as well. The dynamic nature of sea lion haulouts necessitates using the same or similar haulouts at the same time of the year to determine 'normal' sea lion behaviour at that location. Another shortcoming of my study was the inability to determine where sea lions were going and what they were doing following the research disturbance. This would only be possible through large scale monitoring and tracking. In addressing factors that influence the numbers of animals on shore it would have also been preferable to include weather data such as temperature, precipitation, wind and water state. Future studies should incorporate weather station data, as it likely affects the hauling out behaviour of sea lions (Withrow, 1982; Watts, 1996; Porter, 1997).

Topography and the propensity of animals to move among sites limited the numbers of animals that could be observed at any given time, as is the case with most land and ship-based surveys. It was assumed that prior to the research disturbance, animals were hauled out in preferred areas at each site, and that the numbers of animals visible from the research blinds represented typical distributions of animals on the haulouts. Redistribution of sea lions in other areas or islands was certainly possible, as was recovery during night hours.

Longer observation periods (additional weeks) would likely have resulted in full recovery being observed at additional haulout locations, depending on recovery assessment. However, recovery periods had not been assessed for Steller sea lions prior to my study, and there was no information to better guide my study design. Tolerance and habituation levels likely varied by location, but were not evaluated. Finally, differences in age and sex composition might also have accounted for some of the site-specific response to various disturbance stimuli and the additional non-research disturbances might also have affected recovery levels or had cumulative effects.

Implications

Establishing site-specific hauling out patterns for Steller sea lions could improve the interpretation of census counts that are used to monitor and assess population trends. There is a need to continue to examine how environmental variables and sea lion behaviour can affect the accuracy of population estimates, especially in terms of estimating variation in observed numbers of sea lions and the percentage of animals that might be missed during survey efforts.

Knowledge of these effects can further future field study designs and help to determine appropriate analyses for data collected under varying environmental conditions.

Short-term effects of human intrusion include disruptions of sea lion daily activities and potential redistribution of animals. It is important to determine whether research disturbance results in short-term changes in spatial distribution of sea lions, or if it ultimately results in reduced use of preferred habitat. Long-term effects of human interference that significantly reduces the amount of time sea lions haul out, or substantially interferes with hauling out patterns, could potentially have consequences on life cycles and activities (Orsini, 2004).

Using an assortment of recovery measures can lead to inappropriate comparison of studies that will likely influence the interpretation of results. In presenting various methods to document recovery, I hope to invoke discussion to determine appropriate local recovery criteria for wildlife populations experiencing human disturbance. Recovery percentages and time to reach recovery levels have direct bearing on conservation and management plans and these numbers should not be reported or used casually. Realizing that research activities are affecting sea lion hauling out behaviour may be the first step in addressing the tradeoff between obtaining information needed to monitor and conserve the population, and the cost to the animals of obtaining it.

Future studies are needed to assess the influence of disturbance on sea lion redistribution within a critical recovery period, as well as to determine the physiological effects that sea lions might experience with repeated human intrusion. Results will further our understanding of group dynamics and the behavioural response of Steller sea lions when presented with major disruptions to their daily activities. It is essential to determine how human disturbance affects sea lions in order to limit the potential adverse effects of scientific investigations, population monitoring and recreational disturbance, as well as to provide managers with the best conservation policies for local situations. Assessing the severity of the effects of disturbance has important practical consequences for management and conservation initiatives.

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