MULTI-SCALE ANALYSIS OF EELGRASS HABITAT (*Zostera marina*) IN NEWMAN SOUND, NEWFOUNDLAND

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MULTI-SCALE ANALYSIS OF EELGRASS HABITAT (*Zostera marina*) IN NEWMAN SOUND, NEWFOUNDLAND

by

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ABSTRACT

The scale of observation affects how we perceive all ecological patterns and processes. The problem of scale is in finding ways to relate observations across space and time. In this study, I quantified two measures of eelgrass (*Zostera marina*) habitat structure as a function of spatial scale. I determined a scaling law comparing perimeter-to-area ratios of eelgrass habitat over a range of resolutions. I then used this function to compute juvenile cod abundance across scales. I also investigated the effect of spatial scale on the frequency distribution of eelgrass patch sizes. Due to temporally and spatially lagged mechanisms within eelgrass systems, I hypothesized that the frequency distribution of patch sizes for eelgrass would fit a power law. My results support this hypothesis, regardless of observation scale. In this thesis, I demonstrate that measurements taken at coarse resolutions can be used to estimate eelgrass habitat structure and cod abundance at finer resolutions using a simple scaling law. Thus, the frequency distribution of patch sizes at one scale can be computed from the frequency distribution at a scale that may be logistically more convenient to obtain.

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CHAPTER 1: INTRODUCTION AND OVERVIEW

Recognition of the importance of scale in ecology has increased radically in recent years (Gardner et al. 1989, O'Neill 1989, Weins 1989, Holling 1992, Levin 1992, Schneider 1994, Pickett et al. 1997, Gustafson 1998, Peterson et al. 1998, Ludwig et al. 2000). However, this insight has not progressed much beyond the observation that the scale of investigation does make a difference. The fundamental problem of scale is in finding ways to relate observations across space and time, and revealing what is maintained or lost in the process. One way to address the problem of scale is to find a way to compute across spatial scales. However, before investigating methods for computing information across spatial scales, we need to consider the limited range of scales for which information currently exists.

Kareiva and Anderson (1988) reviewed six years of experimental community ecology studies published in *Ecology* and found that plots used in half the studies were no larger than a meter in diameter. Their review confirmed that many ecologists study problems at scales far smaller than the scale of biological interaction and ecological patterns. In this example, spatial and temporal extent is sacrificed for experimental control; however, it is also sacrificed for increased resolution (Folt et al. 1998). Ecological studies that are conducted at spatial scales that are either too fine or too coarse can often be unsuitable, as they may fail to reveal significant relationships between the ecological variables of concern (Levin 1992).

Biological processes, such as predator-prey or competitive interactions, occur at multiple spatial scales. The impact of such processes on the distribution and abundance of organisms may only be detectable at specific scales (Pecharsky et al. 1997). For instance, correlation with prey has been reported as scale-dependent for zooplankton (Mackas and Boyd 1979. Star and Mullin 1981). marine birds (Schneider and Piatt 1986, Hunt and Schneider 1987. Logerwell and Hargreaves 1996. Logerwell et al. 1998), and Atlantic cod (Horne and Schneider 1997. Rose and Leggett 1990). It is therefore crucial that investigations be designed to integrate biological interactions with ecological patterns (e.g.. habitat structure). which are often at different spatial scales.

The effect of spatial scale on measurement is not only evident in interactions occurring between organisms. but also in associations between organisms and their habitat. Such relationships can be expected to be scale-dependent: yet. multi-scale studies of organisms and habitat are rare. Most multi-scale studies are limited to a few selected scales and may fail to detect ecologically significant distributional patterns at other scales. Murphy et al. (1998) found that the aggregation of stream invertebrates on artificial leaf packs decreased with increasing patch size (i.e. grain). as well as decreasing spatial extent of patches. The processes influencing the distributions of these invertebrates were suggested as intrinsic aggregation and resource partitioning. In another multi-scale study. Schneider et al. (1987) found the association between epibenthic megafauna and substrate to be stronger at large than at smaller spatial scales in swimming animals. The opposite was true for sessile. discretely motile and crawling animals. Thus. processes such as movement and migration can determine the spatial scale(s) over which the densities of organisms are associated with substrate variability.

Like most animals. fish associate with their habitat over a range of spatial scales. Their distributions are a result of ecological processes that operate within this range.

Associations between the density of fish and habitat are strong at some scales and non-existent at others. The scale of observation has been suggested to determine the perceived importance of a habitat variable, such as % substrate cover or vegetation density (Bult et al. 1998). In a study examining the influence of spatial scale of observation on perception of substrate use by benthic fishes, Welsh and Perry (1998) suggested that substrate use should be examined across several spatial scales They found estimates of substrate use were sensitive to small changes in spatial scale. Thus, multi-scale studies of fish-habitat interactions and multi-scale habitat models may be better at describing how fish associate with their habitat than single-scale studies and models. Despite such insights, the field of ecology has not progressed much beyond the observation that measurement scale has an effect on results. Moreover, multi-scale studies are not always logistically feasible at all relevant spatial and temporal scales. Therefore, the next logical step is to develop ways to compute across spatial scales.

In this study I quantified the complexity of eelgrass (*Zostera marina*) habitat structure as a function of spatial scale. Eelgrass is a significant habitat component for many species of fish. More fish species (Edgar and Shaw 1995) and more individuals (Branch and Grindley 1979, Orth and Heck 1980, Beckley 1983, Stoner 1983, Bell et al. 1987, Heck et al. 1989, Sogard 1989, Ferrell and Bell 1991) are associated with seagrass habitat than with unvegetated habitat. The recent collapse of northern stocks of Atlantic cod in the northwest Atlantic has sparked new interest in the ecology of juvenile Atlantic cod (Taggart et al. 1994). This commercially important species remains under fishing moratoria in some areas. Cod produces large numbers of eggs that hatch in the water column, are pelagic for a 90 day period, then settle into limited areas of suitable benthic habitat (Schneider et al. 1997). Eelgrass habitats are important nurseries for juvenile cod in the northern part of their range, providing refuge from larger predators (Gotceitas et al. 1997). Limitation of this critical habitat may be important for this species (Gotceitas et al. 1997, Linehan et al. 2001). However, we also need to consider habitat structure in addition to the total amount of eelgrass habitat. We need to take into account the effect of spatial scale on the way we perceive structure in habitat, and how this changes our estimates of organism abundance at different scales.

There are several methods that quantify habitat structure as a function of spatial scale. The first, and most common method is the 'dividers method' for measuring length by using different ruler steps (Sugihara and May 1990). The second is the 'box counting' method for 2 dimensional surfaces, such as habitat. The box counting method overlays a 2-dimensional surface with various grids of different box sizes, and counts the number of boxes containing some part of the habitat (Sugihara and May 1990, Milne 1991). These two methods produce estimates of the 'fractal dimension' (Sugihara and May 1990). The third method, derived from box counting calculates perimeter/area at each scale (Sugihara and May 1990). In this thesis, I examined this traditional method of scaling habitat using measures of perimeter and area. In addition, I also tried a novel method using frequency distributions.

A SCALING LAW FOR PERIMETER-TO-AREA RATIOS

In Newfoundland most sites with eelgrass have high densities of juvenile cod (Ings in prep.). However, eelgrass cover by itself is a poor predictor of cod abundance. The differences in abundance may be attributable to the considerable variation in size and complexity of shape of eelgrass beds. Because community and population characteristics differ between the interior and the edge of a habitat (Forman and Godron 1981). comparing such characteristics with the edge (perimeter) to interior (area) ratio of habitat is useful in evaluating the ecological importance of habitat complexity (Hamazaki 1996). The development of scaling laws that describe pattern across scales (Ludwig et al. 2000) allows for measurement of habitat complexity across spatial scales. Scaling laws are power laws that can be used to express the change in measurement for the perimeter or area of a habitat as the function of spatial scale (e.g.. resolution). The exponent of a scaling law (i.e. the scaling exponent) quantifies the change in length or area. and can be estimated by regression of perimeter-to-area against resolution. Thus. the ability to compute the perimeter-to-area ratio at any spatial measurement scale depends upon the presence of a power law relationship between perimeter-to-area ratio and resolution. Scaling laws are linked to the fractal dimension of a habitat. because the fractal dimension is calculated using the exponent of the scaling law (Mandelbrot 1982. Pennycuick and Kline 1986. Sugihara and May 1990).

Population characteristics such as gastropod density (Beck 1998). epifaunal community structure (Gee and Warwick 1994). distributions of arthropods (Morse *et a.l*1985). locust swarm formation (Despland *et al.* 1988). and feeding in ungulates (Milne *et al.* 1992) are known to be strongly associated with the fractal dimension of habitat. In red-cockaded woodpeckers (Wigley *et al.* 1999). landscape variables (including fractal dimension) were more strongly related to reproductive success than were measures of foraging substrate or area in suitable foraging habitat. This suggests that the fractal dimension is a habitat measure superior to traditional variables. such as non-scaled measures of area or perimeter (Wigley *et al.* 1999). Pennycuick and Kline (1986) also propose that the fractal dimension of coastline described the density of bald eagle nests better than perimeter alone. Scaling laws. which include fractal techniques. appear to be useful in the analysis of scaling population characteristics driven by perimeter-to-area ratios. Such analyses can quantify changes in habitat complexity across measurement scales and may allow for calculations of organism abundance across such scales. Despite this potential use. fractal techniques and scaling laws have not been widely applied to quantify population characteristics in ecology.

FREQUENCY DISTRIBUTIONS OF PATCH SIZE

Another critical issue in ecology is the effect of patchy landscapes on the distribution and abundance of species. Yet. there is no characteristic scale over which an organism's response to habitat patchiness should be measured (Hart and Horwitz 1991). It is therefore important to examine the effect of spatial scale on observations of patch sizes. High macrofaunal biomass combined with a wide range of patchiness makes eelgrass an ideal system for assessing the effects of habitat patchiness on animal abundance (Robbins and Bell 1994. Bell et al. 1995. Fonseca 1996. Eggleston et al. 1998). Eelgrass patchiness may affect populations through a variety of mechanisms. including alteration of predator distribution. abundance and foraging behaviour (Leber 1985. Main 1987. Bell and Hicks 1991. Irlandi 1994. Irlandi et al. 1995). modifications of water flow (Eckman 1983. Bell et al. 1995). and changes in animal behaviour (Heck and Crowder 1991).

Habitat patchiness is usually quantified using simple data summaries such as means. variances. or any of a variety of indices (e.g.. Taylor's Index of patchiness. Relative Richness Index. Diversity Index. Fragmentation Index: Turner 1989). Although frequency distributions are rarely used. they provide more information about the observed pattern of any given habitat characteristic than any single index. A linear regression of a frequency distribution at various resolutions can be used to characterize the effect of spatial scale on the frequency distribution of a habitat characteristic. The slope of this frequency distribution on a log-log plot is called the 'Korčak exponent' (Korčak 1940, Korvin 1992). A comparison of Korčak exponents across resolutions provides a measure of how the frequency distribution changes across spatial scale. For this investigation the effect of spatial scale on the Korčak exponent was examined using the distribution of eelgrass patch sizes in a fjord located on the northeast coast of Newfoundland, Canada. The number of small patches lost at coarse resolutions can be expected to drive the change in slope of the frequency distributions.

My intention was to determine how eelgrass characteristics could be computed across spatial scales of study, and how this may enable us to calculate abundances of juvenile Atlantic cod. The goals were to: 1) test for and characterize scaling regions for perimeter-to-area ratios in eelgrass habitats; 2) identify the extent of acceptable scaling regions; 3) to compute estimates of juvenile cod abundance within appropriate scaling regions, using a previously known model of juvenile cod abundance in eelgrass habitat (Wells et al. in prep.); 4) to calculate changes in the Korčak Exponent for patch size frequency distributions over a range of spatial scales; and 5) to develop a model that can be used to compute the frequency distribution at one spatial scale (i.e. resolution), from that at another spatial scale.

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CO-AUTHORSHIP STATEMENT

Chapter 2: A Scaling Law for Eelgrass Habitat in Newman Sound, Newfoundland

Miriam O designed and identified the research proposal, collected all field (i.e. CASI) and computational data, performed the data analysis, and prepared the manuscript. David C. Schneider contributed with development of ideas, methods and statistical analysis. Nadine J. Wells contributed data for the application section. Robert S. Gregory organized and helped with fieldwork, and the acquisition and processing of the CASI image. All co-authors contributed with the development of thoughts and editing of the manuscript.

Chapter 3: Using Power Laws to Quantify the Patch Size Distribution of Eelgrass Habitat

Miriam O designed and identified the research proposal, collected all field and computational data, performed the data analysis, and prepared the manuscript. David C. Schneider reviewed the manuscript, suggested revisions and contributed with development of ideas, methods, statistical analysis.

CHAPTER 2: A SCALING LAW FOR EELGRASS HABITAT IN NEWMAN SOUND, NEWFOUNDLAND

ABSTRACT

Ecology is a scale-dependent science. All ecological patterns and processes are affected by scale to some degree, and attempts to interpret ecological data or to apply findings are constrained by scale. The fundamental problem of scale is in finding ways to relate observations across space and time, and revealing what is maintained or lost in the process. In this study we quantified the complexity of eelgrass (*Zostera marina*) habitat structure, calculated as the ratio of perimeter-to-area, as a function of spatial scale. We then used this function to compute estimates of juvenile cod abundance across scales. We determined a scaling law comparing perimeter-to-area ratios of eelgrass habitat over a range of resolutions in a fjord on the northeast coast of Newfoundland, Canada. Consistent values were found for the exponent of the scaling law over spatial scales spanning two orders of magnitude. This indicates that large-scale features are simply magnified versions of smaller ones within this range of spatial scales. We show that measurements taken at coarse resolutions (e.g., satellite imagery) can be used to estimate eelgrass habitat structure and cod abundance at finer resolutions (e.g., aerial photography) using a simple scaling law.

INTRODUCTION

Many of the major problems in ecology require predictions at large scales, based on calculations across space and time. The problem lies in trying to understand patterns observed at one level of detail, in terms of processes that are operating on other levels. One of the main objectives in ecology is to explain the pattern of distribution and abundance of species or populations (Krebs 1978). However, ecology is a scale-dependent science, with patterns of abundance and distribution that change with measurement scale. Recognition of the importance of scale in ecology has increased in recent years (Gardner et al. 1989, O'Neill 1989, Weins 1989, Holling 1992, Levin 1992, Schneider 1994, Pickett et al. 1997, Gustafson 1998, Peterson et al. 1998, Ludwig et al. 2000). Yet, this insight has not progressed much beyond the observation that the scale of investigation makes a difference on how we perceive our environment. Applying this concept in ecology requires taking the next step, which is to develop ways to compute across spatial scales.

One way to measure habitat complexity across spatial scales is to develop scaling laws that link scale with pattern in nature (Ludwig et al. 2000). Scaling laws can be developed to quantify the effect of spatial scale resolution on the measurement of perimeter or area of a habitat. Lengths and areas of natural objects differ when we change the scale at which objects are measured (van Hees 1994). Changes in length or area with scale can be quantified using a scaling exponent. The scaling exponent can be calculated as the slope of the regression of perimeter-to-area of an object against resolution—i.e. the power law exponent for the log-linear function. It is to be expected that a highly complex (i.e. convoluted) habitat would have a greater scaling exponent than less complex habitat because changing resolutions would have a greater effect on the perimeter-to-area ratio of a highly convoluted habitat. If the relationship between perimeter-to-area ratio and resolution can be expressed as a power law, then it is possible to compute the perimeter-to-area ratio at any spatial scale of measurement. Since community and population characteristics in the interior of a habitat differ from those at the edge (Forman and Godron 1981), comparing these characteristics with the edge (perimeter) to interior (area) ratio of habitat proves useful in evaluating the ecological importance of 2-dimensional habitat complexity (Hamazaki 1996).

Fractals are a special type of scaling law, where a fractal dimension is calculated using the exponent of a scaling law (Mandelbrot 1982, Pennycuick and Kline 1986, Sugihara and May 1990). Developing scaling laws can thus be considered a prerequisite to fractal techniques. The fractal dimension of habitat is known to be strongly associated with population characteristics such as gastropod density (Beck 1998), epifaunal community structure (Gee and Warwick 1994), locust swarm formation (Despland et al. 1988), feeding in ungulates (Milne et al. 1992), and distributions of arthropods (Morse *et al.* 1985). Fractal dimension has also been suggested as a habitat measure superior to traditional variables, such as non-scaled measures of area or perimeter (Wigley et al. 1999). In a study relating reproduction of red-cockaded woodpeckers to habitat attributes, Wigley et al. (1999) found that reproductive success was more strongly related to landscape variables--including fractal dimension--than to measures of foraging substrate or area in suitable foraging habitat. Pennycuick and Kline (1986) proposed that the fractal dimension of coastline described the density of bald eagle nests better than perimeter alone. Thus, it is possible that fractal analyses of habitat can be used in scaling population dynamics driven by perimeter-to-area ratios. Such analysis can determine the nature of changes in habitat complexity across scales of study and may permit calculations of organism abundance across such scales. Despite the potential for using fractal techniques and scaling laws to quantify population parameters in ecology, few such applications currently exist.

In this study we examined whether a scaling law could be used to quantify structural complexity in eelgrass habitat (*Zostera marina*). We then used the scaling law to estimate abundance of juvenile Atlantic cod (*Gadus morhua*) in a fjord located on the northeast coast of Newfoundland, Canada. Eelgrass is a significant habitat in Newfoundland coastal waters. Past studies have shown that fish species diversity and density are associated more with seagrass habitat than with less complex unvegetated habitat, such as sand or mud (Branch and Grindley 1979, Orth and Heck 1980, Beckley 1983, Stoner 1983, Bell *et al.* 1987, Heck *et al.* 1989, Sogard 1989, Ferrell and Bell 1991, Edgar and Shaw 1995, Gotceitas et al. 1997). The recent collapse of *Gadus morhua* in the northwest Atlantic has sparked interest in the ecology of juveniles of this species. This once commercially dominant demersal species has been under a fishing moratorium in many Canadian areas since 1992 (Taggart et al. 1994). Atlantic cod produce large numbers of eggs that hatch in the water column, are pelagic for an approximately 90 day period (Anderson and Dalley 1997), then settle to the bottom in limited areas (Schneider et al. 1997). After *Gadus morhua* settle, eelgrass habitats are considered important nurseries for juvenile cod, providing refuge from larger predators (Gotceitas et al. 1997, Linehan et al. 2001). Limitation of this critical habitat is believed to be important for this species (Tutin 1942. Tveite 1984. Gotceitas et al. 1995). However. because the structure of habitat is known to influence quality of refuge (Gotceitas and Colgan 1989). the structure of this habitat also needs to be considered. in addition to the total amount of eelgrass cover.

Our intention was to quantify eelgrass structure as a function of different spatial scales. and then use this function to estimate the abundance of juvenile Atlantic cod in this critical habitat. In this study we: 1) determined the scaling law between perimeter-to-area ratios and resolution for eelgrass habitats. 2) identified the range of scales over which this scaling law was applicable (i.e. the 'scaling region'). and 3) estimated juvenile cod abundance within this scaling region. using a model of juvenile cod abundance in eelgrass habitat (Wells et al. in prep).

METHODS

Study Area

Our study area was located in Newman Sound. a fjord located in southwestern Bonavista Bay. on the northeastern coast of Newfoundland. Canada (48°35' N. 53°55' W). The maximum depth within the sound ranges between 55 m (inner sound) to ~300 m (outer sound). Nearshore (<10 m deep) substrate includes mud. silt. sand. gravel. cobble. and bedrock. Eelgrass was associated with mud. silt. sand. and gravel substrates. Macroalgae (*Laminaria digitata* Lamouroux. *Agarum cribrosum* Bory. *Chondrus crispus* Stackhouse. *Fucus vesiculosus* L.. and *Ascophyllum nodosum* (L.) Le Jolis) was associated with the coarse cobble and bedrock substrates (Linehan et al. 2001). Where present, eelgrass was generally restricted to depths shallower than 6 m in Newman Sound. Winter sea conditions in this area are severe due to the Labrador Current and its transport of pack ice and icebergs formed in Greenland and the Labrador Sea, occurring generally between March and July each year (Murray 1969, Dinsmore 1972, NORDCO 1980). Coves within and outside Newman Sound often freeze over during the winter, due to freshwater input from streams and rivers.

Newman Sound was selected as our study area because eelgrass was present along much of the shallow nearshore environment in a wide range of structural complexities. Furthermore, data from previous and concurrent juvenile cod studies were available for the Newman Sound area (Crocker et al. in prep, Gorman et al. in prep, Gregory et al. 2001, Ings et al. in prep, Norris et al. in prep, Sargent et al. in prep, Wells et al. in prep).

Habitat Mapping

We used a compact airborne spectrographic imager (CASI) to obtain thematic images of eelgrass habitat in the study area. CASI is a multispectral imager operating in the visible and near infrared (470-876 nm) region of the light spectrum. This imager can be configured for quantitative digital mapping of marine habitats (Ritter and Lanzer 1997). CASI imagery was collected July 26-31, 1999, from a maximum height of 3600 m. Habitat was classified using previously known spectral signatures, and then further calibrated using extensive on-site ground truth data. The resulting thematic image consisted of shallow marine habitats spanning the entire coastline of Newman Sound (Figure 2.1).

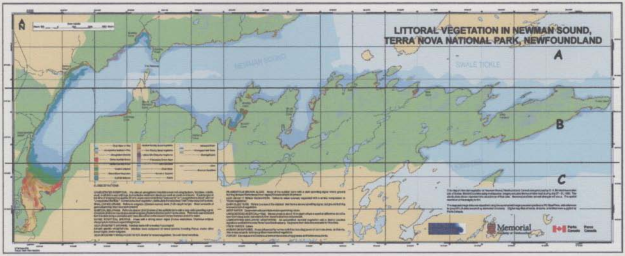

Figure 2.1. Map of shallow marine habitat in Newman Sound, Newfoundland. Green and turquoise areas represent eelgrass habitat. To determine if the scaling exponent of eelgrass was constant across the study area, we divided the imagery of Newman Sound into three subsections of equal area: A) Image 1 contained the North Subsection of the imagery; B) Image 2 contained the Middle Subsection of the imagery; and C) Image 3 contained the South Subsection of the imagery.

Ground Truth Methods

We obtained extensive habitat data to calibrate the spectral signatures applied in the habitat classification. In total, we collected data from 322 ground truth points within the study area. The imagery was revised based on pixel characteristics from these points of known habitat composition. All of the areas mapped in Newman Sound were ground truthed using a 4m aluminum boat, at low tide, and as close as possible to the dates of the CASI flights. Sites of all areas of significant interest were surveyed (e.g., major eelgrass and algae beds). Within these sites, areas of relatively uniform habitat were surveyed at 50 m intervals along the shoreline. When possible, 2-3 points were surveyed at each interval perpendicular to the shore, from shallow into deeper water. In areas of heterogeneous habitat, surveys were performed in the same manner, but more often, in order to record as many habitat types as possible. Surveys were restricted where possible to pure, dense and extensive features. We used large features because positioning error was about 3 pixels (12 x 12 m), even with differential GPS. Thus, selected features had to be at least 5 x 5 pixels (20 x 20 m) to be useful as a ground truth point.

CASI data were obtained in line transects flown under varying conditions of illumination, tide, and visibility. To account for possible variations in spectral signal from different sections of the imagery, which were acquired over six days, we ground truthed data from all parts of the image over 21 days. Different areas of the same habitat type can have slightly different spectral characteristics depending on factors such as desiccation, physiological state, degree of substrate coverage, and presence of other species. CASI data for several sites of the same habitat type provided the expected variability in the spectral characteristics for that class (G. Borstad unpublished).

At every site surveyed, overlying water was measured using a weighted length of line. Tide height was recorded at the time of ground truth. Landmarks were used to mark every site on a map as a backup of position. We recorded data on substrate type, % coverage of the vegetation, dominant vegetation (or relative proportion in a mixed vegetation bed), and the presence of any coloured organism (e.g., smooth cord weed, *Chorda filum*) or geological features.

Box-counting method

We used a box-counting method (Rodriguez-Iturbe and Rinaldo 1997) to quantify eelgrass habitat at varying scales of resolution. The imagery was in raster (i.e. grid) format, therefore, boxes represented pixels in the imagery. Box-counting consisted of gathering contiguous pixels into boxes, and then quantifying the habitat characteristic at each successive resolution or box size. The outcome was a series of counts of grid boxes containing habitat for various box sizes.

We began the box-counting process with a map of eelgrass habitat mapped at a pixel size of 16 m^2 (4m x 4m pixel). We quantified potential habitat by first counting the number of 16 m^2 pixels that contained 100 % eelgrass habitat. The number of pixels was then converted to the area of eelgrass (m^2). We quantified perimeter by counting the boxes containing 100 % eelgrass along the perimeter of the habitat, and converting this number to a measure of length (m). After these conversions we then took the ratio of the perimeter to the area. The pixels were then aggregated by 2 on a side (8m x 8m), 3 on a side (12m x 12m), and so on up to 20 on a side (80m x 80m). The next 5 maps of eelgrass distribution were produced by aggregating pixels by 10 on a side, to 30 x 30 pixels (120m x 120m), 40 x 40 pixels (160m x 160m), 50 x 50 pixels (200m x 200m), 60 x 60 pixels (240m x 240m), and 70 x 70 pixels (280m x 280m). After every aggregation we then counted all the boxes that contained at least 50% eelgrass by area, as well as boxes along the perimeter of the habitat. We did not use maps at coarser resolutions because the box size became too large to accurately measure perimeter and area of eelgrass habitats. For instance, a cove containing 30-40 % eelgrass would be classified as a non-eelgrass area if the size of the box exceeded the size of the cove. Nevertheless, the resolutions of these maps provide a range of nearly four orders of magnitude in box size.

Data Analysis

We described the structural complexity of eelgrass habitat as the perimeter to area ratio, and measured this parameter across a wide range of scales. To determine if the scaling exponent of eelgrass was constant across the study area, we divided the imagery of Newman Sound into three subsections of equal area. Image 1 contained the North Subsection of the imagery, Image 2 contained the Middle Subsection of the imagery, and Image 3 contained the South Subsection of the imagery (Figure 1). Within each of the three regions, all eelgrass patches were aggregated in calculating the P/A ratio. Our criteria for identifying a 'scaling region' were 1) the relation between perimeter to area ratio and resolution could be expressed as a power function (linearity on a log-log plot), and 2) the slopes for all three images were homogeneous (determined using ANCOVA). We examined the residuals from the regression to verify that these were homogeneous.

independent and normal. Logarithms were taken for both the ratio of perimeter to area [P (m)/A (m^2)] of eelgrass and the corresponding box area, or resolution (R). Thus, the relation between the two was:

$$Log_e(P/A) = \alpha + \beta \cdot Log_e R \qquad (2.1)$$

This is equivalent to the power law:

$$P/A = e^{\alpha} R^{\beta} \qquad (2.2)$$

where β is the slope of the regression.

The exponent of the power law is also known as the scaling exponent, which is the slope of the plot for the range of scales over which the power law relationship applies.

We used ANCOVA to compare the relationship between P/A and resolution across the three images, in order to find a scaling region with a slope β common to all images. The model for this ANCOVA was:

$$Log_e(P/A) = \beta_o + \beta_R \cdot Log_e R + \beta_I \cdot I + \beta_{RI} \cdot Log_e(R \cdot I) \qquad (2.3)$$

where P = perimeter (m), A = area (m^2), β_o = overall mean, β_R = overall slope, R = resolution (m^2), β_I = mean for each image , I = image (i.e. 1, 2, or 3), and β_{RI} = slope for each image. This model results in a power law with two exponential terms:

$$P/A = e^{\beta_o} R^{\beta_R - \beta_{RI} I} e^{\beta_I I} \qquad (2.4)$$

RESULTS

We found that the perimeter-to-area relationship for eelgrass habitat did not fit a power function over the entire range of resolutions examined (Figure 2.2 A). However, an intermediate section described by a power law was found between the resolutions of 784

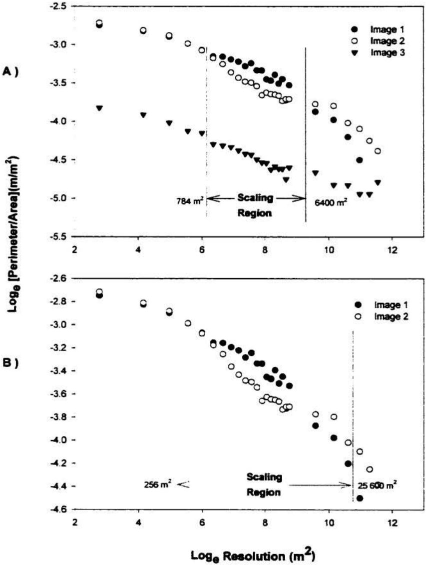

Figure 2.2. The relationship between perimeter-to-area ratios and resolution for eelgrass habitat in Newman Sound. A) Including all CASI images. B) Including Image 1 and Image 2 only.

m^2 and 6400 m^2, which we called the 'scaling region'. This intermediate section was determined as the region where a power law was applicable, and where the slope was the same for all three images ($F_{2,36}=0.69$, $p=0.507$, $SS_{total}=11.23$). Because the interaction between resolution and image was not significant, this term was removed from the model. The slope (β_R), or scaling exponent of the revised model, within the scaling region was –0.202. After substituting the parameter estimates for the overall slope (β_R) and the overall mean (β_o) into Equation 2.3, the formal model was:

$$Log_e\,(P/A) = -3.8197 + -0.202\,Log_e R - \beta_I I. \tag{2.5}$$

which expressed as a power function becomes:

$$P/A = e^{-3.8197} R^{-0.202} e^{\beta_I I} \tag{2.6}$$

($F_{1,36} = 275.14$, $p<0.001$, $SS_{total}=11.23$).

The South Subsection (i.e. Image 3) contained very little eelgrass, and did not have the range of patchiness seen elsewhere in the study area. After removing this image from the analysis, the resulting scaling region included resolutions between 256 m^2 and 25,600 m^2 (Figure 2.2 B). The slope (β_R), or scaling exponent, within the scaling region was –0.203. The image (I in Equation 2.3) and resolution by image ($R \cdot I$ in Equation 2.3) terms were removed from the model because they were not significant ($F_{1,34} = 2.21$, $p=0.147$, $SS_{total}=2.41$ and $F_{1,34} = 0.56$, $p=0.461$, $SS_{total}=2.41$ respectively). Equation 2.2 shows the formal model for the ANCOVA. After substituting the parameter estimates for the overall slope (β_R) and the overall mean (β_o) into Equation 2.3, the formal model was:

$$Log_e\,(P/A) = -3.4491 + -0.203\,Log_e R \tag{2.7}$$

This equation can also be expressed as the power function:

$$P / A = e^{-3.4491} R^{-0.203} \quad (2.8)$$

($F_{1,34} = 354.36$, $p<0.001$, $SS_{total} = 2.41$).

For the analysis including all three subsections, and the analysis including only the North and Middle Subsections (i.e. Image 1 and 2), we found that the relation of the perimeter-to-area ratio to resolution fit a power function over a wide range of resolutions. Thus, we were able to determine a scaling exponent for eelgrass habitats over these resolutions.

DISCUSSION

The search for consistent scaling relations (Bak et al. 1988) and the dynamic processes that generate them (Tainaka 1994, Loreto et al. 1995, Vespignani et al. 1995, Grassberger and Zhang 1996, Milne 1998) are essential to understanding complex ecological systems. Scaling relations (Stanley et al. 1996) are a major analytical tool in studying complexity, in which the behaviour of a system can be described as a function of a parameter, temporal scale, spatial scale, or all three. Scaling relations indicate that the system is controlled by rules that propagate across a wide range of scales (Meakin 1993). The limits of power law relations reveal domains of scale over which particular processes operate (Krummel et al. 1987, Weins 1989, Weins and Milne 1989). Domains of scale are interpreted as evidence of hierarchical organization in nature (Allen and Star 1982, King 1997).

In this study, we have described the complexity of the eelgrass habitat in terms of its perimeter-to-area ratio, and measured this parameter across a wide range of scales, as defined by the resolution of the remotely sensed imagery. Over the entire range of resolutions. the relationship between perimeter-to-area ratio and resolution was not linear. However. an intermediate range. the 'scaling region' (Nikora et al. 1999). was found where a power function was applicable. and the slope was the same for all images. The significance of this finding is that a coarse measurement of the perimeter-to-area ratio can be taken at a low resolution (e.g.. 6400 m^2) and calculated to high resolutions (e.g.. 784 m^2) using a simple power function. Furthermore. we can apply this function to new data sets within the scaling region because the scaling exponent was constant for all images. A non-linear function would be required to calculate beyond the scaling region. After removing Image 3 from the analysis. the resulting scaling region included the resolutions between 256 m^2 and 25.600 m^2. Thus. a coarse measurement taken at a resolution of 25.600 m^2 can be calculated down to the scale of 256 m^2 using a simple power function. Consistent values for the scaling exponent. $\beta = -0.203$. were obtained over spatial scales spanning two orders of magnitude. The removal of the image inconsistent with the rest of the study area resulted in a significant increase in the range of the scaling region. Therefore. we will focus our discussion on inferences derived from the analysis of the first two images.

Different processes affect the distribution of eelgrass at various scales. A power function did not describe the system over the widest range of spatial scales. However. it is likely that an object does not have the same structure over all measurement scales. Hence. a scaling region spanning a limited range of resolutions is to be expected. Furthermore. the biological and physical processes generating these power functions are expected to operate over a restricted range of scales (Bradbury *et al.* 1984). These restricted ranges. or 'scaling regions' are found in geomorphology (Rodriguez and Iturbe 1997). and in various measures of landscape heterogeneity (Nikora *et al.* 1999). A constant scaling exponent over a range of resolutions indicates that within this region large-scale features are magnified versions of smaller ones. A sudden change in scaling exponents reflects a scale-dependent threshold that is probably caused by different landscape processes operating within distinct scaling regions (Ludwig et al. 2000). Thus, the shift in scaling exponent at either end of the scaling region defines the limits within which interpolation is possible (Sugihara and May 1990). There may be 'domains' of scale (i.e., scaling regions), within which functional relationships remain relatively constant and interpolation is possible (Weins 1989, Ludwig et al. 2000).

It is expected that structuring mechanisms of eelgrass, a type of seagrass, would change within each domain of scale. In general, seagrass beds exhibit 'domains of scale' in biological structure, ranging from individual rhizomes and groups of shoots (centimetres to metres), to discrete patches of seagrass (metres to tens of metres), to seagrass landscapes (tens of metres to kilometres) (Duarte and Sand-Jensen 1990a and b, Duarte et al. 1994, Olesen and Sand-Jensen 1994, Robbins and Bell 1994, Irlandi et al. 1995, Turner et al. 1996, 1999). For eelgrass systems on the northeast coast of Newfoundland, it is likely that the physiology of eelgrass would affect growth patterns (e.g., by underground root systems called rhizomes) at small scales (<10m^2). At intermediate scales (100s of m^2) freshwater input, depth, or substrate could affect discrete patches. Wind exposure, ice scouring, temperature and coastline structure may regulate the structural complexity of eelgrass landscapes at large scales (100s of m^2 to 1000s of m^2). And at even larger scales (> km^2), oceanographic processes could determine the distribution of eelgrass along this coast. For example, alongshore currents could transport eelgrass seeds from one cove to the next, where successful colonization would depend upon a combination of suitable substrates, temperature, wind exposure, salinity and coastline structure. The constant scaling exponent within our scaling region suggests the possibility of processes generating self-similar eelgrass structure within this intermediate range of resolutions (256 m^2 to 25, 600 m^2). The processes dominating eelgrass structure within this scaling region are unknown. We can however, speculate that the break point at either end of the scaling region suggests changes in the domain of scale, signalling a switch in ecological or environmental processes.

Computing Juvenile Cod Abundance from the Scaling Exponent of Eelgrass Habitat

Many biological variables cannot be remotely sensed. Hence, there is need for scaling relations that connect remotely sensed variables (i.e., habitat variables) to population variables, such as density, biomass, production, movement, recruitment, and mortality. Ideally, studies linking population variables to habitat should be performed at the scale at which information is obtained in the field. However, fine resolution maps that span large areas are expensive and inconvenient to produce. As a result, coarse scale maps are most commonly used in large-scale population studies that span large areas (e.g., Anderson and Dalley 1997). This creates a need for calculating population variables across spatial resolutions. Using remotely sensed imagery, scaling exponents can be estimated over a scope wide enough to be useful, from large areas down to small-scale plots practical for experiment and direct measurement of population and community dynamics.

Estimates of fish abundance are normally required at both local (e.g., point source habitat changes) and global scales (e.g., stock assessment), but field measurements are limited to small scales (Figure 2.3). Eelgrass is an important habitat for age 0 Atlantic cod within a narrow band off the coast of northeast Newfoundland (Linehan et al. 2001). Thus, scaling relations can link population abundance of age 0 cod to eelgrass habitat within this zone. Here, we attempt to demonstrate how scaling laws can be derived and applied to calculations of population estimates from habitat complexity. This catch estimate is dependent upon factors that affect catch per seine haul, including type of site, time of day, tide cycle and seasonal timing. We used the fish catch data for the months of September and October only, since juvenile cod abundance is most predictive of year-class strength during these months in Newfoundland (Gregory et al. 2001). We assumed that distributional patterns among eelgrass habitats are most apparent during these months. This calculation assumes that no age 0 cod exist outside the 55m reach of the beach seine; an assumption we know to be false. However, Methven and Schneider (1998) found most age 0 cod within this 55m reach, suggesting this assumption is not far off. It is also important to note that the sites that were seined do not necessarily represent all sites along the coastline. Many sites within Newman Sound are not seinable and may have lower abundances of juveniles due to the nature of unseinable substrate or habitat (e.g., sandy/rock substrate, rocky/vertical cliff shorelines). Our intent here is to demonstrate the use of a scaling function to obtain a first cut estimate that recognizes the dependence of ecological variables on spatial scale. This demonstrates how scaling laws can be derived and applied to calculations of population estimates from habitat complexity.

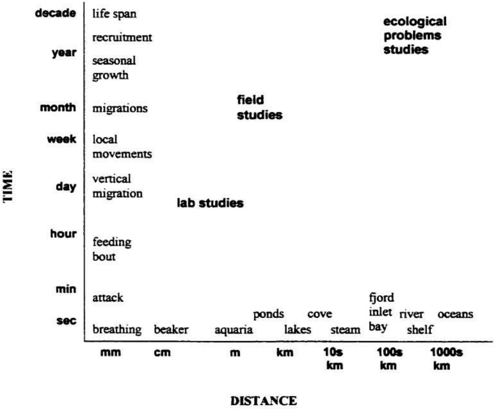

Figure 2.3. The gap between the temporal and spatial scales of the ecological problems we are trying to understand, and the mechanisms observed in field and lab studies.

Using the scaling exponent of eelgrass habitat, we calculated fish abundance within a 55 m band (i.e. the scale of typical field measurements using a beach seine: Methven and Schneider 1998, Linehan 2001). Wells et al. (in prep.) found that catch of age 0 cod increased with the scaling exponents of eelgrass habitats (Figure 2.4). The scaling exponent for eelgrass habitat in Newman Sound ($\beta = 0.202$) and fish catch can be used to estimate the density of age 0 cod as 50.1 fish per seine haul (area=880 m^2).

Further, we can calculate the number of 16-metre wide beach seines that fit along the coastline of Newman Sound, and estimate how many age 0 cod are in the sound, assuming that there were no age 0 cod beyond the 55 m extent of the seine from the beach. This can be accomplished by using the dividers method (Mandelbrot 1982, Sugihara and May 1990) to calculate the fractal dimension of the coastline for Newman Sound. The dividers method consists of measuring the length of the coastline using different ruler sizes. The lengths of the coastline were regressed against size of the measurement ruler, and the fractal dimension was then calculated from the slope of the regression (methodological details in Ings, in prep.). We calculated the fractal dimension of the Newman Sound coastline to be $D = 1.2188$ using a topographic map (scale 1: 50,000). We calculated the number of 16-metre beach seines that fit along the Newman Sound coastline by:

$$CL_{fine} = CL_{coarse} (L_{fine} / L_{coarse})^{1-D}. \qquad (2.9)$$

where CL_{fine} is the coastline length at the scale of 16m, CL_{coarse} is the coastline length at 180m, L_{fine} is the length of the ruler at 16m, L_{coarse} is the length of the ruler at a 180m, and D is the fractal dimension of the Newman Sound coastline (see Appendix 1 for derivation of Equation 2.9). Through substituting values for CL_{coarse}, L_{coarse}, L_{fine} and D

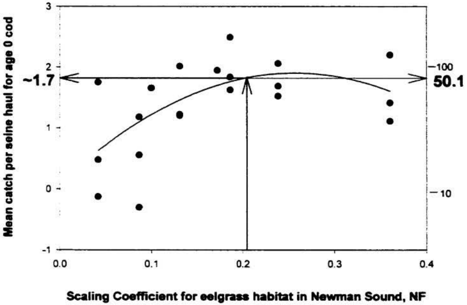

Figure 2.4. Catch of age 0 cod increased with the scaling exponents of eelgrass habitats. The scaling exponent for eelgrass habitat in Newman Sound (ß = 0.202) and fish catch can be used to estimate the density of age 0 cod as 50.1 fish per seine haul (area=880 m2). Data from Well et al. (in prep.).

into Equation 2.9, we calculated the coastline length to be:

$CL_{fine} = CL_{16m}$ = 17,820 m (16 m /180 m) $^{1-1.22}$ = 30,350 m = 30.350 km

Therefore, the number of 16 m beach seines that fit along the coastline of Newman Sound can be calculated by dividing CL_{16m} by 16 m:

# of 16 m beach seines = CL_{16m} / 16 m = 30,350 m / 16 m = 1,896.88 beach seines

To calculate an estimate of how many juvenile Atlantic cod are within 55 m of the shore in Newman Sound, we took the product of beach seines and catch per seine haul to obtain:

1,896.88 beach seines x 50.1 fish per seine haul ≈ 95,000 juvenile Atlantic cod along the coastline of Newman Sound. This calculation needs a final correction that computes the proportion of sites at the scale of a 16m beach seine that contain eelgrass habitat within 55 m of the shore.

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CHAPTER 3: USING POWER LAWS TO QUANTIFY THE PATCH SIZE DISTRIBUTION OF EELGRASS HABITAT

ABSTRACT

The scale of observation affects how we perceive all ecological patterns and processes. As a result, attempts to interpret ecological data or to apply ecological findings are often constrained by scale. The fundamental problem of scale is in finding ways to relate observations across space and time, and revealing what is maintained or lost in the process. In this study, we investigated the effect of spatial scale on the frequency distribution of eelgrass (*Zostera marina*) patch sizes in a fjord on the northeast coast of Newfoundland, Canada. Based on the dynamics of this system, we hypothesized that the frequency distribution of patch sizes for eelgrass would fit a power law. We found that the patch size distribution fit a power law, which is consistent with complexity generated by competing exponential rates. We show that the full frequency distribution of patch sizes at one scale can be computed from the frequency distribution at a scale that may be logistically more convenient to obtain. Thus, less expensive coarse resolution maps may be used to calculate the patch size frequency distribution at the smaller scales common for many population field studies.

INTRODUCTION

One of the key goals of ecology is to explain patterns of distribution and abundance of species or populations (Krebs 1978). However, such patterns change with the scale of measurement. The description of any system depends on the spatial and temporal perspective chosen. All ecological patterns and processes depend on scale of measurement, and attempts to make sense of ecological data or to use ecological findings in management are constrained by scale (Peterson et al. 1998). Hence, it is essential to understand not only how patterns and dynamics vary with scale, but also how patterns at one scale are expressions of processes operating at other scales (Holling 1992). The fundamental problem of scale is in finding ways to relate observations across space and time, in understanding how information is transferred across scales, and revealing what is maintained or lost in the process. Although recognition of the importance of scale in ecology has greatly increased in recent years (Gardner et al. 1989, O'Neill 1989, Weins 1989, Holling 1992, Levin 1992, Schneider 1994, Pickett et al. 1997, Gustafson 1998, Peterson et al. 1998, Ludwig et al. 2000), this insight has not progressed much beyond the observation that the scale of investigation does make a difference. The next logical step is to develop methods to compute across spatial scales.

The effect of patchy landscapes on the distribution and abundance of species is a critical issue in applied ecology. Habitat patchiness affects population dynamics, such as recruitment (Minchinton 1997, Eggleston et al. 1998, Hertzberg et al. 2000), settlement (Bologna and Heck 2000), feeding (Turner et al. 1991) and predation (Gorman et al. in prep, Irlandi et al. 1995). Yet, there is no single scale at which an organism's response to habitat patchiness should be measured (Hart and Horwitz 1991). Thus, it is important to examine the effect of spatial scale on observations of patch sizes in habitat. High macrofaunal biomass combined with a wide range of patchiness, makes eelgrass an ideal system for assessing the effects of habitat patchiness on animal abundance (Robbins and Bell 1994, Bell et al. 1995, Fonseca 1996, Eggleston et al. 1998). Eelgrass patchiness may affect populations through a variety of mechanisms, including alteration of predator distribution, abundance and foraging behaviour (Leber 1985, Main 1987, Bell and Hicks 1991, Irlandi 1994, Irlandi et al. 1995), modifications of water flow (Bell et al. 1995), and changes in animal behaviour (Heck and Crowder 1991). In this study, we investigated patchiness of eelgrass habitats as a function of spatial scale for the northeast coast of Newfoundland, Canada.

Quantification of habitat patchiness is usually accomplished with simple data summaries such as means, variances, or any of a variety of indices (e.g., Taylor's Index of patchiness, Relative Richness Index, Diversity Index, Fragmentation Index; Turner 1989). However, a more informative method of measuring the 'patchiness' of a habitat across spatial scales is to compare the frequency distribution of patch sizes to map resolution (i.e. spatial scale). A full frequency distribution provides more information than any single summary statistic or index used to describe habitat. Further, any index can be computed from the frequency distribution. The frequency distribution of patch sizes (at the scale specific to a biological mechanism) can be used to calculate the impact of a mechanism on a population. For example, if the scale is known at which animal numbers depend on habitat, then the patch size frequency distribution at that scale can be used to quantify the abundance of this animal in this habitat. From this frequency distribution simple data summaries such as means, variances, or any of a variety of indices can be calculated.

Frequency distributions that fit a power law result from two competing exponential rates that are temporally or spatially lagged (Stanley et al. 1996). The contest between these rates must be unequal. For example, unequal accumulation and release of energy occurs during earthquakes along faultlines (Bak and Chen 1995, Stanley et al. 1996), or during forest-fires (Loreto et al. 1995). Sole and Manrubia (1995) found that the size distribution of gaps in a rainforest fit a power law. They attributed this finding to processes of gap formation (i.e. treefall) and regeneration, which are major influences in tropical ecosystems (Whitmore 1991). A gap in the rainforest is formed, not only by a single tree, but also by vines attached to neighbouring trees. This causes a domino-like collapse, resulting in a much larger gap than would be formed by the fall of a single tree. Successional phases then slowly begin to regenerate the forest within this opening (Jonsson and Esseen 1990). For eelgrass systems on the northeastern coast of Newfoundland, ice scouring events and growth act as competing rates that are both temporally and spatially lagged. Growth and ice scouring occur on two very different time scales. While growth is steady throughout the summer months (June to August), ice scouring events occur rapidly and episodically during the winter months (December to May). Furthermore, it is likely that the destruction caused by ice scouring events occurs at a much larger spatial scale than the regeneration of eelgrass shoots. Based on these dynamics, we hypothesize that the frequency distribution of patch sizes for eelgrass will fit a power law.

The slope of a frequency distribution that follows a power law distribution is called the 'Korčak exponent' (Korčak 1940, Korvin 1992). In geography it is well known that the size of islands follows a power law distribution, that is called Korčak's (1940) law:

$P [A > a] = k\, a^{-b}$,

where $P [A > a]$ is the frequency of islands of size $A > a$, and b is the Korčak exponent. The Korčak exponent is assumed to remain constant over different spatial scales (Mandelbrot 1975, Rodriguez-Iturbe and Rinaldo 1997). To investigate the effect of spatial scale on the size distribution of eelgrass patches we compared Korčak exponents across resolutions of imagery.

We investigated whether patch size distributions for eelgrass habitat on the northeast coast of Newfoundland changed over spatial scales. We hypothesized: 1) the frequency distribution of patch sizes for eelgrass habitat would fit a power law called Korčak's Law (Korčak 1940), and 2) the slope of the frequency distribution (the Korčak exponent) of patch size, would change depending on the resolution of the imagery.

METHODS

Study Area

Our study area was Newman Sound, a fjord located in southwest Bonavista Bay, on the northeastern coast of Newfoundland, Canada (48°35' N, 53°55' W). The maximum depth within the sound ranges between 55m (inner sound) to ~300 m (outer sound). Nearshore (<10 m deep) substrate includes mud, silt, sand, gravel, cobble and bedrock.

Eelgrass (*Zostera marina*) is associated with mud, silt, sand and gravel substrates. Macroalgae (*Laminaria digitata* Lamouroux, *Agarum cribrosum* Bory, *Chondrus crispus* Stackhouse, *Fucus vesiculosus* L., and *Ascophyllum nodosum* (L.) Le Jolis) is associated with the coarse cobble and bedrock substrates. Where present, eelgrass is generally restricted to depths shallower than 6 m in Newman Sound. The cold Labrador Current transports icebergs from Greenland and pack ice formed in the Labrador Sea along the northeast coast of Newfoundland between March and July each year (Murray 1969, Dinsmore 1972, NORDCO 1980). Coves in the vicinity of Newman Sound often freeze over during the winter, due to freshwater input from streams and rivers.

Newman Sound was selected because eelgrass was present along much of the shallow nearshore environment (<10 m deep) and occurred in a wide range of structural complexities. Further, data from previous and concurrent studies on nearshore interactions between juvenile cod and eelgrass habitat were available for the Newman Sound area (Crocker et al. in prep, Gorman et al. in prep, Ings et al. in prep, Norris et al. in prep, Sargent et al. in prep, Wells et al. in prep, Gregory et al. 2001, Linehan et al. 2001).

Habitat Mapping

We used a compact airborne spectrographic imager (CASI) to obtain thematic images of eelgrass habitat in the study area. CASI is a multispectral imager operating in the visible and near infrared (470-876 nm) region of the light spectrum, which was configured for quantitative digital mapping of marine habitats (Ritter and Lanzer 1997). CASI imagery was collected July 26-31, 1999, from a height of 3600 m. Habitat was classified using previously known spectral signatures, then further calibrated using extensive on site ground truth data. The resulting thematic image consisted of shallow marine habitats spanning the entire coastline of Newman Sound (Figure 3.1).

Ground Truth Methods

We obtained extensive habitat data to calibrate the spectral signatures applied in the habitat classification. In total, we collected data from 322 ground truth points within the study area. The imagery was revised based on pixel characteristics from these points of known habitat composition. All of the areas mapped in Newman Sound were ground truthed using a 4m aluminum boat, at low tide, and as close as possible to the dates of the CASI flights. Sites of all areas of significant interest were surveyed (e.g., major eelgrass and algae beds). Within these sites, areas of relatively uniform habitat were surveyed at 50 m intervals along the shoreline. When possible, 2-3 sites were surveyed at each interval perpendicular to the shore, from shallow into deeper water. In areas of heterogeneous habitat, surveys were performed in the same manner, but at a greater frequency, in order to record as many habitat types as possible. Surveys were restricted where possible to pure, dense and extensive features. We used large features because positioning error was about 3 pixels (12 x 12 m), even with differential GPS. Thus, selected features had to be at least 5 x 5 pixels (20 x 20 m) to be useful as a ground truth point.

CASI data were obtained in line transects flown under varying conditions of illumination, tide, and atmosphere. We ground truthed data from all parts of the image

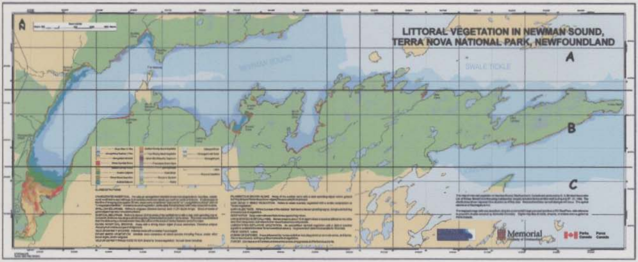

Figure 3.1. Map of shallow marine habitat in Newman Sound, Newfoundland. Green and turquoise areas represent eelgrass habitat. To determine if the scaling exponent of eelgrass was constant across the study area, we divided the imagery of Newman Sound into three subsections of equal area: A) Image 1 contained the North Subsection of the imagery; B) Image 2 contained the Middle Subsection of the imagery; and C) Image 3 contained the South Subsection of the imagery.

over 21 days, thereby accounting for possible variations in spectral signal from different sections of the imagery acquired over 5 days. Different areas of the same habitat type can also have slightly different spectral characteristics depending on factors such as desiccation, physiological state, degree of substrate coverage, and presence of other species (G. Borstad, unpublished).

At every site surveyed, overlying water was measured using a weighted length of line, and tide height was recorded at the time of ground truth. Landmarks were used to mark every site on a map as a backup of position. We recorded data on substrate type, % coverage of the vegetation, dominant vegetation (or relative proportion in a mixed vegetation bed), and the presence of any coloured organism (e.g., smooth cord weed, *Chorda filum*) or geological features.

Box-counting method

We used a box-counting method (Rodriguez-Iturbe and Rinaldo 1997) to quantify eelgrass habitat at varying scales of resolution. The imagery was in raster (i.e. grid) format, therefore, boxes represented pixels in the imagery. Box-counting consisted of gathering contiguous pixels into boxes, and then quantifying the habitat characteristic at each successive resolution or box size. The outcome was a series of counts of grid boxes containing habitat for various box sizes.

The box-counting method was initially performed with imagery of eelgrass habitat mapped at 4m x 4m pixel size. Using the GROUP module in the IDRISI 32 software package, we determined contiguous groupings of eelgrass habitat cells in an image. Cells belonging to the same contiguous grouping were given a unique 'patch' identifier. We included diagonals in defining groups, or patches. Cells were considered to belong to the same group if they had the same value and they touched in any of the eight possible directions, N, E, S, W, NW, NE, SW, SE. Holes within eelgrass patches were removed from the analysis by overlaying this image with a Boolean (i.e. binary) image that classified all non-eelgrass pixels as 'zero'. As a result, all non-eelgrass pixels were multiplied by zero, thereby cancelling them out of the patch size analysis.

The subsequent map was produced by aggregating the pixels by 2 on a side (i.e. to 8m x 8m). We then classified all the boxes that contained at least 50% eelgrass as "eelgrass" boxes, and repeated the GROUP module process. The pixels were then aggregated by 3 on a side (to 12m x 12m), 4 on a side, 5 on a side and so on until the frequency distribution consisted of only 3 patch sizes (i.e. the number of data point necessary for a regression analysis). Thus, the number of patch size categories limited the range of scales used in our analyses.

Data Analysis

We used ordinary least squares regression to estimate the slope and intercepts of the patch size frequency distributions. Logarithms were taken for both the frequency of eelgrass patches (N) and the corresponding patch size [P (m^2)]. Thus, the relation between the two was:

$$log_e N = \alpha - \beta \, log_e P \qquad (3.1)$$

which is equivalent to the power function:

$$N = e^{\alpha} P^{\beta} \qquad (3.2)$$

where β is the slope of the regression, and α is the Y-intercept for the log-log regression.

The exponent of the power function is also called the Korčak exponent when used to characterize frequency distributions (Korvin 1992). We examined the residuals from the regression to verify that there were no systematic deviations of the data from the model, and that the residuals were homogeneous, independent and normal.

The parameters of the patch size frequency distributions (i.e. β and α) were then regressed against resolution. This was done to detect if the effect of spatial scale on these parameters could be modeled linearly. The logarithm was taken for resolution (R), but not for slope (β) since the slopes were negative. To keep the analysis consistent, the logarithm was taken for R, but not the parameter α.

The relation between resolution and Korčak exponent was:

$$\beta = \gamma_1 - \gamma_2 \log_e R \tag{3.4}$$

which is equivalent to the function:

$$e^{\beta} = e^{\gamma_1} R^{\gamma_2} \tag{3.5}$$

where γ_2 is the slope of the regression.

The relation between resolution and parameter α was:

$$\alpha = \gamma_3 - \gamma_4 \log_e R \tag{3.6}$$

which is equivalent to the function:

$$e^{\alpha} = e^{\gamma_3} R^{\gamma_4} \tag{3.7}$$

where γ_4 is the slope of the regression.

Again, the residuals from the regression were examined to verify that there were no systematic deviations of the data from the model, and that the residuals were homogeneous, independent and normal.

We chose to divide the imagery of Newman Sound into three subsections of equal area: image 1) North Subsection, image 2) Middle Subsection, and image 3) South Subsection (Figure 3.1). We divided the imagery to determine if the same power law function was common across subsections, as well as holding for the frequency distribution of eelgrass patches in the full CASI imagery. Only the middle subsection maintained a sufficient sample of patches over more than three resolutions, which was the minimum number of data points needed to make an estimate. Therefore, only this middle subsection was compared to the overall imagery of eelgrass in Newman Sound.

Size classes that had a frequency of one caused a 'tail' at the end of the patch size frequency distribution. These tails represented a few very large patches, resembling meadows rather than patches typical within this area. Because these large patches were rare, their true frequency was poorly estimated. Due to their undue influence on the regression, these poorly estimated size classes were removed from the analysis.

RESULTS

Power law functions for eelgrass patch size frequency distributions

Eelgrass patch size distributions for all resolutions fit power law functions for the Middle Subsection (Figure 3.2 A). The power law functions for each resolution, and the corresponding power law exponents (i.e. the Korčak exponent) are shown in Table 3.1. The analysis of residuals could not be done on coarser resolutions (>400 m^2), as the sample size declined to three or fewer patches. It was evident that the frequency

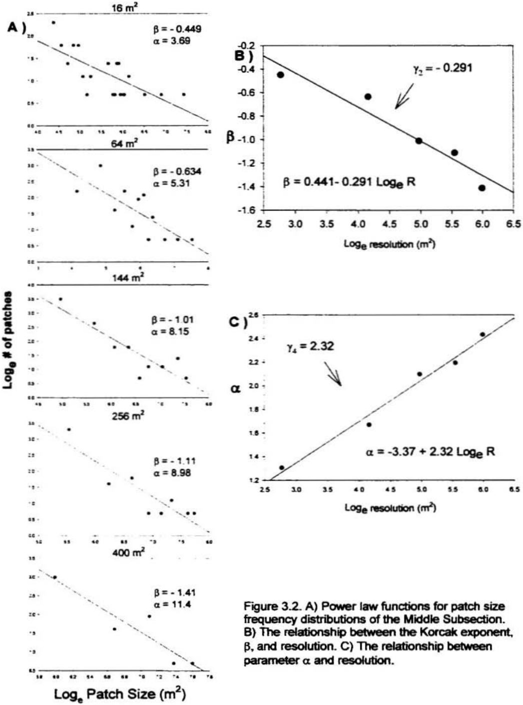

Figure 3.2. A) Power law functions for patch size frequency distributions of the Middle Subsection. B) The relationship between the Korcak exponent, β, and resolution. C) The relationship between parameter α and resolution.

Table 3.1. The parameter estimates for the model, $N = e^{\alpha} P^{\beta}$, of the frequency distributions at 5 resolutions for the Middle Subsection of the CASI imagery. F ratios relate to H_o: $\beta=0$.

Resolution	Parameter α	Korčak Exponent (β)	P-values	SS_{total}	F-values
16 m^2	3.69	- 0.449	<0.001	4.4626	18.49
64 m^2	5.31	- 0.634	0.003	6.53	15.12
144 m^2	8.15	- 1.01	<0.001	6.93	27.15
256 m^2	8.98	- 1.11	0.002	5.83	25.22
400 m^2	11.4	- 1.41	0.023	3.71	18.35

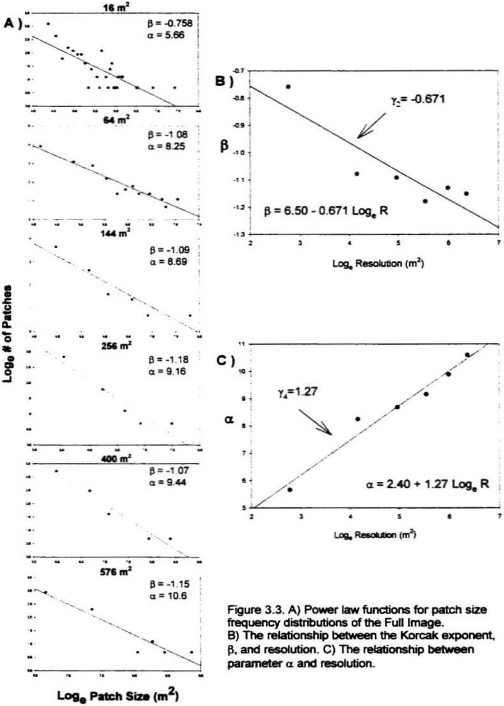

Figure 3.3. A) Power law functions for patch size frequency distributions of the Full Image.
B) The relationship between the Korcak exponent, β, and resolution. C) The relationship between parameter α and resolution.

Table 3.2. The parameter estimates for the model, $N = e\ \alpha\ P\ \beta$, of the frequency distributions at 6 resolutions for the Full Image of the CASI imagery. F ratios relate to H_o: $\beta=0$.

Resolution	**Parameter α**	**Korčak Exponent (β)**	**P-values**	**SS_{total}**	**F-values**
16 m^2	5.66	- 0.758	<0.001	12.15	40.25
64 m^2	8.25	- 1.08	<0.001	10.16	102.75
144 m^2	8.69	- 1.09	0.006	6.74	27.67
256 m^2	9.16	- 1.18	0.013	3.30	28.22
400 m^2	9.44	- 1.07	0.004	4.95	59.97
576 m^2	10.6	- 1.15	0.005	4.78	31.49

distribution changed with resolution. Appendix 2 contains the complete regression analysis of all resolutions for the Middle Subsection.

Power law functions emerged again for the eelgrass patch size distributions of all resolutions of the Full Image (Figure 3.3 A). Table 3.2 lists the power law functions for each resolution and the corresponding power law exponents. Appendix 3 contains the complete regression analysis for the Full Image.

The relationship between the Korčak exponent and resolution

For the Middle Subsection, the slopes of the frequency distributions (i.e. the Korčak exponent, β) became increasingly negative as resolution decreased (Figure 3.2A). We regressed β against resolution to produce a loglinear function relating patch size frequencies to resolution (Figure 3.2 B). We found the exponent of the function, γ_2, to be -0.291. Through substituting for this exponent, γ_2, as well as γ_1 into Equation 3.4, the formal model was:

$$\beta = 0.441 - 0.291 \, Log_e \, R \qquad (3.8)$$

This equation is equal to the function:

$$e^{\beta} = e^{0.441} \, R^{-0.291} \qquad (3.9)$$

The exponent γ_2 differed significantly from zero ($F_{1,3} = 40.33$, $SS_{total} = 0.588$, $p = 0.008$).

The power law distributions for each resolution and the corresponding Korčak exponent for the Full Image are shown in Table 3.2. It was clear that changing resolutions modified the frequency distributions of eelgrass patch sizes. We were not able to perform the residual analysis on resolutions coarser than 576 m^2, as the sample size declined to three or fewer patches. The slopes of the frequency distributions, β, became increasingly negative as resolution decreased (Figure 3.3 A). We regressed β against resolution, which resulted in a loglinear function relating the Korčak exponent to resolution (Figure 3.3 B).

The exponent of the function, γ_2, was found to be -0.671. Through substituting for γ_2 and γ_1 into Equation 3.4, the formal model was:

$$\beta = 6.50 - 0.671 \, Log_e \, R \tag{3.10}$$

This equation can also be expressed as the function:

$$e^{\beta} = e^{6.5} R^{-0.671} \tag{3.11}$$

The exponent γ_2 differed significantly from zero ($F_{1,3} = 10.57$, $SS_{total} = 0.115$, $p = 0.031$).

The relationship between parameter α and resolution

To calculate a frequency distribution at one resolution, from the frequency distribution at another, we need to have linear relationships between resolution and: 1) the slope of the distributions (the Korčak exponent, β), and 2) the parameter α of the frequency distribution. We know from the analysis above that the Korčak exponents over a range of resolutions fit a loglinear function. To determine the relationship between parameter α and resolution, we regressed α against the resolution of the imagery. Similar to the analysis of the Korčak exponent, a loglinear relationship emerged between the parameter α and resolution.

For the Middle Subsection, the values for the α parameters of the frequency distributions increased as resolution decreased (Figure 3.2 A). When we regressed α against resolution, a linear function emerged (Figure 3.2 C) with an exponent γ_4 of 2.32. Through substituting for γ_4, as well as γ_3 into Equation 3.6, the formal model was:

$$\alpha = -3.37 - 2.32 \, Log_e \, R \tag{3.12}$$

This equation can also be expressed as the function:

$$e^{\alpha} = e^{-3.37} R^{2.3} \tag{3.13}$$

The exponent γ_4 differed significantly from zero ($F_{1,3} = 44.33$, $SS_{total} = 37.135$, $p = 0.007$).

Again, the α parameters of the frequency distributions for the Full Image increased as resolution decreased (Figure 3.3 A). The regression of α against resolution confirmed that the relationship between the parameter α of the distributions and resolution fit a loglinear function (Figure 3.3 C). The exponent γ_4 of this function was found to be 1.27. After substituting for γ_4, as well as γ_3 into Equation 3.6, the formal model for this analysis was:

$$\alpha = 2.40 - 1.27 \, Log_e \, R \tag{3.14}$$

This equation can also be expressed as the function:

$$e^{\alpha} = e^{2.40} R^{1.27} \tag{3.15}$$

The exponent γ_4 differed significantly from zero ($F_{1,3} = 113.03$, $SS_{total} = 14.681$, $p < 0.001$).

Scaling Relationships for Frequency Distributions

Having the scaling coefficient (γ) for β and α over various resolutions, we can now compute the slope and parameter α for a frequency distribution at one resolution from the frequency distribution at another, using the following relationships:

$$\beta_{course} = \beta_{fine} \left(\frac{R_{course}}{R_{fine}} \right)^{\gamma} \tag{3.16}$$

$$\alpha_{course} = \alpha_{fine} \left(\frac{R_{course}}{R_{fine}} \right)^{\gamma} \qquad (3.17)$$

where β = slope or the Korčak exponent, α = parameter α, R = resolution of the imagery, and γ = the rescaling coefficient. Therefore, the frequency distribution at any given resolution can be calculated from the frequency distribution at a resolution that may be logistically more convenient to obtain. From the full frequency distribution we can calculate commonly used summary statistics, such as the mean or variance.

DISCUSSION

Habitat patches differ in origin and dynamics. Patchiness emerges from the interaction between physical and biotic processes (Levin 1976, Levin 1978) and is apparent at any scale of resolution (Marquet et al. 1993). Descriptions of patchiness in marine, freshwater and terrestrial systems present different problems, particularly regarding mechanisms of patch formation (García-Moliner et al. 1993). In pelagic environments, ecological processes that are dependent on spatio-temporal scales of water movement result in 'patchiness' (i.e. continuous habitat interspersed with corridors) rather than discrete patches. However, intertidal and benthic marine ecosystems are similar to terrestrial systems in that open spaces or patches of organisms, substrate or habitat have boundaries that are often discrete (García-Moliner et al. 1993). Intertidal and benthic zones are high energy environments where wave activity dislodges groups of organisms and leaves behind barren patches, which are then open for colonization (Paine and Levin

1981). These barren patches are similar to gaps in forest stands (García-Moliner *et al.* 1993). Similarly, eelgrass habitats on the northeastern coast of Newfoundland are subject to patch formation by high-energy winter storms and ice scouring common to this coastline.

A power law distribution is generated by two competing exponential rates that are temporally or spatially lagged (Stanley et al. 1996). A model system with a power law distribution is a sand pile created by slowly adding grains, where an additional grain stimulates avalanches of all sizes (Bak and Chen 1995). Examples of physical systems with power law distributions are, accumulation of fuel in a forest until fire results (Loreto et al. 1995), earthquakes (Bak and Chen 1995), avalanches (Bak et al. 1987, Bak et al. 1988, Tang and Bak 1988, Bak and Chen 1989) and rainforest gap structure (Solé et al. 1992). We hypothesized that the frequency distribution of patch sizes for eelgrass would fit a power law, because mechanisms for this system exist as competing rates that are temporally and spatially lagged. Pack ice and icebergs are present in coves all along the northeast coast of Newfoundland during the winter (Dinsmore 1972). As the ice moves, eelgrass shoots encased by ice will be torn or dislodged by the roots (Robertson and Mann 1984). The removal of eelgrass in this way will likely result in the formation of patches of different shapes and sizes. Subsequent annual growth begins in late spring and continues throughout the summer. While the spread of *Zostera marina* is rapid due to the presence of underground runners (Sculthorpe 1967), it can be assumed that the rate of spatial expansion of eelgrass habitat will occur at more limited spatial and temporal scales than the destruction of entire patches by ice scouring.

Our findings show that the frequency distributions of patch sizes fit a power law at each observation scale. These findings are consistent with the hypothesis that distributions were generated by competing exponential rates. We also hypothesized that the slope of the patch size distribution (i.e. the Korčak exponent) would change with resolution. Our results support this hypothesis. The Korčak exponent did indeed change with resolution of the imagery. This finding implies that the assumption (Mandelbrot 1975. Rodriguez-Iturbe and Rinaldo 1997) of a constant Korčak exponent is incorrect. Small habitat patches became less detectable at coarse resolutions. A reduction in the frequency of small patches with decreasing resolution caused the slope of the frequency distribution to become increasingly negative. resulting in a decrease in Korčak exponents.

Not only did the Korčak exponents change with resolution. but the relationship between them emerged as a loglinear function. To determine the frequency distribution at a particular scale. both slope (Korčak exponent) and parameter α need to be computable from a loglinear function. The relationship between the parameter α and resolution also fit a loglinear function. Thus. the frequency distribution of eelgrass patch sizes can be calculated across resolutions (i.e.. spatial scale). As a result. we can calculate the frequency distribution of patch sizes at one scale. from the frequency distribution at a scale that may be logistically more convenient to obtain. Thus. less expensive coarse resolution maps may be used to calculate the patch size frequency distribution at the smaller scales of population field studies.

Species dynamics depend on the size of landscape patches (Forman and Godron 1981). However. the size distribution of landscape patches. and the resulting Korčak exponent change depending upon the scale at which they are observed. Yet. almost all studies of patch dynamics are performed at a single scale. For example. Forman and Godron (1981) justified limiting their study of landscape patches to one scale on the assumption that most of the resulting patterns appear to apply to all levels of scale. However. our results show that the slope of the patch size frequency distribution (the Korčak exponent) is scale-dependent. Thus. the degree of landscape patchiness. as measured by the Korčak exponent depends on the scale of observation (Weins 1997). Because the frequency distribution depends on map resolution. any measure of patchiness will vary with scale for eelgrass habitat. The scaling law for this frequency distribution follows from the dynamics in the system. It is also of wider utility than the scaling law for any single measure. such as a mean or variance. If we can predict the frequency distribution across spatial scales. then we can investigate the dynamics of populations or mechanisms occurring within this habitat at any spatial scale.

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CHAPTER 4: SUMMARY

Ecology is a scale-dependent science. One of the main goals in ecology is to explain the pattern of distribution and abundance of species or populations (Krebs 1978). However, all ecological patterns and processes are affected by scale to some degree, and our attempts to interpret ecological data or to use our findings in management are constrained by scale (Peterson et al 1998). The distribution and abundance of particular species will reveal one pattern at a fine scale, and another when viewed at a coarse scale (Peterson et al 1998). Finding ways to relate observations across space and time, and revealing what is maintained or lost in the process is the fundamental problem of scale. In this study I examined two methods that quantify changes in eelgrass structure over different spatial scales. First, I examined scaling habitat with measures of perimeter and area. Second, I looked at the change in frequency distributions of patch size with spatial scale.

The structural complexity of eelgrass habitat likely affects the population dynamics occurring within this habitat. In Newman Sound, eelgrass habitat is a complex mosaic of various-sized patches, surrounded by unvegetated sand or mud. High macrofaunal biomass combined with spatial distributions that range from meadows that extend over several hundred metres, to fragmented patches (<0.25 m^2), make eelgrass a good habitat for assessing the effects of habitat structure on animal abundance (Robbins and Bell 1994, Bell et al. 1995, Fonseca 1996, Eggleston et al. 1998).

PERIMETER-TO-AREA RATIOS

Emphasis must be placed on how we perceive habitat structure at different spatial scales, if we are to further our understanding of the link between population dynamics and habitat complexity. Habitat boundaries represent locations where the rates of population dynamics change abruptly in relation to those beyond the habitat (Forman and Godron 1981, Turner et al. 1999). Thus, comparing population dynamics with the perimeter-to-area ratio of habitat proves useful in evaluating these dynamics in an area of habitat. One way to measure habitat structure across spatial scales is to develop scaling laws that model the effect of scale on patterns in nature (Ludwig et al. 2000). Scaling laws are power-law relationships that relate measurements on one scale to another. They can describe complexity as a function of temporal or spatial scale. These relations indicate that the system is controlled by rules that are applicable across a wide range of scales (Meakin 1993 as cited by Milne 1998).

In this study, a scaling law was found to quantify the effect of spatial scale (i.e. resolution) on a measurement of habitat structure (i.e. perimeter-to-area ratios). This scaling law was simply a power law with an exponent called the 'scaling exponent' (Stanley et al. 1996). I found a constant scaling exponent over a range of resolutions, which indicates that within this range large-scale features are simply magnified versions of smaller ones. Therefore, perimeter-to-area ratio can be computed within a wide range of spatial scales from other measurements within the same range. However, outside of this range the relationship between perimeter-to-area ratio and resolution suddenly changes. This sudden change in scaling exponents reflects a scale-dependent threshold possibly caused by dissimilar landscape processes operating outside compared to within the scaling region (Ludwig et al. 2000). It is within such scaling regions which one may interpolate (Sugihara and May 1990).

Scaling laws have been suggested (Krummel *et al.* 1987, García-Moliner *et al.* 1993) as a means by which difficult problems in hierarchy theory can be answered, such as how to determine boundaries between hierarchical levels and how to determine the scaling rules for calculating across scales within each scaling domain. These boundaries are indicated by changes in the scaling exponent of the habitat. Supporters of hierarchy theory (Allen and Star 1982, O'Neil et al 1988, Allen et al. 1995, Ahl and Allen 1996, King 1997) propose that scaling domains may be represented as hierarchical levels (Ludwig et al. 2000). Sugihara and May (1990) suggested that fractals, and thus scaling exponents, represent a good method for characterizing hierarchical levels in nature. However, many now question this idea (e.g., Allen and Hoekstra 1992, O'Neill and King 1998), and have stated that scaling domains are not the same as hierarchical levels. While scaling laws can identify domains where scaling is possible, these domains are specific to a parameter and cannot be applied for all parameters contained within that domain or 'hierarchical level' (Allen and Hoekstra 1992, O'Neill and King 1998).

PATCH SIZE DISTRIBUTIONS

Another feature used in characterizing habitat complexity is the measurement of habitat 'patchiness'. This measurement of complexity differs from that of perimeter-to-area, because 'patchiness' is quantified as the number of discontinuous patches of eelgrass habitat (García-Moliner et al. 1993). The effect of habitat patchiness on the distribution and abundance of species is a critical issue in applied ecology (Marquet et al. 1993). Yet, there is no characteristic scale at which an organism's response to habitat patchiness should be measured (Hart and Horwitz 1991. Levin 1992). Therefore, it is important to examine the effect of spatial scale on the perception of patch sizes in habitat.

Eelgrass patchiness affects populations through a variety of mechanisms, including alteration of predator distribution, abundance and foraging behaviour (Leber 1985, Main 1987, Bell and Hicks 1991, Irlandi 1994, Irlandi *et al.* 1995), modifications of water flow (Eckman 1983, Bell *et al.* 1995), and changes in animal behaviour (Heck and Crowder 1991). Patchiness is usually quantified from simple data summaries such as means, variances, or any of a variety of indices (e.g., Taylor's Index of patchiness, Relative Richness Index, Diversity Index, Fragmentation Index; Turner 1989, Monmonier 1974). Frequency distributions, more than any single summary statistic or index used to describe habitat, provide more information (Schneider 1994) about any given habitat characteristic. The frequency distribution of patch sizes—at the scale of population studies—can be used to calculate the impact of a mechanism on a population at that specific scale (e.g., the impact of predator distribution). From this frequency distribution, summary statistics such as means, variances, or any of a variety of indices can be calculated.

The slope of a frequency distribution that follows a power law distribution is called the 'Korčak exponent' (Korčak 1940, Korvin 1992). In geography it is well known that the size of islands follows a power law distribution, which is called Korčak's (1940) law:

$P\ [A > a] = k\ a^{-\beta}$,

where $P\ [A > a]$ is the frequency of islands of size $A > a$, and β is the Korčak exponent. Korčak (1940) analyzed the size distribution of geographical objects (areas of islands and lakes, length of rivers, etc.) and found that the areas of islands follow a power law distribution (Korvin 1992). Size distributions of natural and computer-generated lakes, and lengths of caves were found to fit Korčak's Law (Curl 1960, 1966, 1986, Kent and Wong 1982, Goodchild 1988). Bak and Chen (1995) discuss the occurrence of power law distributions (i.e. Korčak's Law) in earthquakes and found that various features of earthquakes have a power law distribution, including energy released during earthquakes (Bak and Chen 1995), distribution of epicentres (Kagan and Knopoff 1980), and the number of aftershocks as a function of time (Bak and Chen 1995). Stanley et al. (1996) discuss the power law as a tool for scaling in many fields, including biophysics, econophysics, and city growth. DNA sequences (Peng et al. 1992), heartbeat intervals (Peng et al. 1995), urban growth (Makse et al. 1995), company growth (Mantegna and Stanley 1995, Stanley et al. 1995, Stanley et al 1996a, Stanley et al 1996b), and lung inflation (Suki et al. 1994, Barabási et al 1994) all display power law correlations used for scaling.

In ecology, only a few studies have examined full frequency distributions. The distributions of gaps in the rainforest (Sole and Manrubia 1995), forest-fire behaviour (Loreto et al. 1995) and the distribution of patch areas of evergreen vegetation (Milne 1998) have been found to fit power laws. I could find only one ecological study (Nikora et al. 1999) that mentioned Korčak's law or the Korčak exponent for frequency distributions that follow a power law distribution. Nikora et al. (1999) calculated the Korčak exponent using the cumulative size frequency distribution for various sets of patches (Nikora et al. 1999). Their study, and a few others that have mentioned the Korčak exponent (Mandelbrot 1975, Rodriguez-Iturbe and Rinaldo 1997), failed to recognize that frequency distributions change with spatial scale. A measure of how frequency distributions change across spatial scales is provided by comparing the Korčak exponents across resolutions (or scales). For eelgrass patch sizes, the frequency of small patches decreased with coarser resolutions of the CASI imagery. The reduction of small patches caused the slope of the frequency distribution (i.e. the Korčak exponent) to become increasingly negative. My thesis has demonstrated that the frequency distributions of patch sizes fit a power law regardless of observation scale, and that the Korčak exponent itself changes in a regular way with spatial scale.

If a frequency distribution follows Korčak's (1940) law, then the Korčak exponent β is related to the fractal dimension of the coasts of the islands through:

$\beta = 0.5\ D_{coast}$,

where D_{coast} is the fractal dimension of the coastline (Mandelbrot 1975, Rodriguez-Iturbe and Rinaldo 1997). In this thesis, I investigated the perimeter to area ratio rather than coastline length; thus, the Korčak exponent β is interpreted as half of the perimeter-to-area fractal dimension (i.e. $\beta = 0.5\ D_{P/A}$) (Nikora et al. 1999). Because the fractal dimension is derived from the scaling exponent, we should be able to calculate the scaling exponent for eelgrass perimeter-to-area ratios from the slope of the patch size frequency distribution (i.e. the Korčak exponent). Nikora et al. (1999) compared the observed to the expected (see Mandelbrot 1983) Korčak exponent for various sets of patches with power law distributions, and found that the exponents differed by only 7-10%. However, in the lake size studies, the fractal dimensions calculated from the Korčak exponent were found to differ from those calculated by shoreline-length resolution analysis (Kent and Wong 1982, Goodchild 1988). The underlying assumption is that the Korčak exponent is constant over different spatial scales. However, the results of our study suggest that the Korčak exponent changes with resolution, which would explain the discrepancy of this equation.

Not only did the Korčak exponents change with resolution, but the relationship between them also emerged as a loglinear function. If the slope of a distribution can be calculated using a loglinear function, then only the parameter α from Korčak's Law is needed to determine the frequency distribution at a particular spatial scale. The relationship between the parameter α and resolution fit a loglinear function as well. This suggests that the frequency distribution of eelgrass patch sizes is predictable across resolutions of imagery (i.e. spatial scale). As a result, we can calculate the full frequency distribution of patch sizes at one scale, from the frequency distribution at a scale that may be logistically more convenient to obtain. Thus, less expensive coarse resolution maps may be used to calculate the patch size frequency distribution at the smaller scales of population field studies.

WHY DO WE GET POWER LAWS IN EELGRASS SYSTEMS?

With the single exception of the power law distribution, all other size distributions depend on some characteristic parameter such as length or area (Korvin 1992, Stanley et al. 1996). Power laws for size distributions are expected when a system is operating away from equilibrium at or near a threshold of instability (Sole and Manrubia 1995). Recently it has been recognized that many interacting dynamic systems naturally evolve into a 'self-organized critical state', resulting in events of all sizes—many small and few large (Bak et al. 1987, Bak et al. 1988, Tang and Bak 1988, Bak and Chen 1989). Power laws can describe the frequency distributions of these events. This discovery suggests a dynamic mechanism generating scaling behaviour (including fractal structure) in nature (Bak and Chen 1995). This self-organized critical state occurs in systems (Bak et al. 1988) that are regulated by the feedback between the state of the system and its control parameter (Loreto et al. 1995). Examples of self-organized systems include, accumulation of fuel in a forest until fire results (Loreto et al. 1995), and sand piles created by slowly adding grains, where an additional grain stimulates an avalanche (Bak and Chen 1995). In the avalanche example, a self-organized critical state arises when the chain reaction for avalanches becomes unstable, and avalanches of all sizes occur (Bak and Chen 1995).

Competing exponential rates that are temporally or spatially lagged are known to generate power law distributions (Stanley et al. 1996). The contest between these rates must be unequal, as seen in the accumulation and release of energy during earthquakes along faultlines (Bak and Chen 1995, Stanley et al. 1996), and during forest-fires (Loreto et al. 1995). Sole and Manrubia (1995) found that the size distribution of gaps in a rainforest fit a power law. They attributed this finding to processes of gap formation (i.e. treefall) and regeneration, which are major influences on the structure of tropical ecosystems (Whitmore 1991). A gap in the rainforest is formed, not only by a single tree, but also by vines attached to neighbouring trees. This causes a domino-like collapse, resulting in a much larger gap than would be formed by a single tree. Successional phases then slowly begin to regenerate the forest within this opening (Sole and Manrubia 1995). The occurrence of power laws is of great importance in physics, since it indicates the existence of an underlying scale-invariant mechanism (Bak and Chen 1995). For example, the power law generated by the size distribution of earthquakes indicates that the mechanism of small earthquakes is essentially the same as the mechanism for large earthquakes, otherwise their frequency could not be expected to obey the same power law (Bak and Chen 1995). Although power law distributions and scaling laws provide potentially powerful tools for prediction, both physics and ecology are just beginning to develop scaling equations for complex systems. If the processes generating a habitat are conflicting and lagged, it is expected that its structural properties will be expressed as power law distributions and scaling laws. Finding such power laws and scaling regions is the first stage to predicting population characteristics from habitat.

For eelgrass habitats on the northeast coast of Newfoundland, ice scouring events and annual growth act as competing exponential rates that are lagged in space and time. During the winter (December to May), pack ice and icebergs are present in coves all along the northeast coast of Newfoundland and coves in the vicinity of Newman Sound often freeze over due to freshwater input from streams and rivers. Over this icebound period, ice-scouring events occur rapidly and episodically. As the ice moves, eelgrass shoots are encased by ice are either torn or dislodged by the roots in large quantities (Robertson and Mann 1984). This removal of eelgrass may result in the formation of habitat patches of different sizes. Subsequent growth begins in late spring and continues throughout the summer at a steady rate. While the spread of *Zostera marina* is rapid due to the presence of underground runners (Sculthorpe 1967), it can be assumed that the rate of spatial expansion of eelgrass habitat will occur at more limited spatial and temporal scales than the destruction of entire patches by ice scouring. Due to these temporally and spatially lagged mechanisms, I hypothesized that the frequency distribution of patch sizes for eelgrass would fit a power law. In this thesis, I demonstrate that the frequency distributions of patch size fit a power law regardless of observation scale. This is consistent with distributions that are generated by competing exponential rates.

A variety of disciplines have accurately described highly irregular patterns, distributions, and scaling exponents (e.g., Meakin 1993, Solé et al. 1992). These studies have captured the statistical behaviour of these patterns over a wide range of scales (Mandelbrot 1982, Stanley et al. 1996), and have indicated that pattern is a function of process (Solé and Manrubia 1995). These and future studies that search for consistent scaling relations (Bak et al. 1988) and the processes that generate them (Loreto et al. 1995, Vespignani et al. 1995, Grassberger and Zhang 1996) are necessary to gaining a strong understanding of complex systems in general, and ecological systems in particular (Milne 1998).

Population dynamics (e.g., recruitment, competition, predation) change depending on the scale of observation or measurement. Thus, it is essential that eelgrass habitat structure be examined for properties that can be computed across spatial scales, such as perimeter-to-area ratios or the frequency distribution of patch sizes. The ability to calculate these habitat measures across spatial scales allows for computations of estimates of population dynamics at the scale of field studies. Further exploration of scaling laws and patch size distributions should be examined using additional eelgrass habitats in order to determine the applicability of these scaling relations to local, regional or global scales. In order to test the findings presented in this thesis, additional research is needed on population dynamics of organisms dependent on the structure of eelgrass habitats in this area. Another necessary step is to obtain the value of the Korčak exponent from theory (e.g., competing rates). By quantifying the exponential rates (e.g., growth) and the rates of destruction (e.g.. ice scouring). it may be possible to compute the resulting power law of the Korčak distribution for testing against data.

Understanding how eelgrass characteristics relate to ecological processes (e.g.. population dynamics) that generate patterns in benthic systems. and how these processes change with spatial scale. is fundamental to discovering relationships between eelgrass habitats and population dynamics at large scales. The challenge lies in estimating population dynamics based upon perimeter-to-area ratios or patch size. In terrestrial systems. the task of estimating population dynamics at small scales seems manageable. However. the logistics of acquiring quantitative data on population dynamics in aquatic environments (e.g.. predation rates or abundances) has proven to be much more problematic due to the difficulty in directly observing submerged habitats. Thus. it is essential that future research also includes development of new technologies for underwater measurement of these dynamics.

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APPENDIX 1: DERIVATION OF THE COASTLINE LENGTH EQUATION

To calculate the number of 16-metre beach seines that fit along the coastline, we used:

$CL_{fine} / CL_{coarse} = N_{fine} L_{fine} / N_{coarse} L_{coarse}$

Through substituting $N_{fine} / N_{coarse} = (L_{fine} / L_{coarse})^{D}$ into Equation 1, the equation became:

$$CL_{fine} / CL_{coarse} = (L_{fine} / L_{coarse})^{D} (L_{fine} / L_{coarse})^{1}$$

$$= (L_{fine} / L_{coarse})^{1-D}$$

$$CL_{fine} = CL_{coarse} (L_{fine} / L_{coarse})^{1-D}.$$

where CL_{fine} is the coastline length at the scale of 16m. CL_{coarse} is the coastline length at 180 m using a topographic map (scale 1: 50.000). L_{fine} is the length of the ruler at 16m. L_{coarse} is the length of the ruler at a 180 m, and D is the fractal dimension of the coastline.

APPENDIX 2 : COMPLETE ANALYSIS FOR PATCH SIZE FREQUENCY, MIDDLE SUBSECTION

Resolution of 16 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)
model:	The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
     2.40+
         -    *
 Ln F    -
         -
         -
     1.80+       *    * *
         -
         -
         -          *              *   2
         -
     1.20+
         -                *  *             *
         -
         -
         -                 *         ** * *       *     *        *
     0.60-
         -
           ----------+---------+---------+---------+---------+--- Ln P
        4.20      4.80      5.40      6.00      6.60      7.20
```

The regression equation is $\text{Ln } F = 3.69 - 0.449 * \text{Ln } P$

$\alpha_1 = 3.69$ and $\alpha_2 = -0.449$

Therefore, the model is $F = e^{3.69} * P^{-0.449}$

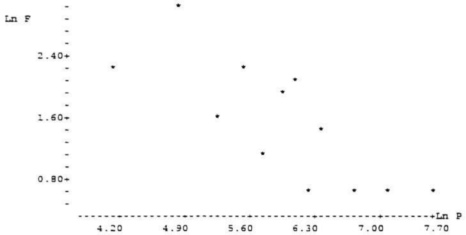
Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	2.3251	2.3251	18.49	0.000
Error	17	2.1375	0.1257		
Total	18	4.4626			

Resolution of 64 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)

model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).



The regression equation is $\text{Ln } F = 5.31 - 0.634 * \text{Ln } P$
$\alpha_1 = 5.31$ and $\alpha_2 = -0.634$

Therefore, the model is $F = e^{5.31} * P^{-0.634}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	3.9285	3.9285	15.12	0.003
Error	10	2.5990	0.2599		
Total	11	6.5275			

Resolution of 144 m^2

response variable: frequency to resolution (F)
explanatory variable: patch size (P)
model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

The regression equation is $\text{Ln } F = 8.15 - 1.01 * \text{Ln } P$
$\alpha_1 = 8.15$ and $\alpha_2 = -1.01$

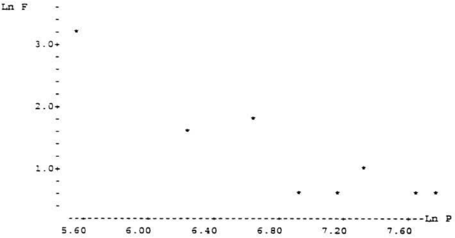
Therefore, the model is $F = e^{8.15} * P^{-1.01}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	5.5126	5.5126	27.15	0.000
Error	7	1.4213	0.2030		
Total	8	6.9339			

Resolution of 256 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)
model:	The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).



The regression equation is $\text{Ln F} = 8.98 - 1.11 * \text{Ln P}$

$\alpha_1 = 8.98$ and $\alpha_2 = -1.11$

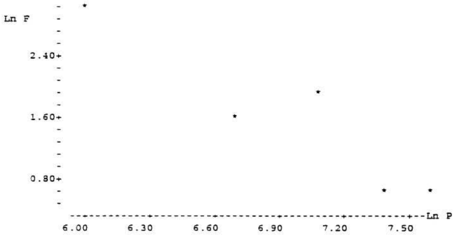
Therefore, the model is $F = e^{8.98} * P^{-1.11}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	4.7104	4.7104	25.22	0.002
Error	6	1.1207	0.1868		
Total	7	5.8310			

Resolution of 400 m^2

response variable: frequency to resolution (F)
explanatory variable: patch size (P)
model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).



The regression equation is $\text{Ln F} = 11.4 - 1.41 * \text{Ln P}$

$\alpha_1 = 11.4$ and $\alpha_2 = -1.41$

Therefore, the model is $F = e^{11.4} * P^{-1.41}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	3.1901	3.1901	18.35	0.023
Error	3	0.5217	0.1739		
Total	4	3.7118			

APPENDIX 3 : COMPLETE ANALYSIS FOR PATCH SIZE FREQUENCY, FULL IMAGE

Resolution of 16 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)
model:	The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
      3.20+
          -    *
  ln F    -
          -
          -       *
      2.40+
          -            *
          -              *          *
          -                **
          -          *
      1.60+                   *         *
          -                     *       *
          -
          -                       *   *    ***
          -
      0.80+
          -                    *   *   * ***       2     *        *
            +---------+---------+---------+---------+---------+---------+----ln P
         4.20      4.80      5.40      6.00      6.60      7.20
```

The regression equation is $\ln F = 5.66 - 0.758 \ln P$

$\alpha_1 = 5.66$ and $\alpha_2 = -0.758$

Therefore, the model is $F = e^{5.66} * P^{-0.758}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	7.4919	7.4919	40.25	0.000
Error	25	4.6535	0.1861		
Total	26	12.1454			

Resolution of 64 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)

model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
          -      *
       3.6+
          -
 ln F     -                  *
          -                         *
          -
       2.4+
          -                             *
          -
          -                                     *  *
          -                                  *       *   *
       1.2+                                                  *    *
          -
          -                                                   *
          -
            ------+---------+---------+---------+---------+---------+lnP
               4.20      4.80      5.40      6.00      6.60      7.20
```

The regression equation is $\ln F = 8.25 - 1.08 \ln P$

$\alpha_1 = 8.25$ and $\alpha_2 = -1.08$

Therefore, the model is $F = e^{8.25} * P^{-1.08}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	9.2581	9.2581	102.75	0.000
Error	10	0.9011	0.0901		
Total	11	10.1592			

Resolution of 144 m^2

response variable: frequency to resolution (F)
explanatory variable: patch size (P)
model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
 ln F     -      *
          -
          -
       3.0+
          -
          -                 *
          -
          -
       2.0+
          -
          -                         *
```

```
          -                                *
          -
       1.0+
          -
          -                                     *              *
           --+---------+---------+---------+---------+---------+---lnP
           4.80      5.40      6.00      6.60      7.20      7.80
```

The regression equation is $\ln F = 8.69 - 1.09 \ln P$

$\alpha_1 = 8.69$ and $\alpha_2 = -1.09$

Therefore, the model is $F = e^{8.69} * P^{-1.09}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	5.8844	5.8844	27.67	0.006
Error	4	0.8507	0.2127		
Total	5	6.7351			

Resolution of 256 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)
model:	The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
          -
      2.80+ *
          -
  ln F    -
          -
          -
      2.10+
          -
          -                   *
          -
          -
      1.40+
          -
          -                               *
          -
          -
      0.70+                                       *               *
           --+---------+---------+---------+---------+---------+---lnP
           5.60      5.95      6.30      6.65      7.00      7.35
```

The regression equation is $\ln F = 9.16 - 1.18 \ln P$

$\alpha_1 = 9.16$ and $\alpha_2 = -1.18$

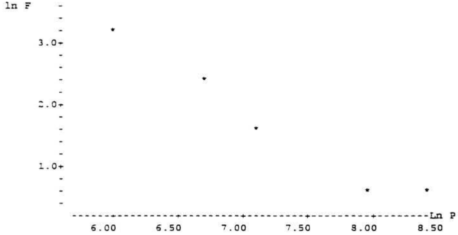
Therefore, the model is $F = e^{9.16} * P^{-1.18}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	2.9786	2.9786	28.22	0.013
Error	3	0.3167	0.1056		
Total	4	3.2953			

Resolution of 400 m^2

response variable: frequency to resolution (F)
explanatory variable: patch size (P)
model: The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).



The regression equation is $\ln F = 9.89 - 1.13 \ln P$
$\alpha_1 = 9.89$ and $\alpha_2 = -1.13$

Therefore, the model is $F = e^{9.89} * P^{-1.13}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	4.7149	4.7149	59.97	0.004
Error	3	0.2359	0.0786		
Total	4	4.9508			

Resolution of 576 m^2

response variable:	frequency to resolution (F)
explanatory variable:	patch size (P)
model:	The slope of the patch size frequency distribution is dependent on the resolution of the imagery (i.e. scale).

```
        -  *
    2.80+
        -
ln F    -
        -
        -                   *
    2.10+
        -
        -
        -
        -
    1.40+
        -
        -                                          *
        -
        -
    0.70+                                    *         *          *
          ----+---------+---------+---------+---------+---------+-lnP
           6.80      7.20      7.60      8.00      8.40      8.80
```

The regression equation is $\ln F = 10.6 - 1.15 \ln P$

$\alpha_1 = 10.6$ and $\alpha_2 = -1.15$

Therefore, the model is $F = e^{10.6} * P^{-1.15}$

Analysis of Variance

SOURCE	DF	SS	MS	F	p
Regression	1	4.2497	4.2497	31.49	0.005
Error	4	0.5399	0.1350		
Total	5	4.7896			