TEMPORAL VARIATION IN LEOPARD SEAL PRESENCE AND PREDATION NEAR AN ANTARCTIC PENGUIN ROOKERY

by

Tracey Rae Mader

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

In

Biological Sciences

MONTANA STATE UNIVERSITY – BOZEMAN
Bozeman, Montana

April 1998

APPROVAL

of a thesis submitted by

Tracey R. Mader

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Wayne Z. Trivelpiece — Wayne Z. Trivelpiece (Signature) — 4-14-98 Date

Approved for the Department of Biology

Ernest Vyse — E R Vyse (Signature) — 4/14/98 Date

Approved for the College of Graduate Studies

Joseph J. Fedock — Joseph J. Fedock (Signature) — 4/15/98 Date

STATEMENT OF PERMISSION TO USE

Signature Tracey Mader

Date April 14, 1998

ACKNOWLEDGEMENTS

I would like to thank Erica Goetze and Piotr Ciaputa for their help in collecting data during the 1995/1996 field season and for making this project a reality. Committee members, Dr. Wayne Trivelpiece, Dr. Kevin O'Neill, and Dr. Robert Garrott, have provided guidance and discussion for this research. I am grateful to Dr. Robinson-Cox, Kristie Allen, and Kasia Salwicka for statistical assistance. I thank the captain and crew of the R/V Polar Duke and members of the 1995/1996 Polish Expedition, Arctowski Station, for their logistical support. This study was conducted under Dr. Wayne Trivelpiece with funding from the National Science Foundation – Division of Polar Programs, grant OPP-9121952.

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ABSTRACT

Temporal and spatial variability in sea ice are hypothesized to impact all trophic levels of the Antarctic marine food web. The leopard seal, *Hydrurga leptonyx*, is a pack ice obligate and a generalist feeder. Information on the life history attributes of leopard seals has generally been limited to population censuses, diet studies of harvested animals, and observations of activity near penguin rookeries. Knowledge of the physical and biological parameters that regulate leopard seal distribution in the Antarctic Peninsula and the extent of their association with penguin rookeries is uncertain. Between 1984/85 - 1996/97 leopard seal sightings near a penguin rookery were recorded at the Admiralty Bay field station, a long-term research site, on the southwestern shore of King George Island (KGI), South Shetland Islands. Records of weekly leopard seal censuses and opportunistic leopard seals sightings were investigated to determine annual presence and predation patterns. Leopard seals were most often sighted in October and declined in each subsequent month of the austral summer. Annually, leopard seal numbers at the penguin rookery were highest in years following moderate ice winters when the October pack ice edge was in the vicinity of KGI. When the position of the ice edge was distant from our site, in years of both high and low ice winters, the numbers of leopard seal sightings were low. In addition to the long-term studies, we initiated a systematic study of intrannual variation in leopard seal presence and behavior near the rookery during the austral summer of 1995/96. Observations of leopard seals and associated physical and biological factors were recorded in fixed 3-hour blocks between 8 October and 11 February. Local sea ice condition, time of day, day of year, and penguin activity to and from the rookery were investigated as correlates of intrannual leopard seal presence. A logistic regression model for the 1995/96 data determined that the independent variables, day of year and ice condition, explained 31% of the variation in leopard seal presence near the rookery. Leopard seals were more likely to be present early in the season than later and there was a positive correlation between increasing local ice cover and leopard seal presence. Analysis of leopard seal predation observations indicated both diel and seasonal trends in the 1995/96 study and the long-term monitoring records. In October and early November, leopard seal predation behavior and penguin activity occurred throughout the day. During this time, Adélie penguins arrived at the rookery with 1-2 kg body fat to sustain them over their prolonged courtship period. In December and January, leopard seal predation behavior was concentrated between 1500-2100 hr., as was the number of penguins arriving to the rookery. During this time adult breeding Adélie penguins made frequent trips to sea in order to feed their growing chicks and carried up to 600g of krill upon their return. These findings indicated that leopard seal predation behavior was correlated with penguin activity and that as leopard seals frequented the coast near the rookery they preyed on those penguins which best afforded a fat, energy rich source of food at various times of the year.

INTRODUCTION

Studies of the Antarctic Peninsula marine ecosystem have recently focused on the variability of sea ice and its impact on predator and prey populations dynamics (Fraser et al. 1992; Siegel and Loeb 1995; Trathan et al. 1996; Trivelpiece and Fraser 1996; Loeb et al. 1997; Trivelpiece and Trivelpiece in press). Annual variation in sea ice extent in this region ranges from an average maximum coverage in September to an average minimum coverage in February (Stammerjohn 1993; Stammerjohn and Smith 1996). Recent declines in the extent of Antarctic Peninsula sea ice have been correlated with a 50-year warming trend in air temperatures (Fraser et al. 1992; King 1994; Stark 1994; Smith et al. 1996). Between the 1940s and 1960's, winter temperatures were sufficiently cold for sea ice to extend north of the South Shetland Islands an average of 4 out of 5 years (Fraser et al. 1992). However, an analysis of microwave satellite imagery since 1973, indicates that annual winter sea ice currently reaches this region of the Antarctic Peninsula only 1-2 years in each 5-7 year period (Stammerjohn 1993; Stammerjohn and Smith 1996; Hewitt 1997). These cycles in the temporal and spatial distribution of sea ice are hypothesized to affect all trophic levels of Southern Ocean community including krill populations (Siegel and Loeb 1995; Loeb et al. 1997) and krill dependent predators such seabirds and seals (Fraser et al. 1992; Trivelpiece and Trivelpiece in press). The leopard seal, *Hydrurga leptonyx*, is a top predator in the Antarctic marine ecosystem known to eat krill, penguins, and seals (Ørtisland 1977; Siniff et al. 1979; Kooyman 1981; Laws 1984; Siniff and Stone 1985). If temporal and spatial variability in sea ice impacts all levels of the Antarctic marine food web, an examination of leopard seal abundance and predatory behavior might reveal correlations between environmental parameters and predator-prey interactions.

The leopard seal, a pack ice obligate of the Southern Ocean has been relatively unexploited and understudied by humans because of its solitary existence and inaccessibility. An estimated 220,000 - 400,000 leopard seals live in the Antarctic with a circumpolar distribution, concentrated between 50^0 S and 79^0 S (Laws 1984). Leopard seals range from the coasts of the Antarctic continent to the edge of the pack ice with seasonal migrations or dispersals to Antarctic and Subantarctic islands (Müller-Schwarze and Müller-Schwarze 1975; Rousevell and Eberhard 1980; King 1983; Borsa 1990). During the austral summer, most leopard seals are found in the outer 100 km of the northern edge of the Antarctic pack ice (Gilbert and Erickson 1977). The leopard seal is generally a solitary species (Erickson et al. 1971), with females giving birth to pups in the pack ice from November to December (Laws 1984). Reports by Testa et al. (1991) suggest that the annual north-south movement of leopard seals may be cyclic and correlated with oceanographic features that influence Antarctic pack ice.

Information on the life history attributes of leopard seals has generally been limited to population censuses of distribution and short-term harvest studies. Analyses of stomach contents in such studies have indicated that leopard seals take both vertebrate and invertebrate prey. The major invertebrate prey species include krill (*Euphausia spp.*) and cephalopods which make up approximately 50% and 6% of the diet, respectively. Vertebrates in the diet of the leopard seal include penguins (20%), seals (14%) and fishes (9%) (Ørtisland 1977; Kooyman 1981; Laws 1984). Siniff and Stone (1985) reported temporal variation in the prey species eaten by leopard seals in the Antarctic Peninsula region. Krill were important in the diet late in September and again in March, and most likely remained essential throughout the winter. Cephalopods were taken throughout the year. November through February young crabeater seal pups, *Lobodon carcinophagus*, were consumed as available (Siniff et al. 1979) and penguins were important to the leopard seal diet in mid-February when fledglings entered the water (Siniff and Stone 1985).

Though seasonal prey preferences may depend on availability, leopard seal presence is associated with most rookeries where penguins congregate to breed in the austral summer (Penney and Lowry 1967; Müller-Schwarze 1971; Müller-Schwarze and Müller-Schwarze 1975; Hunt 1973). However, the extent to which leopard seals associate with specific sites and their distribution in the Antarctic Peninsula during the austral summer is uncertain. Previous studies have examined leopard seal hunting methods and rates of predation and suggested that leopard seal behavior was influenced by environmental variables such as seasonal-effects, time of day, sea ice conditions, tide, and surf (Penny and Lowry 1967; Müller-Schwarze 1971; Müller-Schwarze and Müller-Schwarze 1975; Siniff and Stone 1985). The objective of this study was to determine the extent to which temporal and spatial variability in environmental factors affected the presence and predatory behaviors of leopard seals. I described and quantified leopard seal behavior and environmental variables near an Antarctic penguin rookery in 1995/96 and summarized long-term abundance data collected at the site between 1984/85 and 1996/97. Specifically, I wanted to determine if leopard seal behavior varied daily, seasonally, or annually and what biological and/or physical factors influenced this variance. I hypothesized that daily and seasonal leopard seal presence and predation near the Admiralty Bay rookery was correlated to penguin activity, sea ice conditions, time of day, and time of season. To investigate temporal variation over a larger scale, I sought to correlate annual leopard seal presence with long-term data records of penguin abundance and mortality, and the extent of regional sea ice.

METHODS

Study Area

King George Island (KGI) is the largest of the South Shetland Islands and lies approximately 100 km northwest of the Antarctic Peninsula at 62^0 10' S, 58^0 27' W (Figure 1). KGI is bordered by the Drake Passage to the northwest and Bransfield Strait to the southeast. Currents from both these waters move in a northeasterly direction along the shores of KGI. The prevailing winds in this region are westerly which causes pack ice to consolidate against the northwestern side of the island, leaving the shores of the southeastern side open (Trivelpiece et al. 1987; 1990; Trivelpiece and Fraser 1996). Admiralty Bay, on the southeast side of KGI, is 5 km wide at its mouth and opens up into the Bransfield Strait where wind and ocean currents sweep ice in and out of the bay. The penguin rookery is located along the western shore of Admiralty Bay (Figure 1) and is designated a Special Site of Scientific Interest (SSSI #8) by the Antarctic treaty which prohibits visitors without a permit. The rookery is largely composed of two species of penguins: 5000-10000 Adélie (*Pygoscelis adeliae*) and 1500-2500 gentoo (*P. papua*) penguin pairs. An additional 3000-4000 pairs of chinstrap penguins (*P. antarctica*) breed at three nearby rookery sites along the western shore of Admiralty Bay.

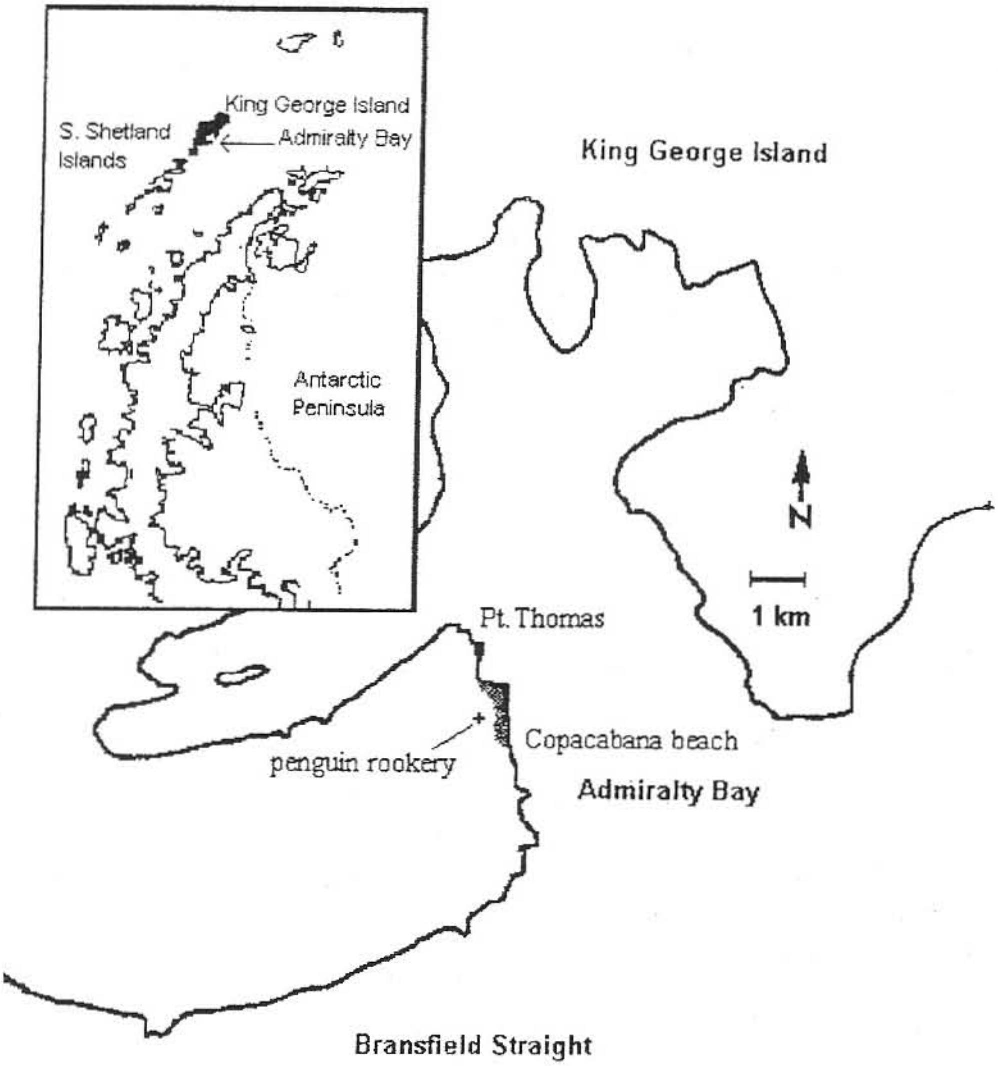

Figure 1. The location of Admiralty Bay on the southeastern shore of King George Island, South Shetland Islands, Antarctic Peninsula (adapted from Trivelpiece et al. 1990).

Data Collection

1995/96 Intrannual Leopard Seal Study

In the austral summer of 1995/96, a study of intrannual variation in leopard seal behavior was conducted at the Admiralty Bay field station. Observations of leopard seals were made between 8 October and 11 February from a blind overlooking the bay. The wooden blind was located on a hill approximately 30 m above the beach and 100 m from the tidal zone. The blind had windows on three sides which made it possible to observe the beach (200 x 1150 m) (Figure 1), as well as the surrounding ocean to approximately 1 km. Observations were made in fixed 3-hour blocks that were randomly scheduled starting at daylight and ending at dusk. Duration of daylight varied seasonally from 12 to 23 hours during the study. A total of 651 hours of observations were conducted (approximately 33 hours every week with a maximum of 9 hours recorded daily). Binoculars (10 X 40) and/or a spotting scope (45X) were used to locate leopard seals. At the beginning of each observational period, the following information was recorded: date, time of day, ice type (bergs or pack) and ice cover in bay and along shore (scale from 0 to 9 - no ice in bay to bay completely covered by ice). Leopard seal behavior, the number and species of penguins arriving and departing the rookery beach, and the occurrence and identity of flying bird species above or within the study area were recorded at intervals throughout the observations.

An attempt was made to document all occurrences of leopard seal behavior during each observation period. This method of sampling was possible because leopard seal behaviors above water were obvious enough to attract the attention of an observer, and behavioral events were not too frequent to record. The identification of individuals during or between observation periods was not feasible; however, the probability of seeing any one seal at one time was random which provided a relatively unbiased sample of behaviors in the group as a whole. The following information was documented for each seal sighting: time, seal location (distance and direction from blind), size, sex, and behavior (four categories of leopard seal behavior included: haul out - resting on ice or land, patrol - swimming along beach, chase - chasing penguin, and kill - killing penguin. Predation events were timed in discreet phases: chase, kill (jerk-bite: throwing penguin back and forth with head and eating), or escape, recapture. Penguin species and age (adult or fledgling) were recorded for each predation event.

The number of penguins arriving and departing the rookery were censused every 30 minutes during the 3-hour observation period. A complete scan sample (Altmann 1974) took 60-120 seconds. To facilitate the census, the entire beach was divided into 50 m sections, marked by orange painted rocks that could be seen from the blind. Species and numbers of penguins entering or exiting the beach through each 50 m segment were recorded. Orientation of penguins towards the water as well as movement, behavior (i.e., shaking off water to dry feathers, preening), and the appearance of the underside flipper (penguins exiting the water display pink vascilated flippers to dissipate heat) were used to confirm whether birds were arriving or departing the rookery.

Birds flying above the study area were censused at these same 30 minute intervals (30 second scan sample). The abundance of each of the following species was noted: kelp gull *(Larus dominicanus*), giant petrel (*Macronectes giganteus*), Wilson's storm petrel (*Oceanites oceanicus*), cape petrel (*Daption capense*), brown skua (*Catharacta lonnbergi*), south polar skua (*Catharacta maccormicki*), and snow petrel (*Pagodroma *nivea*). The presence of flying birds or feeding flocks on or above the water were particularly influential in locating leopard seal predation events. Birds circling and/or vocalizing over the kill drew the attention of the observer to the kill. The arrival sequence of flying bird species was of interest in determining which species were involved in locating prey and which species used other birds to locate this food source.

1984/85 – 1996/97 Annual Leopard Seal Study

During the austral summers of 1984/85 through 1996/97, surveys of leopard seal abundance were conducted in two ways: a weekly beach census and daily opportunistic sightings. Weekly beach censuses were made once each Sunday at mid-day from October through February. The censuses included leopard seals in the water, hauled out on the beach or on ice flows along a 2.5 km stretch from Pt. Thomas to Copacabana beach (Figure 1). In addition, daily opportunistic records were kept on leopard seal presence and predation behavior during consistent effort field studies at the Admiralty Bay field station. This documentation was considered opportunistic or *ad libitum* (Altmann 1974) in that no sampling regime was followed.

Census numbers from representative colonies of breeding penguins at the rookery provided annual estimates on the relative number of penguins breeding at the rookery between 1984/85 and 1996/97 (Trivelpiece et al. 1990). Records were also kept on 200 banded reproductive study birds each year. Nest sites of these breeding penguins were visited daily throughout each austral season and penguins that did not return to relieve their mates and/or feed their chicks were assumed to have been killed by leopard seals, as other known sources of adult mortality during the breeding season are limited. Banded penguins that were considered lost to leopard seals in one season were never observed at the rookery in a subsequent year. A large percentage of these bands were recovered from carcasses of penguins that washed up on the beach each season, further supporting the assumption that penguin mortality was the result of leopard seal predation.

Long-term data concerning the extent of sea ice in the Antarctic Peninsula is based on summaries from Stammerjohn (1993), Stammerjohn and Smith (1996), and Hewitt (1997).

Data Analysis

The 1995/96 intrannual data of leopard seal presence and behavior and penguin activity to and from the rookery were summarized as frequencies and are presented as trends. Annual leopard seal presence and ice conditions at Admiralty Bay are presented as means ± one standard deviation. Logistic regression was used to determine the affect of 4 independent variables (date, time of day, ice condition, and penguin activity) on leopard seal presence/absence. To increase the independence of each sample, the analysis was based on 3-hour observation periods in which leopard seal presence were recorded as present (1) or absent (0). The regression model selection of subsets of independent variables and all their interactions were made using SAS proc logistic (SAS Institute 1988) and Wald chi-square values. Nonparametric two-way contingency table analyses (Fisher's exact test) were conducted to compare leopard seal presence in each month of the 1995/96 austral summer.

Multiple regression was used to analyze annual differences in leopard seal presence, penguin prey abundance, opportunistic leopard seal kill sightings, and penguin mortality records between the years 1984/85 –1996/97. Non linear regression helped determine the relationship between the annual ice index and leopard seal presence. Nonparametric two-way contingency table analyses (Pearson's Chi square) were conducted to compare the frequencies of seal behaviors that were recorded by two different sampling schemes - systematic sampling during the 1995/96 field season and *ad libitum* sampling from 1984/85 –1996/97. STATISTICA (StatSoft 1994) was used for both parametric and non-parametric analyses. Parametric tests were applied if the residuals were normally distributed.

RESULTS

1995/96 Behavioral Observations

During the 1995/96 austral summer, 304 observations of leopard seals were recorded during 651 hours of observations. Haul out behavior accounted for 47% (n=142) of all leopard seal sightings. Thirty-six percent of the observations were patrols (n=110), 10% chases (n=31) and 7% kill (n=21). All leopard seal predation behaviors observed were timed, but only 2 of the 21 records captured the entire sequence of events from patrol to chase to kill. The times for these two records were 9.20 and 12.15 min. The mean time documented for all partial predation observations was 9.0 $\pm$ 11.0 minutes (chase: mean=1.7 $\pm$ 1.8 minutes; kill: mean= 6.0 $\pm$ 4.0 minutes). Leopard seals kill their prey by violently jerking the bird from side to side above the surface of the water. Mouthfuls of flesh are separated from the penguin carcus for the leopard seal to consume in "jerk-bites" (Müller-Schwarze and Müller-Schwarze 1975). After each jerk-bite, the leopard seal must retrieve the carcus to repeat the process. The mean number of leopard seal jerks-bites documented per kill was 24.0 $\pm$ 23.0. Of the penguin prey being chased and/or killed, 16 times the penguin was identified as an Adélie and once as a gentoo. Thirty-two observations were made of leopard seals waiting near ice bergs or pack ice for what appeared to be a surprise attack on incoming penguins. The seabird that most often congregated at kills was the kelp gull which arrived first 15 of the 21 times the event was recorded, followed by cape petrel (10 times), giant petrel (6 times), south polar skua (3 times), brown skua (2 times).

1995/96 Leopard Seal Presence and Correlated Variables

The results of a logistic regression using the dependent variable presence/absence (77 presences and 111 absences) and 4 independent variables (date, time of day, ice condition, and penguin activity) indicated that date (χ^2=9.1, p <0.01) and ice (χ^2=5.7, p=0.02) were the only two independent variables which added significantly to the model (penguin χ^2=0.09, p=0.77; time χ^2=1.08, p=0.29). Maximum likelihood estimation procedures (stepwise selection, forward selection, and backward elimination of best subsets in SAS) and Akaike Index Criteria (AIC) values were used to select the most parsimonious model for the data (Burnham and Anderson 1992). The model that included both date and ice accounted for 31% of the variance in leopard seal presence/absence and had the lowest AIC value (Table 1).

Once the Date + Ice model was chosen, a second best subsets procedure (SAS) was run to include potential interactions between the four independent variables. AIC values were used to rank the models in descending order of preference. The 2-3 variable models selected are presented in Table 2. Comparison of the Date + Ice model with the interaction models concluded that all models (Table 2) were within 2 AIC values of each other (i.e. a 90% confidence interval) and therefore comparable in parsimony and fit (Sakamoto et al. 1986). Correlation matrix graphs depicted the interactions between these variables and indicate that samples were well distributed across all dates and times, and that all types of ice conditions were represented (Appendix).

Table 1. Model selection of independent variables used in logistic regression to predict leopard seal presence in 1995/96. The variable date refers to the day of the austral summer. Ice represents ice coverage in the study area. Penguin refers to the number of penguins censused. Time represents the time of day.

Model	R-square	Variation %	AIC
Date	0.52	26.78	156.20
Ice	0.45	20.65	159.87
Penguin	0.26	6.76	170.46
Time	0.04	0.15	177.12
Date + Ice	0.56	31.14	150.24
Date + Ice + Penguin	0.56	31.32	150.98
Date + Ice + Penguin + Time	0.56	31.33	152.90

Table 2. Best subsets models of independent variables (date, ice, time, penguin) and their interactions obtained from SAS proc logistic for regression of 1995/96 leopard seal presence data.

Model	AIC
Date + Ice(Time)	148.65
Date + Date(Ice)(Time)	149.02
Date + Date(Penguin) + Date(Ice)(Time)	149.93
Date + Date(Ice)	149.98
Date + Ice	150.24
Date + Penguin + Date(Ice)(Time)	150.34
Date + Date(Ice) + Date(Penguin)	150.53

Date

Date explained 26.8% of the variation in the model used to predict leopard seal presence during the 1995/96 austral summer. There was a negative correlation between leopard seal presence and date (Julian calendar 1 =October 1) (Figure 2) indicating leopard seals were more likely to be present earlier in the season than later. Results of a Fisher's exact test indicated that the frequency of 3-hour observation periods in which a leopard seal was present was significantly higher in October (30 of 37 observations) than in any other month ($p<0.01$). Significantly more leopard seals were seen in November than in January or February ($p<0.01$). Leopard seal size also varied with date. In October and November, adult (>age 3) leopard seals (i.e. those with a length of >2.5 m (Laws 1958)) of both sexes were recorded. Smaller individuals were observed in December and January (five leopard seals < 2.5 m were hauled out on 1 December 1995). The sex of leopard seals observed in predation behavior was undetermined.

The number of leopard seal behaviors recorded per 3-hour period also declined from October through February (Table 3). Leopard seals were seen hauled out as well as patrolling and chasing in close proximity to one another during the month of October. On 13 October two leopard seals were observed patrolling side by side (within 3 m of one another) while a third seal was recorded chasing a penguin within 50 m. Twenty-eight adult leopard seals (both male and female) were observed hauled out on ice on 30 October.

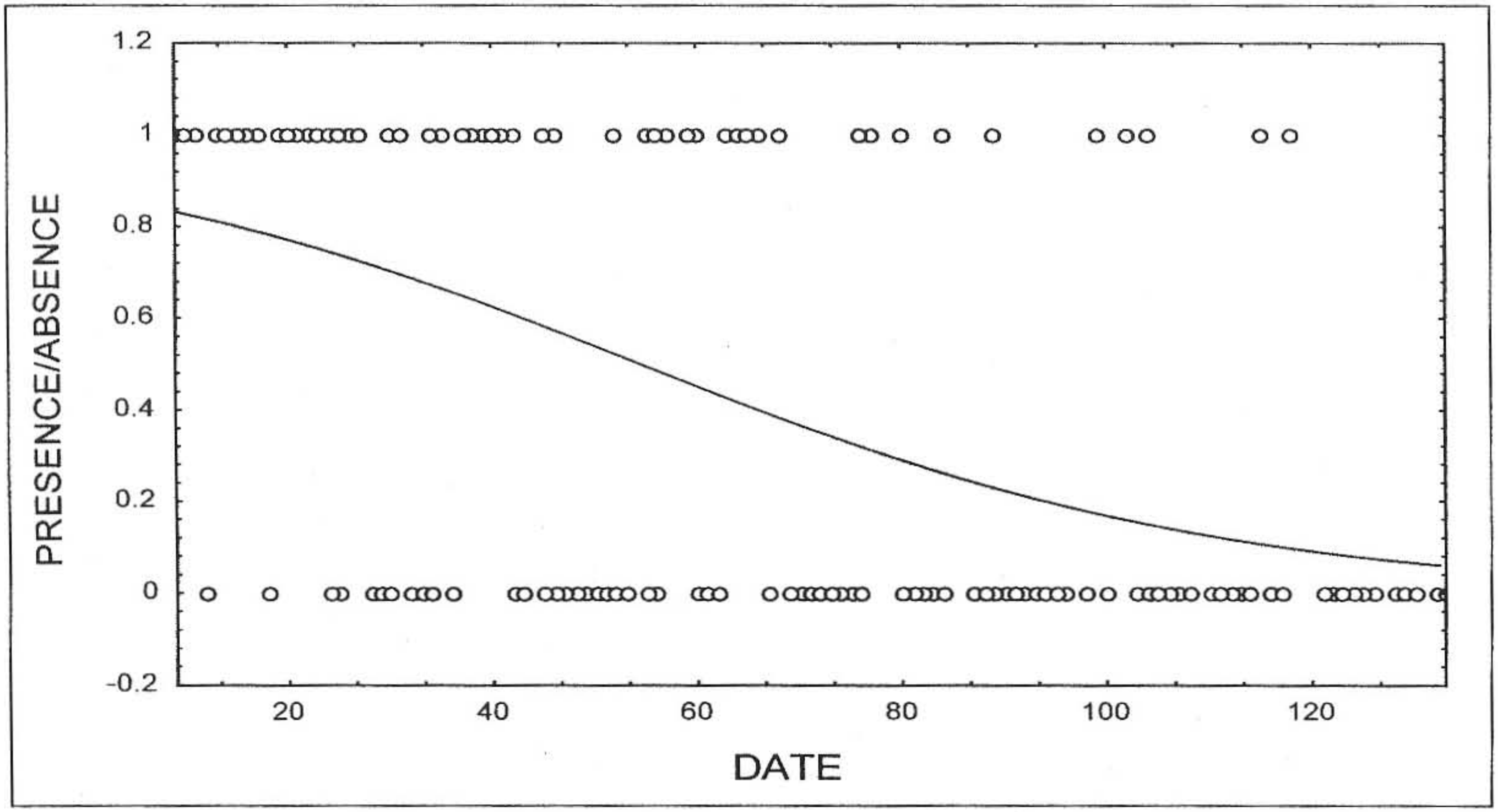

Figure 2. Non-linear estimate of 1995/96 leopard seal presence/absence (1/0) near the Admiralty Bay Rookery and date, or day of season (Julain date 20=October 20, 120=January 28).

Table 3. A summary of 651 hours of leopard seal behavioral observations including the number of observations of each behavior per month and the frequency of behaviors recorded in each 3-hour observation period for the 1995/96 austral summer.

	October		November		December		January		February	
Behavior	N	Freq.	N	Freq.	N	Freq.	N	Freq.	N	Freq.
Haul out	57	1.3	67	1.3	18	0.3	0	0.0	0	0.0
Patrol	71	1.7	10	0.2	17	0.3	11	0.2	1	0.1
Chase	20	0.5	7	0.1	4	0.1	0	0.0	0	0.0
Kill	13	0.3	3	0.1	4	0.1	1	0.0	0	0.0
Total obs.	161	3.8	87	1.7	43	0.8	12	0.2	1	0.1
No.3hr obs. per month	43		52		56		48		18	

Ice Conditions

There was a positive correlation between the extent of ice cover in Admiralty Bay at the time of each observation period and leopard seal presence (Figure 3). Ice condition explained 20.7% of the variation in the model used to predict leopard seal presence. As ice cover increased to fill half of the study area, the likelihood of seeing a leopard seal increased. The mean and range of ice conditions near the penguin rookery were larger in October (mean= 2.3 ± 2.4, range 0-9) and November (mean=2.3 ± 2.7 range 0-9) and then declined in December (mean=0.9 ± 1.4, range 0-5) and January (mean=0.1 ± 0.4, range 0-1), and increased slightly in February (mean= 0.5 ± 0.5, range 0-1).

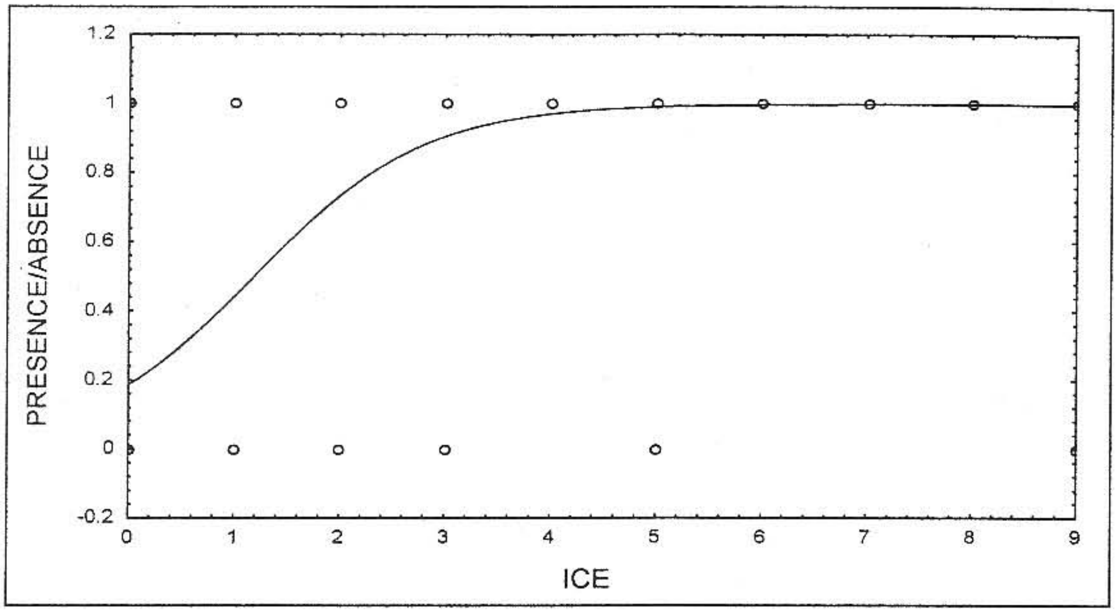

Figure 3. Non-linear estimate of 1995/96 leopard seal presence/absence (1/0) near the Admiralty Bay Rookery and ice condtions (ordinal scale 0-9).

Time of Day

There was no significant correlation between time of day and whether or not leopard seals were present near the penguin rookery in 1995/96 (p=1.08) (Figure 4). However, the number of leopard seal behavioral observations per 3-hour period did show diel patterns. When both predation (patrol, chase, kill) and haul out behavior (resting on ice) were combined, peak numbers occurred between 1200-1800 hrs in all months of the austral summer. When predation and haul out behaviors were separated, we found that in October both behaviors occurred throughout the day. In November, more predation behavior was observed between 0600-1200; whereas haul out behavior was greater in the afternoon and evening between 1200-1800. During December and January, both predation and haul out behavior was highest between 1500-2100 (Figure 5).

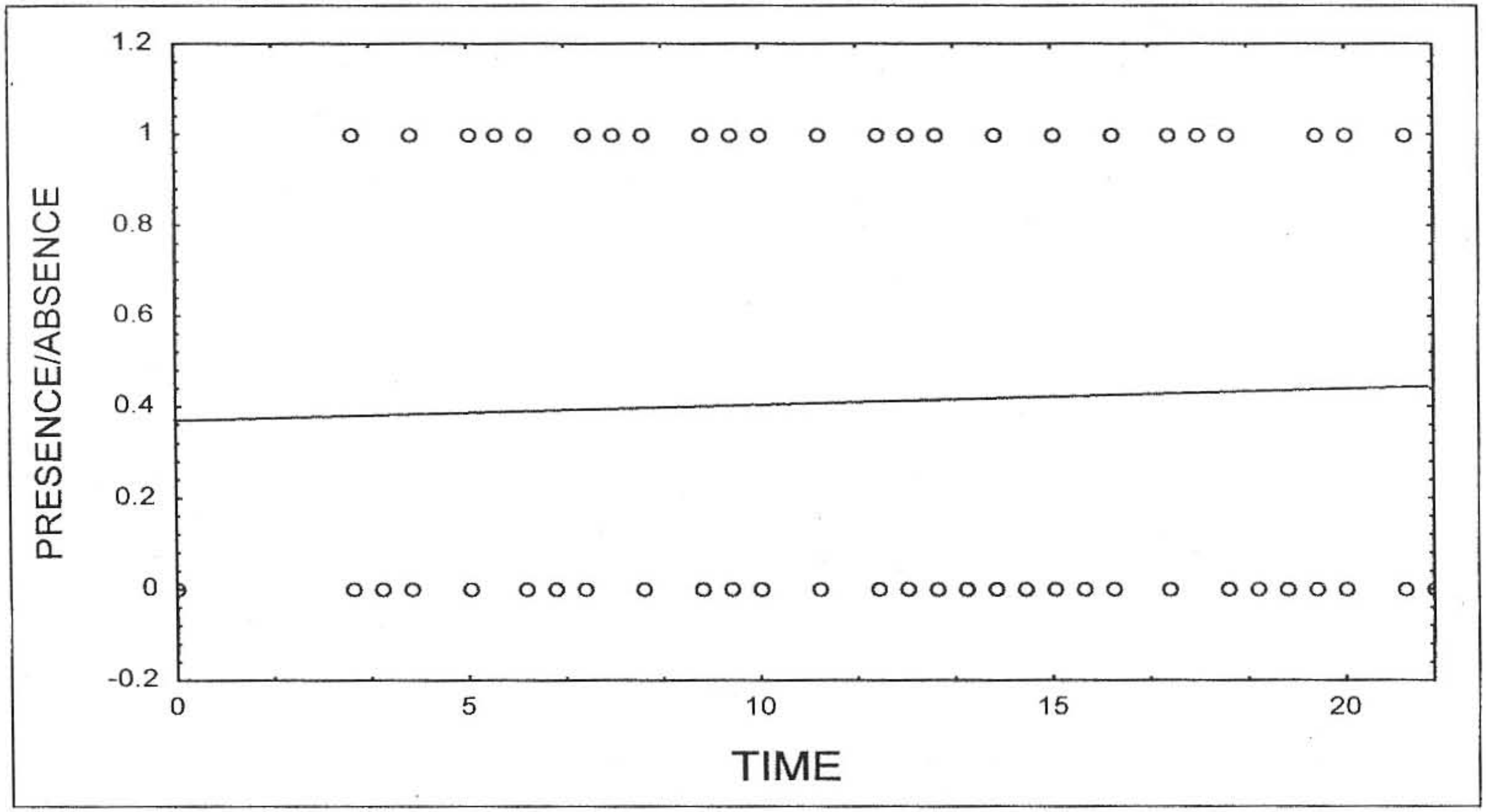

Figure 4. Non-linear estimate of 1995/96 leopard seal presence/absence (1/0) near the Admiralty Bay Rookery and time of day (0000-2300 hr).

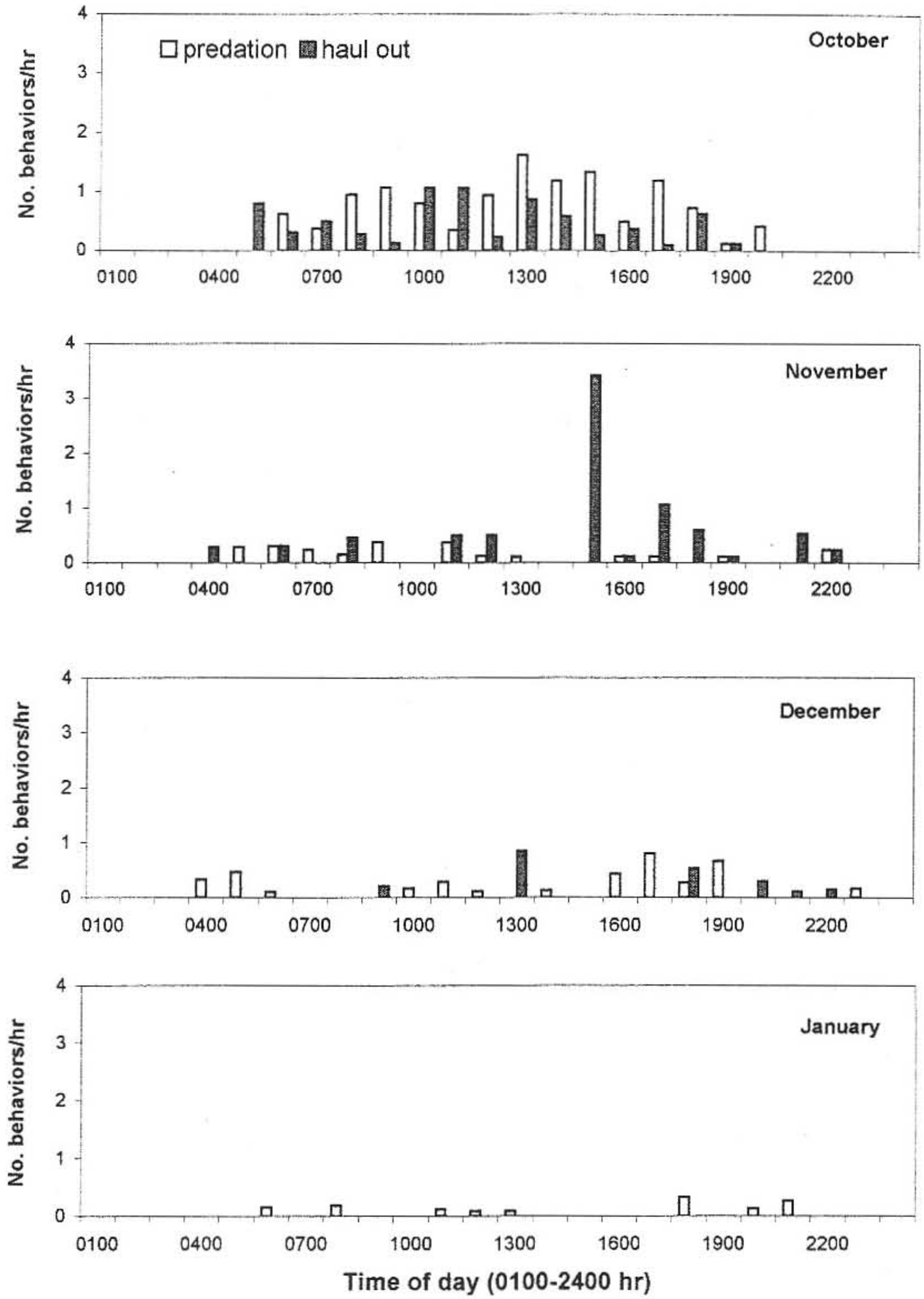

Figure 5. Diel variation in leopard seal predation behavior (patrol, chase, kill) and resting behavior (haul out) near the penguin rookery based on 651 hours of observation during the 1995/96 austral summer.

Penguin Activity

Penguin activity alone explained only 6.8% of the variation in leopard seal presence at the penguin rookery (Figure 6). The scan samples of Adélie, gentoo, and chinstrap penguins were averaged per 3-hour period to provide a comparison of penguin activity throughout the summer. These censuses indicated that penguin activity increased from October to January (October mean of 92.5 ± 103.4, November mean=233.5 ± 147.0, December mean = 524.5 ± 218.4, January mean = 594.9 ± 343.7) and then declined in February (mean = 124.4 ± 72.0).

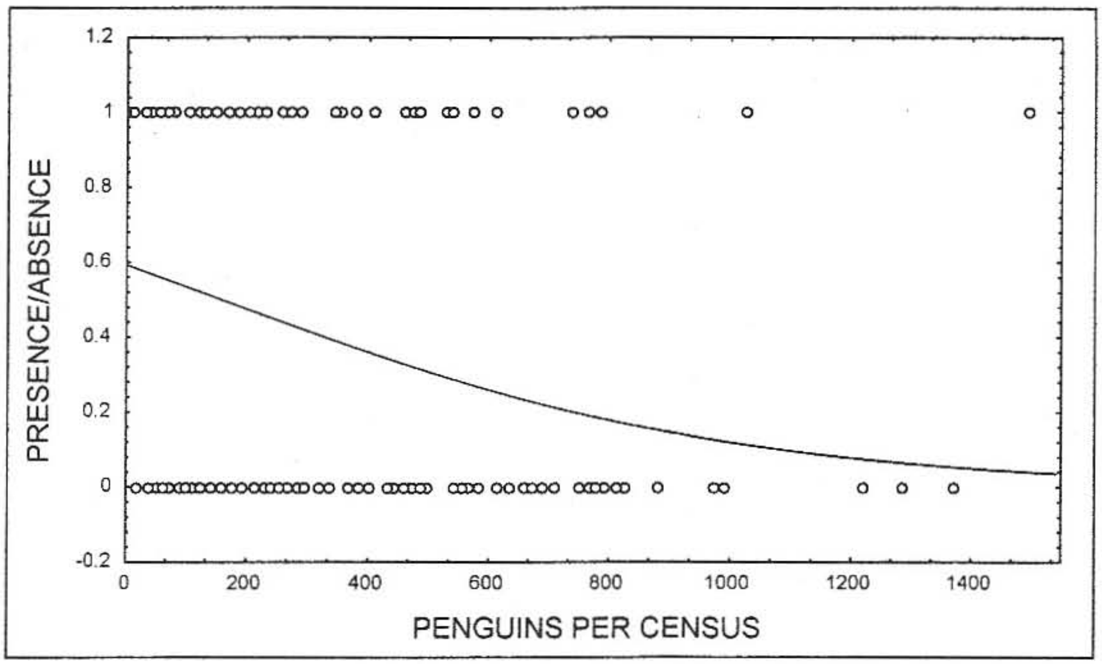

Figure 6. Non linear estimate of 1995/96 leopard seal presence/absence (1/0) near Admiralty Bay and penguin activity.

Diel penguin activity remained relatively constant, peaking at different hours each month of the austral summer. In October penguin numbers peaked between 0600-1200, November and December 1800-2400, January and February 1200-1800. The increased range in activity hours coincided with increased day length. Penguin activity was further separated into penguins arriving or departing the rookery and then compared to leopard seal predation behavior by time of day for October - January 1995/96 (Figure 7). In every month except October, the number of penguins arriving at the rookery generally increased throughout the day, with numbers peaking between 1500 and 2100 hours. In all months, penguins departing the rookery peaked in the morning hours (0600-1200) and then declined slightly throughout the day. Overall, leopard seal predation behavior didn't seem to follow the trend of penguins arriving or departing the rookery largely due to the fact that there were no penguin differences in October when most of the leopard seals were recorded. Graphs of only Adélie penguins arriving or departing the rookery through each month of the season depicted the same basic trends in activity as all penguins combined.

1984/85-1996/97 Annual and Intrannual Variation

Weekly Seal Census

A total of 123 leopard seal sightings were recorded in 220 weekly seal censuses between 1984/85-1996/97. A mean of 0.5 ± 0.5 leopard seals were recorded per census. Three to four year oscillations in peak leopard seal abundance occurred during those years (Figure 8). Adélie penguin abundance and leopard presence between 1984/85 – 1996/97 were not directly correlated (R^2 =0.19, p=0.15). However, Hewitt's (1997) annual sea ice index and leopard seal presence were strongly correlated. When the ice index variable was transformed quadratically, and analyzed in a non-linear regression, ice

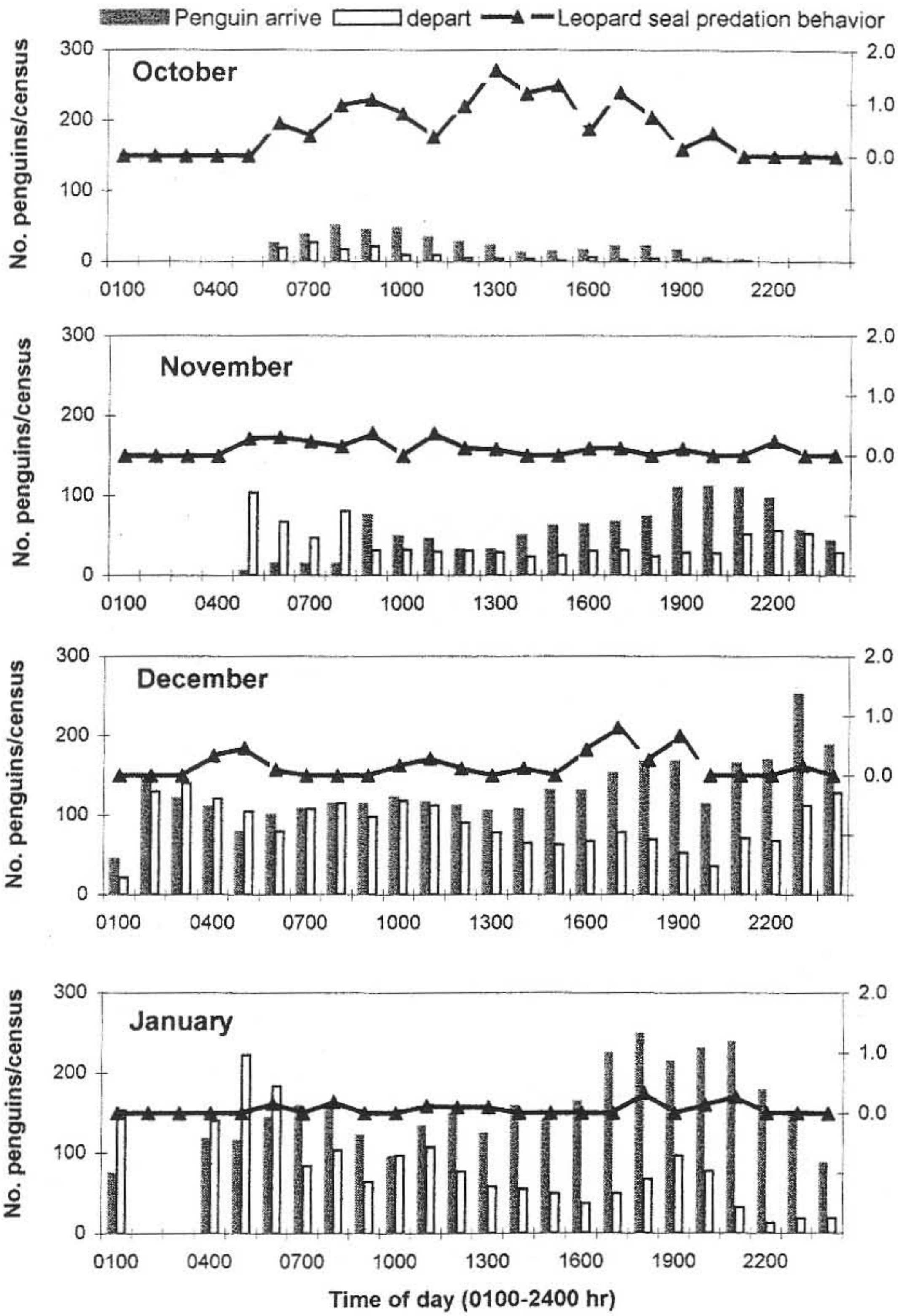

Figure 7. Diel variation in 1995/96 penguin activity and leopard seal predation behaviors (patrol, chase, kill) per hour for the months of October through January.

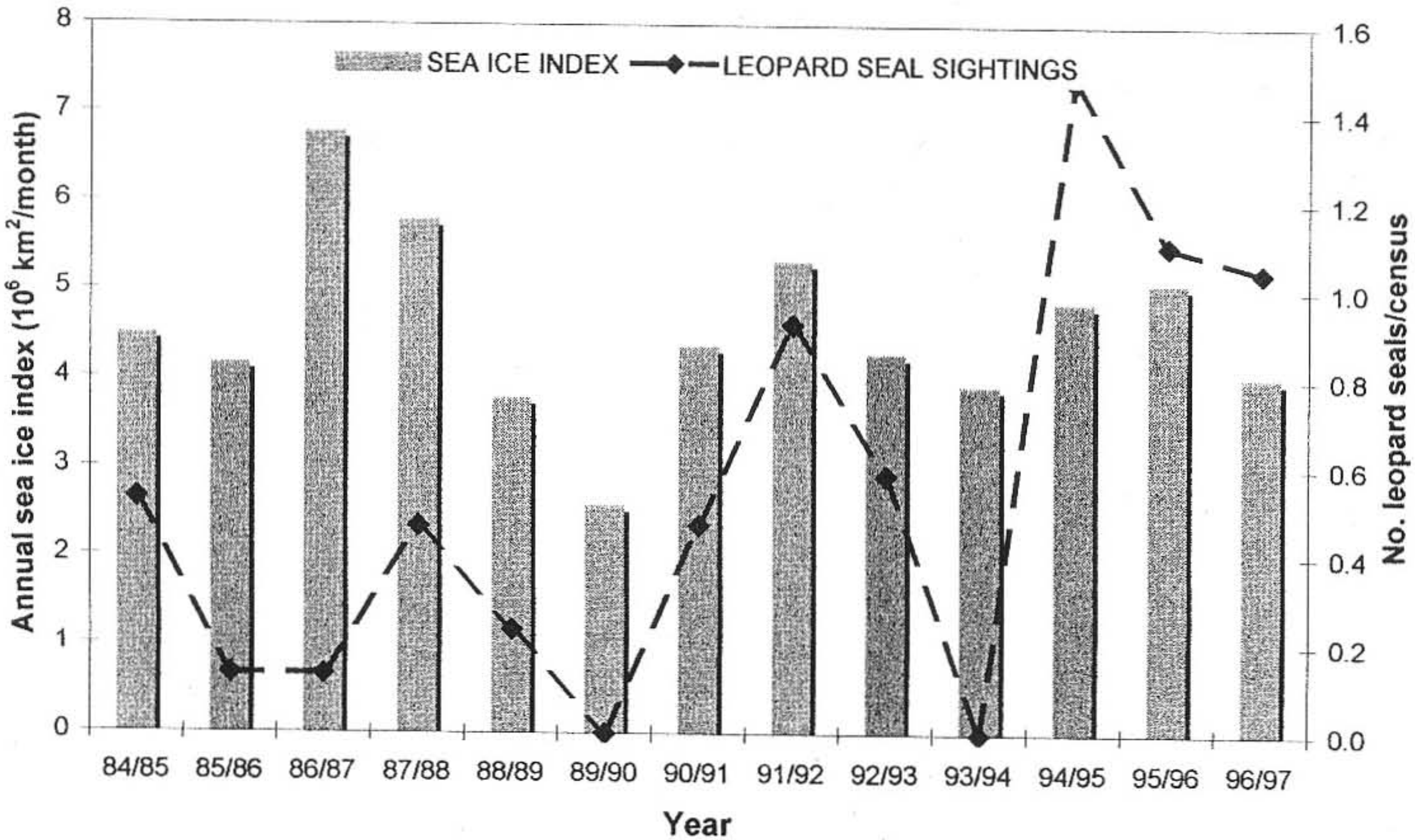

Figure 8. Variation in the number of leopard seals observed per weekly seal census near the Admiralty Bay penguin rookery and Hewitt's (1997) annual sea ice index for the years 1984/85 - 1996/97. The annual ice index (1,000,000 km sq./month) was derived from microwave imagery data in Stammerjohn (1993) for the northwestern side of the Antarctic Peninsula.

explained 59% of the variance in (R^2=0.35) in leopard seal presence between 1984/85-1996/97. In years when the annual ice extent was relatively low or high, few leopard seals were seen in Admiralty Bay. When censuses were separated by month for intrannual comparisons, the number of leopard seals recorded declined though the austral summer: October mean = 16.7 ± 2.0, November mean = 8.5 ± 1.0, December mean = 7.3 ± 1.0, January mean = 1.3 ± 0.0, February mean = 0.0 ± 0.0.

Opportunistic Leopard Seal Sightings

At the Admiralty Bay field station, a total of 662 sightings of leopard seals were made between 1984/85 and 1996/97. The greatest number of sightings occurred in 1990/91 (16%) with additional high numbers in 1988/89 (12%), 1991/92 (12%), 1992/93 (12%) and 1994/95 (11%). Predatory behavior (patrol, chase, kill) accounted for 87% of all observations (Table 4). The was no direct correlation in the percent Adélie penguins presumed killed by leopard seals and the number of opportunistic sightings of leopard seals near the rookery (R^2=0.08, p=0.18).

The number of leopard seal sightings per day was highest in October (n=9.0) followed by December (n=7.0), November (n=5.0), January (n=2.0), February (n=1.0). Sixty-nine percent of all leopard seal sightings were made between 1200 and 1800 as were 81% of all haul outs. This trend in daily activity was the same as that found in the 1995/96 study where leopard seals were more likely to be seen when the number of penguins arriving (rather than departing) the rookery was highest (Figure 9).

A comparison of the 1995/96 behavioral data collected through systematic sampling and the 1984/85 – 1996/97 behavioral data collected opportunistically was

Table 4. A summary of 662 opportunistic sightings of leopard seals near the penguin rookery between 1984/85 - 1996/97. Behaviors include patrol, chase, kill, and haul out.

Behavior	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	Total
Patrol	7	19	11	10	12	15	27	20	9	5	13	3	9	160
Chase	1	1	2	1	5	1	7	5	7	1	3	0	1	35
Kill	3	11	2	20	54	38	71	36	55	12	43	18	27	390
Haul out	0	0	1	3	7	1	3	17	9	1	15	17	3	77
Total	11	31	16	34	78	55	108	78	80	19	74	38	40	662

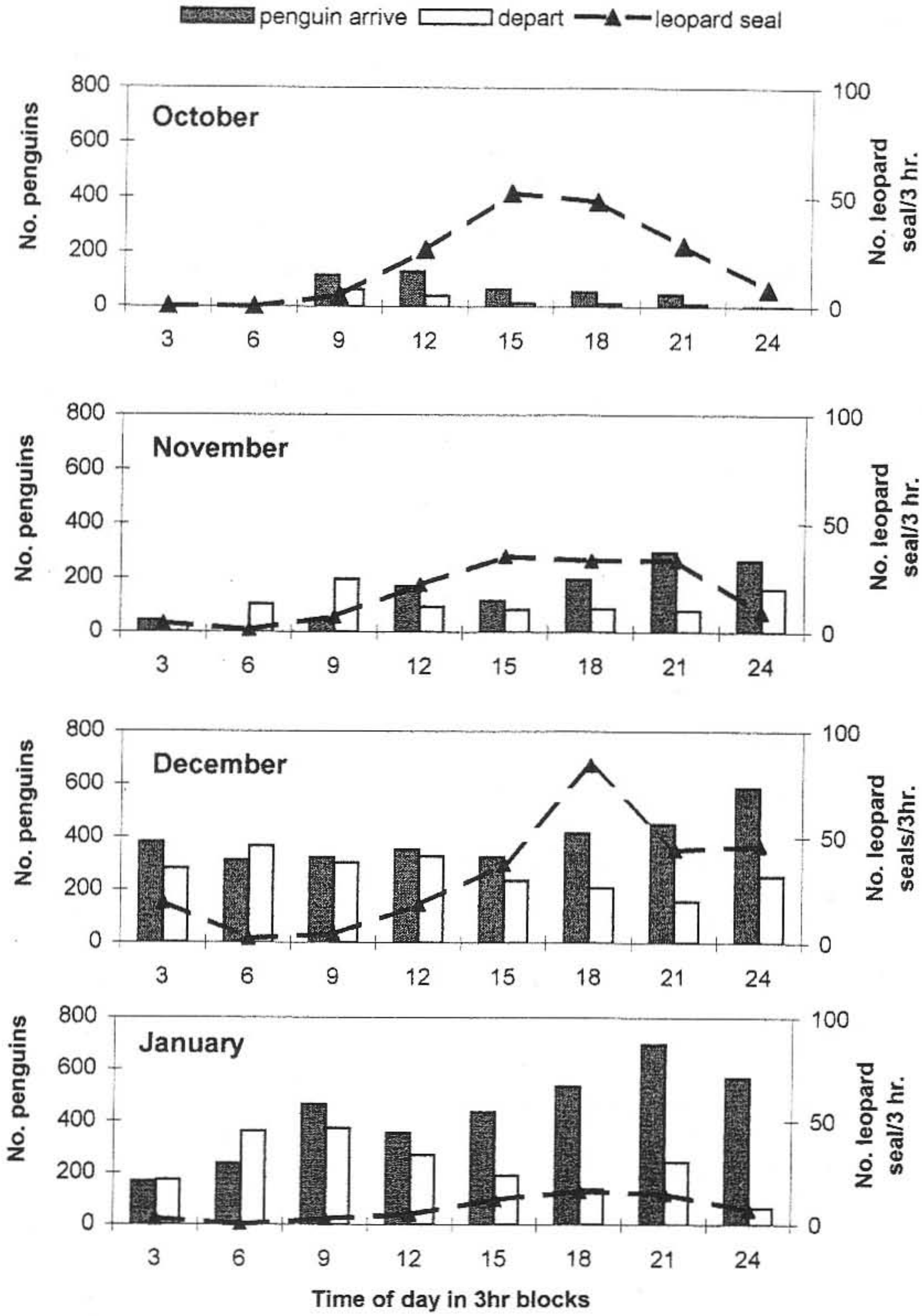

Figure 9. A comparison of opportunistic leopard seal sightings 1984/85 -1996/97 and diel penguin activity 1995/96 by time of day.

made using Pearson's Chi-square analyses. Table 5 shows the results of the analyses that indicated that the frequency of all behaviors recorded by the two methods were significantly different ($p<0.01$).

Table 5. A comparison of the frequencies of leopard seal behavior near the penguin rookery recorded through opportunistic sampling between 1984/85 - 1996/97 and systematic sampling in 1995/96. Statistical results of a 2x2 frequency table with Pearson's chi-square and p values.

Behavior	1984/85-1996/97 Opportunistic	1995/96 Systematic	Pearson Chi-square	p
Patrol	160	110	13.88	<0.01
Chase	35	31	8.06	<0.01
Kill	390	21	228.92	<0.01
Haul out	77	142	147.93	<0.01
Total	662	304		

Penguin Abundance and Predation Rates

Adélie penguin numbers declined significantly between 1984/85-1996/97 ($R^2=0.55$, $p<0.01$) (Figure 10). The percentage of banded Adélie penguins in the reproductive studies that did not return during each breeding season (i.e. birds assumed to have been killed by leopard seals) ranged from 4.7 - 19.8% and was highest in 1987/88 and 1990/91. In examining the peaks in predation, oscillations seem to occur every 2-3 years between 1987/88 and 1996/96. A comparison of the percent Adélie penguins presumed killed by leopard seals and reproductive data on Adélie breeding success between 1984/85 –1996/97 revealed that the four highest years of presumed kills (1987/88, 1989/89, 1990/91 and 1996/97) corresponded to the four lowest years of Adélie breeding success (Trivelpiece unpublished data).

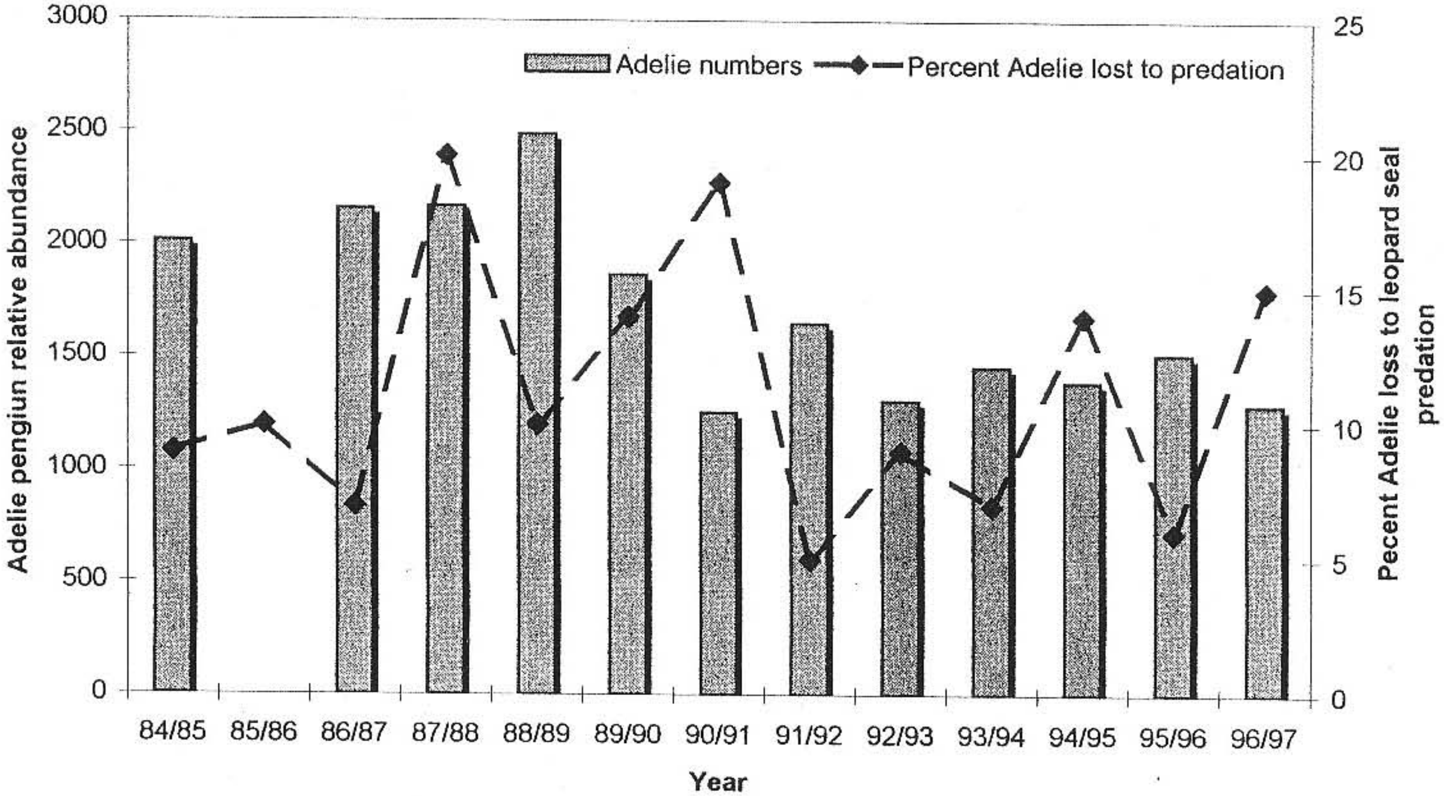

Figure 10. Relative abundance and percent non-returning Adelie penguins at the rookery from 1984/85 - 1996/97. The same, representative penguin colonies were censused each year for comparison. The percentage of Adelie penguins predated by leopard seal were derived from the number of breeding penguins banded that year who did not return to their nest sites.

DISCUSSION

Diel, seasonal, and annual variation in 1) leopard seal presence, and 2) leopard seal predation behavior were investigated using three data sets. An intrannual study in 1995/96 and two long-terms studies between 1984/85 – 1996/97 were analyzed to determine correlates for temporal variation in leopard seal occurrences. Seasonal variation in the presence of leopard seals at Admiralty Bay was recorded in both the 1995/96 study and the long-term data. This seasonal variation was most strongly correlated with sea ice conditions. Leopard seal were present in significantly greater numbers in the early season (October - November) and were more likely to be observed when pack ice was present in Admiralty Bay. This same correlation was found in comparisons of annual leopard seal sightings and regional sea ice extent. Weekly counts of leopard seals were low during summers that followed either low and high ice years, but increased in years following moderate pack ice winters. This presence/absence data suggests that leopard seals in the Admiralty Bay area utilize penguin prey when environmental factors such as season and ice bring the seals in proximity of the penguin rookery.

Leopard seal behavioral data from both 1995/96 and 1984/85-1996/97 depicted seasonal as well as diel patterns in leopard seal sightings. Leopard seal predation behavior was highest in October and declined thereafter through February; inversely, penguin activity began low and increased throughout the summer. Leopard seal predatory behavior (patrol, chase, kill) in October and November occurred throughout the day, but increased between 1200-2100 hrs. in the latter half of the austral summer suggesting that leopard seals are influenced by the large number of penguins returning to the rookery at that time.

Effects of Season

Date, or season, had the greatest influence on leopard seal presence and predation behavior near the penguin rookery during the 1995/96 summer. This same trend was evident in the long-term data collected over 13 seasons between 1984/85-1996/97. Both the weekly seal censuses and the opportunistic sightings revealed a decline in leopard seal numbers as the season progressed. This presence early in the season with a decline throughout the summer suggests a seasonal pattern of movement through Admiralty Bay. It is unknown whether or not leopard seals undertake an annual migration (King 1983; Siniff 1991); however, reports of spatial segregation of age classes and distinctions in breeding and non breeding distributions suggest this is likely (Laws 1984). Mature leopard seals are thought to reside on the edge of the pack ice, moving southward with ice in the summer and northward in the winter (Gilbert and Erickson 1977). Leopard seals of age 3 – 9 years have been observed near the coast of the Antarctic Peninsula during the austral summer (Hofman et al. 1977). Juveniles are thought to disperse or migrate northward in the austral fall and winter where they often congregate at sub-Antarctic islands (Borsa 1990; Rounsevell and Eberhard 1980). However, no information is available regarding the annual movement or individually marked adult leopard seals during the austral summer.

The winter and spring diet of leopard seals on the outer edge of the pack ice is not known, though it is thought that leopard seals forage heavily on krill while near the pack ice and specialize on pinnipeds or birds while near rookeries. Intraspecific competition for food in the winter, and/or for mates in spring, may be one reason for the seasonal movement of leopard seals (Borsa 1990; Rounsevell and Eberhard 1980). Siniff and Stone (1985) hypothesized that interspecific competition might be greatest during the winter and early spring when leopard seals of all ages compete with Adélie penguins and crabeater seals, both of whom specialize in eating krill and dwell in the pack ice. The presence of crabeater seals in the leopard seal diet has been found to increase through the summer as pups become available (Siniff et al. 1991; Siniff and Stone 1985). Øritsland (1977) found crabeater seal remains in 3% of the stomachs of leopard seals in September and October, compared to 25% in November through March. In late September and October before crabeater seal pups are abundant, penguins in breeding condition may provide a reliable, albeit temporary, source of food before the leopard seal begins its own breeding season in the pack ice in November and December. Observations of adult leopard seal in Admiralty Bay in October and November and juvenile seals in December and January support this hypothesis.

Effects of Ice Cover

Regional ice cover in the eastern Antarctic Peninsula is strongly correlated with date. Annual cycles show a 5-6 month advance with maximum ice coverage in September and a 5-6 month ice retreat with minimum winter pack in February (Stammerjohn and Smith 1996). The regional effects of westerly winds and a northeastern current consolidate sea ice on the western side of King George Island, providing open water on the eastern side earlier in the austral summer. This early open water allows penguins access to land (Trivelpiece and Fraser 1996). Admiralty Bay is on the southeastern side of King George Island and perhaps it is this predictable open water and congregation of penguins in October that influence the movement of leopard seals though this region in spring.

Stammerjohn and Smith (1996) report a 5-7 year periodicity since 1973 in the extent of winter sea ice in the Antarctic Peninsula. Two to four years of low ice are followed by 1 to 2 years of high ice coverage. The annual ice cover index compiled by Hewitt (1997) for this same period, indicated three periods of extensive ice cover in the Antarctic Peninsula in 1986, 1991, and 1995. The leopard seal weekly census numbers showed a periodicity of three to four years that was strongly correlated with the winter sea ice index. The number of leopard seals recorded in Admiralty Bay were low following low ice or high ice winters; whereas leopard seal numbers increased in years of moderate sea ice winters. Similar 4 -5 year oscillations were reported in the abundance of wintering immature leopard seals at Macquarie Island between 1949 and 1979 (Rounsevell and Eberhard 1980). Such oscillations in leopard seal numbers have been linked with date (the start of winter), mean annual temperature, and oceanographic variation such as the El Niño Southern Oscillation (Laws 1984; Testa et al. 1991).

The relationship between high leopard seal numbers in moderate ice years and low numbers following light and heavy sea ice winters, suggests that the September/October position of the pack ice edge might best explain the variation leopard seal presence near the Admiralty Bay rookery. In the case of moderate winters, when the pack ice edge is near the South Shetland Islands (Stammerjohn 1993; Stammerjohn and Smith 1996), leopard seals migrate to Adélie penguin rookeries nearby. However, when the ice edge is well north or south of these islands in high and low ice winters respectively, the presence of leopard seals recorded at Admiralty Bay is reduced accordingly.

Local ice conditions examined in the 1995/96 study differ from the annual or regional ice extent that was analyzed between 1984/85 - 1996/97. Local ice conditions in the Admiralty Bay area changed daily and were relatively independent of date with no significant differences in mean ice cover throughout the 1995/96 austral summer. Leopard seal presence was positively correlated with the amount of ice near the penguin rookery during the 1995/96 study. In addition, both predation and haul out behavior were most often observed when there was a greater range of ice cover conditions (i.e. October and November). This relationship has two likely explanations, first the presence of ice in the study area affords leopard seals a haul out platform, which would lead to more sightings. Secondly, leopard seals were more often observed using ice as a hiding place from which to ambush penguins. This hunting technique would likely increase the seal's probability of capturing a penguin and would also help explain the positive correlation found between the presence of ice and leopard seals in the study area in 1995/96.

Diurnal Variation

Relatively little diurnal variation was observed in the presence of leopard seals at Admiralty Bay in 1995/96 because of the large number of seals seen in October that were active throughout the day. However, in examining the number of leopard seal behaviors per hour, diel patterns are evident. Both predation and haul out behaviors were most often seen between 1200 and 1800. Erickson et al. (1971) found that daily fluctuations in temperature influenced crabeater and leopard seal activity levels. Minimum body temperatures were correlated with the peak haul-out periods (maximum incoming solar radiation) between 1100-1400. Similarly, Müller-Schwarze and Müller-Schwarze (1975) reported that leopard seals tended to be more active during hours of decreasing light intensity (including nocturnal activity), with highest haul out records between 0800-1200. The range in hours of leopard seals observed near the Admiralty Bay rookery increased as the length in day increased suggesting that leopard seals are likely present at night, but such presence could not be confirmed. Øritsland (1977) found that leopard seals appear to feed throughout the day. Both Hofman et al. (1977) and Müller-Schwarze and Müller-Schwarze (1975) claimed that leopard seals were most active at night, presumably feeding at that time. As daylight hours increased from October through December, we were able to make observations throughout a 24-hour period. The results of this study indicate there was some leopard seal activity between 2100 and 2400, but show no evidence of a period of maximum activity during this time.

Effects of Penguin Activity and Abundance

There was no correlation between penguin activity and leopard seal presence during this 1995/96 study. Neither seasonal nor diurnal penguin trends appeared to affect whether leopard seals were present in Admiralty Bay. Again, this data was biased towards the high presence of seals observed in October which in effect masks the influence of increased penguin activity in later months when leopard seals were recorded less often near the rookery. Adélie penguins winter on the pack ice and return to the coast to initiate breeding in October. I found that during October, total penguin activity was relatively low as birds fast ashore during a 3-week courtship period. Conversely, penguin activity was highest in December and January when both the male and female breeding penguins made frequent trips to sea in order to feed their rapidly growing chicks. I found leopard seal activity during these months was low relative to October. The increased abundance of leopard seals in October likely results from the need of a reliable food source to prepare for their subsequent pupping and mating activities in November and December. Adélie penguin arriving at the Admiralty Bay rookery have 1-2 kg of body fat to sustain them over their prolonged courtship period (Trivelpiece and Trivelpiece 1990). Furthermore, the arrival pattern of Adélie penguins which starts with males and is followed by females, then younger breeders, assures a steady influx of birds to the rookery throughout October and early November. Leopard seals frequenting the coast near the rookery are afforded a steady stream of fat, energy rich penguins at a time of the year when other resources (e.g. krill, crabeater pups) are scarce.

Other studies report that leopard seal predation was highest as penguin chicks depart the rookery (Penny and Lowry 1967; Müller-Schwarze and Müller-Schwarze 1975). This is not the case at Admiralty Bay. No leopard seals were seen during the 1995/96 fledgling period, nor were any leopard seals censused during late January and early February in the weekly seal surveys in the years 1984/85-1996/97. I cannot explain why leopard seals do no frequent our area during the penguin fledgling period when vulnerable chicks enter the sea for the first time. It appears that leopard seal foraging behavior differs at different locales for as yet unknown reasons.

Total penguin activity at the rookery was recorded throughout the day, though peaks varied by month. In December and January when I found penguins to be most active, the birds were more likely to be in the water near the rookery between 1800-2400. Leopard seal behavior during these months was also higher between 1500-2100. This contrasts the findings of Müller-Schwarze and Müller-Schwarze (1975) who reported penguins and leopard seals to be active in the water at different hours. Other studies have suggested that leopard seals preferential prey on penguins arriving at the rookery (rather than those departing) (Penny and Lowry 1967). The combined results of this 1995/96 study and the long-term data supported this hypothesis. When the greatest numbers of penguins were most often arriving to the rookery in December and January, the leopard seal behaviors observed also peaked during this time. However, this correlation between leopard seal activity and penguin arrivals is confined to the December and January period when Adélie penguins are making daily trips to sea to feed their chicks. Targeting returning penguins would have two major advantages to foraging leopard seals. First, penguins returning to the rookery are carrying an average 600 g of krill in their stomachs (Volkman et al 1980; Karnovsky 1996) a substantial amount of additional energy per bird captured. Secondly, incoming penguin with large food loads would be less maneuverable and likely tired at the end of their foraging trips and therefore easier to capture.

Systematic Vs. Opportunistic Sampling

Systematic observations of leopard seal behavior for the 1995/96 austral summer indicated that haul out and patrol were the most prevalent behaviors observed, followed by chases and kills. In contrast, the opportunistic data between 1984/85-1996/97 recorded kills as the most common behavior. Behavioral observations made during the 1995/96 study, found that the time required to kill and eat a penguin is greater than that spent patrolling or chasing. In addition, the presence of birds vocalizing and feeding near kills may explain why kills were so commonly recorded in the opportunistic data. These findings suggest that the opportunistic data underestimates the abundance of leopard seals at the rookery.

Leopard Seal- Penguin Population Interactions

Leopard seal presence and predation at penguin rookeries has been related to rookery size and species (Laws 1984). Müller-Schwarze and Müller-Schwarze (1975) found that leopard seal activity near penguin colonies of less than 10,000 pairs was limited, though leopard seals at Kerguelen Island and South Georgia appeared near colonies of fewer penguins (Borsa 1990; Laws 1984). Penguin populations at the Admiralty Bay rookery varied between 8000-12000 pairs during the 1984/85-1988/89 period, then declined by 30% after 1988 (Trivelpiece and Trivelpiece, Ecology in press). However, the abundance of leopard seals recorded between 1984/85 – 1996/97 in both the weekly seal census and opportunistic sightings near the rookery does not reflect the changes in overall abundance of penguins at the rookery. Likewise, the number of Adélie penguins at the rookery and the percentage of banded non-returning Adélie penguins that were assumed to be predated by leopard seals were not correlated (Figure 10).

Some attempts at predicting when and where predators occur by indentifying physical and biological factors (such as sea ice conditions, hydrographic processes, and availability of the krill) have been successful (Plötz et al. 1991; Trivelpiece and Fraser 1996). The leopard seal is a top predator in a krill-based food web and krill make up approximately 50% of their diet. The Antarctic Peninsula is the major spawning site of krill (Marr 1962). In the spring, both juvenile and adult krill move northeasterly with the prevailing current to waters off the South Shetland Islands (Siegel 1988; Siegel and Loeb 1995). Years of good or bad krill recruitment (Siegel and Loeb 1995) do not appear to correspond with leopard seal presence near the Admiralty Bay rookery. However, when we examined the relationship between the precent of Adélie penguins assumed lost to leopard seal predation and Adélie breeding success for the 1984/85 to 1996/97 period (Trivelpiece unpublished data), we found that the four highest years of losses to leopard seals corresponded to the four lowest years of Adélie breeding success. This implies that leopard seals are indeed a major factor affecting annual Adélie penguin breeding success and demography.

The lack of data on physical parameters and their correlation with leopard seal data have been demonstrated. Testa et al. (1991) found no correlation between leopard seal data and temperature or sea ice coverage in the Antarctic Peninsula between 1973-1981. Leopard seals are long-lived and presumably adapt to changes in their physical and biological environments (Siniff 1991). Variability in environmental factors such as the frequency and extent of sea ice, the abundance and availability of krill, crabeater seals, and other prey, and how leopard seals compete for these resources is largely unknown. Scientists working in the Antarctic have recorded increased variability in physical and biological parameters such as temperature, sea ice extent, krill, and Adélie penguin populations. Knowledge of the biological and ecological interactions among top predators, their prey, and the pack ice environment is essential in determining how the present regional warming and global climate change will result in changes in behavior, movement patterns, and/or populations parameters of Antarctic species.

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APPENDIX

Logistic Regression Correlates of Leopard Seal Presence

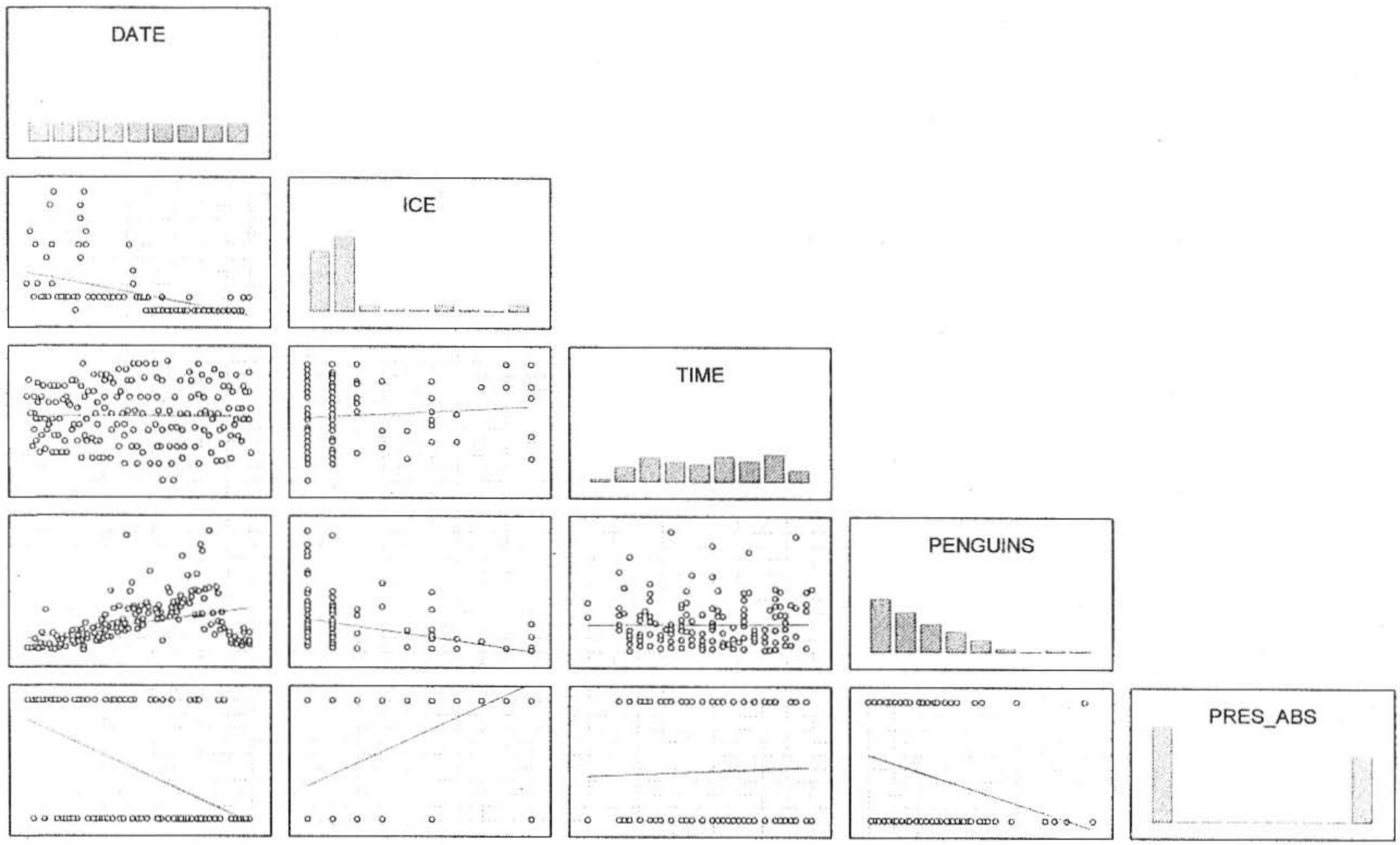

Figure 11. Logistic regression correlates of 1995/96 leopard seal presence/absence near the Admiralty Bay penguin rookery. Independent variables (date, ice, time, and penguins) and all their interactions are presented.