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Environmental Drivers of Spatial and Temporal Variability in Lakes

Mark David Scheuerell

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

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Abstract

Environmental Drivers of Spatial and Temporal Variability in Lakes

Mark David Scheuerell

Chair of the Supervisory Committee:

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Lakes are heterogeneous, three-dimensional landscapes, but are rarely appreciated as such. Organisms distribute themselves throughout these aquatic landscapes in a variety of ways, depending on the abiotic (e.g. temperature, oxygen, light) and biotic (e.g. predators, prey) features of the environment. Therefore, change in habitat use by an organism usually reflects temporal variation in the spatial distributions of the physical, chemical, and biological characteristics of lakes, or the constraints they impose on aquatic organisms. Integrating the effects of these changes across multiple scales requires knowledge of the external and internal functions of ecosystems. This task is often hindered by our inability to separate ecological process and pattern from underlying natural variability, especially when comparing the results of small experiments to observations made at larger scales. New development and application of geographic information systems (GIS), remote sensing, computer simulation models, spatial statistics, and sampling techniques has shown how emergent patterns in variability can indicate important spatial features of the landscape. Similar advances in time-series

analyses allow us to track dynamic changes in the underlying trends or periodic effects in time-ordered data.

I examined patterns in the spatial and temporal variance within and among several components of aquatic ecosystems. Through a combination of field sampling and quantitative methods, I offered ecological explanations for, and statistical descriptions of temporal and spatial patterns in the variance of observed data. Using ecological data from a variety of different lake ecosystems including relatively pristine Alaskan lakes and others from Washington state that were heavily impacted by human activities, I found that patterns in the spatial or temporal variance of observed data could often be explained by environmental drivers such as the amount of light, lake basin morphology, or the intensity of human disturbance. In all cases, I paid particular attention to the scope of the study and its influence on the results. My results highlight opportunities for ecologists to explicitly consider the role of dynamic changes in the spatial and temporal distribution of organisms in empirical and theoretical studies of aquatic ecosystems.

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Dedication

To my parents for their love, kindness, and generosity.

Chapter 1: Overview

Background

All of the ecosystems of the earth are inherently heterogeneous. Some of this heterogeneity is associated with the geophysical template that ecosystems lie on such as mountain ranges and river valleys, and climatic effects like temperature, precipitation, and wind patterns. Other important aspects of this heterogeneity arise from changes in the temporal and spatial distribution of the organisms that inhabit the landscape. While ecologists have long recognized heterogeneity and complexity in terrestrial and aquatic ecosystems (Whittaker 1956, MacArthur 1972, Steele 1978, Pickett and White 1985, Forman and Godron 1986, Carpenter 1988, Rose and Leggett 1990), they have had limited success interpreting the consequences of temporal and spatial patterns and processes for ecosystem structure and function (Levin 1992). However, interest in the subject has grown considerably in recent years (Kareiva 1994, Wennergren et al. 1995, Tilman and Kareiva 1997), partially due to the development of quantitative methods designed to deal with the temporal and spatial dependency implicit in all ecological interactions (Carroll and Pearson 2000).

Lakes are heterogeneous, three-dimensional lanscapes, but are rarely appreciated as such (Schindler and Scheuerell 2002). Organisms distribute themselves throughout these aquatic landscapes in a variety of ways, depending on the abiotic (e.g. temperature, oxygen, light) and biotic (e.g. predators, prey) features of the environment (Breck 1993, Hugie and Dill 1994, Hughes and Grand 2000, Tyler and Brandt 2001, Lima 2002). Therefore, change in habitat use by an organism usually reflects temporal variation in the spatial distributions of the physical, chemical, and biological characteristics of lakes, or the constraints they impose on aquatic organisms (Werner and Gilliam 1984). Integrating the effects of these changes across multiple scales requires knowledge of the external and internal functions of ecosystems (Levin 1992, Polis et al. 1997, Mason and Brandt 1999). This task is often hindered by our inability to separate ecological process and pattern from underlying natural variability (Kaitala and Ranta 2001, Jonzen et al. 2002), especially when comparing the results of small experiments to observations made at larger scales (Schindler 1998, Carpenter et al. 2001, Power 2001). New development and application of geographic information systems (GIS), remote sensing, computer simulation models, spatial statistics, and sampling techniques has shown how emergent patterns in variability can indicate important spatial features of the landscape (Horne and Schneider 1995, Kracker 1999, Schneider 2001). Similar advances in time-series analyses allow us to track dynamic changes in the underlying trends or periodic effects in time-ordered data (Pole et al. 1994).

Presently, lake ecosystems are subjected to a variety of anthropogenic stresses such as the disruption of nutrient cycles resulting in eutrophication (National Research Council 1992, Carpenter et al. 1998), habitat modification (Christensen et al. 1996, Radomski and Goeman 2001), and the exploitation of fishes by recreational and commercial fisheries (Pauly et al. 1998, Pauly et al. 2001, Post et al. 2002). As the global human population grows we will rely more heavily on aquatic resources for food, clean drinking water, recreation, and a variety of industrial uses (Botsford et al. 1997, Naiman et al. 1998). In light of these increasing demands, ecologists are challenged with making predictions about the response of aquatic ecosystems to changes in the abiotic and biotic environment under a variety of natural and anthropogenic disturbances (Pace 2001, Carpenter 2002). Central to these predictions are models that incorporate predator feeding and prey mortality rates; these models depend implicitly on the temporal and spatial distributions of interacting organisms. Qualifying the utility of models also depends on the goals of the study, rather than relying on statistics alone (Guisan and Zimmermann 2000). Fortunately, confronting models with existing data permits one to define the range of suitable model predictions and applications (Hilborn and Mangel 1997, Gotelli 2000).

Research Overview

In the following sections, I outline my dissertation research where I examined patterns in the spatial and temporal variance within and among several components of aquatic ecosystems. Through a combination of field sampling and quantitative methods, I offer ecological explanations for, and statistical descriptions of temporal and spatial patterns in the variance of observed data. In all cases, I pay particular attention to the scope of the study and its influence on the results. Contemporary ecologists are becoming increasingly aware of the importance of informing the public about the relevance of their work (Ehrlich 2002). Closing the gap between academic institutions and the public will allow for more cooperation and effective application of management policies. We must increasingly devote a portion of our careers to educational activities that will help promote an active conservation ethic to reduce environmental degradation and the associated loss of biodiversity. It is my sincerest hope that this body of work represents a step in that direction.

Chapter 2. Ecologists are often interested in the extent of aggregation within species or guilds, the amount of association between trophic levels, and the persistence of patterns over space and time (Coomes et al. 1999). The spatial distribution of aquatic organisms is almost always patchy and the degree of heterogeneity usually varies with the scale (resolution and extent) of analysis (Schneider 2001). An accurate description of the observed spatial pattern across a range of scales is critical when modeling the processes that generated the observed distribution (Levin 1992) and designing appropriate sampling strategies (O'Driscoll et al. 2000). Pattern analysis in terrestrial systems typically involves counts of individuals over a sampling grid or complete spatial maps of organism locations, but this is often quite difficult in aquatic systems (O'Driscoll et al. 2000). However, advances in hydroacoustics technology have allowed aquatic ecologists to generate detailed data on the spatial locations of individual organisms (Horne 2000). The challenge remains to develop robust statistical methods for describing the aggregation and association of predators and prey in aquatic systems, and using these data to understand predator-prey interactions.

Here I developed a statistical methodology for analyzing patterns in the aggregation and association of predators and prey inhabiting pelagic ecosystems that are inherently three-dimensional. The first method only considered data on the nearest neighbors of individuals whereas the second approach took advantage of the measured distances among all of the sampled individuals in the population. Hydroacoustics can be used to measure the three-dimensional positions of organisms in pelagic ecosystems and therefore I also developed an edge correction to account for the biases associated with sampling by hydroacoustics. I used empirical data on the locations of predatory and prey fishes obtained with hydroacoustics in Lake Washington to illustrate how three-dimensional patterns of aggregation and association of predators and their prey could be assessed with these metrics. I found that prey fish were aggregated at small spatial scales (1 m) and only during the day. Their potential predators on the other hand were aggregated at all spatial scales less than or equal to 5 m during the day, but only at scales <3 m at night. Predators and prey were positively associated with one another at scales of 0.5 – 1 m during the day, but not at all during the night, reflecting the visual foraging nature of the predators and their high mobility relative to their prey. Predators and prey were negatively associated during the night and at scales >2 m during the day, which may reflect predator avoidance. These results highlight how high-resolution, three-dimensional data on the spatial positions of aquatic organisms can improve our understanding of the spatial scaling of predator-prey interactions in pelagic ecosystems.

Chapter 3. Lakeshores throughout North America are increasingly being developed and altered by humans (Jennings et al. 1999, Radomski and Goeman 2001). Accompanying this development are anthropogenic stresses to lake ecosystems such as the disruption of nutrient cycles resulting in eutrophication (Carpenter et al. 1998, Garrison and Wakeman 2000, Moore et al. 2002), introduction of exotic species (Jackson et al. 2001), and the exploitation of predatory fishes by recreational and commercial fisheries (Pauly et al. 2001, Post et al. 2002). Some direct impacts of lakeshore residential development on the physical structure of lake habitats include the removal of coarse woody debris (Christensen et al. 1996) and aquatic vegetation (Radomski and Goeman 2001), and bottom substrate modifications (Beauchamp et al. 1994). These alterations of nearshore habitats can adversely affect fish communities (Olden and Jackson 2001). Researchers and managers alike often rely on empirical models to predict the effect of human actions on lake ecosystems(Carpenter and Gunderson 2001). For simplicity, these models assume that there is no change in the spatial distribution of organisms with human disturbance. However, this critical assumption remains untested (Boisclair 2001).

Here I evaluated the cumulative effect of lakeshore residential development on the spatial distribution of fishes in 23 lakes in western Washington and southwestern British Columbia. Detecting changes in fish assemblages brought on by human disturbance usually requires observations before and after the disturbance (Lester et al. 1996). However, in this case I took a comparative approach across lakes, which is useful in ecosystem studies where experimental replication is impossible (Schindler 1998).

These lakes spanned an urban to rural gradient, with the intensity of lake shoreline disturbance by humans highest nearest the Seattle urban area and then generally decreasing with distance from the urban center. I also examined the potential role of lake geomorphology on fish spatial distributions because of the natural interaction between geomorphology and physical habitat (Wetzel 2001). I found a decrease in the level of fish spatial aggregation with an increase lakeshore residential development, such that fishes in highly developed lakes were randomly distributed whereas those in relatively pristine lakes were highly aggregated. I also found that the geophysical attributes of the lakes affects the spatial aggregation of fish, such that lakes with a high perimeter to surface area ratio and a relatively shallow littoral zone had higher aggregation among fish. The implications of this interaction between the spatial distribution of aquatic organisms and anthropogenic disturbances have yet to be explored in aquatic ecosystems.

Chapter 4. Diel vertical migration (DVM) is a common behavioral phenomenon among many aquatic taxa (Stich and Lampert 1981, Levy 1987, Wurtsbaugh and Neverman 1988). Among freshwater fishes, DVM by juvenile sockeye salmon and kokanee (*Oncorhynchus nerka*) has received considerable attention (e.g. Narver 1970, Levy 1987, 1990, Steinhart and Wurtsbaugh 1999). While residing in the pelagic zone of their nursery lakes, juvenile sockeye typically occupy much deeper waters during the day than they do at night, with migrations often covering tens of meters (Levy 1987, Clark and Levy 1988, 1990). The ecological explanation for the evolution of this behavior has remained elusive. Three general hypotheses have been proposed to account for the adaptive significance of DVM: bioenergetic efficiency, foraging opportunity, and predator avoidance (Brett 1971, Eggers 1978, Levy 1987, Clark and Levy 1988, 1990, Bevelhimer and Adams 1993, Steinhart and Wurtsbaugh 1999). However, given the visual foraging nature of both juvenile sockeye and their predators, the interaction between light and the distribution of both predators and prey on sockeye DVM has yet to be considered.

I evaluated changes in the timing and amplitude of juvenile sockeye DVM caused by seasonal changes in the light environment with concomitant changes in the vertical distribution of their zooplankton prey and predators. I examined juvenile sockeye DVM among three lakes in southwestern Alaska in early summer when the nights were short and two of those lakes again near the end of summer when the nights were considerably longer. If the sockeye indeed balance predation risk and foraging gain (or growth), I hypothesized that sockeye would change their migratory behavior to match changes in the light environment so they would exploit the so-called "antipredation window" (Clark and Levy 1988). I discovered that juvenile sockeye appear to time their daily migrations such that they maintain a roughly constant light environment, which is bright enough for them to forage by, yet affords them protection from their visually foraging predators. Furthermore, this antipredation window was continuous in early summer, but was split into two discrete time periods during the crepuscular hours in late summer. These data support the hypothesis that changes in habitat use by juvenile sockeye salmon reflect a dynamic strategy to minimize the ratio of predation risk to foraging gain that changes dramatically over the course of diel cycles in pelagic ecosystems.

Chapter 5. Much of the current emphasis in food web studies attempts to predict the degree to which food web structure controls primary producers and the efficiency with which primary production is transferred to upper trophic levels (e.g. Carpenter and Kitchell 1993, Polis and Winemiller 1994). In aquatic ecosystems zooplankton grazers affect their phytoplankton food directly through grazing (Sommer et al. 1986) or indirectly through nutrient recycling (Lehman 1980). In turn, the nutritional quality of primary producers can control the composition of the herbivore community and rates of secondary production (Gulati and DeMott 1997). In addition to algal quality, algal quantity may also limit zooplankton production (Lynch 1989). Furthermore, the body size of an individual may also affect its fecundity (Lampert 1993) and therefore, the size structure of the zooplankton community may play an important role in overall secondary production rates in aquatic ecosystems. However, much of our understanding to date has relied on lab experiments (e.g. Elser et al. 2001) or comparative studies of different ecosystems (e.g. Brett et al. 2000, Dobberfuhl and Elser 2000). Furthermore, strong intra- and interannual variation in the physical, chemical, and biological properties of lakes may produce an environment with large differences in the interaction among trophic levels. Fortunately, time series analyses provide a robust statistical means for differentiating ecological patterns from natural variation in the environment (Berryman 2001).

I investigated whether there were seasonal changes in the relationship between *Daphnia* fecundity and the physical-chemical environment, algal community characteristics, and *Daphnia* length using dynamic linear time series models (DLM) to analyze a high-resolution, 16-year time series from Lake Washington. I used two metrics to describe algal quality: the percent of blue-green algae, and the light to total phosphorus (TP) ratio as an indirect metric for algal C:P (Sterner et al. 1997). Chlorophyll *a* concentration and algal biovolume served as measures of algal quantity. As expected, both the light:TP ratio and the percent of blue-green algae had negative effects on *Daphnia* fecundity, and chlorophyll *a* concentration and biovolume had positive effects on fecundity. However, I found a comparatively stronger effect of *Daphnia* length on fecundity, although it was negative and therefore opposite to expectation. In all cases, I observed strong seasonal differences in environmental effects, but no temporal change in the fundamental relationships between our indices of algal quantity and quality, allometry, and *Daphnia* reproduction. My results supported a hypothesis of physical-chemical coupling to algal quality and zooplankton production, but highlight the importance of temporal variation in this forcing.

Chapter 2: Quantifying aggregation and association of predators and prey in three-dimensional landscapes

ABSTRACT

Interactions between predators and prey depend on their spatial distributions. In particular, meaningful interpretations of the role of these interactions in structuring population, community, and ecosystem dynamics depend on the scale of analysis. Here I develop two statistical methods for analyzing patterns in the aggregation and association of predators and prey inhabiting pelagic ecosystems that are inherently three-dimensional. The first method only considers data on the nearest neighbors of individuals, whereas the second approach takes advantage of the measured distances among all of the sampled individuals in the population. Hydroacoustics can be used to measure the three-dimensional positions of organisms in pelagic ecosystems, and therefore I also develop an edge correction to account for the biases associated with sampling by hydroacoustics. I used empirical data on the locations of predatory and prey fishes obtained with hydroacoustics in Lake Washington to illustrate how three-dimensional patterns of aggregation and association of predators and their prey can be assessed with these metrics. I found that prey fish were aggregated at small spatial scales (1 m) and only during the day. Their potential predators on the other hand were aggregated at all spatial scales less than or equal to 5 m during the day, but only at scales <3 m at night. Predators and prey were positively associated with one another at scales of

0.5 – 1 m during the day, but not at all during the night, reflecting the visual foraging nature of the predators and their high mobility relative to their prey. Predators and prey were negatively associated during the night and at scales >2 m during the day, which may reflect predator avoidance. These results highlight how high-resolution, three-dimensional data on the spatial positions of aquatic organisms can improve our understanding of the spatial scaling of predator-prey interactions in pelagic ecosystems.

Key words: aggregation; association; predator; prey; spatial statistics; Ripley's K; nearest neighbor; hydroacoustics; Lake Washington

INTRODUCTION

All ecological interactions exhibit some level of spatial dependence (Koenig 1999, Carroll and Pearson 2000). In particular, the spatial relationship among predators and their prey has important implications at the population, community, and ecosystem levels (Lundberg et al. 2000). In many cases the role of space in ecology was previously viewed as a means for explaining unexpected results without explicitly considering its function (Kareiva 1994). Recently, spatial autocorrelation and variance in ecological systems has been more often treated as a source of useful information, due to developments in geographic information systems and spatial statistics (Legendre 1993, Horne and Schneider 1995). Nevertheless, many studies fail to match the spatial scale of the experiment or observation to the ecological process or patterns being evaluated, due to difficulties with terminology, methodology, and the large data sets often required for analyses (Bult et al. 1998).

The importance of spatial scale in evaluating ecological interactions has been increasingly emphasized in recent years (Wiens 1989, Allen and Hoekstra 1992, Levin 1992). Issues of spatial scale are important for assessing overall species richness (Karlson and Cornell 2002), productivity-biodiversity relationships (Chase and Leibold 2002), and the effective management of fisheries (Folt et al. 1998) and other natural resources (Lovell et al. 2002). In particular, the relationship between organisms and the physical environment (Crook et al. 2001, Li et al. 2001, Thompson et al. 2001) and between predators and prey (Schneider and Piatt 1986, Rose and Leggett 1990, Muotka and Penttinen 1994, Fauchald et al. 2000) depend on the spatial scale of analysis. In some cases a lack of consideration for the spatial scale of the study can lead to erroneous conclusions about the relationships between predators and their prey (Rose and Leggett 1990, Cummings et al. 1997).

Much progress has been made in analyzing the scale-dependence of spatial patterns in terrestrial (e.g., Clark and Evans 1954, Haase 1995, Coomes et al. 1999, Freeman and Ford 2002) and stream (Muotka and Penttinen 1994, Bult et al. 1998, Crook et al. 2001, Li et al. 2001) ecosystems using two-dimensional data. In these cases, methods that use surface (density) or point (individual locations) patterns have both been used because data collection often benefits from stationary or sedentary organisms and the relatively small spatial extent of the studies (Bult et al. 1998, O'Driscoll et al. 2000).

Similar studies in much larger pelagic ecosystems have also been restricted to two-dimensional approaches using surface pattern data due to difficulties in sampling the locations of organisms in three dimensions over large regions of space (Schneider and Piatt 1986, Rose and Leggett 1990, O'Driscoll et al. 2000, Swartzman and Hunt 2000). However, pelagic ecosystems are inherently heterogeneous and three-dimensional in nature, whose physical, chemical, and biological environments can change dramatically across all dimensions (Schindler and Scheuerell 2002). Recent advances in hydroacoustics technology are allowing researchers to identify and track both predators and prey in three dimensions (Gerlotto et al. 1999, Horne 2000, Axelsen et al. 2001), which allow us to explicitly address the predator-prey dynamics occurring across the third dimension. Nevertheless, to date there has been no formal development and ecological application of methods for explicitly quantifying patterns of aggregation and association of aquatic organisms using three-dimensional point pattern data.

In this paper I develop two metrics for gauging the degree of aggregation among organisms in three-dimensions as a means for investigating the role of spatial scale in predator-prey interactions in aquatic environments. Both statistics use point pattern data; the first is based on nearest neighbor data only, whereas the second utilizes information on all of the measured distances among individuals. I then illustrate how the second statistic can be modified to test the degree of spatial association between predators and prey. In all cases the functional forms of the models follow the methodology outlined by Coomes et al. (1999) for two-dimensional data. As an example, I apply these tests to spatial data on predator and prey fishes from Lake Washington to illustrate how the spatial scale of fish aggregations and predator-prey interactions respond to daily fluctuations in the light environment.

METHODS

Nearest-neighbor statistical analyses. Consider the situation where we wish to test whether the spatial distribution of some population of organisms is statistically different than that expected by random chance. One approach is to compare the observed distances of nearest neighbors to those expected under complete spatial randomness (CSR, Diggle 1983). Under CSR, the distribution of organisms will follow a three-dimensional Poisson process across an infinite universe. Define $P(R \leq r)$ to be the probability that the distance (R) from an individual to its nearest neighbor is less than or equal to a specified distance r. If $P(R \leq r)$ exceeds the expected probability for small r, the population has an aggregated distribution. If the density of organisms is ρ, the expected number of neighbors within a sphere of radius r is $4/3\rho\pi r^3$ and the probability that there are no neighbors within the same sphere is then $\exp(-4/3\rho\pi r^3)$. For a Poisson distribution, the probability (G) that an individual has at least one neighbor within a distance r becomes

$$G_{P\infty}(r,\rho) = P(R \leq r) = 1 - \exp(-\tfrac{4}{3}\rho\pi r^3). \qquad (1)$$

$G_{P\infty}(r,\rho)$ is a cumulative density function (cdf) such that $G_{P\infty}(0,\rho) = 0$ and $G_{P\infty}(\infty,\rho) = 1$.

While these relationships hold in theory, the practical aspects of field sampling require that we measure the locations of individuals within a sub-sample of the environment. For example, when sampling with hydroacoustics, some fish will be closer to the edge of the sound beam than their nearest neighbor. Calculating $G_{P\infty}$ from these data thus requires an edge correction (Ripley 1981, Cressie 1993, Coomes et al. 1999). I calculated the edge correction with Monte Carlo simulations of a three-dimensional Poisson process in a restricted volume indicative of the typical geometry and volume sampled along a hydroacoustic transect. I used 500 Monte Carlo simulations of a three-dimensional Poisson process in volume of 10^5 m^3 based upon a 500 m transect, with a depth of 40 m, and a beam angle of 6.7°, a common geometry for hydroacoustics equipment (Figure 2.1). I varied the population density in the simulations from 0.001 – 1.0 m^{-3} to mimic a range of fish densities typically encountered in field surveys (Scheuerell, unpublished data). For each simulated pattern, I computed $P(R \leq r)$ for all points with r ranging from 0.1 – 31.6 m (-1.0 – 1.5 on a $\log_{10}$ scale). I then calculated the average observed cdf, $G_{PV}(r,\rho)$, as the mean of the 500 simulations. The edge correction (ξ) is the difference between the mean and the expected cdf:

$$\xi(r,\rho) = G_{PV}(r,\rho) - G_{P\infty}(r,\rho). \qquad (2)$$

Finally, I used nonlinear regression to describe the relationship between r, ρ, and ξ (Figure 2.2).

To estimate the degree of spatial aggregation among individuals, I computed the cdf of the observed nearest neighbor distances $G_{obs}(r,\rho)$ and compared it to $G_{PV}(r,\rho)$ as expected under CSR (Figure 2.2). Again following the notation of Coomes et al. (1999), the test statistic equals the maximum distance between the observed and expected cdf across all values of r, such that

$$dw = \max[G_{\mathrm{obs}}(r,\rho) - G_{\mathrm{PV}}(r,\rho)]. \tag{3}$$

This statistic therefore tests for aggregation over all spatial scales within the range of radii considered (Coomes et al. 1999). I estimated the null distribution of dw by comparing $G_{\mathrm{PV}}(r,\rho)$ to the $G_{\mathrm{obs}}(r,\rho)$ from 1000 Monte Carlo simulations of a three-dimensional Poisson process. The critical values of dw were then calculated from the upper tail of the null distribution such that the 95th percentile indicated dw_{crit} for $P = 0.05$ (sensu Coomes et al. 1999). Calculating dw_{crit} for every statistical test is cumbersome and time-consuming (Coomes et al. 1999). Therefore, I characterized the relationship between dw_{crit} and density (ρ) based on 1000 Monte Carlo simulations for distributions again containing 0.001 – 1.0 individuals m^{-3} (Figure 2.3).

Multi-neighbor statistical analyses. The previous analyses only make use of the nearest-neighbor statistics. However, useful information is also contained in the distances to other neighbors as well. To account for these higher order statistics, I assessed the degree of aggregation between prey organisms (i) and their association with their predators (j) by modifying Ripley's K statistic (Ripley 1981). First assume there are N_i individuals distributed randomly in a volume V. The expected number of neighbors within a radius r of any randomly chosen individual is $\mathrm{E}\{N_{ii}\} = 4/3\pi r^3\,(N_i - 1)/V$. Thus, I express the index of aggregation $I_A(r)$ as

$$I_A(r) = \frac{V}{\frac{4}{3}\pi r^3 N_i (N_i - 1)} \cdot \sum_{1}^{N_i} N_{ii} \qquad (4)$$

where N_{ii} is the number of neighbors within a radius r of each individual i. An $I_A(r) > 1$ indicates clumping whereas $I_A(r) < 1$ indicates regular spacing.

Now assume we also have a population of predators distributed within the same volume V. If the predators and prey are distributed randomly following a Poisson process, the expected number of prey i within a given distance r of a predator j is $E\{N_{ji}\} = 4/3\pi r^3 N_i/V$. The index of association between the predators and the prey $I_S(r)$ becomes

$$I_S(r) = \frac{V}{\frac{4}{3}\pi r^3 N_i N_j} \cdot \sum_{1}^{N_j} N_{ji} \qquad (5)$$

where N_{ji} is the number of neighboring prey i within a radius r of each predator j. When $I_S(r) > 1$, the predators and prey are positively associated, whereas $I_S(r) < 1$ denotes negative association among them.

I also estimated the statistical significance for both I_A and I_S through Monte Carlo simulation. Both predators and prey were distributed randomly within a sample volume based on their respective densities and the I_A and I_S were calculated for each simulation. The critical values were then calculated from the upper tail of the null distribution such that the 95th percentile indicated the critical value for $P = 0.05$. For the example data from Lake Washington described below, I used 1000 simulations with a predator density of 0.004 m^{-2} and a prey density of 0.02 m^{-2}.

Field Data. As an example of the above methodology, I used information on the spatial distributions of predatory and prey fish from Lake Washington. Lake Washington is a large (87.6 km^2), relatively deep (mean depth = 40 m), mesotrophic lake located largely within the city of Seattle, Washington. The pelagic prey fish community is dominated by sockeye salmon (*Oncorhynchus nerka*), longfin smelt (*Spirinchus thaleichthys*), peamouth chub (*Mylocheilus caurinus*), and yellow perch (*Perca flavescens*). The pelagic predator fish community is primarily comprised of cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*Oncorhynchus mykiss*) and northern pikeminnow (*Ptychocheilus oregonensis*). For my purposes, I combined all potential prey fish into one group (prey) and all of the predator fish into another (predators) based on their relative sizes (Werner and Gilliam 1984).

For measuring fish locations in three-dimensions, I used a BioSonics DT4000 split-beam echosounder operating at 200 kHz with an elliptical transducer consisting of -3 dB beam angles of 6.7 and 13.5 degrees. I used a 0.4 ms pulse at a rate of 4 s^{-1} with the lower threshold set at -70 dB. All incoming signals were digitized at the transducer and then stored on a computer hard drive for later analysis. The transducer was towed alongside the boat at a speed of 10 km hr^{-1} as the survey followed 4 predetermined transects across the lake over a total distance of 20.0 km (sample volume = 7.09×10^6 m^3). The day survey occurred between 13:30 and 15:30 on 5 August 1998; the night survey occurred between 22:00 and 0:00 on the same day. The depth and size of individual echoes were obtained using the BioSonics DT Analyzer 4.0 software. I classified all targets less than -46 dB as prey fish and all targets greater than -37 dB as predators. According to Burczynski and Johnson (1986), these sound intensity thresholds correspond to fish lengths of <100 mm and >282 mm respectively. I obtained simultaneous measurements on the x-y coordinates of the fish by coupling the hydroacoustics to a sub-meter accurate Trimble® AgGPS 132 differential global positioning system (DGPS).

RESULTS

Model results. The edge correction (ξ) to account for the geometry of the hydroacoustics was a nonlinear function of density and the scale of examination (Figure 2.3). As density increased, the magnitude of the edge correction decreased, as did the radius at which the maximum edge correction occurred. This results from tighter packing of individuals, which reduces the expected distance to a nearest neighbor and thereby reduces the influence of the sample volume's edge. Contrary to expectation, G_{PV} did not underestimate $G_{P\infty}$ across all densities and radii that I examined. For densities approaching 1.0 m^{-3}, the edge correction was positive at small radii. The critical values for testing the difference between G_{obs} and $G_{P\infty}$ (dw) were also a nonlinear function of density (Figure 2.4). As density decreased, dw_{crit} increased such that when the density was 0.001 m^{-3}, the critical value at $P<0.05$ was at least 20% of the possible range in dw.

Lake Washington fishes. The spatial distribution of the prey fish differed from their predators. Using the G statistic, which only accounts for nearest neighbor distances and is independent of spatial scale over the range of *r* examined, the distribution of prey fish was significantly aggregated during the day, but not at night ($dw_{\mathrm{day}} = 0.0646$, $dw_{\mathrm{night}} = 0.00540$, $dw_{0.01} = 0.0546$; Figure 2.5). The predatory fish however showed significant spatial aggregation during both day and night ($dw_{\mathrm{day}} = 0.745$, $dw_{\mathrm{night}} = 0.612$, $dw_{0.01} = 0.174$; Figure 2.5). The differences in the expected cdf of the random distribution between predators and prey reflects the difference in their observed densities, with prey fish being 20 times more dense than their predators (0.04 and 0.002 m^{-3} respectively).

The index of aggregation that accounts for all neighbors within a given distance (I_A) yielded different results and allowed for comparisons at specific spatial scales. I found that in this case the prey fish demonstrated significant aggregation during the day at scales between 0.5 and 1.0 m (Figure 2.6). At night however, prey fish were not aggregated at any of the spatial scales I examined. The prey fish were significantly more uniform than random at scales greater than 1.5 m during the day and greater than 1 m night (Figure 2.6).

The spatial distribution of the predators on the other hand was quite different from their prey (Figure 2.6). During the day, the predators showed significant aggregation at all of the spatial scales I tested, with two prominent modes occurring at 0.2 and 0.8 m. At night, their spatial distribution shifted toward random and I only observed significant aggregations at scales <2.8 m. Furthermore, the magnitude of aggregation at all of the significant spatial scales during the night was lower than those observed during the day. I only observed significant departures from random toward a uniform distribution among predators at night at spatial scales >4.2 m.

The degree of association between the prey fish and their predators also changed between day and night (Figure 2.6). During the day, predators and prey were positively associated with one another at spatial scales between 0.6 and 1.1 m, but this pattern was no longer evident during the night. Furthermore, during the day the predators and prey were negatively associated with one another at scales >2.2 m. The predators and prey were also negatively associated during the night at all spatial scales >0.8 m.

DISCUSSION

Many of the recent studies in aquatic ecosystems investigating the effect of spatial scale on the observed spatial patterns among organisms and their environment have concentrated on surface pattern analyses that consider discrete samples from a continuous spatial distribution (Bult et al. 1998, O'Driscoll et al. 2000). For example, some researchers have used hydroacoustics data to examine the spatial relationships among fish predators and prey using density estimates across two dimensions (Rose and Leggett 1990, Horne and Schneider 1997). Point pattern analyses based on the distances between discrete objects have proven effective in terrestrial systems (Coomes et al. 1999, Freeman and Ford 2002). However, these have largely been avoided in pelagic ecosystems due to difficulties in obtaining detailed spatial maps over larger areas (or volumes) (O'Driscoll et al. 2000). As further technological improvements provide better information on the spatial locations of organisms in three dimensions (e.g., Gerlotto et al. 1999, Axelsen et al. 2001), statistical techniques such as those outlined here to analyze point patterns will provide better insights into the spatial distribution of organisms in three dimensions, and the relevance of these spatial distributions to predator-prey interactions.

Descriptions of scale-dependent spatial patterns require that we pay particular attention to the limits of our inference due to sampling effects (Levin 1992, Coomes et al. 1999). For my analyses, an edge correction was necessary for measuring inter-fish distances due to biases associated with the hydroacoustic beam pattern. Upon first inspection, the edge correction appeared most critical at low densities when the probability of a fish's nearest neighbor being outside the sample volume was relatively high. However, at high densities, examination of the edge correction (ξ) and the test statistic critical value (dw_{crit}) revealed a surprising result. Although lower in absolute magnitude, the edge correction became increasingly important at high densities when dw_{crit} was also quite small. In these cases, the edge correction equaled a higher proportion of dw_{crit} in the typical region of interest (i.e., low probabilities). This indicated that at high fish densities, the edge correction would be critical when looking for statistically significant differences between an observed spatial distribution and the underlying null distribution.

The edge correction was often positive at small radii for high organism densities. Coomes et al. (1999) found a similar phenomenon for the two-dimensional case, but did not offer any explanations why. Most likely, the positive edge corrections necessary at high densities are an artifact of the underlying statistical distribution. For a Poisson process in three-dimensions, the variance in the expected distance to a nearest neighbor is inversely proportional to the cube root of density. Consequently, at high densities the sampled points within the restricted volume lack some of the extreme events that theoretically occur in an infinite universe. As a result, the random Poisson distribution will appear more uniform at high densities and therefore over-predict the number of neighbors less than some small *r* away.

Both of the statistical methods I used provided information on the spatial distribution of organisms, but yielded different results. The criterion based only on nearest neighbor distances (*G*) merely provided a means for assessing the overall patterns in aggregation, independent of the spatial scale of examination. This approach is based upon the probability of observing at least one neighbor within a given radius. In this case, I found that the prey fish in Lake Washington were aggregated and statistically different from a random Poisson distribution during the day, but not at night (Figure 2.5). Unfortunately, the statistical test involving *dw* is not designed to test for departures from a Poisson random distribution toward uniformity or regular spacing.

Greater insights can be gained by using information on the distances between all of the individuals within a sample volume (Andersen 1992), whereby comparisons are based on the actual number of neighbors within a given radius of an individual. Indeed, the prey fish appeared aggregated at small spatial scales (≤ 1.0 m) using the index that accounts for multiple neighbors (Figure 2.6). These aggregations are typically thought to improve foraging opportunities and act as a predator defense mechanism (Brock and Riffenburgh 1960, Eggers 1978, Pitcher et al. 1988). However, this pattern only held for the daytime distribution. Previous qualitative observations indicated that pelagic prey fishes in Lake Washington form aggregations that disperse at night, presumably due to a lack of light for orienting to their conspecifics (Eggers 1978). Several studies in other systems have also found substantial differences in the spatial distribution of prey fishes between day and night and attributed them to changes in the light environment (Bohl 1980, Clark and Levy 1988, Sogard and Olla 1993). At scales generally >1 m, this approach also revealed significant regular spacing among the prey fish that was obscured in the former analysis. This tendency toward a uniform distribution at large scales is evident upon qualitative inspection of the hydroacoustics echograms as the size of fish aggregations appeared quite small.

The predators also demonstrated significant aggregation using both the nearest- and multiple-neighbor statistics (Figures 2.5 & 2.6). However, their aggregation behavior was likely a response to prey rather than an anti-predator defense given the relatively low predation risk among these large piscivores. Predators will often move to track the distribution of their prey (Holling 1966, Kareiva and Odell 1987, Krebs 1997). For mobile organisms such as fish, the association between predators and their prey is thought to occur at spatial scales similar to a few body lengths of the predator (Horne and Schneider 1997). In Lake Washington the predators and prey were positively associated at spatial scales of 0.6-1.1 m, which is equivalent to a few body lengths of the predators.

Rose and Leggett (1990) estimated that the spatial scale of cod actively feeding on capelin was also small (3.5 m) and reflected the predator's ability to pursue its prey. I also found that predators and prey fish were positively associated with one another during the day, but not at night (Figure 2.6). This likely reflects the visual foraging nature of the piscivores in this system (Beauchamp et al. 1999). The negative association between predators and prey at relatively larger spatial scales (>2 m) may reflect consumption by the predators or active predator avoidance by the prey (Rose and Leggett 1990, Horne and Schneider 1997).

Previous work on the spatial correlation between predators and prey has highlighted the importance in considering a range of spatial scales (Schneider and Piatt 1986, Rose and Leggett 1990, Fauchald et al. 2000). Toward that goal, several recent studies have used methods based on potential or extra contacts (Bult et al. 1998, O'Driscoll et al. 2000), variance power laws (Horne and Schneider 1997), or spectral analyses (Logerwell et al. 1998). Other researchers have used statistical tests based on Ripley's *K* to examine the relationships between seabirds and their fish prey (O'Driscoll and McClatchie 1998), aquatic invertebrate predators and their prey (Muotka and Penttinen 1994), and the relationship between fish and habitat characteristics (Essington and Kitchell 1999, Crook et al. 2001). However, these analyses have been restricted to two-dimensional data. This study represents another step in the direction toward understanding the role of spatial scale in ecology by offering a methodology for analyzing the spatial aggregation and association of predators and prey in pelagic ecosystems that are inherently three-dimensional in nature.

ACKNOWLEDGMENTS

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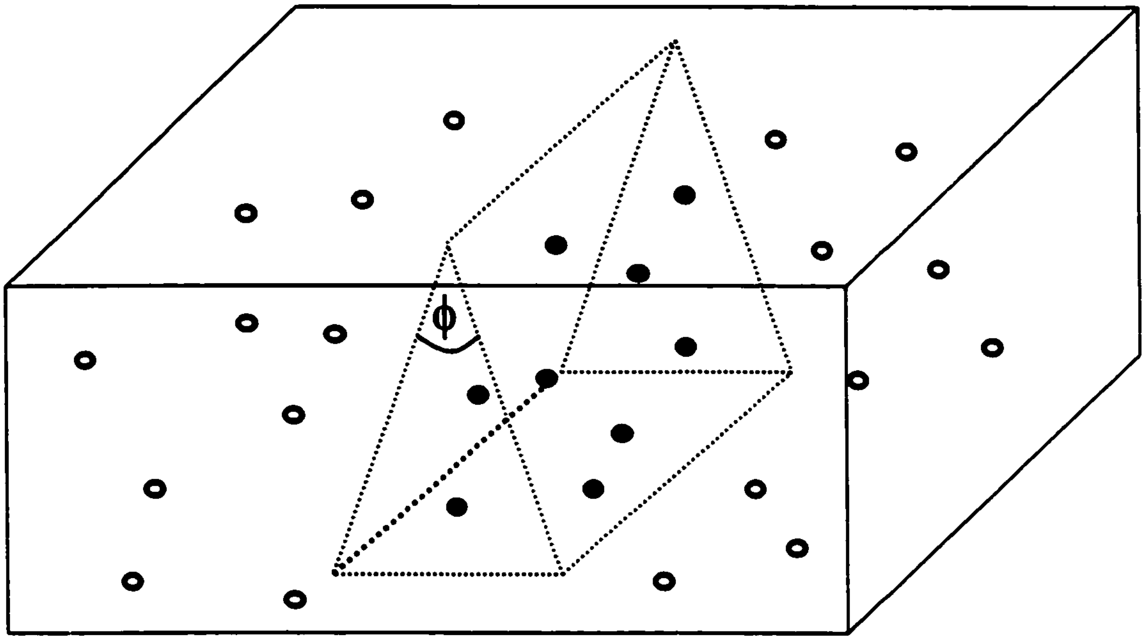

Figure 2.1. Schematic illustrating the sampling volume obtained with a theoretical hydroacoustic transect. As an example, solid circles indicate targets that were included in the sample. The transect length was 500 m long and the sample volume was held constant at 10^5 m^3.

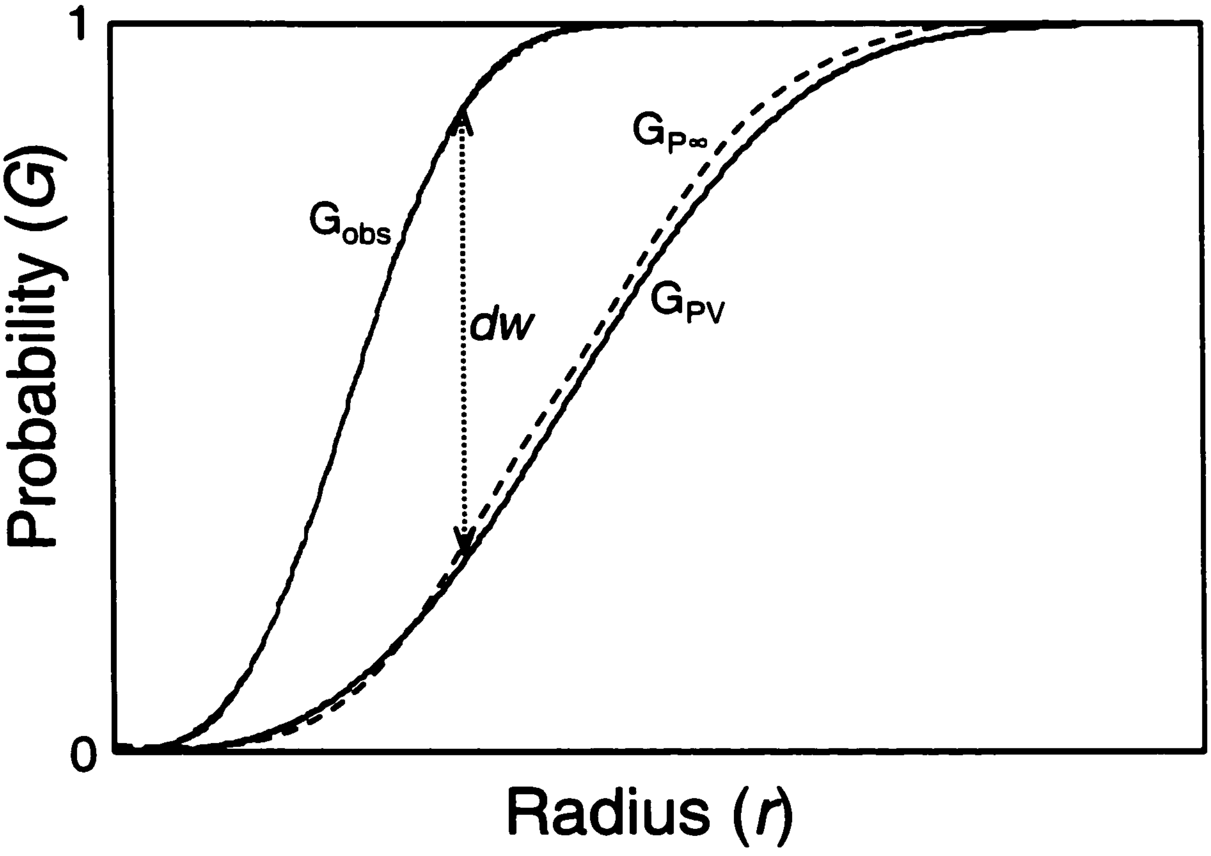

Figure 2.2. The probability G of an individual fish having a nearest neighbor within a sphere of a given radius r for spatial patterns of equal density generated by 1) a three-dimensional Poisson process within an infinite universe ($G_{P\infty}$), 2) a three-dimensional Poisson process within a sampling volume (G_{PV}), and 3) an aggregated distribution (G_{obs}). The test statistic *dw* equals the maximum difference between G_{obs} and G_{PV}.

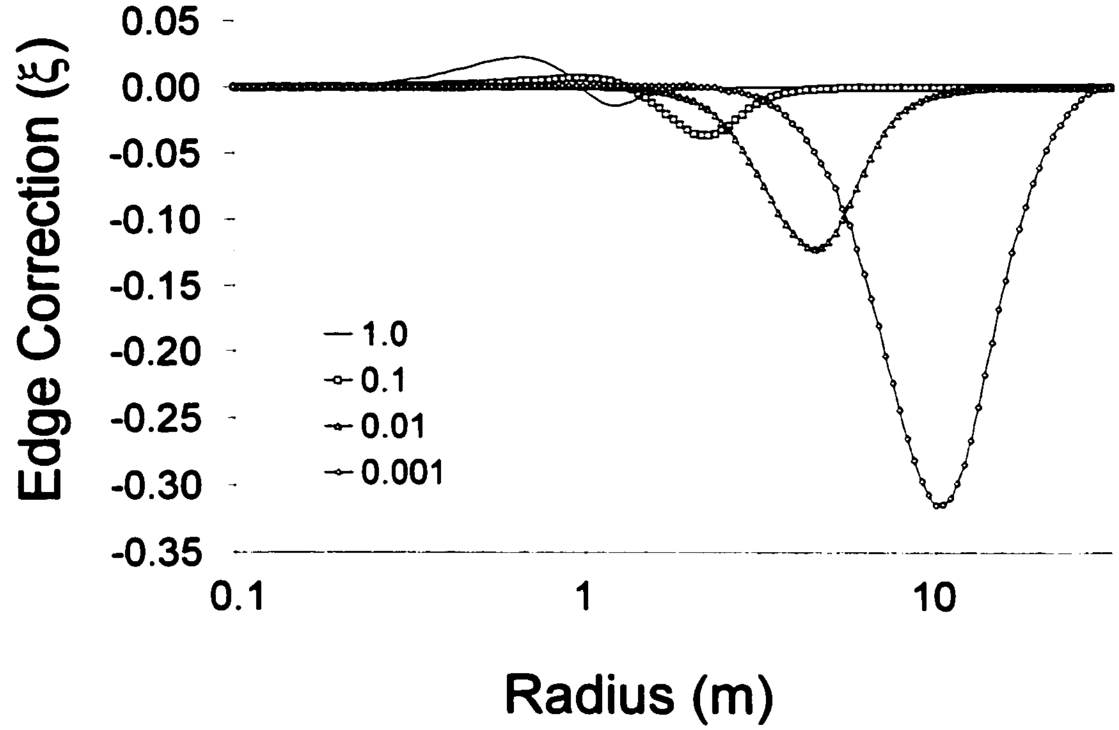

Figure 2.3. Edge correction (ξ) for G_{PV} in relation to the sphere radius (r, m) and fish density (ρ, m^{-3}). The nonlinear edge correction was fitted to data from Monte Carlo simulations ($r^2 = 0.95$) and has the form $\xi(r,\rho) = \beta_0 r(1 + \beta_1 r)(1 + \beta_2 \log_{10}[\rho]) \times \exp[\beta_3 r(1 + \beta_4 \log_{10}[\rho]) + \beta_5 r^2(1 + \beta_6 \log_{10}[\rho])]$. The regression coefficients are $\beta_0 = 0.0340$, $\beta_1 = -0.834$, $\beta_2 = 0.322$, $\beta_3 = -0.468$, $\beta_4 = 0.600$, $\beta_5 = -0.111$, $\beta_6 = 0.256$. The form of the regression equation was taken from Coomes et al (1999).

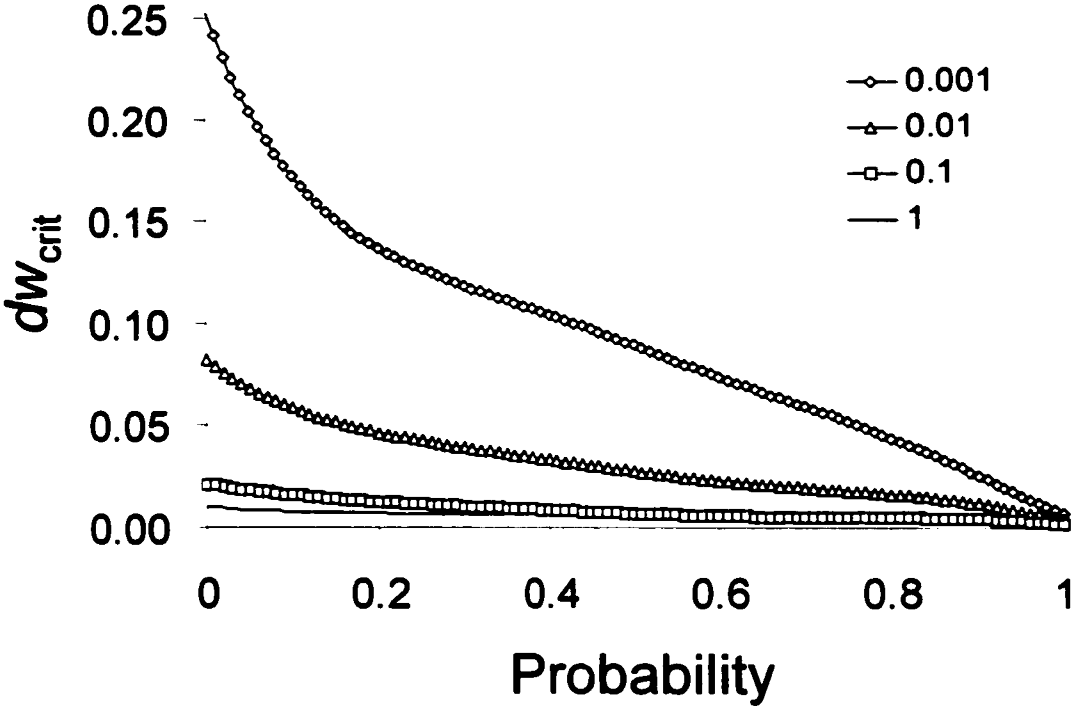

Figure 2.4. Critical values of *dw* in relation to fish density (ρ, m^{-3}) and the probability (P) at which a pattern is indistinguishable from a random three-dimensional Poisson process. The relationship was derived through a nonlinear fit to data from Monte Carlo simulations ($r^2 = 0.99$) and has the form $dw_{crit}(\rho) = \beta_1(1 - \rho^{\beta_2})$, where the regression coefficients are $\beta_1 = -0.0116 + 0.0208P - 0.00260P^2 - 0.0133P^3$ and $\beta_2 = -0.453 + 0.435P - 1.83P^2 + 1.75P^3$. The regression equation is a reduced form of that offered by Coomes et al. (1999).

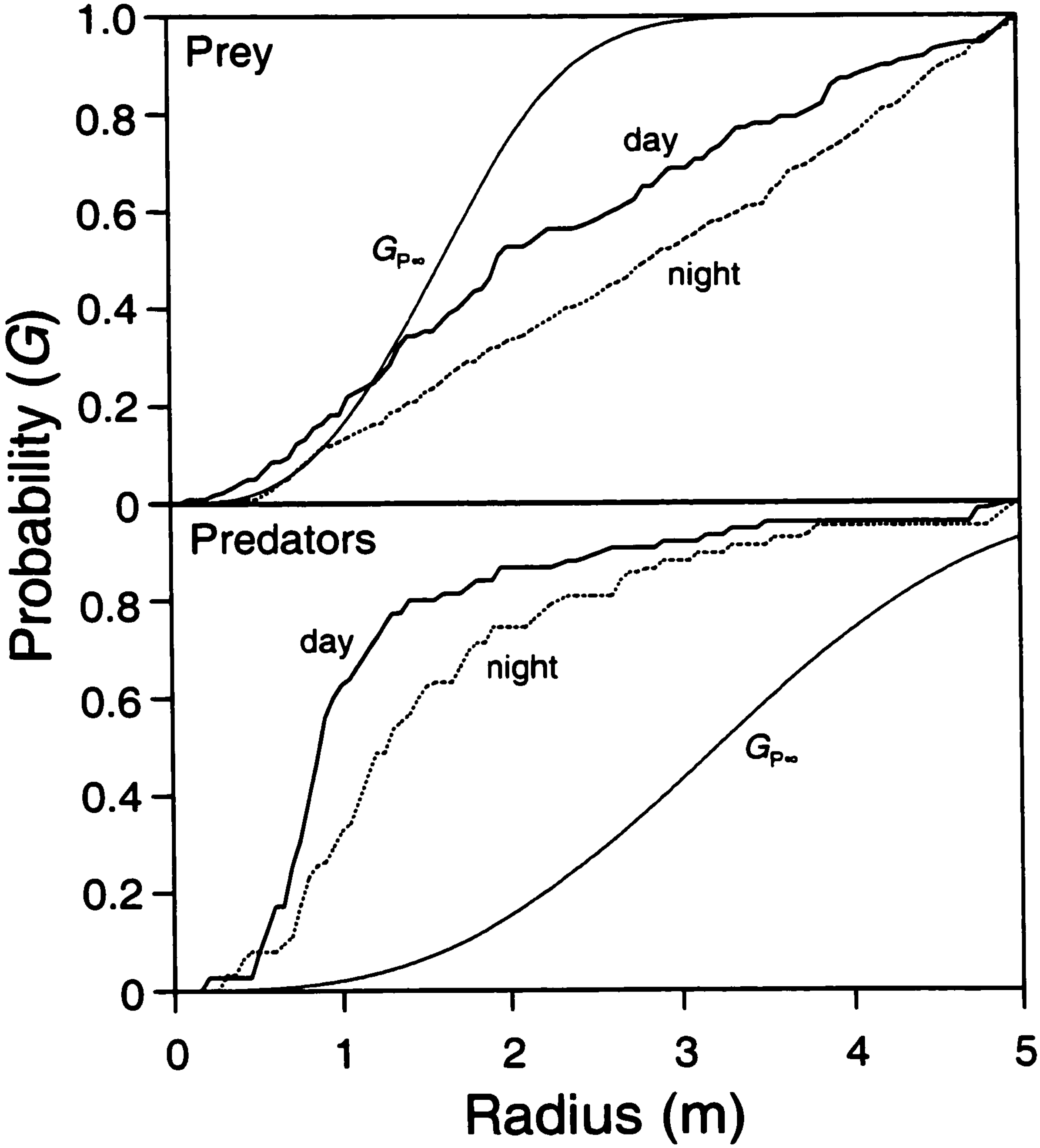

Figure 2.5. The probability *G* of a fish having a nearest neighbor within a sphere of radius *r* for prey fish and their potential predators during the day and night compared to the expected probability assuming a random distribution ($G_{P\infty}$). The test statistic *dw* equals the maximum distance between the observed and expected cdf's across all radii and is therefore scale independent. Data are based on hydroacoustic surveys in Lake Washington on 5 August 1998.

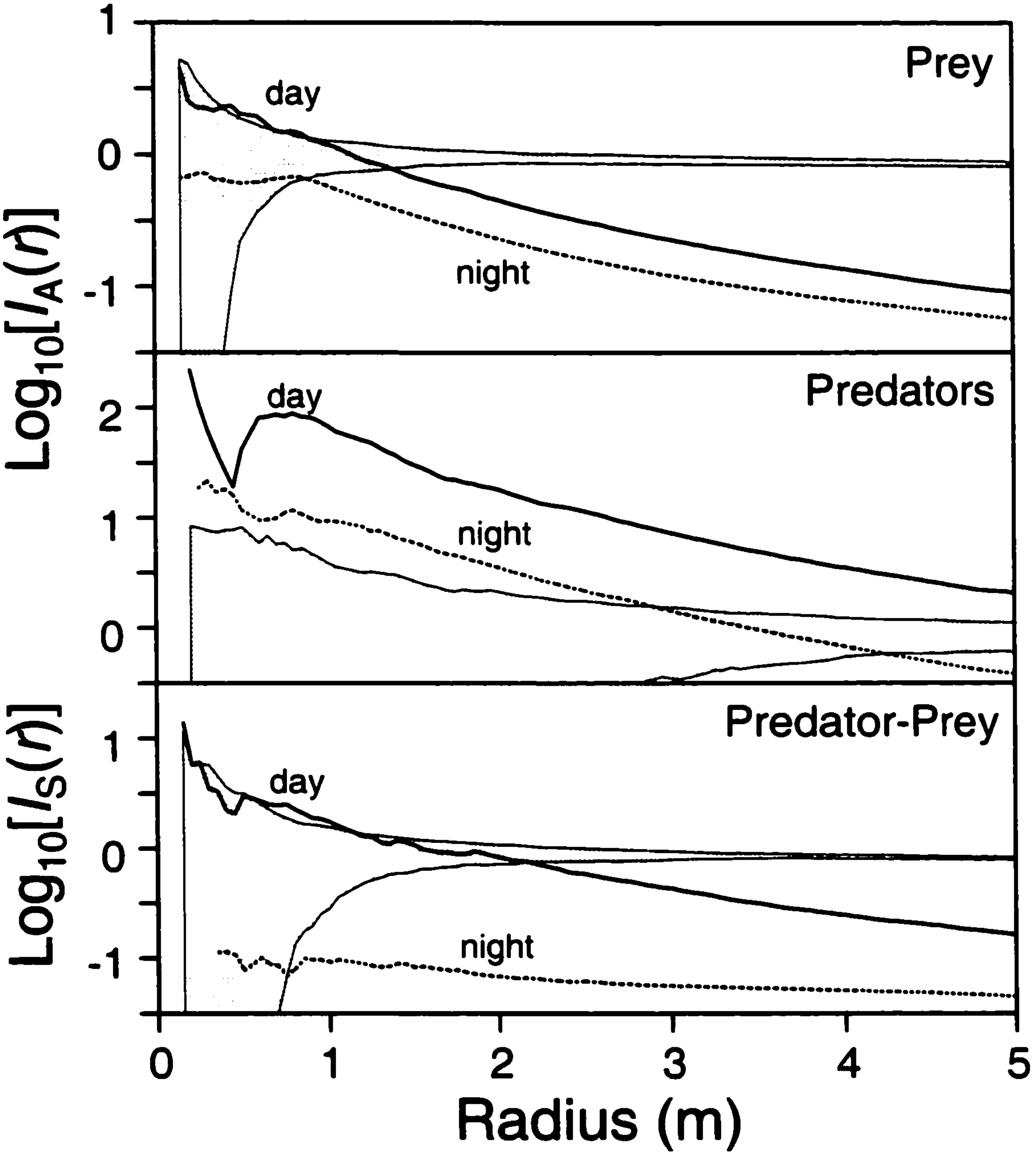

Figure 2.6. Indices of aggregation (I_A) for prey fish and their predators, and the index of association (I_S) between the predators and their prey during the day (solid line) and night (dotted line) for spatial scales <5 m. The shaded region denotes the 95% confidence interval around the expected values obtained through Monte Carlo simulation. Observations outside and above the shaded region are significantly aggregated whereas those outside and below are significantly regularly spaced. Points inside the shaded region are not significantly different from a random Poisson distribution. Data are based on hydroacoustic surveys in Lake Washington on 5 August 1998.

Chapter 3: Human development of lakeshores alters the spatial distribution of fishes[1]

Humans increasingly impact all of the world's ecosystems through a variety of disturbances such as changing land use, species introductions and extinctions, alteration of nutrient cycles, and the use of >50% of the available fresh water (Vitousek et al. 1997). While terrestrial ecology has long apprecated the effects of human-mediated habitat transformation and fragmentation on the spatial distribution of organisms (Kareiva and Wennergren 1995, Debinski and Holt 2000, Haila 2002), similar studies in aquatic ecosystems have been neglected. Recent research in lakes shows that human development of lakeshores simplifies the physical habitat (Christensen et al. 1996, Jennings et al. 1999, Jackson et al. 2001, Olden and Jackson 2001) and alters nutrient cycles (Garrison and Wakeman 2000, Moore et al. 2002). However, no studies to date have examined the influence of shoreline disturbance by humans on the spatial distribution of aquatic organisms. Here we quantify the effect of lakeshore development on the spatial distribution of fishes in 23 lakes in the U.S. Pacific Northwest. We found that the spatial distribution of fishes became significantly less aggregated with increased shoreline development by humans. We also found that the geophysical attributes of the

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[1] This chapter follows the format of the journal *Nature* and was submitted with my co-author Daniel E. Schindler.

lakes affect the spatial aggregation of fish; lakes with a high perimeter to surface area ratio and a relatively shallow littoral zone had much higher levels of fish aggregation. The implications of this interaction between the spatial distribution of aquatic organisms and anthropogenic disturbances have yet to be explored in aquatic ecosystems.

Lakeshores throughout North America are increasingly being developed and altered by humans (Christensen et al. 1996, Jennings et al. 1999, Radomski and Goeman 2001). Accompanying this development are anthropogenic stresses to lake ecosystems including disruption of nutrient cycles resulting in eutrophication (Carpenter et al. 1998, Garrison and Wakeman 2000, Moore et al. 2002), introduction of exotic species (Jackson et al. 2001), and the exploitation of predatory fishes by recreational and commercial fisheries (Pauly et al. 2001, Post et al. 2002). Transformation of nearshore habitats can also adversely affect fish communities because they form the physical template on which lake ecosystems lie (Olden and Jackson 2001). Some direct impacts of lakeshore residential development on the physical structure of lake habitats include the removal of coarse woody debris (Christensen et al. 1996) and aquatic vegetation (Radomski and Goeman 2001), and bottom substrate modifications (Beauchamp et al. 1994). These modifications are also associated with a reduction of fish growth rates (Schindler et al. 2000).

As the global human population grows we will rely more heavily on aquatic resources for food, clean drinking water, and recreation (Botsford et al. 1997, Naiman et al. 1998). In light of these increased demands, ecologists are challenged with making predictions about the response of aquatic ecosystems to changes in the abiotic and biotic environment under a variety natural and anthropogenic disturbances (Pace 2001, Carpenter 2002). Central to these predictions are models that incorporate predator feeding and prey mortality rates; these models depend implicitly on the spatial distributions of interacting organisms. Furthermore, these models also assume that there is no change in the spatial distribution of organisms with human disturbance. However, this critical (and unlikely) assumption remains untested for aquatic systems (Boisclair 2001) whereas in terrestrial systems, anthropogenic habitat loss and fragmentation has altered the spatial distribution of organisms, changed competitive and predator-prey interactions, reduced biodiversity, and led to increased extinction risk (Debinski and Holt 2000, Fahrig 2002, Haila 2002). Here we explored whether human disturbance to lakeshores has any consequences for the spatial distribution of fishes.

Detecting changes in fish assemblages caused by human disturbance usually requires observations before and after the disturbance (Lester et al. 1996), but such studies are often protracted, expensive, and confounded by multiple time-dependent processes. We took an alternative, comparative approach across lakes, which is useful in ecosystem studies where experimental replication is impossible (Schindler 1998) and more rapid feedback is desired. To evaluate the cumulative effect of lakeshore development on the spatial distribution of fishes, we sampled 23 lakes in western Washington, USA, and southwestern British Columbia, Canada. These lakes spanned a residential development gradient in the greater Seattle, WA metropolitan area, which has a current population near 2 million that grew almost 20% in the last 10 years. The intensity of lake shoreline disturbance by humans is highest near the Seattle urban center and then generally decreases with distance from the urban area. We also examined the potential role of the lakes' physical morphology on fish spatial distributions because of the natural interaction between morphology and physical habitat available to aquatic organisms. Lakes with high perimeter : area ratios can receive relatively high inputs of terrestrial matter compared to more circular lakes (Wetzel 2001). Similarly, lakes with very steep sides have relatively little littoral habitat compared to pelagic habitat (Wetzel 2001).

We used the number of nearshore houses per km of shoreline as an index of the intensity of human disturbance, as a high density of lakeshore homes has been correlated with reduced coarse woody debris (Christensen et al. 1996) and aquatic vegetation (Radomski and Goeman 2001), altered nutrient cycling (Garrison and Wakeman 2000), and reduced fish growth rates (Schindler et al. 2000). We chose two simple metrics to describe the physical morphology of our study lakes. First, we used the volume development index as a measure of the lake basin morphometry. The index is expressed as the ratio of a lake's mean depth to its maximum depth (Wetzel 2001), such that a conical basin would have an index of 0.33 and a perfectly cylindrical basin would have an index of 1.0. Second, we used the shoreline development index (D_L) to classify the shape of the lake shoreline relative to its area, where $D_L = 0.5P(\pi A)^{-0.5}$, P is the length of shoreline, and A is the lake surface area (Wetzel 2001). For these purposes we adopt the convention of referring to D_L as the shoreline morphometry index to avoid confusion with our classification of the intensity of human shoreline development.

We assessed the degree of spatial aggregation among fishes using the method developed for three-dimensional point process patterns (Chapter 2). This method involves measuring the locations of individual organisms in three dimensions with hydroacoustics coupled to a differential global positioning system (DGPS), and then calculating the nearest neighbor distances among organisms. For each lake, we compared the observed probability (G_{obs}) of a fish having a nearest neighbor within a given radius to that expected in a random distribution (G_{PV}) assuming a three-dimensional Poisson process. We compared the two probability distributions through the test statistic dw_{obs}, which equals the maximum difference between G_{obs} and G_{PV} over all radii examined. The critical value of dw was calculated through Monte Carlo simulation (Chapter 2). When the ratio of $dw_{obs}:dw_{crit} > 1$, the spatial distribution is significantly aggregated. We used this ratio as a measure for the intensity of aggregation among fishes such that large values indicate strong aggregation and values approaching zero are uniformly distributed in space.

Both human development of lakeshores and lake morphometry were related to the spatial distribution of fishes. We found that the basin morphometry index had a negative effect on the degree of spatial aggregation among fishes (Figure 3.1a) (linear regression: $b = -7.94$, $s.e. = 2.90$, $P < 0.05$, $r^2 = 0.26$), indicating that as the lake basin became more cylindrical in shape, fish aggregation decreased. Once the ratio of mean depth to maximum depth reached 0.5, the fish showed essentially no aggregation behavior. We also found a significant positive effect of lakeshore morphometry on the degree of spatial aggregation among fishes (Figure 3.1b) (linear regression: $b = 2.35$, *s.e.* $= 0.851$, $P < 0.05$, $r^2 = 0.27$), demonstrating that fish were more aggregated in lakes with increasingly complex shorelines. Together the morphometric indices explained 40% of the variation in fish aggregation patterns ($P < 0.01$) and there was a significant interaction between basin and lakeshore morphometry (linear regression: $b = -7.94$, *s.e.* $= 2.90$, $P < 0.05$).

We used the residual variation in fish aggregation from the previous multiple regression of morphometric indices to illustrate the cumulative effect of lakeshore development by humans on the spatial distribution of fishes (Figure 3.2). We discovered a significant negative effect of housing density on the residual variation in fish aggregation (linear regression: $b = -0.0375$, *s.e.* $= 0.0102$, $P < 0.005$, $r^2 = 0.40$), indicating that fish became less aggregated as housing density increased. Removing Angle Lake from the analysis (a statistical outlier with the highest dwelling density at 55.1 houses km^{-1}), we found a somewhat stronger effect of human disturbance on fish aggregation (linear regression: $b = -0.0517$, *s.e.* $= 0.0119$, $P < 0.001$, $r^2 = 0.49$). We also found a very strong relationship between all three of the predictor variables (basin, shoreline, houses) and the level of fish aggregation when we combined them into a backward stepwise regression including all interaction terms (aggregation = $-0.0365 \times$ houses $+ 3.62 \times$ shoreline $- 4.98 \times$ shoreline $\times$ basin, $P < 0.0001$, $R^2 = 0.84$). The intercept in this model was not significant ($P > 0.99$).

All natural populations demonstrate spatial and temporal variation in their numbers. Some of this variability is associated with the physical structure of their habitat. For many years terrestrial ecologists have paid particular attention to the role of human-mediated habitat fragmentation in determining the distribution and interaction among species. These studies have shown that changes in habitat structure often lead to subsequent variation in the spatial distribution of organisms and that these changes must be considered when conserving or restoring ecosystems (Debinski and Holt 2000, Fahrig 2002, Haila 2002). Only recently have we begun to appreciate analogous anthropogenic disturbances in aquatic ecosystems. Evidence is accumulating which shows that human development of lakeshores affects the physical habitat of lakes and the fish community associated with it (Beauchamp et al. 1994, Christensen et al. 1996, Jennings et al. 1999, Schindler et al. 2000, Jackson et al. 2001, Olden and Jackson 2001, Radomski and Goeman 2001). This study represents the first to demonstrate the effects of human disturbance along lakeshores on the spatial distribution of organisms in lakes. We do not know what the principal drivers are of our observed change in fish spatial distribution with changes in residential shoreline development. Nevertheless, we suspect that a combination of eutrophication and associated water clarity (Carpenter et al. 1998), changes in trophic structure associated with fish exploitation (Post et al. 2002), and degradation of nearshore habitats (Schindler and Scheuerell 2002) all contribute to this response.

Researchers and managers alike often rely on empirical models of fish production, nutrient cycling, or contaminant flows to predict the effect of human actions on lake ecosystems (Carpenter and Gunderson 2001). For simplicity, these models often ignore or average spatially explicit features of the biotic and abiotic environments. However, lakes are heterogeneous, three-dimensional landscapes whose structure is influenced by physical, biological, and human activities (Riera et al. 2001). Therefore, consideration of the underlying assumptions is critical when the model is used to evaluate changes within or among ecosystems (Boisclair 2001). As an example we show how lakeshore development changes the underlying spatial distribution of fishes, which is usually assumed constant across systems. Most of the anthropogenic disturbances to aquatic ecosystems associated with lakeshore development occur gradually over time (Jennings et al. 1999), which should allow for proactive management in areas where development of lakeshores is just beginning (Moore et al. 2002). In these cases, incorporating knowledge about the interaction between humans and the environment will prove critical to understanding and predicting ecosystem dynamics (Carpenter 2002). Given the wide-ranging negative effects of anthropogenic habitat transformations on organisms in terrestrial ecosystems, we suspect that similar effects are prevalent, but unexplored, in aquatic ecosystems.

METHODS

Lake data. All of the study lakes were located in western Washington, USA, and southwestern British Columbia, Canada, in a region east of Puget Sound and west of the

Cascade Mountains in an attempt to control for differences in geology, elevation, lake size, and morphometry. Information on lake surface area, shoreline length, mean depth, and maximum depth was obtained from the Washington State Lake Survey Data (Bortleson et al. 1976) and the British Columbia Ministry of Sustainable Resource Management (http://www.gov.bc.ca/srm). The elevation of all lakes ranged from 35–520 m above sea level. The average lake surface area was 22 ha (± 3.4 SE), the mean depth across all lakes was 8.6 m (± 1.1 SE), and the average maximum depth was 18 m (± 2.5 SE). All of the WA lakes had public access for boating and fishing, but the BC lakes were located at the University of British Columbia Malcolm Knapp Research Forest and therefore had neither public access nor shoreline development.

Fish data. We sampled all of the lakes during 11-20 August 1998 and 23-31 August 1999. We obtained direct estimates of the fish community composition in each lake with gill nets and minnow traps. Further information on the fish community composition was gathered through Washington Department of Fish and Wildlife internet sources (http://www.wa.gov/wdfw). The fish community was similar among all lakes and consisted of naturally reproducing and stocked populations of 3-6 of the following species: Centrarchidae (*Micropterus salmoides*, *M. dolomieui*, *Lepomis macrochirus*, *L. gibbosus*, *Pomoxis nigromaculatus*), Percidae (*Perca flavescens*), Ictaluridae (*Ictalurus nebulosus*), and Salmonidae (*Oncorhynchus mykiss*, *O. clarkii*). The average density of prey fishes in the study lakes was 0.097 m^{-3} (± 0.024 SE) and the mean density of predatory fishes was 0.0011 m^{-3} (± 0.00038 SE). Neither the density of prey fishes nor predatory fishes varied across the residential shoreline development gradient (linear regression, prey: $P > 0.70$, $R^2 = 0.005$; predators: $P > 0.90$, $R^2 = 0.0004$).

We measured the three-dimensional locations of fish using a BioSonics DT6000 split-beam echosounder operating at 200 kHz with an elliptical transducer consisting of -3 dB beam angles of 6.7 and 13.5 degrees. We used a 0.4 ms pulse at a rate of 4 s^{-1} with the lower threshold set at -70 dB. All incoming signals were digitized at the transducer and then stored on a computer hard drive for later analysis. The transducer was towed alongside the boat at a speed of 10 km hr^{-1} as the survey followed 8-14 predetermined transects across each lake over a total distance of 1300-4200 m (mean = 2500 ± 130 SE). The total sample volume was 5800-160000 m^3 (mean = 30000 ± 8300 SE). All hydroacoustic surveys occurred between 11:30 and 17:30 on 11-20 August 1998 and 23-31 August 1999. The depth and size of individual echoes were obtained using the BioSonics DT Analyzer 4.0 software. For these analyses we combined all potential prey fish together and classified all targets less than -46 dB as prey fish, which correspond to fish lengths <100 mm (Burczynski and Johnson 1986). We obtained simultaneous measurements on the x-y coordinates of the fish by coupling the hydroacoustics to a sub-meter accurate Trimble® AgGPS 132 differential global positioning system (DGPS).

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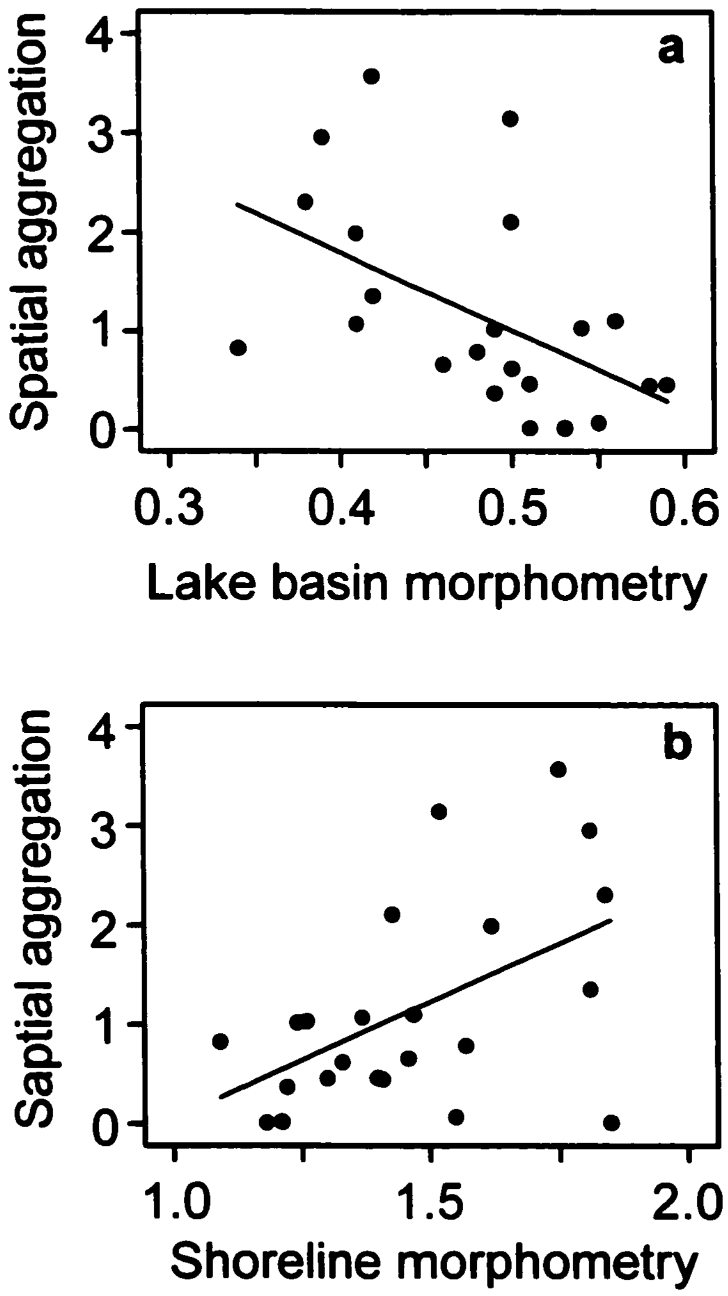

Figure 3.1. Relationship between the degree of spatial aggregation among fishes and lake geophysical morphology. **a**, Lake basin morphometry expressed as the ratio of mean depth to maximum depth; **b**, Lake shoreline morphometry equals $0.5P(\pi A)^{-0.5}$ where P is the length of shoreline and A is the lake surface area. Both morphometric indices are dimensionless. The degree of spatial aggregation equals the ratio of dw_{obs} to dw_{crit}. Values >1 indicate significant aggregation at $\alpha = 0.0022$ (= 0.05 / 23 comparisons).

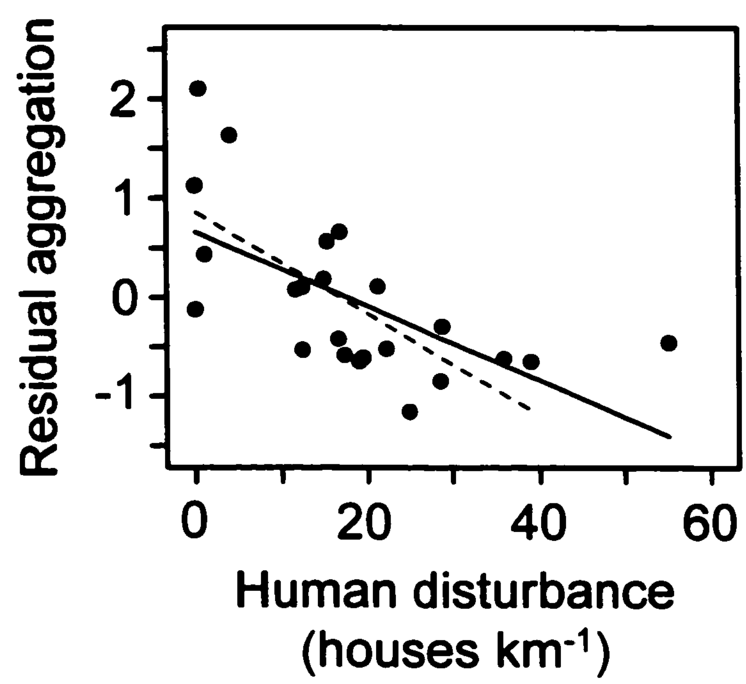

Figure 3.2. Relationship between the residual degree of spatial aggregation and the intensity of human lakeshore disturbance expressed as the number of houses km^{-1} ($n = 23$, $r^2 = 0.40$, $P < 0.05$). The residuals were obtained from the regression of the morphological indices in Figure 1 against the degree of spatial aggregation. The dashed regression line is for all points <50 houses km^{-1}.

Chapter 4: Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window[2]

ABSTRACT

Diel vertical migration (DVM) is a widespread phenomenon in aquatic organisms, yet the adaptive significance of this behavior is still unclear. In particular, diel vertical migration by juvenile sockeye salmon (*Oncorhynchus nerka*) has received considerable attention. We studied how changes in the light environment affect juvenile sockeye DVM through changes in foraging rates and predation risk to test three competing hypotheses to explain DVM in Alaskan lakes. Using hydroacoustics to track temporal changes in fish distribution, we found that in early summer when daylength was long (~21 hours), the sockeye delayed their nighttime migration and did not migrate up as high into the water column as they did in late summer when the daylength was much shorter (~16 hours). Given a lack of diel vertical migration in the zooplankton community, it appears that juvenile sockeye were not simply tracking their food supply. We found clear patterns of DVM and a strong, significant correlation between the mean depth of the sockeye and the amount of light at the lake surface. However, fish large enough to be sockeye predators demonstrated no diel changes in vertical distribution. Calculations of the *in situ* light

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[2] This paper is in review at *Ecology* and was submitted with my co-author Daniel E. Schindler.

experienced by individual juvenile sockeye suggested that they were migrating to maintain a constant light environment. This light environment allowed the sockeye to exploit an antipredation window whereby they could forage on zooplankton while reducing the odds of visual detection by their predators. Furthermore, this antipredation window was continuous in early summer, but was split into two discrete time periods during the crepuscular hours in late summer. These data support the hypothesis that changes in habitat use by juvenile sockeye salmon reflect a dynamic strategy to minimize the ratio of predation risk to foraging gain that changes dramatically over the course of diel cycles in pelagic ecosystems.

INTRODUCTION

Diel vertical migration (DVM) is a common behavioral phenomenon among many aquatic taxa (Stich and Lampert 1981, Levy 1987, Wurtsbaugh and Neverman 1988). The typical pattern is for organisms to be found deep in the water column during the day, followed by a migration upward at dusk, and then a downward migration at dawn (Lampert 1989, Levy 1991). Among freshwater fishes, DVM by juvenile sockeye salmon and kokanee (*Oncorhynchus nerka*) has received considerable attention (e.g. Narver 1970, Levy 1987, 1990b, Steinhart and Wurtsbaugh 1999). While residing in the pelagic zone of their nursery lakes, juvenile sockeye typically occupy much deeper waters during the day than they do at night, with migrations often covering tens of meters (Levy 1987, Clark and Levy 1988, 1990b). The ecological explanation for the evolution of this behavior remains elusive. Three general hypotheses have been proposed to account for the adaptive significance of DVM: bioenergetic efficiency, foraging opportunity, and predator avoidance (Brett 1971, Eggers 1978, Levy 1987, Clark and Levy 1988, 1990b, Bevelhimer and Adams 1993, Steinhart and Wurtsbaugh 1999).

The bioenergetic efficiency hypothesis is based on vertical differences in temperature within the lake, and proposes that the juvenile sockeye select temperatures to maximize their growth rate (Brett 1971, Biette and Geen 1980, Bevelhimer and Adams 1993). Because sockeye salmon are visually foraging planktivores (Eggers 1977), they often feed on zooplankton in the warmer surface waters that have enough light for prey detection (Doble and Eggers 1978, Eggers 1978). The sockeye then presumably migrate to colder, deeper waters to decrease metabolic costs while not feeding (Bevelhimer and Adams 1993). The foraging opportunity hypothesis suggests that fish should track their prey in space and time to maximize foraging and subsequent growth rates (Narver 1970, Levy 1990a, b). However, this hypothesis alone is often rejected because juvenile sockeye typically demonstrate DVM while their zooplankton prey do not and instead remain in the nearsurface waters (Clark and Levy 1988, Levy 1990a, Stockwell and Johnson 1999). Finally, the predator avoidance hypothesis predicts that juvenile sockeye move vertically in the water column in response to piscivores. In this case, the juvenile sockeye are thought migrate up in the water column once light levels have diminished enough to reduce detection by visually feeding piscivores (Eggers 1978, Levy 1987, Clark and Levy 1988).

In all likelihood, a combination of these three hypotheses affects changes in the timing and amplitude of the juvenile sockeye DVM (Clark and Levy 1988). Certainly we expect daily or seasonal changes in the depth distributions of light, temperature, zooplankton, and piscivores. These temporal and spatial fluctuations in the abiotic and biotic environments should alter the relative response of juvenile sockeye to a given stimulus over the growing season (Clark and Levy 1988, Bevelhimer and Adams 1993). Several recent studies have concentrated on evaluating the potential causes of DVM in the absence of other factors. For example, Bevelhimer and Adams (1993) examined bioenergetic costs and benefits of DVM in the absence of predation. Steinhart and Wurtsbaugh (1999) studied the effects of light and foraging on sockeye DVM under the ice in the absence of a thermal gradient. However, given the visual foraging nature of both juvenile sockeye and their predators, the interaction between light and the distribution of both predators and prey on sockeye DVM has yet to be considered. A frequently cited behavioral model suggests that the timing of DVM should occur at the intermediate light levels that occur during crepuscular periods (Clark and Levy 1988). During these times, referred to as the "antipredation window", the light levels allow for a visual range that minimizes the ratio of predation risk to feeding rate ($\mu:f$) for the juvenile salmon. Thus far, empirical evidence of the antipredation window is lacking.

Here we evaluated changes in the timing and amplitude of juvenile sockeye DVM caused by seasonal changes in the light environment with concomitant changes in the vertical distribution of their zooplankton prey and predators. We examined juvenile sockeye DVM among three lakes in southwestern Alaska in early summer when the nights were short and two of those lakes again near the end of summer when the nights were considerably longer. If the sockeye indeed balance predation risk and foraging (or growth) gain, we hypothesized that sockeye would change their migratory behavior to match changes in the light environment so they would exploit the so-called "antipredation window" (Clark and Levy 1988). We discovered that juvenile sockeye appear to time their daily migrations such that they maintain a roughly constant light environment, which is bright enough for them to forage by, yet affords them protection from their visually foraging predators. We also found seasonal differences in the timing and duration of the antipredation window.

METHODS

We examined the influence of light, predators, and zooplankton prey on the spatial distribution of juvenile sockeye salmon in 3 lakes in SW Alaska during the summer of 2000. All three lakes (Kulik, Nerka, and Little Togiak) are located within the Wood River Lakes system and ultimately drain into Bristol Bay (59°20' N, 158°40' W). During the summer of 2000, we surveyed Lake Kulik on 8-9 July and 25-26 August, Lake Nerka on 3-4 July and 1-2 September, and Little Togiak Lake on 11-12 July. Our surveys ran from pre-dusk through dawn with an additional 1-2 hour sampling period during mid-day.

We used hydroacoustics to measure changes in the spatial distribution of both juvenile sockeye salmon and their predators. We used a BioSonics DT4000 split-beam echosounder operating at 200 kHz with an elliptical transducer consisting of -3dB beam angles of 6.5 and 13.5 degrees. We used a 0.4 ms pulse at a rate of 2 s^{-1} with the lower threshold set at -70 dB. All incoming signals were digitized at the transducer and then stored on a computer hard drive for later analyses. Only echoes from depths less than 80 m were analyzed to eliminate potential electrical noise problems. The size and depth of individual echoes were obtained using the BioSonics DT Analyzer 4.0 software. We classified all fish less than –46 dB as juvenile sockeye and all fish greater than –37 dB as predators. According to the equation of Burczynski and Johnson (1986), these sound intensity thresholds correspond to fish lengths of <100 mm and >282 mm respectively. Although the hydroacoustics cannot distinguish the species of fish, juvenile sockeye salmon constitute >75% of the pelagic fish abundance in the Wood River lakes (Hilborn et al., UW Alaska Salmon Program, unpublished data, Rogers 1961, Pella 1964, Burgner et al. 1969), and therefore the hydroacoustics provide a reasonable estimate of juvenile sockeye salmon density and depth distribution.

The split-beam hydroacoustics provided us with estimates of the size and depth of individual fish, but we required a correction for the relative over-sampling of deeper depths due to the cone-shaped geometry of the sound beam. Therefore, we calculated a maximum likelihood estimate of the weighted mean fish depth for juvenile sockeye based on targets grouped into five-minute intervals for each survey. We calculated the weights as

$$w = [\pi z^2 \tan(\theta/2) \tan(\phi/2)]^{-1}, \qquad (1)$$

where z is the depth of an individual target in meters, and θ and ϕ are the hydroacoustic beam angles in degrees. Our transducer is elliptical, such that $\theta = 6.5°$ and $\phi = 13.5°$; a transducer with a circular beam would have equal parameters. These weighted mean depths were based on a mean of 46 (±2.4 SE) individual fish per five-minute sampling interval. For each lake and month combination (n = 5), we grouped all of the predators together before calculating their depth distribution. We based this decision on the observation that the predators were approximately 200 times less dense than the juvenile sockeye in July and about 30 times less dense in August and September, which resulted in small sample sizes for calculating summary statistics over the same sampling interval as the juvenile sockeye. We also assumed that the vertical distribution of predators did not change over a diel cycle based on the lack of any observable vertical migration among predators (see Results).

During the hydroacoustic surveys, we measured incident light levels at the lake surface with a Li-Cor Model 192SA light meter, which measures light in the 400-700 nm range. Light levels were averaged over a five-minute interval and recorded to a Li-Cor Model 1400 data logger. We calculated the light extinction coefficient (K) on each sampling occasion by measuring the light intensity at one-meter intervals down to 25 m depth and fitting a least-squares regression through the standard equation for exponential light extinction:

$$L_d = L_0 \exp(-Kd), \tag{2a}$$

where L_0 is the light level just below the water's surface and L_d is the light level at a given depth d. Estimates of the *in situ* light level experienced by an individual fish ($L_{i,t}$) at a given time t was predicted as

$$L_{i,t} = L_{0,t} \exp(-Kz_i) \tag{2b}$$

using the estimated extinction coefficient K, and the measured fish depth z_i and incident light level $L_{0,t}$. We then computed weighted-means of the *in situ* light over one-hour intervals for juvenile sockeye salmon and their predators using the maximum likelihood analysis described above. It is important to note that the *in situ* light level does not equal the average light and depth for the same one-hour interval inserted into Eqn. 2b due to the nonlinear light extinction with depth. Instead, the weighted mean is based on individual estimates of *in situ* light for individual fish and the vertical distribution of fish.

To assess day-night changes in the vertical distribution of zooplankton, we sampled Lake Kulik on 12 July 2001 at 02:00 and 14:00, and Lake Nerka on 29 August 2001 at 01:00 and 14:00. We collected duplicate samples from 6 discrete depths (1, 10, 20, 30, 40, 50 m) with a 28.8 L Schindler-Patalas trap fitted with an 80-µm mesh cod end. Zooplankton taxa were counted and identified at 25X with a Wild dissecting scope. Zooplankton were initially classified into the following taxonomic groups: *Daphnia longiremis*, *Eubosmina longispina*, *Holopedium gibberum*, *Cyclops columbianus*, calanoid copepods (*Diaptomus gracilis*, *D. pribilotensis*, *Eurytetomra yukonensis*), and copepod nauplii. However, we subsequently lumped all species together for our analyses due to similar patterns in their vertical distribution and the wide diet breadth of juvenile sockeye.

To evaluate the antipredation window and the optimal timing of juvenile sockeye DVM, we calculated the ratio of predation risk to foraging gain (μ:f) over time. For these analyses we combined all of our data from all of the lakes in July and again in August/September. We estimated potential foraging rates (f) of juvenile sockeye salmon as a function of reactive distance according to the model of Clark and Levy (1988) as

$$f_{i,t} = \frac{\varepsilon\pi(r_{i,t} + b)^2 v\rho}{1 + h\pi(r_{i,t} + b)^2 v\rho}, \tag{3}$$

where $r_{i,t}$ is the reactive distance of an individual juvenile sockeye salmon i at a given time t, b is the radius of an individual zooplankter, v is the average fish swimming speed, ρ is the density of zooplankton, ε is the number of zooplankton eaten per attack, and h is the average attack and handling time. All parameter values and their units are listed in Table 4.1. We modeled the reactive distance (r) of juvenile sockeye as a function of the *in situ* light level based on the experimental work of Henderson and Northcote (1985) for juvenile Dolly Varden, *Salvelinus malma*. We generated the following saturating relationship for $r_{i,t}$ (measured in m):

$$r_{i,t} = \begin{cases} 0 & \text{for } \log_{10}(L_{i,t}) \le -3.60 \\ 0.0491\log_{10}(L_{i,t}) + 0.0177 & \text{for } -3.60 < \log_{10}(L_{i,t}) \le -1.97, \\ 0.080 & \text{for } \log_{10}(L_{i,t}) > -1.97 \end{cases} \tag{4}$$

where $L_{i,t}$ is the *in situ* light level (W m^{-2}) from Eqn 2b.

Predation risk for juvenile sockeye was modeled as a product of predator-encounter probability and the predator's reactive distance. The probability of an individual juvenile sockeye encountering a predator ($p_{i,t}$) at time t was modeled as the normalized pdf of the predator vertical distribution such that

$$p_{i,t} = \frac{\exp\left[-\frac{(\ln z_i - m)^2}{2s^2}\right]}{\int_z \exp\left[-\frac{(\ln z_i - m)^2}{2s^2}\right] dz}. \qquad (5)$$

Here, z_i is the depth of the individual juvenile sockeye, m is the mean of the $\log_e$-transformed predator depths, and s^2 is the variance in $\log_e$-transformed predator depths. We assumed that the vertical distribution of predators did not change over a diel cycle based on the lack of any observable vertical migration among predators (see Results). This resulted in predator sample sizes of 51 in July and 450 in August. After $\log_e$ transformation, $m = 2.87$ and $s^2 = 0.0226$ for July, and $m = 2.91$ and $s^2 = 0.0235$ for August/September.

Although most of the predators on juvenile sockeye in our study lakes are arctic char (*Salvelinus alpinus*) (Ruggerone and Rogers 1984), we could not find a model of their reactive distance. Therefore, we based the reactive distance of predators on a model for lake trout (*Salvelinus namaycush*), a similar salmonid piscivore (Vogel and Beauchamp 1999). Following Beauchamp et al. (1999), reactive distance (R) of a predator is a saturating function where

$$R_t = \begin{cases} 17.37\, I_{z,t}^{0.4747} & \text{for } I_{z,t} < 0.0757 \\ 101.2 & \text{for } I_{z,t} \geq 0.0757 \end{cases} \tag{6}$$

and the *in situ* light level ($L_{i,t}$) is from Eqn 2b (measured in W m^{-2}). We assumed turbidity to be zero in their model given the high water transparency in these lakes (extinction coefficient K ranged from -0.18 to -0.21). Relative predation risk for an individual juvenile sockeye ($\mu_{i,t}$) then becomes

$$\mu_{i,t} = p_{i,t}\, R_t. \tag{7}$$

Finally, we calculated the average ratio of foraging gain to predation risk over five minute sampling intervals τ using the weights from Eqn. 1 as

$$\left(\frac{\mu}{f}\right)_\tau = \frac{\sum_{i,t\in\tau} w_{i,t} \frac{\mu_{i,t}}{f_{i,t}}}{\sum_{i,t\in\tau} w_{i,t}}. \tag{8}$$

RESULTS

We observed clear diel vertical migrations of juvenile sockeye salmon in all of the lakes (Figure 4.1). During early July, sockeye began their upward migration around 22:00 from their daytime depth near 75 m. They then reached their average nighttime depth of approximately 15 m around 02:30 where they remained for about one hour before migrating back down, again reaching their daytime depth around 07:30. During this time, the $\log_{10}$ of the incident light level (W m^{-2}) at the lake surface ranged from approximately

2.5 at 21:00 to –2.0 at 03:00, and then back up to 2.5 by 09:00. During late August the juvenile sockeye began their upward migration earlier and reached shallower depths than in July (Figure 4.1). The juvenile sockeye began their upward migration around 20:00, reaching their average nighttime minimum depth between 7-10 m around 23:00, where they remained approximately 5 hours longer than in July. They began their downward migration around 05:30 and reached their average daytime depth near 75 m around 09:00. During late August, light levels were generally lower than in July (Figure 4.1). At the onset of vertical migration, the $\log_{10}$ of the incident light level (W m^{-2}) was near 2.0 at 21:00, reached a minimum of –3.5 around 02:00, and rose back up to 2.0 by 09:00. The variation in light levels between 00:00-06:00 during late August was caused by a combination of moonlight and changes in cloud cover.

The vertical limits of the distribution of predators across all sampling dates varied between 10-75 m, but these fish were generally found between 20-40 m (Figure 4.1). This depth distribution remained relatively constant over the diel period, as linear regression of predator depth as a function of the $\log_{10}$ of incident light explained <10% of the variation in predator depth. Furthermore, we only found significant, but very weak, regressions in August (Kulik: $R^2 = 0.017$, F-ratio = 4.04, $p = 0.046$) and September (Nerka: $R^2 = 0.088$, F-ratio = 27.4, $p < 0.0001$).

The vertical distribution of the zooplankton community changed very little between day and night in Lake Kulik (Figure 4.2), but the zooplankton community tended to shift deeper at night in Lake Nerka. However, we found no significant difference in the zooplankton depth distributions in either lake (Kolmogorov-Smirnov 2-sample test, maximum difference = 0.5, $p > 0.10$), and zooplankton were generally found in the top 30 meters of the water column. The day and night mean depths for Lake Kulik were 27.2 m (±4.6 SE) and 26.2 m (±4.9 SE) respectively. The day and night mean depths for Lake Nerka were 25.6 m (±5.0 SE) and 30.0 m (±4.9 SE) respectively. Excluding copepod nauplii, the zooplankton community was dominated by cyclopoid copepods, and to a lesser extent *Eubosmina* and calanoid copepods. This pattern generally held across all lakes and times of the day.

The temperature profiles in early July showed a slight thermocline near 8 m in Little Togiak, with more pronounced thermoclines near 10 m and 15 m in Kulik and Nerka respectively (Figure 4.3). By late August, the thermocline in Kulik was around 10 m, and it remained near 15 m in Nerka although the thermal stratification was less pronounced. In July, the maximum temperature was near 12°C for all lakes. In August, the maximum temperature in Kulik had increased to above 14°C, but remained near 12 in Nerka. The minimum temperature ranged from 4.2-4.9°C across all lakes and dates.

We found a significant positive relationship between the amount of incident light at the lake surface and the depth of the juvenile sockeye salmon during the crepuscular periods and night (Table 4.1, Figure 4.4). As the light level increased, the mean depth of the juvenile sockeye also increased. In lakes Kulik and Nerka, the slope of the regression line through the data points was steeper in July than in late August (Kulik: $t = 3.00$, df = 139, $p = 0.0016$) and early September (Nerka: $t = 3.81$, df = 117, $p = 0.00011$). These differences in slope indicated a stronger response of juvenile sockeye to the same unit change in light level earlier in the year. During the juvenile sockeye DVM, the light levels at the lake surface changed by 4-5 orders of magnitude (Figures 4.1 & 4.4). However, the amount of *in situ* light that the juvenile sockeye experienced during their migration changed by only 1-2 orders of magnitude (Figure 4.5). During the juvenile sockeye migration in July, the mean of the log *in situ* light levels began near –1 and decreased to around –3 just after midnight, where they remained through the remainder of the night and into the following morning during their downward migration. During late August and early September, the mean of the log *in situ* light levels began near –3, fell slightly to –3.7 by 01:00, and then increased to near –3 again by the end of the migration at 09:00 (Figure 4.5). during both sampling periods

The predators demonstrated a different response than their sockeye prey to changing light levels (Figure 4.5). During the time when the juvenile sockeye were vertically migrating, the predators remained at roughly the same depth. This resulted in a dramatic change in the predators' *in situ* light levels from dusk through dawn, which spanned 5-6 orders of magnitude. This large change in the predators' *in situ* light levels essentially reflected the change in incident light at the lake surface (Figure 4.1). The times where the curves of *in situ* light levels for the juvenile sockeye and their predators cross indicates temporal and spatial overlap of predators and prey.

Plots of the ratio of foraging gain to predation risk (μ:*f*) illustrated substantial changes in this ratio over the course of DVM by juvenile sockeye (Figure 4.6). In July,

μ:f was minimized for one continuous 6 hour period from 0:00-6:00. However, later in the summer, this antipredation window was split into two discrete periods. The ratio of μ:f was minimized for roughly one hour from 22:00-23:00 and again from around 7:00-8:00. In both early and late summer, inspection of the mean incident light function (Figure 4.6) indicated that the antipredation window was bounded by surface light levels of 100 and 0.01 W m^{-2}.

DISCUSSION

We found strong patterns of diel vertical migration by juvenile sockeye salmon in all three of our study lakes, in both early and late summer (Figure 4.1). The juvenile sockeye were found deep in the water column during the day, began their migration upward at dusk, and remained in relatively shallow waters until dawn, when the process reversed. This behavioral phenomenon has been reported for other populations of juvenile sockeye throughout their range in North America (Narver 1970, Clark and Levy 1988, Beauchamp et al. 1997). Levy (1987) outlined several hypotheses to explain diel vertical migration by juvenile sockeye salmon: maximizing bioenergetic efficiency, maximizing foraging gain, and minimizing predation risk. These hypotheses focus on the sensory mechanisms of the fish, especially those pertaining to temperature and light (Levy 1987, 1990b).

The bioenergetic efficiency explanation for diel vertical migration centers around water temperature, whereby the fish are thought to migrate to shallow, warm water to feed on zooplankton and then retreat to deeper, cool water where they remain while digesting their prey and minimizing the energy required for maintenance (Brett 1971, Bevelhimer and Adams 1993, Stockwell and Johnson 1997). Levy (1991) found that changes in the vertical distribution of juvenile sockeye in a British Columbia lake tracked movements of an internal thermal seiche. Brett (1971) found that sockeye growth rates were maximized at 15°C, but Biette and Geen (1980) found that sockeye grew best when exposed to a cyclic temperature environment similar to that encountered during diel vertical migration. Using a bioenergetics model, Bevelhimer and Adams (1993) also found a growth advantage to diel vertical migration in a North Carolina population of adult kokanee (*O. nerka*). However, the authors also noted that predation was not a factor for the size class of adults they examined. Among several Idaho lakes, Beauchamp et al. (1997) suggested that only those juvenile sockeye exposed to limited food resources and high predation risk appeared to maximize bioenergetic efficiency. In our case, we generally observed juvenile sockeye below 70 m during the day, but the thermocline was generally between 8-15 m. If the fish were merely tracking cooler temperatures during the day to maximize bioenergetic efficiency, it is unclear why they should go so deep when the temperature was a constant 4-6°C below 30 m (Figure 4.3). Furthermore, the energetic costs associated with the hydrostatic effects on the swim bladder during vertical migration of this amplitude would likely diminish any metabolic advantage associated with migration (Levy 1987). Finally, Steinhart and Wurtsbaugh (1999) documented diel vertical migrations among three populations of *O. nerka* during the winter. The 3-5°C homothermal environment under the ice led them to propose that foraging was more important than temperature in structuring the observed vertical distribution patterns.

The light environment within lakes has previously been shown to affect the vertical distribution of many pelagic fishes (Luecke and Wurtsbaugh 1993, Appenzeller and Leggett 1995) including juvenile sockeye salmon (Levy 1987, 1990b). Juvenile sockeye salmon are visual foragers (Eggers 1977) and they largely feed on zooplankton during their residence in lakes (Doble and Eggers 1978). Given the generally positive relationship between body size and survival (Miller et al. 1988), juvenile fish may attempt to maximize their foraging opportunities and hence growth rate. If so, diel vertical migrations by juvenile sockeye may reflect an attempt to maximize their spatial and temporal overlap with populations of vertically migrating zooplankton (Levy 1987, 1990a, 1990b, Stockwell and Johnson 1999). Furthermore, at dusk a vertically ascending planktivore could take advantage of the contrast between its zooplankton prey and the backlit surface of the water, which would render the zooplankton prey more vulnerable to detection (Zaret and Kerfoot 1975, Zaret 1980). However, given the apparent lack of vertical migration among the zooplankton communities in our study lakes (Figure 4.2), the juvenile sockeye would not appear to be merely tracking the vertical movements of their prey. Similarly, if the juvenile sockeye had adopted the strategy of simply maximizing prey intake, they should have remained in the upper 30 m of the water column throughout the daylight hours. Again, this was not the case in our lakes where juvenile sockeye were essentially absent from the upper 50 m of water during the day.

Indeed, Levy (1990a) cites the lack of spatial overlap between juvenile sockeye and their zooplankton prey as evidence against the foraging efficiency hypothesis.

The vertical distribution of predators can also affect the timing and amplitude of diel vertical migrations by juvenile sockeye salmon (Levy 1987, Clark and Levy 1988, Levy 1990b, Bevelhimer and Adams 1993). Most of the pelagic predators of juvenile sockeye salmon are also visual foragers, occupying relatively shallow depths throughout the day and night (this study, Beauchamp et al. 1999). The avoidance of upper waters by juvenile sockeye during the daylight hours is likely a response to the presence of visually-foraging predators there. In lakes where juvenile sockeye are found high in the water column during the day, they often form schools (Eggers 1977, Levy 1990a), a common defense against predators (Brock and Riffenburgh 1960, Sogard and Olla 1993). Large piscivores also experience a rapid decrease in visual range with a decrease in light level (Beauchamp et al. 1999, Vogel and Beauchamp 1999). In our study lakes, we found that the large fish were generally found in the upper 40 m of water during all times of the day (Figure 4.1). Data from Bevelhimer and Adams (1993) showed that growth rates based on observed diel vertical migration patterns were on average only 50% of those predicted by an optimal DVM pattern, again suggesting that the fish were migrating to reduce their vulnerability to predators rather than merely maximizing their growth rate.

We found a strong correlation between the light intensity at the lake surface and the mean depth of juvenile sockeye (Figure 4.4). Appenzeller and Leggett (1995) found that the modal depth of rainbow smelt (*Osmerus mordax*) in Lake Memphremagog was strongly related to the incident light at the lake surface, and they hypothesized that the smelt were actively avoiding a light threshold rather than tracking some optimal light level. Among several British Columbia lakes, Levy (1990b) found that juvenile sockeye salmon in very clear lakes were much deeper in the water column during the day than those in comparatively darker lakes. Using his empirical relationship between the light extinction coefficient (K) and mean daytime depth (Depth = $-15.4\ K^{-1} - 1.23$, $r^2 = 0.83$, $p<0.05$), we would predict sockeye in our lakes to reside between 73-86 m during the day. Indeed, we recorded daytime depths of juvenile sockeye greater than 70 m in all of the lakes (Figure 4.1).

The predator avoidance hypothesis suggests that fish should seek out isolumes where the visual foraging ability of the predators is greatly diminished (Eggers 1978, Clark and Levy 1988, Levy 1990b). In Lake Washington, Eggers (1978) found that during dusk, the isolume at 7.3×10^{-4} W m^{-2} separated individuals from schools of juvenile sockeye salmon; the schools were presumably affording some level of predator protection. In our case we found that juvenile sockeye appeared to track light levels in the range of 10^{-2} to 10^{-4} W m^{-2} throughout the course of their migration (Figure 4.5). Levy (1990b) hypothesized that evolution would favor fish that selected light levels below the saturation irradiance threshold (SIT) of their predators. The SIT is the minimum irradiance that maximizes a predator's reactive distance, below which the predator's reactive distance declines dramatically (Henderson and Northcote 1985). For adult lake trout feeding on salmonid prey, Vogel and Beauchamp (1999) estimated SIT to be 0.0756

W m^{-2}. We indeed found that the juvenile sockeye occupied depths with light levels below the SIT for lake trout (Figure 4.5), suggesting that the juvenile sockeye migrated to avoid predators. The Wood River Lakes lack lake trout, but they do have sizable populations of arctic char (*Salvelinus alpinus*), which are quite similar to lake trout and account for high levels of juvenile sockeye mortality in our study system (Nelson 1966, Burgner et al. 1969, Ruggerone and Rogers 1984, Burgner 1991).

It is also conceivable that the juvenile sockeye salmon would select isolumes that allow them to forage effectively while simultaneously reducing the probability of detection by predators (sensu Werner and Gilliam 1984). Henderson and Northcote (1985) measured the minimum prey detection threshold (VIT) for juvenile cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*) feeding on zooplankton prey at 1.08×10^{-3} and 2.53×10^{-4} W m^{-2} respectively. If we assume that the visual acuity of juvenile sockeye salmon is an average of these values, we see that in early July the juvenile sockeye are always found above the VIT and could theoretically forage on zooplankton (Figure 4.5). However, in late summer the juvenile sockeye were near or below the same threshold, suggesting that predator avoidance may have been more important than foraging during that time.

Clark and Levy (1988) hypothesized that juvenile sockeye migrate to select light levels sufficient enough to detect their prey while minimizing the detection ability of their predators, thus allowing them to exploit an "antipredation window". Their hypothesis suggests that fish should alter their depth distribution in response to changing light levels to minimize the ratio of predation risk to foraging gain and therefore maximize their fitness. Furthermore, Clark and Levy's (1988) dynamic optimization model predicts that this antipredation window will occur around the crepuscular periods when light levels change most rapidly. Interestingly, in July we found only one antipredation window when $\mu{:}f$ was very low for approximately six hours that encompassed both crepuscular periods (Figure 4.6). Due to the relatively high latitude of our study lakes, light levels in early July were apparently high enough to facilitate foraging throughout the evening hours (Figure 4.5), which led to low $\mu{:}f$ values. Later in the summer however, when the nights were nearly an order of magnitude darker, the ratio of $\mu{:}f$ was lowest during two distinct time periods (Figure 4.6). In this case, these two antipredation windows were about one hour long and coincided with the times when the incident light was changing most rapidly. As the evening progressed, the light levels became insufficient for foraging and the ratio of $\mu{:}f$ increased until dawn when light levels rose again and foraging rates increased relative to predation risk. Indeed, our results provide strong evidence in support of Clark and Levy's (1988) hypothesis.

Clark and Levy's (1988) dynamic optimization model also predicts that juvenile sockeye will balance their predation risk and foraging gain based on their present state and an ultimate goal. Assuming that the juvenile sockeye are attempting to reach some minimum size threshold before the winter, and subsequent smoltification the following spring, they might be willing to accept more predation risk in favor of better foraging opportunities in the early summer. As the summer progresses and they approach or exceed their size requirement, juvenile sockeye may opt for safer water and only forage enough to meet energy maintenance requirements. In early July, juvenile sockeye responded more rapidly to a unit change in light than they did in late August (Figure 4.4, Table 4.2). We also found that on average, juvenile sockeye were found in a brighter environment in early July than in late August (Figure 4.5). This could have resulted from the greater number of predators that we observed later in the summer; a reflection of the midsummer movement of arctic char out of river mouths and into the pelagia of lakes (Ruggerone and Rogers 1984). These seasonal differences in light response and *in situ* light levels reflect a dynamic change in habitat utilization by the juvenile sockeye during their first year of life.

Given the spatial overlap of the zooplankton prey and predators in our lakes, we expect that juvenile sockeye salmon should select their depth in the water column based a trade-off between foraging gain and predation risk. Given the visual foraging nature of both the sockeye and their predators, changing light levels likely structure the vertical distribution of juvenile sockeye salmon. This response to light was apparent in the timing and amplitude of our observed diel vertical migrations. We found that the juvenile sockeye shifted the timing of their upward migration earlier in the day and their downward migration later after dawn to match the seasonal changes in light intensity (Figure 4.1). Furthermore, the amplitude of the juvenile salmon migration extended into shallower depths later in the summer when the light intensity was an order of magnitude darker (Figure 4.1). Our data support Clark and Levy's (1988) prediction that DVM patterns by juvenile sockeye salmon reflect a strategy of balancing the conflicting demands of minimizing their predation risk while maximizing their growth rates.

ACKNOWLEDGMENTS

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Table 4.1. Descriptions and values for the parameters in the juvenile sockeye foraging model (from Clark and Levy 1988).

Symbol	Parameter	Value	Units
h	Handling time	1.8	s
v	Mean swimming speed	0.05	$m\ s^{-1}$
ρ	Mean zooplankton density	10^{4}	m^{-3}
b	Radius of individual zooplankter	5×10^{-4}	m
ε	Zooplankton consumed per encounter	1	-

Table 4.2. Regression results for the relationship between the weighted depth of juvenile sockeye salmon and the $\log_{10}$ of the incident light hitting the lake surface. Regression results are for the data plotted in Figure 4.4 without the outliers (open circles).

Lake	Month	n	R^2	Intercept (SE)	Slope (SE)	F-ratio	p-value
Nerka	July	90	0.77	-9.07 (3.34)	15.4 (0.890)	298.6	<0.0001
	Sept	89	0.93	10.0 (1.05)	11.7 (0.366)	1021	<0.0001
Kulik	July	75	0.82	4.34 (2.23)	12.8 (0.687)	346.1	<0.0001
	August	87	0.87	17.7 (1.22)	10.4 (0.422)	602.7	<0.0001

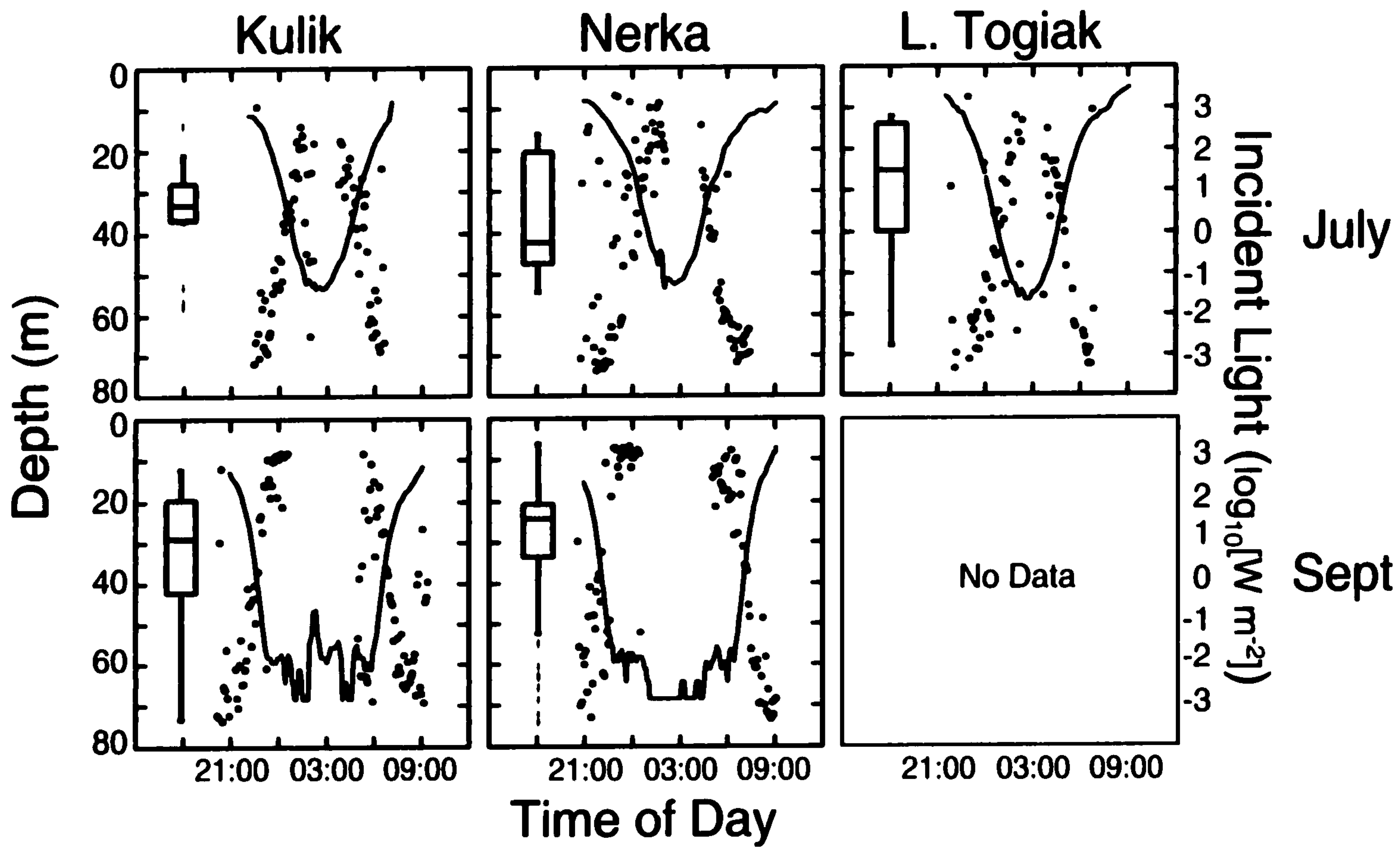

Figure 4.1. Depth distribution of piscivorous fishes (box-and-whisker plot) combined with time series of the mean depth of juvenile sockeye (black dots) and the log of light intensity at the lake surface (solid line) for Kulik, Nerka, and Little Togiak lakes, in July and September. Each data point for the depth of juvenile sockeye represents an average over a five-minute interval. See Methods section for details.

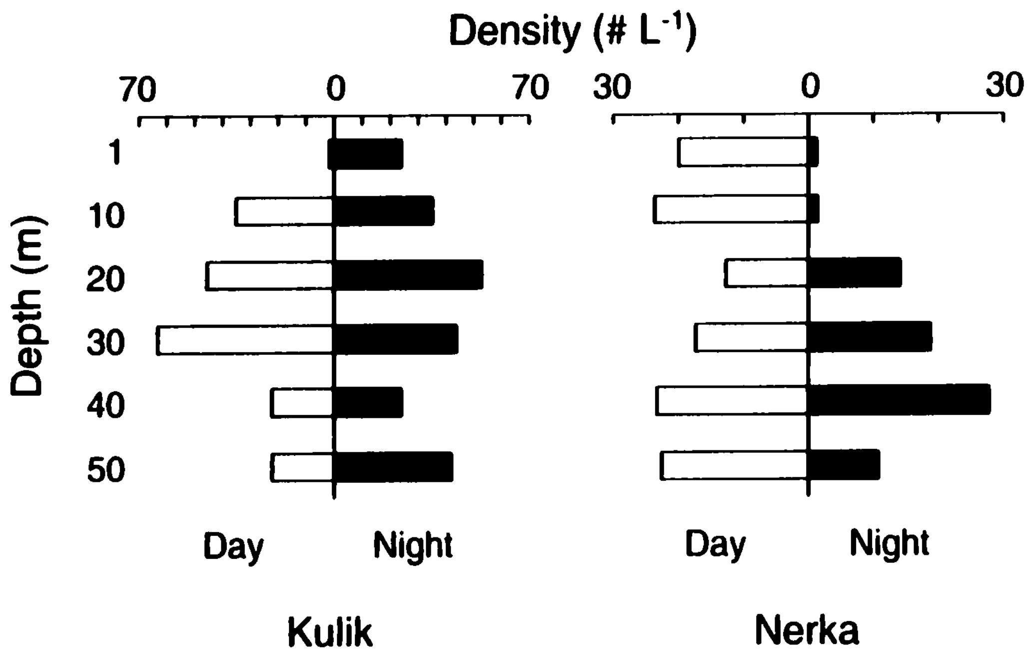

Figure 4.2. Depth distribution of the zooplankton community during the day (open bars) and night (solid bars) for Lakes Kulik and Nerka. See Methods section for details on the zooplankton taxa that were included in the analysis.

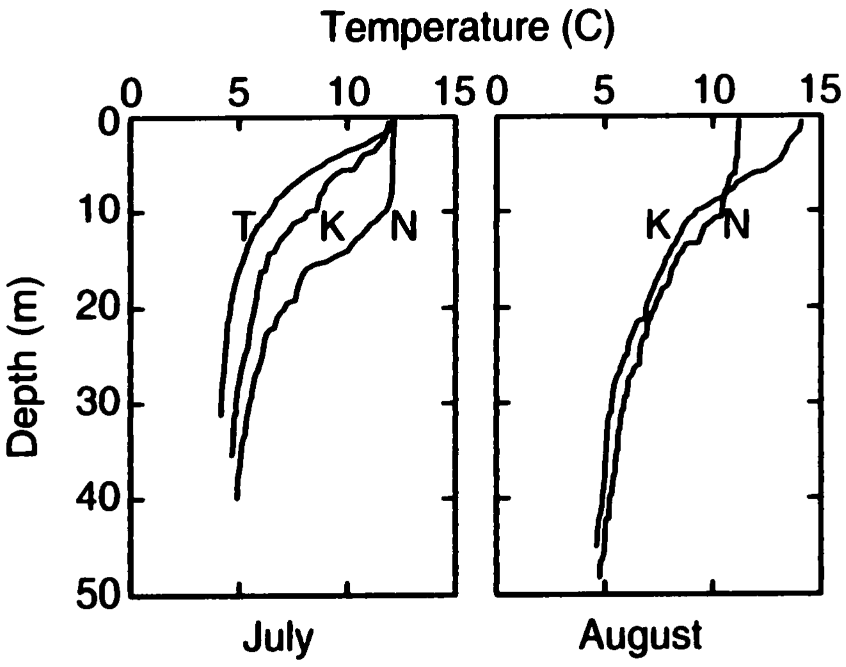

Figure 4.3. Temperature-depth profiles for Little Togiak (T), Nerka (N) and Kulik (K) lakes in early July and late August.

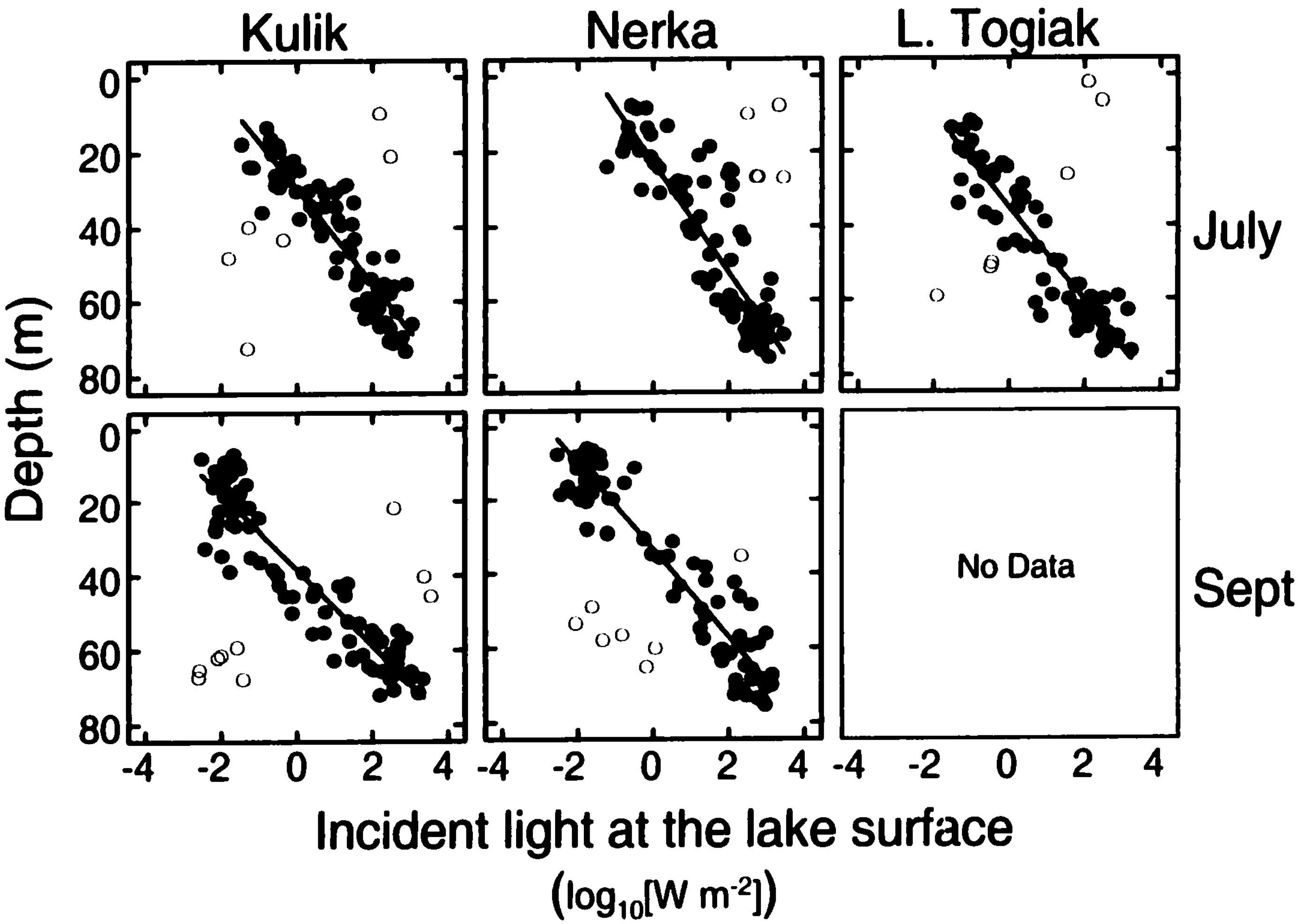

Figure 4.4. Relationship between light intensity at the lake surface and the depth distribution of juvenile sockeye salmon for Kulik, Nerka, and Little Togiak lakes, in July and September during crepuscular periods and night. Regression coefficients of determination (R^2) listed in Table 4.2 are for the solid circles only; open circles represent statistical outliers.

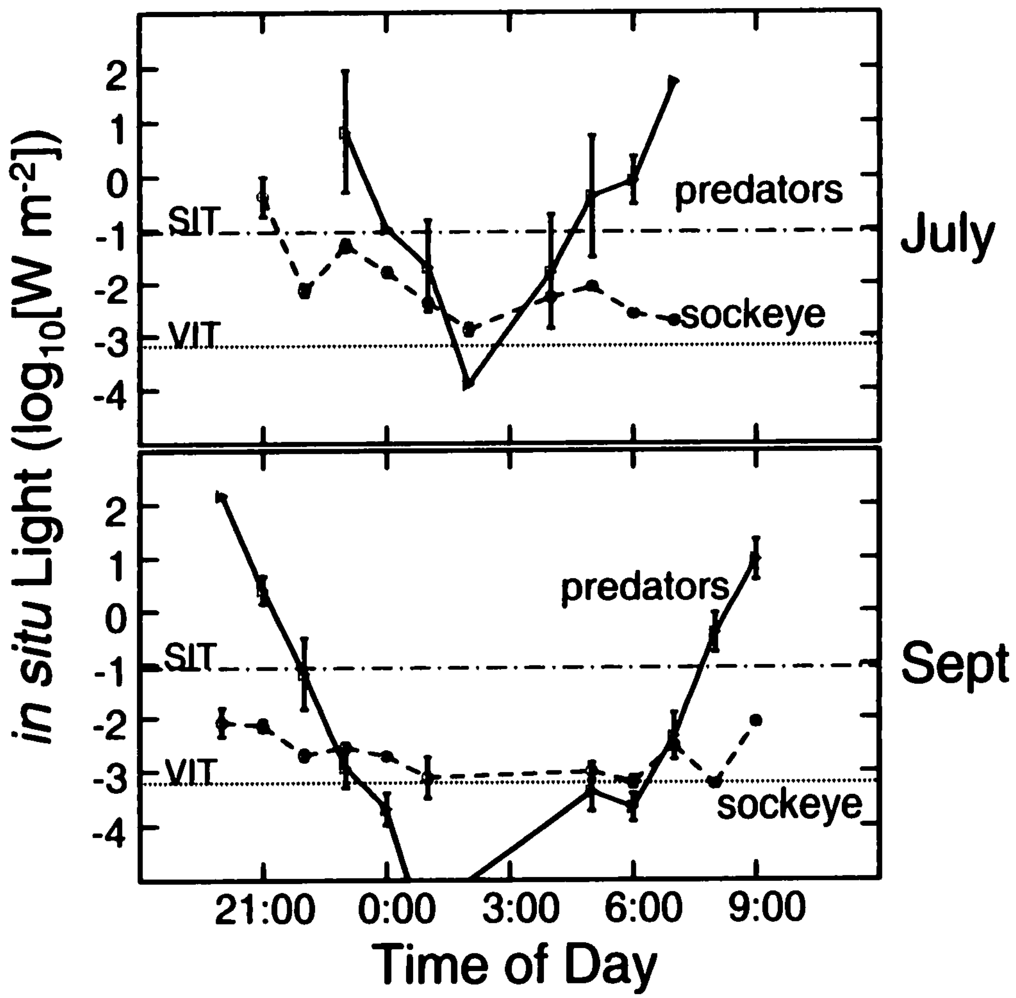

Figure 4.5. Time series of hourly averages of the ambient light levels for predators (solid line) and juvenile sockeye salmon (dashed line), in July and September. Error bars represent 95% confidence intervals. For comparison, the horizontal dashed line at −1.1 indicates the saturation irradiance threshold (SIT) for the detection of juvenile salmonid prey by adult lake trout, and the horizontal dotted line at −3.2 indicates the average lower light threshold (VIT) for zooplankton prey detection by juvenile salmonids .

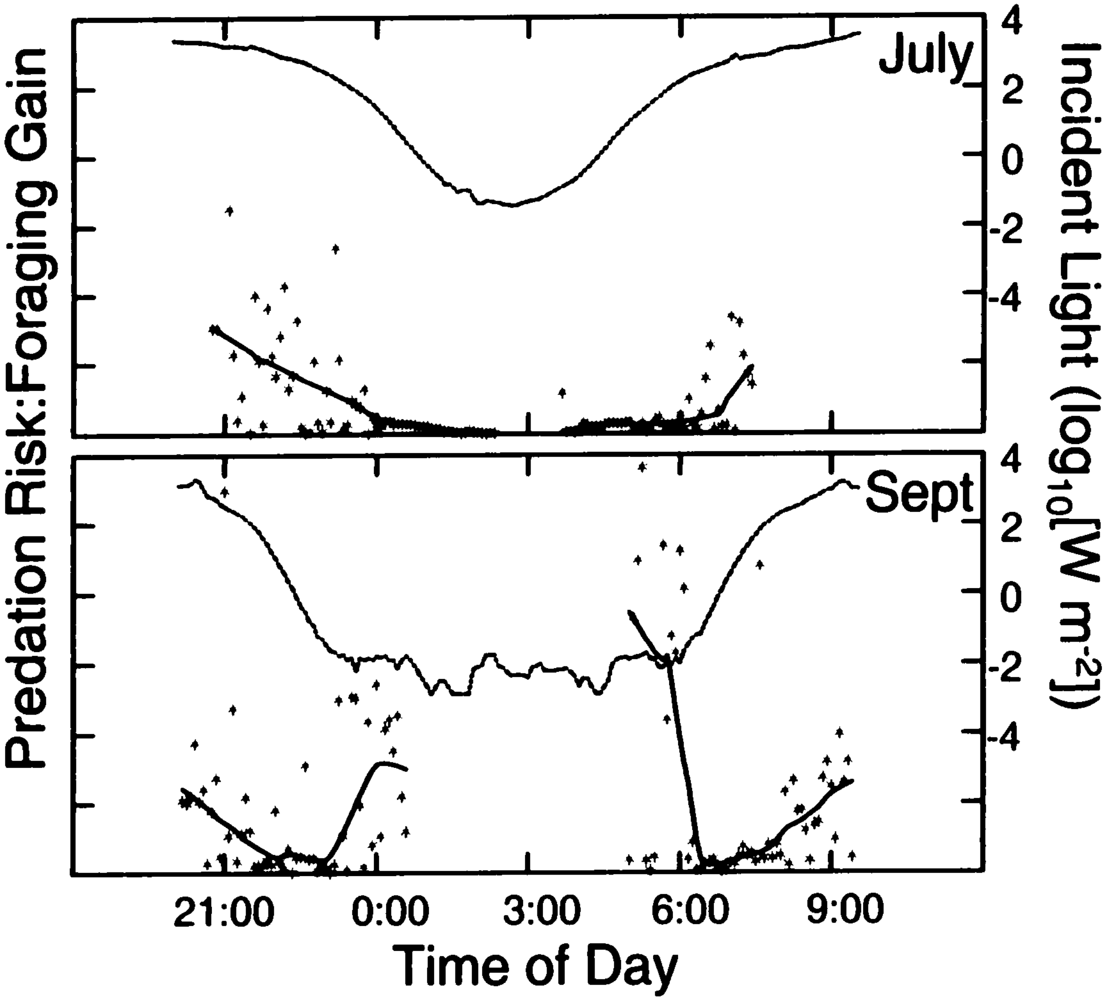

Figure 4.6. Time series of the ratio of predation risk to foraging gain (μ:*f*) for juvenile sockeye salmon in July (upper panel) and September (lower panel). The asterisks represent the mean μ:*f* from 5-minute sampling intervals. The solid lines are local area regression (LOWESS) estimates through the observed data to aid in visualization. The dotted line is the mean incident light across all lakes.

Chapter 5: Environmental and algal forcing of *Daphnia* production dynamics[3]

ABSTRACT

Recent studies of lakes suggest that the relative availability of light and phosphorus in the mixed layer helps determine the quality of phytoplankton consumed by herbivorous zooplankton. In turn, increases in algal quality positively affect zooplankton growth and reproductive rates. However, these studies have concentrated on explaining variation among lakes over relatively short time periods and have not evaluated the temporal dynamics in the physical-chemical forcing on zooplankton production. We investigated whether there were seasonal changes in the relationship between *Daphnia* fecundity and the physical-chemical environment, algal community characteristics, and *Daphnia* length using dynamic linear models (DLM) to analyze a high-resolution, 16-year time series from Lake Washington. We used two metrics to describe algal quality: the percent of blue-green algae, and the light to total phosphorus (TP) ratio as an indirect metric for algal C:P. Chlorophyll *a* concentration and algal biovolume served as measures of algal quantity. As expected, both the light:TP ratio and the percent of blue-green algae had negative effects on *Daphnia* fecundity, and chlorophyll *a* concentration

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[3] This paper will appear in *Limnology & Oceanography* in 2002 with my co-authors Daniel E. Schindler, Arni H. Litt, and W. T. Edmondson.

and biovolume had positive effects on fecundity. However, we found a comparatively stronger effect of *Daphnia* length on fecundity, although it was negative and therefore opposite to expectation. In all cases, we observed strong seasonal differences in environmental effects, but no temporal change in the fundamental relationships between our indices of algal quantity and quality, allometry, and *Daphnia* reproduction. Our results support a hypothesis of physical-chemical coupling to algal quality and zooplankton production, but highlight the importance of temporal variation in this forcing.

INTRODUCTION

Much of the current emphasis in food web studies attempts to predict the degree to which food web structure controls primary producers and the efficiency with which primary production is transferred to upper trophic levels (e.g. Carpenter and Kitchell 1993; Polis and Winemiller 1994). In aquatic ecosystems zooplankton can exert strong control over phytoplankton. These grazers affect their phytoplankton food directly through grazing (Sommer et al. 1986) or indirectly through nutrient recycling (Lehman 1980). In turn, the nutritional quality of primary producers can control the composition of the herbivore community and rates of secondary production (Gulati and Demott 1997). In addition to algal quality, algal quantity may also limit zooplankton production (Lynch 1989). Furthermore, the body size of an individual may also affect its fecundity (Lampert 1993) and therefore, the size structure of the zooplankton community may play an important role in overall secondary production rates in aquatic ecosystems. However, there have been no formal quantitative analyses of the relative importance of each of these factors in governing secondary production rates in zooplankton.

The emergence of ecological stoichiometry has lead to a greater understanding of the relationship between grazers, their food source, and the abiotic environment (Elser and Urabe 1999). Because the C:N:P ratios vary among different zooplankton taxa, the relative rates at which zooplankton acquire and recycle these nutrients have important implications for zooplankton growth rates (Main et al. 1997) and phytoplankton dynamics (Sarnelle 1992). When consuming low-quality food, zooplankton growth can be constrained by their ability to synthesize and maintain vital biochemical cell constituents (Elser et al. 1996). In particular, *Daphnia* have high requirements for P and are therefore susceptible to P-nutritional constraints on growth (Urabe et al. 1997). The C:P ratio is one representation of the "quality" of the phytoplankton as a food source for zooplankton. Other aspects of food quality include algal fatty acid content (Müller-Navarra et al. 2000) and phytoplankton community composition (Demott 1999).

Predicting the effects of environmental conditions on the relative importance of algal quality versus algal quantity on zooplankton production remains an important goal in aquatic ecology (Brett et al. 2000). Variation in the ratio of light exposure to nutrient supply has been suggested as a principle driver of the carbon to phosphorus ratio (C:P) (Sterner et al. 1997). At a fixed level of phosphorus, increased light leads to increased C-fixation and thereby decreases the relative amount of P in the algae, resulting in a decrease in algal quality. However, the mechanism and extent to which the abiotic environment control algal quality in lakes remains poorly understood. Much of our understanding to date has relied on lab experiments (e.g. Elser et al. 2001) or comparative studies of different ecosystems (e.g. Dobberfuhl and Elser 2000). Strong intra- and interannual variation in the physical, chemical, and biological properties of lakes may produce an environment with large differences in the interaction among trophic levels. However, there has been essentially no exploration of the temporal organization of environmental forcing on algal quality and subsequent patterns of secondary production in lakes.

The plankton of Lake Washington have been studied intensively since 1949 (Edmondson 1994). The time series data derived from these studies allowed us to investigate how seasonal changes in the physical and chemical environment are transmitted to zooplankton production dynamics via temporal changes in surrogates of algal quality and quantity in Lake Washington. Specifically we measured the relative strengths of algal quality, algal quantity, and *Daphnia* length as predictors of *Daphnia* fecundity. Our results support the contention that the physical-chemical environment controls zooplankton production through its effect on food quality while emphasizing the importance of temporal organization in the coupling between phytoplankton and zooplankton production.

METHODS

We used the chlorophyll a concentration and total algal biovolume as metrics for algal quantity (Felip and Catalan 2000), and the proportion of blue-green algae and the light:TP ratio and as surrogates for algal quality. We based the latter assumption on the findings of Sterner et al. (1997) who found a strong positive relationship between light:TP and algal C:P ($r^2 = 0.85$). Rather than first predict algal C:P from light:TP and then calculate the effect of C:P on *Daphnia* fecundity, we used light:TP as a predictor of *Daphnia* fecundity to avoid compounding the errors from the first regression. Furthermore, our goal was to explore whether simple measures of the physical and chemical environment such as light and TP have any ability to predict *Daphnia* fecundity. Therefore, we adopt the convention of using algal quality to refer to the effects of blue-green algae and light:TP, and algal quantity to refer to the effect of chlorophyll *a* concentration and algal biovolume.

Limnological data. Lake Washington is a large (87.6 km^2), mesotrophic lake located within the city of Seattle, Washington. Standard limnological data from Lake Washington including zooplankton abundance, chlorophyll *a* concentration, algal biovolume and community composition, total phosphorus, thermal profile, and Secchi depth, were collected over weekly to monthly intervals from 1977-1992. We concentrated on this time period because *Daphnia* were rare in the lake before 1975, and then found only sporadically until 1977 (Edmondson 1994). Lake water was collected from 0-10 m using an integrated-depth tube sampler. Following persulfate digestion and subsequent reaction with molybdate and stannous chloride, total phosphorus (TP) concentration was determined colorometrically by reading the samples on a spectrophotometer at 720 nm and comparing them to a standard curve (Anonymous 1999). Chlorophyll *a* concentration was determined by filtering lake water through 0.7 μm membrane filters, grinding the filters, and dissolving them in acetone. Following centrifuging, the samples were read on a spectrophotometer at 663 nm, corrected for pheopigments, and compared to a standard curve (Strickland and Parsons 1972). We estimated algal biovolume using simple geometric analogues. At least 50 cells or colonies were measured to characterize the size range in the population, and then individual size was multiplied by density to obtain total biovolume.

Zooplankton were collected from 0-20 m with a Clark-Bumpus sampler fitted with a 130 μm net and a flow meter to calculate the total sample volume (Edmondson and Litt 1982). We combined all *Daphnia* species (*D. pulicaria*, *D. thorata*, *D. galeata mendotae*) and based their sexual maturity upon the relative size of the first two processes on the post-abdominal claw (Edmondson and Litt 1982). Mean fecundity was calculated as the mean number of eggs per adult female. *D. pulicaria* averaged 70% of the *Daphnia* biomass across all samples and should therefore help to minimize species composition effects. Finally, we averaged all of these data over monthly intervals in an attempt to maximize within-year samples and minimize the number of missing values. This produced a time series of 192 observations. To determine *Daphnia* mean length, we measured at least 50 *Daphnia* to the nearest 0.01 mm and averaged them over monthly intervals. However, we were only able to reconstruct a shorter time series of *Daphnia* length data from 1985-1992 (n = 65 = 94 - 29 missing data points). Therefore, from here on we will refer to the two time series as "long" and "short" respectively.

Following the notation of Sterner et al. (1997), we calculated the mean light in the mixed layer (I_m, dimensionless) as a fraction of the surface light using the formula

$$I_m = \frac{1 - e^{-Kz_m}}{Kz_m} \qquad (1)$$

where the extinction coefficient (K, m^{-1}) is calculated from the Secchi depth (z_{sd}, m) using the relationship $K = 1.54/z_{sd}$. We calculated the depth of mixing (z_m, m) as the maximum depth where the water temperature varies ≤ 1 °C relative to the temperature at 0.5 m.

Time Series Analyses. We used Dynamic Linear Models (DLM) fit to times series data (Pole et al. 1994) as a tool for evaluating the ability of food quality, food quantity, and allometric hypotheses in predicting *Daphnia* fecundity dynamics. We also added an environmental effect to the model to allow for additional seasonal effects on *Daphnia* fecundity dynamics. This environmental effect represents an aggregate of exogenous variables that we have not accounted for explicitly (e.g., actual light intensity, water temperature, specific algal species composition), but allows us to evaluate the seasonal variation in *Daphnia* fecundity dynamics. This technique has been applied effectively to ecological data and the methodology has been described in detail elsewhere (e.g. Cottingham and Carpenter 1998; Lamon et al. 1998) so we will only describe it briefly here.

Our model formulation begins with the familiar general linear model

$$\mathbf{Y} = \mathbf{X}\theta + \nu, \tag{2}$$

where an n x 1 vector of response variables (**Y**) are set equal to an n x m matrix of predictor variables (**X**) times an m x 1 vector of regression parameters, plus an n x 1 vector of observation errors (ν). In our case, the vector **Y** would represent the observed eggs per female *Daphnia* and the different forms of matrix **X** would represent the various competing models. For our first analysis of the long time series, **X** contained all one- and two-variable combinations of the following four variables: chlorophyll *a* concentration, algal biovolume, the light:TP ratio, and the proportion of blue-green algae (total of 10 combinations). For the second analysis of the short time series, **X** contained each of the previous four variables alone, plus *Daphnia* mean length alone, plus each of the original four variables combined with *Daphnia* length (total of 9 combinations).

For the dynamic form of the model, we express the relationship in a similar fashion, but introduce an explicit time-ordered index to the vectors and matrices. In this case, at each time step t the observed response variable (Y_t, a scalar) is sequentially fitted to the 1 x m vector of predictor variables ($\mathbf{X}_t$) with the m x 1 regression parameter vector (θ_t) plus an error term (ν_t, a scalar) according to the observation equation

$$Y_t = \mathbf{X}_t\theta_t + \nu_t \qquad\qquad \nu_t \sim N[0,V_t]. \tag{3}$$

This model formulation has two features that distinguish it from the time invariant model (2). First, the observed data are explicitly time ordered (i.e. $Y_1, Y_2, \ldots, Y_t$) and second, the regression parameters are allowed to vary through time. The observation errors ν_t have a variance V_t that is time-dependent and is usually not known well enough to approximate it with a fixed value. Therefore, as the analysis proceeds through time, V_t is estimated from all of the prior data by assuming it is equal to the inverse of the precision ($V_t = \phi_t^{-1}$). Following Pole et al. (1994), we assume that ϕ_t is gamma distributed as

$$\phi_t \sim G[n_{t-1}/2, d_{t-1}/2\,], \tag{4}$$

such that n_{t-1} is the degrees of freedom and d_{t-1} is the sum of squared errors. The discounting scheme described below also applies to V_t.

The parameter set in the general linear model (2) is the same for all observations (i.e. every observation contains information on each parameter). However, the DLM makes use of changes in the parameter set over time through a system equation. Using prior information from Bayesian learning, the m x 1 vector of regression parameters (θ_t) evolves through time according to the first-order Markov process

$$\theta_t = \mathbf{G}\theta_{t-1} + \omega_t \qquad\qquad \omega_t \sim N[\mathbf{0}, \mathbf{W}_t]. \tag{5}$$

The m x m system evolution matrix **G** dictates how the parameters change systematically through time while the m x 1 variance vector ω_t describes the stochastic change in each of the parameter estimates (θ_t) over time. The system variance matrix ($\mathbf{W}_t$) has the variance in ω_t along the diagonal and zeros elsewhere. It is determined by the component discount factors applied to the previous time step's posterior covariance matrix (Pole et al. 1994).

One-step forecasts are generated at each time step and the parameters are updated as new information becomes incorporated into the model. Through the use of discounting, priors are given weights that determine how influential the prior data are when updating the parameter estimates. These discounts represent the rate of exponential decay of useful information such that when the discount is 1 (its maximum value), all of the prior information is retained whereas a discount of 0 means no prior information is used at all. In general, the lower the discount value, the faster a parameter can change through time. For example, in our case setting the discount to 0.9 would use the last 26 data points. We selected the discounts by varying them systematically and then minimizing the negative log-likelihood of the overall model.

As an example, consider the case where we wish to predict the effect of chlorophyll *a* concentration on *Daphnia* fecundity, while including the seasonal effect of month, and assuming a constant trend (i.e. an underlying intercept or "level", but no increase or decrease in the series over time). At $t = 1$, the parameter (θ_t) and predictor vectors ($\mathbf{X}_t$) would be generated from the level (α_t), predictor (β_t), and seasonal ($\mu_{\text{month},t}$) effects respectively to give

$$\theta_1 = (\alpha_1\ \beta_1\ \mu_{1,1}\ \mu_{2,1}\ \mu_{3,1}\ \mu_{4,1}\ \mu_{5,1}\ \mu_{6,1}\ \mu_{7,1}\ \mu_{8,1}\ \mu_{9,1}\ \mu_{10,1}\ \mu_{11,1}\ \mu_{12,1})' \tag{6}$$

and

$$\mathbf{X}_1 = (1\ [\text{chlorophyll } a]_1\ 1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\,). \tag{7}$$

The evolution matrix (**G**) would have the form

$$\mathbf{G}=\left(\begin{array}{c:c:cccccccccccc}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\hdashline
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\hdashline
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{array}\right). \tag{8}$$

The dotted lines within **G** delineate the 3 square sub-matrices along the diagonal representing the transition rules for the level (n = 1), regression predictor (n = 1), and seasonal (n = 12) parameters respectively. At each permutation of (3), the evolution matrix **G** causes the 12 seasonal parameters within θ_t to shift such that only one monthly parameter corresponding to the current month is included when multiplied by $\mathbf{X}_t$ in (2). Pole et al. (1994) offer a more detailed discussion of the general model development and Lamon et al. (1998) provide a comprehensive example of the methodology applied to ecological data.

We began by comparing each competing model to 1) a reference model containing an underlying level plus a seasonal effect, but no regression effect, and 2) the same model minus a specific seasonal component. Lastly, we compared each of the models minus their seasonal component to the reference model. For the first two comparisons, we assessed model performance through the use of a likelihood ratio test, which is appropriate for testing nested models (Hilborn and Mangel 1997). To compare any full model A with a reference model B, the test statistic (R) was computed as twice the difference in negative log-likelihood, $\mathrm{L}(x|\cdot)$, according to

$$\mathrm{R} = 2[\mathrm{L}(x|B) - \mathrm{L}(x|A)] \qquad \mathrm{R} \sim \chi^2(df). \tag{9}$$

The degrees of freedom (df) for the test equal the difference in the number of parameters between models A and B. The same comparison was then made for a full model A with its comparable non-seasonal model C. We then ranked the competing predictive models in order of increasing performance according to the Bayes Information Criterion (BIC), where

$$\mathrm{BIC} = 2\mathrm{L}(x|\cdot) + p \log_e(n), \tag{10}$$

L is the negative log-likelihood and p equals the number of parameters in the model, and n is the sample size (Box et al. 1991).

For pair-wise comparisons between any 2 models i and j ($i < j$), we used the Schwarz criterion (Kass and Raftery 1995)

$$\mathrm{S}_{ij} = (\mathrm{BIC}_j - \mathrm{BIC}_i) / 2. \tag{11}$$

The Schwarz criterion is an approximation to a true Bayes Factor (B_{ij})

$$\mathrm{S}_{ij} \cong \log_e(\mathrm{B}_{ij}). \tag{12}$$

According to Kass and Raftery (1995), when $2\mathrm{S}_{ij} = 2\log_e(\mathrm{B}_{ij})$ is 0 to 2, the evidence favoring the higher ranked model is "not worth more than a bare mention"; 2 to 6 indicates "positive", 6 to 10 offers "strong", and <10 provides "very strong" evidence for model *i* over model *j* (see Tables 3 and 5). The Schwarz criterion also allowed us to compare all non-seasonal models with a model including only seasonal effects.

RESULTS

The time series data from Lake Washington demonstrated considerable inter- and intra-annual variation (Figure 5.1), but closer examination of the monthly mean values revealed consistent intra-annual trends (Figure 5.2). Light and TP were negatively correlated, with the peak in light occurring in May-June and the peak in TP occurring in January-March. Chlorophyll *a* concentration and algal biovolume both reached their maximum values in April and May although they were also most variable during these months as well, largely as a function of the timing of spring stratification. Blue-green algae constituted a small percent of the phytoplankton community throughout the winter and spring before rising in May and then peaking in August. *Daphnia* fecundity was bimodal with consistent peaks in April and September whereas *Daphnia* mean length remained relatively constant across months with a slight increase during late summer. Although we do not have direct estimates of algal C:P ratios, we made predictions about the likely range of their values in Lake Washington based on the relationship of Sterner et al. (1997). We found that the predicted algal C:P ratio in Lake Washington varied between 250-350 and rose into the region where it constrains zooplankton production in May-October (Figure 5.3).

Simple linear regressions using the metrics of food quantity, food quality, and *Daphnia* length to predict *Daphnia* fecundity demonstrated mixed results (Table 5.1). We found a weak, but significantly positive relationship between algal quantity (both chlorophyll *a* and biovolume) and fecundity. We observed no significant relationship between algal quality (percent blue-green algae and the surrogate, light:TP) and *Daphnia* fecundity. Finally, we found a marginally significant negative relationship between *Daphnia* length and fecundity. However, these results are conservative estimates of the relationships because simple linear regression assumes that each of the data points is independent. This is not the case here where the time series data are temporally autocorrelated and the time ordering of the data may represent a substantial source of information about the relationships between variables. Using the DLM approach, which explicitly accounts for the temporal organization of the time series, we found a significant relationship between all of the predictor variables and *Daphnia* fecundity, and greatly improved the predictive capability of the models (Table 5.1).

The DLM method indicated that food quality models (light:TP and percent blue-green algae) fit the observed data best (Table 5.2). The next 3 highest ranked models all included chlorophyll *a* (i.e. food quantity) as a predictor (Table 5.2). According to the Schwarz criterion, the light:TP model had essentially no evidence favoring it over the percent blue-green algae model (Table 5.3), but both of the food quality models had very strong evidence favoring them over any of the food quantity or mixed models (Table 5.3). The effects of algal quality and quantity on *Daphnia* fecundity, measured as the product of the predictor variable and its regression coefficient ($X_t\theta_t$), matched our predictions. The distribution of effect sizes from the DLMs indicated a negative effect of the food quality metrics on *Daphnia* fecundity as illustrated by light:TP and the amount of blue-green algae (Figure 5.4). Conversely, food quantity as represented by chlorophyll *a* had a positive effect on *Daphnia* fecundity. However, biovolume actually had a negative effect when it was added as a second predictor with chlorophyll *a* (Figure 5.4).

Analyses of the short time series indicated a strong relationship between *Daphnia* length and fecundity (Table 5.4). Indeed, the top 5 models all included length as a predictor variable and had very strong evidence favoring them over any non-length model (Table 5.5). Based on BIC, the mixed model of length plus chlorophyll *a* performed best. However, the Schwarz criterion provided very little evidence to support it over the second-ranked length-only model (Table 5.5). While *Daphnia* length provided the best fit to the observed fecundity, its effect on fecundity was strongly negative and therefore the opposite of what we expected (Figure 5.5).

Finally, we found no significant difference in any of the main effects across months (ANOVA, $F_{1,11} < 0.5$, $p > 0.9$ for all comparisons). However, the aggregate seasonal effect varied significantly across months (ANOVA, $F_{1,11} > 230$, $p < 0.0001$ for all comparisons). A negative-exponentially weighted least squares fit through the seasonal data from the top 5 long series models plus the length-only model from the short time series, indicated a positive effect of the aggregate environmental variable in late spring (April-May) and again in September (Figure 5.6). The aggregate environmental variable had the greatest negative effect in mid-summer (June and July) and a slight negative effect in late fall and early winter (November-January). In all cases, the models that included a seasonal effect were better predictors than their non-seasonal counterparts (Tables 3 & 5). However, all but one of the non-seasonal models provided "very strong" evidence favoring them over the season-only reference model (Table 5.6). This suggests that ecological structure by itself is still more important than just accounting for seasonal effects.

DISCUSSION

Physical and chemical conditions have been proposed to control the nutrient use efficiency at the base of lake food webs (Sterner et al. 1997). In particular, when light energy in the mixed layer is high relative to phosphorus availability, algae are carbon-rich and nutrient-deficient, leading to poor algal quality as food for zooplankton grazers (Sterner et al. 1998; Urabe and Sterner 1996). Furthermore, several studies have shown the important effect of algal quality on zooplankton production (Elser et al. 1998; Müller-Navarra et al. 2000; Sterner and Hessen 1994). As the elemental stoichiometry of zooplankton taxa varies, so does their relative requirement for C, N, and P. Relative to copepods, the *Daphnia* N:P ratio is generally lower due to their relatively high requirement of P for cell constituents such as phospholipids, ATP/ADP, and nucleic acids (Elser et al. 1996). Subsequently, when their food sources are relatively high in P, *Daphnia* exhibit increased growth rates due to greater requirements for P-rich ribosomal RNA (Main et al. 1997).

Combining the above models for the effect of light:TP on algal quality and the subsequent effect of algal quality on *Daphnia* production, we expected a negative relationship between light:TP and *Daphnia* fecundity (sensu Sterner et al. 1997). Indeed, we found a strong negative relationship between light:TP and *Daphnia* fecundity (Figure 5.4) across all months of the year. Sterner et al. (1997) also found that the month and temperature affected the slope of the relationship between light:TP and algal C:P. Therefore we might expect seasonal differences in the effect of light:TP on zooplankton production. While we found no significant change in the slope of the main effect between light:TP and *Daphnia* fecundity over time, we did find a strong seasonal effect of the environment on *Daphnia* fecundity (Figure 5.6). This suggests that additional environmental variation (e.g. changes in solar irradiance, water mixing, algal community composition) causes seasonal differences in algal quality. At the phytoplankton community level, the concentration of blue-green algae negatively affects *Daphnia* reproduction (Demott 1999; Ferrao et al. 2000). We found a significantly negative effect of blue-green algae on *Daphnia* fecundity (Figure 5.4), although not as strong as the light:TP effect (Table 5.2). It is therefore likely that the extent to which various aspects of food quality limit *Daphnia* production in Lake Washington varies with changes in phytoplankton community composition, which in turn varies within and across years (Schindler et al. 2001).

Most studies of the effect of algal quality on zooplankton reproduction have concentrated on lab experiments (e.g. Sterner et al. 1998) or comparative studies of different ecosystems (e.g. Brett et al. 2000; Dobberfuhl and Elser 2000). Testing hypotheses about the effects of food quality on zooplankton reproduction with time series of field data are rare. A 9-year study of 3 hypereutrophic lakes in The Netherlands found an inverse relationship between algal quality (C:P ratio) and *Daphnia* abundance in 2 out of 3 lakes (Demott and Gulati 1999). The molar C:P ratio of the algae in the Dutch lakes ranged from 250-500, and were generally higher than the ~300 threshold, above which *Daphnia* production is expected to be constrained by food quality (Hessen 1992). Our prediction of algal C:P from light:TP based on the findings of Sterner et al. (1997) indicates values near or above the threshold (Figure 5.3), and therefore support our result of a negative effect of light:TP on *Daphnia* fecundity.

In addition to algal quality, algal quantity directly affects zooplankton production. An increase in food concentration has caused increased *Daphnia* reproductive rates in the lab (Lynch 1989) and field (Wu and Culver 1994). Indeed, our time series analysis revealed a strong positive effect of algal quantity (chlorophyll *a* concentration) on *Daphnia* fecundity (Figure 5.4), both within and across years. When we combined chlorophyll *a* and biovolume together, the observed effect of biovolume was negative and opposite of what we expected (Figure 5.4). This could result from the residual effect of biovolume as a potential indicator of algal quality. However, we might expect that the other two direct measures of algal quality would outperform the more indirect residual effect of biovolume, but this was not the case. Alternatively, it could be an artifact of multicollinearity whereby when two regression predictor variables are highly correlated, the observed sign of one of the coefficients may be opposite of the expected (Sokal and Rohlf 1995). Indeed, in our data set from Lake Washington chlorophyll *a* concentration and algal biovolume are strongly correlated (Pearson, $r = 0.88$, $p < 0.0001$).

Several possibilities exist for our observed difference in the negative effect of algal quality versus the positive effect of food quantity (Figure 5.4). The smaller effect of the light:TP ratio on *Daphnia* fecundity, relative to the chlorophyll *a* effect, may reflect the relatively rapid uptake of soluble nutrients by algae compared to the response of *Daphnia* to changes in its food resource. Furthermore, we relied on the light:TP ratio as a metric of algal C:P (Sterner et al. 1997). However, other biochemical components of food quality such as highly unsaturated fatty acids can be important determinants of *Daphnia* growth (see review by Brett and Müller-Navarra 1997), and the relative importance of these fatty acids varies across phytoplankton P content and taxa (Sundbom and Vrede 1997). Furthermore, the relative importance of algal quality for zooplankton production may decrease with a decrease in algal quantity (Brett et al. 2000; Sterner 1997). This phenomenon occurs at low food abundance when a larger fraction of the energy consumed goes toward metabolism instead of growth. Finally, we observed a switch in the relative performance of the algal quality versus quantity models in the analyses of the short time series (Table 5.5). However, we downplay this result as it likely reflects the loss of overall descriptive power when decreasing the sample size by 66% while also introducing several missing values in the short time series.

Daphnia body size might also explain observed variation in fecundity due to allometry; larger individuals often have larger clutch sizes than smaller individuals (Peters 1983). Given that the size distribution of Daphnids is often highly variable (Lampert 1993), we might expect that variation in *Daphnia* length could explain the variation in fecundity over time. Lampert (1993) also found that fish predation caused a decrease in *Daphnia* size and subsequent fecundity over the summer. However, we found subtle seasonal differences in *Daphnia* length (Figure 5.2). In fact, the slight increase in *Daphnia* length over the summer suggests weak predation effects by fish in Lake Washington. The unusual negative effect of *Daphnia* length on fecundity (Figure 5.5) apparently resulted from the slight increase in *Daphnia* length from spring into late summer coincident with a substantial decrease in fecundity during the same time (Figure 5.2). Thus we expect that this relationship is simply coincidental.

Daphnia did not become abundant in Lake Washington until 1977 (Edmondson and Litt 1982), but since then they have come to dominate the grazer community and exert strong control on their phytoplankton food resource (Edmondson 1994). Predicting the response of *Daphnia* to changes in its food quantity and quality is a critical part of understanding the food web dynamics in Lake Washington and other systems as well. By combining information on the physical, chemical, and biological characteristics of lakes in a temporally explicit framework, we were able to distinguish the effects of seasonal changes in the environment from other fundamental factors influencing *Daphnia* reproduction. By using formal time series analyses, we found considerable temporal organization in plankton dynamics that were not evident in a static representation of this system. This highlights the importance of temporal variation in algal quality and quantity effects on zooplankton production and suggests that simple experiments are conservative tests of these effects.

Predicting environmental stochasticity is nearly impossible, but we also found regular intra-annual patterns in the seasonal effects of the environment on *Daphnia* reproduction. At present, we do not know what the exact drivers of this seasonal forcing are, but temperature and day length are obvious factors. Ecosystems are not static, but rather change through time following changes in their various abiotic and biotic components, sometimes undergoing dramatic changes in their state (Scheffer et al. 2001). However, as we demonstrated here, some of this change is predictable across time. Our results should aid in future model formulation by offering insight into the temporal organization of ecosystem dynamics.

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Table 5.1. Comparison of regression performance to predict *Daphnia* fecundity for a simple linear regression model and the seasonal DLM, based upon the r^2 and p-value of the full regression model. The predictor variables are chlorophyll *a* concentration (Chl *a*), algal biovolume (BV), the light:TP ratio (L:TP), proportion of blue-green algae (BG), and *Daphnia* mean length (length).

	Simple linear		DLM	
Predictor	r^2	p-value	r^2	p-value
Chl *a*	0.12	<0.001	0.36	0.002
BV	0.032	0.016	0.33	0.006
BG	0.010	0.17	0.34	<0.001
L:TP	0.0013	0.63	0.35	<0.001
length	0.042	0.080	0.70	<0.001

Table 5.2. DLM results for the analysis of the long time series (1977-1992, n = 192) using models that explicitly account for monthly seasonal effects. Models are ranked in terms of overall performance in predicting *Daphnia* fecundity. Rank is assigned in order of increasing BIC. The "Ref" model represents a simple random walk. Class refers to the type of predictor variable(s) in terms of algal food constraints on *Daphnia* fecundity. The predictor variables are described in Table 5.1, with the sign of the regression coefficient for each predictor variable in parentheses following it. See Methods section for description of BIC calculations. The likelihood ratio (R) p-values indicate whether any given model performs significantly better than the reference model and its comparable non-seasonal model.

		Predictors				R p-values	
Rank	Class	X_1	X_2	Parameters	BIC	Reference	Non-Season
Ref				13	178.3	-	<0.001
1	quality	L:TP(-)		14	154.8	<0.001	<0.001
2	quality	BG(-)		14	156.3	<0.001	<0.001
3	mixed	Chl *a*(+)	BV(-)	15	166.8	<0.001	<0.001
4	quantity	Chl *a*(+)		14	173.8	0.002	<0.001
5	mixed	L:TP(-)	Chl *a*(+)	15	174.1	0.001	<0.001
6	mixed	BG(-)	Chl *a*(+)	15	175.3	0.001	<0.001
7	mixed	BV(+)	L:TP(-)	15	175.3	0.001	<0.001
8	quantity	BV(+)		14	176.0	0.006	<0.001
9	mixed	BV(+)	BG(-)	15	176.9	0.003	<0.001
10	mixed	L:TP(-)	BG(-)	15	177.6	0.004	<0.001

Table 5.3. Pair-wise comparisons of DLM model performance for the long time series based on twice the Schwarz criterion (2S). Model numbers refer to those in Table 5.2. See Methods for statistical description and equations. Any model at the top of a column can be compared to any lower ranked model in subsequent rows (e.g. Model 1 versus 5 = 39, 3 versus 4 = 14). According to Kass and Raftery (1995), a number from 0 to 2 means the evidence favoring the higher ranked model is "not worth more than a bare mention"; 2 to 6 indicates "positive", 6 to 10 offers "strong", and >10 provides "very strong" evidence.

	Model								
Model	1	2	3	4	5	6	7	8	9
2	1.5								
3	12	10							
4	19	17	7.0						
5	19	18	7.3	0.33					
6	20	19	8.5	1.6	1.2				
7	21	19	8.5	1.6	1.2	0.0082			
8	21	20	9.2	2.2	1.9	0.69	0.68		
9	22	21	10	3.2	2.8	1.6	1.6	0.93	
10	23	21	11	3.8	3.5	2.2	2.2	1.5	0.62

Table 5.4. DLM results for the analysis of the short time series (1985-1992, n = 65) to include the effect of *Daphnia* length, using models that explicitly account for monthly seasonal effects. Descriptions of the table columns are the same as those in Tables 1 & 2.

		Predictors				R p-values	
Rank	Class	X_1	X_2	Parameters	BIC	Reference	Non-Season
Ref				13	93.3	-	0.017
1	mixed	length(-)	Chl *a*(+)	15	73.2	<0.001	0.060
2	allometric	length(-)		14	73.2	<0.001	0.016
3	mixed	length(-)	BV(+)	15	75.4	<0.001	0.020
4	mixed	length(-)	BG(-)	15	75.8	<0.001	0.019
5	mixed	length(-)	L:TP(-)	15	76.2	<0.001	0.019
6	quantity	Chl *a*(+)		14	83.6	<0.001	0.038
7	quality	BG(-)		14	91.8	0.018	0.014
8	quantity	BV(+)		14	92.4	0.025	0.014
9	quality	L:TP(-)		14	92.6	0.028	0.009

Table 5.5. Pairwise comparisons of DLM model performance for the short time series based on twice the Schwarz criterion (2S). Model numbers refer to those in Table 5.3. Column and row descriptions are the same as Table 5.3.

	Model							
Model	1	2	3	4	5	6	7	8
2	0.026							
3	2.2	2.2						
4	2.6	2.6	0.40					
5	3.0	3.0	0.80	0.40				
6	10	10	8.2	7.8	7.4			
7	19	19	16	16	16	8.2		
8	19	19	17	17	16	8.8	0.60	
9	19	19	17	17	16	9.0	0.80	0.20

Table 5.6. Schwarz criterion (2S) values for the comparisons of DLM predictive models lacking a seasonal effect to season-only reference models for the long and short time series (from Tables 2 & 4). Model numbers for the non-seasonal predictive models refer to those in Tables 3 (long) and 5 (short) respectively. See Table 5.2 for description of the critical values for the Schwarz criterion.

	Non-seasonal Predictive Model									
Season-only	1	2	3	4	5	6	7	8	9	10
Long	47	40	35	28	27	26	16	15	12	3.5
short	50	45	44	43	43	38	26	26	24	-

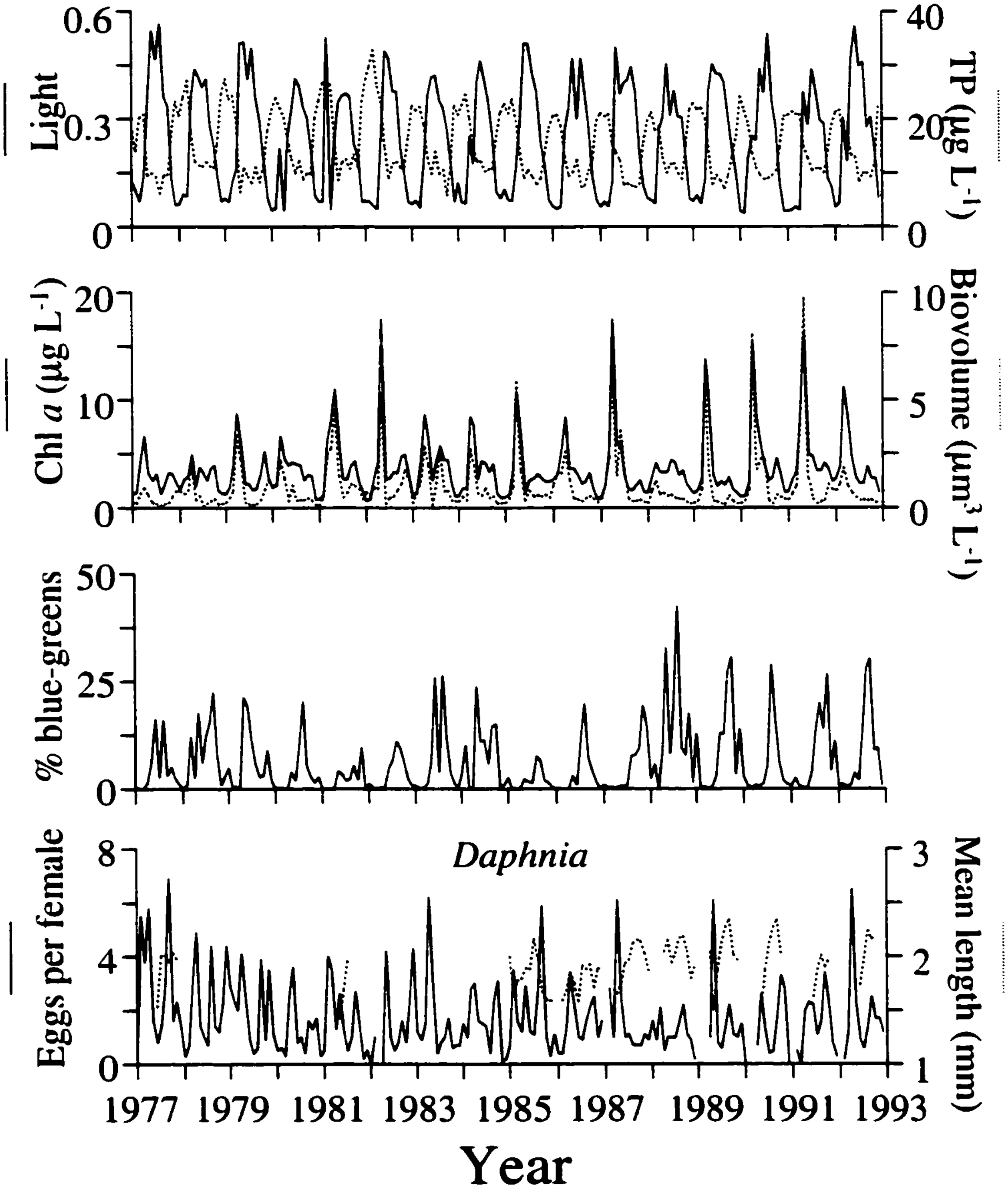

Figure 5.1. Lake Washington time series data from 1977-1992 for the amount of light in the mixed layer (Light), total phosphorus (TP), chlorophyll a concentration (Chl *a*), algal biovolume (Biovolume), percent of blue-green algae by biovolume (% Blue-greens), *Daphnia* fecundity, and *Daphnia* mean length. Note that *Daphnia* length data only exist for parts of 1977, 1982, and 1985-1992. The variable "Light" is a dimensionless fraction of the surface light; see Methods for a description of the formula used.

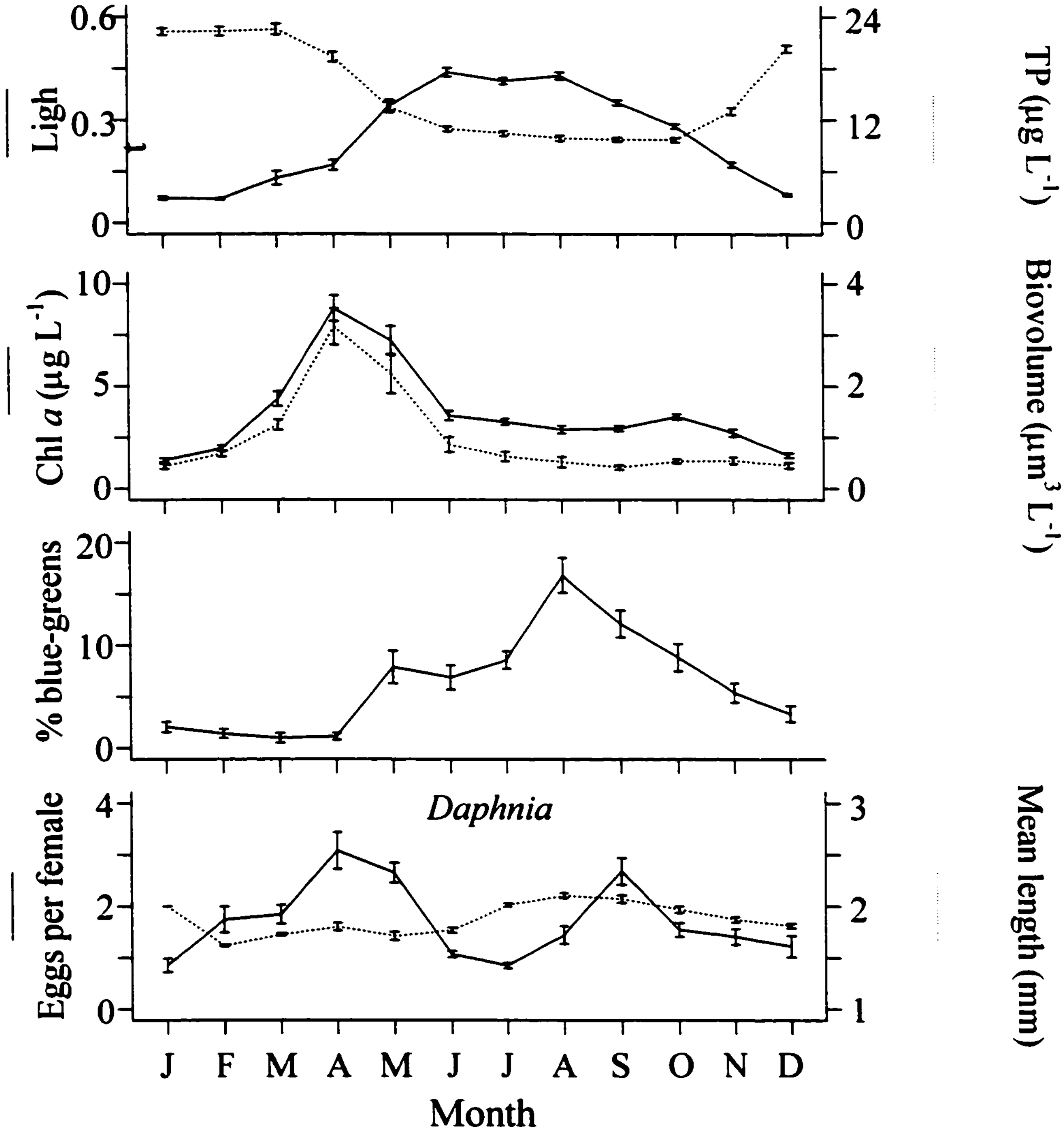

Figure 5.2. Monthly means of the Lake Washington time series data (1977-1992) described in Figure 5.1. Error bars represent 95% confidence intervals (n = 16 per month). Mean *Daphnia* length is based upon partial years of data from 1977, 1982, and 1985-1992, with n = 1-8.

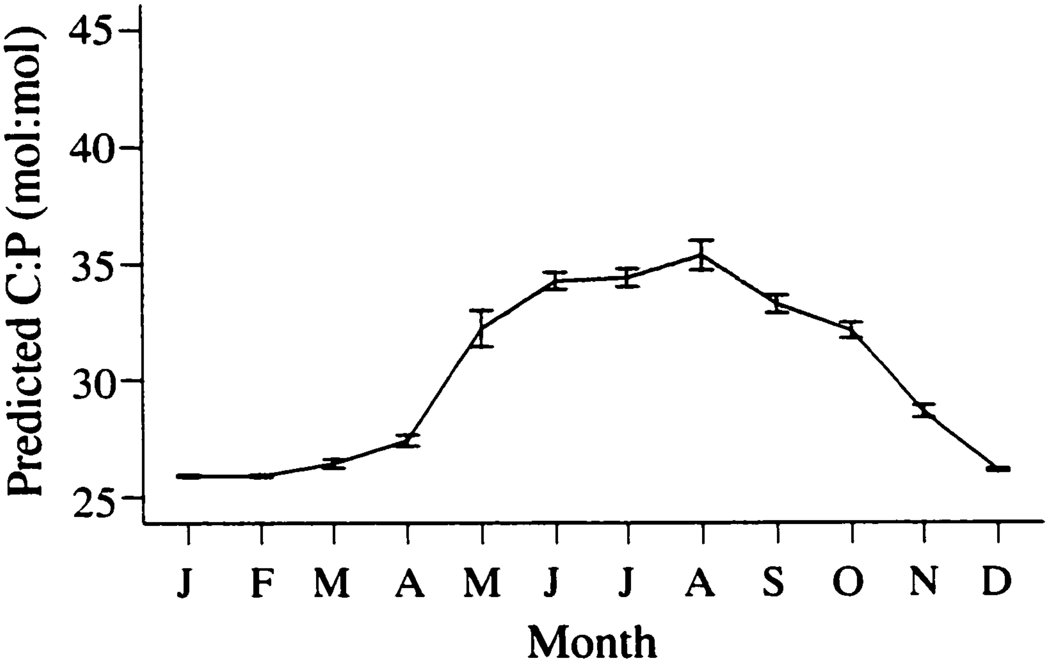

Figure 5.3. Monthly means (±95% C.I.) of the C:P ratio predicted from light:TP based on the relationship of Sterner et al. (1997) (C:P = 252 + 71·light:TP, r^2 = 0.85). The shaded region of the graph indicates the lower range of C:P ratios where algal food quality is thought to be a limiting factor in *Daphnia* production (Hessen 1992).

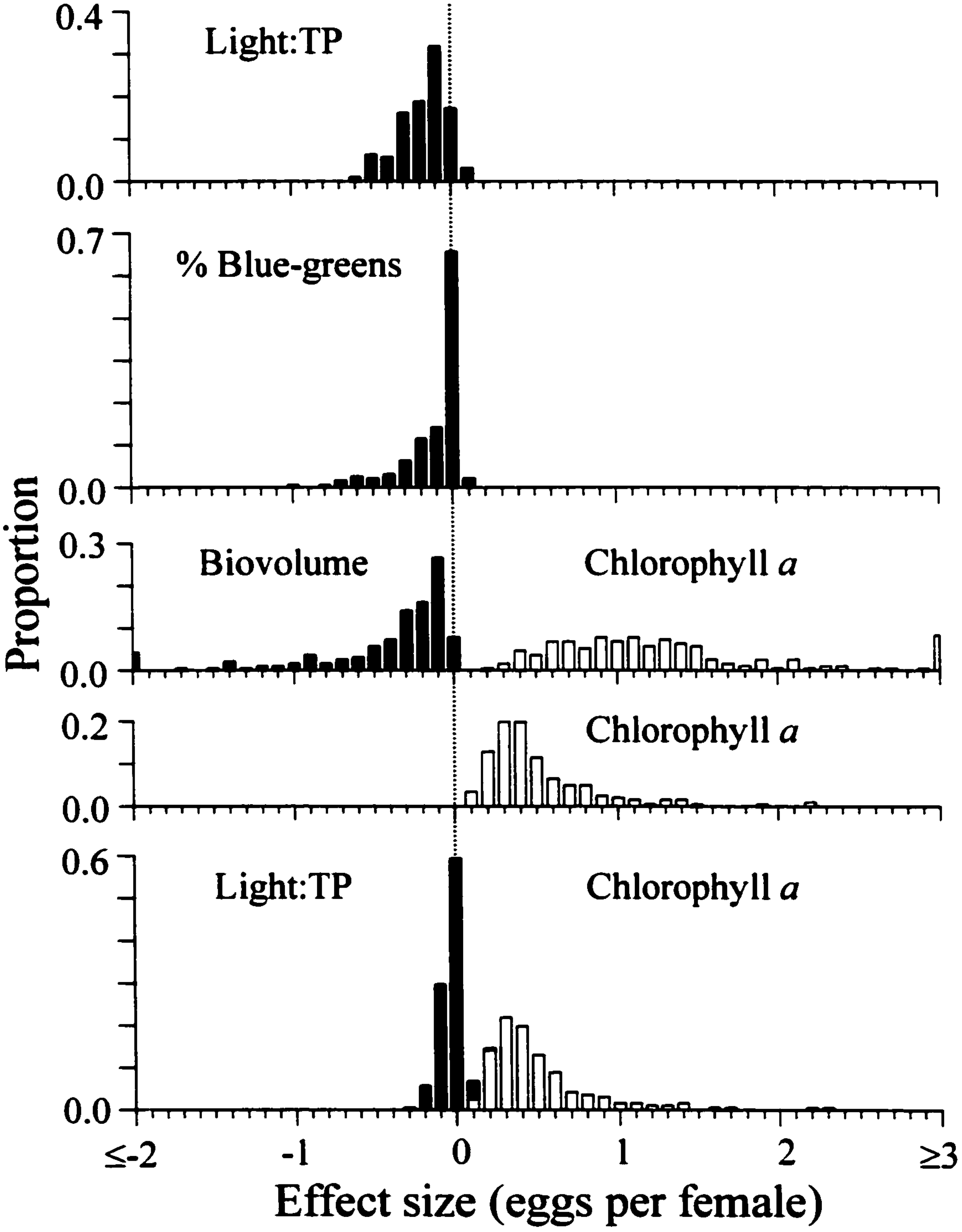

Figure 5.4. Distribution of DLM effect sizes for the 5 highest ranked models listed in Table 5.1.

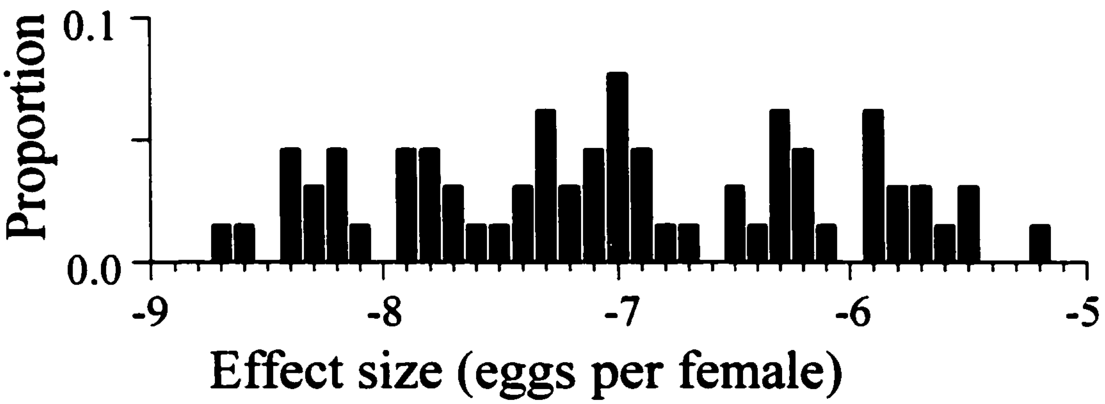

Figure 5.5. Distribution of DLM effect size with only *Daphnia* length as a predictor of *Daphnia* fecundity (model 2) based on the DLM for the short time series (1985-1992).

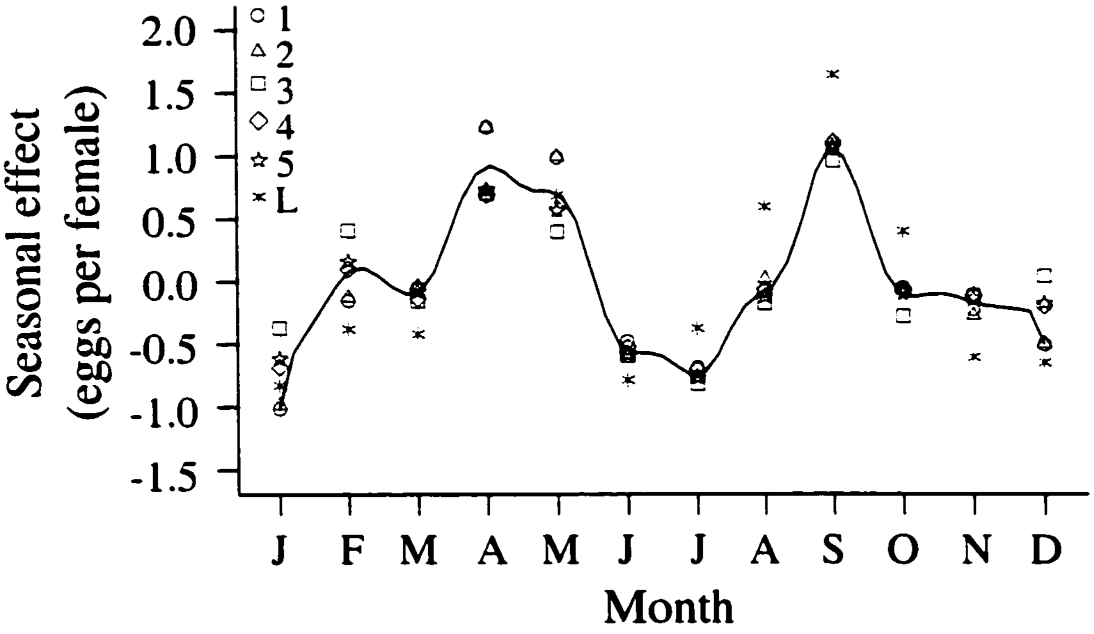

Figure 5.6. Seasonal effects of environmental forcing from the DLM analyses of the 5 models shown in Figure 5.4 (numbers 1-5) plus the seasonal effect from the length-only model shown in Figure 5.5 (L). The line represents a best-fit curve based upon a negative exponential weighting function.

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Appendix A: Matlab code for the modified 3D Ripley's K(d) described in chapter 1.

```
function Kd3D

% This program calculates every neighbor distance from acoustic data
% based on single target detections and TS to length conversions.
% It requires text files from the BioSonics DT6000 Visual Analyzer software
% with 7 columns (target depth, TS, along, athwart, bottom depth, lat, lon).

% Output is 2 *.txt files: 1) the cdf of neighbor distances
%                          2) the 3D K(d) function described in Scheuerell (2002)

% original version created by Mark Scheuerell on 02.01.09

% last modified by MDS on 02.04.22

% initialization routines
clear;
close;
echo off;
format long;
pack;

% model parameters
PredLength = 28;     % min length (cm) of a "predatory" fish
PreyRatio = 2;       % min length ratio of pred:prey
MinFishSize = 2;     % min length (cm) of "prey" fish
MaxPreySize = 10; % max length (cm) of "prey" fish

d = [0.5:0.5:50]';

tic; % starts stopwatch


%--------------------
% DATA INPUTS
%--------------------

cd C:\1sims\3D;

% load the data file
FileName = input('Which file do you want to analyze? ','s');
```

```
% variables are target depth, TS, along, athwart, bottom depth, lat, lon
AcData=dlmread([FileName,'.txt'],'\t');;

% prompt for the sample Volume
Volume = str2num(input('What is the sample volume? ','s'));


%-------------------------------
% DATA CONVERSIONS
%-------------------------------

% convert degrees to meters lon
AcData(:,7)=AcData(:,7).*60.*1852.*cos(AcData(:,6)*pi/180)...
        +tan(AcData(:,4)*pi/180).*AcData(:,1);

% convert degrees to meters lat
AcData(:,6)=AcData(:,6).*60.*1852+tan(AcData(:,3)*pi/180).*AcData(:,1);

% convert TS to bodylength (cm)
% using Burczynski and Johnston (1986) for sockeye at 420 kHz
AcData(:,8)=10.^((AcData(:,2)+66)/20);

% variables are: target depth, TS, along, athwart, bottom depth, lat, lon, fish length
% drop extra columns
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
% new cols are Target Depth (m), Lat (m), Lon (m), Fish Length (cm)

% drop all of the targets less than the minimum fish size
AcData(find(AcData(:,4)<MinFishSize),:)=[];
% drop all prey<targets<predators
AcData(find(AcData(:,4)<PredLength & AcData(:,4)>MaxPreySize),:)=[];
NumTargets=length(AcData);

AcData(find(AcData(:,4) < MaxPreySize),5) = 0; % it's a prey
AcData(find(AcData(:,4) > PredLength),5) = 1; % it's a predator in general
```

```
%-------------------------
% PROGRAM BODY
%-------------------------

% initialize some matrices
NewX=zeros(NumTargets,1);
NewY=zeros(NumTargets,1);
NewZ=zeros(NumTargets,1);

Prey2Prey = zeros(1,length(d))'; % histogram of inter-prey distances
Prey2Pred = zeros(1,length(d))'; % histogram of prey-predator distances
Pred2Pred = zeros(1,length(d))'; % histogram of inter-predator distances
Pred2Prey = zeros(1,length(d))'; % histogram of predator-prey distances

NumPreds = length(find(AcData(:,4) > PredLength));
NumPrey = NumTargets - NumPreds;

% loop through all of the fish to compute distances
for i=1:NumTargets

  NewX = AcData(:,3) - AcData(i,3);
  NewY = AcData(:,2) - AcData(i,2);
  NewZ = AcData(:,1) - AcData(i,1);

  % compute distances
  rho = sqrt((NewX.^2 + NewY.^2 + NewZ.^2));

  % compute distance histograms based on fish type
  if AcData(i,5)==0 % it's a prey fish
    p = histc(rho(find(AcData(:,5)==0&rho~=0)),d);
    if length(p)>0
      Prey2Prey = Prey2Prey + p;
    end;
    q = histc(rho(find(AcData(:,5)>0)),d);
    if length(q)>0 & size(q,2)==1
      Prey2Pred = Prey2Pred + q;
    end;
  elseif AcData(i,5)>0 & size(histc(rho(find(AcData(:,5)>0)),d),2)==1 % it's a predator
    Pred2Pred = Pred2Pred + histc(rho(find(AcData(:,5)>0)),d);
    Pred2Prey = Pred2Prey + histc(rho(find(AcData(:,5)==0)),d);
  end;
```

```
end

% compute cdf's
y2y = cumsum(Prey2Prey);
y2d = cumsum(Prey2Pred);
d2d = cumsum(Pred2Pred);
d2y = cumsum(Pred2Prey);

% compute modified Ripley's K
KdPrey = y2y*Volume./(4/3*pi*(d.^3)*NumPrey*(NumPrey-1));

KdP_P = y2d*Volume./(4/3*pi*(d.^3)*NumPrey*NumPreds);

KdPreds = d2d*Volume./(4/3*pi*(d.^3)*NumPreds*(NumPreds-1));

KdD_Y = d2y*Volume./(4/3*pi*(d.^3)*NumPrey*NumPreds);

Prey_Density = NumPrey/Volume
Preds_Density = NumPreds/Volume


%------------------------
% PLOT THE DATA
%------------------------

subplot(4,1,1)
plot(d,KdPrey)

subplot(4,1,2)
plot(d,KdP_P)

subplot(4,1,3)
plot(d,KdPreds)

subplot(4,1,4)
plot(d,KdD_Y)


%---------------------------
% OUTPUT THE DATA
%---------------------------
```

```
cd C:\1sims\3D;
FinalMatNN = cat(2,y2y,y2d,d2d,d2y);
save([FileName,'_cdf_out.txt'],'FinalMatNN','-ascii');
FinalMatKd = cat(2,KdPrey,KdP_P,KdPreds,KdD_Y);
save([FileName,'_Kd_out.txt'],'FinalMatKd','-ascii');


RunTimeInMin = toc/60 % end stopwatch
```

Appendix B: Matlab code for calculating the 3D transform of Besag's (1977) transform of Ripley's K(d).

```
function Ld3D

% This program calculates every neighbor distance from acoustic data
% based on single target detections and TS to length conversions.
% It requires text files from the BioSonics DT6000 Visual Analyzer software
% with 7 columns (target depth, TS, along, athwart, bottom depth, lat, lon).

% Output is 2 *.txt files: 1) the cdf of neighbor distances
%                          2) the 3D L(d) function described in Scheuerell (2002)

% original version created by Mark Scheuerell on 02.01.09

% last modified by MDS on 02.04.17

% initialization routines
clear;
close;
echo off;
format long;
%pack;

% model parameters
PredLength = 28;      % min length (cm) of a "predatory" fish
PreyRatio = 3;        % min length ratio of pred:prey
MinFishSize = 2;      % min length (cm) of "prey" fish
MaxPreySize = 10; % max length (cm) of "prey" fish

d = [0:0.02:10]';

tic; % starts stopwatch

%------------
% DATA INPUTS
%------------

cd C:\1sims\3D;

% load the data file
```

```
FileName = input('Which file do you want to analyze? ','s');
% variables are target depth, TS, along, athwart, bottom depth, lat, lon
AcData=dlmread([FileName,'.txt'],'\t');;

% prompt for the sample volume
volume = str2num(input('What is the sample volume? ','s'));

%-----------------
% DATA CONVERSIONS
%-----------------

% convert degrees to meters lon
AcData(:,7)=AcData(:,7).*60.*1852.*cos(AcData(:,6)*pi/180)...
        +tan(AcData(:,4)*pi/180).*AcData(:,1);

% convert degrees to meters lat
AcData(:,6)=AcData(:,6).*60.*1852+tan(AcData(:,3)*pi/180).*AcData(:,1);

% convert TS to bodylength (cm)
% using Burczynski and Johnston (1986) for sockeye at 420 kHz
AcData(:,8)=10.^((AcData(:,2)+66)/20);

% variables are: target depth, TS, along, athwart, bottom depth, lat, lon, fish length
% drop extra columns
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
% new cols are Target Depth (m), Lat (m), Lon (m), Fish Length (cm)

% drop all of the targets less than the minimum fish size
AcData(find(AcData(:,4)<MinFishSize),:)=[];
% drop all prey<targets<predators
AcData(find(AcData(:,4)<PredLength & AcData(:,4)>MaxPreySize),:)=[];
NumTargets=length(AcData);


%-------------
% PROGRAM BODY
%-------------

% initialize some variables
```

```
N_con = 0;
N_pred = 0;

% initialize some matrices
NewX=zeros(NumTargets,1);
NewY=zeros(NumTargets,1);
NewZ=zeros(NumTargets,1);

TypeVec=zeros(NumTargets,1); % tag vector for fish type (e.g. predator or prey)

Prey2Prey = zeros(1,length(d))'; % histogram of inter-prey distances
Prey2Pred = zeros(1,length(d))'; % histogram of predator-prey distances
Pred2Pred = zeros(1,length(d))'; % histogram of inter-predator distances

NumPreds = length(find(AcData(:,4) > PredLength));
NumPrey = NumTargets - NumPreds;

% loop through all of the fish to compute distances
for i=1:NumTargets

  TypeVec=zeros(NumTargets,1); % reset type code
  TypeVec(find(AcData(:,4) > PredLength)) = 1; % it's a predator in general
  TypeVec(find(TypeVec==1 & (AcData(:,4)/PreyRatio > AcData(i,4)))) = 2;
      % it's a predator to this fish

  NewX = AcData(:,3) - AcData(i,3);
  NewY = AcData(:,2) - AcData(i,2);
  NewZ = AcData(:,1) - AcData(i,1);

  % compute distances
  rho = sqrt((NewX.^2 + NewY.^2 + NewZ.^2));

  NND = TypeVec(find(min(rho(find(rho~=0)))));
  if NND==0
    N_con = N_con+1;
  else N_pred = N_pred+1;
  end;

  % compute distance histograms based on fish type
  if TypeVec(i)==0 % it's a prey fish
    p = histc(rho(find(TypeVec==0&rho~=0)),d);
    if length(p)>0
```

```
      Prey2Prey = Prey2Prey + p;
    end;
    q = histc(rho(find(TypeVec==2)),d);
    if length(q)>0 & size(q,2)==1
      Prey2Pred = Prey2Pred + q;
    end;
    r = histc(rho(find(TypeVec>0)),d);
    if length(r)>0 & size(r,2)==1
      Pred2Pred = Pred2Pred + r;
    end;
  elseif TypeVec(i)>0 & size(histc(rho(find(TypeVec>0)),d),2)==1
    Pred2Pred = Pred2Pred + histc(rho(find(TypeVec>0)),d);
  end;

end

% compute cdf's
y2y = cumsum(Prey2Prey);
y2d = cumsum(Prey2Pred);
d2d = cumsum(Pred2Pred);

% compute Besag's (1977) transform
LdPrey = (volume*y2y/(NumPrey*(NumPrey-1))/pi).^(1/3) - d;
[Maxi MaxDist] = max(LdPrey);
[Mini MinDist] = min(LdPrey);

% compute Besag's (1977) transform
LdP_P = (volume*y2d/(NumPrey*NumPreds)/pi).^(1/3) - d;
[Mxi MxDist] = max(LdP_P);
[Mni MnDist] = min(LdP_P);

% compute Besag's (1977) transform
LdPreds = (volume*d2d/(NumPreds*(NumPreds-1))/pi).^(1/3) - d;

% compute Dixon's (1994) stat
Sii = log(N_con/N_pred*NumPreds/(NumPrey-1))

%----------------
% OUTPUT THE DATA
%----------------

subplot(2,1,1)
```

```
plot(d,LdPrey) % Besag (1977) transform
axis([0 10 -5 5])
title(['max = ',num2str(Maxi,3),' @ d = ',num2str(MaxDist/50,3)...
    '  min = ',num2str(Mini,3),' @ d = ',num2str(MinDist/50,3)...
        '  n = ',int2str(NumPrey)])

subplot(2,1,2)
plot(d,LdP_P) % Besag (1977) transform
title(['max = ',num2str(Mxi,3),' @ d = ',num2str(MxDist/50,3)...
    '  min = ',num2str(Mni,3),' @ d = ',num2str(MnDist/50,3)...
        '  n = ',int2str(NumPrey)])


cd C:\1sims\3D;
FinalMatNN = cat(2,y2y,y2d,d2d);
save([FileName,'_out.txt'],'FinalMatNN','-ascii');
FinalMatLd = cat(2,LdPrey,LdP_P,LdPreds);
save([FileName,'_Ld_out.txt'],'FinalMatLd','-ascii');

RunTimeInMin = toc/60 % end stopwatch
```

Appendix C: Matlab code for calculating the edge correction necessary for analyzing 3D point positions obtained with hydroacoustics.

```
function edge_dw25

% This program calculates nearest neighbor distances from simulated data
% based on a 3D Poisson random process. It then computes an edge correction
% between the theoretical and observed cdf's of Pr{NN < r} where r is the
% radius of a sphere.

% Output is 2 *.txt files:
% 1) mean measured cdf in the sample volume
% 2) edge corrections for various denisties & r's
% row_index = r and col_index = density

% original version created by Mark Scheuerell on 02.02.28

% last modified by MDS on 02.03.10

%------------------------
% initialization routines
%------------------------

clear all;
tic % starts stopwatch
%close;
%echo off;
format long;

cd C:\1sims\3D;

rand('state',sum(100*clock));

%-----------------
% model parameters
%-----------------

d = [-1:0.02:1.5]';       % bins for log10 n-n distances histogram

NumRuns = 1000;           % number of MC simulations
```

```
start = 2;                      % start # of fish (log10)
endpt = 5;                      % ending # of fish (log10)
step = 0.1;           % increment for log10 density gradient

phi = 6.5*pi/180;     % 1/2 beam angle of the transducer in radians = deg*pi/180

% to base density on a sample vol of 10^5 m3
l = 500;                                     % length (m) of the volume
z = sqrt(200/tan(phi));   % depth (m) of the cone
w = z*tan(phi);                         % 1/2 width (m) of the cone @ z

%--------------
% program body
%--------------

time = num2str(now,9)

dwDistFile = ['dwDist','_',num2str(phi,3),'_',num2str(start,2),'_',...
    num2str(step,2),'_',num2str(endpt,2),'_',time,'.txt'];

k = 1; % counter for storing edge corrections

dw = zeros(1,NumRuns);

for nf = start:step:endpt % loop over the various fish log10(density)

  nf % where we are in the log10(density) loop

  Gpq = zeros(1,length(d)); % histogram of inter-prey distances

  NumFish = round(10^nf);

  window = round(30*nf-50);

  count = 0; % initialize the fish counter

  fid = fopen('MeanGpqOut.txt');
  MeanGpq = fscanf(fid,'%g');
  MeanGpq = MeanGpq([1:126] + round(6300*(nf-2)))';

  for mc = 1:NumRuns
```

```
% generate the fish data
SimData = zeros(NumFish,3);
SimData(:,1) = l*rand([NumFish 1]); %X pos of the fish
SimData(:,2) = 2*w*rand([NumFish 1]); %Y pos of the fish
SimData(:,3) = z*rand([NumFish 1]); %Z pos of the fish

% sample with acoustics
SampledFish = sortrows(SimData(find(SimData(:,2)<w+SimData(:,3)*tan(phi)...
  & SimData(:,2)>w-SimData(:,3)*tan(phi)),:));
clear SimData;

NumSampled = length(SampledFish(:,1));

% pad with "99" to eliminate false N-N at beginning & end of transect
SampledFish = cat(1,zeros(window,3)+99,SampledFish,zeros(window,3)+99);

count = count+NumSampled;               % running count of sample size

% initialize some matrices
NewData = zeros(2*window,3);  % to become the basis-shifted fish matrix

Nearest = zeros(1,NumSampled);% collection of N-N distances

% loop through the fish to compute distances
for i=(1+window):(NumSampled+window)

  NewData = SampledFish([(i-window):(i+window)],:)...
    - repmat(SampledFish(i,:),[2*window+1 1]);

  % compute distances
  rho = sqrt((NewData(:,1).^2 + NewData(:,2).^2 + NewData(:,3).^2));

  % find nearest neightbor
  Nearest(i-window) = min(rho(find(rho>0)));

end % loop for each fish

% compute cdf's
p = histc(log10(Nearest),d);
Gpq = cumsum(p)/sum(p); % cdf

dw(mc) = max(Gpq - MeanGpq);
```

```
  end; % mc loop for MC

  clear MeanGpq;

  k=k+1;

  % output the dw Distn
  fid = fopen(dwDistFile,'a');
  OtPt = cat(1,nf*ones(1,NumRuns),[1:NumRuns],sort(dw));
  fprintf(fid,'%2.1f\t%4f\t%.4e\n',OtPt);
  clear OtPt;
  fclose(fid);

end; % nf loop for varying fish #

RunTimeInHrs=toc/3600 % end stopwatch
```

Appendix D: Matlab code for calculating the nearest-neighbor distances from 3D data obtained with hydroacoustics.

```
function NND

% This program calculates nearest neighbor distances from acoustics data
% based on a 3D Poisson random process. It then computes an edge correction
% between the theoretical and observed cdf's of Pr{NN < r} where r is the
% radius of a sphere.

% It requires text files from the BioSonics DT6000 Visual Analyzer software
% with 7 columns (target depth, TS, along, athwart, bottom depth, lat, lon).

% Output is  1) the observed dw value
%            2) the critical dw value
%            3) *.txt file with mean measured cdf in the sample volume

% the program also requires the following functions
% EdgeCor.m
% dwCrit.m

% original version created by Mark Scheuerell on 02.04.19

% last modified by MDS on 02.04.30

%------------------------
% initialization routines
%------------------------

clear all;
close;
echo off;
format long;

% model parameters
PredLength = 28;       % min length (cm) of a "predatory" fish
PreyRatio = 2;         % min length ratio of pred:prey
MinFishSize = 2;       % min length (cm) of "prey" fish
MaxPreySize = 10; % max length (cm) of "prey" fish

d = [0.05:0.05:10]';
```

```
P = 0.002; % desired p-value (accounting for 25 multiple comparisons)

%tic; % starts stopwatch

%------------
% DATA INPUTS
%------------

cd C:\1sims\RRF;

% load the data file
FileName = input('Which file do you want to analyze? ','s');
% variables are target depth, TS, along, athwart, bottom depth, lat, lon
AcData=dlmread([FileName,'.txt'],'\t');;

% prompt for the sample volume
volume = str2num(input('What is the sample volume? ','s'));

%-----------------
% DATA CONVERSIONS
%-----------------

% convert degrees to meters lon
AcData(:,7)=AcData(:,7).*60.*1852.*cos(AcData(:,6)*pi/180)+tan(AcData(:,4)*pi/180).
            *AcData(:,1);

% convert degrees to meters lat
AcData(:,6)=AcData(:,6).*60.*1852+tan(AcData(:,3)*pi/180).*AcData(:,1);

% convert TS to bodylength (cm)
% using Burczynski and Johnston (1986) for sockeye at 420 kHz
AcData(:,8)=10.^((AcData(:,2)+66)/20);

% variables are: target depth, TS, along, athwart, bottom depth, lat, lon, fish length
% drop extra columns
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
AcData(:,2)=[];
% new cols are Target Depth (m), Lat (m), Lon (m), Fish Length (cm)
```

```
% drop all of the targets less than the minimum fish size
AcData(find(AcData(:,4)<MinFishSize),:)=[];
% drop all prey<targets<predators
AcData(find(AcData(:,4)<PredLength & AcData(:,4)>MaxPreySize),:)=[];
NumTargets=length(AcData);

PredsFish = AcData(find(AcData(:,4)>= PredLength),:);
PredsFish(:,4)=[];
NumPreds = length(PredsFish);
PredsDens = NumPreds/volume
GpqPreds=[];

PreyFish = AcData(find(AcData(:,4) <= MaxPreySize),:);
PreyFish(:,4)=[];
NumPrey = length(PreyFish);
PreyDens = NumPrey/volume

  if NumPreds > 4
  window = floor(20*log10(PredsDens)+100);

    % pad with "99" to eliminate false N-N at beginning & end of transect
    PredsFish = cat(1,zeros(window,3)+99,PredsFish,zeros(window,3)+99);

    % initialize some matrices
    NewData = zeros(2*window+1,3);  % to become the basis-shifted fish matrix

    NearestPreds = zeros(1,NumPreds);       % collection of N-N distances

    % loop through the fish to compute Predator distances
    for i=(1+window):(NumPreds+window)

      NewData = PredsFish([(i-window):(i+window)],:) -
              repmat(PredsFish(i,:),[2*window+1 1]);

      % compute distances
      rho = sqrt((NewData(:,1).^2 + NewData(:,2).^2 + NewData(:,3).^2));

      % find nearest neightbor
      NearestPreds(i-window) = min(rho(find(rho>0)));

    end % loop for each fish
```

```
  % compute cdf's
  p = histc(NearestPreds,d);
  GpqPreds = cumsum(p)/sum(p); % "cumulative" cdf
  InfGpqPreds = 1-exp(-4/3*pi*PredsDens*(10.^d).^3)'; % theoretical G across infinite
            universe
  EdgeCorPreds = EdgeCor(d,PredsDens);
  dwPredsObs = max(GpqPreds - InfGpqPreds - EdgeCorPreds')
  dwPredsCrit05 = dwCrit(PredsDens,P)
  MeanNNPreds = mean(NearestPreds)
end



window = floor(27*log10(PreyDens)+100);

  % pad with "99" to eliminate false N-N at beginning & end of transect
  PreyFish = cat(1,zeros(window,3)+99,PreyFish,zeros(window,3)+99);

  % initialize some matrices
  NewData = zeros(2*window,3);   % to become the basis-shifted fish matrix

  NearestPrey = zeros(1,NumPrey);          % collection of N-N distances

  % loop through the fish to compute Predator distances
  for i=(1+window):(NumPrey+window)

    NewData = PreyFish([(i-window):(i+window)],:) -
            repmat(PreyFish(i,:),[2*window+1 1]);

    % compute distances
    rho = sqrt((NewData(:,1).^2 + NewData(:,2).^2 + NewData(:,3).^2));

    % find nearest neightbor
    NearestPrey(i-window) = min(rho(find(rho>0)));

  end % loop for each fish

  % compute cdf's
  p = histc(NearestPrey,d);
  GpqPrey = cumsum(p)/sum(p); % "cumulative" cdf
```

```
    InfGpqPrey = 1-exp(-4/3*pi*PreyDens*(10.^d).^3)'; % theoretical G across infinite
            universe
    EdgeCorPrey = EdgeCor(d,PreyDens);
    dwPreyObs = max(GpqPrey - InfGpqPrey - EdgeCorPrey')
    dwPreyCrit05 = dwCrit(PreyDens,P)

    MeanNNPrey = mean(NearestPrey)

    if length(GpqPreds)==0
      GpqPreds = zeros(1,length(GpqPrey));
    end;

FinalMatNN = cat(2,GpqPrey',GpqPreds');
save([FileName,'_NNcdf_out.txt'],'FinalMatNN','-ascii');

plot(d,InfGpqPrey,d,GpqPrey,d,EdgeCorPrey)
legend('InfGpqPrey','GpqPrey','EdgeCorPrey')

%RunTimeInMin=toc/60 % end stopwatch
```

Appendix E: Matlab code for calculating the critical values for the nearest-neighbor aggregation test.

```
function dwc=dwCrit(rho,P)

% this funciton calcuates the critical value for the "dw" test statistic from
% Coomes et al. (1999) based on the given density (rho) and desired p-value (P)

b1 = -0.0116 + 0.0208*P - 0.00260*P^2 - 0.0133*P^3;
b2 = -0.453 + 0.435*P - 1.83*P^2 + 1.75*P^3;

dwc = b1*(1-rho^b2);
```

Appendix F: Matlab code for calculating the edge correction used in the nearest-neighbor aggregation test.

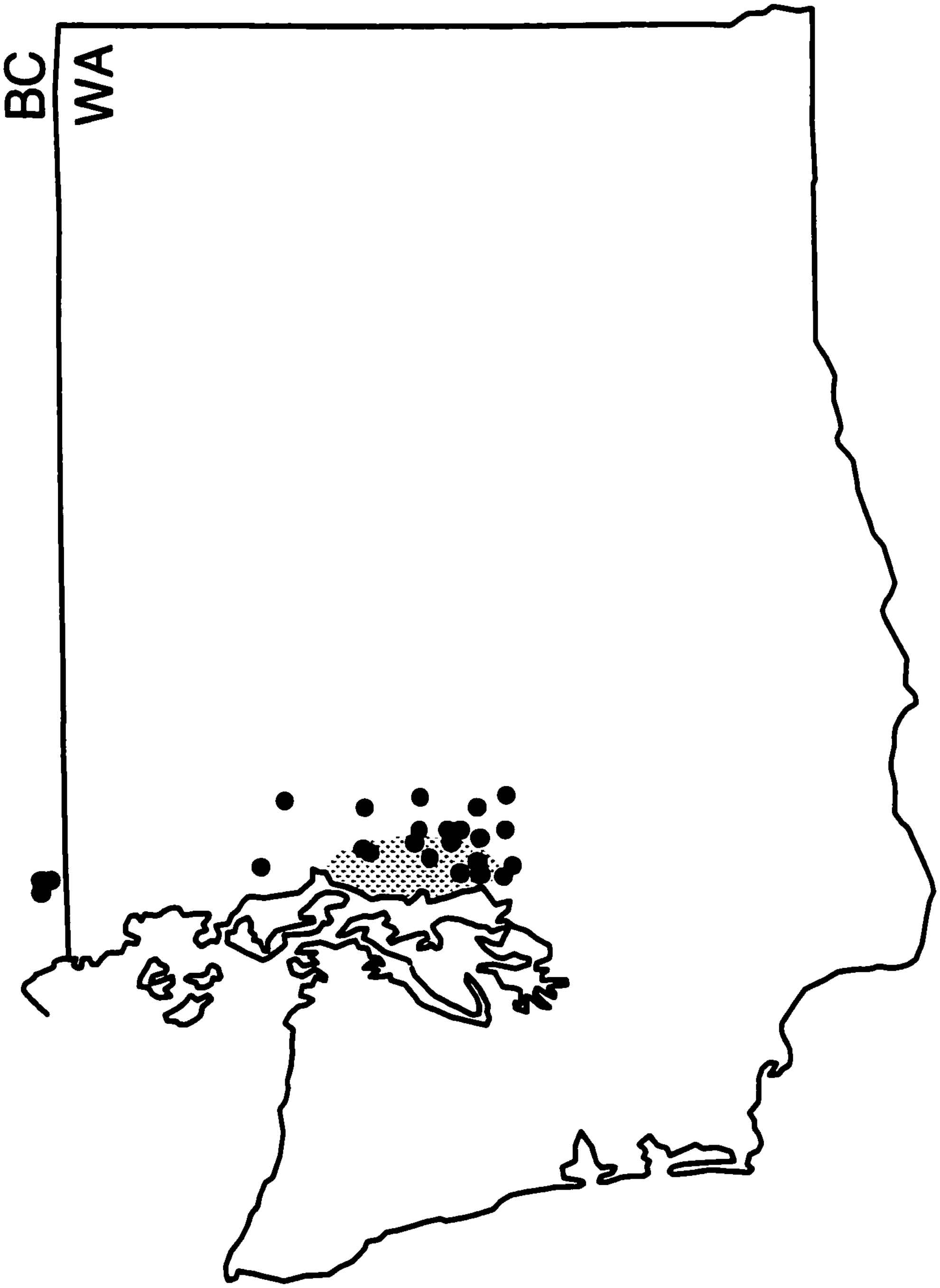
```
function ec = EdgeCor(r,rho)

% this function calculates the edge correction necessary for a 6.7 degree
% hydroacoustic transducer based on the density (rho) and sphere radius (r)

b0 = 0.0340;
b1 = -0.834;
b2 = 0.322;
b3 = -0.448;
b4 = 0.600;
b5 = -0.111;
b6 = 0.256;

ec = b0*r.*(1+b1*r)*(1+b2*log10(rho)).*exp(b3*r.*(1+b4*log10(rho))...
        +b5*r.^2*(1+b6*log10(rho)));
```

Appendix G: Map of the Pacific northwest indicating the locations of the study lakes used in Chapter 3.



Appendix H: Table of morphometric data for the study lakes used in Chapter 3.

Lake	Elevation (m)	Surface area (ha)	Drainage area (ha)	Mean depth (m)	Max depth (m)	Shoreline length (km)	Lakeshore houses
Angle	110	40.5	207	7.6	15.8	3.5	195
Beaver	123	25.1	295	6.4	16.4	3.2	54
Boren	317	7.3	277	5.5	10.3	1.1	22
Deep	233	15.0	1015	11.0	22.0	2.1	1
Devils	135	5.3	52	7.0	13.6	1.1	19
Echo	145	6.9	60	5.2	15.2	1.0	29
Eunice	480	18.2	191	15.8	42.0	2.8	0
Fenwick	35	9.7	228	3.9	9.4	1.9	8
Geneva	118	10.5	91	5.8	13.9	1.6	35
Gwendoline	522	13.0	81	13.4	27.0	1.8	0
Langlois	37	15.8	96	16.1	29.7	1.8	3
Loon	340	48.6	306	27.5	62.0	5.2	1
Margaret	242	18.2	616	5.5	13.0	2.7	52
McMurray	48	64.8	842	8.8	15.8	4.2	64
Meridian	112	60.7	300	12.4	27.3	4.0	157
Neilson	120	7.7	75	5.5	9.4	1.4	16
North	119	22.7	197	4.2	10.3	2.7	58
Otter	150	27.5	181	5.8	9.7	2.4	36
Pine	118	34.8	269	6.1	11.8	3.9	96
Riley	157	12.1	114	6.7	13.6	1.5	19
Shadow	164	19.8	184	6.7	13.6	1.9	24
Shady	158	8.5	88	6.4	12.1	1.3	45
Star	97	14.2	153	7.6	15.2	1.8	51
Wilderness	142	27.9	171	6.4	11.5	2.9	50
Mean	176	22.3	254	8.6	18.4	2.4	45
SE	26	3.4	49	1.1	2.5	0.23	10

Vita

Mark Scheuerell was born in Milwaukee, Wisconsin to his wonderful parents Judy and Robert. He has an incredible younger brother Steven, a fantastic sister-in-law Annie, and a smiley new nephew River. After brief stays in Detroit and Boston, his family settled down in Sartell, Minnesota along the banks of the beautiful Mississippi River where Mark spent many hours with Steve playing in and around the water. It was during these formative years that he developed a fascination for water and everything in it. Fortunately, his parents are adventurous, love the outdoors, and took Steve and him on many short trips and long vacations all over the United States and Canada.

Mark spent four years (1987-1991) in Madison at the University of Wisconsin finishing my Bachelor of Science degree in Zoology during which time he met several dear friends and learned endless lessons of life. After a two-year hiatus from school when he worked at the University of Wisconsin's Center for Limnology and the Cornell University Biological Field Station, Mark entered graduate school in the Department of Natural Resources at Cornell University in June of 1993. There his research focused on fish spatial dynamics and he received a Master's degree in Fisheries and Aquatic Science in December of 1995.

After finishing his M.S., Mark traveled in South America for awhile and then moved to Avon Park, FL and began working with a group of researchers from the University of Massachusetts and the Massachusetts Audubon Society on the federally endangered Florida Grasshopper Sparrow. Since September 1997 he has been living in

Seattle, WA where in his spare time he enjoys alpine and Nordic skiing, mountain and road biking, canoeing, and ultimate frisbee. Mark spent the last three summers in beautiful southwest Alaska doing research on the food web dynamics of sockeye salmon. In 2002 Mark earned a Doctor of Philosophy degree at the University of Washington in the Department of Zoology.