12-2001

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EFFECTS OF AN INCREASING HARBOR SEAL POPULATION ON CHANGES IN SITES USED FOR PUPPING

By

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B.S. The Evergreen State College, 1994

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

December, 2001

Advisory Committee:

James R. Gilbert, Professor of Wildlife Ecology

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EFFECTS OF AN INCREASING HARBOR SEAL POPULATION ON CHANGES IN SITES USED FOR PUPPING

By Nikolina Guldager

Thesis Advisor: Dr. James R. Gilbert

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
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Aerial survey data from 1981 to 1997 of an increasing harbor seal (*Phoca vitulina concolor*) population in Penobscot and Blue Hill bays, Maine, were used to evaluate spatial and temporal patterns of use of pupping sites by mother-pup pairs. Pupping sites refer to haul-out sites where pups were observed during surveys, and are assumed to be used consistently from birth to weaning. Sites with pups were spatially clustered to remove spatial autocorrelation, reduce temporal variability and provide biologically cohesive and independent sample units. Spatial, temporal and habitat analyses were completed for 2 spatial scales: individual sites and clusters of sites.

The temporal and spatial distribution of the population increase was examined for individual sites (individual site scale) and clusters of sites (cluster scale) to predict behavioral and environmental characteristics that may effect pupping site use at different population densities. On the site scale, Taylor Power Law (TPL) and Analysis of Variance (ANOVA) results revealed that numbers of pups at all sites increased at an equal rate providing no strong evidence for aggregation or repulsion behavior. However,

increased use of new sites at high densities decreased spatial pattern, implying some degree of spatial limitation. Clusters of sites that were used during all survey years had the highest number of pups and increased steadily with the overall increase, while clusters used less frequently (< all survey years) maintained low numbers of pups and had higher temporal variability.

Logistic and multiple regression were used to relate frequency of pupping site use and numbers of pups per site and cluster to physical characteristics of sites. Initial site selection was for clusters of sites with a high availability of haul-out space, access to close alternative haul-outs, and seclusion from humans (significant variables ($\alpha = 0.05$): area of intertidal zone, number of sites in a cluster, and minimum distance to an site ≥ 2000 ha). Individual site use, however, was poorly related to physical site characteristics, and is likely more dependent on unmeasured dynamic characteristics such as wind direction, surf, tidal phase, human use patterns, harbor seal behavior, and food availability. Physical characteristics of sites are poor to moderate indicators of pup production and distribution on the individual site and cluster scales, respectively.

Spatial autocorrelation in pup counts was incorporated into multiple regression models using trend surface analyses. Spatial autocorrelation accounted for a moderate amount of variation in pup counts ($r^2 \leq 0.35$) on both the individual site and cluster scales. On the individual site scale, this likely represents species aggregation (patchy spatial pattern), while on the cluster scale it likely represents a larger scale spatial gradient across the study area resulting from an unmeasured environmental gradient in resources.

ACKNOWLEDGMENTS

Funding for this project was provided by the National Marine Fisheries Service (Northeast Fisheries Science Center and Maine Agriculture and Forest Experiment Station). I would like to thank Dr. James Gilbert, my major advisor, for his continual support, encouragement, flexibility and friendship. I would also like to thank the other members of my graduate committee, Dr. William Krohn and Dr. Joseph Kelley whose comments and suggestions were greatly appreciated. Thank you to Dr. Raymond O'Connor for his thoughtful input, and a special thanks to Dr. William Halteman for making statistics fun and challenging and for his many patient hours of consultation.

I am especially grateful to Randy Boone, Cathy Johnson, Jeff Hepinstall and Stephanie Painton for their friendship and laughter, and for the time they spent patiently guiding me through lengthy Geographic Information System tasks. I would like to acknowledge the hours of technical assistance that Jared Austin and Birgitta Pahl provided in the field, viewing endless slides and conducting tedious computer tasks. I would like to give a special thanks to Sarah Dooling for her camaraderie and late night laughter in Nutting Hall, and her invaluable partnership in the field. Lastly, I would like to thank my family and Ed for putting up with me during my years in graduate school.

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CHAPTER 1

INTRODUCTION

The Maine harbor seal population has been rapidly increasing since the early 1980's. Over 3,000 islands and intertidal ledges along the Maine coastline provide sheltered, easily accessible terrestrial habitat for harbor seals to rest, thermoregulate, molt, give birth to and nurse their young (Gilbert and Wynne 1984, Richardson 1976). These terrestrial sites are referred to as "haul-out sites." A peak in the number of seals at haul-out sites occurs during the birthing and nursing period (Allen et al. 1988, Allen et al. 1989, Brown and Mate 1983, Kreiber and Barrette 1984, Sullivan 1980, Temte et al. 1991), which is in late May to early June in Maine. This period of haul-out activity is referred to as the "pupping period," and a "pupping site" is defined as a haul-out site where pups are born and mother-pup pairs haul-out frequently during the nursing period of roughly 24 – 30 days (Boulva and McLaren 1979, Thompson et al. 1994). The pupping period provides an optimal time to survey harbor seals because: 1) animals are more congregated for pupping and subsequent breeding, 2) more animals are hauled-out for longer time periods (Jeffries 1986, Thompson et al. 1989, Thompson 1993, Thompson et al. 1994), and 3) counts of pups provide an index to productivity. Coast-wide aerial surveys conducted during pupping indicated a 3-fold increase in hauled-out seals in Maine between 1981 (10,543 seals) and 1997 (30,990 seals). Estimated pup production in Maine also increased from 676 individuals in 1981 to 5,539 in 1997, as did numbers of haul-out sites (Gilbert and Guldager 1998). These harbor seal survey data (Gilbert and

Guldager 1998, Gilbert and Stein 1981, Gilbert and Wynne 1983, Kenney 1994, Kenney and Gilbert 1994) provide data to examine effects of increase in pup counts on sites used by pups.

Examining a scale-specific pattern of a species' population change through time is important to a) develop hypotheses regarding a species' population ecology and its relationship with resources, b) identify and understand habitat associations relative to population density, and c) design monitoring protocols that are sensitive to biologically significant population change.

Patterns of population change through time are often not constant across all habitats (i.e. space). Depending on a species' population ecology, high quality (optimal) and poor quality (sub-optimal) habitats may have different rates of population change. A territorial species is one where unrelated individuals of a population maintain territories to maximize survival, while an aggregating species is one where unrelated individuals of a population group together to maximize survival (Pulliam 1973). For simplicity, territoriality and aggregation are generally defined in this paper as mutually exclusive behaviors; however, there are instances in nature where these strategies overlap. Species that are territorial will exclude (either actively or passively) other individuals from optimal sites at a certain site density (Brown 1969, Fretwell 1972, Fretwell and Lucas 1970, Oyler 1993), causing sub-optimal sites to become colonized or have an increased density at higher population levels. This would cause optimal sites to maintain high stable densities through population fluctuations, while densities at sub-optimal sites tend to fluctuate with changes in population size (Figure 1.1a).

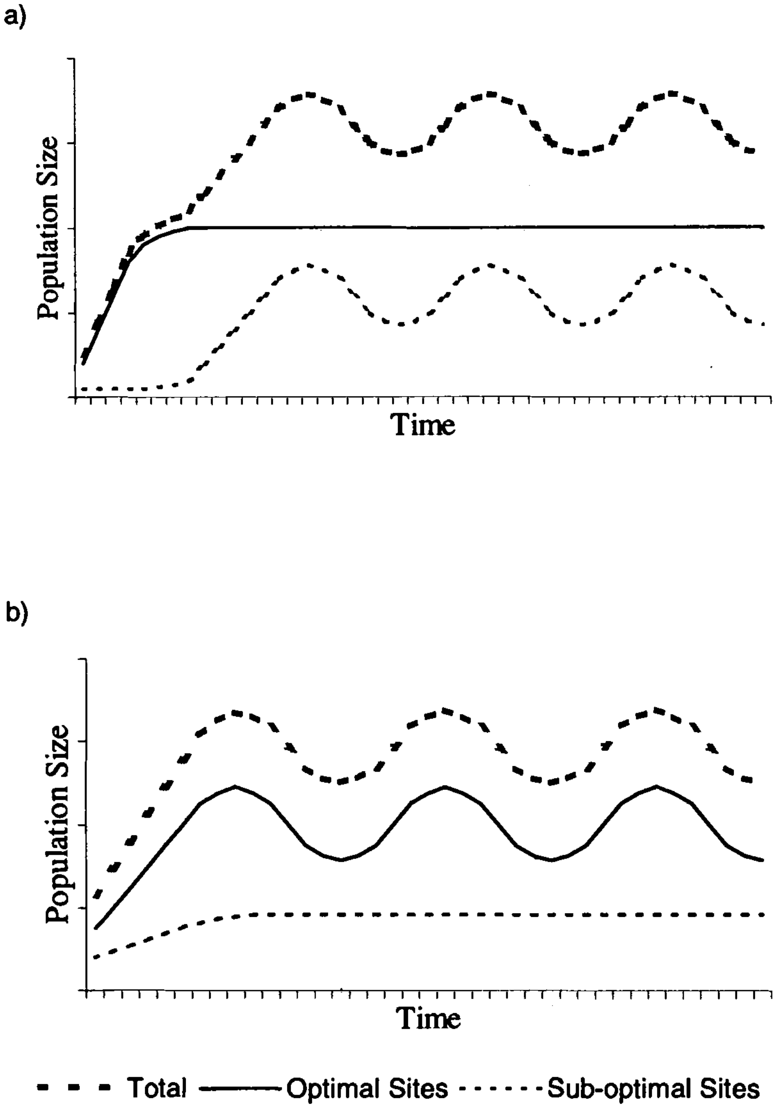

Figure 1.1. Patterns of population change for a fluctuating population for a) a territorial species, and b) an aggregated species (Adapted from Oyler, 1993).

A species that benefits more from aggregation will have a different spatial pattern of population change than a species that benefits more from territorial behavior. Conspecific attraction would result in fluctuation of optimal sites with population change, while sub-optimal sites would remain relatively stable at low site densities through time (Figure 1.1b) (McArdle et al. 1990). Most species have a strategy somewhere within the continuum between highly territorial and highly aggregated behaviors, creating different patterns of population change (Taylor and Taylor 1977).

Understanding scale-specific patterns of population change is central to being able to develop and interpret habitat relationships from resource selection analyses for a given snapshot in time. Habitat analyses may yield different results depending on a species' stage of population growth (O'Connor 1986) and their population ecology. For example, one would predict that a territorial species would have the greatest differences in density between optimal and sub-optimal sites during periods of low to moderate population densities, and the smallest differences during periods of higher overall population densities (Figure 1.1a). In this instance, differences between optimal and sub-optimal sites during high-density years may be masked, making associations between habitat parameters and site quality harder to detect. An aggregating species, however, would have the greatest differences in density between optimal and sub-optimal sites during periods of higher overall population density relative to periods of lower overall population density (Figure 1.1b), making associations between habitat parameters and site quality easier to detect.

It is also important to understand these varying patterns of population change in order to detect biologically significant changes with monitoring protocols (Wilcove and

Terborgh 1984). This is especially important for the conservation of species in peril. For instance, if a territorial species were to decline and optimal sites were solely monitored, only extreme population changes would be detected, while solely monitoring sub-optimal sites would be relatively more sensitive to minor changes in populations. Understanding species' spatial patterns of population change allows one to identify areas of particular biological importance and assess the sensitivity of monitoring protocols to detect change (Wilcove and Terborgh 1984).

In the chapters that follow a process for identifying and incorporating spatial and temporal patterns of animal distributions into resource selection models will be used to evaluate the resource selection strategy for an increasing population of harbor seals in Penobscot and Blue Hill bays, Maine. Chapters 2 through 5 explore spatial and temporal patterns of pupping site use, compare spatial and temporal patterns of pupping site use for coarse and fine spatial scales, identify changes in distribution of pupping site use with changes in overall pup production at 2 spatial scales, and identify habitat associations for different spatial scales and pup densities, respectively. Chapter 6 summarizes conclusions drawn from each of the preceding chapters.

STUDY AREA

The study area encompassed the terrestrial and aquatic habitat of Penobscot and Blue Hill bays, which are located in the central part of the Maine Coast. Study area boundaries were the west edge of Penobscot Bay, excluding the Muscle Ridges area and the outer islands, to the eastern edge of Blue Hill Bay and Swan Island (south of Mount

Desert Island) (Figure 1.2). This area was chosen because of its high number of pupping sites.

SURVEY DATA

Aerial surveys of harbor seal haul-out sites were conducted in the study area during the pupping period in 1981, 1982, 1986, 1993 and 1997. In Maine, peak haul-out occurs at low tide when extensive intertidal zones surrounding islands and intertidal ledges expose accessible haul-out space (Richardson 1976). Surveys were therefore flown within 2 hours on either side of low tide. All sites were surveyed for seals, and if present, a visual count was made and photographs were taken of the site. Separate counts were tallied for pups and all seals combined. Given that only hauled-out harbor seals were surveyed, total counts were interpreted as minimum population estimates for Maine (Gilbert and Guldager 1998, Gilbert and Stein 1981, Gilbert and Wynne 1983, Gilbert and Wynne 1984, Kenney and Gilbert 1994, Waring et al. 2000). Survey results are presented in Table 1.1.

Counts of harbor seals (including pups) on each site in the study area for each survey year were geo-referenced using a Geographic Information System (GIS) (Arc/Info, Version 7.03, ESRI, Redlands, CA). Count data were joined to U.S. Geological Survey (USGS), 1:24,000 scale digital maps of the coast mapped to mean high tide. The USGS coverage was edited prior to joining it to the count data so that each site was represented by only one polygon. Due to the common use of intertidal sites as haul-outs and their absence in the USGS high tide coverage, a separate point coverage was digitized to include them. These additional sites were digitized on-screen using

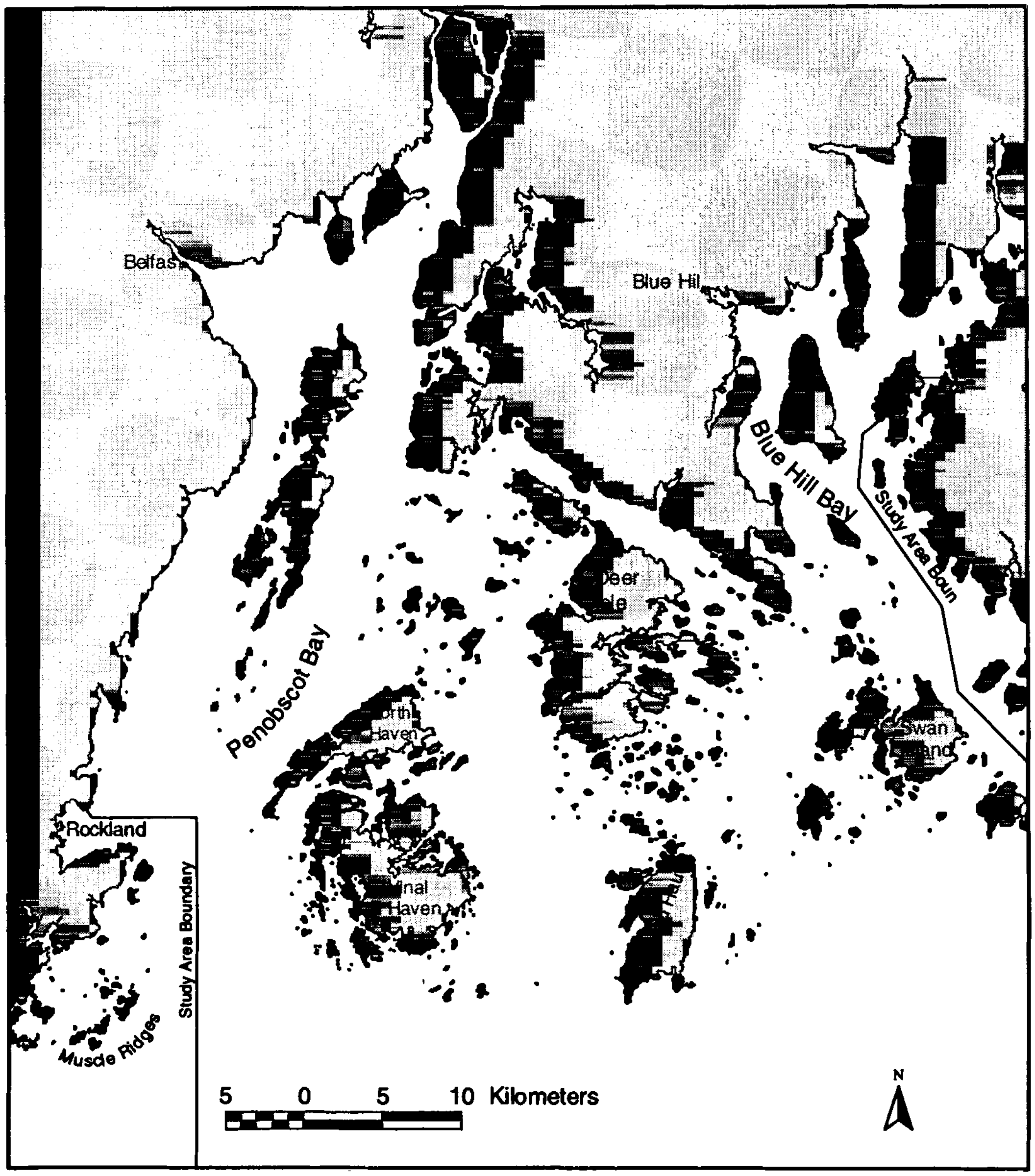

Figure 1.2. Study area map of mid-coastal Maine, which includes all sites from the west edge of Penobscot Bay to the eastern edge of Blue Hill Bay, except as noted in text.

Table 1.1. Numbers of harbor seals, pups, and haul-out sites with seals in the study area from 1981 – 1997 surveys.

	Total Seals	Pups	% Pups	# Sites with Seals	# Sites with Pups
1981	3,606	337	9.35	122	73
1982	3,785	605	15.98	123	77
1986	4,197	673	16.04	102	74
1993	10,628	1,769	16.64	211	156
1997	10,653	2,219	20.83	217	168

scanned mylar images of National Oceanic and Atmospheric Administration (NOAA) navigational charts, 1:40,000 scale.

The term "site" refers to all individual islands and intertidal ledges. Separations of sites were determined at low tide. For example, a site that appears to be 2 islands at high tide may become 1 island at low tide due to a connecting intertidal zone. By this low-tide definition this area was a single site. Similarly, a seemingly separate island at high tide that was connected to the mainland by an intertidal zone at low tide was considered part of the mainland by this definition.

This study only examines patterns of pupping site use. Pups were used as indicators of pupping sites, and analyses of pup counts were interpreted as patterns of use by mother-pup pairs. It is important to note that all spatial, temporal and habitat analyses in the following chapters were completed for sites that had pups present in ≥ 1 survey year, and there were additional sites within the study area that were used as haul-outs by adults but were not included due to the absence of pups. One exception to this is in

Chapter 3; all haul-out sites were included when creating a coarser spatial scale to ensure that all available haul-outs were incorporated. However, all subsequent analyses completed for the coarser spatial scale only included units used by pups. It was also assumed throughout this study that survival of pups among sites is equal, therefore, increased pup counts at pupping sites are synonymous with increased site quality.

Examining patterns of pupping site use targets individuals with more critical haul-out site habitat requirements. Mother-pup pairs have more limited mobility (Jeffries 1986, Thompson et al 1989, Thompson 1993, Thompson et al. 1994), nursing females have increased energy demands, and pups have special habitat requirements such as easily accessible haul-out sites and calm water (Kovacs et al. 1990, Sullivan 1980, Wilson 1978). Haul-out requirements of sub-adults, males and non-breeding females are likely less restrictive given their large ranges, flexibility in accessing alternative haul-outs, and ability to remain at sea for longer time periods. Solely examining pupping sites also avoids problems associated with density being used as an indicator of site quality (Van Horne 1983). Loss of pupping sites may have serious repercussions to the long-term health of the population, therefore understanding use patterns of mother-pup pairs is most important.

CHAPTER 2

A PRELIMINARY INVESTIGATION OF SPATIAL AND TEMPORAL PATTERNS OF PUPPING SITE USE

INTRODUCTION

Examination of space and time patterns of site use for pupping reveals information about the scale at which sites are selected. Intensity of use of a pupping site may be dependent on the use of neighboring pupping sites. This spatial autocorrelation occurs when an observed value of a variable at one site is correlated with the values of the variable at neighboring sites (Sokal and Oden 1978). Identifying the distance at which site use becomes independent of use at surrounding sites is critical to identifying the proper spatial scale to examine other influences on site selection. Grouping spatially autocorrelated sites into cohesive, independent clusters is likely to provide biologically and statistically valid sample units for further analyses.

Changes in the spatial scale of the sample unit alters the apparent temporal patterns of use, therefore, evaluating the temporal variability of pup counts at different scales will help define an appropriate spatial scale to further examine patterns of site use. Temporally random counts may imply 1) true random use, 2) selection for dynamic characteristics, or 3) the spatial scale may be too fine or too course for consistent patterns of use to be apparent. Testing for spatial and temporal randomness provides a means for identifying the spatial scale at which temporal patterns of site use become detectable. To identify proper spatial scale for further analyses, this chapter explores spatial and temporal patterns of site use by harbor seals for pupping.

METHODS

The Mantel test (Mantel 1967) was used to test for spatial and temporal randomness in pup counts at sites, using the Mantel Nonparametric Test Calculator V2.0 (Liedloff 1999). The Mantel test (Sokal and Rohlf 1994) estimates the association between 2 independent dissimilarity matrices describing the same set of entities (X, Y), and tests whether the association is stronger than one would expect from chance. The Mantel coefficient Z is equal to the sum of the products of the corresponding elements in the 2 matrices ($Z = \Sigma \Sigma X_{ij}Y_{ij}$) (Sokal and Rohlf 1994). Randomization techniques were used to evaluate the significance of the observed Z statistic by randomly permutating the rows and the columns of one of the matrices one thousand times, re-computing the Mantel coefficient Z each time. The observed Z statistic was compared with the generated distribution of Z statistics in order to determine its significance. The Mantel test addresses the null hypothesis that there is no association between the two distance matrices X and Y (Fortin and Gurevitch 1993).

Mantel tests were used to test for spatial autocorrelation in pup counts in each of the 5 survey years. Matrix **X** was composed of geographic distances (m) between all pairs of sites, and matrix **Y** was composed of differences in pup counts between all pairs of sites. Sites were included in all spatial analyses given pups were present in the given survey year.

Given that Mantel tests simply determine the presence or absence of spatial autocorrelation, correlograms were used to graphically illustrate changes in autocorrelation with distance (Upton and Fingleton 1985). Correlograms were created using Systat 8.0, with the correlogram coefficient equal to the standardized covariance. The correlogram coefficient is a ratio of covariances and was calculated as

$$\rho\,(h) = C\,(h)\,/\,C\,(0),$$

where $C\,(h)$ is the covariance for pairs of sites separated by a given distance h, and $C\,(0)$ is the finite covariance for all pairs of occupied sites (Kaluzny 1998). Geographic distances between pairs of sites were categorized, and h was the average distance between sites for each distance category. The coefficient $\rho\,(h)$ was plotted against distance h to create the correlogram. A correlogram illustrates changes in coefficient values as distance h increases, providing information about the pattern of spatial autocorrelation across the study area. Individual coefficient values within a correlogram are interpreted as a measure of how similar or dissimilar pup counts are between sites for a given distance category h, relative to all pairs of sites in the entire study area. High positive coefficient values imply that sites that are separated by distance h have similar pup counts, while high negative coefficient values imply that sites that are separated by distance h are dissimilar to each other (Sokal 1979). Figure 2.1 illustrates how correlogram shape is directly related to the spatial distribution of the response variable (Sokal 1979).

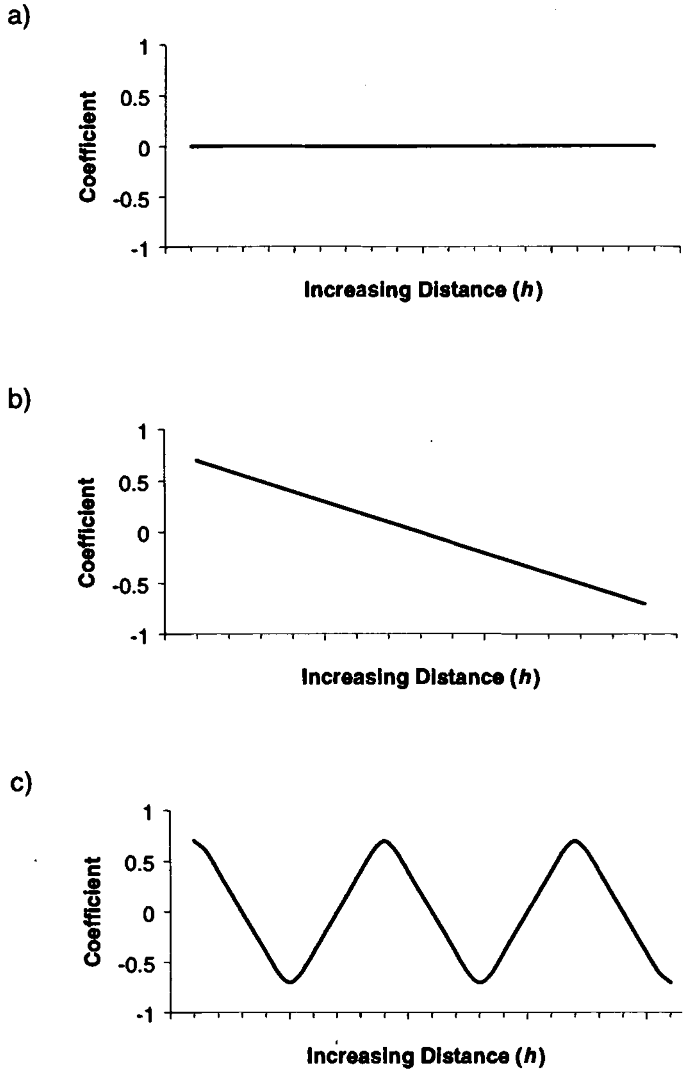

Figure 2.1. Representations of correlograms that illustrate the following patterns of spatial autocorrelation: a) no spatial autocorrelation, b) a gradual cline in numbers across the entire study area; sites that are closest together are the most similar and sites become less similar as the distance (*h*) between them increases, and c) 3 clines, or patches, within the study area. Symmetrical ordering of patches causes the long distance positive autocorrelation in the latter example, which causes similarity between far-away response values (Sokal 1979).

Since distance categories with small sample sizes produce unreliable coefficients, the longest distance categories were not examined. Correlograms were only examined for inter-site distances up to 30,000 m (equal to approximately 1/2 the maximum between-site distance). Correlograms were examined for spatial pattern for each of the 5 survey years.

The Mantel test was used to determine if pupping site use was random between all possible pairs of survey years (5 surveys = 10 comparisons). Matrix **X** was an n x n matrix composed of differences in pup counts between sites for year A, and matrix **Y** was composed of differences in pup counts for year B. Sites were included in the analyses given pups were present in at least 1 of the 5 survey years. P-values were adjusted for joint estimation using the Bonferonni inequality before determining significance.

RESULTS

Use of individual sites by pups was spatially autocorrelated in 1982 ($P = 0.001$) and 1986 ($P = 0.004$), while Mantel tests were insignificant in other survey years (1981: $P = 0.209$, 1993: $P = 0.305$, 1997: $P = 0.245$). Correlograms showed a stronger pattern of spatial arrangement of pup counts in 1982 and 1986 (Figure 2.2). The 1982 and 1986 correlogram coefficients oscillated between positive and negative values with increasing distance categories, as would be characteristic of a patchily distributed species (Sokal

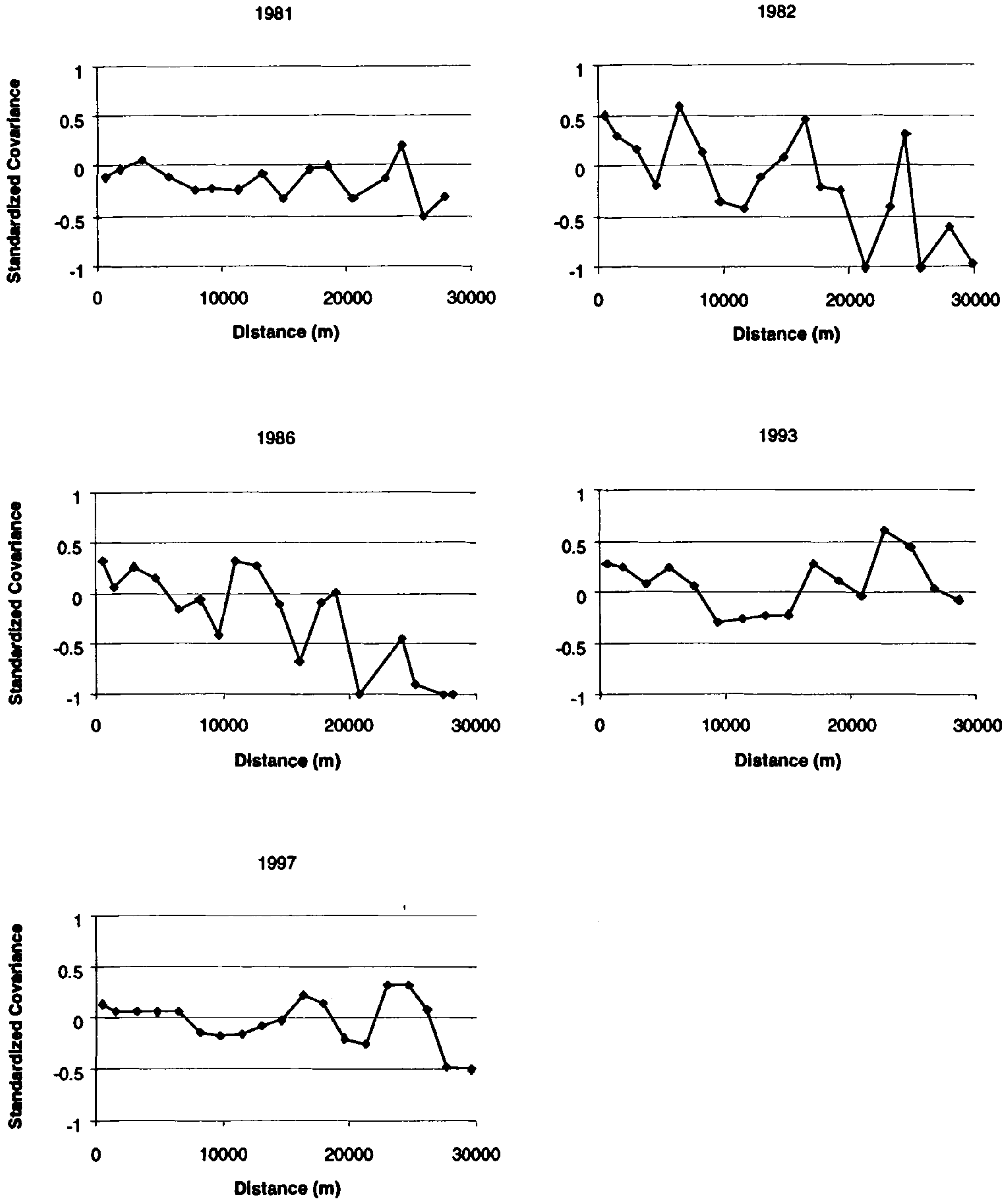

Figure 2.2. Annual spatial correlograms of pup counts, 1981 – 1997.

1979). Pupping sites were more likely to be near other pupping sites in 1982 and 1986. The general downward trend illustrated in 1982 and 1986 is likely due to smaller sample sizes in distance categories greater than 18,000 m for these survey years, therefore biological interpretations are unwarranted.

In years with similar pup densities (1981, 1982 and 1986; and 1993 and 1997), numbers of pups at pupping sites were dependent on use in previous years, but use was random between years with large differences in pup counts (1980's compared to 1990's). Three of the 4 Mantel tests between years of similar densities were significant, while only 1 of the 6 tests between years of low and high pup counts was significant ($\alpha < 0.05$) (Table 2.1).

Table 2.1. Results from Mantel tests for temporal random use of sites by pups. P-values (P) are from the randomized distribution generated from 1000 permutations.

	1982	1986	1993	1997
	P	P	P	P
1981	0.005[a]	0.014	0.057	0.027
1982		0.004[a]	0.021	0.026
1986			0.108	0.002[a]
1993				0.005[a]

[a] Significant ($\alpha = 0.05$) after adjusting for joint estimation of independently significant results using the Bonferonni inequality.

DISCUSSION

Significant spatial autocorrelation of pup counts during lower density survey years (1982 and 1986) and moderate temporal variability between years is evidence that a coarser spatial scale is appropriate for examining harbor seal pupping site use. Examining patterns of use on a coarser spatial scale may reduce spatial and temporal variability and reveal patterns of use otherwise masked. Given that islands used by harbor seals occur in a naturally clustered distribution in the study area, spatially grouping sites within these natural clusters may mimic patch size and provide biologically cohesive sample units for further harbor seal analyses. Chapter 3 presents methods for accomplishing this.

CHAPTER 3

A PRELIMINARY INVESTIGATION OF SPATIAL AND TEMPORAL PATTERNS OF PUPPING SITE USE FOR A COARSE SPATIAL SCALE

INTRODUCTION

Significant spatial autocorrelation of harbor seal pup counts during lower density survey years (1982 and 1986) and variable use of sites by pups between survey years have suggested that harbor seals were using patches of sites rather than individual sites. Therefore, a coarser spatial scale that mimics the patch size used by mother-pup pairs is appropriate for examining pupping site use (Chapter 2). This chapter presents methods to create a coarser spatial scale for further analyses for all survey years. This is warranted given: 1) significant spatial autocorrelation in 1982 and 1986 is evidence that a coarser spatial scale is appropriate, however, its absence in other survey years (1981, 1993 and 1997) is not evidence that a coarser spatial scale is inappropriate, 2) pupping sites occur in a naturally clustered distribution in all survey years, and 3) pupping site use is temporally variable among all survey years, implying that the individual site spatial scale is inappropriate for detecting temporal trends. Spatial scales identified in this chapter will be used in the following chapters to examine spatial and temporal patterns of habitat use for pupping by an increasing population of harbor seals, and environmental characteristics of sites associated with these patterns.

METHODS

Pupping sites were spatially grouped into naturally occurring geographic clusters in order to create biologically significant sample units for different scales of analyses. Systat (Version 9.0) was used to geographically group sites into clusters using single linkage, hierarchical cluster analysis. Sites were clustered based on their X and Y coordinate values that were in Universal Transverse Mercator (UTM) units; therefore, distance measurements between points could be directly interpreted in meters.

Sites were included in cluster analyses given seals (pup or non-pup) were present during at least 1 of the 5 survey years. All haul-out sites were included in cluster analyses rather than solely including pupping sites to insure that all potentially available sites were incorporated into clusters. This allows cluster sample units to be applied to future studies and management strategies related to harbor seal pupping and general haul-out site use.

Graphical trees illustrate the hierarchical cluster process. Each site begins as a single branch at zero distance. The 2 closest sites are the first branches to be joined. In a step-wise manner, the next closest sites or clusters (branches) are joined to form a new cluster, with branch length being a function of distance. This process continues until all sites are joined into one cluster (branch). The single linkage method defines between site and cluster distance (branch length) as the distance between the closest members of the clusters.

Hierarchical trees were examined to define the minimum distance that was to separate one cluster of sites from another cluster, which is also the maximum between site distance within a cluster. The first step for determining an optimum clustering distance was to identify the distance range where the majority of the site and cluster (branch) joining was occurring by visual examination of the hierarchical trees. The best cluster distance within this range was identified by examining total number of clusters (n), and the distribution of the total number of sites per cluster for selected distances. This prevented choosing a cluster distribution with small sample sizes (n), as well as insured a more even distribution of sites within a cluster. For example, a distribution of 3 clusters (n) with 4, 50 and 293 sites in each is not desirable, and neither is a distribution of 300 clusters (n) with most of the clusters consisting of only 1 site.

The spatial distribution of the selected clusters was visually examined in ArcView (Version 3.1, ESRI, Redlands, CA) to insure that clusters were distinct units and naturally followed the geographic landscape. For example, one cluster consisting of a string of sites spanning the entire study area would be undesirable when one would expect a more grouped distribution based on the spatial arrangement of sites. Given the selection of the best cluster distance, each site was assigned a cluster identifier and combined with its other cluster members to form 1 sample unit. Seal counts per site were summed and X and Y coordinates were averaged for each cluster for further analyses. The best cluster scenario will be used in further analyses in this study and will be referred to as the cluster scale, while analyses that use individual sites as the sample unit will be referred to as individual site scale analyses.

Mantel tests (Chapter 2) were used to test for spatial autocorrelation in pup counts for the best cluster scenario within each of the five survey years. Matrix **X** was composed of geographic distances (m) between all pairs of clusters, and matrix **Y** was composed of differences in pup counts between all pairs of clusters. All clusters were included in all spatial analyses. Given that Mantel tests simply determine the presence or absence of spatial autocorrelation, correlograms were used to graphically illustrate changes in autocorrelation with distance (Upton and Fingleton 1985) (Chapter 2). Correlograms were examined for spatial pattern for each of the 5 survey years.

The Mantel test was used to determine if pup use was random between all possible pairs of survey years (5 surveys = 10 comparisons) for the best cluster scenario. Matrix **X** was an n x n matrix composed of differences in pup counts between clusters for year A, and matrix **Y** was composed of differences in pup counts between clusters for year B. All clusters were included in all temporal analyses. P-values were adjusted for joint estimation using the Bonferonni inequality before determining significance.

RESULTS

Examination of hierarchical trees identified inter-site distances between 500 and 1000 m to be the distance range where most of the sites were joined into clusters. Inter-site distances less than 500 m would produce clusters that mostly consist of 1 site, while clustering at distances greater than 1000 m would produce fewer clusters, with some clusters heavily weighted with large numbers of sites. The observed increase in joining frequency between 500 and 1000 m represents the natural geographic clustering of sites in the study area.

Total number of clusters (n) and the distribution of the total number of sites per cluster were examined for distances 500, 600 and 900 m. Clusters that were joined at 500, 600 and 900 m had sample sizes (n) of 234, 205 and 115 respectively. The frequency distribution of numbers of sites per cluster for different cluster distances

(Figure 3.1) showed that the 900-m cluster distance had the most even frequency distribution. The number of clusters with only 1 site was 167, 136 and 54 for 500, 600 and 900-m clusters respectively, while the number of clusters with greater than 10 sites per cluster was 0, 0 and 6 for 500, 600, and 900-m clusters, respectively. The 900-m cluster distance was selected as an appropriate compromise between having many clusters with only 1 site, and a few very large clusters. Joining clusters at distances less than 900-m would have increased the sample size (n), however many sites would not be incorporated into clusters; while joining clusters at distances greater than 900 m would have decreased the sample size and the clusters would have been too large.

Spatial examination of the 900-m clusters illustrated the appropriateness of the chosen cluster distance (Figure 3.2). The clusters well match the natural geographic groupings of sites used by harbor seals.

Significant spatial autocorrelation in pup counts among individual sites in 1982 and 1986 (Chapter 2) was eliminated by geographically clustering sites. Insignificant Mantel tests for spatial autocorrelation showed that haul-out use by pups was spatially random for clusters of sites (cluster scale) in all survey years ($\alpha > 0.05$). Cluster scale correlograms (Figure 3.3) illustrated that clustering sites removed the patchy spatial pattern found for individual sites (Figure 2.2, Chapter 2).

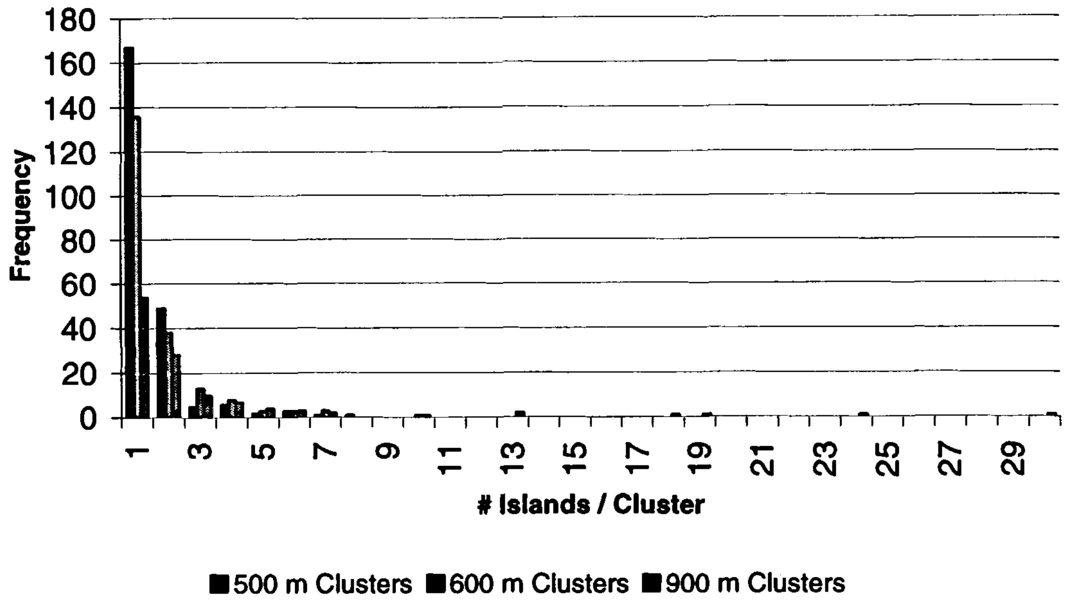

Figure 3.1. Frequency distribution of number of sites per cluster for different cluster distances x (500, 600 and 900 m). Clusters with 900-m maximum within site distances display the most even frequency distribution; number of clusters with only one site is less frequent than the 500 and 600 m clusters, while the number of clusters with > 10 sites is minimal (6).

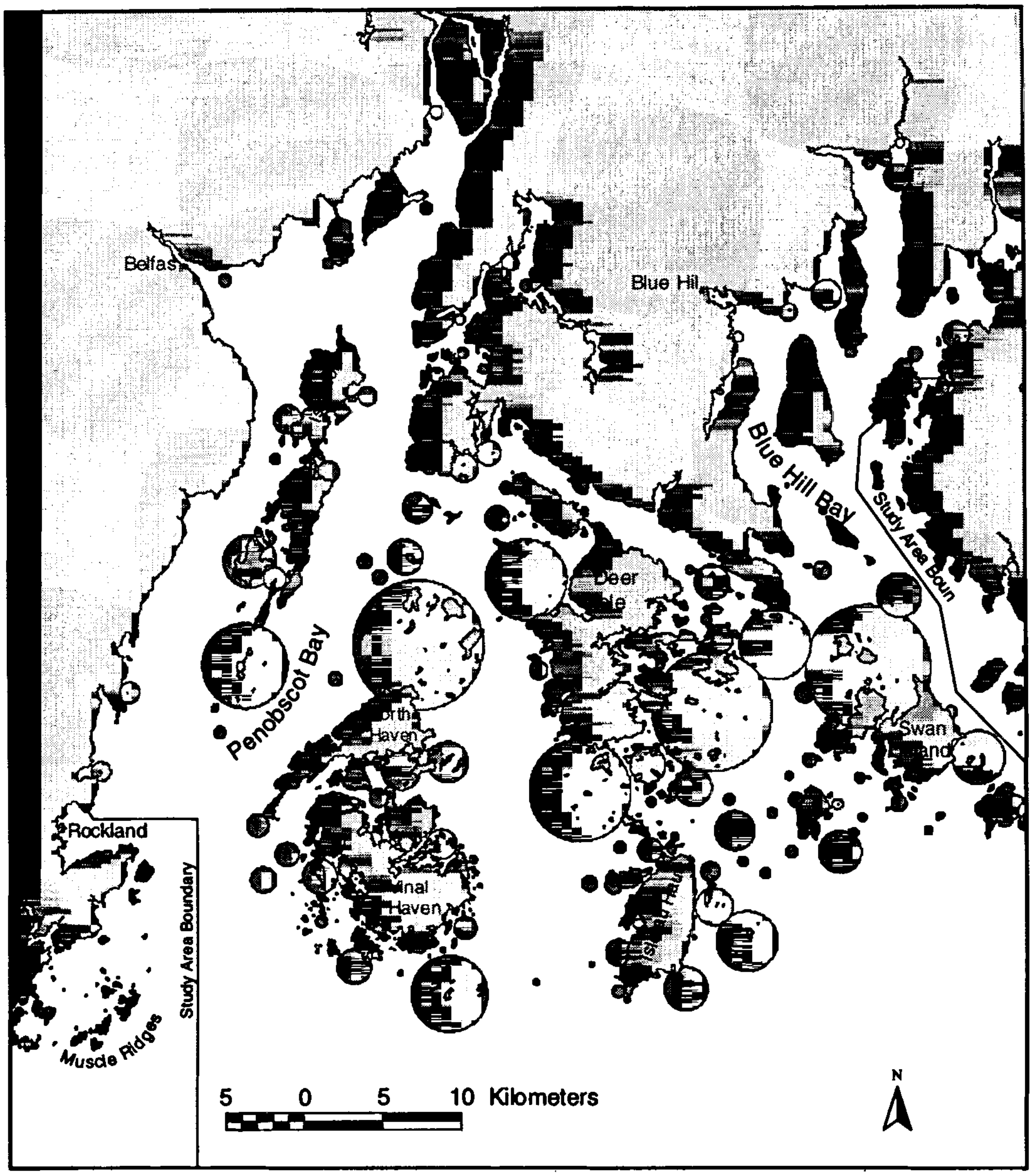

Figure 3.2. Map of clusters of pupping sites defined by a 900-m maximum distance between sites. All sites within a circle represent a single cluster. Circles do not represent area of haul-out space; rather they bound all individual sites within a cluster.

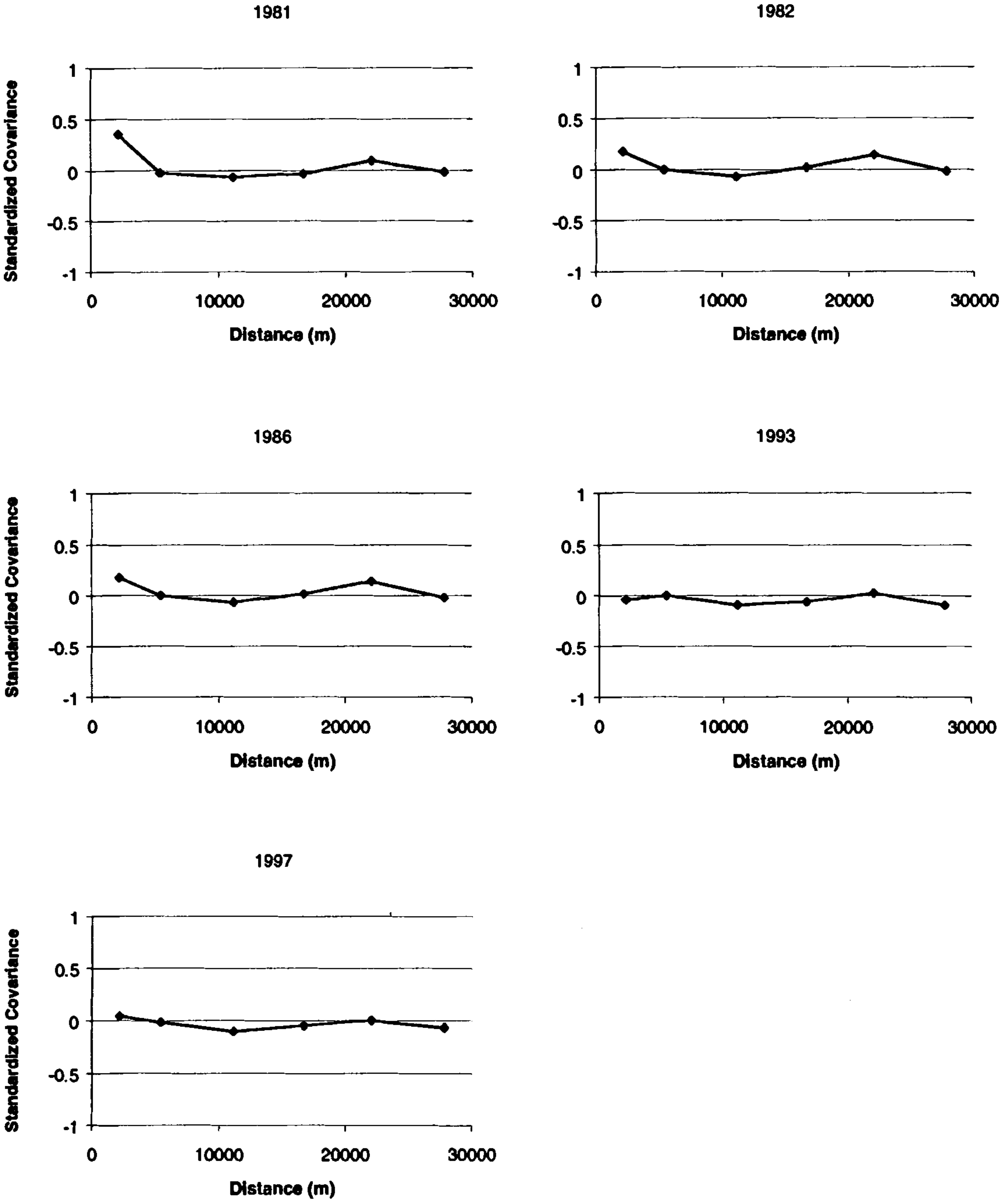

Figure 3.3. Annual spatial correlograms of pup counts for clusters of sites defined by 900-m distance, 1981 – 1997.

Geographically clustering sites decreased temporal variability relative to the moderate levels observed on the individual site scale (Chapter 2). All between year Mantel tests were significant ($\alpha > 0.05$), implying that a cluster's use was dependent on its use in other years (Table 3.1). Thus, cluster use for pupping was consistent between survey years; the erratic temporal use identified for the individual site scale in Chapter 2 was no longer apparent.

Table 3.1. Results from Mantel tests for temporal random use of haul-outs by pups for clusters of sites. P-values (P) are from the randomized distribution generated from 1000 permutations.

	1982	1986	1993	1997
	P	P	P	P
1981	≤ 0.001[a]	≤ 0.001[a]	≤ 0.001[a]	≤ 0.001[a]
1982		≤ 0.001[a]	≤ 0.001[a]	≤ 0.001[a]
1986			≤ 0.001[a]	≤ 0.001[a]
1993				≤ 0.001[a]

[a] Significant ($\alpha = 0.05$) after adjusting for joint estimation of independently significant results using the Bonferonni inequality.

DISCUSSION

Geographically clustering sites that were separated by < 900 m created biologically cohesive sample units for further analyses. Clustering sites eliminated patchy spatial autocorrelation identified on the individual site scale (Chapter 2) and increased temporal stability of use between years. This is evidence that the selected clusters mimicked the patch size actually used for harbor seal pupping. Temporal stability on the cluster scale is evidence that seals may be initially using clusters of sites due to static characteristics, while more variable use between survey years on the individual site scale (Chapter 2) is evidence that selection within a cluster is based on more dynamic processes. This would indicate that harbor seals are selecting pupping sites on multiple spatial scales. Both the cluster scale and the individual site scale will be used in the following chapters to examine spatial and temporal patterns of habitat use for pupping by an increasing population of harbor seals, and environmental characteristics of sites associated with these patterns.

CHAPTER 4

SPATIAL AND TEMPORAL PATTERNS OF PUPPING SITE USE FOR AN INCREASING POPULATION

INTRODUCTION

This chapter examines changes in harbor seal pupping site use in space and time relative to the increase in pup production between 1981 and 1997 in order to: 1) assess the influence of aggregation on harbor seal pup distribution, 2) develop predictions regarding the characteristics of habitat associations at different densities, and 3) design monitoring protocols that are capable of detecting biologically significant changes. As discussed in previous chapters, examining these patterns on appropriate spatial scales is an important component to detecting biologically meaningful patterns. Therefore, all analyses will be completed for the individual site and cluster scales, which refer to analyses that use sites and clusters of sites (aggregated using 900-m distance) as sample units, respectively.

METHODS

Analysis of Variance

Analysis of Variance (ANOVA) was used to determine if harbor seal pup counts increased at all locations at the same rate on the individual site and cluster scales. Mean numbers of pups were tested for differences between different frequencies of use and among survey years. A site's frequency of use was the number of survey years (1 – 5) where pups were observed. Given significant results, Tukey pair-wise comparisons were used to determine which year, frequency, and (year * frequency) interaction term groups were significantly different from one another. Temporal patterns of use were examined for different frequency groups.

Taylor Power Law

The Taylor Power Law (TPL) (Taylor 1961) was used to examine spatial and temporal variation in pup counts on the individual site and cluster scales. The TPL is a relationship between species' mean density and variance and can be used to identify important patterns of population change. The TPL equation

$$s^2 = a\,m^b \qquad (1)$$

states that the variance (s^2) around the mean (m) is equal to the mean raised to the power (b), modified by coefficient (a) (Oyler 1993, Taylor 1961). Coefficient (a) is considered a sampling or computing factor, and coefficient (b) represents the degree of species aggregation (Taylor 1961, Taylor 1984, Taylor 1992, Taylor and Woiwod 1980, Taylor and Woiwod 1982, Taylor et al. 1978, Taylor and Taylor 1977).

A species that has evenly distributed changes in population across sites will have a coefficient (b) equal to 2. If all sites used by a population increase in time by the same factor (k) the mean density will also increase by factor (k), however, the variance will increase by factor (k^2). The slope coefficient from the regression of the log (variance) against the log (mean) is equal to (b), and log (a) is the intercept. A regression of population variance on mean density on a log scale will therefore yield a slope of 2. Aggregating populations, however, will have concentrated changes in density at high-use sites, and will therefore have increased variances as population density increases. A regression of population variance on mean density on a log scale would therefore yield a slope greater than 2. A population that tends to have increased use of low-use sites at high population densities will have lower variances at higher population densities. The TPL equation would have a coefficient (b) that is less than 2.

The Taylor Power Law can be applied to evaluate spatial and temporal relationships of variance to mean density (McArdle et al. 1990). Spatial TPL coefficients (b_s) that calculate species variance and mean density across sites within a year are useful for examining a species within year spatial variance relative to it's overall population density. Temporal TPL coefficients (b_t) calculate the relationships between species variance and mean density within sites across years. Temporal TPL coefficients (b_t) can be used to examine site variation through time relative to a site's mean density. McArdle et al (1990) interpreted values of (b) for spatial and temporal TPL as follows:

a) $b_s = 2$. Within year spatial variability across sites is constant between low and high-density years.

b) $b_s > 2$. Higher density years have higher spatial variability across sites than lower density years, with good sites (high-density sites) increasing proportionately faster in good years than poor sites (low-density sites).

c) $b_s < 2$. Higher density years are less spatially variable across sites than lower density years, with poor sites increasing proportionately faster in good years than good sites.

d) $b_t = 2$. Variability over time is equal across all good and poor sites.

e) $b_t > 2$. Good sites are more variable across years than poor sites.

f) $b_t < 2$. Good sites are less variable across years than poor sites. Good sites remain stable across years and poor sites fluctuate.

Combinations of temporal and spatial TPL can be jointly interpreted to understand patterns of site use and population dynamics (McArdle et al 1990).

The Taylor Power Law was used to examine the spatial and temporal variation in pup counts in relation to overall counts for the individual site and cluster scales of use. T-tests were used to determine if the (b) coefficients were significantly different from 2.

RESULTS

Individual Site Scale of Use

There were significant differences in mean number of pups per site for different survey years, frequencies, and (survey year * frequency) interactions on the site scale (ANOVA) (Table 4.1). Mean number of pups per site was greater in the 1990s than in the 1980s, however, pup counts were not significantly different between 1981, 1982 and 1986 or between 1993 and 1997 (Figure 4.1). Average number of pups per site also increased with number of years the site was used (Figure 4.2) illustrating that frequency of use is a good indicator of pup density and site quality. Pair-wise comparisons showed significant differences between all frequency categories except 2 and 3 (Figure 4.2).

Sites that were used in 2 to 5 of the 5 survey years increased in mean number of pups per site between survey years, while sites that were used in only 1 survey year did not significantly increase with the overall increase in density (Figure 4.3). The significant (year * frequency) interaction term implies different rates of change between different frequencies of use; however, the overall increasing trend between survey years for the different use frequencies is of most interest. All sites are increasing with the overall increase in population density within the study area (Figure 4.3).

Table 4.1. Analysis of Variance of mean numbers of pups per site among survey years, frequency categories, and (frequency * year) interaction terms.

Analysis of Variance					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Year	10395.9	4	2598.9	40.21	≤ 0.001
Frequency	15860.7	4	3965.1	61.35	≤ 0.001
Year*Frequency	2861.7	16	178.8	2.76	≤ 0.001
Error	64627.9	1000	64.6		

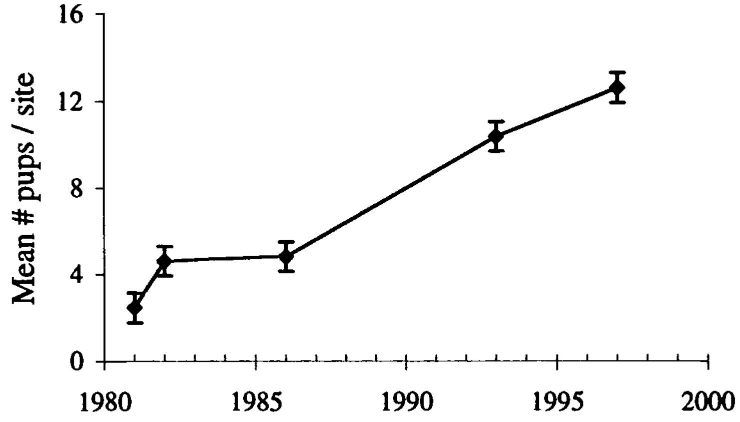

Figure 4.1. Mean number of pups per occupied site (± SE) for each survey year.

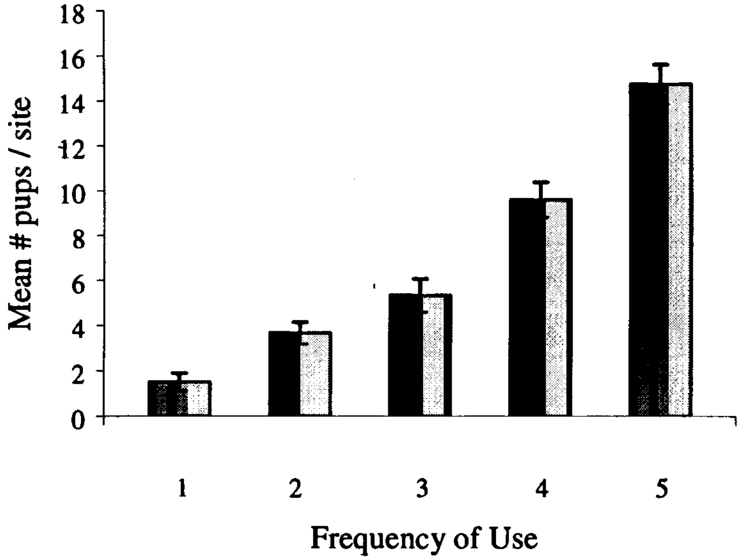

Figure 4.2. Mean number of pups per occupied site (± SE) for sites used 1, 2, 3, 4 and 5 survey years.

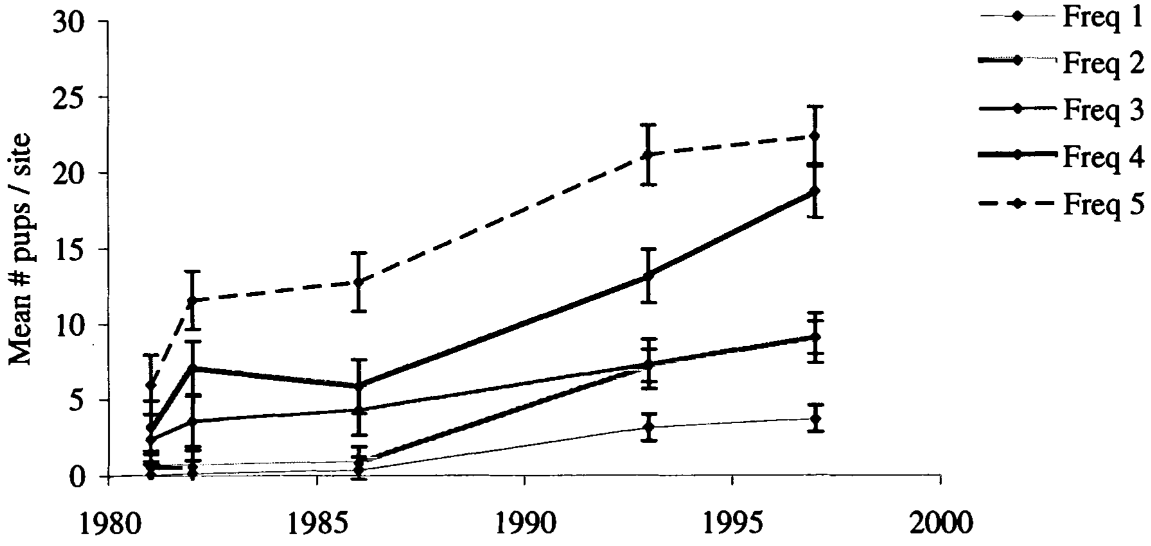

Figure 4.3. Mean number of pups per occupied site (± SE) for each year by frequency of use.

Taylor Power Law results showed that the relative temporal variability of pup counts among individual sites was not different ($b_t = 2$) (Table 4.2). This is consistent with the individual site scale ANOVA results and implies that all sites had increased pup production causing similar temporal variability among sites.

Spatial TPL results indicated that pup production increased proportionately faster at unused or marginal sites than optimal sites, causing decreased spatial variation at increased population levels (Table 4.2). Unused sites, or those with low numbers of pups, filled during years of high overall pup production causing relatively decreased spatial variance. These findings are consistent with those in Chapter 2; significant spatial autocorrelation in pup counts that was detected in 1982 and 1986 was absent in years with higher pup production (1993 and 1997), which implies higher relative spatial variability in lower density survey years. Spatial TPL results should be interpreted with caution given small sample sizes (n = 5 years), though high r^2 values (Table 4.2) imply well-fit regression models.

Table 4.2. Estimated coefficients (b), standard errors (SE), sample sizes (n), and r^2 values for temporal and spatial Taylor Power Law evaluations at two spatial scales.

	Individual Site Scale		Cluster Scale	
	Temporal	Spatial	Temporal	Spatial
b	1.985	1.624[a]	1.862[a]	2.144
SE	0.046	0.160	0.048	0.217
n	256	5	83	5
r^2	0.881	0.972	0.950	0.970

[a] Significantly ($\alpha = 0.05$) less than 2.0.

Cluster Scale of Use

Clusters consistently used (5 of 5 survey years) for pupping increased in population numbers as total population increased, while less frequently used clusters did not similarly increase in pup counts. On the cluster scale, the mean numbers of pups per cluster for different survey years, frequencies of use, and (survey year * frequency) interactions were significantly different (ANOVA) (Table 4.3). Mean numbers of pups per site were significantly greater in the 1990s than in the 1980s, however, pup counts per cluster were not significantly different between 1981, 1982 and 1986 or between 1993 and 1997 (Figure 4.4). Significantly higher mean pup counts were observed in clusters that were used during all survey years compared to less frequently used clusters, while clusters used 1 – 4 times did not have significantly different mean number of pups (Figure 4.5).

High-use clusters (frequency = 5) increased in pup counts between survey years and low frequency clusters (frequency = 1, 2, 3 and 4) maintained constant low pup levels (Figure 4.6), explaining the significant (year * frequency) interaction in the Analysis of Variance (Table 4.3). Clusters used 1, 2, 3 and 4 times showed no significant difference in mean number of pups between survey years (Figure 4.6). However, clusters that were used 5 times had significantly higher numbers of pups in 1993 and 1997 than in previous survey years, and all other (year * frequency) combinations (Figure 4.6). Those clusters that were used during all survey years are shown in Figure 4.7, and number of pups per cluster per year is presented in Table 4.4. Five (cluster numbers 2, 11, 14, 34 and 40) of the 19 clusters consistently comprise 54.8 % (95 % CI: ± 8.7 %) of all pup production in the study area during years of increasing population density.

Table 4.3. Analysis of Variance of mean numbers of pups per cluster among survey years, frequency categories, and (frequency * year) interaction terms.

Analysis of Variance					
Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Year	24234.9	4	6058.7	5.771	≤ 0.001
Frequency	163880.9	4	40970.2	39.026	≤ 0.001
Year*Frequency	64549.8	16	4034.4	3.843	≤ 0.001
Error	409427.1	390	1049.8		

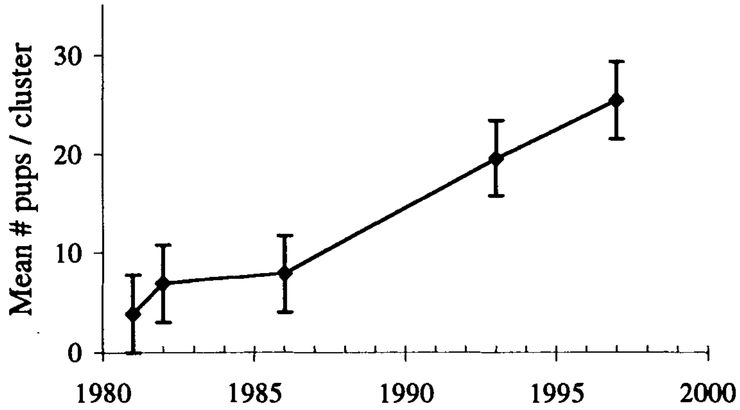

Figure 4.4. Mean number of pups per occupied cluster (± SE) for each survey year.

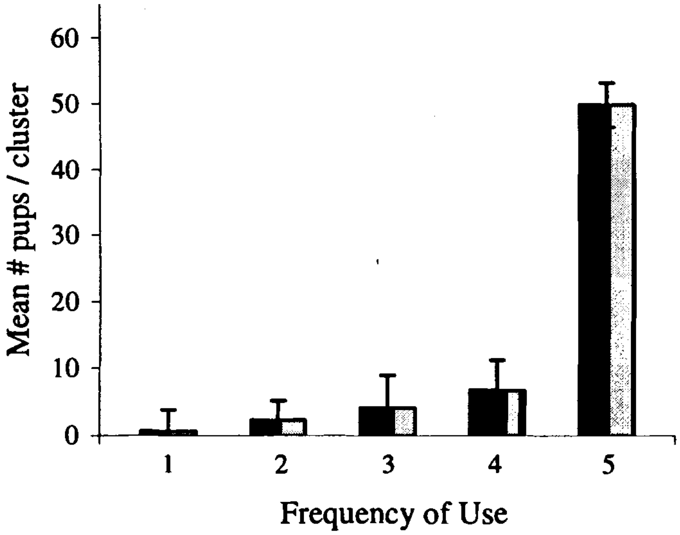

Figure 4.5. Mean number of pups per occupied cluster (± SE) for clusters used 1, 2, 3, 4 and 5 survey years.

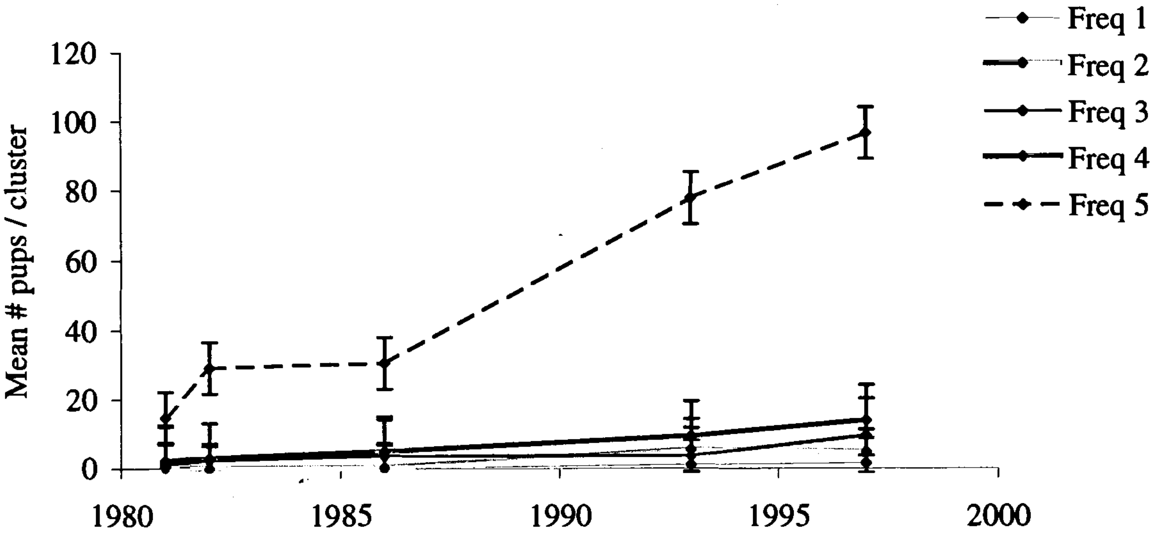

Figure 4.6. Mean number of pups per occupied cluster (± SE) for each year by frequency of use.

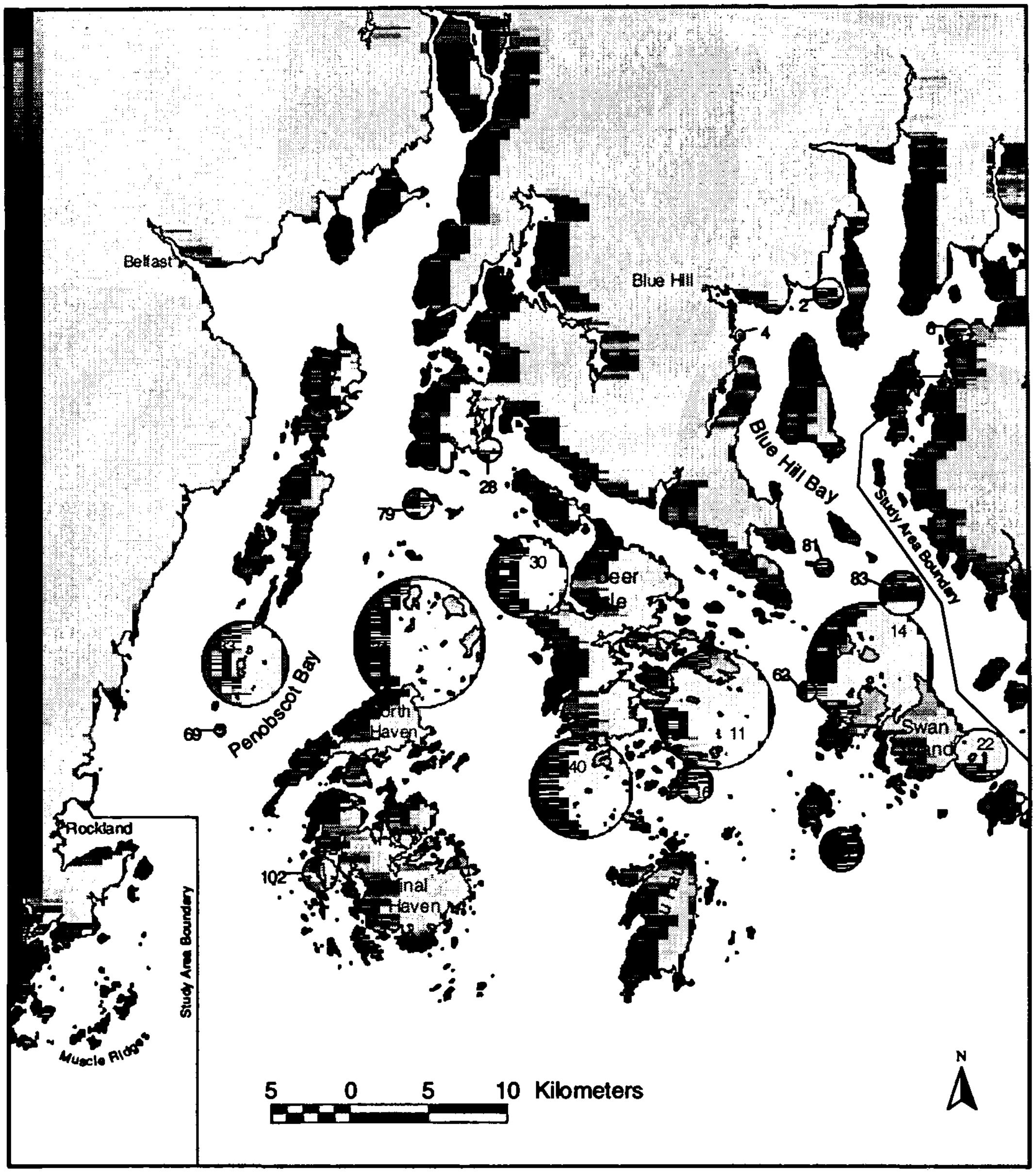

Figure 4.7. Clusters used during all 5 survey years for pupping. These areas had the highest numbers of pups in the study area.

Table 4.4. Number of pups per cluster per year for clusters used during all 5 survey years.

			YEAR		
CLUSTER ID	1981	1982	1986	1993	1997
2	36	131	73	111	167
4	4	8	20	11	7
6	8	46	25	22	49
11	26	49	34	225	341
14	72	111	78	382	288
16	4	3	20	80	40
22	2	4	14	17	13
28	8	22	19	21	19
30	3	4	37	59	99
33	21	22	37	81	71
34	39	76	59	161	324
40	17	11	48	95	137
61	3	2	3	13	12
62	7	13	9	20	49
69	9	13	17	29	38
79	9	8	28	35	41
81	6	19	11	58	64
83	6	11	46	50	73
102	1	1	4	10	4
Total	281	554	582	1480	1836

Taylor Power Law results showed that the relative temporal variability of clusters was lower for clusters with higher pup counts than for those with lower pup counts ($b_t < 2$) (Table 4.2). Clusters that had high mean numbers of pups maintained high densities relative to overall pup production in every survey year and were magnitudes greater than counts at other clusters. These high-use clusters likely drove the TPL results. Very low-use clusters (≤ 2 pups) were stable; they maintained low pup counts in all survey years relative to overall pup production in every survey year, however, they likely had minimal influence on TPL results.

Relative spatial variability among clusters of sites was not different among survey years ($b_s = 2$) (Table 4.2). Pup production changed at similar rates across clusters (space), causing consistent spatial variation at different population levels. Spatial TPL results should be interpreted with caution given small sample sizes ($n = 5$ years), though high r^2 values (Table 4.2) imply well-fit regression models.

DISCUSSION

Patterns of Pupping Site Use

Aggregation and space limitations of mother-pup pairs likely affect pupping site use on the individual site scale. Aggregation is likely important for increased predator detection and resting time (Krieber and Barrette 1984, Terhune 1985), while sufficient haul-out space may be required for mother-pup bonding by minimizing aggressive conspecific interactions (Godsell 1988, Neuman 1999, Thompson 1989). The 180 % increase in pups in the study area between 1981 and 1982 (Table 1.1) was accompanied with an increase in spatial autocorrelation in pup distribution (Chapter 2), and consistent site use (Table 1.1, and Chapter 2). However, the 263 % increase in pup counts between 1986 and 1993 (Table 1.1) was accompanied with the removal of significant spatial autocorrelation (Chapter 2), a decrease in spatial variability, and an increase in number of pupping sites used (Table 1.1). The former is evidence of aggregation at low densities, while the latter illustrates some degree of spatial limitation at higher population densities. TPL results that suggest neither high degrees of aggregation or repulsion likely reflect a balance between these two behaviors (Taylor and Taylor 1977) that is required for successful production of young.

High-use clusters acted as pupping refugia that consistently maintain significantly higher pup counts at different population sizes. This concept of pupping refugia was derived from TPL results and differs from that defined by McArdle et al. (1990). McArdle et al. (1990) defined a refugia distribution in terms of TPL results; good sites have lower temporal variability than bad sites ($b_t < 2$), and in good years poor sites increased to similar densities as good sites, decreasing spatial variation ($b_s < 2$) (Figure 4.8a). Clusters used for pupping were found to have similar relative temporal variability to that described above ($b_t < 2$), however both good and poor clusters increased with population size and good clusters consistently maintained higher pup counts. Poor clusters never increased to densities similar to good clusters, creating equal spatial variability at different population levels ($b_s = 2$) (Figure 4.8b). High-use clusters act as refugia that are not yet limited by resources, however, increased use of less optimal clusters is evidence that resources (i.e., space) at high-use clusters are nearing saturation.

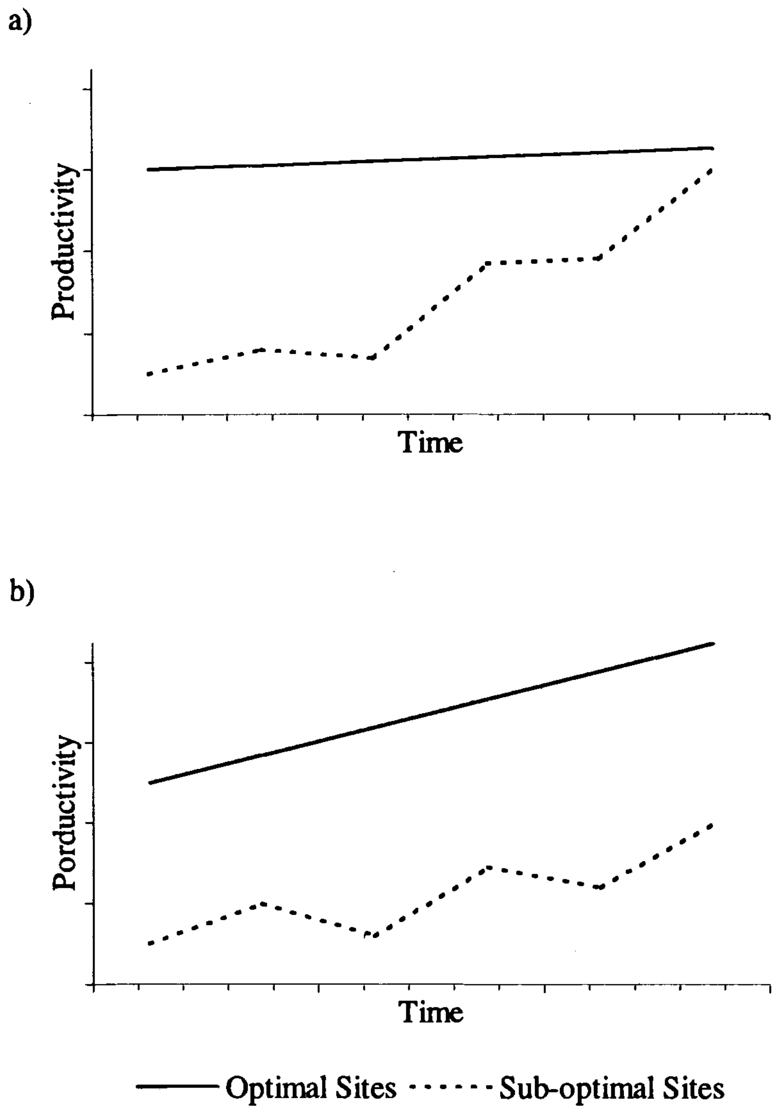

Figure 4.8. Two examples of refugia distributions. Example (a) illustrates the model described by McArdle et al. (1990) ($b_t < 2$, $b_s < 2$), and example (b) illustrates the distribution of increase of pup counts within the study area for the cluster scale ($b_t < 2$, $b_s = 2$).

If the population were to continue to increase, the spatial pattern of use may: 1) continue to increase at high-use and low-use clusters, with high-use clusters maintaining significantly higher pup densities than low-use clusters; or 2) level out at high-use clusters and increase proportionately faster at low-use clusters causing pup counts to approach the magnitude of those at high-use clusters. The former scenario would suggest that pupping habitat at high-use clusters is superior to low-use clusters at all densities and pup counts at high-use clusters will consistently track changes in pup production at densities beyond those observed in this study. The latter scenario suggests that pupping habitat is similar in quality across clusters at high overall pup densities (ideal free distribution (Fretwell and Lucus 1970)), and high-use clusters would poorly track changes in pup production at densities beyond those observed in this study. Evaluation of spatial patterns of future changes in pup production would provide valuable information regarding the stability of quality and carrying capacity of different habitats.

Predicting Patterns of Habitat Use

Knowledge of the spatial and temporal patterns of pupping site use provided the following information for understanding habitat relationships and developing habitat models for mother-pup pairs: 1) the distribution of site quality, i.e., are sites simply good or bad (binomial response) or is there a continuum of site quality (continuous response); 2) the type of resources that may be selected for, i.e., dynamic or static characteristics; and 3) the population levels that will yield the strongest habitat relationships.

The following predictions were made regarding factors affecting pupping site use on the individual site scale:

1) There is a continuous range in quality between marginal and optimal pupping sites within the study area. This is supported by the continuous distribution of pup counts between low and high-use sites in all survey years. Therefore, a continuous response representing this full range is appropriate when examining factors affecting pupping site use at this spatial scale.
2) High between year temporal variability (Chapter 2) suggests that sites may be selected for based on dynamic characteristics, i.e. surf, wind, tidal phase, fish distributions. Static characteristics that are descriptive of sites are likely important predictors of suitable pupping sites, however, dynamic attributes may cause use to be temporally variable.
3) Habitat associations relating pup production to environmental characteristics should be similar for all survey years given all sites increased at similar rates with the overall increase in pup production. However, associations should be strongest at higher densities (1993 and 1997) due to differences in pup counts between different quality sites being of a greater magnitude and more sites being used.

Different use patterns are apparent for clusters of sites. The following predictions were made regarding factors affecting pupping site use on the cluster scale:

1) Clusters seem to be dichotomously good or bad, with consistently used clusters (used during all survey years) having significantly more pups than all other less frequently used clusters. Clusters do not well represent a continuous range of pup counts between low and high-use clusters. Threshold values of environmental characteristics may simply determine if a cluster is good or

bad, making a binomial response (high-use / low-use) appropriate for examining factors affecting use.

2) Cluster use is likely dependent on static characteristics associated with a cluster. Consistent use of high-density clusters (Chapter 3) and low temporal variability suggests that dynamic characteristics may have limited affects on pupping site use on the cluster scale.
3) Habitat associations relating pup production to environmental characteristics should be similar for all survey years given all high-use clusters (used in all survey years) had significantly more pups than low-use clusters (used in 1 – 4 survey years) in all survey years. However, due to the increased differences in pup counts between high and low-use clusters during years of increased pup production, associations should be strongest at higher densities (1993 and 1997).

Management Implications

Harbor seal pupping habitat should be conserved as clusters of sites. Consistent high-use of the same clusters through years of low and high overall pup production identifies these clusters as immobile core production areas in the study area. Harbor seal mother-pup pairs consistently used clusters of sites from 1981 – 1997, while individual site use within these clusters was variable. Conserving the coarser unit should therefore provide for cluster and site scale habitat requirements that are important to successful production.

Annual trend counts of high-use clusters, or a subset of high-use clusters (cluster numbers 2, 11, 14, 34, and 40), would allow managers to inexpensively track temporal changes in harbor seal population productivity. High-use clusters made up a consistent fraction of total pup counts in the study area, and were sensitive to overall changes in pup production. One should use caution, however, when overall pup counts are greater or lesser than those observed between 1981 and 1997. Increased pup production may cause low-use clusters to increase proportionately faster than high-use clusters causing pup counts to approach the magnitude of those at high-use clusters. In this instance, increases in pup production within the study area will not be detected with trend counts of high-use clusters, and number of hauled-out pups will be underestimated relative to surveys conducted at lower pup densities. Very low-use clusters, however, will likely become unused at very low pup densities and number of hauled-out pups will be overestimated relative to surveys conducted at higher densities. Trend counts would, however, be an effective means to monitor changes in production within the wide range of counts observed between 1981 and 1997. Power analyses should be completed to determine the ability of such monitoring protocols to detect significant changes in pup production. Similar analyses that examine the spatial pattern of increase of total hauled-out harbor seals (pup and non-pup) would provide useful information for designing trend count surveys that track overall changes in population size.

CHAPTER 5

CHARACTERISTICS OF PUPPING SITES

INTRODUCTION

Results from Chapter 4 were used to postulate 1) the effects that behavioral mechanisms have on pupping site use, 2) types of environmental characteristics that may affect pupping site use, and 3) the effects that density may have on habitat use. This chapter addresses 2) and 3) directly by examining associations between pupping site use and static environmental factors for different population densities at the individual site and cluster scales (identified in Chapter 3). Including previously identified spatial structure into habitat models indirectly incorporates behavioral mechanisms affecting site use. Results from Chapter 4 were also used to identify a proper response for habitat models (binomial vs. continuous) for each spatial scale.

METHODS

Physical Characteristics of Sites

A spatial database of environmental variables was generated using a GIS (Arc/Info, Version 7.03, ESRI, Redlands, CA). Variables were chosen based on information known about important characteristics of pupping sites. Variables were descriptive of the sites themselves, area surrounding the sites, and distance measurements from the sites to other features in the landscape.

National Wetlands Inventory (NWI) (Cowardin and Carter 1979) digital coverages, 1: 24,000 scale, were transformed to 5-m resolution raster format. NWI coverages were used to calculate the area of intertidal zone (substrate exposed and flooded by tides), area of upland (above mean high tide), and area of sub tidal zone (substrate continuously submerged) within 500 m, 1 km, and 2 km. Centered label points of polygons from the geo-referenced USGS coverages, and point locations from the digitized point coverage, were used as site center points from which to generate a circle for each radius of 500 m, 1 km, and 2 km. The number of intertidal, upland and sub tidal cells within each radius were then tallied for each site and converted to area.

Rasterized NWI coverages were also used to calculate the minimum distance (m) to a site greater than 10 ha, and minimum distance to a site greater than 2000 ha. Most sites > 10 ha have a private home or structure. Sites greater than 2000 ha included the human populated islands within the study area: Deer Isle, Little Deer Isle, Isle au Haut, Swan Island, North Haven, Vinal Haven, and Islesboro. Raster format allowed distances to be calculated from the low tide edge of one site to the low tide edge of another. Areas of each site's intertidal zone, upland, total site (intertidal zone + upland), rocky intertidal zone (intertidal zone with rock > 75% and vegetation < 30%), and aquatic bed (intertidal zone dominated by plants) were also calculated using NWI coverages (m^2).

Areas of shoal water within 500 m, 1 km, and 2 km were calculated using a bathymetry coverage generated by Johnson (1998). Johnson used preliminary bathymetric contour data acquired from the Maine Geologic Survey and digitized additional contours using 1992 NOAA bathymetric charts. She merged the two coverages and transformed them to a 60-m resolution raster format. I then re-sampled the coverage to 5-m cell resolution in order to maintain the same units used in other analyses. Shoals were defined as waters ≤ 10 m in depth from mean high water. Area of shoal water was calculated using the same method as described above for area of upland, intertidal and sub tidal zones within the given radii.

Maximum site elevations (m) were obtained from USGS topographic maps that were transformed to 5-m resolution raster format. Distance to a deep-water channel was also calculated for each site from the Coastal Maine Geological Environment Survey coverages (citation) (5-m resolution raster format). Preliminary correlation analyses eliminated area of rocky intertidal zone, area of aquatic bed, and distance to deep-water channel from further analyses. I defined the set of characteristics summarized in Table 5.1 for individual site scale analyses, including transformations required to meet modeling assumptions of normality.

Cluster scale analyses (Table 5.2) included the average minimum distance to a site greater than 10 and 2000 ha. Total areas of intertidal zone, upland, total site, rocky intertidal zone, and aquatic bed intertidal zone were calculated for clusters. Maximum elevation per cluster, and number of used sites in each cluster was also determined.

Table 5.1. Explanatory variables considered in habitat association models on the individual site scale.

Variable	Transformation	Description
Mindist2000	$x^{0.5}$	Distance to first site greater than 2000 hectares (km)
Mindist10	$x^{0.5}$	Distance to first site greater than 10 hectares (km)
Intertidal	ln	Area of intertidal zone (m^2)
Upland	ln	Area of land above mean high-tide (m^2)
Totarea	ln	Intertidal + Upland (m^2)
Maxelev	$(x^{0.5})^{0.5}$	Maximum site elevation (m)
Intertid1km	ln	Area of intertidal zone within 1 kilometer (m^2)
Upland1km	ln	Area of land above mean high-tide within 1 kilometer (m^2)
Subtidal1km	x^3	Area of water below mean low-tide within 1 kilometer (km^2)
Shoal1km	none	Area of water $\leq$ 10 meters deep within 1 kilometer (km^2)

Table 5.2. Explanatory variables considered in habitat association models on the cluster scale.

Variable	Transformation	Description
Mindist2000[a]	$x^{0.5}$	Distance to first site greater than 2000 hectares (km)
Mindist10[a]	$x^{0.5}$	Distance to first site greater than 10 hectares (km)
Intertidal[b]	ln	Area of intertidal zone within cluster (m^2)
Upland[b]	ln	Area of land above mean high-tide within cluster (m^2)
Totarea[b]	ln	Intertidal + Upland (m^2)
Maxelev[c]	$(x^{0.5})^{0.5}$	Maximum elevation within cluster (m)
Numclus	ln	Number of sites within cluster

[a] Variable was averaged across sites within a cluster to obtain cluster scale values.

[b] Variable was totaled across sites within a cluster to obtain cluster scale values.

[c] The maximum value from all sites within a cluster was used for cluster scale values.

Habitat Model Development

Categorical Response: Frequency of Use by Pups

Multinomial and binomial logistic regressions were used to examine associations between frequency of use (used 1, 2, 3, 4 or 5 survey years for pupping) and characteristics of individual sites and clusters. Frequencies that did not have significantly different mean pup counts (Chapter 4) were collapsed into the same frequency category. Individual sites that were used 2 and 3 survey years were combined into the same frequency category creating 4 categories of site use: sites used 1, 2 + 3, 4 and 5 survey years. These categories of use for the individual site scale will be referred to A – D accordingly. Clusters that were used 1, 2, 3 and 4 survey years were combined into the same frequency category, creating 2 categories of cluster use (clusters used 1 to 4, and 5 survey years). Multinomial logistic regression was used on the individual island scale where number of frequency categories was greater than 2, and binomial logistic regression was used on the cluster scale where 2 frequency categories were identified.

Variables were transformed where appropriate in order to meet assumptions of normality for logistic regression models. Prior to including variables in multivariate analyses, preliminary univariate analyses were completed for all variables in Tables 5.1 and 5.2. Variables were considered in multivariate analyses if $\alpha < 0.300$. Spearman correlations were calculated between all variable pairs to be considered in multivariate analyses. To avoid problems with multicollinearity (Neter et al. 1996), pairs of variables with correlations > 0.50 were not included in the same model. All remaining possible models were examined for each year separately, from which the most predictive and parsimonious model was chosen.

Goodness-of-fit was evaluated using McFadden's Rho-squared (ρ^2). McFadden's ρ^2 values that were greater than 0.20 were considered to be very satisfactory (Hensher and Johnson 1981). The Wald test statistic and derivative tables were examined in addition to the above statistic for multinomial models. The Wald test statistic was used to determine the overall significance of the variable in the full model (Hosmer and Lemeshow 1989, Steinberg and Colla 1999). Derivative tables provided a means to examine how changes in independent variables affected the predicted probability of the response for multinomial logistic regression models. Derivative tables showed how the predicted probability changed across dependent variable levels for each unit of increase in the independent variable (Steinberg and Colla 1999).

On the site scale, a random subset of 20 % of all sites from each of the five frequency-of-use categories was reserved for model validation (test data). Model robustness was examined for site scale analyses by calculating predicted values for all observations in the test data set using the parameter estimates from the model-building data set. Percent correctly classified sites were then compared between the learning and test data sets.

Continuous Response: Numbers of Pups

Multiple and trend surface regression analyses were used on the individual site and cluster scales at different population densities to develop habitat models between pup counts and site characteristics and model spatial pattern, respectively. The spatial component (trend surface analysis) was incorporated into habitat analyses in order to account for spatial autocorrelation in the data sets, and hence control for violation of model assumptions and provide additional information for model interpretation. The response variable in all regression models was log (ln) transformed pup counts.

Habitat characteristics were modeled for each survey year using multiple regressions. Variables were transformed where appropriate in order to meet assumptions of normality. Prior to including variables in multivariate analyses, preliminary univariate analyses were completed for all variables in Tables 5.1 and 5.2. Variables were considered in multivariate analyses if $\alpha < 0.250$. Spearman correlations were completed between all variables to be considered in multivariate analyses. Due to problems with multicollinearity (Neter et al. 1996), pairs of variables with correlations > 0.50 were not included in the same model. Within these parameters, all possible models were examined for each year separately, from which the most predictive and parsimonious model was chosen.

Spatial structure was modeled by completing forward step-wise selection from a cubic trend surface regression:

$$z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

with x and y representing geographic UTM coordinates (Bocard et al. 1992). Due to the exceptionally large numbers generated from UTM coordinates, the minimum value from each variable was subtracted from all cases and was then divided by 1,000 (converted from m to km). A significance level of $\alpha = 0.15$ was used to enter and remove variables from the model.

On the individual site scale, models were tested for robustness using an external validation data set (test data) for models developed for 1993 and 1997. The validation data set was a random subset of 20% of all sites chosen from each of the five frequency-of-use categories. Models were independently developed for the test data using the variables from the best model from the learning data set. Coefficients, standard errors, r^2 and p-values were compared.

Pup count variance was partitioned between habitat and spatial components in order to incorporate shared variation resulting from spatial autocorrelation in the independent and response variables (Bocard et al. 1992). Species variation was partitioned into 4 categories: (a) non-spatial habitat, (b) spatially structured habitat, (c) spatial structure, and (d) unexplained variation (Bocard et al. 1992). This was accomplished by: 1) regressing pup counts on habitat and spatial variables; 2) regressing pup counts on habitat variables; and 3) regressing pup counts on spatial variables (Boone 2000). The (r^2) values from each regression analysis were combined as follows in order to obtain the percent variation explained for each of the above 4 categories (Bocard et al. 1992):

(a) = habitat r^2 – (b);

(b) = habitat r^2 + space r^2 – (habitat + space) r^2;

(c) = space r^2 – (b);

(d) = 1 – (habitat + space) r^2.

RESULTS

Frequency of Use by Pups

Individual Site Scale of Use

The frequency with which seals used sites for pupping was poorly related to habitat variables on the site scale. Multinomial logistic models were significant for 'minimum distance to a site $\geq$ 2000 ha' and 'area of sub tidal zone within 1 km' (α = 0.05) (Table 5.3). Model fit was poor with McFadden's ρ^2 equal to 0.028 and 0.018 respectively. Significant p-values for the 'Mindist2000' model within the category A (used 1 year) vs. category B (used 5 years) sub-model indicates that the model does best at separating sites used during 1 survey year from those that were used 5 survey years (Table 5.3). Sub-models that compared other frequency categories did poorly for all models.

Minimum distance to a site $\geq$ 2000 ha, and sub tidal area within 1 km were significantly associated with frequency of use (α = 0.05) (Table 5.4). One unit of increase in these predictor variables corresponded to a decrease in probability of a site being used once and an increase in probability of a site being used 2, 3 or 4 times (Table 5.4). Sites that are farther from large islands and are surrounded by a greater area of water are more likely to be used frequently than those that are within closer proximity to large islands and surrounded by less water.

Though model fits were unsatisfactory, results were consistent between the learning and test data sets (Table 5.5). Models did best at classifying sites that were used once. High correlation (Spearman rank correlation > 0.500) between variables prevented the development of good multivariate logistic regression models.

Cluster Scale of Use

The frequency with which clusters were used for pupping was related to many of the habitat variables at the cluster scale (Table 5.6). Area of intertidal zone (ρ^2 = 0.245) and number of sites in a cluster (ρ^2 = 0.293) were positively associated with clusters that were used during 5 survey years. The probability of a cluster being used 5 times compared to < 5 times increased as the area of intertidal zone increased and the number of sites in a cluster increased. The positive relationship between frequency of use and area of upland, total cluster area and maximum site elevation in a cluster are likely surrogates of the more biologically significant variables 'area of intertidal zone' and 'number of sites in a cluster' due to high variable correlation.

Predictions made from the logistic models were variable and inconsistent. Significant models did well at predicting use of clusters with frequency of use less than 5 survey years (78.4 – 84.5 % correct), however, they were poor predictors of clusters that were used during all five survey years (27.2 – 47.9 % correct) (Table 5.6). High correlation between variable pairs prevented the development of good multivariate logistic models.

Table 5.3. Results of best univariate logistic regression habitat models ($\alpha < 0.300$) for harbor seal pupping on the site scale. McFadden's Rho-squared (ρ^2) and chi-square p-values are presented. The multinomial response is categories that represent frequency-of-use (A = used 1 survey, B = used 2 or 3 survey, C = used 4 surveys, and D = used 5 surveys). Level D is the reference category within sub-models; i.e., sub-model A vs. D compares category A to D, etc. n = 205.

Overall Model			Explanatory Variables				
Model	ρ^2	P	Sub-model	Variable	Estimate[a]	SE	P
Mindist2000	0.028	0.004	A vs. D	Constant	3.671	0.835	0.000
				Mindist2000	-1.472	0.512	0.004
			B vs. D	Constant	2.763	0.843	0.001
				Mindist2000	-0.814	0.507	0.108
			C vs. D	Constant	1.110	0.990	0.262
				Mindist2000	-0.589	0.606	0.331
Subtidal1km	0.018	0.031	A vs. D	Constant	3.287	0.982	0.001
				Subtidal1km	-0.074	0.040	0.062
			B vs. D	Constant	2.450	1.000	0.014
				Subtidal1km	-0.039	0.040	0.336
			C vs. D	Constant	0.165	1.265	0.896
				Subtidal1km	0.002	0.050	0.970
Intertidal	0.012	0.134	A vs. D	Constant	3.569	1.598	0.025
				Intertidal	-0.212	0.169	0.210
			B vs. D	Constant	3.881	1.606	0.016
				Intertidal	-0.257	0.171	0.131
			C vs. D	Constant	-0.231	2.003	-0.908
				Intertidal	0.047	0.209	0.823
Shoal1km	0.008	0.257	A vs. D	Constant	0.783	0.489	0.110
				Shoal1km	0.717	0.387	0.064
			B vs. D	Constant	0.786	0.491	0.110
				Shoal1km	0.654	0.389	0.093
			C vs. D	Constant	-0.714	0.631	0.258
				Shoal1km	0.771	0.459	0.093

[a] Signs associated with estimates are intuitively reversed given the assignment of the reference level. Negative estimates may be interpreted as a positive relationship between frequency of use and the predictor variable for that sub-model.

Table 5.4. Individual site scale multinomial logistic regression models. Wald test statistic chi-square P-values and derivative tables are presented. Categories represent frequencies of use (A = used 1 survey, B = used 2 or 3 survey, C = used 4 surveys, and D = used 5 surveys).

Model	Variable	Wald P[a]	Category[b]			
			A	B	C	D
Mindist2000	Constant[c]	0.000	0.361	0.016	-0.162	-0.216
	Mindist2000	0.006	-0.186	0.069	0.040	0.078
Subtidal1km	Constant[c]	0.000	0.370	0.038	-0.218	-0.191
	Subtidal1km	0.044	-0.011	0.003	0.005	0.004
Intertidal	Constant[c]	0.007	0.235	0.331	-0.322	-0.243
	Intertidal	0.161	-0.011	-0.027	0.023	0.015
Shoal1km	Constant[c]	0.009	0.092	0.086	-0.131	-0.046
	Shoal1km	0.302	0.033	0.006	0.013	-0.052

[a] The *t* ratios normally used to assess the significance of individual parameters in binomial logistic regression cannot be used to assess overall significance of a variable in multinomial regression given that each variable corresponds to more than one parameter. The Wald test statistic is used to determine the overall significance of the variable in the full model (Hosmer and Lemeshow 1989, Steinberg and Colla 1999).

[b] Derivative tables provide a way to examine how changes in independent variables will affect the predicted probability of the response in multinomial logistic regression. The values under each category represent how the predicted probability will change for each unit of increase in the given variable for that frequency category (Steinberg and Colla 1999).

[c] There is no useful interpretation of constant results (Steinberg and Colla 1999).

Table 5.5. Comparison of percent correctly classified sites for site scale multinomial logistic regression models. Results are for the learning (model) and test data sets. Categories represent frequencies of use (A = used one survey, B = used 2 or 3 survey, C = used 4 surveys, and D = used 5 surveys).

Model	Data	n	Percent Correctly Classified			
			A	B	C	D
Mindist2000	Model	205	45.4	39.6	10.8	11.1
	Test	51	45.7	38.9	9.6	12.9
Subtidal1km	Model	205	44.4	39.3	11.3	9.2
	Test	51	49.4	37.9	11.9	10.5
Intertidal	Model	205	42.3	39.6	11.5	8.9
	Test	51	42.7	39.1	11.5	8.3
Shoal1km	Model	205	42.6	39.0	10.3	10.1
	Test	51	43.1	39.0	10.2	12.1

Table 5.6. Results of univariate logistic regression habitat models for the cluster scale. McFadden's Rho-squared (ρ^2), and P-values are presented. Response = (pup use frequency = 5); reference = (pup use frequency < 5). n = 83.

Overall Model					Explanatory Variable			
Variable	ρ^2	Percent Correctly Classified			Variable	Estimate	SE	P
		Freq = 5	Freq < 5	Overall				
Mindist2000	0.055	27.4	78.4	66.8	Constant	-2.430	0.661	≤ 0.001
					Mindist2000	0.982	0.456	0.031
Mindist10	0.004	23.2	77.2	64.8	Constant	-1.520	0.577	0.008
					Mindist10	0.440	0.727	0.545
Intertidal	0.245	43.1	83.1	74.0	Constant	-11.336	2.848	≤ 0.001
					Intertidal	0.935	0.253	≤ 0.001
Upland	0.209	39.3	82.0	72.2	Constant	-2.901	0.651	≤ 0.001
					Upland	0.239	0.066	≤ 0.001
Totarea	0.218	41.1	82.5	73.0	Constant	-9.162	2.295	≤ 0.001
					Totarea	0.719	0.199	≤ 0.001
Maxelev	0.104	31.7	79.7	68.7	Constant	-5.962	1.743	≤ 0.001
					Maxelev	2.362	0.832	0.005
Numclus	0.293	47.9	84.5	76.1	Constant	-4.487	0.940	≤ 0.001
					Numclus	2.356	0.624	≤ 0.001

Numbers of Pups

Individual Site Scale of Use

Habitat analyses indicated significant relationships between habitat variables and numbers of pups in 1982, 1993 and 1997, however, models explained little variability (Table 5.7). Significant positive associations were found between number of pups per site and area of intertidal zone, area of sub tidal water within 1 km, and area of shoal water within 1 km. Minimum distance to sites ≥ 2000 ha was both negatively (1982) and positively (1993) associated with number of pups per site. Biological explanation for this difference is unclear, causing reliability of coefficient values to be questionable. Given these weak model results, validation was not appropriate.

Variation in pup counts per site explained by spatial trend surface models ranged between 8.0 – 42.3 % (Table 5.8), and habitat variables accounted for 0 – 17.5 % (Table 5.7) of the variation. Variance was partitioned between these two components (Bocard et al. 1992) in order to incorporate shared variation resulting from spatial autocorrelation in the independent and response variables. Spatial structure accounted for 8.0 – 35.1 % of the variance in pup counts when the shared gradient of habitat was removed, and habitat variables accounted for 0 – 10.2 % when the shared gradient with spatial structure was removed (Figure 5.1). The percent of the explained variation in pup counts attributed to habitat and space interaction was also minimal (0 – 7.2 %) (Figure 5.1).

Total explained variation was consistently low for all site scale analyses (Figure 5.1). Spatial structure accounted for the largest proportion of the explained variation in pup counts, with a peak occurring in 1982. These findings are consistent with previously observed significant spatial autocorrelation in 1982 (Chapter 2). Though minimal, habitat accounts for a higher proportion of explained variation during the high-density years (1993 and 1997).

Table 5.7. Results of best linear regression habitat models for each survey year for the site scale. Coefficients of determination (r^2) for each model, explanatory variables used, and their coefficients are presented.

	Overall Model			Explanatory Variables			
Year	n	r^2	P	Variable	Estimate	SE	P
1981	No significant results						
1982	77	0.111	0.013	Constant	0.889	0.782	0.259
				Mindist2000	-0.524	0.207	0.014
				Intertidal	0.147	0.081	0.074
1986	No significant results						
1993	64	0.113	≤ 0.001	Constant	0.682	0.590	0.250
				Mindist2000	0.279	0.157	0.078
				Intertidal	0.092	0.058	0.116
1997	65	0.175	≤ 0.001	Constant	0.448	0.368	0.225
				Subtidal1km	0.424	0.129	≤ 0.001
				Shoal1km	0.048	0.012	≤ 0.001

Table 5.8. Results of best cubic trend surface regression models for each survey year for the site scale. Coefficients of determination (r^2) for each model, explanatory variables used, and their coefficients are presented.

Overall Model				Explanatory Variables			
Year	n	r^2	P	Variable	Estimate	SE	P
1981	73	0.080	0.015	Constant	0.793	0.161	≤ 0.001
				XY	0.001	0.000	0.015
1982	77	0.423	≤ 0.001	Constant	2.418	0.588	≤ 0.001
				X	-0.127	0.040	0.002
				X^2	0.002	0.001	0.005
				XY	0.001	0.000	≤ 0.001
1986	74	0.195	≤ 0.001	Constant	1.373	0.145	≤ 0.001
				XY	0.001	0.000	≤ 0.001
1993	126	0.193	≤ 0.001	Constant	2.570	0.369	≤ 0.001
				X	-0.061	0.015	≤ 0.001
				XY	0.002	0.001	0.082
				X^2Y	0.001	0.000	0.004
				XY^2	-0.001	0.000	≤ 0.001
1997	133	0.229	≤ 0.001	Constant	2.455	0.266	≤ 0.001
				X	-0.047	0.011	≤ 0.001
				XY	0.002	0.000	≤ 0.001
				Y^3	-0.001	0.000	≤ 0.001

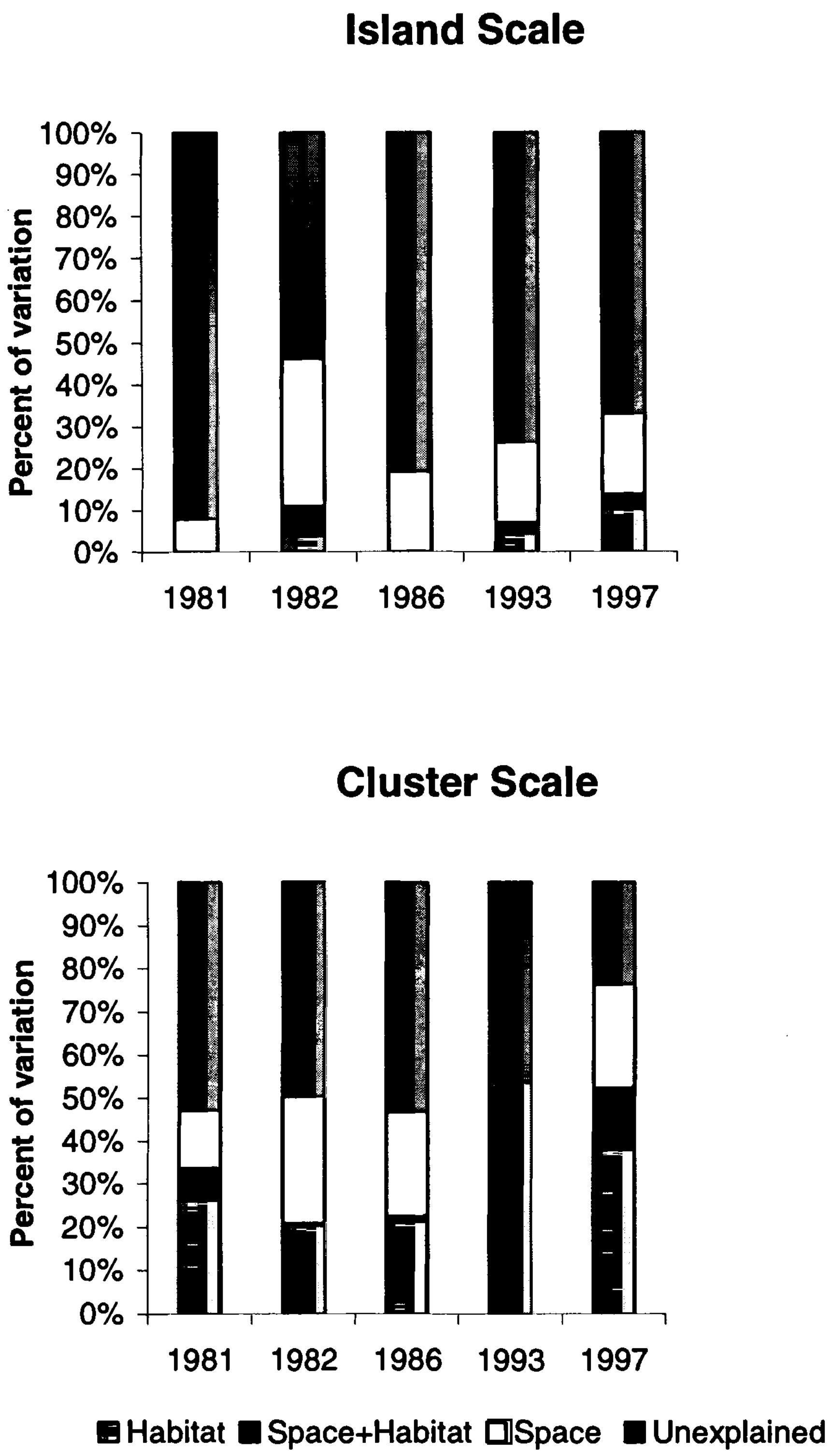

Figure 5.1. Percent variation in pup counts due to habitat; spatially structured habitat; spatial structure; and unexplained variation for each survey year on the individual site and cluster scales.

Cluster Scale of Use

Number of seal pups per cluster was related to many of the habitat variables ($\alpha = 0.05$) (Table 5.9). Minimum distance to sites greater than 2000 ha was positively associated with pup counts in 1997 only. There were significant positive relationships with minimum distance to 2000 ha sites, area of intertidal zone, upland, total site area, maximum elevation and number of sites in a cluster in 1981, 1993 and 1997 (Table 5.9). With the exception of 1997, multivariate habitat models were compromised by correlated variables (Spearman rank correlation > 0.500) (Table 5.10).

Variation in pup counts per cluster explained by spatial trend surface models ranged between 0 – 38.6 % (Table 5.11), and habitat variables accounted for 20.8 – 53.6 % (Table 5.10) of the variation. Variance was partitioned between these two components (Bocard et al. 1992) in order to incorporate shared variation resulting from spatial autocorrelation in the independent and response variables. Spatial structure accounted for 0 – 24.3 % of the variance in pup counts when the shared gradient of habitat was removed, and habitat variables accounted for 20.3 – 53.6 % when the shared gradient with spatial structure was removed (Figure 5.1). The percent of the explained variation in pup counts attributed to habitat and space interaction was minimal (0 – 14.6 %) (Figure 5.1).

When compared across survey years, the spatial gradient accounted for the largest proportion of the explained variation in 1982, 1986 and 1997 on the cluster scale. 1981 had a minimal amount of variation explained by the spatial regression analyses, and spatial structure was completely absent during 1993 (Figure 5.1). Habitat characteristics accounted for a larger percent of variation in pup counts during the highest density survey years.

Table 5.9. Univariate linear regression habitat models for the cluster scale. Coefficients of correlation (r) for each model and P-values are presented. Results in bold type signify significant results ($\alpha = 0.05$).

		YEAR				
Variable	Statistic	1981	1982	1986	1993	1997
Mindist2000	r	0.100	-0.211	0.105	0.154	**0.343**
	P	0.533	0.271	0.563	0.225	**0.005**
Mindist10	r	0.079	-0.284	0.063	0.092	0.105
	P	0.625	0.135	0.726	0.470	0.405
Intertidal	r	**0.393**	**0.406**	0.343	**0.533**	**0.510**
	P	**0.011**	**0.029**	0.051	**0.000**	**0.000**
Upland	r	**0.399**	0.283	0.270	**0.493**	**0.504**
	P	**0.010**	0.137	0.129	**0.000**	**0.000**
Totarea	r	**0.383**	**0.370**	0.292	**0.505**	**0.493**
	P	**0.014**	**0.048**	0.099	**0.000**	**0.000**
Maxelev	r	**0.459**	**0.456**	0.317	**0.426**	**0.506**
	P	**0.003**	**0.013**	0.072	**0.000**	**0.000**
Numclus	r	**0.580**	**0.427**	**0.474**	**0.732**	**0.698**
	P	**0.000**	**0.021**	**0.005**	**0.000**	**0.000**

Table 5.10. Results of best linear regression habitat models for each survey year for the cluster scale. Coefficients of determination (r^2) for each model, explanatory variables used, and their coefficients are presented.

Overall Model				Explanatory Variables			
Year	n	r^2	P	Variable	Estimate	SE	P
1981	41	0.336	≤ 0.001	Constant	0.049	0.328	0.881
				Numclus	0.860	0.194	≤ 0.001
1982	29	0.208	0.013	Constant	-1.383	1.344	0.313
				Maxelev	1.721	0.646	0.013
1986	33	0.225	0.005	Constant	1.317	0.425	0.004
				Numclus	0.686	0.229	0.005
1993	64	0.536	≤ 0.001	Constant	0.413	0.246	0.099
				Numclus	1.361	0.161	≤ 0.001
1997	65	0.525	≤ 0.001	Constant	-0.403	0.375	0.287
				Numclus	1.478	0.203	≤ 0.001
				Mindist2000	0.530	0.239	0.030

Table 5.11. Results of best cubic trend surface regression models for each survey year for the cluster scale. Coefficients of determination (r^2) for each model, explanatory variables used, and their coefficients are presented.

Overall Model				Explanatory Variables			
Year	n	r^2	P	Variable	Estimate	SE	P
1981	41	0.211	0.011	Constant	0.218	0.399	0.588
				Y	0.085	0.027	0.003
				Y^3	-0.001	0.000	0.008
1982	29	0.302	0.002	Constant	1.244	0.340	≤ 0.001
				XY	0.001	0.000	0.002
1986	33	0.255	0.003	Constant	1.628	0.313	≤ 0.001
				Y	0.046	0.014	0.003
1993	64	No significant results					
1997	65	0.386	≤ 0.001	Constant	0.553	0.375	0.146
				Y	0.181	0.036	≤ 0.001
				Y^2	-0.004	0.001	≤ 0.001
				XY	0.001	0.000	0.017

DISCUSSION

Initial use of pupping sites may simply be dependent on groups of sites containing close alternative haul-out locations, large areas of intertidal zone, and seclusion from areas of human population. Similarly, Krieber and Barrette (1984) showed that harbor seals in Forillon National Park, Canada aggregated more than expected on the basis of the distribution of suitable haul-out sites, and were selecting sites that were in close proximity to other available sites. Dynamic conditions such as wind direction, surf, tidal phase, and human use patterns may cause site suitability to change (Allen et al. 1984, Boulva and McLaren 1979, Richardson 1976, Schneider and Payne 1983, Sullivan 1980), therefore, making the proximate location of alternative sites important. High use clusters are used consistently between survey years (Chapter 4), while use of pupping sites within clusters is temporally variable. It follows that static characteristics such as sufficient haul-out space and distance from human activity, best determined the quality of clusters and initial use of an area, and that individual site use within clusters was dependent on more dynamic characteristics (predicted in Chapter 4 and shown in Chapter 5).

Similar proportions of the total variation in pup counts are represented by spatial structure independent of the environmental variables for the cluster and individual site scales. This proportion of variation in pup counts reflects an unmeasured underlying process. Given that pup counts and environmental variables did not have similar spatial structuring, the major causes of spatial pattern in pup counts are not explained by the chosen descriptors. Spatially structured variation in the species data independent of habitat variables likely represents social aggregation (Bocard et al. 1992), or selection for spatially structured unmeasured environmental characteristics (additional habitat variables), or both.

At the individual site scale, the spatial structure in pup counts may be partially due to conspecific attraction. It is reasonable to conclude on this scale that harbor seals benefit from being close to other populated sites. Group hauling increases safety and conserves energy by increasing predator detection and providing more rest time (Krieber and Barrette 1984, Terhune 1985). Effects of unmeasured environmental characteristics are likely to also contribute to the observed spatial pattern. Dynamic characteristics may cause availability to change, forcing aggregation on groups of sites. For example, a strong south wind may make southerly exposed sites unavailable due to surf conditions, forcing seals to haul-out on more sheltered northerly sites.

Spatial structure in pup counts on the cluster scale may be best explained by unmeasured landscape scale environmental descriptors. It is improbable that spatial structure on the cluster scale was due to species aggregation behavior; seals are unlikely drawn to sites based on the presence of conspecifics > 900 m away.

Comparisons of site use among years of different densities are difficult to make given the high proportion of unexplained variation, however, some patterns that were expected based on Chapter 4 findings were weakly detected. Though differences were minimal, habitat accounted for the most variation in pup counts for the high-density years (1993 and 1997), and the least amount of variation for the lowest density year (1981) on the site scale. This was likely due to an increased magnitude of counts and an increased number of used sites at high densities, while associations developed for low-density years (1981) may be weak due to low pup counts across sites (Chapter 4). Spatial variables accounted for the most variation in pup numbers in 1982. These results are also consistent with previous site scale findings due to significant spatial autocorrelation in 1982 and 1986 (Chapter 2), and decreased spatial variance at increased population densities (Chapter 4). On the cluster scale, habitat associations were strongest during high-density years. This was expected due to increased differences in pup counts between high and low use sites during years of increased pup production (Chapter 4). The amount of explained variability in pup counts due to spatial variables on the cluster scale fluctuated between surveys unpredictably.

Unexplained variation in pup counts was considerable on the cluster and site scales. This may be due to true random use, unmeasured habitat characteristics, or harbor seal behavior. Explanatory variables in habitat models were limited to coarse physical characteristics of sites. Many important aspects of harbor seal habitat were not included in models, such as: fine spatial scale site attributes; subsurface marine characteristics; prey species abundance and distribution; and dynamic environmental characteristics known to effect site use patterns (i.e. tidal phase, weather conditions, and surf). This study addresses the effects of coarse site characteristics and spatial structure on pup density only, and ignores all other aspects relevant to the life history of harbor seals. Stagnant characteristics of sites are poor to average indicators of pup production and distribution on the individual site and cluster scales, respectively. Animals are likely responding to conspecifics, dynamic processes and to attributes that describe the marine portion of their habitat.

CHAPTER 6

SUMMARY

Spatial and temporal patterns of use of pupping sites were identified and incorporated into habitat association models. Harbor seal survey data collected during pupping from 1981 – 1997 from an increasing population in Penobscot and Blue Hill bays, were used in a series of analyses to arrive at conclusions regarding behavioral and environmental characteristics that may affect use of pupping sites:

1) Spatial autocorrelation and consistency of site use for pupping between survey years was examined to determine the appropriateness of the spatial scale (individual site as the sample unit). Significant patchy spatial autocorrelation and inconsistent site use implied that a coarser spatial scale might be appropriate for further examination of space and time patterns. Inconsistent site use between survey years also implied that use is dependent on dynamic environmental characteristics at this scale (Chapter 2).
2) Pupping sites were geographically clustered into patches. Clusters provided biologically cohesive sample units for further analyses that were not spatially autocorrelated and had relatively consistent cluster use between survey years. Consistent site use between survey years also implied that use is dependent on static environmental characteristics at this scale (Chapter 3).
3) The temporal and spatial distribution of increase in pup production was examined for individual pupping sites (site scale) and clusters of sites (cluster scale) in order to make predictions regarding behavioral and environmental

characteristics that may affect site use at different population densities, and design monitoring protocols that are capable of detecting biologically significant changes (Chapter 4).

   a) On the site scale, Taylor Power Law (TPL) and Analysis of Variance (ANOVA) results revealed that count variability through time was constant across all sites, and all sites increased at an equal rate providing no strong evidence for aggregation or repulsion behavior. Increased use of marginal and new sites at high densities decreased spatial variability. This increased use of marginal and new sites, and increased magnitude of counts at high densities, may make habitat associations more detectable at high densities.
   b) On the cluster scale, TPL and ANOVA results revealed that low-use and high-use clusters increased in pup counts at proportionately similar rates, though high-use clusters maintained significantly higher numbers of pups in all survey years (refugia), and low-use sites had higher relative temporal variability. This pattern of increase created larger differences in pup counts between low-use and high-use clusters at high population densities causing habitat associations to be most detectable at this time.

4) Habitat association models between pup counts and environmental characteristics were examined for the individual site and cluster scales at different population densities. Space was incorporated into models in order to account for variation that was attributable to behavioral aspects such as

aggregation, and for unmeasured spatially structured environmental characteristics associated with pup counts (Chapter 5).

a) On the site scale, pup counts and frequency of site use were poorly related to static environmental characteristics in all years (0 – 10.2 % of total variation in pup counts), though slightly more variation in pup counts was explained by these characteristics in higher density years. High temporal variability indicates that dynamic characteristics may be better predictors of site quality at this scale. Variation attributable to space was also similar in all years (8.0 – 35.1 % of total variation in pup counts), though it accounted for slightly more variation at lower densities (1982 and 1986). This may indirectly represent aggregation behaviors at low densities or selection for spatially structured environmental characteristics.

b) Static environmental characteristics explained more variation in pup counts (20.3 – 53.6 % of total variation in pup counts) on the cluster scale than on the individual site scale (0 – 10.2 % of total variation in pup counts). The amount of variation in pup counts explained by environmental characteristics on the cluster scale was similar in all survey years, with slightly more variation was explained at higher population densities. At the cluster scale, variation attributable to space (0 – 24.3 % of total variation in pup counts) fluctuated between survey years unpredictably.

This study was able to identify scales of use, identify the spatial distribution of increase in pup counts, hypothesize types of behavioral and habitat characteristics effecting site use at different densities, and weakly confirm habitat use predictions. This information was directly useful for harbor seal management; analyses identified 1) the scale that habitat conservation is appropriate, 2) monitoring protocols capable of detecting biologically significant changes in productivity and 3) environmental characteristics associated with suitable sites. In this study, environmental characteristics were poorly defined, but the scale for habitat conservation and approach for monitoring protocols were successfully determined.

Harbor seal pupping habitat should be conserved as clusters of sites. Consistent high-use of the same clusters through years of low and high overall pup production identifies these clusters as immobile core production areas in the study area. Harbor seal mother-pup pairs consistently used clusters of sites from 1981 – 1997, while individual site use within these clusters was variable. Conserving the coarser unit should therefore provide for cluster and site scale habitat requirements that are important to successful production.

Annual trend counts of high-use clusters, or a subset of high-use clusters (cluster numbers 2, 11, 14, 34, and 40), would allow managers to inexpensively track temporal changes in harbor seal population productivity. One should use caution, however, when overall pup counts are greater or lesser than those observed between 1981 and 1997. Due to low-use sites potentially increasing at a faster rate than high-use sites at increased densities, trend count surveys of high-use clusters may underestimate the number of hauled-out pups at very high densities (> 1991 counts) relative to surveys conducted at lower pup densities. Trend count surveys may also overestimate the number of hauled-out pups at very low densities (< 1981 counts) relative to surveys conducted at higher densities due to low use sites becoming unused. Similar analyses that examine the spatial pattern of increase of total hauled-out harbor seals (pup and non-pup) would provide useful information for designing trend count surveys that track overall changes in population size.

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