

AN APPROACH TO THE QUANTIFICATION AND CLASSIFICATION OF AQUATIC LANDSCAPES

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ABSTRACT: *Every ecosystem presents a unique set of processes specific to the environmental variables and resources found there. Quantifying the important landscape components that drive ecosystem processes has been the focus of landscape ecology. The patch/corridor/matrix model has been developed as a framework for quantifying the interaction between elements in terrestrial landscapes. An alternative model may be required for the quantification of aquatic landscapes. Spatial distributions of resources are important to species interactions and fish growth in aquatic ecosystems. This paper will identify important processes in aquatic landscapes, present appropriate tools for spatial analysis of these landscapes, and outline a methodology for classifying aquatic landscapes according to spatial characteristics.*

BACKGROUND

The study of spatial phenomena and quantification of spatial patterns provide a common ground for the fields of geography and ecology. Spatial patterns are a result of variation across space. Recently, variability or heterogeneity has been recognized as an important aspect in ecological studies (Legendre and Fortin, 1989; Levin, 1992; Horne and Schneider, 1995). Heterogeneity or the uneven distribution of resources within landscapes results in a mosaic of aggregated objects, with distinct boundaries between patches, corridors, and the background matrix (Forman, 1995). A landscape of agricultural fields separated by hedgerows, spotted with patches of forest, and bisected by a road is an example of a heterogeneous landscape. Landscape heterogeneity plays an important role in how ecosystems function by influencing the flow of energy and organisms (Turner and Gardner, 1990).

The field of aquatic ecology is concerned with interactions among biological, physical, and chemical components of freshwater ecosystems. In the study of fish distributions in large lake systems, focus has shifted from whole lake estimates of fish abundance to collecting multiple parameters of high resolution ecological data over a greater extent of the lake. With the development of high resolution, remote sampling techniques, environmental heterogeneity in aquatic systems can be examined (Buczynski and Johnson, 1986; Nero et al., 1990; Luo and Brandt, 1993). Maps of species distribution in large lakes can be produced to represent

the density of fish targets within a vertical slice of the water column. Rather than treating landscapes as a homogeneous unit, high-resolution sampling reveals heterogeneity of resources. Quantifying the heterogeneity or patterns observed in the aquatic environment is the focus of this paper. By quantifying the spatial arrangement of landscape features important to predator-prey interactions, aquatic landscape function may become evident.

The science of fisheries has long been interested in the spatial distribution of aquatic species, as well as the relationship of species distribution to the physical environment (Magnuson et al., 1979; Mackas, 1984; Olson et al., 1988; Nero et al., 1990; Brandt, 1993). The complexity of large lake ecosystems calls for a classification system that aids in describing the interactions between the physical, chemical, and biological components of these systems. In this regard, landscape ecology, which deals with the quantification of landscape components and the impact of their interrelationships on landscape function, may be applicable in describing the interactions of fish populations in the Great Lakes. For resource managers interested in sustainability of fish populations, defining the spatial relationships or patterns of predator, prey, and water temperature will provide information on the ability of predators to utilize prey, resulting in refined estimates of potential fish growth.

Quantification of landscape structure and its relationship to ecosystem function has been the focus of landscape ecology over the past decade (Forman and Godron, 1981; Turner and Gardner, 1990; Forman,

1995). Landscape structure refers to the specific arrangement and spatial relationships of landscape elements, typically the arrangement of patches and corridors across a background matrix. Landscape ecology emphasizes the spatial arrangement of energy, materials, and species in relation to the composition, characteristics, and configuration of landscape elements and the effect of these spatial relationships on landscape function (Turner and Gardner, 1990). Landscape ecology is based on the premise that pattern and distribution of landscape elements reflect underlying processes (Turner and Gardner, 1990). Similarly, the approach presented here will rely on the assumption that spatial distributions of important aquatic landscape elements are reflective of underlying ecological processes, such as predator-prey interactions. In a terrestrial landscape ecology model, spatial elements include patch, corridor, and matrix. A model that describes the arrangement of important spatial elements in aquatic environments will be presented here.

HIGH RESOLUTION ACOUSTIC DATA

The acquisition of data in aquatic systems has been enhanced by the use of acoustic instruments that send a signal through the water column and estimate the depth, size, and location of objects in the water column by interpreting the echo or returned signal. As a research vessel travels along a transect, a downward facing transducer, deployed off the side of the ship, projects and receives soundwaves (Figure 1 inset). As the sonar signal is reflected by fish and received at the transducer, a series of echoes are integrated to calculate the total echo for each cell or volume of water sampled along the transect. This integrated echo is a relative measure of biomass density within that volume of water. Typically, estimates of fish abundance can be integrated at a resolution as fine as one meter in depth by approximately 40 meters along the transect. In addition to fish biomass, the size of individual fish targets can be estimated. As a result, analysis of fish abundance can be based on size classes and, with some assumptions, fish abundance can be separated into classes representing prey and predators. Although acoustic technology can not as yet differentiate between species, knowing something about the ecology of a particular ecosystem increases the certainty about the species being detected. In Lake Ontario, the pelagic (open water) fish community is dominated by chinook

salmon and lake trout as top predators and alewife and smelt their primary prey (Goyke and Brandt, 1993). Since these prey species rarely exceed 200 mm in Lake Ontario, it can be assumed that anything above 250 mm is one of the two predatory species.

Geo-referenced, acoustic data can be converted to maps of fish distribution. This allows for the inclusion of spatially explicit data in species interaction models. The data used in this study were collected by the Great Lakes Center, Buffalo, New York (Kracker et al., 1996). The survey design involved the collection of georeferenced, high resolution acoustic measures of fish distribution of a three-dimensional grid sampled over a 24 hour period in three seasons (July, October, and April) (See Figure 1). A single transect is a 20 minute snapshot of fish distribution throughout the water column. The grid is composed of five north-south and five east-west transects covering one square nautical mile (1852 m x 1852 m). One complete grid is sampled approximately every four to six hours. This is repeated throughout a 24-hour period resulting in four complete grids collected in each of the three seasons.

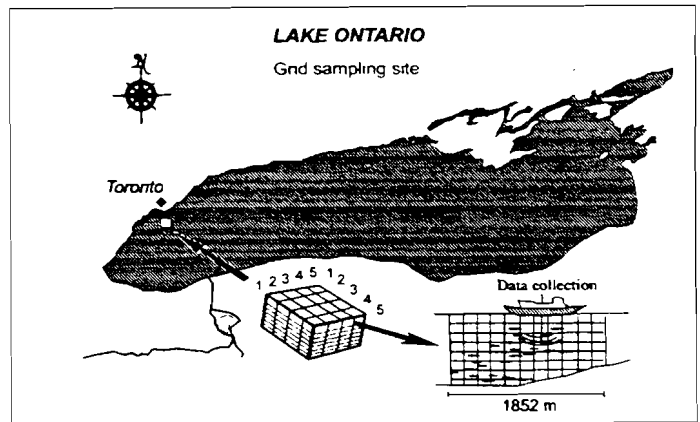


Figure 1. Lake Ontario grid sampling site

Each acoustic transect represents a vertical slice of the water column that is 1852 meters in length at the surface and extends to the bottom of the lake (approximately 40-60 meters deep). Within each transect, fish abundance is estimated for every one meter in depth and approximately 40 meters along the transect, resulting in a resolution of 1 by 40 meters. Water temperature data were collected simultaneously along the same transects, using a towed device that samples the water column at various depths. When interpolated to the resolution of the acoustic data, maps of water temperature representing the same slice of the water column can be generated.

This grid sampling design makes it possible to compare changes in landscape composition and configuration within the study area both spatially (across the extent of the grid) and temporally (over 24 hours and three seasons). Recent efforts to analyze transect data collected in this manner has involved visualization and non-spatial statistical techniques (Brandt and Kirsch, 1993; Goyke and Brandt, 1993). However, efforts to quantify and analyze the spatial arrangement of these variables, as presented here, have not been fully developed.

OBJECTIVES

Aquatic features important to ecological processes include physical, chemical, and biological components of the ecosystem. The distribution of predators, prey, and water temperature (Figure 2) has been identified as important features affecting potential fish growth (Brandt, 1993). In this paper, I will present a method for quantifying and characterizing the spatial arrangement (both composition and configuration) of predators, prey, and water temperature. By characterizing

ecologically significant spatial elements for each remotely sensed acoustic transect in the Lake Ontario grid, changes in landscape structure can be compared daily and seasonally, identifying characteristics most significant in explaining spatial and temporal changes related to predator-prey interactions.

This paper will focus on the first of the overall project objectives: (1) develop a set of landscape measures to quantify the characteristics, composition, and configuration of aquatic landscape features related to predator-prey interactions; (2) determine if the characteristics, composition, and configuration of aquatic landscape features change significantly over time and space, and; (3) identify changes in aquatic landscapes that are most significant in characterizing the differences between transects collected at different locations and times.

LANDSCAPE ELEMENTS

A terrestrial landscape ecology model is comprised of three basic elements - patch, corridor, and matrix. The characteristics, configuration, and interactions between these elements affect ecological processes, such as species movement and diversity, recolonization, and habitat preferences (McLaughlin and Roughgarden, 1993; Forman, 1995). The three basic landscape elements are defined as: (1) patch - a relatively homogeneous non-linear area that differs from its surroundings; (2) corridor - a strip of a particular type that differs from the adjacent land on both sides that can function as a conduit, barrier, and habitat, and (3) matrix - the background ecosystem or land-use type in a mosaic, characterized by extensive cover, high connectivity, and/or major control over dynamics (Forman, 1995).

Developing a model for aquatic systems will require identifying ecologically significant processes and the resources or elements that impact those processes. For this analysis, predator-prey interactions will be the primary ecological process under study. There are many factors that affect the distribution of fish throughout their life history, such as suitable substrate during spawning. However, factors that are of primary importance in terms of foraging and growth include the distribution of prey, water temperature, and predators (Figure 2) (Magnuson et al., 1979; Brandt, 1993; Rose and Leggett, 1990).

Turner and Gardner (1990) refer to landscape structure as the size, shape, number, kinds, and

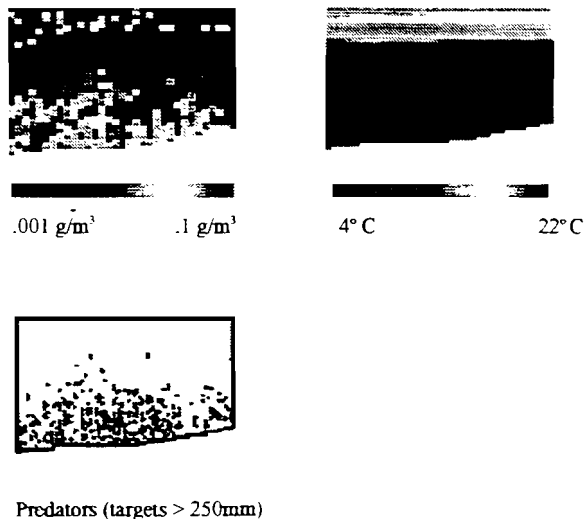


Figure 2. Distribution of prey density, temperature, and predator in a typical transect.

configurations of its component ecosystems, each consisting of a unique distribution of energy, materials, and species. Landscape function refers to the flow of energy, materials, and organisms among the component ecosystems. The structure of the landscape (characteristics, composition, and configuration) affects landscape function by influencing the flow of energy and organisms (Turner and Gardner, 1990). Change in both structure and function occurs over time. In determining whether or not the landscape ecology approach is appropriate for the study of fish population dynamics in the Great Lakes, it is necessary to examine whether or not these concepts have a counterpart in aquatic systems. For instance, are the basic landscape elements and their characteristics applicable to aquatic landscapes? Do the same principles of interaction between landscape elements and ecological processes apply to aquatic ecosystems?

Patches

Patches are communities or species assemblages surrounded by a matrix of a dissimilar type (Forman and Godron, 1981). The patchiness of plankton and the schooling behavior of fish support the premise that patches exist in aquatic systems. "This basic aggregation pattern of individuals of a species into assemblages underlies the patchiness of vegetation and animal communities found in nature (Forman and Godron, 1981 p. 734)". Measuring the aggregation of fish populations in the Great Lakes has, until recently, been limited by sampling methodology. Traditional sampling, such as net trawling, provides an estimate of biomass density within a sampled volume, but provides little information regarding the spatial arrangement or heterogeneity within that volume. Remotely sensed acoustic techniques have recently been used to examine heterogeneity of fish populations at a much finer resolution (Luo and Brandt, 1993; Nero and Magnuson, 1989). As a result, spatial variation or patchiness of fish can be observed in aquatic systems.

Forman and Godron (1981) identify important patch characteristics such as degree of isolation, accessibility, interaction, diversity, minimum viable population, shape, convolution, roughness, and compactness and suggest that these patch characteristics affect the function of the patch within the landscape. For instance, increased patch size may result in increased species diversity. Similarly, the patch shape, which determines the relative amount of interior, may provide varying degrees of protective habitat for schooling fish.

Orientation of a patch may also affect species movement or habitat use. The orientation of patches along fronts is well documented in marine systems (Mackas and Shefton, 1982). In freshwater systems, variation in the degree of patchiness may occur as a response to physical and biological forcing functions related to the daily vertical migrations of plankton in response to sunlight, seasonal and daily variations in temperature, the degree of active mobility by individuals within the ecosystem, and the movement of water. The system of landscape metrics developed here will be used to describe the characteristics of patches and their composition and configuration within the landscape. Whether or not patch characteristics vary spatially or temporally in aquatic ecosystems can be addressed by classifying landscapes according to these characteristics and examining how those characteristics change.

Thermal Corridor

Temperate lakes, such as the Laurentian Great Lakes, thermally stratify in the summer months, creating a much warmer water mass above and a cold water mass below the thermal gradient. This extreme temperature gradient can occur within a relatively short vertical distance (a range of 4° C to 22° C can occur within a few meters in a lake 200 m deep). The thermocline is an aquatic counterpart to the terrestrial corridor in several

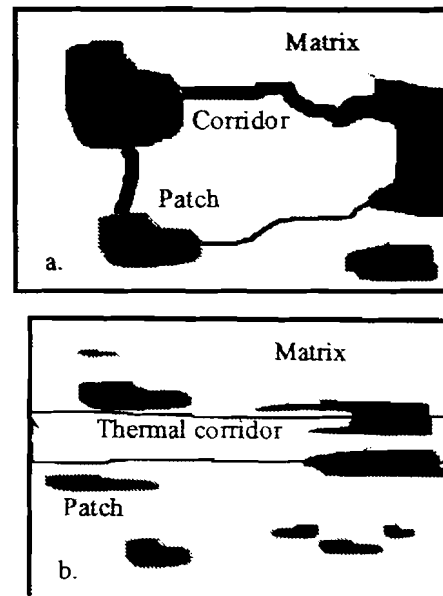


Figure 3. (a) Patch/corridor/matrix model (after Forman and Godron, 1981) (b) patch/thermal corridor/matrix model.

regards. First, the temperature gradient differs from adjacent areas on both sides. Secondly, this structure acts as a barrier and provides a type of refuge for species from their predators (Rose and Leggett, 1990). The thermocline also acts as habitat. The vertical and horizontal extent of fish species distributions in relation to the thermocline in Lake Ontario has been roughly delineated into salmonid and prey habitats (Olson et al., 1988). Finally, the thermocline is a zone of very high productivity. It is a significant physical structure with ecological consequences (Magnuson et al., 1979). The thermocline functions as a corridor in many ways. Therefore, the term "thermal corridor" will be used as the equivalent to the terrestrial corridor. The characteristics and configuration of the thermal corridor within the landscape will be measured using the system developed here.

Matrix

Patches of prey are arranged across the background matrix of water, which can be equated to the terrestrial matrix. This aquatic matrix has a chemical makeup of nutrients, oxygen, and possibly, toxins. The fluid nature of water is inherently connective and greatly controls the dynamics of elements within the matrix, mimicking the properties of the terrestrial matrix.

Given that patches, thermal structures, and a matrix exist in large lake systems, this aquatic landscape model should be applicable in describing the basic components of the aquatic landscape (Figure 3). The actual measures for identifying the arrangement and characteristics of these landscape elements will be applied in terms of relevant ecological processes.

ECOLOGICAL PROCESSES

Forces driving the distribution of fish and potential growth rates include availability of prey, behavioral response based on a preferred temperature, or a function of both prey availability and temperature (Brandt, 1993). How might the arrangement or configuration of aquatic landscape elements, such as thermal gradients and heterogeneity of prey, impact predator-prey interactions and potential growth rates? Water temperature affects metabolic rates and the efficiency with which prey are converted into positive growth of the predator (Brandt, 1993). Therefore, if prey reside outside a predator's preferred temperature, growth

rates may be affected. Likewise, if prey are not found within the vicinity of predators, the inability of fish to utilize prey will adversely affect growth. Describing the composition and configuration of predators, prey, and water temperature will provide information about the spatial relationship of these landscape elements in the context of predator-prey interactions. For instance, measures of landscape composition and configuration can be based on ecological questions such as: Do fish cluster? Does the presence of a predator affect clustering of prey? Are species spatially associated with a preferred temperature? Is the distribution of fish related to the presence of a thermal structure? Do species distributions exhibit daily or seasonal changes? These questions relate to the spatial relationships and potential interactions between predators, their prey, and temperature. By developing a set of metrics that captures the spatial arrangement and characteristics of aquatic landscape elements at any one place and time, changes in that arrangement can be identified, resulting in refined estimates of growth that incorporate daily and seasonal changes in landscape function.

LANDSCAPE METRICS

Landscape metrics are a set of measures designed to quantify the characteristics of landscape elements and the spatial relationship of those elements in terms that address ecological processes. Efforts to quantify terrestrial landscape features by developing a set of metrics relevant to ecological processes include Fragstats (McGarigal and Marks, 1995), a program designed to quantify landscape patterns to study function and change. Analysis of aquatic data includes Nero et al. (1990), who tested patch finding algorithms and analyzed differences in patch characteristics of fish within a Gulf Stream front, correlating patch features with the type of water mass in which they were located. The landscape metrics applied to the Lake Ontario grid transects will identify characteristics of the landscape that may impact fish growth.

METHODOLOGY

To quantify and compare the composition and configuration of aquatic landscape features among

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transects it will be necessary to identify landscape elements, determine appropriate landscape metrics, characterize the composition and configuration of elements and transects, differentiate between elements and between transects, and analyze results spatially and temporally (Figure 4).

Identify landscape elements

The landscape features or elements of interest in this study are those variables that have been previously identified as having an impact on predator-prey interactions and fish growth (the distribution of prey, predators, and water temperature). The characteristics of these elements may impact predator-prey interactions. In addition, the composition and configuration of these elements within the landscape may affect function.

Determine appropriate aquatic landscape metrics

A set of measurements developed to capture spatial relationships relevant to ecological processes is needed to define aquatic structure and classify landscapes. These aquatic landscape metrics are based on an ecological principle or question related to predator-prey interactions. For instance, fractal dimension of patches is used as a measure of patch complexity. This could be useful in interpreting the vulnerability of a patch to predation, hypothesizing that a more compact shape is less vulnerable. A full list of landscape metrics to be applied at both the element level and the landscape level is introduced below and given in Table 1. There are three basic types of metrics: characteristics of elements, composition of landscape, and configuration of landscape.

As a landscape element, prey patches may exhibit characteristics such as fractal dimension, area, density, size distribution of fish lengths within the patch, and mean and range of temperatures in which the patch resides. The thermal structure will be characterized by presence or absence of a spatial structure. The characteristics of predators will include size and the temperature in which the predator resides. These measures of element characteristics can be calculated for any single element in the landscape and also averaged to provide a landscape level measure of that characteristic (McGarigal and Marks, 1995).

The composition of the landscape refers to the numbers and types of elements that make up a landscape.

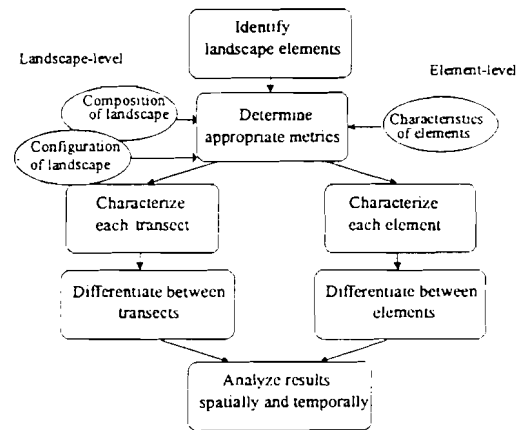


Figure 4. Methodology

This includes measures of total edge, numbers, and area of each element type, as well as the average characteristics of each element applied as a landscape indice. The spatial configuration of landscape elements refers to the actual location of elements and includes measures such as intensity, which is indicative of clustering or randomness. Intensity over a range of distances provides information about mean nearest neighbor distance (NND), distance where heterogeneity begins, distance where clustering becomes significant, and the distance where maximum clustering is observed (Getis and Franklin, 1982). Contagion is a measure of landscape configuration based on the probability of adjacent cells being occupied (Gardner and O'Neill, 1991) and is indicative of the degree to which patches of prey are clumped.

Characterize each element type and transect

In these steps, characterizing each element type and transect means applying the system of metrics defined in Table 1 to the elements and transects as appropriate. There are two levels at which transects can be characterized - the element-level and landscape-level. For instance, the fractal dimension of a patch can be measured for each individual patch, while the fractal dimension also can be measured for the entire transect. At the element-level, the characteristics of element types can be differentiated regardless of the transect in which they are found.

Table 1. Aquatic Landscape Metrics

Landscape Elements	Element Characteristics	Landscape Composition	Landscape Configuration
Temperature	Absence/presence of thermal corridor	% of landscape occupied by thermal corridor	% of total depth where thermal corridor begins
	Range of temperature	Mean temperature	Directionality of corridor in thermal structure Components of thermal structure (from variogram)
Prey patches	Area	Total patch area	Global spatial autocorrelation (I)
	Perimeter	Total patch perimeter	Contagion of prey
	Fractal dimension	Mean patch fractal dimension	1st order intensity (clustering/randomness)
	Mean density and variance within patch	Mean density and variance of patches	2nd order intensity (K function)
	Temperature in which patch resides	% of landscape occupied by patches	Mean temperature in which patch resides
	Depth of patch	# of patches	Mean NNDs to other patches, thermal gradient, and predator
	Patch orientation	Density (# patches/landscape)	Std. dev. and variance of NNDs
	NNDs to other patches, thermal corridor, predator	Mean patch size	
Predators	Size distribution w/in patch (min., max., std. dev, var.)	Size distribution of prey (min., max., std. dev, var.)	
	Temp. in which predator resides	Ave. temp. in which predator resides	Mean NNDs to other predators, thermal corridor, and patch
	Size of predator (mm)	Ave. size of predator (mm)	Std. dev. and variance of NNDs

This effort will focus on the landscape or transect level characteristics because the aim is to make comparisons between transects, not between types of elements within each transect (although patches will be differentiated). The characteristics measured at the element level will be averaged to provide a landscape level indice. The descriptors of temperature and predator characteristics will be limited by the type of information that can be derived from the original data.

At the landscape scale, each transect can be defined in terms of the spatial configuration and composition. Measures of spatial configuration include existence of structures, clustering, heterogeneity, and spatial association of predator to prey, prey density to

temperature, predators to thermal structure, as well as averages of element-level measures. Measures of composition include numbers, kinds, diversity of landscape elements. Measures of landscape configuration and composition are used to differentiate between these attributes of each transect.

Differentiate between elements and transects

Following through with the landscape level approach, principal components analysis (PCA) can be used to determine which descriptors of average landscape characteristics, composition, and configuration contribute most in differentiating transects. PCA is a data reduction

technique used to reduce a dataset of correlated variables to a few classes that can account for a large proportion of the total variance in the original variables (Dunteman, 1989).

Analyze results spatially and temporally

The analysis of classes of transects identified through PCA will be examined relative to the space and time in which the transects were sampled, by simply noting the time and location of transects within each class. Comparisons of transects collected at the same time (i.e. a set of 10 transects that make up a grid) could be examined in terms of eigenvalues that describe those transects. Temporal comparisons can be made with more specificity by including in the PCA only those time periods of interest. For example, a PCA of all transects in a single grid taken at night for each of the three seasons could be used to determine if there are differences in the characteristics that contribute to night transects in July versus night transects in October.

SUMMARY

The sustainability of fish communities in Lake Ontario has been a concern in recent years. Current efforts to model predator-prey interactions are motivated by the need to estimate available prey against predator demand in a heavily managed system (Jones et al., 1993). Improved estimates of fish consumption and growth can be obtained by studying the organization of species distribution within the water column, the proximal relationship between prey densities and predator distribution, partitioning of the environment used by pelagic fish, and seasonal variation in habitat characteristics. Therefore, it is important to retain the spatial characteristics of the landscape when quantifying landscape processes.

The patch/thermal corridor/matrix model developed here retains the spatial features of the aquatic transect. By applying this model, it will be possible to identify specific biological and physical characteristics that distinguish one aquatic landscape from another. The approach developed here also can be applied to transects from other ecosystems that were sampled in the same manner to compare how landscapes vary from one system to another. This method for measuring the composition and configuration of aquatic landscape elements

addresses questions such as: is predator abundance related to thermal structures, and do spatial measures indicative of schooling or predator avoidance behavior vary spatially and temporally? If pattern is a realization of a process, then identifying specifically what changes about the pattern could lead to hypotheses about processes. By defining spatial features of the aquatic environment in ecologically relevant terms, any changes in the pattern observed can be examined for its relevance or potential impact on predator-prey interactions.

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REFERENCES

- Brandt, S. B. 1993. The Effect of Thermal Fronts on Fish Growth: A Bioenergetics Evaluation of Food and Temperature. *Estuaries* 16(1):142-159.
- Brandt, S.B., and Kirsch, J. 1993. Spatially-explicit Models of Striped Bass Growth Potential in Chesapeake Bay. *Transactions of the American Fisheries Society* 122:845-869.
- Burczynski, J.J., and Johnson, R.L. 1986. Application of Dual-Beam Acoustic Survey Techniques to Limnetic Populations of Juvenile Sockeye Salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:1776-1788.
- Dunteman, G.H. 1989. *Principal Components Analysis*. New York: Sage Publications.
- Forman, R.T. 1995. *Land Mosaics*. Washington: Cambridge Press.
- Forman, R.T., and Godron, M. 1981. Patches and Structural Components for a Landscape Ecology. *Bioscience* 31(10):733-740.
- Gardner, R.H., and O'Neill, R.V. 1991. Pattern, Process, and Predictability: The Use of Neutral Models for Landscape Analysis. In *Quantitative Methods in Landscape Ecology*, ed. M.G. Turner and R.H. Gardner, pp. 289-308.
- Getis, A., and Franklin, J. 1987. Second-order Neighborhood Analysis of Mapped Point Patterns. *Ecology* 68(3):473-477.
- Goyke, A.P., and Brandt, S.B. 1993. Spatial Models of Salmonid Growth Rates in Lake Ontario. *Transactions of the American Fisheries Society* 122:870-883.
- Horne, J.K., and Schneider, D.C. 1995. Spatial Variance in Ecology. *Oikos* 74:1-9.
- Jones, M.L., Koonce, J.F., and O'Gorman, R. 1993. Sustainability of Hatchery-Dependent Salmonine Fisheries in Lake Ontario: The Conflict between Predator Demand and Prey Supply. *Transactions of the American Fisheries Society* 122:1002-1018.
- Kracker, L.M., Brandt, S.B., and Horne, J.K. 1996. Spatial Modelling of Fish Growth Rates: A 3-Dimensional View of Lake Ontario. Presented at American Fisheries Society 1996 Annual Meeting. Dearborn, Michigan.
- Legendre, P., and Fortin, M-J. 1989. Spatial Pattern and Ecological Analysis. *Vegetatio* 80:107-138.
- Levin, S.A. 1992. The Problem of Pattern and Scale in Ecology. *Ecology* 73(6):1943-1967.
- Luo, J., and Brandt, S. B. 1993. Bay Anchovy *mitchili* Production and Consumption in Mid-Chesapeake Bay based on a Bioenergetics Model and Acoustic Measures of Fish Abundance. *Marine Ecol. Progress Series* 98: 223-236.
- Mackas, D.L. 1984. Spatial autocorrelation of Plankton Community Composition in a Continental Shelf Ecosystem. *Limnology and Oceanography* 29(3):451-471.
- Mackas, D.L., and Shefton, H.A. 1982. Plankton Species Assemblages off Southern Vancouver Island: Geographic Pattern and Temporal Variability. *Journal of Marine Research* 40:1173-1200.
- McGarigal, K., and Marks, B.J. 1995. *Fragstats: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. Gen. Tech. Rep. PNW-GTR-351. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.
- Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an Ecological Resource. *American Zoologist* 19:331-343.
- McLaughlin, J.F., and Roughgarden, J. 1993. Species Interactions in Space. In *Species Diversity in Ecological Communities*, ed. R.E. Ricklefs and D. Schluter, pp. 89-98. Chicago: University of Chicago Press.
- Nero, R.W., and Magnuson, J.J. 1989. Characterization of Patches Along Transects Using High-Resolution 70-kHz Integrated Acoustic Data. *Canadian Journal of Fisheries and Aquatic Sciences* 46:2056-2064.
- Nero, R.W., Magnuson, J.J., Brandt, S.B., Stanton, T.K., and Jech, J.M. 1990. Fine scale Biological Patchiness of 70 kHz Acoustic Scattering at the Edge of the Gulf Stream-Echo Front 85. *Deep Sea Research* 37:999-1016.
- Olson, R.A., Winter, J.D., Nettles, D.C., and Haynes, J.M. 1988. Resource Partitioning in South-Central Lake Ontario. *Transactions of the American Fisheries Society* 117:552-559.

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Rose, G.A., and Leggett, W.C. 1990. The Importance of Scale to Predator-Prey Spatial Correlations: An Example of Atlantic Fishes. *Ecology* 71:33-43.

Turner, M.G., and Gardner, R.H. 1990. *Quantitative Methods in Landscape Ecology*. New York: Springer-Verlag