INFLUENCE OF INDIVIDUAL ANIMAL BEHAVIOR ON SPATIAL AND TEMPORAL VARIABILITY IN NUTRIENT DEPOSITION

by

SHANNON E. ALBEKE

(Under the Direction of Nathan P. Nibbelink)

ABSTRACT

Cross-habitat movement of energy and other materials can spatially link ecosystems, resulting in changes to trophic interactions, ecosystem function and community diversity. Pulses of nutrient inputs, like pulses of productivity, may generate reserves of resources that affect ecological interactions long after the pulse has subsided. However, spatial linkages between ecosystems may be disrupted by temporal discontinuity in transport processes. In order to understand these complex ecological properties and model their effects on the landscape, we must explore the spatial and temporal variation of phenomena, such as variation in nutrient transport (allochthonous inputs). As with seabirds, piscivory by coastal river otters (Lontra canadensis) in nearshore coastal areas provide a pathway for nutrient transport between sea and land, thus extending the resource shed of the terrestrial community into the ocean. Marinederived carbon (C), nitrogen (N), and phosphorus (P) transported by river otters to terrestrial latrine sites (specific locations along the shoreline) can be several orders of magnitude higher than other nutrient inputs in this system. The following dissertation research represents the synthesis component of an NSF funded project, aimed at developing mechanistic models that will allow the exploration of potential current landscape response to changes in resource availability and otter behavior, as well as forecasting future changes anticipated from climate change. Otters choose latrine sites based on specific environmental characteristics. My results

suggest Boundary convexity is the strongest environmental characteristic influencing otter latrine site selection. Additionally, results from the individual-based model (IBM) overwhelmingly indicate otter behavior is almost entirely driven by prey availability. The IBM was able to reproduce observed patterns in nutrient transport, facilitated by the behavioral response of otters to pelagic fish schools and the subsequent creation of social groups. The inclusion of vision, olfaction and memory as viable forms of otter sensing and their quantifiable response to these stimuli provide a strong behavioral foundation for the IBM. The conceptual design of this IBM is applicable to any ecosystem in which variation is caused by behavior, genetic or physiological traits of individuals, and we believe this research provides an excellent working example.

INDEX WORDS: Lontra canadensis, coastal river otter, latrine selection, boundary convexity, nutrient deposition, individual-based model, pelagic fish, model selection, maximum entropy, adaptive behavior

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DEDICATION

This is dedicated to my daughter, Piper, whose unconditional love was simply inspirational.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW OF COASTAL RIVER OTTER

Cross-habitat movement of energy and other materials can spatially link ecosystems (Polis et al. 1997, Anderson and Polis 1998, Ben-David et al. 1998, Huxel and McCann 1998, Power and Rainey 2000, Nakano and Murakami 2001, Holt 2004) resulting in changes to trophic interactions (Polis et al. 2004), ecosystem function and community diversity (Holt 2004). Pulses of nutrient inputs, like pulses of productivity, may generate reserves of resources that affect ecological interactions long after the pulse has subsided (Sears et al. 2004). However, spatial linkages between ecosystems may be disrupted by temporal discontinuity in transport processes. In addition, community and ecosystem responses to subsidies may co-vary with other temporally variable factors (such as temperature and rainfall). Thus, the ecological properties of a defined point in space are marked by both past and present events (Reiners and Driese 2001, Meyer et al. 2002, Anderson and Polis 2004).

To understand these complex ecological properties and model their effects on the landscape, we must explore the spatial and temporal variation of phenomena, such as variation in nutrient transport (allochthonous inputs) (Power and Rainey 2000, Thompson et al. 2001). When allochthonous inputs are mediated by animal behaviors, spatial and temporal variability in nutrient transport are especially high. Dispersal and food availability are major determinants of space use by animals, but they are not the sole factors. In fact, population density, demography, social interactions and avoidance of predation risk may alter the space use predicted by resource patterns alone (Rosenzweig 1981, Hobbs and Hanley 1990, Bernstein et al. 1991, Lima and Zollner 1996, Manly et al. 2002). The spatial and temporal variation (topology) of

animal-mediated nutrient transport may result in complex emergent community properties and increased landscape heterogeneity (i.e., variability in diversity and productivity; Holt 2004). Because reductions in biodiversity and landscape heterogeneity may alter the resilience of ecosystems to environmental change (Tilman and Downing 1996, Paine et al. 1998, Chapin III et al. 2000, Carpenter 2003, Soule et al. 2003), understanding ecological topology is critical. Developing mechanistic models explaining this variation will allow us to forecast a range of potential ecosystem responses to important human-induced stressors (e.g., climate change, resource extraction, habitat alteration).

RIVER OTTER (Lontra canadensis)

The North American river otter is an aquatic member of the weasel family (*Mustelidae*) (Liers 1951, Hall 1981). In Alaska, river otters are found in both freshwater and marine habitats, feeding primarily on fish and crustaceans (Melquist and Hornocker 1983, Larsen 1984, Ben-David et al. 1998, Blundell et al. 2002a). River otters are nearly ubiquitous in coastal areas of the Gulf of Alaska, including the study area in Prince William Sound, Alaska (PWS; Hall 1981, Bowyer et al. 1995). Coastal river otters are different from inland populations in that they prey upon marine fishes and invertebrates inhabiting the nearshore environment (Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994, Bowyer et al. 1995, Ben-David et al. 1998).

River otter display sexual dimorphism in body size with average male size 5% larger than female size (Jackson 1961, Lariviére and Walton 1998). In non-oiled areas of PWS, Duffy et al. (1994) found adult male and female otters to average 9.4 and 8.4 kg, respectively. River otters typically reach sexual maturity at age 2 with some female yearlings reaching sexual maturity as an exception (Hamilton Jr. and Eadie 1964, Docktor et al. 1987, Bowyer et al. 2003). Litter size most often ranges between 1 to 3 young, but can reach up to 5 offspring (Lariviére and Walton 1998). Blundell et al. (2002b) found natal dispersal to have a low probability with sex biased

patterns where females dispersed less often, but further than males. Otters can live up to 13 years in the wild (Docktor et al. 1987), although the average age of all otters captured in PWS was 3.5 years (Bowyer et al. 2003). Blundell et al. (2004) found the sex ratio of river otter in PWS to be approximately 66% male. This finding is supported by data collected during the 2006 field season within the same study area (Kaiti Ott, unpublished data). River otter neither hibernate nor migrate (Melquist and Hornocker 1983, Bowyer et al. 2003).

The abundance of river otters within the study area has been estimated to be between 0.28 and 0.8 otter per km of coastline (Testa et al. 1994). This density is lower than estimates of the European otter, *Lutra lutra*, (1.2 otter per km of coast) in coastal areas of Shetland, United Kingdom (Kruuk et al. 1989), which may reflect the influence of the *Exxon Valdez Oil Spill*. River otter inhabiting coastal areas of PWS exhibit an atypical social behavior in comparison to other mammals (Blundell et al. 2002a, Blundell et al. 2004). The social structure of river otter within the coastal environment consists of large groups of males (Rock et al. 1994, Blundell et al. 2002a). These large groups (3-18 otters) serve to improve foraging efficiency of schooling pelagic fish within the nearshore environment (Blundell et al. 2002a, Blundell et al. 2002a, Ben-David et al. 2005). As the number of pelagic fish schools decrease, group size of male otters also decrease (Blundell et al. 2002a). On the other hand, female otters and a few male otters are solitary in their behavior, foraging primarily on intertidal demersal fish, but occasionally joining a large group of males to opportunistically forage on pelagic fish (Blundell et al. 2002a).

As with other mustelids, river otters communicate through scent marking (Lariviére and Walton 1998, Ben-David et al. 2005). Scent marking takes place at specific locations along the coast, also known as latrine sites, through feces, urine and anal gland secretions (Blundell et al. 2002a, Bowyer et al. 2003, Ben-David et al. 2005). Communication through scent marking appears to have two different uses within the social structure of coastal river otters. Social otters appear to use latrine sites for intra-group communication, signaling resource use or enabling otters that have become separated from the group to reunite for social foraging (Ben-

David et al. 2005). Conversely, solitary otters use latrine site scent marking to indicate territorial boundaries and encourage mutual avoidance (Ben-David et al. 2005).

Use of the coastal landscape by social otters is different than that of solitary otters. Social otter groups are comprised primarily by males while solitary otters are either female or an occasional male (Blundell et al. 2002a, Ben-David et al. 2005). Blundell et al. (2001) found male otters to have a home-range of more than twice the size of female otters. Concurrently, male otter home-ranges tended to have a higher proportion of overlap while females had low spatial overlap and distinct core areas of use (Blundell et al. 2001). Social otters tend to visit fewer latrine sites than do solitary otters, but social otter latrine sites have a higher frequency of use than do solitary otter latrines (Ben-David et al. 2005).

Because river otters forage in an aquatic environment and use latrine sites exclusively for urination and defecation, nutrients are moved in the opposite direction of the typical nutrient-flow diagram (i.e. nutrients are typically viewed as flowing 'downstream' within a watershed). This source of nutrients has been labeled as the resource shed of the terrestrial community (Power and Rainey 2000), with the ocean acting as a reservoir of additional nutrients and river otter being the transport mechanism for the nutrients. With this concept in mind, Ben-David et al. (2005) estimate the average amount of nitrogen excreted by an otter to be 5.15 g per defecation event, with an average of 7.7 events per day. Regardless of the intensity, the input of marine derived nutrients to the coastal landscape at latrine sites is much greater than non-latrine areas.

TERRESTRIAL VEGETATION

The study area has a maritime climate with cool and wet summers followed by winters of deep snow accumulation (Ben-David et al. 2001). The coastal landscape is typically snow-free from early May to early November. The structure of the coastline is primarily steep and rocky with some flat, low gradient openings and numerous bays and inlets (Bowyer et al. 1995). The

coastal vegetation is primarily old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), having a well-developed under-story comprised of *Oplopanax horridus*, *Vaccinium spp.*, *Menziesia ferruginea*, and *Rubus spp*. (Ben-David et al. 2001). Alder (*Alnus*) is also present and occurs on disturbed sites or near the terrestrial vegetation/intertidal zone interface (Bowyer et al. 1995).

NEARSHORE ENVIRONMENT

The nearshore subtidal zone is defined as any marine environment < 20m in depth. The bathymetric gradient of the nearshore environment is highly variable, ranging from near vertical to slopes of only a few degrees. The substrate is also variable, with sizes ranging from large boulders to fine sediment. Therefore, a resulting mosaic of available habitat types has created a heterogeneous marine vegetative community.

The nearshore habitat is the most heavily vegetated portion of this marine environment (Dean et al. 2000). Large tidal fluctuations in this habitat (annual maximum tide of 4.66 m and a minimum tide of -1.13 m) (NOAA 2007) greatly affect the vegetative community. Two kelp species (*Agarum cribrosum* and *Laminaria saccharina*) dominate rock within sheltered bays and less exposed coastline (Dean et al. 1996, Dean et al. 2000). For rocks existing on exposed points, bull kelp, *Cereocystis luetkeana*, comprise the canopy and *Laminaria bongardiana* the understory (Dean et al. 1996, Dean et al. 2000). Eelgrass, *Zostera marina*, dominates softer substrate usually found in bays (McRoy 1968, 1970, Dean et al. 1998, Dean et al. 2000). The majority of the intertidal region of the coastline is dominated by *Fucus gardneri*, interspersed with red and green algae (Gilfillan et al. 1995, Stekoll et al. 1996, Dean et al. 2000).

NEARSHORE FISHES AND INVERTEBRATES

The nearshore environment also supports a multitude of fish species. Two groups of prey are typically found: demersal, intertidal species and migratory, pelagic species. The intertidal species are primarily comprised of the families *Cottidae*, *Scorpaenidae*, *Hexagrammidae*, *Cancridae*, chiton and clams (Larsen 1984). These species are non-migratory residents and provide a consistent food base to coastal river otter (Blundell et al. 2002a, Mecklenburg et al. 2002, Ben-David et al. 2005). *Salmonidae*, *Ammodytidae*, *Clupeidae*, and *Gadidae* (Larsen 1984, Ben-David et al. 1998, Blundell et al. 2002a) are the primary migratory, pelagic fish species found within the study area. These schooling pelagic fish species typically enter the study area in the beginning of May for spawning and move back out to the open ocean or expire (salmon) by November (Blundell et al. 2002a, Mecklenburg et al. 2002). As otter prey, the schooling pelagic fish have a higher energy density than the intertidal-demersal fish (Anthony et al. 2000, Blundell et al. 2002a).

STUDY OBJECTIVES

The effect upon the production and composition of the vegetative community through the use of latrine sites by coastal river otter behavior differs spatially and temporally via individual movements, group membership and association with prey resources (Figure 1.1). In our study area located in Prince William Sound, Alaska, differences in vegetative response to river otter activity include increased growth of trees (Roe et al. 2010) and increased uptake of marine-derived nutrients by shrubs and trees (Ben-David et al. 1998, Roe et al. 2010), but because of physical disturbance from otter activity, a decrease in shrub density and species specific use of nutrients occurred (Roe et al. 2010). As previously described, the frequency of latrine use by otters, and the subsequent transport of marine-derived nutrients, is mediated by the availability of prey. The behavior of individual otters in response to prey (i.e., cooperative foraging by

males, solitary females) and the physical characteristics of the coastal environment affect the spatial and temporal patterns at the landscape level. Individual-based models (IBMs) are often developed to gain a deeper understanding of system dynamics through individual behavior and implemented because classical approaches ignore individual differences and local interactions (Grimm and Railsback 2005). Given the current understanding of the relationships between otters, their prey, and the physical environment, an appropriate method for modeling the system's effect on individuals and the individual's interaction with the environment, as well as with other individuals, is to use an IBM (Grimm and Railsback 2005).

The following dissertation research represents the synthesis component of an NSF funded project designed, "to investigate the effects of spatial and temporal variation in allochthonous inputs of C, N, and P by coastal river otters on ecosystem processes, emergent community properties, and landscape heterogeneity in the land-margin of PWS" (Ben-David et al. 2004). In the proposal, Ben-David et al. (2004) outlined 5 primary objectives:

Quantify the spatial and temporal variability across the landscape in nutrient transports
 (C, N, and P) from sea to land by river otters as a function of otter sociality.

2. Explore the diversity of soil microorganisms, rates of nutrient cycling, and the creation of nutrient pools in the soil in response to spatial and temporal variability in availability of C, N, and P given the effects of other temporally variable factors (e.g., temperature, precipitation).

3. Investigate the degree to which variation in C, N, and P, nutrient cycling, and nutrient pools in the soil affect plant biomass, NPP, reproductive output and community composition given the effects of other temporally variable factors.

4. Derive estimates of spatial heterogeneity by extrapolating information from sampled latrines to the landscape level.

5. Parameterize an individual-based, spatially-explicit model that will simulate changes to the terrestrial landscape based on spatial and temporal variation in distributions of schooling fish, otter activity, and C, N, and P transport by river otters.

While my colleagues are exploring transport rates, patterns, mechanisms of nutrient uptake and consequences for the terrestrial community, my work synthesizes all of these components. My research is aimed at developing mechanistic models that will allow the exploration of potential current landscape response to changes in resource availability and otter behavior as well as forecasting future changes anticipated from climate change. The following chapters build the necessary elements to parameterize the individual-based model, describe the model implementation and then assess the model's performance. Specifically, Chapter 2 describes the development of a novel landscape metric, Boundary Convexity, to help describe the coastline shape and the associated influence on otter latrine site selection; Chapter 3 compares different modeling approaches used to assess the likelihood of coastal river otter use of the coastal environment, a necessary component to modeling adaptive behavior and variability in nutrient deposition; Chapter 4 describes the individual-based model developed to measure the spatial and temporal fluxes in nutrient deposition to the nearshore environment by river otter through adaptive responses to pelagic fish availability.

The model system I assemble in this dissertation provides a unique framework for the study of ecosystem responses to spatial and temporal variation in nutrient inputs. The strengths of the model system, rarely found elsewhere, are (1) the detailed understanding we have of the mechanisms that create the variation in nutrient inputs (i.e., the relations between fish distributions, otter sociality, and latrine use), and (2) the 14 years of data collected on latrine use by otters (since 1990 following the *Exxon Valdez oil spill*). Although otters directly influence only a small part of the land-margin, indirect effects on the landscape may be large, and include propagation across the landscape of genotypes generated on otter latrines (e.g., spruce seeds)

or greater plant diversity that could support high diversity of consumers. Regardless, lessons learned from this model system are applicable to any ecosystem in which variation is caused by the behavior (e.g., migrations, roosting, breeding) or genetic/physiological traits of individuals.

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Figure 1.1: Conceptual model of otter latrine use in relation to season and prey availability as proposed by Ben-David et al. (2004). Abundance and distribution of schooling fish influences social behavior in male otters, which use latrines for intra-group communication. Social otters use fewer latrines at high frequency; nonsocial otters foraging on demersal fishes visit numerous latrines infrequently. Females join male groups when non-reproductive. Thus, latrine use will vary within a season and among years as a function of the abundance of schooling fishes and otter demography.
CHAPTER 2

MEASURING BOUNDARY CONVEXITY AT MULTIPLE SPATIAL SCALES USING A LINEAR "MOVING WINDOW" ANALYSIS: AN APPLICATION TO COASTAL RIVER OTTER HABITAT SELECTION¹

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ABSTRACT

Landscape metrics have been used to quantify ecological patterns and to evaluate relationships between animal presence/abundance and habitat at multiple spatial scales. However, many ecological flows occur in linear systems such as streams, or across patch/landscape boundaries (ecotones). Some organisms and flows may depend on the boundary shape, but metrics for defining linear boundary characteristics are scarce. While sinuosity and fractal dimension address some elements of shape, they fail to specify the dominate shape direction (convexity / concavity). We propose a method for measuring boundary convexity and assess its utility, along with sinuosity and fractal dimension, for predicting site selection by coastal river otters. First, we evaluate the characteristics of boundary convexity using a hypothetical boundary. Second, to compare convexity with other linear metrics boundary convexity, sinuosity and fractal dimension were calculated for the coastline of a set of islands in Prince William Sound, AK. Finally, we use logistic regression in an information-theoretic framework to assess site selection of river otters as a function of these linear metrics. Boundary convexity, fractal dimension and sinuosity are relatively uncorrelated at all scales. Otter latrine sites occurred at significantly more convex locations on the coastline than random sites. Using logistic regression and convexity values at the 100 meter windowsize, 69.5% of the latrine sites were correctly classified. Coastal terrestrial convexity appears to be a promising landscape-scale metric for predicting otter latrine sites. We suggest that boundary convexity may be an important landscape metric for describing species use or ecological flows at ecotones.

INTRODUCTION

The use of landscape and patch metrics to measure broad-scale ecological patterns has become increasingly more common (Hopkins 2009; Kearns et al. 2005; Turner 1989; Wu 2004),

in particular for describing relationships between animals and their habitat (Forester et al. 2007; Grober-Dunsmore et al. 2008; Hamer et al. 2006). Patch shape is often identified as important for determining species presence (Heegaard et al. 2007; Taylor et al. 2008), animal density (Ewers and Didham 2007), the distribution of organisms within a patch (Haynes and Cronin 2006) and has been shown to influence the movement of nutrients (Polis and Hurd 1996). Patch shape is most often measured as the perimeter-to-area ratio or patch fractal dimension (McGarigal et al. 2002; Rempel 2008). However, some ecological relationships may depend more heavily on characteristics of patch boundaries than on whole patch properties (such as animal-habitat relationships when "edge" habitat characteristics are important to the species). To measure characteristics of boundaries we have largely been limited to the conventional whole patch metrics, or relatively simple measures on boundary segments themselves, such as sinuosity. In order to improve our understanding of how boundary shape may influence ecological processes or animal habitat selection, we need more refined metrics for defining boundary shape. One such metric is boundary convexity. The degree of convexity (or concavity) for a defined boundary may be important to organisms or flow under a variety conditions much in the same way that topographic concavity (valleys) or convexity (ridges) are important to habitat use by elk (Kie et al. 2005) or movement of soil particles (Ruiz et al. 2006). However, in an extensive literature search, we have not found an ecological study that has substantially dealt with convexity of an ecotone, edge, or boundary as important to ecological processes or organism-environment relationships. Here we offer an approach for calculating boundary convexity at multiple spatial scales (script available free online; Albeke et al. 2009), then we demonstrate the value of boundary convexity for describing habitat selection for coastal river otters.

Any understanding of animal habitat selection necessitates consideration of spatial scale. Each organism's perspective dictates the scale at which it observes the physical world (Allen and Hoekstra 1992). The scale, shape and juxtaposition of landscape patches can affect

species abundance and distribution. For example, McGrath et al. (2003) found a reduced ability to discriminate northern goshawk (*Accipiter gentilis*) nest sites from available habitat as landscape scale increased while Mitchell et al. (2001) found that coarser landscape characteristics are most important for prediction of migratory bird species breeding habitat. Additionally, Nams et al. (2006) found that variables most important for predicting grizzly bear (*Ursus arctos*) habitat selection varied depending on the spatial scale at which the variables were averaged. Thus, investigating the influence of scale in determining (and measuring) how organisms respond to their environment has been, and still is, a critical area of research. This work can help tackle scale-related issues of geospatial data analysis in general, and avoid scale traps such as ecological fallacy (Robinson 1950) and aggregation effects (King et al. 2004).

Fractals can be used to represent many kinds of patterns and all spatial scales can be represented through self-similarity (Li 2000). The fractal dimension can be calculated for any portion of a patch's boundary for any scale. This value can be used to quantify the complexity of the feature at the given scale. Unfortunately, the fractal dimension will not describe the direction of a complex feature relative to the adjacent features. Our research required a method to quantify the shape of a portion of a patch's boundary convexity, a new landscape metric that quantifies the shape of a patch boundary (ecotones, edges or other linear features). We define boundary shape as either convex or concave. Convexity is considered a pattern metric in landscape ecology (Trani and Giles 1999). The degree of convexity can be unique for any point along the patch (or landscape) boundary and will vary with spatial scale. Because of this trait, convexity may provide a biologically meaningful measurement describing the use of boundaries by wildlife.

Coastal river otters forage for fish within the intertidal zone of islands located in Prince William Sound, Alaska and choose specific locations for their latrines along the coastline (Ben-David et al. 2005; Ben-David et al. 1998; Bowyer et al. 2003). This results in the transport of

nutrients from the marine environment to the coastal terrestrial community (Ben-David et al. 1998) which has a significant influence on the vegetation community, both through nutrient enrichment and disturbance by river otters (Roe et al. 2010). Otter latrines are used as communication tools, with social otters advertising group associations and dominance while solitary otters use latrines to facilitate mutual avoidance (Ben-David et al. 2005; Rostain et al. 2004). Ben-David et al. (2005) hypothesized that the combination of large intertidal rock (scent marking platforms) and the presence of old-growth forest (prevention of scent-mark dehydration) provide the greatest influence on otter latrine site selection. Because appropriate scent-marking platforms are often on points (Larsen 1983), and the fact that scent dispersal may be facilitated by wind, we hypothesize that coastal shape will be a significant driver of latrine site selection. In particular, we hypothesize that otters are more likely to choose latrine sites whose coastline is sinuous (has more points and bays) at broader scales (500-1000 m), and more convex at local scales (10-200 m). The objectives of our study are threefold: (1) to characterize boundary convexity using a hypothetical boundary of known dimensions; (2) to calculate boundary convexity of a coastline in Prince William Sound, Alaska, and compare its characteristics to sinuosity and fractal dimension; and (3) determine the spatial scale and linear metric most appropriate for describing coastal river otter latrine site selection.

METHODS

Process for quantifying boundary convexity

The boundary convexity measure we propose can be used to quantify the relative convexity/concavity for any measure-point along a linear feature (e.g. patch boundary). Using route-events in ArcGIS[™] (ESRI 2006) to represent the linear boundary feature, the spatial location of a given measure-point along the feature can be stored. The calculation of convexity becomes easier if the boundary is simplified. To simplify the boundary, a three-point circular arc

representing the boundary segment is created. The circular arc uses, in sequential order, the start-point (measure-point - (1/2 * window-size)), measure-point, and end-point (measure-point + ($\frac{1}{2}$ * window-size)) measures of the boundary segment (Figure 2.1). The circular arc represents the relative shape of the boundary at the measure-point. The orientation (clockwise or counterclockwise) of the circular arc, in relation to the boundary segment, determines whether the patch portion is concave or convex (i.e. clockwise = convex). The degree of convexity is determined by obtaining the mid-point of the circular arc, mid-point of the chord connecting the start and end points, and finding the chord height between the mid-points (Figure 2.1, Step 5). The value quantifying convexity is then a combination of the circular arc orientation (sign is positive for convex and negative for concave) and the chord height value described above. Boundary convexity can range from 0 to $\pm \frac{1}{2}$ the window-size (scale), with 0 indicating a straight boundary (on average) at the given scale, a positive value indicating a convex boundary, and a negative value indicating a concave boundary. Because the convexity value is calculated in map units (e.g. meters) it may be valuable for defining the relative size of landscape boundary features. However, because scale-independence is a valuable feature of a landscape metric we calculate the boundary convexity index (BCI) as:

$$BCI = {}^{BC}/_{BC_{max}}$$
(1)

where BC is the unscaled convexity value in meters and BC_{max} is equal to $\frac{1}{2}$ the scale (windowsize). The BCI values are scale-independent and range between -1.0 and +1.0. Figure 2.2 demonstrates how BCI values can vary using an example patch boundary.

With the information gathered to calculate convexity, one can also calculate sinuosity (S):

$$S = \frac{TL}{EL}$$
(2)

where *TL* is the total segment length (i.e. window-size) and *EL* the Euclidean distance between start and end points. Sinuosity values can range between 1 (straight line) and the total segment length and is scale-independent. The Boundary Convexity Tool (BCT, Albeke et al. 2009) can be used to calculate both sinuosity and convexity at multiple window-sizes (scales) and steps (positions along the feature).

The purpose for using route-events is twofold. First, routed layers allow for easily managed references to any location along the linear feature of interest via route measures. The route measures, in turn, allow for easy interpretation of the location (a measure is simply the distance in meters from the start of the line), easy manipulation (simple math to move a specified distance along the route) and simple & accessible storage of output (event tables).

Construction of known dimension dataset

We constructed a 'saw-toothed' shaped line to mimic a portion of a hypothetical patch boundary with known dimensions to illustrate the range of convexity values given a range of boundary shape conditions. In the horizontal direction, the peaks and troughs of the hypothetical patch boundary (Figures 2.3 & 2.4) are 200 meters apart and the line segment connecting these extreme locations is 282.8 meters in length. First, to demonstrate how different locations along a patch's boundary can affect boundary convexity, five separate locations on the patch boundary and a window-size of 200 meters was used. The chosen measurement points were located at 0% (trough), 25%, 50%, 75% and 100% (peak), of a patch boundary line. Second, to demonstrate how changes in scale affect boundary convexity, four different window-sizes were applied to a constant location (at a peak) of the hypothetical patch boundary. The chosen window-sizes were 200, 500, 1000 and 1132 meters (Figure 2.4 A-D). The saw-toothed design was used (as opposed to a more "natural" shape) due to the simplicity for creation, visualization and interpretation. Results of analyzing a more curvilinear feature would have been similar; however the arcs demonstrating the calculation would have been more difficult to see.

Comparing Boundary Metrics

In order to characterize the behavior of the boundary convexity metric across a range of natural conditions, we compared BCI values to two other metrics commonly used for linear features, sinuosity and fractal dimension. In addition, because statistical analysis of speciesenvironment relationships often depends on independent predictor variables, we wanted to determine whether boundary convexity was a unique metric. Our test area was a coastline (marine-terrestrial boundary) located in southwestern Prince William Sound, Alaska. Coastlines in the Knight Island complex (including Disk, Eleanor and Ingot Islands; 147°43'W, 60°30'N) were digitized using IKONOS 1-meter panchromatic images, at a scale of 1:1,500, creating a coastline 245 km in length. The island polygons were then converted into a route feature class, which is required for the BCT (Albeke et al. 2009). BCI (eq. 1) and sinuosity (eq. 2) were calculated for the entire coastline at seven window-sizes, 10, 20, 50, 100, 200, 500 and 1,000 meters and a step-size (moving-window increment) of 10 meters using the BCT. Fractal dimension was also calculated for each window-size. To calculate fractal dimension, each coastline segment spatial extent was found and the maximum difference between the X coordinates and the Y coordinates was stored. Next, five separate ruler sizes were created by taking 1%, 5%, 10%, 20% and 40% of the maximum coordinate difference. The rulers are then placed end-to-end along the boundary segment to give a total segment length given the ruler size. The fractal dimension was calculated using the log-log relationship:

$$Log(L(s)) = (1-D)Log(s) + b$$
(3)

where L is the length of the ruler (s) multiplied by the number of rulers needed to measure the total boundary segment, 1-D is the slope and D is the fractal dimension (Mandelbrot 1982).

Fractal dimension values are scale-independent and can range between 1 (straight line) and 2 (highly complex line) (Mandelbrot 1982; Turchin 1996).

For each window-size (scale), BCI, the absolute (or directionless) BCI, sinuosity and fractal dimension were compared using Pearson's *r* correlation coefficient to assess similarity between the metrics. All statistical analyses were performed using SAS 9.1 (SAS Institute Inc., Cary, NC).

Application to Coastal River Otters

During the summer of 2006, 326 river otter latrine sites were identified along the coastline and GPS locations were recorded. GPS locations were snapped to the island boundaries (coastline route features) with Knight Island having 257, Disk Island 23, Eleanor Island 38, and Ingot Island 8 latrine locations, respectfully. To determine whether linear metrics, including convexity index, sinuosity and fractal dimension, influence otter latrine site selection, 326 random locations were identified. Random locations were a minimum of 100 meters from an existing latrine or other random location.

Logistic regression with an information-theoretic approach was used to determine which boundary metric (across a range of spatial scales) best fit the data. Twenty-eight candidate models, each consisting of a single variable; BCI, absolute BCI, sinuosity and fractal dimension at each of the spatial scales (10, 20, 50, 100, 200, 500, 1000 m), were compared. Methods followed the approach of Anderson et al. (2000). To test for goodness-of-fit (GOF), the Hosmer-Lemeshow GOF statistic was calculated for the global model (Hosmer and Lemeshow 2000). The global model consisted of the entire set of available variables.

Akaike's Information Criteria (AIC) uses maximum likelihood to estimate the relative model fit (Burnham and Anderson 2001). However, this approach may create biased results for small samples size. Burnham and Anderson (2001) suggest correcting for small sample size:

$$AIC_{c} = -2 \ln(L(\hat{\theta} \mid data)) + 2K + (2K(K+1)/(n-K-1))$$
(4)

where $\ln(L(\hat{\theta} \mid data))$ is the maximized log-likelihood over the unknown model parameters (θ) given the data, and K is the number of parameters in the approximating model. As sample size (n) increases, AIC_c approaches the same AIC value. Models with lower AIC_c values are deemed to be better representations of the process being modeled. Akaike weights were calculated to determine the weight of evidence (*w*) for each model within the candidate set:

$$w_{i} = \frac{\exp(-\Delta AIC_{c_{i}}/2)}{\sum_{r=1}^{R} \exp(-\Delta AIC_{c_{r}}/2)}$$
(5)

where ΔAIC_{c_i} is the ΔAIC_c value for the *i*th model in the set of R candidate models (Burnham and Anderson 2001). The value of w_i can range from 0 to 1. The candidate model with the largest w_i can be said to be the best approximating model.

Two methods were used to assess relative precision of the logistic models. First, a leaveone-out cross-validation technique was used to determine the expected model error rate (Steyerberg et al. 2001). To perform leave-one-out cross-validation, each sample record is left out, while the rest of the records are used to generate a model. This model is then used to predict presence or absence of the latrine for the left out record. The process is repeated so that each record is excluded from model fitting once, allowing for prediction and classification error rates to be determined. Model predictions \geq 0.5 indicated latrine presence and predictions < 0.5 indicated latrine absence. Secondly, Receiver Operating Characteristic (ROC) plots were generated and area under the curve (AUC) was calculated.

RESULTS

Changes in convexity with location

Boundary convexity index (BCI) values range from -1 (concave) to +1 (convex), the magnitude of which depends both on the position of the measure-point on the boundary (Figure 2.3) and on the window-size (Figure 2.4). As the measure-point moves from the trough to the peak (with window-size = 200 m and 4 equal steps), the BCI value ranges from -0.70 to -0.17, 0.0, 0.17, and finally 0.70 (Figure 2.3A-E). In the hypothetical boundary, because of the regular geometry, the value of concavity at the trough is equal to and opposite the convexity at the peak. In reality, the maximum convexity will be driven in part by the maximum distance from peak to trough (points to bays in case of a coastal boundary), and in part by the window-size.

Changes in convexity with scale

As window-size (scale) increases from 200 to 500 meters, unscaled boundary convexity increases because the 200 m window-size is substantially shorter than the trough to trough distance of the hypothetical boundary, whereas the 500 m window-size approaches the trough to trough distance (Figure 2.4 A & B). However, because BCI is scale independent, the values are nearly identical. In this example, the maximum unscaled boundary convexity value would be measured when the measure-point is at a peak and the window-size is equal to the wavelength, 566 meters, whereas BCI would remain relatively unchanged. As window-sizes increase in scale beyond the wavelength, the convexity values decrease until reaching a value of 0 when the window-size (1,132 meters) encompasses the two adjacent peaks to the measure-point (Figure 2.4 C & D). A value of zero will occur whenever the conditions of the boundary conspire to create a straight line between the endpoints and the measure-point, regardless of intervening boundary complexity.

Comparison of Patch Boundary Metrics

Comparisons between BCI, absolute BCI, fractal dimension and sinuosity indicate that these linear metrics are relatively uncorrelated for our study area at all scales (Figure 2.5). The mean absolute Pearson's *r* was greatest between absolute BCI and sinuosity (μ = 0.45) and smallest between BCI and fractal dimension (μ = 0.04; Figure 2.5). One exception is absolute BCI and sinuosity, which are correlated for window-sizes < 200 m (Pearson's *r* > 0.5, Figure 2.5). This was not unexpected given that both sinuosity and absolute BCI measure aspects of line complexity (how much it "meanders" between two points) and ignore shape direction. However, at larger scales, the relationship between absolute BCI and sinuosity weakens, seemingly because sinuosity values increase in range at larger scales (Table 2.1). We must note here that the sinuosity calculation can produce outlying values (erroneously high) when the two end points are very close, but the scale (window-size) is very large, as in the case of islands. We excluded these outliers (< 1% of our data) from our analysis.

The correlation coefficient varied with window-size (scale). For BCI vs. sinuosity, absolute BCI vs. sinuosity, BCI vs. absolute BCI and sinuosity vs. fractal dimension, the correlation coefficient decreased as window-size increased (Figure 2.5). Conversely, as scale increased, the correlation between BCI and fractal dimension also increased. The correlation coefficient did not significantly change with scale for absolute BCI vs. fractal dimension. These results indicate that boundary convexity is a unique linear metric.

Coastal River Otter Latrine Site Selection

Model selection results indicate that BCI values at the 100 meter window-size best approximated latrine presence (Table 2.2). Additionally, models of BCI at any of the windowsizes were found to be more parsimonious than any of the other metrics compared in the

candidate set (Table 2.2). Because the global model was found to fit the data (no overdispersion; Hosmer-Lemeshow GOF, p > 0.05), all candidate models will also fit the data.

To test the accuracy of the best-fitting models, models with the highest *w_i* for each patch boundary metric were assessed using leave-one-out cross-validation. Overall correct classification rate was highest for the model containing BCI at the 100 meter scale (C100), with total prediction accuracy equaling 69.5% (Table 2.3). For each of the three additional models tested for accuracy, results demonstrate that total prediction accuracy is not much better than a coin-flip (Table 2.3). This observation is further supported by the relatively low AUC values for the three additional models, absolute convexity at 100 meters, sinuosity at 500 meters, and fractal dimension at 10 meters (Figure 2.6; Swets 1988).

DISCUSSION

The value of a landscape metric is often specific to the landscape and species combination unique to a study area (Ritters et al. 1995). Li and Wu (2004) suggest that field or map based metrics will most often provide the greatest amount of inference because of their simplicity and ease of interpretation. Additionally, a landscape metric must be biologically meaningful and capture different aspects of spatial pattern (Hargis et al. 1998; Li and Wu 2004; Ritters et al. 1995). The boundary convexity index (BCI) meets these criteria for several reasons: 1) the metric is easily interpreted (positive or negative value); 2) the metric is scaleindependent; 3) the metric captures different aspects of spatial pattern (i.e. not correlated with sinuosity or fractal dimension); 4) the metric is calculated at the 'sub-patch' scale; and 5) the metric was demonstrated to be biologically meaningful to coastal river otters (logistic regression analysis). Therefore, we feel that boundary convexity is an important new landscape metric that can be applied to any linear feature(s) of interest such as patch or landscape boundaries.

The shape of a boundary is specific to each unique location along that boundary and the shape is scale dependent. For example, a segment of coastline viewed using a 100 meter frame may appear to be convex. However, the same location, when viewed at a scale of 1000 meters, may be concave in shape because the location may be within a larger bay. Thus, for any ecological problem, measuring variables at an appropriate scale (or range of scales) will require system and/or organism-specific knowledge (Allen and Hoekstra 1992). Measurements of boundary convexity performed to expectations when applied to a line with known dimensions. Boundary convexity values were consistently concave for troughs and convex for peaks and the values were identical in magnitude (with signs reversed) when measured from complementary locations on the regular artificial boundary. These measurements serve to characterize the boundary convexity metric and further, to demonstrate the range of values to expect under known conditions. However, we caution that comparing boundary convexity values between two datasets that have different 'reference scales' (i.e. 1:1,500 vs. 1:24,000) is not appropriate, even if the window-sizes are the same. This is true also for sinuosity and fractal dimension because the degree of generalization of line features from reality can differ greatly depending on the scale at which the data was digitized (acquired).

As mentioned above, the use of the coastline (a patch boundary) by coastal river otters within the study area is nearly ubiquitous, yet otter latrine site locations are found only where habitat conditions meet certain criteria (Bowyer et al. 2003). Using the shape (convexity) of the surrounding coastline as a variable influencing latrine site selection appears to be a promising landscape-scale metric. The logistic regression analysis supports our hypothesis that river otters may be selecting "points" as latrine sites, presumably to facilitate social communication via maximum dispersal of scent-marks. The measurement of boundary convexity for latrine sites at multiple scales allowed us to determine the scale at which otters most strongly respond to the shape of the coastline. This result improves our understanding of the scale at which river otters are interacting with their environment, and also will allow us to predict nutrient deposition

by river otters in unsampled areas based in part on coastal shape. Using only a single variable (BCI at the 100 meter scale), we were able to correctly classify nearly 70% of coastal locations as latrines. While previous attempts to determine habitat variables driving otter latrine site selection correctly classified 80% to 87% of locations, these studies measured habitat variables intensively at fine scales (Bowyer et al. 2003). The ability to predict otter latrine locations using data derived from satellite imagery will be invaluable for the management of coastal river otters and for understanding their role in nutrient transport from sea to land.

Boundary convexity could be applied to similar ecological questions where species depend on ecotones (unique conditions of patch boundaries). For example, Howell et al. (2007) found that brown-headed cowbird (*Molothrus ater*) use of forest edge varied by landscape context. Highly fragmented forests were used more completely than less fragmented forests. Would telemetry locations of female cowbirds demonstrate a relationship with boundary convexity? Taylor et al. (2008) found that the noisy miner (*Manorina melanocephala*) in Victoria, Australia were more likely to occur with edge geometry characteristics that were described as 'projections' and 'clumps'. Boundary convexity may provide a more quantitatively derived metric for describing the habitat use of this avian species. Other potential ecological situations in which boundary convexity could be applied are flying squirrel (*Pteromys volans*) dispersal which can be affected by landscape structure (Selonen and Hanski 2004) and arthropod densities that rely on algal wrack and carrion washed ashore on islands located in the Gulf of California (Polis and Hurd 1996).

In conclusion, boundary convexity measures spatial patterns at the sub-patch scale and can be used to help explain some ecological processes occurring along patch boundaries. Our research demonstrates how boundary convexity can be used to assess animal habitat selection based on this pattern. We hope the boundary convexity metric finds wide application, and further that the Boundary Convexity Tool (Albeke et al. 2009) will assist in the expanded use of

not only boundary convexity, but also other linear metrics in a scalable, moving-window framework.

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Table 2.1: The mean (SD) and minimum, maximum values for each linear metric at each window-size (scale). For window-sizes greater than 100 meters, the maximum sinuosity value has been adjusted by removing small islands having perimeters less than or very near the window-size (denoted with *).

Window-	Boundary		Fractal
size	Convexity Index	Sinuosity	Dimension
10 m	0.032 (0.265)	1.12 (0.19)	1.06 (1.32)
	-0.804, 0.827	1.00, 3.26	1.00, 1.16
20 m	0.083 (0.306)	1.24 (0.37)	1.07 (0.03)
	-0.906, 1.0	1.00, 4.46	1.00, 1.17
50 m	0.084 (0.314)	1.42 (0.46)	1.09 (0.04)
	-0.963, 1.0	1.00, 4.56	1.00, 1.21
100 m	0.092 (0.303)	1.59 (0.62)	1.12 (0.05)
	-1.0, 0.867	1.01, 8.09	1.01, 1.37
200 m	0.079 (0.29)	1.85 (1.56)	1.13 (0.05)
	-0.720, 1.0	1.03, 10.86*	1.03, 1.38
500 m	0.051 (0.256)	3.10 (7.82)	1.16 (0.06)
	-0.860, 1.0	1.04, 9.75*	1.01, 1.45
1000 m	0.044 (0.259)	5.02 (17.52)	1.17 (0.05)
	-0.777, 0.817	1.08, 10.59*	1.05, 1.37

Table 2.2: Summary of model selection statistics for the set of candidate models (i) predicting presence of otter latrines. Model descriptions are boundary convexity index (C), absolute boundary convexity index (AC), sinuosity (S) and fractal dimension (FD) followed by the window-size.

Model	AIC _c	Δ AIC _c	Wi
C100	750.565	0	0.9993
C200	765.086	14.521	0.0007
C50	789.712	39.146	0
C500	802.806	52.241	0
C1000	816.431	65.865	0
C20	856.201	105.636	0
C10	866.632	116.067	0
AC100	891.434	140.869	0
S500	892.539	141.974	0
S1000	895.998	145.432	0
AC50	896.77	146.205	0
AC200	900.393	149.827	0
FD10	902.736	152.17	0
S200	906.24	155.675	0
S10	907.376	156.811	0
FD20	907.617	157.051	0
AC20	908.016	157.451	0

FD200	908.791	158.226	0
FD50	908.97	158.405	0
FD1000	909.001	158.436	0
AC10	909.086	158.521	0
AC1000	909.263	158.698	0
AC500	909.474	158.909	0
S100	909.716	159.15	0
FD100	909.841	159.275	0
FD500	909.853	159.287	0
S20	909.895	159.33	0
S50	909.901	159.336	0

Table 2.3: Percent of correctly classified observations using the best-fitting model for each patch boundary metric and leave-one-out crossvalidation. Model descriptions are boundary convexity index (C), absolute boundary convexity index (AC), sinuosity (S) and fractal dimension (FD) followed by the window-size.

Model	Latrine	Random	Total
C100	69.6%	69.3%	69.5%
AC100	51.5%	66.0%	58.7%
S500	19.0%	84.4%	51.7%
FD10	51.5%	58.9%	55.2%



Figure 2.1: The procedure to calculate boundary convexity: 1) Obtain start, measure and end points (0%, 50% and 100% of the length) of the boundary segment (Steps 1 & 2); 2) Draw circular arc through the three points (Step 3); 3) Determine circular arc orientation (clockwise or counterclockwise); 4) Draw a chord between start and end points (Step 4); 5) Obtain the midpoint of the circular arc and chord (Step 5); 6) Calculate the chord height. For this particular example, the boundary convexity value is equal to 15.8 meters, indicating the measure-point is convex given a window-size of 100 meters.



Figure 2.2: An example of boundary convexity index (BCI) values for a window-size of 50 meters (A) and 100 meters (B) and a step-size of 20 meters. Positive values indicate convexity while negative values indicate concavity. Please note the BCI value differences between the same measure-points at the two scales (window-sizes).



Figure 2.3: An example of how boundary convexity index values change as the measure-point (POM) changes using a window-size of 200 meters. The measure-point begins at a trough of the wave (A), 25% of the segment distance (B), 50% of the segment distance (C), 75% of the segment distance (D), and ends at a peak of the wave (E).



Figure 2.4: An example of how boundary convexity (BC) in meters and boundary convexity index (BCI) values change as window-size (scale) increases for the same measure-point (POM). The window-sizes are 200 meters (A), 500 meters (B), 1,000 meters (C), and 1,132 meters (D).



Figure 2.5: Scatter plots of absolute Pearson's *r* correlation coefficients across all window-sizes for each patch boundary metric combination (CS = convexity-sinuosity, ACS = absolute convexity-sinuosity, CFD = convexity-fractal dimension, ACFD = absolute convexity-fractal dimension, CAC = convexity-absolute convexity, SFD = sinuosity-fractal dimension). Solid symbols indicate significance at the 95% confidence level (p < 0.05) and hollow symbols are not significant. Mean(SD) Pearson's *r* across all window-sizes, trend lines, the associated linear equations and R^2 values are included.



Figure 2.6: ROC plots demonstrating discriminatory accuracy for otter latrine site selection for models: boundary convexity index at 100 meters (A), absolute boundary convexity index at 100 meters (B), sinuosity at 500 meters (C) and fractal dimension at 10 meters (D); and the calculated area under the curve (AUC).

CHAPTER 3

LATRINE SITE SELECTION BY COASTAL RIVER OTTERS: A COMPARISON OF MODELING ALGORITHMS AND MODEL SELECTION USING AREA UNDER THE CURVE

(AUC)¹

¹Shannon E. Albeke, Nathan P. Nibbelink, and Merav Ben-David. To be submitted to Journal of Wildlife Management

ABSTRACT

Wildlife managers and researchers have an increasingly growing number of available algorithms from which to develop species distribution models. These approaches use environmental variables, coupled with species observation data, to estimate the probability that habitat is suitable for a species in a given area. Because different algorithms may behave differently across species and datasets, testing multiple approaches to assess the most supported environmental variables, as well as the best fitting model, is desirable. Coastal river otters inhabiting the nearshore environment in Prince William Sound, AK prey on benthic and schooling pelagic fish. The otters transport marine derived nutrients to specific locations along the coastline through the use of latrine sites. Latrine sites are chosen based on specific environmental characteristics, and developing accurate models to estimate potential latrine locations can provide wildlife managers with tools to make informed management decisions. Three algorithms (logistic regression, k-nearest neighbor, and maximum entropy) were used to predict otter latrine site selection for two separate datasets using environmental variables calculated at multiple spatial scales. Variables having the greatest support were identified via model selection using area under the curve (AUC) derived from receiver operating characteristic (ROC) plots. Boundary convexity was found to be the strongest parameter estimating latrine presence for each dataset and algorithm combination. However, the degree of influence for each parameter differed between logistic regression and Maxent. Maxent performed consistently better in estimating latrine occurrence, for both within-sample and out-of-sample datasets, than KNN and logistic regression. Using the best fitting model, the Herring Bay (HB) within-sample AUC values were 0.855, 0.824 and 0.785 while the out-of sample values were 0.713, 0.735, and 0.738 for Maxent, logistic regression and KNN algorithms, respectively. While there were no variables at a specific scale that were supported in the top model across all algorithms, the top models did not differ significantly from a biological perspective. Thus,

managers have multiple options from which to choose to accurately predict otter latrine occurrences.

INTRODUCTION

Determining important habitat for animal species is critical for management and conservation (Elith et al. 2006; Gillison 1997; Guisan and Zimmermann 2000; Hernandez et al. 2006; Thuiller 2003). Although measuring habitat use in the field provides the greatest confidence that important areas have been identified, it is often not feasible to survey all areas in a landscape (Fielding and Bell 1997; Stockwell and Peterson 2002). Therefore, estimating probability of use with models developed from samples, often limited in geographic extent, must be used until surveys can be completed.

Species distribution modeling and the myriad of available approaches has increased significantly in recent history (Elith et al. 2006; Guisan and Thuiller 2005; Guisan and Zimmermann 2000; Remm 2004; Wisz et al. 2008). These approaches use environmental variables along with observations of species presence (and absence or pseudo-absence) to estimate the probability that unsampled areas have suitable conditions for the species to occur. Because different algorithms have been shown to behave differently across species and datasets (Elith et al. 2006; Graham et al. 2008; McPherson and Jetz 2007; Reese et al. 2005), it is desirable to test several algorithms, use multiple validation approaches in order to determine the best model, and to look for the best support for environmental variables across different modeling algorithms (Pearce and Ferrier 2000b; Stockwell and Peterson 2002).

Coastal river otters (*Lontra canadensis*) in Prince William Sound, AK are an important meso-predator in nearshore environments (Ben-David et al. 1998; Blundell et al. 2002; Bowyer et al. 2003), consuming both benthic prey and schooling pelagic fish (when available) (Cote et al. 2008; Larsen 1983; Stenson et al. 1984). Otters then deposit feces and urine at latrines,

aiding in the transfer of marine-derived nitrogen to the terrestrial landscape, thereby influencing coastal vegetation communities (Ben-David et al. 1998; Roe et al. 2010). River otters exhibit high fidelity to latrine sites, returning repeatedly to the same location (Bowyer et al. 1995). River otters choose latrine sites based on specific characteristics of the coastal environment (Bowyer et al. 2003). Developing the ability to estimate potential latrine site locations using remotely-sensed data may provide wildlife managers with several useful tools. First assessing the potential distribution of otters, and ultimately their abundance, is essential for making informed management decisions (Alaska Department of Fish and Game 2009). In addition, estimating latrine abundance along a portion of coastline may provide researchers a quantifiable method for estimating effects of allochthonous nutrient influx onto the nearshore environment.

Otter visitation to specific latrine sites is variable through time and depends on the demography of the population (i.e., sex ratio), the distribution of prey, and the physical characteristics of the shoreline (Ben-David et al. 2005; Bowyer et al. 2003). Previous studies have demonstrated at the site-scale, river otters select for steep tidal slope, large intertidal rock, high exposure to waves, extensive beds of kelp, and high overstory cover (Ben-David et al. 2005; Ben-David et al. 1996; Bowyer et al. 2003; Bowyer et al. 1995). Water depth, tidal slope, and wave action are correlated with the distribution and abundance of fishes and invertebrates (Ben-David et al. 1996; Dean et al. 2000). Large trees provide shelter while root holes and crevices serve as dens (Bowyer et al. 1995). In addition, these shaded areas may reduce desiccation of scent marks used for communication (Ben-David and others 2005). At larger spatial scales, Dubuc et al. (1990) demonstrated that river otters select for more convoluted shorelines, which are characterized by productive shallow-water habitats. Also, convoluted shorelines offer numerous exposed points that could aid in the long-range dispersion of scent which may facilitate social communication (Albeke et al. 2010). The objective of this study is to determine the algorithm best estimating coastal river otter latrine site selection for both withinsample and out-of-sample datasets. We chose to examine three different types of algorithms, a

classical parametric method (logistic regression), a nonparametric method (k-nearest neighbor), and a machine learning method (maximum entropy). Because an organism's perspective dictates the scale at which the landscape is viewed (Albeke et al. 2010; Allen and Hoekstra 1992), environmental variables were calculated at multiple spatial scales. Because both KNN and Maxent approaches do not lend themselves to calculation of the Akaike's Information Criterion (AIC), we use the area under the curve (AUC), derived from receiver operating characteristic (ROC) plots to select from a set of candidate models evaluating both the bestfitting spatial scale for each environmental variable, as well as choose a best-fitting overall model.

METHODS

Study Area

The study area is located in the southwestern portion of Prince William Sound (PWS), Alaska (60.47 N, 147.75 W) and includes four islands: Knight Island, Disk Island, Ingot Island and Eleanor Island (Figure 3.1), on which 143.6 km of coastline were surveyed for otter latrines in 2006. Prince William Sound experiences mild, wet summers and winters that result in heavy snow accumulation (Ben-David et al. 2001; Bowyer et al. 1995). The coastal landscape is dominated by old-growth forests comprised of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), having an understory of *Vaccinium spp.*, rusty menziesia (*Menziesia ferruginea*), *Rubus spp.*, and devil's club (*Oplopanax horridus*) (Ben-David et al. 2001; Bowyer et al. 1995). Riparian zones or areas of disturbance are often characterized by alder (*Alnus spp*) (Bowyer et al. 1995).

The marine environment is highly diverse. Subtidal zones vary with depth and slope with some areas characterized by vertical walls while others have shallow slopes of only a few

degrees (Dean et al. 2000). Tidal fluctuations range from -1.13 m to 4.66 m (NOAA 2007). Marine vegetation communities vary with substrate and exposure to waves and currents. Typically, rocky exposed points are inhabited by bull kelp (*Cereocystis luetkeana*) and split kelp (*Laminaria bongardiana*) while colander weed (*Agarum cribrosum*) and sugar kelp (*Laminaria saccharina*) inhabit rocky areas within sheltered bays and protected coastline (Dean et al. 2000; Dean et al. 1996). Bays with finer substrates support eelgrass (*Zostera marina*) communities (Dean et al. 2000; Dean et al. 1998; McRoy 1968, 1970). Much of the intertidal zone is dominated by rock weed (*Fucus gardneri*) and red and green algae (Dean et al. 2000; Gilfillan et al. 1995; Stekoll et al. 1996).

Data Preparation

For the study area, IKONOS® 1-meter panchromatic stereo-pairs and 4-meter multispectral satellite imagery were obtained and manipulated to create the necessary datasets describing the landscape. First, the coastline was digitized, at a 1:1,500 scale, using the panchromatic imagery. Second, using the Leica Photogrammetry Suite (LPS) within ERDAS IMAGINE (ERDAS, Inc., Norcross, GA), an existing DOQQ aerial image was used as a reference for creating tie-points linking the two 1-meter panchromatic IKONOS® stereo images (GeoEye, Thornton, CO). Because of shading issues related to the date of image capture (September 24, 2007), the DEM was incomplete for some north facing areas. To correct this problem, the DEM was converted from a raster to a point feature class and additional points were manually added to fill areas of missing data. The elevation values for the additional points were set at zero and placed outside of the island polygons or was obtained from an existing 2-arc-second DEM (http://ned.usgs.gov/). Using the point feature class, a new 10-meter DEM was created using the Inverse Distance Weighted (IDW) tool within ArcGIS 9.3.1 (ESRI, Redlands, CA).
To perform a supervised classification of landcover types, a 1-meter pan-sharpened image was created by combining the 1-meter panchromatic image and the 4-meter multispectral image. A set of five landcover classes (alder, conifer, muskeg, rock and water) were chosen. Each landcover type was manually digitized, using low-elevation aerial photography and the 1-meter pan-sharpened image, to create 'areas-of-interest' (AOI, training polygons) needed to perform a supervised classification. The AOI's were limited to be within 35 meters of the shoreline. This choice was made for two reasons: 1) otter use of the landscape is typically limited to areas near the shoreline (Larsen 1983) and 2) verified locations of field-collected landcover type were then created for each AOI. Finally, the ERDAS IMAGINE Classifier tool and the Mahalanobis distance algorithm were used to create the classified landcover dataset, with 1-meter resolution, for the 35 meter area nearest the shoreline. To test the classification error, an internal assessment of classification success was performed by obtaining the majority landcover class for each AOI. The internal classification error was less than 12%.

The marine portion of the landscape used by otters was derived from bathymetric sounding points. The bathymetric sounding points were obtained from the National Geophysical Data Center (NGDC 2007). The points occurred at approximately 30-meter intervals and occupied the entire study area, extending to near the coastline. To assist in accurately modeling depth, additional point locations obtained from the digitized coastline were included and their values set to zero. The Inverse Distance-Weight (IDW) technique was then employed to generate a 10-meter interpolated raster of ocean depth.

Dataset Manipulation

All spatial data analyses were performed in ArcGIS 9.3.1. The 10-meter DEM and bathymetry datasets were resampled to 5-meter resolution using bilinear interpolation. The

increased resolution of these datasets allowed the mean raster value to be calculated using zonal statistics (the square cells better fitting the round edges of the zone), thus providing an accurate representation of the local variability by calculating a more accurate area-weighted mean value for each habitat variable at each buffer-size (see below). The degree of slope was calculated for the terrestrial and marine habitats using the resampled DEM and bathymetry datasets and the Spatial Analyst extension for ArcGIS. To test for the potential effects of aspect, the *Area Solar Radiation* tool (Spatial Analyst) was used with the resampled DEM as input to create a dataset estimating the total incoming solar radiation. We chose to estimate total radiation once a week in one-hour intervals for dates occurring between May 15 and August 30, 2006. With Spatial Analyst and the resampled DEM, a three step hydrologic modeling process was used to create a flow accumulation dataset representing the amount of potentially available freshwater. First the *Fill* command was used to remove small imperfections; then the flow direction was calculated and used to generate the final flow accumulation dataset.

Landscape Variables

A suite of variables describing the coastal and nearshore landscapes were generated at every 10 meter interval along the study area coastline, referred to as point-locations (Table 3.1).To the best of our ability, the choice of metrics follow that of Bowyer et al. (2003; 1995) and Larsen (1983). The difference between this study's metrics and previous studies is that all data were derived from satellite imagery or bathymetric sounding points instead of collected directly at each latrine site in the field.

Mean coast height, flow accumulation, solar radiation, terrestrial slope, depth and marine slope were calculated through a five-step process: 1) Initially, a 30-meter buffer was generated for both sides of coastline to represent the areas of highest river otter use (Larsen 1983; Ben-David unpublished data). The interior portion of the buffer represents the terrestrial landscape

and the exterior portion represents the marine landscape (Figure 3.2a); 2) To create the terrestrial-only mask, the 30-meter buffer was intersected with the island polygon feature class while the marine-only mask was created by using the erase tool; 3) To quantify the landscape variables at different spatial scales, a set of four buffer sizes were created for each point location having diameter equal to 10, 25, 50 and 100 meters (Figure 3.2b); 4) Each point-location at each buffer-size was iteratively intersected with the terrestrial-only and marine-only masks, creating a masked-polygon representing the area of otter use for each habitat type (marine or terrestrial) and scale (Figure 3.2c); 5) Finally, the mean zonal statistic was calculated for each masked-polygon for each raster dataset (Albeke and Nibbelink 2009). Using the same method as previously described, the percent conifer was iteratively calculated for each masked-polygon using the Tabulate Area tool and the 1-meter classified landcover dataset.

Larsen (1983) found that coastal river otter habitat use was most often restricted to convex portions of the coastline. To measure this feature of the terrestrial landscape, the boundary convexity index was calculated for each point-location (Albeke et al. 2010). The boundary convexity tool (Albeke et al. 2009) conducts a linear "moving window" analysis at user-defined intervals and window-sizes. For our study we chose an interval of 10 meters and used window-sizes of 10, 25, 50, and 100 meters (approximately equal to the diameter of the buffer sizes). The final landscape variable measures the cost-distance of each point-location to the open ocean. The open ocean was defined as the minimum convex polygon (MCP) derived from the extent of the digitized coastline (see data preparation section; Figure 3.1). To calculate the cost-distance, a 5-meter raster having the terrestrial portion of the landscape assigned a value of 10,000 and the marine portion a value of one, in conjunction with the MCP, was used. The cost-distance values were calculated using ArcGIS Spatial Analyst's *Cost Distance* tool. The calculated values were extracted from the raster for each point-location.

Data Collection

A total of 326 individual river otter latrine sites were identified along the study area coastline and GPS locations were recorded during the summer of 2006. These locations were snapped to the digitized coastline and assigned the nearest point-location. Identification of latrine sites within Prince William Sound and surrounding areas is highly accurate (Ben-David and Golden 2007). Therefore, we are confident that latrine identification within the study area represents an accurate estimate of the number and location of existing otter latrines. To create geographically distinct datasets to facilitate within-sample and out-of-sample model validation, the study area was split into two separate groups, labeled Herring Bay (HB) and Lower Passage-Eleanor Island (LPEI; Figure 3.1). Thus, HB had 175 and LPEI 151 identified latrines. In addition, a set of random locations (175 for HB and 151 for LPEI), were created and placed a minimum of 100 meters from an existing latrine or other random location.

Model Comparison

Three modeling algorithms were compared with respect to their ability to discriminate between latrine and random sites using both within-sample and out-of-sample validation. The modeling approaches include logistic regression (Pearce and Ferrier 2000b), K-nearest neighbor (KNN; Williams et al. 1994), and Maximum Entropy (Maxent; Phillips and Dudík 2008; Phillips et al. 2006). Each modeling approach was used to generate the probability of a pointlocation being a latrine given the binary response variable. The logistic and KNN models were created using SAS 9.1 (SAS Institute Inc., Cary, NC) and Maxent created using the freely available tool (Phillips and Dudík 2008; Phillips et al. 2006). The HB dataset was used to develop within-sample models and then applied to the LPEI dataset for out-of-sample validation. Conversely, the same process was applied using the LPEI dataset for model creation and the

HB dataset for out-of-sample validation. The following methodological descriptions apply to each modeling approach.

The formulation of the candidate set of models required a multiple-step process for each dataset (HB & LPEI). First, Pearson's r correlation coefficients were calculated using SPSS 11.5 (SPSS Inc., Chicago, IL). Variables having correlation coefficients \geq 0.5 were removed to avoid multicollinearity (Table 3.1). Next, single variable models were run for each landscape variable at each scale (buffer-size). The area under the curve (AUC), derived from receiver operating characteristic (ROC) plots, was then calculated, using SPSS 11.5, to allow for a globally consistent comparison between the modeling approaches (Hernandez et al. 2006; Zweig and Campbell 1993). The scale having the highest AUC for each landscape variable was retained for inclusion in the global model(s) (Table 3.2). The global model, using the logistic regression approach only, was tested for model goodness-of-fit using the Hosmer-Lemeshow GOF statistic (Hosmer and Lemeshow 2000). The global model was deemed to be an adequate fit of the data if the p-value was ≥ 0.05 .

The KNN approach requires an optimal number of neighbors be chosen. Prior to performing the model selection process for this algorithm, the parameters within the logistic regression global model were used to determine the optimal number of neighbors. This was accomplished by iteratively testing model accuracy using k = 2 through k= 30. Thus, the optimum number of neighbors was determined to be k= 17.

An information theoretic process was used to find the best fitting model for each modeling approach. Initially candidate models were developed a priori for each model type (Burnham and Anderson 2001). However, because KNN is nonparametric and Maxent does not output loglikelihood, Akaike's Information Criterion (AIC) cannot be globally used for model selection. Instead, AUC was used as the common statistic for assessing the best fitting model. To perform model selection from the candidate set, models with higher AUC values were deemed to be better representations of the process being modeled. For models having the same AUC

(rounded to the nearest 1/100th), the more simple model was chosen (i.e. fewer parameters). To calculate a comparable AUC statistic (as well as confusion matrices, see below) for the Maxent algorithm, the same sample locations used for the logistic and KNN approaches were extracted from the predicted surface of the Maxent model. This was necessary because the default AUC calculated by Maxent is an area-corrected AUC statistic based on a sample of 10,000 pseudo-absence locations (Phillips et al. 2006). As an additional validation of using AUC for model selection, AIC values were for the logistic regression models (Akaike 1973; Burnham and Anderson 2002). The AUC and AIC were then plotted and regressed to assess the relationship between the two metrics. To correct for differences in AIC values between the two datasets, each AIC value was divided by the sample size.

In addition to AUC values, confusion matrices were created to estimate model accuracy of both within and out-of-sample datasets. The probability threshold required for matrix creation was chosen by maximizing the function [sensitivity - m(1 - specificity)] where m was held constant = 1 for each model (Zweig and Campbell 1993). The confusion matrices were then used to calculate model accuracy, sensitivity and specificity using Program R 2.11.1 (Fielding and Bell 1997; R Development Core Team 2010).

RESULTS

Model Development

Prior to determining the best scale for each landscape variable, Pearson's r correlation coefficients were calculated. Three variables were removed because of multicollinearity including marine slope, terrestrial slope and solar radiation (Table 3.1). The remaining landscape variables, at the 10, 25, 50 and 100 meter scales, were then used in single variable models for each dataset and modeling approach. The CostToOcean variable is not scalable and

therefore only has one AUC calculated for each model approach and was included in all subsequent global models (see below). The best fitting scales varied between the datasets and modeling approaches (Table 3.2). For the Herring Bay (HB) dataset, five 10m, one 25m, four 50m and five 100m variables were the best fitting, while the Lower Passage/Eleanor Island (LPEI) dataset had two 10m, three 25m, three 50m and seven 100m variables. Boundary convexity was found to be the most influential variable for each dataset and algorithm. The AUC values for each best fitting variable ranged between 0.482 (poor discrimination capacity) and 0.78 (reasonable discrimination capacity; Table 3.2), indicating no single variable was entirely adequate for discriminating between latrine and random locations (Pearce and Ferrier 2000a; Swets 1988).

The best fitting variables for the logistic global model, using the HB dataset, includes convexity at 50m, CostToOcean, depth at 10m, elevation at 10m, flow accumulation at 100m, and percent conifer at 50m. For the LPEI dataset the variables were convexity at 100m, CostToOcean, depth at 25m, elevation at 10m, flow accumulation at 100m, and percent conifer at 10m. The KNN approach consisted of convexity at 100m, CostToOcean, depth at 25m, elevation at 100m, and percent conifer at 50m for the HB dataset and convexity at 100m, CostToOcean, depth at 50m, elevation at 100m, flow accumulation at 50m, and percent conifer at 50m for the HB dataset and convexity at 100m, CostToOcean, depth at 50m, elevation at 100m, flow accumulation at 50m, and percent conifer at 25m for the LPEI dataset. Lastly, the Maxent global model was comprised of convexity at 50m, CostToOcean, depth at 10m, elevation at 10m, flow accumulation at 100m, and percent conifer at 10m, flow accumulation at 100m, CostToOcean, depth at 25m, elevation at 10m, flow accumulation at 100m, and percent conifer at 50m. For the logistic approach, two variables with the same scale were shared between the datasets while only one variable with the same scale was shared for the KNN and Maxent approaches. The lack of correspondence between the variables and datasets may indicate a geographic distinction between the two datasets.

Model Selection

The logistic global models for both datasets were found to fit the data, for the Hosmer-Lemeshow GOF statistic was not significant (p > 0.05). Thus, each subsequent candidate model, regardless of model approach, was treated as also fitting the data. Logistic model selection results, for the HB dataset, indicate convexity at 50m, CostToOcean, depth at 10m, elevation at 10m, and percent conifer at 50m to be the best fitting while convexity at 100m, CostToOcean, depth at 25m, elevation at 10m, and percent conifer at 10m for the LPEI dataset (Table 3.3). For each dataset, the best fitting model did not include flow accumulation at 100m, presumably due to the exceptionally poor discriminating capacity of the variable (Table 3.2). Using the best fitting logistic model for each dataset, AIC was also calculated. The scatterplot between AUC and AIC (adjusted by sample size) indicates a high degree of correspondence between AUC and AIC (Figure 3.3). Thus, confirming AUC as a similar model selection statistic to AIC for this group of data.

The best fitting model for KNN was convexity at 100m, CostToOcean, depth at 25m, elevation at 10m, and percent conifer at 50m for the HB dataset, behaving similar to the logistic approach in which flow accumulation once again was removed from the global model (Table 3.3). However, for the LPEI dataset only three variables (convexity at 100m, CostToOcean, and elevation at 100m) remained in the best fitting model. Maxent model selection found the global model to be the best fitting for both datasets.

Parameter estimates using logistic regression were calculated for both datasets (Table 3.4). For the HB dataset boundary convexity, mean marine depth and percent conifer were positively related to latrines while cost to ocean and mean elevation were negatively related (mean depths were measured as meters below sea-level, thus a negative parameter estimate indicates a positive response). Boundary convexity was the strongest predictor of latrine occurrence (Table 3.4). For every 10m increase in convexity a latrine was 1.64 times more likely

to occur. The LPEI dataset parameter estimates are similar to the HB dataset. Boundary convexity, mean depth and percent conifer were positively related while mean elevation was negatively related. Additionally, boundary convexity was also the strongest predictor of latrine occurrence, having a 1.43 greater chance of a latrine being present for every 10m increase in convexity. The one difference in parameter estimates between the LPEI and HB datasets is that CostToOcean was positively related to latrine presence for the LPEI model. However, the influence of this parameter upon either model is relatively small.

The relationship of latrine occurrence to the parameters follows the patterns previously measured at the site-specific scale (Bowyer et al. 2003; Bowyer et al. 1995). For example, Bowyer et al. (1995) found otter latrine site selection to be positively related to old-growth forest and steeper tidal slopes and were negatively related to steep vegetated slopes. Regardless of the dataset, the logistic regression analyses follow the same relationships, having a positive related with percent conifer (old-growth) and mean depth (tidal slope) and negatively related with mean elevation (vegetated slope). Thus, providing confidence that variables derived from satellite imagery can measure characteristics of the nearshore environment similar to field collected data.

The Maxent algorithm differed with logistic regression in ranking the most influential variables for estimating latrine occurrence. For both datasets boundary convexity, mean depth and mean elevation were the top three contributors to the model (Table 3.5). Boundary convexity, similar to the logistic regression results, was the most influential parameter contributing 58% for the HB model and 62% for the LPEI model. One noticeable difference between Maxent and logistic regression was the percent contribution of percent conifer for the HB dataset. Percent conifer was the second strongest parameter for logistic regression (Table 3.4), but was ranked fifth by Maxent (Table 3.5, 6.2% contribution).

Model Accuracy

The best fitting model for each dataset and approach were used to predict the probability of a point-location as a latrine site for both within-sample and out-of-sample data. ROC plots were then used to find the optimal mix of false-positive and false-negative results for each model/dataset combination (Zweig and Campbell 1993). The threshold values obtained from the ROC plot analysis (Table 3.6) were then used to create confusion matrices. Using the confusion matrices, model accuracy, sensitivity and specificity were calculated for each algorithm, as well as AUC (Table 3.7). For every model comparison metric, within-sample values were better than out-of-sample values. Maxent had the highest within-sample metric values for the HB dataset and the highest specificity and AUC for the LPEI dataset. KNN accounted for the remaining highest LPEI within-sample metric values. Conversely, KNN had the highest out-of-sample metric values for the HB dataset, except for sensitivity (logistic), and Maxent the highest out-of-sample metric values for LPEI.

The difference between within-sample and out-of-sample values was calculated for each metric (Table 3.8). KNN had the smallest amount of difference for every metric within the HB dataset, indicating the algorithm estimated otter latrine sites more consistently between the datasets than logistic regression and Maxent, but not necessarily more accurately. For LPEI, Maxent had the smallest difference in accuracy and sensitivity and logistic regression the smallest difference in specificity and AUC. Concurrently, Maxent also has the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in accuracy and sensitivity and logistic regression the smallest mean difference in specificity and AUC. The average rank (1, 2 or 3) across all metrics was calculated. The mean rank for the Maxent algorithm was 1.5, 2.1 for KNN and 2.3 for logistic (Table 3.8). Thus, of the algorithms compared, Maxent was more consistent in estimating latrine occurrence than KNN and logistic regression.

DISCUSSION

A pressing wildlife management need is the ability to estimate coastal river otter abundance for Prince William Sound, AK and surrounding coastline. This research has demonstrated that it is possible to predict otter latrine sites along coastlines, with nearly 80% accuracy, using landscape variables derived from satellite imagery. The discriminatory success of the models could then potentially be used to estimate otter abundance, creating a potentially powerful management tool (Nielsen et al. 2005). For example, using data from this NSF research project, there are 326 latrines and an estimated 62 resident otters (Ott et al. in Prep), giving an occupation rate of 0.19 otters/latrine. Using the HB Maxent model to predict latrines for HB and LPEI, 343 latrine sites were estimated. Using the previously stated rate, one could infer that approximately 65 otters occupied the 143.6 km of coastline within the study area. Of course, one should use caution assuming a consistent relationship far outside the area in which the model was parameterized. However the Maxent model showed relatively good transferability between our study areas.

Maxent performed more consistently across the range of within and out-of-sample datasets when compared to the other two algorithms. The AUC for the Maxent models were higher for three out of the four datasets. This result is not unexpected as Maxent exhibits additivity to the contribution of each variable and predicted pixel (Phillips et al. 2006).

The model development and selection processes provided an interesting story in relation to spatial scale, geographic location and algorithm type. Not a single variable at a single scale occurred in all of the algorithms for both datasets. Previous analyses using data from this particular study (Albeke et al. 2010) as well as other research (McGrath et al. 2003; Mitchell et al. 2001; Nams et al. 2006), have demonstrated the importance of scale in understanding animal habitat selection. This research indicates that our interpretation of an animal's response to an environmental variable is directly influenced by the chosen algorithm. For example, Albeke

et.al (2010) found that coastal river otters respond most strongly to boundary convexity at the 100m scale using logistic regression. However, in this study, even though the same convexity values were used, Maxent and logistic regression both found the strongest support (AUC) for convexity at the 50m scale when using the HB dataset. The LPEI dataset had convexity at 100m chosen for all three algorithms. Although the scales differ, they do not invalidate the previously reported result because the dataset used within Albeke et al. (2010) included the entire study area whereas this study split the dataset into two areas. Secondly, the biological relevance between boundary convexity measured at 50m versus 100m may not necessarily be significant. However, the finding does demonstrate the nuance involved with species distribution modeling, and the necessity of putting seemingly different results into a biological context to evaluate whether the difference observed is meaningful.

The results of this modeling exercise also support prior work demonstrating that with modeling approaches, 'one size does not fit all' (Guisan and Zimmermann 2000). The geographic range of the study area (Figure 3.1) is small compared to the distribution of river otter in coastal Alaska. However, not only did variables differ in the 'best' scale for each algorithm, the global models for each algorithm differed between datasets. Additionally, as is most often the case, each algorithm was less accurate when applied to the out-of-sample dataset. In fact, using Landis and Koch's (1977) strength of agreement scale, virtually every algorithm's strength would be considered 'moderate' for within-sample and only 'fair' for out-of-sample. Thus, the question remains as to the 'generality' of the tested models to provide 'precise' predictions to coastal areas within Prince William Sound, AK and beyond (Guisan and Zimmermann 2000; Levins 1966).

Several steps may be taken to help better understand the performance of each algorithm, and assist in making the most informed management decisions as possible. Given the high ratio of non-latrine to latrine sites, a Monte-Carlo approach to selection of random sites and/or increasing the number of random sites, in which multiple models are run using different sets of

random sites, may provide a better understanding of the performance for the logistic and KNN algorithms within this model system. Finally, adopting an Adaptive Resource Management (ARM) approach may provide the necessary framework for determining which approach to apply to future study areas by making predictions of the new coastline and then quantifying algorithm accuracy through monitoring (Lancia et al. 1996).

Several hurdles exist to applying the ARM approach using the developed models. Most notably will be the 'grain' of the landscape data (Allen and Hoekstra 1992). For this study, access to high resolution imagery (IKONOS 1m) was available, which allowed for the digitization of a highly accurate coastline and interpolation of a 5m DEM. McGrath et al. (2003), Mitchell et al. (2001) and Nams et al. (2006) all found that varying scales of data affected the accuracy of habitat use models by wildlife. If the landscape variables for areas outside of this study are not derived from data collected at the same scale, then applying the algorithms developed with this research would be inappropriate. With that said, because each of the landscape variables was derived from satellite imagery, and the strongest predictor variable (convexity) can be calculated using only a coastline file, there is good potential for applying these models to other areas.

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Table 3.1: Description of landscape metrics that potentially may influence

latrine site selection by coastal river otters.

Variable	Definition	Units
Convexity	Convexity index = scale independent metric measuring maximum protrusion (+) or depth (-) of coast defined by a smooth arc through the three points of the coastline defined by the window size and measurement point (Albeke et al. 2010).	Meters
CostToOcean	Cost-path analysis of marine distance from point-location to nearest intersection with minimum- convex boundary of study area.	Num. of cells
Depth	Mean depth within the marine buffer	Meters
Elevation	Mean elevation with the terrestrial buffer.	Meters
Flow Accumulation	Mean number of accumulated raster cells, based on a watershed analysis using a digital elevation model, within the terrestrial buffer.	Num. of cells
Percent Conifer	Proportion of coniferous forest within the terrestrial buffer.	Percent area
Marine Slope †	Mean degree slope within the marine buffer	Degrees
Solar Radiation †	Mean total amount of incoming solar radiation, based on the DEM, within the terrestrial buffer.	Watt hours/m ²
Terrestrial Slope †	Mean degree slope within the	Degrees

Table 3.2: AUC values for single-variable models to subsequently be included in model selection (* indicates use in global model for each approach). Please note the CostToOcean variable is not scalable. The values are placed in the 10m columns for convenience.

	Scale (radius in meters)											
Study Group		10m			25m			50m			100m	
Herring Bay (HB)	LR	KNN	ME	LR	KNN	ME	LR	KNN	ME	LR	KNN	ME
Convexity	0.645	0.627	0.636	0.688	0.665	0.693	0.738*	0.742	0.716*	0.727	0.751*	0.687
Depth	0.701*	0.684	0.658*	0.699	0.685*	0.647	0.654	0.655	0.601	0.615	0.636	0.572
Elevation	0.591*	0.630*	0.614*	0.578	0.628	0.612	0.567	0.655	0.601	0.551	0.636	0.534
CostToOcean	0.585*	0.580*	0.559*	-	-	-	-	-	-	-	-	-
Percent Conifer	0.524	0.476	0.544	0.523	0.516	0.546	0.564*	0.594*	0.574	0.555	0.547	0.590*
Flow Accumulation	0.408	0.522	0.583	0.431	0.565	0.552	0.437	0.583	0.587	0.482*	0.625*	0.617*
Lower Passage- Eleanor Island (LPEI)												
Convexity	0.687	0.688	0.703	0.718	0.709	0.725	0.725	0.717	0.726	0.779*	0.772*	0.780*
Depth	0.636	0.642	0.645	0.642*	0.635	0.659*	0.626	0.652*	0.634	0.578	0.577	0.579
Elevation	0.631*	0.625	0.631	0.627	0.644	0.656	0.619	0.652	0.663	0.602	0.690*	0.678*
CostToOcean	0.624*	0.702*	0.675*	-	-	-	-	-	-	-	-	-
Percent Conifer	0.539*	0.510	0.576	0.520	0.624*	0.574	0.524	0.590	0.625*	0.539	0.601	0.610
Flow Accumulation	0.618	0.601	0.639	0.639	0.662	0.639	0.640	0.669*	0.651	0.670*	0.653	0.675*

Table 3.3: Model selection using Area Under the Curve (AUC). The least complex models having AUC values rounded to the nearest 1/100 for each approach was deemed the best fitting model. † indicates the global model.

HB Dataset	AUC
Logistic	
Convex50m CostToOcean Depth10m Elev10m PctConf50m	0.817
Convex50m CostToOcean Depth10m Elev10m FlowAcc100m PctConf50m †	0.824
Convex50m CostToOcean Depth10m Elev10m	0.789
Convex50m Depth10m PctConf50m	0.777
Convex50m CostToOcean Depth10m	0.776
Convex50m Depth10m Elev10m	0.772
Convex50m Depth10m	0.762
Convex50m CostToOcean Elev10m	0.755
KNN	
Convex100m CostToOcean Depth25m Elev10m PctConf50m	0.785
Convex100m CostToOcean Depth25m Elev10m	0.764
Convex100m Depth25m PctConf50m	0.753
Convex100m CostToOcean Depth25m	0.753
Convex100m Depth25m Elev10m	0.751
Convex100m Depth25m	0.745
Convex100m CostToOcean Elev10m	0.734
Convex100m CostToOcean Depth25m Elev10m FlowAcc100m PctConf50m †	0.607
Maxent	
Convex50m CostToOcean Depth10m Elev10m FlowAcc100m PctConf100m †	0.855
Convex50m CostToOcean Depth10m Elev10m PctConf100m	0.840
Convex50m CostToOcean Depth10m Elev10m	0.821
Convex50m Depth10m Elev10m	0.799
Convex50m CostToOcean Depth10m	0.797
Convex50m Depth10m PctConf100m	0.793
Convex50m Depth10m	0.780
Convex50m CostToOcean Elev10m	0.776
LPEI Dataset	
Logistic	
Convex100m CostToOcean Depth25m Elev10m PctConf10m	0.817

Convexioum Cost roucean Deptn25m Elevitum PctContitum	0.817
Convex100m CostToOcean Depth25m Elev10m FlowAcc100m PctConf10m †	0.818
Convex100m CostToOcean Depth25m Elev10m	0.811
Convex100m CostToOcean Elev10m	0.809
Convex100m Depth25m Elev10m	0.806

Convex100m Depth25m PctConf10m	0.789
Convex100m CostToOcean Depth25m	0.787
Convex100m Depth25m	0.777

KNN

46
348
34
33
318
314
'84
'82

Maxent

Convex100m CostToOcean Depth25m Elev100m PctConf50m 0.86	
Convex room CostroOcean Depth25m Elev room r cicomoni 0.00	52
Convex100m CostToOcean Elev100m 0.84	45
Convex100m CostToOcean Depth25m Elev100m 0.84	42
Convex100m Depth25m Elev100m 0.82	26
Convex100m Depth25m PctConf50m 0.80	07
Convex100m CostToOcean Depth25m 0.80	25
Convex100m Depth25m 0.78	32

Table 3.4: Parameter estimates for the best-fitting logistic regression model. The estimates and 95% CI were scaled by the magnitude of the assumed effect to standardize interpretation of each variable.

				Scaled	Scaled	95% CI
		Unit	Scaled	Odds		
Parameter	Estimate (SE)	Change	Estimate	Ratio	Lower	Upper
HB Dataset						
Intercept	-1.2046 (0.5595)		-1.205		-2.301	-0.108
Convex50m	0.0496 (0.0103)	10	0.496	1.643	0.295	0.697
CostToOcean	-0.0003 (0.0001)	100	-0.026	0.974	-0.040	-0.013
Depth10m	-0.1874 (0.0514)	1	-0.187	0.829	-0.288	-0.087
Elev10m	-0.0432 (0.0108)	1	-0.043	0.958	-0.064	-0.022
PctConf50m	0.0348 (0.0074)	10	0.348	1.416	0.203	0.493
LPEI Dataset						
Intercept	-1.1617 (0.5125)		-1.162		-2.166	-0.157
Convex100m	0.0354 (0.0062)	10	0.354	1.425	0.233	0.476
CostToOcean	0.0003 (0.0001)	100	0.026	1.026	0.007	0.044
Depth25m	-0.1049 (0.0531)	1	-0.105	0.900	-0.209	-0.001
Elev10m	-0.0232 (0.0073)	1	-0.023	0.977	-0.038	-0.009
PctConf50m	0.0075 (0.0038)	10	0.075	1.077	0.000	0.149

Table 3.5: Estimates of relative contribution of each environmental variable to the Maxent model. For comparison, the rank of variable importance derived from the log-odds of the best fitting logistic regression model is included (Table 4).

	Percent	Logistic
Parameter	contribution	Rank
HB Dataset		
Convex50m	58	1
Depth10m	17.9	3
Elev10m	8.3	4
CostToOcean	6.5	5
PctConf100m	6.2	2
FlowAcc100m	3.2	-
LPEI Dataset		
Convex100m	61.9	1
Depth25m	16.6	2
Elev100m	9.5	5
Pctconf50m	6	3
CostToOcean	4	4
FlowAcc100m	2.1	-

	HB Da	ataset	LPEI Dataset		
	Within-sample	Out-of-sample	Within-sample	Out-of-sample	
Logistic	0.520	0.600	0.469	0.508	
KNN	0.474	0.500	0.471	0.676	
Maxent	0.404	0.374	0.296	0.393	

Table 3.6: Threshold values derived from ROC curves for each best fitting model and dataset.

Table 3.7: Model comparison metrics for each dataset derived from the confusion matrices.

Model/Metric	HB Dataset		LPEI D	ataset
	Within-sample	Out-of-sample	Within-Sample	Out-of-sample
Logistic				
Accuracy	0.757	0.689	0.772	0.643
Sensitivity	0.765	0.702	0.753	0.606
Specificity	0.750	0.677	0.793	0.719
AUC	0.824	0.735	0.817	0.685
KNN				
Accuracy	0.731	0.705	0.791	0.631
Sensitivity	0.710	0.678	0.772	0.620
Specificity	0.758	0.742	0.814	0.646
AUC	0.785	0.738	0.846	0.644
Maxent				
Accuracy	0.786	0.695	0.772	0.700
Sensitivity	0.781	0.679	0.720	0.668
Specificity	0.791	0.715	0.853	0.747
AUC	0.855	0.713	0.866	0.716

	Accuracy	Sensitivity	Specificity	AUC
Logistic (HB)	0.068	0.063	0.073	0.089
KNN (HB)	0.026	0.032	0.016	0.047
Maxent (HB)	0.090	0.102	0.075	0.142
Logistic (LPEI)	0.129	0.147	0.074	0.132
KNN (LPEI)	0.160	0.152	0.169	0.202
Maxent (LPEI)	0.072	0.052	0.107	0.150
Logistic (Mean)	0.099	0.105	0.073	0.110
KNN (Mean)	0.093	0.092	0.092	0.124
Maxent (Mean)	0.081	0.077	0.091	0.146

Table 3.8: Calculated difference between within-sample and out-of-sample

metric values measuring classification accuracy.



Figure 3.1: Study area with the two geographic datasets (Herring Bay-HB, and Lower Passage/Eleanor Island-LPEI) differentiated by color.



Figure 3.2: Masked buffer process. For example, a 30m of the coastline representing the terrestrial or marine portion of the environment (A), then a point-buffer of a given radius is created (B) and intersected with the 30m marine portion of the nearshore environment (C).



Figure 3.3: Scatterplot of AUC and AIC values for both datasets and the corresponding regression line. AIC values were obtained from the logistic regression analysis. The raw AIC values were divided by the sample number to create a comparable metric between the datasets. Regression line equation and associated R² also included.

CHAPTER 4

MODELING BEHAVIOR OF COASTAL RIVER OTTER (*LONTRA CANADENSIS*) IN RESPONSE TO PREY AVAILABILITY IN PRINCE WILLIAM SOUND, ALASKA: A SPATIALLY-EXPLICIT INDIVIDUAL-BASED APPROACH¹

¹Shannon E. Albeke, Nathan P. Nibbelink, and Merav Ben-David. To be submitted to Ecological Monographs

ABSTRACT

The transport of nutrients between sea and land by coastal river otters is an important process affecting the productivity of nearshore terrestrial vegetation. The social behavior of otters is directly associated with the presence of schooling pelagic fish. Social otters cooperatively forage on fish schools and use latrine sites to communicate group associations and dominance. Conversely, solitary otters feed primarily on intertidal fish and use latrines to communicate mutual avoidance. This behavioral mechanism creates variable nutrient deposition rates to the nearshore environment. To increase our understanding of system processes, a spatially-explicit individual-based model (IBM) was developed to investigate landscape-level effects of spatial and temporal variation in nutrient transport by coastal river otter. The IBM simulated behavioral responses by otters based on variability in abundance, spatial location and timing of schooling fish, coupled with the relative habitat quality of the nearshore environment. Additionally, a sensitivity analysis was performed to determine which processes (i.e. parameters) most affected otter behavior and subsequent nutrient deposition. A set of nine simulation experiments were completed, each having 10 replicates. Results from the IBM overwhelmingly indicate otter behavior is almost entirely driven by prey availability. Of the six measured response variables (daily fecal counts, defecation rate, hours of activity, fish school forage success, social groups, and coastline use), five of the twenty-four possible variable combinations experienced noticeable variation. The response variables were always significantly different for simulation experiment R03 (no schools), and the behavioral response was always to the detriment of otter fitness. The spatial pattern of fecal deposition was heterogeneous across the coastal landscape, mimicking the observed variation recorded during the 2006 and 2007 sample periods. The IBM was able to reproduce observed patterns in nutrient transport, facilitated by the behavioral response of otters to pelagic fish schools and the subsequent creation of social groups. The inclusion of vision, olfaction and memory as viable

forms of otter sensing and their quantifiable response to these stimuli provide a strong behavioral foundation for the IBM.

INTRODUCTION

As with seabirds (Anderson and Polis 1998, Hobson et al. 1999, Mulder and Keall 2001), piscivory by coastal river otters (*Lontra canadensis*) in nearshore coastal areas provide a pathway for nutrient transport between sea and land (Ben-David et al. 1998), thus extending the resource shed of the terrestrial community into the ocean (Power and Rainey 2000). Marinederived carbon (C), nitrogen (N), and phosphorus (P) transported by river otters to terrestrial latrine sites (specific locations along the shoreline) can be several orders of magnitude higher than other nutrient inputs in this system (Giblin et al. 1991, Lilleskov et al. 2001).

In Prince William Sound (PWS), Alaska, social otters use latrine sites as communication tools, advertising group associations and dominance (Rostain et al. 2004, Ben-David et al. 2005). Predominantly male, social otters that forage cooperatively on schooling pelagic fish in the nearshore environment (Blundell et al. 2002a) use fewer latrines at high frequency. In contrast, nonsocial otters (mostly females and some males) tend to feed on intertidal/benthic fishes and visit numerous latrine sites with low frequency (Ben-David et al. 2005). This behavioral mechanism, determined by otter demography and the distribution of pelagic fishes in the nearshore environment, creates variation in nutrient transport from sea to land. The effect of spatial and temporal variation in allochthonous inputs of C, N, and P on the nearshore ecosystem and the emergent landscape heterogeneity in PWS is not well understood. To increase our understanding of system processes, Ben-David et al. (2005) proposed a need to develop a spatially explicit individual-based model of otter behavior which will identify the important factors underlying the subsequent variation in nutrient transport to the terrestrial community.

Individuals are the building blocks of inherently complex ecological systems (Grimm and Railsback 2005), and provide a natural scale at which to make measurements of ecological interactions (Pascual and Levin 1999). Railsback (2001) has stated that modeling individuals may be an easier task than modeling populations because individuals are more limited in their range of responses and their behavioral response may be more predictable than a population response. Individuals respond to internal changes and the external environment by seeking 'fitness' through adaptive behavior (Grimm and Railsback 2005). From these behaviors, system level properties emerge (Grimm 1999, Railsback 2001, Grimm and Railsback 2005). These characteristics comprise the foundation of individual-based modeling.

Individual-based models (IBM) have been used since the 1970's (Grimm 1999), and are simulation models that treat individuals as unique and discrete entities. These discrete entities have at least one property, in addition to age, that changes during the cycle of the model (Grimm 1999). IBMs are often developed to gain a deeper understanding of system dynamics through individual behavior and implemented because classical approaches ignore individual differences and local interactions (Grimm and Railsback 2005). Spatially explicit IBMs incorporate population dynamics within heterogeneous landscapes by specifying the explicit location of objects (organism, population, habitat patch) and their spatial relationship to other landscape features (Dunning Jr. et al. 1995).

Individual-based models have several advantages. First, IBMs allow researchers to consider aspects of a system typically ignored in analytical models, including variability among individuals, local interactions, complete life cycles, and adaptive behavior to internal and external stimuli (Grimm et al. 2006). Additionally, an IBM allows for the testing of a theory under many different conditions, an attribute typically not available in natural systems (Grimm and Railsback 2005). This attribute is desirable given the myriad of potential climate change scenarios.
The objective of this research is to investigate landscape-level effects of spatial and temporal variation in nutrient transport by coastal river otters via a spatially explicit, individualbased model. We hypothesize that the arrangement and availability of high quality prey (pelagic fish schools) will result in differing patterns of deposition to the coastal landscape. As otters forage, communication of located sources of pelagic fish to other otters through feces will create a variable pattern of deposition across the landscape. First, to test the sensitivity of the model to variations in parameterization, a set of six simulation scenarios testing three model parameters will be compared with the baseline simulation scenario. Each of these scenarios will use an 'informed' pelagic fish model. To test the response of otters to variation in pelagic fish availability, two additional simulation scenarios, one randomly placing pelagic fish within the landscape network and the other removing pelagic fish entirely from the model, will be run. The response of individual otters to prey availability and the resulting pattern of fecal deposition will be tested against observed data.

BIOLOGICAL BACKGROUND

Study Area

The study area is located in the southwestern portion of Prince William Sound (PWS), Alaska and includes four islands: Knight Island (60.47 N, 147.75 W), Disk Island (60.49 N, 147.65 W), Ingot Island (60.53 N, 147.64 W) and Eleanor Island (60.55 N, 147.59 W) (Figure 4.2). The study area is approximately 240 km2, encompassing 245 km of coastline. The study area has a maritime climate with cool and wet summers followed by winters of deep snow accumulation (Ben-David et al. 2005). The coastal landscape is typically snow-free from early May to early November. The structure of the coastline is primarily steep and rocky with some flat, low gradient beaches and numerous bays and inlets (Bowyer et al. 1995). The coastal

vegetation is primarily old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with a well-developed under-story layer comprised of *Oplopanax horridus*, *Vaccinium spp.*, *Menziesia ferruginea*, and *Rubus spp*. (Ben-David et al. 1998).

The bathymetric gradient of the nearshore environment is highly variable, ranging from near vertical to slopes of only a few degrees. The substrate is also variable with sizes ranging from large boulders to fine sediment (Bowyer et al. 2003). Large tidal fluctuations in this habitat (annual maximum tide of 4.66 m and a minimum tide of -1.13 m) (NOAA 2007) greatly affect the vegetative community. Two kelp species (*Agarum cribrosum* and *Laminaria saccharina*) dominate rock within sheltered bays and less exposed coastline (Dean et al. 1996, Dean et al. 2000). On exposed points, bull kelp, *Cereocystis luetkeana*, comprises the canopy and *Laminaria bongardiana* the understory (Dean et al. 1996, Dean et al. 2000). Eelgrass, *Zostera marina*, dominates softer substrate usually found in inner bays (McRoy 1968, 1970, Dean et al. 1998, Dean et al. 2000). The majority of the intertidal region of the coastline is dominated by *Fucus gardneri*, interspersed with red and green algae (Gilfillan et al. 1995, Stekoll et al. 1996, Dean et al. 2000).

The nearshore environment supports a diverse fish community. The community can be described as two distinct groups: resident intertidal-demersal species and migratory pelagic species. The intertidal species primarily belong to the families *Cottidae*, *Scorpaenidae*, *Hexagrammidae*, *Cancridae*, together with invertebrates such as mussels (*Mytilus trossulus*), crabs (*Metacarcinus gracilis*, *M. magister* and others), chiton (*Tonicella lineata*) and clams (*Pelecypoda*) (Larsen 1984, Boehm et al. 2004). These species are a ubiquitous, non-migratory prey base for coastal river otter (Dean et al. 2000, Blundell et al. 2002a, Mecklenburg et al. 2002, Ben-David et al. 2005). *Salmonidae*, *Ammodytidae*, *Clupeidae*, and *Gadidae* comprise the pelagic fish species using the study area for spawning (Larsen 1984, Blundell et al. 2002a). These schooling pelagic fish species typically migrate into the study area in early May and return to the open ocean or expire (salmon) by November (Brown et al. 1999, Blundell et al.

2002a, Brown 2002, Mecklenburg et al. 2002). As otter prey, the schooling pelagic fish have a higher energy density than the intertidal-demersal fish (Anthony et al. 2000, Blundell et al. 2002a).

Coastal River Otter

The North American river otter (*Lontra canadensis*) is an aquatic member of the weasel family (Liers 1951, Hall 1981) and neither hibernates nor migrates (Melquist and Hornocker 1983, Bowyer et al. 2003).River otters are nearly ubiquitous in coastal areas of the Gulf of Alaska, including the study area (Hall 1981, Bowyer et al. 1995) and prey upon marine fishes and invertebrates inhabiting the nearshore environment (Larsen 1984, Stenson et al. 1984, Bowyer et al. 1994, Bowyer et al. 1995, Ben-David et al. 1998). Blundell et al. (2004) found the sex ratio of river otter in PWS to be approximately 66% male. This finding is supported by additional data collected within the study area (Ott et al. in Prep). River otter abundance within the study area has been estimated to be between 0.28 and 0.8 otter per km of coastline (Testa et al. 1994). This estimate is similar to recent abundance estimates of 0.442 otters/km derived by Ott et al. (*in Prep*).

River otters inhabiting coastal areas of PWS exhibit an atypical social behavior in comparison to other mammals (Blundell et al. 2002a, Blundell et al. 2004). In this system river otters occur in large groups of males (Rock et al. 1994, Blundell et al. 2002a). These aggregations (3-18 otters) facilitate foraging efficiency on schooling pelagic fish within the nearshore environment (Blundell et al. 2002a, Blundell et al. 2004, Ben-David et al. 2005). As the number of pelagic fish schools decrease, so does group size (Blundell et al. 2002a). In contrast, female otters and some males remain solitary year round, foraging primarily on intertidal-demersal fish, but occasionally joining a male group to opportunistically forage on pelagic fish (Blundell et al. 2002a).

Similar to other mustelids, river otters communicate through scent-marking (Lariviére and Walton 1998, Ben-David et al. 2005).Scent-marking through feces, urine and anal gland secretions occurs at specific locations along the coast, known as latrine sites (Blundell et al. 2002a, Bowyer et al. 2003, Ben-David et al. 2005, Guertin et al. 2010). Communication through scent marking appears to have two different functions: social otters use latrine sites for intragroup communication, signaling resource use and facilitating group cohesion (Ben-David et al. 2005); solitary otters use latrine site scent marking to indicate territorial boundaries and encourage mutual avoidance (Ben-David et al. 2005).

Blundell et al. (2001) found that male otters occupy a home-range of more than twice the size of female otters. Concurrently, male otter home-ranges tended to have a higher proportion of overlap while females had low spatial overlap and distinct core areas of use (Blundell et al. 2001). In addition, social otters (largely males) tend to visit fewer latrine sites than do solitary otters, but social otter latrine sites have a higher frequency of use than do solitary otter latrines (Ben-David et al. 2005).

Because river otters forage in an aquatic environment and use latrine sites exclusively for urination and defecation, nutrients are transported in the opposite direction of the typical downstream nutrient-flow within a watershed. This nutrient transport extends the resource shed of the terrestrial community into the ocean (Power and Rainey 2000). With this concept in mind, Ben-David et al. (2005) estimate that on average the input of marine derived nutrients to the coastal landscape at latrine sites is much greater than non-latrine areas.

Data Collection

In May 2006, 326 otter latrines were identified along the 144 km of shoreline surveyed within the study area. Point-locations were recorded at the entrance to each latrine site using a Garmin 12xl GPS unit. The identified latrines account for over 95% of existing sites within the study area (Ben-David and Golden 2007). All other sites in the study area were classified as

non-latrine. During the summer months (May – August) of 2006 and 2007, otter feces were counted on 100 of these latrines using a stratified random approach. The stratification was based on island (Knight, Disk, Ingot and Eleanor) and the initial (2006) fecal counts (<100 representing low use and >100 representing high use). For example, because 54% of all sites occurred in Herring Bay on Knight Island, 54 sites were monitored for fecal deposition in that location. Of these 54 sites, 21 were high-use latrines, in accordance with the 39% occurrence of high use sites in the entire study area. Each fecal deposit was recorded and marked with glitter (Glitterex Corp., Cranford, NJ) to avoid duplicate counts on subsequent surveys. Each latrine was sampled 9 times in 2006 and 5 times in 2007.

THE MODEL

The individual-based model description follows the 'Overview', 'Design concepts' and 'Details' (ODD) protocol proposed by Grimm et al. (2006). The IBM was developed using Microsoft Visual Studio 2010 TM and Visual Basic.NET v4.0. All random values from statistical distributions were obtained using Program R via the statconnDCOM interface (Heiberger and Neuwirth 2009, R Development Core Team 2010). Microsoft Access TM was used to store all model input and output.

4.1. Overview

4.1.1 Purpose

The individual-based model (IBM) was designed to simulate the behavior of coastal river otter in response to changes in prey availability within the study area using a spatially-explicit approach. Several processes directly affect the behavior of otters and the subsequent variability in fecal deposition along the coastline, including prey availability, abiotic habitat structure and unique social behaviors facilitating communication. The IBM aims to shed light on

these processes and ascertain which process most influences otter behavior and the subsequent consequences for the nearshore environment.

4.1.2 State variables and scales

Individual otter variables are age, sex, activity-state (active or resting), number of hours in current activity-state, defecation-state (defecated or not), number of hours since defecating, satiation-state (fed on pelagic fish school or not), and spatial location. For females only, the central point along the landscape network 'edge' of the individual's 50% core home range, as well as the habitat encompassed by the home range, are also included as static state variables in the model. The model is constructed to hourly track the activity of each individual for a period of 92 days (2208 hours), beginning on May 15, 2006 and ending August 15, 2006, matching the timeframe of field collected data. Otter movements were restricted to a landscape network comprised of 245 km of coastline and an additional 80 km of 'virtual lines' (Figure 4.2; Section 4.4) (Vuilleumier and Metzger 2006). All movement distances and home range sizes are measured in meters.

The landscape network has three state variables assigned to each point-location, the abiotic habitat quality (likelihood of being an otter latrine), a radial-extent scaling factor, and potential pelagic fish spawning habitat. Using the variable and model selection approach described in Chapter 3, Maximum Entropy (Maxent) was used to estimate the probability of use of each point-location as a latrine site (MEP) (Phillips et al. 2006, Phillips and Dudík 2008). The Maxent model was developed using the entire study area dataset. The variables used for the Maxent model include convexity of the shoreline within 50m, distance to open ocean, mean depth within a 10m radius, mean elevation within 10m, mean flow accumulation within a 100m radius and percent area having coniferous vegetation within 50m. These variables were chosen to follow the abiotic conditions known to affect otter latrine site selection (Larsen 1983, Bowyer et al. 1995, Bowyer et al. 2003, Ben-David et al. 2005, Albeke et al. 2010).

The radial-extent scaling factor was required to accurately represent female home-range size (Section 4.3). Because the landscape network was highly connected (i.e. island coastlines connected to themselves, etc.), a randomly drawn home-range size, if applied as a radius (½ the home-range size) onto the network, would encompass a greater extent of habitat than expected. The extent of occupied habitat exceeding the randomly drawn value varied for each 10m location along the coastline, referred to as a point-location. To account for this phenomenon, the actual extent of habitat was calculated for each point-location at seven different radii (100, 500, 1000, 2000, 4000, 6000, and 10,000 meters). The ratio between the expected and actual network distances was calculated and an exponential curve was fit for each point-location. The estimated parameters were then used to scale the randomly drawn home-range value, given the point-location of the female otter (Section 4.3).

The most common pelagic fish occurring in the study area were Pacific herring (*Clupea pallasi*), Pacific capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus*) (Blundell et al. 2002a). These fish species become available to otters during seasonal spawning migrations to the nearshore environments (Robards et al. 1999, Norcross et al. 2001, Brown 2002). The preferred spawning habitats of these fishes are typically shallow coastline areas, sheltered from heavy wave action and contain submerged marine vegetation (Haegele and Schweigert 1985). Pacific herring most commonly choose spawning areas < 10m in depth (Haegele and Schweigert 1985), Hay et al. 2009). However, depths of < 3m have been suggested as most preferable by herring (Bargmann 1998). Additionally, sand lance tend to spawn in fine-grained substrate at depths of approximately 1.55m (Penttila 2007). Thus, using the depth at 25m variable (see Chapter 3), point-locations having a value \geq -3.04m were included as potential spawning habitat for pelagic fish during simulations (8,108 out of 24,520 locations).

The temporal scale for fish schools was treated slightly differently than the scale of otters. Fish schools were randomly placed onto the network for each simulated hour. The assignment of school locations was restricted to the point-locations meeting the depth requirement (unless

otherwise specified). However, the number of schools available during a given time step was calculated at the beginning of each 24 hour period (i.e. once per day) and held static for the entire day.

4.1.3 Process overview and scheduling

The model simulates individual otter movement and behavior through foraging, recuperation and olfactory communication processes (Figure 4.1). The model begins at midnight, May 15, 2006, with each otter having predetermined states (Section 4.3). During a given time step, the activity-state of each otter was assessed. The majority of simulated behaviors occur for otters that are currently active. Active otter's foraging behavior is influenced by the presence of otter feces and/or fish schools. The completed foraging event is followed by defecation behavior that is driven by the defecation-state, satiation-state and spatial location of the individual. The maintenance of an individual's current activity-state is driven by the hours within the current activity-state and the satiation-state. Recuperating otters (i.e. resting at a static location) assess the maintenance of their current state and proceed with defecation behavior if switching to the active-state. The simulation process repeats every hour for a total of 2208 hours (i.e. 92 days) until 12:00am on August 16th, 2006 is reached.

The placement of pelagic fish schools along the coastline also occurs on an hourly basis. Each fish school is randomly placed at an available unique point-location and remains there only for the given time step. The timing and random placement reflect the dynamic movement of the pelagic fish schools within the 1-hour window (Brown et al. 1999). The number of fish schools is calculated at 12:00am for each day of the simulation. This value is held constant for the 24-hour period.

4.2. Design concepts

4.2.1 Emergence

There are two system-level patterns that emerge from the otter behavior model. The first, and primary objective of this modeling exercise, is to assess the spatio-temporal distribution of fecal deposits by otters. The resulting patterns will describe if the simulated nutrient deposition by otters are randomly occurring, creating homogenous nutrient input to the coastal environment, or if a heterogeneous pattern arises. A heterogeneous distribution pattern of nutrient deposition would create an influx of nutrients to specific locations along the coastline and influence landscape heterogeneity (Ben-David et al. 2005, Roe et al. 2010).

The social behavior of coastal river otters has been well documented (Testa et al. 1994, Blundell et al. 2000, Blundell et al. 2002a, Ben-David et al. 2005). Social otters use scentmarkings to communicate group association while solitary otters mark territorial boundaries (Ben-David et al. 2005). Thus, a second emergent pattern may arise from otter defecation behavior and communication through scent (feces) markings. The aggregation of virtual otters into social groups because of food dispersion would follow field observed social behavior and potentially explain some the heterogeneous fecal deposition patterns observed through field collected data.

4.2.2 Adaptation

The model allows for each otter, while in an active-state, to directly adapt to their current surroundings. First, foraging otters use a 50m visual-sense to locate fish schools and/or best available habitat conditions. This relatively short distance was chosen because otters are adapted to forage underwater, and are therefore nearsighted (Chapman and Feldhamer 1982). If a fish school is located, the otter stops moving along the network to feed on the school for the remainder of the time step. In addition to using sight, male otters use olfaction to detect potential

prey availability. While traversing the landscape network on a foraging excursion, males have the chance to detect scent-markings left by other otters. If a scent-marking is detected, the male chooses to move in the direction of the detected scent in hopes of finding high quality prey.

4.2.3 Fitness

The defecation behavior of each otter is directly related to the type of prey consumed. Pelagic fish have higher lipid content, providing greater caloric value than demersal fish (Anthony et al. 2000). Additionally, the schooling behavior of pelagic fish provides a greater density of prey per unit area. Therefore, otters locating and feeding on a fish school increase their own fitness and potentially that of other nearby foraging otters. The individual otter locating a fish school gains additional energy per hour of foraging and increases the likelihood of reaching satiation. A more satiated otter is less likely to be in an active-state; thus hypothetically reducing the risk of predation (mortality is not included in this model) or injury through foraging excursions. Concurrently, an otter feeding on a fish school is more likely to defecate after feeding. The defecation behavior of the individual otter, coupled with other males' attraction to scent-markings, increases the likelihood of multiple otters congregating in the location of the located fish school. A group of otters have higher efficiency in capturing pelagic fish than solitary otters through cooperative foraging (Blundell et al. 2002a).

4.2.4 Prediction

As was described in Section 4.2.2, otters use detection of scent-markings as an indicator of high-quality prey availability (Kruuk et al. 1991). The assumption, and subsequent prediction, made by each otter is that if a cohort defecates, pelagic fish schools must be nearby.

4.2.5 Sensing

Each otter uses three separate types of sense: olfactory, visual and memory. The male otter uses olfaction to imperfectly detect scent-markings from other otters (see eq. 6). The otter

can smell a scent-marking up to 1km from its current location. This type of sense directly influences the choice of movement direction along the landscape network. The otter continually uses its visual sense during foraging excursions. It was assumed an otter would be acutely aware of the biotic and abiotic conditions within 50m of its current location, allowing the otter to sense nearby fish schools and the highest quality habitat. Finally, otters were assumed to have perfect memory of the local habitat. M. Ben-David has observed (unpublished data; personal observation) telemetered otters foraging on pelagic fish schools. In these observations, upon completion of the feeding, the otters often travelled long distances to a preferred latrine site usually with a well-established den to rest. Thus, a virtual otter transitioning from active-state to inactive-state will choose the point-location on the network having the highest habitat score (probability of being a latrine; MEP) within 1km of its current location.

4.2.6 Interaction

Individual otters are assumed to cooperatively forage during active-state interactions. It is possible for two otters to cross paths and not forage together, but only if a fish school is not present. Female otters were assigned exclusive 50% core home-ranges during model initialization (Blundell et al. 2000). However, during foraging excursions females can cross into another female otter's core area without repercussion.

4.2.7 Stochasticity

Stochasticity was introduced into the model through four separate otter-specific processes and the behavioral parameters were expressed as probabilities or drawn from empirical statistical distributions:

 The movement distance for an individual foraging excursion was randomly drawn from a truncated normal distribution (distance > 0) using a mean (SD) derived from 8 telemetered otters within the study area (Table 4.1; M. Ben-David unpublished data). M.

Ben-David and colleagues measured the behaviors of otters to the nearest second, for a 24 hour period for a full summer in 1991.

- 2. At each landscape network node, the next path chosen by a male otter was first assessed through the detection of scent-markings. For the nearest fecal deposit to the otter's current location, a Bernoulli trial was conducted to determine if the scent was detected. The probability of successful detection was derived from a pair of equations combining the effect of distance and age of the fecal deposit (see eq. 6, 7). If no scent was detected, the next movement-path was randomly drawn from all possible paths, excluding the previously traveled path.
- 3. Having a successful defecation event by an otter was determined using a Bernoulli trial in which the probability was derived using a set of equations using the number of hours since the previous defecation event (mean (SD)) and the habitat quality of the currently occupied point-location as parameters (MEP; see eq. 2, 3).
- For an otter currently in the active-state, the transition probability is derived from the mean (SD) of the timed otter behavior from the data collected for 8 telemetered otters in 1991 (M. Ben-David unpublished data; see eq. 4) and tested using a Bernoulli trial.
- 5. The final stochastic process occurs when or an otter currently in the inactive-state. The probability of transitioning to the active-state is derived from the mean (SD) of the timed otter behavior from the data collected for 8 telemetered otters in 1991 (M. Ben-David unpublished data; see eq.5) and tested using a Bernoulli trial.

An additional stochastic process is the random placement of fish schools onto available point-locations. To perform this operation, the list of available point-locations was obtained with all having equal weight. Each fish school is placed onto the network, without replacement of the point-location, for each time step.

4.2.8 Collectives

Otters are known to create social groups to facilitate foraging success (Blundell et al. 2002a, Ben-David et al. 2005). This behavior is not explicitly represented within the model. However, the use of scent-markings as an adaptive behavior by male otters may produce social collectives of otters through emergent behavior (Sections 4.2.1 - 4.2.3).

4.2.9 Observation

All data output were stored within five MS Access database tables. The 'tblOtter' table stores otter specific information, including the otter's age, gender and randomly assigned home range size (female only). The table 'tblOtter' relates to tables 'tblStateValues,' and 'xrefHomeRange'. The table 'xrefHomeRange' stores the route events describing each female's 50% core home range that cannot overlap with another female. The individual information for each otter state-values (time step, spatial location, activity-state, hours of activity-state, defecation-state, hours since defecating, and satiation-state) are stored in the 'tblStateValues' table. The spatial location and time step of each fecal deposition event is tracked in 'tblPoopTracker', while the timing and location of each fish school is managed in 'tblFishSchools' table.

The capture of information at the finest temporal scale allows for the synthesis of model results at hourly, daily, monthly or the entire study period time-scales. The temporal scales can be used to assess otter behavior for individuals, groups or the entire population. The information contained within the database can be used to perform multiple analyses. Fecal deposition rates

and the spatial configuration can be described for the landscape network. On an individual basis, defecation frequency, active-state frequency, satiation-state frequency and social grouping patterns can be extracted from the data.

4.3. Initialization

Portions of the landscape network were initially attributed as either within or outside the study area (Section 4.4). The study area comprised 58% of the total available coastline within the landscape network. Thus, estimates of otter demographic parameters within the study area were extrapolated to the entire landscape network.

4.3.1 Otters

The density of otters within the study area was previously estimated to range between 0.28 to 0.8 otters/km of coastline (40-115 otters; (Testa et al. 1994). Recent abundance estimates, conducted by Ott et.al. (*in Prep*), are within previous estimates and have a 95% CI equal to 55-78 otters. To begin each simulation, a value was randomly drawn from a uniform distribution bounded by Ott et.al. (*in Prep*) 95% CI, representing the number of otters within the study area. The total number of otters assigned the out-of-area coastline was calculated by multiplying the random density by 1.708, rounded to the nearest integer, and the sample area number subtracted from the total.

The state of each otter was also determined prior to the simulation. First, each otter was assigned a gender based on an average M:F ratio (69% male) derived from previous studies (Chapman and Feldhamer 1982, Lariviére and Walton 1998, Blundell et al. 2004, Ott et al. *in Prep*). The age of each otter was randomly assigned by drawing values from a list, without replacement, calculated by the equation:

$$N_i = T^* (0.3703 * Exp(-0.314 * i))$$
(1)

where N_i is the number of otters at age *i* given the proportion of total number of otters (*T*) at age *i*. The equation was derived from age frequency distributions found in Chapman and Feldhamer (1982).

The activity-state was assigned using a Bernoulli trial with the probability of being 'Active' calculated as the ratio of average hours Active:Inactive (1.43:11.69), which was equal to 0.122 (M. Ben-David unpublished data). The number of hours at the current activity-state was randomly assigned using a uniform distribution bounded by 0 and the upper 95% CI for each activity-state, rounded to the nearest integer. The upper 95% CI for 'Active' was 1.88 hours and 15.32 hours for 'Inactive' (Table 4.1; M. Ben-David unpublished data). Ormseth and Ben-David (2000) found captive otters to defecate, on average once every 4.865 hours (used raw-data). Thus, the number of hours since last defecating was randomly drawn from a uniform distribution bounded by 0 and 5.

The final initialization step for each otter was the placement onto the landscape network. This step was performed separately for the study area and out-of-area portions of the landscape network. Point-locations were filtered to include only habitat values > 0.464 (MEP). This optimal threshold value for the MEP was chosen using methods described in Chapter 3. Males were randomly assigned a point-location within the landscape network and potential overlap of locations was allowed. On the other hand, the placement of females onto the landscape network required the individual be first assigned a core home range size. Blundell et al. (2000) estimated mean 50% core female home range to be 4km (SD= 2) of coastline. Using these parameter values, the home range was randomly drawn from a truncated normal distribution (value > 0). Next, a random point-location was chosen and the home range size was adjusted using the radial-scale adjustment equation (Section 4.1.2) for the unique point-location. Next, the home range extent was placed onto the network by dividing the adjusted value in half and radiating out in all available paths for the remaining distance (e.g. 100m home range would be 50m in both directions). Previous studies have indicated that female 50% core home ranges do not

overlap (Blundell et al. 2000, Gorman et al. 2006). Thus, if any portion of the generated home range overlapped with an existing female otter, a new point-location was randomly chosen and the process repeated until all females were placed onto the landscape network.

4.3.2 Pelagic Fish Schools

The timing of the spawning migration of pelagic fish to the nearshore environment varies annually by species and magnitude (Haegele and Schweigert 1985, Brown et al. 1999, Robards et al. 1999, Blundell et al. 2002a, Brown 2002). Because pelagic fish schools have been shown to play an integral role in otter behavior (Blundell et al. 2002a, Ben-David et al. 2005), accounting for the timing and abundance of fish schools is important. In this model, we do not differentiate between fish school species. Rather the presence of a fish school was deemed most important.

Using georeferenced, aerially identified fish school data provided by Ben-David et al. (2005), the number of fish schools within 100m of the coastline, during a one-day period, were counted for years 1996-1999. The minimum (40) and maximum (98) number of schools became the bounds for a uniform distribution used to set the maximum number of schools that could be available during a simulation. The timing of fish schools entering the simulation is explained by eq. 8.

4.4. Input

The coastline portion of the landscape network was digitized from IKONOS® 1-meter panchromatic satellite imagery at a 1:1,500 scale, resulting in 245.3 km of coastline (Figure 4.2). An additional 80.3 km of 'virtual lines' were appended to the network (Figure 4.2) (Vuilleumier and Metzger 2006) to act as travel corridors connecting individual islands, or the same island having a large bay, to each other. The virtual lines were constructed through a multiple step process. First, Thiessen polygons were created using the 10m point-locations (see Chapter 3).

The polygons were then converted into a line feature class. For approximately every 5 km of coastline, the line connecting two islands or a bay was retained and the excess removed. The remaining virtual lines were slightly modified to create a straight-line having only two vertices connecting the coastline(s). The Network Analyst extension within ArcGIS 9.3.1 (ESRI, Redlands, CA) was used to identify network nodes and populate the adjacency table describing the connectivity of network edges.

4.5. Submodels

For each submodel, please review Table 4.1 for parameter values used for each statistical distribution.

4.5.1 Defecation

The probability of an otter defecating during a given time step is driven by three factors, hours since previous defecation event, habitat quality (MEP), and satiation-state. Using the equation:

$$P(de) = (cdf(hr)^{h}) * s$$
⁽²⁾

where the probability of a defecation event (*de*) was equal to the cumulative probability of a normal function (*cdf*) given the hours since the previous defecation (*hr*) raised to the h^{th} (eq. 3) power and multiplied by the satiation-state (*s*). The *cdf* was parameterized using data obtained from Ormseth and Ben-David (2000) and the satiation-state was equal to 2 if the otter had fed on a fish school and 1 otherwise. The h^{th} power is equal to:

$$h = -ln(MEP) * 1.5 \tag{3}$$

For otters having fed on a fish school (s = 2), the probability of a defecation event doubles. The value of P(de) was used as the probability of successfully experiencing a defecation event using a Bernoulli trial. For instances when the satiation-state (s) increased P(de) to become > 1, the value was set equal to 1.

4.5.2 Active-to-Inactive

The probability of an otter transitioning from an active state to an inactive state is calculated by obtaining the cumulative probability of a normal function given the hours of being in the active-state (cdf(hr)) and the satiation-state (s):

$$P(ai) = cdf(hr)^{1/s}$$
(4)

The *cdf* was parameterized using the unpublished telemetry data collected by M. Ben-David. It was assumed that an otter having fed on higher quality prey would be more satiated and require less foraging effort. Thus, the satiation-state was equal to 2 if the otter had fed on a fish school and 1 otherwise. The probability of successfully transitioning to the inactive-state was tested using a Bernoulli trial. The satiation-state will be reset to indicate the otter has not fed on a fish school during the following time step if the otter chooses to remain active.

4.5.3 Inactive-to-Active

The probability of an otter transitioning from an inactive state to an active state is calculated by obtaining the cumulative probability of a normal function given the hours of being in the inactive-state (cdf(hr)) and the satiation-state (s):

$$P(ia) = cdf(hr)^{1/s}$$
(5)

The *cdf* was parameterized using the unpublished telemetry data collected by M. Ben-David. It was assumed that an otter having fed on higher quality prey would be more satiated and be more apt to remain inactive. Thus, the satiation-state was equal to 1 if the otter had fed on a fish school and 2 otherwise. The probability of successfully transitioning to the active-state was tested using a Bernoulli trial. The satiation-state remains constant for the entirety of the otter's resting period and will be reset to indicate the otter has not fed on a fish school once transitioning to the active-state occurs.

4.5.4 Male Movement - Scent Detection

The movement of males within the landscape network is influenced by the detection of scent-markings. The probability of an otter detecting a scent-mark is driven by the distance between the otter and scent-mark and the age (hours) of the scent-mark. It was assumed that a male otter could detect another otter's scent-mark from a distance up to 1km. This assumption is represented by the equation:

$$P(scent) = Exp(-0.003 * m)^D$$
(6)

where the probability of detecting a scent-mark (P(scent)) is negatively related to the distance between the scent-mark and the otter (m), in meters, and the age (D; eq. 7). Ott et al. (*in Prep*) and Guertin et al. (2010) have indicated viable otter fecal samples must not be older than 24 hours because of weathering and desiccation. Therefore, to model the effect of desiccation reducing the amount of 'scent' available for detection, the equation:

$$D = Exp(0.1 * hr) \tag{7}$$

estimates fecal desiccation (*D*) as positively related to the number of hours (*hr*) the scent-mark has been exposed to the environment. In the simulations, fecal deposits older than 12 hours were removed as possible candidates for detection. The value of eq. 6 was used as the probability of successfully detecting the scent-mark in a Bernoulli trial. It is important to note that male otters beginning their foraging excursion will seek (olfaction) scent-markings within 1km of their location in all possible directions. However, for subsequent olfaction events (at network nodes) the otter can only sense in the forward direction, not backward. Additionally, only the scent-mark having the shortest distance to the otter's current location was tested for detection. Finally, for the current time step, all scent-marks occurring along the path traveled by the otter were removed from the list of available fecal deposits for the individual otter. If an otter did not detect a scent-mark, a random direction was chosen from a uniform distribution of all possible paths, excluding the previously traveled path (i.e. cannot move backwards, only forward).

4.5.5 Female Movement - Core Home Range

For female otters, scent-detection is not included as part of their behavior. Instead, the movement of female otters is random when occurring within the 50% core home range. The direction is randomly chosen from a uniform distribution of all possible paths, excluding the previously traveled path. However, if a movement direction and distance results in the female reaching a node or point-location outside the 50% core area, the following movement direction will be toward the central point-location of the home range.

4.5.6 Fish School Timing

As previously described in Section 4.3.2, the timing of pelagic fish school spawning migrations vary. To account for this timing, a meta-analysis was conducted using two separate studies. The first study was conducted in Prince William Sound over an eight year period

beginning in 1923 (Rounsefell and Dahlgren 1931). The study quantified the number of 'barrels of herring' captured by commercial fisherman. The barrels were summed for each date-range across all years and the maximum number of barrels recorded. Next, the percent of the maximum number of barrels was calculated for each date-range. The mid-point of the daterange was used as the measurement date. Concurrently, the number of herring schools was interpreted from fig.1 (Brown et al. 1999, Blundell et al. 2002a) using the 1st and 15th of each month as the day of measurement. Performing the same calculation, the percent of the maximum was calculated for each date. The data were combined by calculating the average percent of the maximum for each Julian date. These data were then fit with a 5th order polynomial regression:

$$Fs = J^{5} * 1.12^{-9} + J^{4} * -9.88^{-7} + J^{3} * 0.00034 + J^{2} * -0.0564 + J * 4.585 -$$
145.489 (8)

estimating the percent of the maximum number of fish schools (Fs) for a given day (J). Thus, for the given Julian day within the simulation, the number of pelagic fish schools available is calculated as:

$$F(J) = Fmax * Fs \tag{9}$$

where *Fmax* is the maximum number of randomly drawn fish schools (Section 4.3.2).

METHODS

Simulations

Each simulation was run using an hourly time step, beginning at 12:00am May 15, 2006 and running to 12:00am August 16th, 2006. A total of nine separate simulation scenarios were conducted (Table 4.2). The amount of run-time for each simulation ranged between 12 and 20 hours to complete. Thus, each simulation scenario was limited to ten replications. Parameter values were held constant for the entire simulation given the conditions of the scenario being tested (Table 4.2).

Sensitivity Analysis

To estimate the relative importance of model parameters on simulated otter behavior, a sensitivity analysis was conducted. The analysis was completed for three separate parameters, requiring 6 simulation scenarios having different parameterization (Table 4.2). The three parameters include foraging movement distance, hours between defecation events, and hours in the active-state. For each parameter, the mean was adjusted positively or negatively:

$$M = \mu * s \tag{10}$$

where the adjusted mean (*M*) is equal to the product of the baseline mean (μ) and the adjuster (s). The adjuster was equal to 0.9 for the negative and 1.1 for the positive adjustment. The following equation was used to adjust the standard deviation:

$$SD = M * CV \tag{11}$$

where the adjusted standard deviation (*SD*) is equal to the adjusted mean (M) multiplied by the coefficient of variation (CV) of the baseline values.

Schooling Fish Scenarios

It is known that otters can successfully forage on demersal, as well as pelagic fish, in the nearshore environment (Larsen 1984, Ben-David et al. 1998). Thus, determining the effect of schooling fish on otter behavior, either through fecal deposition rates or social group formation, is a pressing question. To approach this question, three scenarios were compared to test how the presence of schooling fish may influence otter behavior. The baseline model (R01) uses an informed fish school model in which only point-locations having a depth \geq -3.04 meters were available for spawning habitat. The second scenario (R02) uses random placement of the fish schools onto the landscape network (all point-locations available), and the third scenario (R03) removed schooling fish entirely from the simulation. To test the similarity between each of these scenarios (including R04-R09), a correspondence analysis was completed using SAS 9.2 (SAS Institute, Inc., Cary, NC). For each point-location and simulation, the mean fecal counts were compared for similarity and the coordinates for the first two dimensions captured.

Data Analysis

Sensitivity Analysis

The data from each replicated simulation scenario were compiled into a single database. Data were stored for each otter and fish school for each simulated hour. To account for variability, data were initially summarized for each replication and then for the entire simulation scenario. Tornado diagrams were created to demonstrate the sensitivity of the response variables to changes in parameter values. The diagrams display the range of mean response values and their associated 95% confidence intervals (CI). The vertical axis represents the mean response value of R01 (baseline). The following sections describe the process used to summarize the five response variables for use within the tornado diagram.

1 – Daily Fecal Counts

The number of fecal deposits was summed for each model replication ('tblPoopTracker'). Then the mean (SD) feces calculated for the entire simulation and 95% CI (n = 10). The mean (SD) value was then divided by the total number of days to produce the mean number of feces per simulated day.

2 - Defecation Rate

The defecation rate of otters was calculated as the proportion of hours each individual experienced a defecation event during the simulation ('tblStateValues'). The mean (SD) proportion was then calculated, by gender, for the entire simulation and 95% CI (n = 10). To calculate the average number of defecation events per day, the mean proportion was multiplied by the total number of hours (2209) and then divided by the total number of days (92).

3 - Hours of activity

The number of hours in the active-state was summed for each otter and replication. Next, the mean number of active-state hours for each replication, by gender, was calculated. Finally, the mean (SD) number of hours for each simulation, by gender, and 95% CI (n = 10) was calculated.

4 - Fish school forage success

Obtaining the number of occurrences in which an otter successfully located a fish school required iterating through each record of 'tblStateValues' and extracting only records in which the otter was active and the first record after transitioning from active-state to inactive-state. This data subset was then used to calculate the mean number of fish school encounter events by gender and replication. The mean number of fish school encounters, by gender, was then divided by the mean hours of activity to produce a mean (SD) proportion of active-state fish school forage success with 95% CI (n = 10) for the simulation. As an additional measurement of

the effect of fish schools, the proportion of defecation events having pelagic fish was calculated as:

$$% pelagic feces = \frac{(active-state school location rate)*(hours active)}{(defectation rate)*(total hours)}$$
(12)

where the proportion of active-state hours in which a fish school was successfully located is divided by the proportion of total hours (2209) having a defecation event.

5 - Social group creation

The analysis of social group creation was performed by two separate types of analyses. The first analysis required the creation of a behavioral adjacency table. Using an iterative process within a replicated simulation, a data row was written for each otter within 50m of the current otter for each time step. Next, a list of unique otter-to-otter interactions was created for each replicated simulation. Using the unique interaction list, the number of otters that interacted (were part of a group) with the current otter was counted. Finally, the average number of otter interactions, by gender, was calculated for each replication, then the mean (SD) was calculated for the entire simulation with 95% CI (n = 10).

The second otter group analysis required iterating through each record of the adjacency table to determine group association for each time step and replicated simulation (i.e. which unique otters where found within 50m of each other). Next, the total number of otters, the total number of groups and the average number of otters within a group were calculated for each time step of each replication. These data were then averaged for each day (24 hour period) and replication. To finish, the mean (SD) per day number of otters, number of groups and number of otters per group and 95% CI (n = 92) were calculated for each simulation.

6 - Coastline Use

The total amount of coastline used by each individual otter was calculated for each replicated simulation by obtaining the difference between the minimum and maximum route measures for each occupied network edge. The differences were then summed for each individual and the mean kilometers of use, for each gender, was calculated for each replication. To finish, the mean (SD) amount of total habitat used was calculated for each gender and simulation.

Comparison to Observed

Simulation R01 (baseline), R02 (random schools) and R03 (no schools) was compared to the field collected data to validate the IBM for accuracy. Data were compared to determine similarity at the landscape and site specific scales. The observed data were collected at 100 of the 326 available latrines sites within the study area. A total of nine sampling events occurred between May 27 and August 15, 2006 and five sampling events occurred between June 10 and August 7, 2007. The total number of feces collected was summed for all sites, excluding the number collected on the first sampling event. This exclusion was made because the number of days between the collection of the feces and the actual deposition could not be determined. The number of feces per day was then calculated by dividing the number of feces (8,475) by the number of days (2006 = 80, 2007 = 58). This defecation rate was then compared with results from the simulations.

One issue with comparing simulated to observed fecal counts is that a single latrine observed in the field may encompass many point-locations within the landscape network. To account for the discrepancy in size (i.e. area), point-locations were manually assigned to each latrine site. This process resulted in 861 point-locations being assigned to the 100 latrine sites. The mean number of fecal deposits for each point-location was then summed for each matching latrine site. A correspondence analysis was run to test for similarity between the two years of

observed data and the three schooling fish scenarios (R01, R02 and R03) and the coordinates for the first two dimensions captured and plotted.

To assess the spatial heterogeneity, histograms were plotted for the observed and mean simulated fecal counts. Point-locations having < 50 feces were withheld from the analysis to reduce noise and small-value bias. Additionally, a one-tailed paired t-test and Pearson's r correlation coefficients were performed to compare the observed and mean simulated fecal counts for the same point-locations (n = 100) to ascertain spatial realism.

RESULTS

Simulation scenarios were successfully completed for nine separate parameterizations, each having 10 replicates. Each simulation replicate required approximately 15 hours to complete. The data from each simulation scenario were captured within an Access database with a total of 34,118,297 total records held in storage using nine databases.

Model Sensitivity

1 – Daily Fecal Counts

The mean feces/day was somewhat sensitive to variation in hours between defecation events (R06 & R07) and hours in the active-state (R08 & R09), whereas movement distance (R04 & R05) was not an influential parameter (Figure 4.3). For example, the difference between R09 and R01 is 36 feces/day (Table 4.3). Thus, for the entire period of the model (92 days), an additional 3,312 feces would be deposited onto the coastline, a 12% increase. The mean feces/day for R01 was equal to 294. Assuming that each feces contains 5.15 g of N (Ben-David et al. 2005), an average of 1,514.1 g of N are deposited daily onto the study area coastline.

2 - Defecation Rate

The mean defecation rate was insensitive to the movement distance (R04 & R05) and hours in the active-state (R08 & R09) parameters and only slightly sensitive to changes in the hours between defecation (R06 & R07; Table 4.4; Figure 4.4). The number of defecation events/day was similar between genders and each simulation, averaging 4.25 events/day (Table 4.5). The estimated deposition rates were less than the 7.7 defecations/day reported from captive studies (Ormseth and Ben-David 2000, Ben-David et al. 2005).

3 - Hours of activity

The mean hours of active-state were insensitive to changes in the parameters (Figure 4.5). The mean hours of female active-state were 798 for scenarios using the informed fish model (Table 4.6). Male hours of active-state were not significantly less than females, averaging 773 for the scenarios.

4 - Fish school forage success

Similar to the hours of active-state, the mean percent of active-state hours for which an otter located a fish school was insensitive to changes in the parameters (Figure 4.6), and there was not a significant difference between scenarios for each gender (Table 4.7). The proportion of feces containing pelagic fish was greatest for simulations R01 and R09 and lowest for R06 (Table 4.8). Similar to the frequency of fish school encounters, male otters consistently had higher proportions of feces containing pelagic fish than females. The mean proportion of feces containing pelagic fish for R01 (baseline) was 36.6%, nearly identical to the 39.9% of field collected otter feces that contained pelagic fish (Ben-David et al. 2005).

5 - Social group creation

The mean number of otter interactions, for males and females, was not significantly different between simulation scenarios (Figure 4.7). Regardless of the scenario, males, on

average, interacted with 57% more individuals than females (Table 4.9). Using scenario R01 (baseline), the mean (SD) percent of time each individual spent in a social group, as well as the percent of that time spent with each gender was calculated (Table 4.10). Males spent significantly more time (49%) in groups than females (40%). Of the 40% time spent in social groups, females spent 80% of their time interacting with males, while males in social groups interacted with other males 74% of the time (Table 4.10). These interaction rates are similar to other findings in which females occurred in mixed-gender groups 77.8% and males 37.5% of the time (Blundell et al. 2002a).

The mean daily proportion of the total otter population participating in group behavior was insensitive to changes in the parameters (Figure 4.8), averaging 41.8% of the total population (Table 4.11). A significantly greater number of individual groups were observed when otters were allowed to spend more time in the active-state (R09, Figure 4.9), indicating some model sensitivity to this parameter (Table 4.11). The maximum group size ranged between 11 and 14 otters for the simulation scenarios (Table 4.11). The mean group size for R01 did increase as fish schools became more abundant (Figure 4.10), following the similar pattern found by Blundell et al. (2002a). The mean number of otters/group was insensitive to changes in the parameters (Figure 4.11).

6 - Coastline Use

The mean kilometers of total coastline used by otters did not significantly vary between genders for any of the simulation scenarios (Table 4.12). Male otters used significantly more habitat than did female otters. This is an expected result because the female movement rules (Submodels 4.5.5) preclude individuals from forging in an unrestrained manner. However, male otters did experience some model sensitivity to changes in the movement distance parameter (Figure 4.12). This result is not surprising, for if an individual can move farther distances, the more likely they are to have used previously unused habitat, and vice-verse.

Schooling Fish Scenarios

1 – Daily Fecal Counts

The mean feces/day was statistically similar between scenarios R01 and R02 while scenario R03 (no schools) was statistically different (Table 4.3). Mean feces/day was most sensitive to the absence of fish schools, with otters defecating at a significantly higher rate than when fish schools are present (Figure 4.3). At least initially, the rate of N deposition would increase to 1,987.9 g of N (31.3% increase) if fish schools were not available as prey items compared to the baseline amount of 1,514.1 g of N.

2 - Defecation Rate

The mean defecation rate, for both males and females, was greatly influenced by the absence of fish schools (Figure 4.4). For simulation scenario R01 (baseline), female defecation rate was higher than males (Table 4.4). In contrast, male defecation rates for models R02 (random schools) and R03 (no schools) were higher than females. The number of defecation events/day was similar between genders for scenarios R01 and R02 (Table 4.5). However, for R03 each otter experienced an additional defecation event/day, on average.

3 - Hours of activity

Otters experienced a significantly higher number of hours in active-state when fish schools were excluded from the model (R03). Conversely, random fish schools (R02) significantly reduced the number of active-state hours for females, but not significantly for males when compared to R01 (Table 4.6). Interestingly, R02 was the only scenario in which male activity hours exceeded those of females. Thus indicating the defense of core home range habitat by female otters restricts their ability to locate pelagic fish schools as efficiently as male otters. Additionally, the amount of variation in active-state hours experienced by R03 otters was

remarkably minimal and consistent between genders (Table 4.6). This result further elucidates the observation that female behavior restricts their ability to locate fish schools.

4 - Fish school forage success

Both genders experienced a higher fish school encounter frequency when school placement was random (R02; Table 4.7). Additionally, scenario R02 had females locate fish schools more frequently than males, with the opposite occurring for R01. Also females encountered fish schools significantly more often with random school placement than the informed fish school scenario (Table 4.7), and feces containing pelagic fish were greater (Table 4.8).

5 - Social group creation

The presence of pelagic fish schools greatly affected the creation and composition of social otter groups within the simulation scenarios. Male and female otters encountered a significantly higher number of other individuals when fish schools were absent (R03, Table 4.9). This result can be attributed to male otters becoming increasingly nomadic in search of high quality prey. The process is controlled by male movement because females were required to defend their home range while males were free to roam the entire landscape network.

In the absence of schools (R03), the number of otters participating in group behavior decreased by 25% when compared to R01 (Table 4.11). Concurrently, the mean number of groups declined with the absence of fish schools (Figure 4.9). Scenarios in which fish schools were either random or absent (R02, R03), there were significantly fewer otters/group than if the informed fish school model was applied (Figure 4.11). This pattern follows the previous tests for the no school scenario (R03), but the result for R02 (random school) was unexpected because the proportion of the population and the number of groups were similar to the informed fish school model (R01). This phenomenon may be explained by the observation that otters in R02

were less often in the active-state (Table 4.6) and found pelagic fish more frequently (Table 4.8). Therefore the individuals probably experienced shorter foraging excursions which limited the formation of larger social groups because fish schools were more available.

6 - Coastline Use

Male otters used more of the coastline habitat when schooling fish were absent (R03) then when fish schools were present (R01 & R02). The increase in coastline use for R03 (no schools) can be explained by males being more active because high quality prey was not available (Table 4.6), which encouraged nomadic behavior as a behavioral response. As previously stated, female use of the coastline was constant throughout the simulation scenarios (Table 4.12).

Comparison to Observed

The observed rate of fecal deposition was 345.4 feces/day during 2006 and 365.6 feces/day in 2007. All simulations averaged less than the 2006 observed rate for point-locations within the study area except for R03 (Figure 4.13). The rates were significantly less for R01 and R02, resulting in a potential loss of 24,164 g of N reaching the nearshore environment when compared to the 2006 deposition rate. Additionally, during 2007 the fecal counts were classified as occurring either on rock (no chance for assimilation by plants) or within a vegetated area. Only 71% of the total fecal deposits occurred within the vegetated area. Thus, the estimated loss of nitrogen to the nearshore environment may be even greater.

The spatial configuration of fecal deposits for the simulation scenarios were compared using Correspondence Analysis. The test compared total fecal counts for each point-location for similarity between simulation scenarios (Figure 4.14). The results demonstrate a high correspondence between simulations using the informed fish model, indicating spatial similarity in fecal deposition between scenarios (R01 and R04-R09). Conversely, R02 and R03 were

dissimilar from the other simulations. For the x-axis, as values increase from negative to positive, the average number of otters within each social group increases (Model Sensitivity 5). As values increase along the y-axis, the defecation rate decreases and fish school locations increase (see Section Model Sensitivity 2 and 4).

The Maxent model was used to estimate the relative habitat quality (MEP) for each pointlocation. Using a threshold value of 0.464, 30% of the available point-locations were classified as a 'Latrine' (Table 4.13). Concurrently, using the manually chosen point-locations for the 100 latrine sites (861 point-locations) for reference, a total of 2,807 (extrapolated to the 326 total latrines) out of a possible 14,370 point-locations were estimated to be used as part of a latrine within the study area, equaling 19.5% of the study area coastline. The percent of classified point-locations, 30%, is similar to the amount of observed coastline used by otters within the study area (19.5%). This result provides confidence that the landscape network did not greatly over- or under-estimate the habitat available to otters.

Otters are assumed to only use latrine sites for defecation and urination (Bowyer et al. 1995, Ben-David et al. 1998). For scenario R01 (baseline), 97% of the total feces occurred on point-locations classified as a latrine (Table 4.13). Of this 97%, 73% of the feces occurred at 2% of the point-locations. This result may indicate certain locations are intensely used, hypothetically by social otters, while the remaining locations less intensely by solitary individuals or smaller, transient groups (Ben-David et al. 2005). Pearson's r correlation coefficients were calculated for R01-R03 and the habitat quality (MEP). For point-locations having > 0 feces, the correlation between habitat and fecal deposition was relatively low, having 0.212, 0.219 and 0.227 correlation coefficients for R01-R03, respectively. Each correlation was significant, but the low values indicate that habitat quality is not the determining factor driving fecal deposition.

The spatial pattern of fecal deposition observed for simulation scenarios R01-R03 can be found in Figures 4.15, 4.16 and 4.17, respectively. Spatial variability in fecal deposition was also observed during the 2006 and 2007 sample periods (Figures 4.18 and 4.19). The relative

similarity between the observed and simulated fecal deposition provides evidence that the emergent patterns from the simulations visually mimic the observed patterns. However, the spatial realism of the model did not match the observed data.

The total amount of observed feces for each latrine, by sample year, was compared to the summed fecal deposits of the associated point-locations using a paired t-test. The mean difference for all possible combinations of observation year and simulation scenarios R01-R03 was found to be significantly different (p < 0.0001). These results indicate the simulated otters were defecating in areas different than the observed latrines. To visually display the differences in deposition, Figures 4.18 and 4.19 represent the observed distribution of feces while Figures 4.20, 4.21 and 4.22 are the summed feces for the same point-locations as observed latrines. The most noticeable difference is the higher quantity of observed defecation compared to the three simulation scenarios. The three simulation scenarios appear to be quite similar to each other. A Correspondence Analysis was conducted to test the similarity between the five groups of data (Figure 4.23). The three sets of simulation data appear to correspond well to each other, indicating consistent otter behavior at these specific point-locations between scenarios. However, both sets of observed data appear to be disparate from all other tested data, demonstrating a high degree of temporal variability in the observed data. One can infer from the previously described Correspondence Analysis (Figure 4.14) that during 2006 more fish schools may have been available than during 2007 and that the number of individuals per social group were relatively similar.

DISCUSSION

The individual-based modeling approach is grounded in the belief that adaptive behaviors of individuals emerge as patterns at the system level (Grimm and Railsback 2005). To facilitate the expansion of IBMs in ecological theory, Uchmański and Grimm (1996) proposed four criteria for a model to be considered an IBM: 1) the degree to which an individual's life cycle is

reflected; 2) the dynamics of individual resource use are explicitly represented; 3) real or integer numbers are used to represent population size; and 4) the extent to which variability between same age individuals is considered. We believe that the IBM described within this text meet these criteria: 1) although individual mortality is not explicitly addressed, each individual's daily life cycle is accounted for on an hourly basis. An individual uses stochastic rules, based on previous experience and states, to determine whether to forage or rest; 2) each individual may have the opportunity to locate and prey upon pelagic fish schools, and in turn improve fitness. Concurrently, pelagic fish schools are dynamically interacting with the physical environment instead of behaving in a static manner; 3) pelagic fish school densities are accounted for using real numbers and seasonal models. Otter density is estimated from a known distribution of the study area and; 4) each individual experiences both temporal and spatial variability throughout the modeling process. The variability may occur through spatial location (habitat quality), prey availability, interaction with other individuals, and unique hourly experiences influencing decisions that affect current and future state-values.

Sensitivity Analysis

The objective of a sensitivity analysis is to quantify the response of the IBM output to variation in model parameters (Grimm and Railsback 2005). When using the informed fish school model, the IBM was relatively insensitive to variation of the three adjusted parameters (Table 4.2). Of the six measured response variables (daily fecal counts, defecation rate, hours of activity, fish school forage success, social groups, and coastline use), five parameterization adjustments caused noticeable variation in a response variable. The mean number of feces/day increased under two different parameterization scenarios, simulation scenario R06 (decrease in hours between defecation events) and R09 (increase in active-state hours). For example, the increase in fecal deposition from R09 led to an additional 12%, or 3,312 feces (17,057 g N) reaching the nearshore environment (Table 4.3). This amount of potential N reaching the

nearshore environment is significant given the relatively meager atmospheric N deposition rate of 0.01-0.2 g N/m2/y (Ben-David et al. 2005). Ormseth and Ben-David (2000) did find active otters to have an increased passage rate of consumed prey. Thus, the model response parallels known otter behavior.

The number of social groups was sensitive to variation in the mean number of active-state hours (R09; Figure 4.9, Table 4.11). When compared to the baseline model (R01), an increase in activity induced a response of nearly three additional social groups/day. The consequence of such a response is unclear because of the relative insensitivity of other response variables to change in this parameter. But, an increase in the total number of groups may indicate greater success in locating pelagic fish schools through cooperative foraging and an in-kind increase in latrine visitation rates (Blundell et al. 2002a, Ben-David et al. 2005).

Two additional sensitive response variables were the proportion of time defecating and mean km coastline used. Defecation time was sensitive to changes in the mean number of hours between defecation events (Figure 4.4, Table 4.4). Even though the fecal deposition rate's response was greater than the other parameters, the change resulted in only a 0.3 feces/day/otter increase, or 27.6 total feces/otter, when the parameter value was decreased by 10% (Table 4.5). The second variable is mean coastline use, which was sensitive to increased movement distance for male otters (R05). Male otters were not restricted in their ability to traverse the coastal landscape. Increasing the distance that can be covered during a foraging excursion is bound to increase the likelihood of crossing previously unused habitat, thereby increasing total amount of coastline used.

Fish School Scenarios

Blundell et al. (2002a) and Ben-David et al. (1998, 2005) describe the role of cooperative forging on pelagic fish schools and the subsequent, gender specific behavioral response. Results from the IBM overwhelmingly indicate otter behavior is driven by prey availability
(Figures 4.3 – 4.12). In general, the presence of fish schools, regardless if the informed or random fish model was used, was the dominant factor influencing otter behavior. The response variables were always significantly different for simulation scenario R03 (no schools), and the behavioral response was always to increase time spent foraging. For example, otters in R03 were in the active-state, on average, 415 hours more than otters in R01 (Table 4.6). Concurrently, male otters used an additional 41.5 km of coastline in scenario R03 when compared to males in R01 (Table 4.12). Therefore, in conditions in which fish schools are lacking, river otters need to spend more time foraging for less valuable prey items, thereby potentially increasing both energy expenditure and predation risk.

The number of feces reaching the nearshore environment for R03 increased by 92 feces/day when compared to R01 (Table 4.3). The higher rate of fecal deposition may decrease if the abundance of demersal fish decreased, thus decreasing otter abundance through limited resource availability (Kruuk et al. 1991). Otter behavior was more subtly affected when fish schools were randomly placed (R02) than when removed entirely.

The defecation rate decreased while forage success simultaneously increased when fish school locations were not restricted to specific spawning areas (R02). The variation in response was statistically significant for female otters when compared to R01. This result has several implications. First, by increasing the spatial distribution of fish schools, individual otters were more likely to experience forage success. Specifically, females experienced significantly more success in locating fish schools than when these prey are patchily distributed. Having an increase in the availability of higher quality prey because they were more uniformly dispersed decreased the risk of predation or injury, realized through reduced hours in the active-state and no difference in the amount of habitat use (Tables 4.6, 4.7, & 4.12). Interestingly, the reduction in defecation rate did not reduce the amount of feces reaching the nearshore environment (Table 4.3). This behavioral pattern may be explained by the fact that even though individuals successfully feeding on fish schools are going to recuperate (rest) for longer periods, they are

also more likely to defecate when consuming the higher quality food. Thus, no net loss or gain in fecal quantity.

A second, but highly related response to a more homogenous distribution of fish schools is the decrease in the number of otters per social group (Figure 4.11). With increased forage success and less activity, individuals appear to be less likely to form larger groups. This pattern occurs because fish schools were easier to randomly locate during forage excursions than when the schools are patchily distributed.

Comparison to Observed

The true test of an IBM is how well the system level patterns are reproduced (Grimm and Railsback 2005). A series of comparisons were made to test the IBM's ability to reproduce observed patterns and behavior, and the similarities between the observed and reproduced patterns are encouraging. The results of simulation scenario R01 (baseline) fell within the range of published (or recently measured) values for several characteristics including home range sizes (habitat use), social group behavior, and forage success. The simulation results were also compared to the observed frequency and pattern of fecal deposition from our recent field study.

The mean (SD) km of coastline use from R01, for both genders, are greater than the reported coastline 95% Adaptive Kernel estimates by Blundell et al. (2000) (Table 4.12). Estimated habitat use (100% home range) is 53% greater than Kernel estimates of Blundell et al. (2000) for females and 89% greater for males. However, 95% confidence intervals do overlap with observed values for both genders. Secondly, estimates from the simulation scenarios are measuring total use of the coastline, not 95% of each individual's location points, which potentially could include outliers, as shown by the 95% confidence intervals which are greater than ½ of the mean value (Table 4.12). Although the measurement of home range within linear systems may be less sensitive to autocorrelation (Blundell et al. 2001), great care must be

taken if estimates of home range are to be calculated for the simulated otter population because the vastness of having hourly locations may swamp a statistical model.

Emergent social behaviors obtained from the baseline simulation (R01) appear to match previously measured patterns. Mean group size increased as pelagic fish abundance increased (Figure 4.10), corresponding to a similar pattern observed by Blundell et al. (2002a). The mean group size of 2.5 otters/group, as well as the maximum group size of 14, is also similar to previous observations (Blundell et al. 2002a, Blundell et al. 2004, Ben-David et al. 2005).

Social group formation from R01 corresponds well to observed data in several ways. First, Blundell et al. (2002a) found males to be in social groups for approximately 55% of their telemetry locations and females 26%. Simulation results estimated males to be in a group 49%, and females 40% of the time. Higher incidence of female group behavior in the model, relative to field observations (40% vs. 26%), may have several explanations. One explanation may be the difference between imperfect detection and measurement in the field while perfect detection was obtained within the simulation models (i.e. each simulated hour of behavior was recorded with perfect detection). In addition, the number of telemetered otters within the study area (F: n = 9, M: n = 32), although significant, is measurably fewer than the number of otters within the simulations (mean = 107). Additionally, all otters in R01 were part of a group for at least one time step. In fact, the minimum number of time steps for any otter was 86 (4% of total time). Thus providing further evidence that perfect detection within the simulation model may be increasing the simulation values when compared to observed data.

Social group composition was also similar to that observed in prior studies. Blundell et al. (2002a) found males occurred in mixed-gender groups 37.5% of the time while 77.8% of the time females occurred in mixed-gender groups. The IBM estimated, with remarkable similarity, males to occur in mixed-gender groups 26% while females 80% of the time. This pattern is supported by the fact that males are more nomadic (Blundell et al. 2002b), have larger home

ranges (Blundell et al. 2000) and occur in greater densities than females (Chapman and Feldhamer 1982, Lariviére and Walton 1998, Blundell et al. 2004, Ott et al. *in Prep*).

The frequency of foraging excursions in the location fish schools was higher for males than females (Table 4.7). This result is similar to Blundell et al. (2002a) which found 43% of males and 32% of females switched their diet to pelagic fish. Along these same lines, previous studies measured the presence of schooling fishes in 39.9% of otter feces (Ben-David et al. 2005). Results for model R01 estimated the mean proportion of pelagic-feces to be 38.1% for males and 35% for females (Table 4.8). Once again, demonstrating a high correspondence to observed patterns. However, one significant divergence from observed data is the rate of defecation. Captive otter studies have estimated otters defecate 7.7 times/day (Ben-David et al. 2000, Ormseth and Ben-David 2000, Ben-David et al. 2005) whereas R01 defecation rate was 4.2 times/day. The most plausible explanation for this difference is that the studies were conducted on otters in captivity, were fed to satiation and were more than likely not experiencing the caloric demands of inhabiting the coastal environment.

Spatial Patterns

The field collected data were compiled to provide an estimated rate of fecal deposition reaching the nearshore environment. The observed rate of fecal deposition was 345.4 feces/day during 2006 and 365.6 feces/day in 2007. The simulated rate of fecal counts for R01 (baseline) was 294 feces/day, significantly less than either of the observed rates. The only simulation to include the 2006 fecal rate within the 95% CI was R09, a model having an increased amount of time in the active-state (Figure 4.13). Given that the active-state parameter was derived from a dataset consisting of only 8 otters, as well as the active-state parameter having relatively little effect on the other response variables (except for number of groups), these results may indicate model R09 is a better fit to observed data than R01.

The spatial pattern of fecal deposition by the simulations, regardless of the schooling fish scenario, is heterogeneous across the coastal landscape (Figures 4.15, 4.16 and 4.17), which mimics the observed variation recorded during the 2006 and 2007 sample periods (Figures 4.18 and 4.19). The maps display the range of high-use and lower-use areas. This similarity provides evidence that the IBM is replicating adaptive traits employed by otters as well as using a representative landscape to influence their behavior. However, as previously stated, the explicit spatial deposition pattern from model results did not match observed data.

Ben-David et al. (2005) and Blundell et al. (2002a) hypothesize that social otters may be found less frequently near latrines than nonsocial otters. Our model may support this idea. As previously described, otter socialness is highly influenced by prey availability. The location of fish schools may be driving defecation to occur on areas not as high in habitat quality simply because the resource was nearby. This is evidenced by the low correlation coefficients between fecal counts and the habitat quality (MEP). Another causal factor may be the model-induced 'memory' of otters (Model Section 4.2.5). Having perfect memory of the point-location having the highest value within 1 km of the current location may be somewhat unrealistic and may require some form of stochasticity be added to the point-location selection process.

The comparison between observed site-specific and simulated fecal counts using both the paired t-test and Correspondence Analysis show the lack of spatial 'realism' of the IBM. However, the lack of correspondence between the two years of observed data provides evidence of the highly variable nature of otter behavior (Figure 4.23). Since otter behavior is highly influenced by pelagic fish, factors influencing pelagic fish may have a cascading effect. The Correspondence Analysis axes indicate that in 2006 the otters may have encountered a higher frequency of pelagic fish schools than in 2007. Sea-surface temperatures do influence the seasonal timing of pelagic fish schools (Brown et al. 1999). The mean sea-surface temperature in Prince William Sound was significantly higher in June 2006 than in June 2007 (Figure 4.24; http://www.ndbc.noaa.gov/). Brown et al. (1999) indicate that as water temperature

increases to approximately 10 C, the number of schooling pelagic fish near the surface also increase (interpreted from figure 1). The earlier increase in sea temperature may have increased the availability of schooling fish for otter consumption during 2006.

One potential explanation for the difference in observed and simulated fecal counts at known latrines can be seen in Figure 4.25. In this example there are two observed latrines that had high amounts of fecal deposition. However, for HB001 and HB004, the R01 simulation only had 13 and 17 feces, respectively. Instead R01 simulated otter defecation to occur at a location very nearby, of similar habitat quality (from a statistical standpoint) and at a similar defecation rate to that observed in the field. In this case, the preferred location by the otters happened to occur at a latrine that was not sampled for feces during the study. Thus, it is important to note that even though the spatial realism of the IBM is not precise, the frequency of fecal deposition is similar between observed and simulated values (Figure 4.26), indicating the model is simulating otter defecation behavior with relative accuracy.

Potential Improvements

The complexity of otter behavior represented by this IBM has effectively reproduced observed patterns at both the population and landscape scales. However, the complexity also created long model run-times (12-20 hours), making it difficult to assess the accuracy of parameter estimates. Essentially, the previously described model analysis is merely a review of parameter estimate accuracy. Of the parameters tested, it appears that the initial active-state value may have been underestimated because R09 proved to be the best fit to the observed fecal deposition rate.

Several of the choices during model development may have influenced the results. One such choice involves olfaction influencing male foraging behavior. Male otters were able to sense the presence of fecal deposits and make a prediction that a fish school would be nearby. The assumption that all feces are the same may need to be revisited because feces containing

no pelagic fish may indicate resource depletion instead of resource abundance (Kruuk et al. 1991). Similarly, female movement rules were simplified to be random as long as they occurred within their 50% core home range; otherwise they were 'drawn' back toward the center of their territory. The behavioral consistency between genders would have increased if females, instead of making random movements were to have used olfactory cues. However, the effect of this choice on model results appears to be negligible.

The effect of pelagic fish on otter behavior has been fully described, but pelagic fish are not the only prey source. The density of demersal fish can also affect otter behavior (Ben-David et al. 2005). The IBM did not account for the density and distribution of demersal fish explicitly because we assumed that benthic resources are uniformly distributed, thus unlikely to affect the variability in nutrient deposition. Instead, the marine abiotic conditions were included as variables within the Maxent model predicting otter latrine use (habitat quality). Dean et al. (2000) found differences in the distribution and abundance of benthic fish given characteristics of the marine environment. It may be an enlightening exercise to develop a model using only terrestrial variables for the otter latrine selection model and couple it with a demersal fish habitat model, thus providing a method to assess if the impact of varying demersal fish availability will have similar effects on otter behavior as pelagic fish. Additionally, this approach may allow for fish density to become a parameter, a necessity if the IBM is to be used to forecast nutrient transport given potential climatic changes because pelagic fish may become less abundant and predation pressure will shift to demersal fish. Finally, it is imperative to test additional parameters for their influence on model output. Ideally, an additional 16 scenarios would be tested and model sensitivity calculated.

Conclusion

The IBM provides a first step in modeling individual otter behavior and their role in expanding the resource shed for the nearshore environment (Ben-David et al. 1998, Power and

Rainey 2000, Ben-David et al. 2005). By reproducing coastal river otter behavior from prior studies in an IBM, we were able to reproduce broad scale patterns in quantity and variability in nutrient transport, facilitated by the behavioral response of otters to pelagic fish schools and the subsequent creation of social groups. The inclusion of vision, olfaction and memory as viable forms of otter sensing and their quantifiable response to these stimuli provide a strong behavioral foundation for the IBM. Although the baseline parameterization (R01) may not be perfect, results provide strong evidence that we can represent patterns of latrine use and nutrient deposition and may be able to model potential consequences of changes to schooling fish populations as a result of climate and human factors.

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Table 4.1: Model parameters, the associated values, and the distribution type used for

initialization or stochastic processes.

Parameter	Value	Distribution	Description
Model Initialization			
Density	55 – 78	Uniform	Minimum - Maximum 95% CI from density estimates (Ott et al. <i>in Prep</i>).
Fish Schools	40 – 98	Uniform	Minimum - Maximum number of fish schools (Ben-David et al. 2005).
Gender Ratio	0.69	-	Percent of males in the population (Chapman and Feldhamer 1982; Lariviére and Walton 1998).
Female 50% Core Home Range	4(2)	Normal	Mean (SD), in km, of female 50% Core Home Range (Blundell et al. 2000).
Habitat Quality Threshold	0.464	-	Maximum Entropy optimal threshold value of logistic probability predicting otter latrine site (Chapter 3).
Activity Threshold	0.122	Bernoulli	Probability of otter being in active-state (ratio of mean Active:Inactive hours; M. Ben-David unpublished data).
Active Upper CI	1.88	Uniform	Upper 95% CI value of mean active- state hours (M. Ben-David unpublished data).
Inactive Upper CI	15.32	Uniform	Upper 95% CI value of mean inactive- state hours (M. Ben-David unpublished data).
Run-time			
Movement Distance	941(1731)	Normal	Mean (SD), in meters, of 8 telemetered otters (M. Ben-David unpublished data).
Hours Between Defecating	4.865(1.825)	Normal	Mean (SD) hours between defecation events for captive otters in a 24hr period (Ormseth and Ben-David 2000).
Hours in Active- state	1.433 (1.393)	Normal	Mean (SD) hours of continuous activity of 8 telemetered otters (M. Ben-David

			unpublished data).
Hours in Inactive-state	11.692 (8.286)	Normal	Mean (SD) hours of continuous inactivity of 8 telemetered otters (M. Ben-David unpublished data).
Scent Distance Decay Rate	-0.003	Bernoulli	Parameter estimate in negative exponential equation (eq. 6) calculating probability of detecting scent-mark given a distance.
Feces Desiccation Rate	0.1	Bernoulli	Parameter estimate in exponential equation (eq. 6) calculating expected amount of desiccation (unitless value) given the age, in hours, of the fecal deposit.
Visual Perception Distance	50	-	Assumed visual distance, in meters, at which the otter is acutely aware of the biotic and abiotic conditions of its surroundings.
Memory Perception Distance	1000	-	Assumed memory distance, in meters, at which the otter can perfectly recall the best (MEP) available habitat.
Active/Inactive - Satiation Scaler	2	Bernoulli	A scaling factor that increases (if Active) or decreases (if Inactive) the probability that an otter will switch activity-states if it has foraged on a school of fish (see eqs. 4, 5).
Defecation - Satiation Scaler	2	Bernoulli	A scaling factor to increase the probability of a defecation event if the otter has foraged on a school of fish (see eq. 2).

	Fish		Parameter	Adjustment
Scenario	Schools	Adjusted parameter	value	
R01	Informed	None	-	None
R02	Random	None	-	None
R03	No schools	None	-	None
R04	Informed	Movement Distance	847 (1558)	-10%
R05	Informed	Movement Distance	1035 (1904)	+10%
R06	Informed	Hours Between Defecating	4.379 (1.643)	-10%
R07	Informed	Hours Between Defecating	5.352 (2.008)	+10%
R08	Informed	Hours in Active-state	1.29 (1.254)	-10%
R09	Informed	Hours in Active-state	1.576 (1.532)	+10%

Table 4.2: Simulation scenario parameter values. Parameter values were not modified

from Table 4.1 unless otherwise stated.

Table 4.3: Mean (SD) feces/day for each

simulation scenario. 95% confidence intervals

Model	Mean (SD)	CI95
R01	294.43 (36.59)	22.68
R02	295.83 (30.33)	18.80
R03	385.97 (29.58)	18.33
R04	310.60 (37.25)	23.09
R05	305.54 (28.28)	17.53
R06	317.32 (33.63)	20.85
R07	293.42 (27.42)	16.99
R08	303.31 (32.71)	20.27
R09	330.19 (32.74)	20.30

were calculated having n = 10.

Table 4.4: Mean (SD) defecation rate measured as the ratio between the number of hours an otter experienced a defecation event and the total number of simulated hours. 95% confidence intervals were calculated having n=10.

	Female		Male	
Model	Mean (SD)	CI95	Mean (SD)	CI95
R01	0.175 (0.004)	0.003	0.173 (0.005)	0.003
R02	0.167 (0.006)	0.004	0.170 (0.006)	0.004
R03	0.221 (0.002)	0.001	0.223 (0.001)	0.000
R04	0.177 (0.005)	0.003	0.176 (0.005)	0.003
R05	0.178 (0.004)	0.002	0.176 (0.005)	0.003
R06	0.185 (0.005)	0.003	0.183 (0.006)	0.004
R07	0.172 (0.007)	0.005	0.171 (0.007)	0.005
R08	0.175 (0.004)	0.003	0.175 (0.004)	0.002
R09	0.175 (0.005)	0.003	0.173 (0.006)	0.004

Table 4.5: Mean defecation events/day/otter for each simulation scenario. Values were derived from Table 4.4 by multiplying the ratio and the total number of hours (2209) and dividing by days (92).

Model	Female	Male
R01	4.21	4.15
R02	4.02	4.08
R03	5.32	5.36
R04	4.24	4.24
R05	4.26	4.24
R06	4.45	4.40
R07	4.14	4.10
R08	4.21	4.21
R09	4.21	4.15

Table 4.6: Mean (SD) hours in active-state for each simulation

	Female	•	Male	
Model	Mean (SD)	Cl95	Mean (SD)	CI95
R01	780.63 (39.36)	24.39	749.91 (46.91)	29.07
R02	715.17 (55.16)	34.19	729.24 (57.76)	35.80
R03	1182.91 (2.62)	1.62	1182.65 (3.17)	1.97
R04	800.25 (41.67)	25.83	782.19 (45.75)	28.35
R05	806.27 (35.58)	22.05	784.35 (41.32)	25.61
R06	810.07 (43.70)	27.09	784.31 (46.63)	28.90
R07	813.16 (61.59)	38.18	785.21 (66.06)	40.95
R08	771.70 (32.32)	20.04	755.28 (32.46)	20.12
R09	801.52 (44.13)	27.35	769.30 (52.63)	32.62

scenario. 95% confidence intervals were calculated having n = 10.

Table 4.7: Mean (SD) proportion of time an otter encountered a fish school while in active-state.95% confidence intervals were calculated having n = 10.

	Female		Male	
Model	Mean (SD)	CI95	Mean (SD)	CI95
R01	0.174 (0.027)	0.017	0.194 (0.033)	0.020
R02	0.219 (0.044)	0.027	0.209 (0.043)	0.027
R03	0.000 (0.000)	0.000	0.000 (0.000)	0.000
R04	0.161 (0.024)	0.015	0.172 (0.029)	0.018
R05	0.156 (0.022)	0.013	0.169 (0.027)	0.017
R06	0.155 (0.026)	0.016	0.170 (0.031)	0.019
R07	0.154 (0.037)	0.023	0.172 (0.043)	0.026
R08	0.170 (0.023)	0.014	0.180 (0.022)	0.014
R09	0.170 (0.029)	0.018	0.189 (0.037)	0.023

Table 4.8: Mean ratio of feces containing

pelagic fish (see eq 12).

	Female	Male
Model	Mean ratio	Mean ratio
R01	0.350	0.381
R02	0.424	0.405
R03	0.000	0.000
R04	0.329	0.344
R05	0.320	0.341
R06	0.307	0.330
R07	0.329	0.358
R08	0.338	0.351
R09	0.352	0.380

Table 4.9: Mean (SD) number of individual otter interactions

for each gender and simulation scenario. 95% confidence

	Fema	Female		•
Model	Mean (SD)	CI95	Mean (SD)	CI95
R01	34.24 (4.14)	2.56	53.86 (6.46)	4.00
R02	36.26 (4.44)	2.75	56.63 (6.66)	4.13
R03	47.14 (3.55)	2.20	73.87 (5.26)	3.26
R04	33.69 (4.09)	2.54	53.01 (6.13)	3.80
R05	37.83 (3.92)	2.43	59.08 (6.59)	4.08
R06	35.39 (3.91)	2.42	56.13 (5.70)	3.53
R07	34.98 (3.38)	2.10	55.03 (5.53)	3.43
R08	35.54 (4.13)	2.56	55.47 (6.63)	4.11
R09	38.42 (4.77)	2.96	61.18 (7.53)	4.67

intervals were calculated having n = 10.

Table 4.10: Mean (SD) percent of time an otter was within a

social group and the percent of that time spent with each

gender for simulation scenario R01 (baseline).

	% Time in	% with	% with
Gender	Group	Female	Male
Female	40% (3%)	20% (2%)	80% (2%)
Male	49% (4%)	26% (2%)	74% (2%)

Table 4.11: The daily mean (SD) social group composition of active otters. Also included are the mean number of fish schools, mean number of total otters, the proportion of otters in social groups, and the maximum group size for each simulation scenario (n = 92).

	Total in						
	Groups	Num.	Otters in	Mean	Mean	% Total	Max.
	Mean	Groups	Group	Num.	Total	in	Group
Model	(SD)	Mean (SD)	Mean (SD)	Schools	Otters	Groups	Size
	44.70	17.82	2.51				
R01	(4.36)	(1.25)	(0.08)	51.17	106.80	41.85	14
	47.25	19.25	2.46				
R02	(3.90)	(1.30)	(0.05)	49.08	112.20	42.11	13
	33.39	14.05	2.38				
R03	(0.79)	(0.27)	(0.04)	1.00	110.40	30.24	11
	46.53	18.60	2.50				
R04	(4.43)	(1.27)	(0.08)	48.35	111.80	41.62	13
	44.22	17.76	2.49				
R05	(4.08)	(1.19)	(0.08)	38.13	107.80	41.02	13
	44.34	17.76	2.50				
R06	(4.29)	(1.26)	(0.08)	42.57	108.00	41.05	12
	43.96	17.67	2.49				
R07	(4.21)	(1.22)	(0.08)	42.90	107.40	40.94	11
	46.34	18.37	2.53				
R08	(4.26)	(1.17)	(0.09)	47.05	109.20	42.44	12
	51.87	20.55	2.53				
R09	(4.72)	(1.44)	(0.07)	49.21	119.50	43.40	12

Table 4.12: The mean (SD) of total km of coastline habitat used by individual otters for each simulation scenario. 95% confidence intervals were calculated having n = 10. For the confidence interval for Blundell et al. 2000 was calculated with females n = 9 and males n = 20.

	Female		Mal	e
Model	Mean (SD)	CI95	Mean (SD)	CI95
R01	22.9 (1.9)	14.2	113.5 (9.0)	70.3
R02	23.1 (1.5)	14.3	116.6 (7.8)	72.3
R03	24.9 (1.0)	15.4	154.9 (5.1)	96.0
R04	22.9 (1.8)	14.2	105.8 (3.8)	65.6
R05	25.3 (1.9)	15.7	124.4 (8.3)	77.1
R06	23.7 (1.5)	14.7	116.8 (4.1)	72.4
R07	24.9 (1.4)	15.4	116.0 (7.5)	71.9
R08	24.6 (1.4)	15.2	114.1 (6.1)	70.7
R09	23.7 (1.6)	14.7	115.0 (8.7)	71.3
Blundell et				
al. (2000)	15.0 (7.0)	4.6	60.0 (51.0)	22.4

Table 4.13: Fecal deposition amount and frequency for simulation scenario R01 (baseline). Point-locations having a Maxent probability \geq 0.464 were classified as latrines. The number of feces is the summed average (10 replications) for each point-location.

				Within	Within	Total	Total
Classification	Fecal	Num.	Num.	Type %	Type %	%	%
Туре	Range	Feces	Points	Feces	Points	Feces	Points
Latrine	<=20	7398	7090	18%	97%	18%	29%
Latrine	20-50	2397	75	6%	1%	6%	0%
Latrine	>=50	30436	147	76%	2%	73%	1%
Non-Latrine	<=20	1337	17207	98%	100%	3%	70%
Non-Latrine	20-50	25	1	2%	0%	0%	0%
Non-Latrine	>=50	0	0	0%	0%	0%	0%
Totals		41592	24520			100%	100%



Figure 4.1: Flow diagram describing model steps and decisions.



Figure 4.2: Map depicting the entire landscape network including the extent of the study area coastline, the additional outside area and the virtual lines connecting islands and bays.



Figure 4.3: Model sensitivity of mean feces/day as the response variable. The vertical axis represents the mean value for R01 (294 feces/day; baseline). Please see Table 4.2 for parameter adjustments and Table 4.3 for measured values.



Figure 4.4: Model sensitivity of mean proportion of time defecating, by gender, as the response variable. The defecation rate was measured as the ratio between the number of hours an otter experienced a defecation event and the total number of simulated hours. The vertical axis represents the mean value for R01 (baseline) of both genders (0.174). Please see Table 4.2 for parameter adjustments and Table 4.4 for measured values.



Figure 4.5: Model sensitivity of mean hours of activity-state as the response variable. The vertical axis represents the mean value for R01 (baseline) of both genders (765). Please see Table 4.2 for parameter adjustments and Table 4.6 for measured values.



Figure 4.6: Model sensitivity of mean proportion of active-state hours in which a fish school was located as the response variable. The vertical axis represents the mean value for R01 (baseline) of both genders (0.183). Please see Table 4.2 for parameter adjustments and Table 4.7 for measured values.



Figure 4.7: Mean and 95% confidence intervals of the number of interactions with individual otters for each simulation scenario.


Figure 4.8: Model sensitivity of mean proportion of total population participating in group activities as the response. The vertical axis represents the mean value for R01 (0.419; baseline). Please see Table 4.2 for parameter adjustments and Table 4.10 for measured values. The 95% confidence intervals were calculated having n = 92.



Figure 4.9: Model sensitivity of mean number of groups as the response. The vertical axis represents the mean value for R01 (17.82; baseline). Please see Table 4.2 for parameter adjustments and Table 4.10 for measured values. The 95% confidence intervals were calculated having n = 92.



Figure 4.10: Modeled otter group size and number of pelagic fish schools.



Figure 4.11: Model sensitivity of mean number of individuals within a group as the response. The vertical axis represents the mean value for R01 (2.51). Please see Table 4.2 for parameter adjustments and Table 4.10 for measured values. The 95% confidence intervals were calculated having n = 92.



Figure 4.12: Model sensitivity of the mean total coastline use by individual otters. The vertical axis represents the mean R01 (baseline) value for male otters only (113.5). The minimal variability of female coastline use led to the choice of using the mean male value. Please see Table 4.2 for parameter adjustments and Table 4.11 for measured values. The 95% confidence intervals were calculated having n = 10.



Figure 4.13: Mean (95% CI) feces/day for each simulation scenario (n = 10). The y-intercept of the x-axis is the estimated rate of fecal deposition for the 2006 sampling effort (345 feces/day). For reference, the estimated fecal deposition rate for 2007 was 366 feces/day.



Figure 4.14: A scatterplot of the first two dimensions of a Correspondence Analysis between each simulation scenario. The spatial pattern of fecal deposition for scenarios using the informed schools (R01, R04-R09) model were more similar to each other than to R02 (random schools) or R03 (no schools). Scenarios R02 and R03 were dissimilar in their spatial fecal deposition pattern along the coastline.



Figure 4.15: Locations of fecal deposition for simulation scenario R01 (baseline) for the entire landscape network. The study area coastline is highlighted in blue. Only locations having \geq 50 feces are displayed.



Figure 4.16: Locations of fecal deposition for simulation scenario R02 (random schools) for the entire landscape network. The study area coastline is highlighted in blue. Only locations having \geq 50 feces are displayed.



Figure 4.17: Locations of fecal deposition for simulation scenario R03 (no schools) for the entire landscape network. The study area coastline is highlighted in blue. Only locations having \geq 50 feces are displayed.











Figure 4.20: Summed fecal deposition for simulation R01 (baseline) occurring at the same 100 latrine locations as the study area.



Figure 4.21: Summed fecal deposition for simulation R02 (random schools) occurring at the same 100 latrine locations as the study area.



Figure 4.22: Summed fecal deposition for simulation R03 (no schools) occurring at the same 100 latrine locations as the study area.



Figure 4.23: A scatterplot of the first two dimensions of a Correspondence Analysis between observed feces at the 100 latrines sites and the simulated deposition for the associated point-locations of simulation scenarios R01 (baseline), R02 (random schools) and R03 (no schools). The axes labels were inferred from the simulation results (see Figure 4.14) and applied to this analysis. For the corresponding point-locations, the simulation scenarios were similar to each other in the amount of fecal deposition reaching those locations. The observed feces also differed between years and simulation scenarios, demonstrating the high degree of spatial and temporal variability in marine derived nutrients reaching the coastal environment.







Figure 4.25: A comparison of two latrine sites and simulation results from experiment R01. Latrine sites HB001 and HB004 have relatively high amounts of feces, but the simulated amounts were equal to 13 and 17, respectively. In turn, the simulated deposition (the red circle) is nearby and has a similar deposition rate and habitat quality.



Figure 4.26: Histogram of otter fecal deposition amounts for (A) the 2006 observed data (n = 100), (B) scenario R01 (n = 147; baseline), (C) scenario R02 (n = 154; random schools), and (D) scenario R03 (n = 178; no schools). Note for the simulation scenarios, frequencies only include point-locations having fecal counts \ge 50.

CHAPTER 5

CONCLUSIONS AND FUTURE RESEARCH CONSIDERATIONS

The abundance of new theoretical and empirical work aimed at addressing major ecological issues has been fostered by advances in methodologies and technologies, as well as increased funding (Thompson et al. 2001). However, Thompson et al. (2001) suggest more progress is necessary to develop a unified understanding of ecological interactions and their associated spatial and temporal scales. Specifically, Thompson et al. (2001) state, "Even our understanding of food webs generally lacks spatio-temporal context, strongly limiting our ability to explain their origin, maintenance and consequences. We suggest building an ecological topology that addresses these needs." This research has taken the necessary steps to apply this suggestion at a landscape scale.

The development of a new scale-independent, landscape metric (boundary convexity) to describe the shape of the coastline is an important step in relating the physical characteristics of the landscape to the ecological processes driven by animal behavior. This methodological and technological advance provides a metric at finer spatial scales than were previously available. In turn, boundary convexity was the most important abiotic variable in models describing otter latrine site selection in Prince William Sound, AK. The development of a spatially transferable model, based on remotely sensed information, is an important contribution to wildlife managers. Having the methods and tools to develop predictive models of latrine density may provide useful scenarios for otter management. Additionally, this research demonstrated the ability to use remotely sensed data to predict otter latrine usage with nearly the same amount of accuracy as models using site-specific information (Bowyer et al. 2003; Bowyer et al. 1995). The coupling of

a robust habitat-use model and 17 years of otter behavior data has afforded the development of an IBM capable of reproducing observed patterns at the system level.

The IBM performed well in reproducing otter-specific behavior, including cooperative foraging through social group organization and spatial heterogeneity of nutrient deposition. Similar to Ben-David et al. (2005) and Blundell et al. (2002), the resulting patterns were heavily influenced by the presence of schooling pelagic fish. These results are compelling for two reasons. First, as is always the case, the knowledge and understanding of the system was incomplete (Starfield 1997). However, by taking a common-sense, heuristic approach (Grimm and Railsback 2005; Starfield et al. 1993), the problem of determining the dominant mechanism(s) driving the observed pattern of nutrient deposition, in light of incomplete information, was effectively addressed. The primary example being that information regarding the timing, abundance and location of pelagic fish schools was relatively depauperate, yet measured otter behavior was similar to observed patterns. Second, the relatively good fit of the IBM to observed patterns provide confidence in the mechanisms and methods used to develop this model. This result, coupled with the increased understanding of the spatial and temporal effects prey availability impose on otter behavior, creates a strong foundation in which expanding the model to include additional spatial and temporal domains can be undertaken (Thompson et al. 2001).

The importance of understanding the potential shift in nutrient deposition to the nearshore environment is grounded by the fact that the species diversity of flora in Prince William Sound is limited because of recent glaciation and harsh environmental conditions (Heusser 1983; Pärtel et al. 2007). Increased fertilization by otter fecal deposition increased in plant growth and diversity (Ben-David et al. 1998; Roe et al. 2010). The opposite effect may occur if nutrients are removed or the pathways are disrupted (Polis and Hurd 1996; Power and Rainey 2000), potentially reducing ecosystem resilience (Chapin III et al. 2000).

The Gulf of Alaska (GOA) has experienced significant warming in the past few decades (Freeland et al. 1997; Wiles et al. 1998). The increased temperatures may be leading to decreases in ice cover, increases in sea surface temperatures and variable nutrient fluxes, all potentially causing declines in primary productivity (Freeland et al. 1997; Whitney et al. 1998). The change in primary productivity may cause shifts in pelagic fish abundance and demersal fish species composition (Anderson et al. 1997; Anderson and Piatt 1999; Polovina et al. 1995). Cascading up the food-chain, the decline in prey has been accompanied by declines in marine mammals and seabirds (Loughlin 1998; Piatt and Anderson 1996). These findings provide a basis from which to test additional hypotheses and forecast future scenarios involving coastal river otter, prey availability, nutrient transport and the resulting patterns upon the landscape.

Sea surface temperatures (SSTs) play an important role in zooplankton production (Mackas et al. 1998) and the timing of pelagic fish spawn (Brown et al. 1999; Brown 2002; Norcross et al. 2001; Penttila 2007). With SSTs increasing (Cane et al. 1997), future research may need to focus on the potential effect of temporal fluctuations in SSTs on pelagic fish timing and availability to coastal river otters. To accomplish this research, the IBM's spatial and temporal scales could be modified through the calculation of summary statistics to parameterize an additional IBM having a larger time step (i.e. days or weeks). The temporal simplification would allow for models to be conducted across an annual time step and facilitate forecasting behavioral response across multiple years of simulation. Additional parameters would be required, such as individual otter survival, reproductive success and annual SST variation for a given climate scenario. In relation to SST variation, a model of pelagic fish response to SST, as well as the response to predation pressure by otters on demersal fish, would be necessary. The temporally expanded IBM would be similar to the model (Figure 1.1) proposed by Ben-David et al. (2004). The ability to accurately develop an IBM forecasting potential behavioral and associated terrestrial response to changes in SSTs is enhanced by the study area.

The study area has many advantages for expanding the spatial and temporal domains of the model system. First, a great amount of data has been collected during the 17 years since the *Exxon Valdez Oil Spill* (EVOS) (Alaska Department of Environmental Conservation 1993), providing both temporal context and diverse types of information. Also, data collection will continue as part of the EVOS settlement. Secondly, aside from EVOS and commercial fishing, Prince William Sound is relatively undisturbed. Thus, monitoring the nutrient pathways and the effect of broad-scale processes on the coastal landscape can be accomplished with fewer anthropogenic influences confounding measurements. The conceptual design of this IBM is applicable to any ecosystem in which variation is caused by behavior, genetic or physiological traits of individuals, and we believe this research provides an excellent working example.

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