Proximate factors influencing the spatial distribution of a high altitude copepod: *Hesperodiaptomus shoshone*.

Malgorzata A. Marszalek

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements
for the Degree of Master of Science at
Concordia University
Montreal, Quebec, Canada

August 2002

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ABSTRACT

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Spatial distribution shapes almost every aspect of the ecology of populations. Even though the importance of spatial distribution to the ecology of zooplankton is established, little is known about the factors that generate and maintain these aggregations (Megard *et al.* 1997). The role that environmental variables, specifically light intensity, and pond substrate coloration play on the formation and maintenance of aggregations was investigated in the freshwater calanoid *Hesperodiaptomus shoshone*. The spatial distribution *H. shoshone* was determined using traditional methods (i.e. the Morisita's index of dispersion) and spatial methods - trend analyses and autocorrelations- with the aim of clarifying distribution dynamics during a 24hr point interval sampling period. Copepods were found to be aggregated through the day and night with the highest aggregation levels at midday. Spatial patterns were not consistent either between the two ponds studied or between sampling times of the day. Partial regression analyses were used to identify the relative contribution of environmental and spatial factors structuring *H. shoshone* spatial distributions. Although the results were not consistent between the two ponds, light intensity and proximity to logs were two proximate factors influencing the observed copepod heterogeneity. Furthermore results showed that background colours of pond substrate were found to influence the aggregation behaviour of copepods in the water column.

ACKNOWLEDGEMENTS

I would like to thank my committee members, Dr. Paul Albert, Dr. Ian Ferguson and Dr. Jim Grant, for their helpful comments with regards to the thesis. I would also like to thank Dr. Mary Maly and Matthew Norton for all their help with the statistical analysis.

A special thanks goes to Dr. Edward J. Maly who provided me with this amazing opportunity and for being the most understanding and generous supervisor a graduate student could ask for. It's a pleasure to work for you.

I am indebted to Maria Pia Aguilera (my partner in crime) whom I coaxed into sampling at night and who had to brave bears, wild thunderstorms, and my company in order to assist me with the field work in Colorado. This thesis could not have been possible without her help, assistance and knowledge.

I would like to thank the people of the Rocky Mountain Biological Laboratory who willingly devoted their time and knowledge especially Dr. Scott Wissinger and billy barr. Special thanks to the friends I made at RMBL: Jill, Tracy, Corey and Rich. I am thankful to the Colorado Nature Conservancy for the chance to study an unspoiled habitat.

I would also like to thank my parents especially my dad, for the support I've received during my years of education.

Finally, I extend a warm and special acknowledgement to Trevor Lane, who continuously encouraged me, kept me sane and provided invaluable comments on the final draft of the thesis.

ABSTRACT

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Spatial distribution shapes almost every aspect of the ecology of populations. Even though the importance of spatial distribution to the ecology of zooplankton is established, little is known about the factors that generate and maintain these aggregations (Megard *et al.* 1997). The role that environmental variables, specifically light intensity, and pond substrate coloration play on the formation and maintenance of aggregations was investigated in the freshwater calanoid *Hesperodiaptomus shoshone*. The spatial distribution *H. shoshone* was determined using traditional methods (i.e. the Morisita's index of dispersion) and spatial methods - trend analyses and autocorrelations- with the aim of clarifying distribution dynamics during a 24hr point interval sampling period. Copepods were found to be aggregated through the day and night with the highest aggregation levels at midday. Spatial patterns were not consistent either between the two ponds studied or between sampling times of the day. Partial regression analyses were used to identify the relative contribution of environmental and spatial factors structuring *H. shoshone* spatial distributions. Although the results were not consistent between the two ponds, light intensity and proximity to logs were two proximate factors influencing the observed copepod heterogeneity. Furthermore results showed that background colours of pond substrate were found to influence the aggregation behaviour of copepods in the water column.

TABLE OF CONTENTS

PAGE

LIST OF FIGURES vi

LIST OF TABLES vii

INTRODUCTION 1

MATERIALS AND METHODS 7

RESULTS 16

DISCUSSION 22

FUTURE STUDIES 35

CONCLUSIONS 37

BIBLIOGRAPHY 80

LIST OF FIGURES

Page

Figure 1: Mexican Cut Nature Preserve Watershed.................................... 39

Figure 2: Diagram of pond 8.. 41

Figure 3: Diagram of pond 11.. 43

Figure 4: Morisita's Index of Dispersion by sampling time of day for pond 11.... 45

Figure 5: Morisita's Index of Dispersion by sampling time of day for pond 8...... 47

Figure 6: Contour density plots for pond 11.. 49

Figure 7: Contour density plots for pond 8.. 51

Figure 8: Autocorrelograms of *H. shoshone* densities for pond 11.................. 55

Figure 9: Autocorrelograms of *H. shoshone* densities for pond 8..................... 58

Figure 10: Differences in *H. shoshone* densities between deep and shallow midpond samples.. 64

Figure 11: Densities of *H. shoshone* found above background markers in pond U2.. 66

Figure 12: Densities of *H. shoshone* found above background markers in pond U6 68

LIST OF TABLES

PAGE

Table 1: Results of spatial trends of *H. shoshone* densities in pond 11............... 70

Table 2: Results of shallow spatial trends of *H. shoshone* densities in pond 8...... 71

Table 3: Results of deep spatial trends of *H. shoshone* densities in pond 8 72

Table 4: Summary of spatial statistics performed in pond 11......................... 73

Table 5: Summary of spatial statistics performed in pond 8 74

Table 6:Results of partial regression analyses in pond 11 75

Table 7: Results of partial regression analyses in pond 8 77

INTRODUCTION

Zooplankton of the oceans and lakes is distributed patchily and the significance of spatial heterogeneity to zooplankton ecology and evolution is well-recognised (Pinel-Alloul, 1995). Spatial distribution shapes almost every aspect of the ecology of populations. In zooplankton species, spatial heterogeneity is considered to influence predation and mortality rates, reproduction, feeding and species diversity (Megard *et al.*, 1997). Even though the importance of spatial distribution to the ecology of zooplankton is established, little is known about the factors that generate and maintain these aggregations (Megard *et al.*, 1997). The purpose of this study is to determine the role that environmental variables, specifically light intensity and pond substrate colouration play in the formation and maintenance of adult aggregations in the high altitude freshwater calanoid copepod *Hesperodiaptomus shoshone* (Forbes S.A.).

Aggregative behaviour has been studied in terrestrial animals such as mammals (Hurlbert, 1990), birds (Parrish and Edelstein- Keshet, 1999) and insects (Irvine, 2000), in aquatic organisms like fish (Garcia-Charton and Perez-Ruzafa, 2001), and zooplankton such as copepods. Copepods have been reported to form dense aggregations in a wide range of habitats including coral-reef environments (Hamner and Carleton, 1979: Lewis and Boers, 1991), near mangrove cays (Ambler *et al.*, 1991: Buskey and Peterson, 1996: Buskey, 1998), temperate and sub-tropical bays (Ueda *et al.*, 1983) and in freshwater lakes and ponds (Colebrook, 1960: Herbert *et al.*, 1980: Byron *et al.*, 1983: Aguilera, 2002). Zooplankton aggregations can occur on scales ranging from centimetres to meters and greater (Byron *et al.*, 1983: Malone and McQueen, 1983: Pinel-Alloul *et al.*, 1990, 1999: Pinel-Alloul, 1995). Patches, density gradients, aggregations and swarms all refer to zooplankton distributions. However, there is ambiguity on the definition of aggregation and many have been proposed. Aggregations are loosely defined as the non-random distribution of biomass or number of individuals per unit volume of habitat (Haury *et al.*, 1978). Another definition specific to zooplankton refers to the term aggregation as "the horizontal or vertical regions of the distribution of a population of zooplankton that contain densities of individuals, usually 3 to 5 times, above the mean density of the population" (Macas *et al.*, 1985; Ritz, 1994; Mauchline, 1998). Hamner (1988) provided the following definition: "a grouping of conspecific individuals without any connotation of mutual attraction containing densities of zooplankton, at least one standard deviation above the mean density of the population". Although different definitions have been proposed to date, they generally reflect the statistical analysis used in the study. With the recent advances of geostatistical methods in spatial ecology the two former definitions seem obsolete. Therefore, although not ideal, the first general definition was used. Patchiness, heterogeneity and aggregations are used interchangeably in the literature and will be employed in this manner throughout this study.

Aggregations like other ecological phenomena are studied from a proximate or an ultimate point of view. An ultimate analysis has the aim of providing functional explanations at the evolutionary level while a proximate analysis is intended to reveal the underlying mechanistic explanations and environmental factors that cause a given phenomenon to occur. Ultimate causes of aggregations in zooplankton may include increased mating success of the aggregated populations (Herbert *et al.*, 1980: Folt, 1987: Folt and Burns, 1999: Aguilera, 2002) or an increased protection from predators (Hamner and Carlton, 1979: Buskey and Peterson, 1996: Buskey, 1998). Several proximate factors such as presence of predators or competitors (Folt, 1987: Folt and Schulze, 1993), salinity and temperature gradients (Omori and Hamner, 1982: Betsill and van den Avyle, 1994), local food abundance (Larsson, 1997), and light intensity (Buskey and Peterson, 1996: Jensen *et al.*, 1999) may cause spatial heterogeneity in zooplankton. In freshwater zooplankton as in other communities, spatial heterogeneity is the result of both physical and behavioural processes. Hence, zooplankton patchiness is the product of several physical processes interacting with numerous biological processes (Malone and McQueen, 1983: Pinel-Alloul and Pont, 1991: Pinel-Alloul, 1995).

The proximate drivers of aggregations in zooplankton communities depend on the scale of the observations (Avois *et al.*, 2000) and zooplankton spatial heterogeneity occurs at hierarchal spatial scales in both marine and freshwater environments (Pinel-Alloul and Pont, 1991: Pinel-Alloul, 1995). In general, the relative importance of biotic processes is inversely correlated with scale (Pinel-Alloul, 1995). In freshwater ecosystems, zooplankton patchiness found over large scales (>1km) is mainly related to structural and advective processes such as the morphometry of the lake basins (Davis, 1969), river inflows (Gliwicz and Rykowska, 1992) and current patterns (Patalas, 1969). On smaller scales (10m – 1km), proximate factors influencing heterogeneity are more variable and include among others vertical stratification (Colebrook, 1960) wind induced currents (Riley, 1976) and downwind accumulation of organisms (de Nie *et al.*, 1980). On even smaller scales (<1-10m) which is the scale of interest for this study, physical gradients (Pinel-Alloul and Pont, 1991) and langumuir circulation patterns (de Nie *et al.*, 1980) influence the distribution but are less important than biological interactions (Folt and Burns, 1999).

In the natural environment, one physical factor that has been reported to induce aggregation formation in copepods is the occurrence of sharp spatial gradients in light intensity (Leising and Yen, 1997). Aggregations of the marine copepod, *Dioithona oculata*, commonly found near mangrove cays typically form between prop roots in shafts of sunlight that penetrate the mangrove canopy (Buskey and Peterson, 1996; Buskey, 1998). These swarms form at dawn and disperse at dusk (Ambler et al., 1991), and light seems to be the primary cue used in swarm formation of this species (Buskey, 1998). Buskey *et al.* (1995) found that laboratory induced aggregations of *Dioithona oculata* had an endogenous rhythm, as copepods would not aggregate at night under a light shaft. Additionally, a small number of studies indicate that copepod aggregations are associated with some physical feature of the bottom topography, or background coloration. Hamner and Carleton (1979) observed that the marine copepods, *Oithona oculata* and *Acartia australis* preferentially aggregate over bright sandy substrates located in proximity of coral boulders. In another study performed in Lake Tahoe, Byron et al. (1983) found the freshwater calanoid copepod, *Diaptomus tyrrelli* to aggregate over contrasting substrate of shallow water or otherwise above rocks closer to the lake surface or immediately adjacent to rocks protruding above the water surface. In a manipulative study, Herbert et al. (1980), found that *Heterocope septentrionalis*, a large calanoid copepod common in pond and lake habitats of arctic North America, formed aggregations above light coloured panels contrasting with the pond substrate. The aggregations remained above the contrasting panels only during daylight hours and were strongest when light intensity was high and wind strength low. Substrate colour with the greatest attraction varied among experimental ponds, indicating that *Heterocope* was not attracted to colour per se but that the greater contrast of the panel relative to the pond substrate seemed to be of greatest importance. Not all contrast provoked a response: aggregations did not form when dark panels where placed on light substrate. Such contrasts in substrate may serve the role of "background marker" promoting the aggregation of copepods. These types of aggregations may be the result of (1) visual orientation to the marker, (2) aggregation aided by fluid motion over the marker and (3) a combination of individuals reacting to the aggregation marker and subsequent interactions between individuals (Haury and Yamazaki, 1995).

Objectives

In a previous study, Aguilera (2002), identified the presence of aggregations in *Hesperodiaptomus shoshone* with the goal of understanding the possible ultimate reproductive benefits of aggregations. This study intends to complement these findings in order to investigate the proximate factors that might induce aggregations of *Hesperodiaptomus shoshone* in two ponds.

The first objective of this study is to confirm the presence of aggregations and to determine the intensity of the observed spatial pattern across the full pond scale during the course of a day in a sampling season. Aggregation intensity is expected to vary with sampling time of day and be most intense during midday samples, where light intensity is highest and decline or be non-existent at night.

The second objective of this study is to follow aggregations throughout a 24hr period in order to understand the dynamics of the copepod aggregations with the aim of clarifying temporal and spatial variability of *Hesperodiaptomus shoshone* by examining large and small-scale spatial patterns of their distribution. Large-scale spatial patterns should show daily cycles that occur through the sampling season.

The third objective of this study is to identify predictors of aggregative behaviours in *H. shoshone* in order to understand the proximate factors influencing the horizontal variability of their distribution. Light intensity should be one of the major factors affecting the distribution of *H. shoshone*.

The fourth objective of this study is to examine the influence background markers of contrasting colour have on the formation of aggregations of *H. shoshone*. If *H. shoshone* uses light as a means of orientation (Siebek, 1968: Ringelberg, 1969), then the background markers of light colour should show a higher proportion of individuals above them, as compared to dark markers and pond substrate.

MATERIALS AND METHODS

Study organism

The species chosen for this study is the calanoid copepod *Hesperodiaptomus shoshone* (Forbes S.A.). At the Mexican Cut (High altitude ponds in Colorado. see below). *Hesperodiaptomus shoshone* is observed to be univoltine. (Maly and Maly. 1974) and it exhibits aggregative behaviours (Aguilera, 2002). It reproduces sexually. and must copulate before a clutch of eggs can be extruded. On emergence from the egg. this calanoid copepod passes through six naupliar stages (N1-N6) and five copepodite stages (C1-C5) before reaching the adult stage (Ward and Whipple. 1959). *Hesperodiaptomus shoshone* is relatively large and highly visible due to the cartoneoid pigmentation (Byron. 1982), which facilitates visual location for mapping. identification and sorting once in the lab.

Study site

The study was conducted at the Mexican Cut Nature Preserve located in the Elk Mountains of south-central Colorado (Fig1). This watershed is owned by The Nature Conservancy and is managed by the Rocky Mountain Biological Laboratory. The Mexican cut contains clusters of ponds on two plateaus on Galena Mountain of approximately 3400m and 3450m (the "Lower Cut" and the "Upper Cut" respectively). The preserve contains several subalpine fens with numerous open water basins that vary in size (<5 to 4647m^2), water chemistry and hydroperiod (Wissinger and Whiteman. 1992: Wissinger *et al.*. 1999). Basins can be categorized as permanent. temporary autumnal (drying then refilling in autumn in most years). or temporary vernal (filled only after snowmelt and drying during the early summer)(Wissinger and Whiteman. 1992: Wissinger *et al.*, 1999). Although many of the basins at The Mexican Cut are only a few meters apart, they often contain quite distinct assemblages of invertebrates (Dodson. 1970: Wissinger *et al.*. 1999). Shallow montane ponds are used in this study because spatial heterogeneity in oxygen concentrations, an important abiotic factor potentially influencing zooplankton distributions, is typically minimal (Wicklum, 1999).

The experimental period lasted six weeks beginning June 28th and ending August 9th, 2001 inclusively.

Dynamics of copepod aggregations

Samples were obtained from two temporary ponds, 8 and 11 respectively. Pond 8 is up to 1.3m deep and covers an area of 928m^2 and pond 11 is up to 0.8m deep and covers an area of 213m^2 (Wissinger *et al.*, 1999). These ponds were chosen because *Hesperodiaptomus shoshone* aggregations have been previously identified in them (Aguilera, 2002). Samples were collected during a 24hr basis with 3 sampling efforts on each sampling date (approximately at midday, 5:00pm, and midnight). On one occasion in pond 8 after a day of rain one sample was taken in the morning (9:00 am). On each sampling effort, ponds were sampled along 7-9 transects with a maximum of 5 sampling locations along each transect. Transects and sampling locations were determined on the first sampling date for each pond and maintained through all the sampling dates (Fig 2 and Fig 3). For this purpose a coordinate system was arbitrarily centred on the south-western portion of each pond to provide x and y coordinates (in m) for further analysis. Each pond was sampled from an inflatable raft once a week using a 4L plexiglas

Schindler-Patalas trap. Data recorded includes date and time of sampling, density of Schindler-Patalas samples, temperature of the water, surrounding physical variables and light intensity (cd/m^2) at each sampling location. Light measurements were performed with a Minolta spot-reading, reflex-viewing exposure meter for ambient and flash light (range of measurements: 0.28-831900 +/-1.07 cd/m^2). One of the advantages of a spotmeter is its ability to measure small and precise areas without reflected light from other areas being able to affect the readings. The temperature was measured with a MultiLine P4, TetraCon® 325 standard conductivity cell (+/- 0.2K).

Role of background markers

To determine the influence of substrate colour on aggregations, ponds U2 and U6 (Fig 1) were chosen due to their similar depth (0.7m deep)(Wissinger *et al.*, 1999). The substrate of pond U2 was golden brown while that of pond U6 was slightly more grey. Five white and black plexiglass panels (30cm x 30cm) were placed in the ponds and left for 24-48hrs before sampling. After 24hrs, a sample was taken and the marker was replaced by a different coloured one. The same site was then resampled 24hr later at the same time of the day (11 am). Locations of the plastic panels were determined in a random fashion and sampled before the introduction of the markers to serve as control values. Samples were taken above the markers and densities were compared among the control, black, and white treatments. Data includes date and time of sampling, density of Schindler-Patalas samples, temperature and light intensity measurements. This set-up (of 5 markers/pond) was performed 7 times during the summer.

DATA ANALYSIS

Morisita's index of dispersion

The presence of aggregations was established using the Morisita's index of dispersion (I_d) for all sampling times for each sampling date, as outlined in Krebs (1989).

$$I_d = n\left[\frac{\sum x^2 - \sum x}{\left(\sum x\right)^2 - \sum x}\right]$$

where,

I_d = Morisita's index of dispersion

n = Sample size, number of sampled units

$\sum x$ = Total number of individuals in sample

$\sum x^2$ = Total number of individuals in sample squared

Departure from randomness in each pond was statistically tested by comparison to a Chi^2 value (Southwood, 1971).

$$\chi^2 = I_d\left(\sum x - 1\right) + n - \sum x \quad \text{(d.f.= n-1)}$$

This index is considered to be the most reliable, since it is independent of population density and sample size (Hurlbert, 1990). A Kruskal-Wallis test was performed in order to determine if there were differences in the Morisita's index by time of day.

It was assumed that each sampling effort of a pond represented an instantaneous snapshot of *H. shoshone* numbers that is that there was no change in spatial patterns during the time required to sample a pond. On average sampling time lasted an hour in each pond.

Trend analyses and autocorrelations

In order to describe copepod spatial structure. the data were subjected to trend surface analysis (Gittins 1968: Legendre and Legendre 1998) and autocorrelations (Legendre and Legendre. 1998). The trend surface analysis consisted of regressing the density values (dependent variable) on their spatial coordinates (independent variable) for each sampling time. A linear regression or second order polynomial was applied to each sampling effort in order to identify significant spatial trends. Higher order polynomials were not used to minimize the chance of removing any spatial patterns underlying the larger scale trends. A surface fitted by a polynomial regression emphasizes spatial trends (coarse scale pattern) in the data while essentially ignoring. and thus removing. fine scale spatial pattern (Stockwell. 1996). The statistical significance of the trends was evaluated using a classical F-test at $\alpha = 0.05$. Prior to trend surface analysis the dependent variable was log transformed in samples where normality was not met. Classical contour maps were plotted from the trend analyses models. using the Sigma Plot 8.0.

To reveal any smaller scale spatial structure underlying the larger scale trends. autocorrelation analysis was applied to the residuals of the fitted trends (Legendre and Fortin. 1989). In cases were trends were not significant. the original copepod densities were subjected to autocorrelation analysis. A variable is autocorrelated if it is possible to predict its value at a given point in space by knowing its value at other locations. Spatial autocorrelation was measured by Moran's I (1950) statistic (Cliff and Ord. 1981). The general formula for computing Moran's I . as outlined in Legendre and Legendre (1998) is:

$$I(d) = \frac{\frac{1}{W}\sum_{h=1}^{n}\sum_{i=1}^{n} w_{hi}(y_h - \bar{y})(y_i - \bar{y})}{\frac{1}{n}\sum_{i=1}^{n}(y_i - \bar{y})^2} \text{ for } h \neq$$

where y_h 's and y_i 's are the values of the observed variable (in this case copepod densities) at sites h and i. The weights w_{hi} take the value $w_{hi} = 1$ when sites h and i are at distance d and $w_{hi} = 0$ otherwise. In this way, only the pairs of sites (h, i) within the stated distance class (d) are taken into account in the calculation of any given coefficient. W is the sum of the weights w for the given distance class (the number of pairs used to calculate the coefficient).

Moran's I varies between −1 and 1, with 1.0 indicating perfect positive autocorrelation and −1.0 indicating perfect negative autocorrelation. Moran's I will occasionally take on a value outside (-1.0 and 1.0), but these are a consequence of an unusual weight matrix or of averaging within distance classes.

Before computing spatial autocorrelation, a matrix of geographic distances among observation sites was calculated and grouped into distance classes. The number of distance classes is determined by Sturge's rule (Legendre and Legendre, 1998):

$$\text{Number of classes} = 1 + 3.3\text{Log}_{10}(m)$$

where m is the number of distances in the upper (or lower) triangular matrix.

Autocorrelation tests performed over a large number of distance classes are actually a set of simultaneous tests; therefore, the global significance of the autocorrelation function was adjusted by a progressive Bonferroni correction. The autocorrelation is globally significant if any distance class is significant, thus only those distance classes meeting this adjusted significance were interpreted. In general, the number of points (pairs) per distance class decreases as distance increases, and consequently the power of the test decreases as well. The distance classes were truncated to a threshold that retained a sufficient number of observations of pairs (30 pairs of points). Autocorrelations are graphically represented by autocorrelograms with the Moran's I statistic on the y-axis and the distance classes on the x-axis. Patch size was inferred from the autocorrelograms, according to Sokal (1979). Since the samples in pond 8 were taken at different depths the data analysis was separated by depth: shore samples with shallow midpond samples and shore samples with deep midpond samples. In pond 11 only shallow samples were taken thus the data was analysed in whole. Additionally, in pond 8 a paired t test was performed between the shallow and deep midpond samples taken at the same coordinates, for each time of day. Computation of Moran's I and tests of significance were done with the statistical package "R" (Legendre and Vaudor, 1991). All other tests were done using SPSS 10.0.

Partial regression analysis

Partial regression analysis was used to evaluate the relative importance of spatial and environmental factors on the distribution of *H. shoshone*. The total variation of *H. shoshone* distribution was partitioned into four components following Bocard *et al.* (1992) and Bocard and Legendre (1994):

1. Fraction A: Nonspatially structured environmental component, where variation in the species abundances can be explained by the environmental data independent of spatial structure.

2. Fraction B: The spatially structured component of copepod variation that is explained by spatially structured environmental data, which for instance can be represented by environmental gradients.
3. Fraction C: Pure spatial component of copepod variation that is not shared by the environmental data which may be explained by behavioural factors or other spatially structured physical or biological processes not included in the analysis.
4. Fraction D: Unexplained component, the variation in copepod abundances that cannot be explained by the spatial coordinates or the environmental data.

The following independent environmental variables were used in the partial regression analysis in both ponds: light intensity, pond depth, temperature, and distance to logs. In pond 8 only shallow samples were used in the analysis. Additionally, in pond 8 distance to closest edge and presence of rocks was added. A forward selection procedure was applied to the environmental variables in each analysis in order to select the terms that contributed significantly to the total explained variation of the response variable. The terms used for the pure spatial component were obtained from the surface trend analyses. The data analysis was performed on SPSS 10.0.

Role of background markers

Data was analyzed by repeated measures ANOVA (Zar, 1999), where the densities of copepods before, during and after the treatments were compared with each other. The three treatments are the following: no marker (control), white marker and black marker. A *post hoc* repeated polynomial contrast was performed in order to determine which treatments differed. Correlations and single classification ANOVA's were performed on the data in order to examine if the number of individuals was correlated with temperature. Repeated measure ANOVA's were additionally performed on light measurements.

RESULTS

Morisita's index of dispersion

The density of copepods per sample varied from 0 to 80 copepods/L in pond 11 and from 0 to 15 copepods/L in pond 8. The Morisita's index of dispersion equals one for random distributions, less than 1 for uniform distributions and greater than 1 for clumped distributions. Significant aggregations were found in both pond 8 and 11 on all dates, and sampling times of the day (Fig 4 and Fig 5). All the values were statistically different from 1 as given by the χ^2 test with $p< 0.001$ for all sampling times. A significant difference in the Morisita's index was found when time of day was considered both in pond 8 ($\chi^2= 6.267$, $p = 0.044$) and pond 11 ($\chi^2=8.143$, $p = 0.017$).

Trend surface analyses

Tables 1-3 present the results for trend surface analyses for pond 11 and pond 8. Figs. 6 and 7 show the resulting contour plots obtained from the coefficients from Tables 1 - 3. All variables (dependent and independent) were standardized, thus the isobars on the contour plots represent differences in standard deviations from the *H. shoshone* mean density. Both in pond 11 and pond 8 the x-axis runs from north to south and the y-axis from west to east (refer to Fig 2 and Fig 3 for sampling locations).

Pond 11

In pond 11, significant *H. shoshone* spatial trends were found on three sampling dates for each sampling time (Table 1). Two significant linear spatial trends were found on the afternoon sample of July 5th and in the midday sample July 30th. Significant second order trends were found throughout the midday and night samples of July 5th, and all of the three samples from July 19th, as well as the afternoon and night samples of July 30th (Figure 6). In general, copepod density is high in the north-western shore of pond 11 with a negative gradient that extends to the mid and southern portions of the pond, except on the Afternoon and night of July 30th.

Pond 8

Since the samples in pond 8 were taken at different depths, the data analysis was separated according to depth: shore samples with shallow midpond samples and shore samples with deep midpond samples.

Significant *H. shoshone* spatial trends were found on six sampling dates but not for all sampling times (Table 2 and 3) No consistent trends were found throughout the dates, sampling times and depths (Fig 7). A western and eastern offshore gradient , where the offshore region was characterized by relatively low densities and shore region with higher densities, was found on the following sampling times: deep and shallow samples on midday of July 2nd, deep samples on midday of July 9th , shallow samples on the night of July 10th, shallow and deep samples on the night of July 23rd and in the shallow midday sample of August 2nd. The patterns of the remaining trends were inconsistent (Fig 7)

Spatial autocorrelation

Pond 11

The results of spatial autocorrelation analyses (Moran's I autocorrelograms) for pond 11, are shown in Fig 8. Two out of nine sampling times had significant spatial autocorrelations (Fig 8) after removing their larger-scale trends (Table 1): the midday sample of July 5th, and night samples of July 19th. The distance at which the value of spatial autocorrelation crosses the expected value $E(I)=-(n-1)^{-1}$, (where n is the number of observations of pairs in a distance class) is considered the patch size (Legendre and Fortin, 1989: Fortin, 1999). From the significant autocorrelograms the average patch size varies from <1.9 to 4.5m.

Pond 8

The results of spatial autocorrelation analyses (Moran's I autocorrelograms) by depth for pond 8, are shown in Fig 9. The residuals of four "sampling times" had significant spatial autocorrelations (Fig 9) after removing their larger-scale trends (Table 2 and 3), night of July 2nd (deep), afternoon of July 23rd(deep), night of July 23rd (shallow and deep). Autocorrelations were found in the following seven samples where the trends were not significant: afternoon of July 2nd (deep), midday of July 9th (deep), night of July 10th (shallow and deep), morning of July 11th (shallow and deep), and midday of July 16th (deep). From the significant autocorrelograms, the patch size for shallow samples is anywhere from 1.6 or less to 7m in size, and in the deep samples 2.0 or less to 7m in size.

The results from the spatial analysis performed in both ponds are summarized in Table 4 and 5. Fields indicated by a "yes" imply that trend analyses or autocorrelation analysis was found to be significant at that sampling time. Values of the Morisita's index of dispersion > 1 indicate presence of significant aggregations at the given sampling time.

Density differences between shallow and deep midpond samples from pond 8

Differences in *H. shoshone* abundances were found in pond 8 between shallow and deep midpond samples when time of day was taken into consideration. In pond 8, *H. shoshone* were significantly more abundant in the deep than shallow midday samples, while there were no significant differences between the densities of deep and shallow samples collected in the afternoons (Fig 10) or mornings . During the night, significantly more *H. shoshone* were found in shallow than deep samples.

Partial regression analyses

Results of partial regression analysis for pond 8 and 11 are shown in Tables 6 and 7 respectively. Not all environmental factors were measured on each sampling occasion and the environmental factors measured are indicated at each sampling time. Light measurements were not performed during the night due to the insensitivity of the light meter to such low lighting conditions. Additionally, light measurements and temperature measurements were not performed during rain due to the fragile nature of the instruments. Refer to data analysis section for the meaning of each fraction.

Pond 11

The relative importance of the nonspatially structured environmental components (Fraction a) and spatially structured environmental components (Fraction b) varied among sampling times and dates (Table 6). Results from the partial regression analysis showed that variations in the environment (Fraction a) with the environmental gradients (Fraction b) explained between 29 and 79% of the total variation in the distribution of *H. shoshone,* when environmental variables were significant (Table 6). Fraction a alone explained between 0 and 65% of the variability of *H. shoshone* distribution while fraction b from 0-32%. Together, light intensity and distance to logs in pond 11 were the best explanatory variables of the distribution of *H. shoshone*. Water depth at sampling coordinates was included in the models on two occasions, midday of July 5th and July 19th. Unexplained spatial effects (Fraction c: space) explained between 0 and 34% of *H.*

shoshone distribution. Between 18 and 100% of the total variation in the distribution of *H. shoshone* remained unexplained. Between 18 and 64% of the total variation remained unexplained when environmental variables were significant (Table 6).

Pond 8

In pond 8 the relative importance of the nonspatially structured environmental components (Fraction a) varied among sampling dates, but in general explained a small amount of the variation of *H. shoshone* distribution (from 0-25%) (Table 7). Variations in the environment (Fraction a) with the environmental gradients (Fraction b) explained between 15 and 36% of the total variation in the distribution of *H. shoshone*, when environmental variables were significant (Table 7). The following variables were retained in the analysis inconsistently on different occasions, distance to edge (12%), distance to logs (0-7%), temperature (3-18.5%), depth (25.2%) and light (10%). The spatially structured effects (Fraction b) accounted from 0 – 32.9 % of the variability. Between 51 and 100% of the total variation in the distribution of *H. shoshone* remained unexplained (Fraction d) and up to 82% when environmental variables were significant.

Role of background markers

Significant differences in densities of *H. shoshone* were found among the background marker treatments (none, white and black). The repeated measures ANOVA's were significant for both pond U2 (F= 8.04, p = 0.001) and U6 (F = 24.319, p<0.0001). On average, 4x more copepods were found above the white than black markers in pond U2 and 3x more often in pond U6.

In *post hoc* tests, significantly more copepods were found above the white than black markers (Fig 11 and Fig 12) (pond U2: $p = 0.003$, pond U6: $p= 0.0001$). In pond U2, significantly fewer individuals were found above the black markers when compared to the controls ($p = 0.001$) and no significant differences were found between the controls and white markers ($p = 0.968$). In pond U6, there were no significant differences between the controls and black markers ($F =3.126$, $p = 0.082$) but there were significantly more individuals found above the white markers when compared to the controls ($p<0.001$).

There was no significant difference in temperature among the three types of background markers in pond U2 ($F=1.132$, $p=0.340$) and U6 ($F=2.243$, $p= 0.132$). No significant correlation was found between the temperature and number of individuals caught above each marker (pond U2: $r = 0.105$, $p = 0.633$; pond U6: $r<0.0001$, $p= 0.999$). Significant differences in light intensity were found above the background marker treatments (none, white and black) ($F=89$ $p=0.0001$). Since there was no significant interaction in light measurements between the ponds ($F= 0.206$ $p=0.667$), the analysis was performed with a single repeated measures ANOVA with the ponds as between subject factors. Within subject contrasts showed that light intensity measured above the markers was highest for white markers, followed by pond substrate then black markers.

DISCUSSION

Spatial patterns have two aspects: intensity and form (Andrew and Mapstone, 1987; Thrush, 1991). Intensity can be measured by methods such as the Morisita's index that categorize density distributions into aggregated, regular or not significantly different from random. However, two distributions may have a similar intensity pattern yet represent considerably different spatial arrangements (Thrush, 1991). Therefore, there is a need to describe the form of the spatial pattern (i.e. size of gradients and aggregations), using techniques such as trend surface analysis and spatial autocorrelations that utilize the information found in the spatial arrangement of individuals. These techniques allow the significance of patterns to be assessed. The first part of this study was exploratory and sought to determine the intensity and form of *H. shoshone* distributions throughout different sampling times in a season, and identify parameters that might explain the observed distributions. Since very few studies have addressed the issue of copepod aggregations in small ponds, this exploratory step was necessary in order to identify possible predictors that might be used in future experimental studies. The second part of the study was experimental and aimed to determine if background coloration of the pond substrate influenced the number of copepods found above introduced black and white background markers.

Morisita's index of dispersion

The first objective of this study was to confirm the presence of aggregations of *H. shoshone* found by Aguilera (2002). The Morisita's index of dispersion was a useful tool for identifying spatial patterns of *H. shoshone* distributions. Studies using the Morisita's index have been performed on organisms such as earthworms (Jimenez *et al.*. 2001). crinoids (MacCord and Duarte, 2002) and carabid beetles (Niemiela *et al.*. 1992), where aggregations were present for some of the species examined. The evaluation of aggregation indices depends on the measurement scale (Horne and Schneider, 1995) and comparison of aggregation indices among populations are only valid when evaluated at the same spatial scale (Hurlbert, 1990). Thus, the magnitude of the values obtained in this study were not compared to those found in other studies.

Regardless of sampling time, *H. shoshone* individuals were found to be significantly aggregated in all samples (Table 4 and Table 5). Generally, the Morisita's index was higher during the midday samples when light intensity is at its peak (Fig 4 and Fig 5). Ueda *et al.* (1983) also reported that the number of aggregations and copepod density within them were lower during dusk periods than during mid-day. These results indicate that aggregations form throughout the day and do not exhibit similar endogenous rhythms observed in *Dioithona oculata*, where copepods are found to disperse at night (Buskey, 1998). Thus, in these ponds, light cannot be the only driver of *H. shoshone* aggregations.

Trend analyses and autocorrelations

The second objective of this study was to identify patterns in the aggregations in order to determine differences in distribution during night and day sampling efforts throughout a sampling season. The spatial analysis techniques used (trend analyses and autocorrelograms) were useful tools for detecting coarse and fine spatial structures of *H. shoshone* densities in the two study ponds. Studies using similar techniques have been performed on copepods in large lakes (Stockwell, 1996) and other organisms e.g. terrestrial vegetation (Thompson *et. al.*, 1996), benthic macrofauna (Thrush, 1991; Underwood and Chapman, 1996), diatoms (Passy, 2001), mammals (Badgley and Fox, 2000) and leaf-miners (Brewer and Gaston, 2002). Significant trend surfaces found, indicated that the spatial distributions of the copepods were not random.

The use of Moran's (I) requires the data to conform to second-order stationarity. That is, the statistical properties (mean and variance) of the observations must be relatively constant over the study area (i.e., no trend can be present; Legendre and Fortin, 1989). In many cases, this is not true because of larger trends in the data; this is the reason why the data was detrended before autocorrelation analysis was performed.

In pond 11, large surface trends were not found on cloudy and rainy days but almost exclusively on sunny ones, except on the afternoon and night of July 30th, where disturbance by heavy rains could have created currents in the pond (Table 4). Most of the large spatial patterns showed gradients with high densities of *H. shohone* concentrated in the north and north-western shores of the pond except on the afternoon and night of July 30th where heavy thunderstorms disturbed the pond (Fig 6). These high density areas coincide with large logs that in some cases have been present in the pond for 30 years (pers. comm. Dr. E. J. Maly). Thus, these areas may provide hiding places for *H. shoshone* from visual predators such as the tiger salamander, *Ambystoma tigrinum*.

Fine spatial patchiness was only found on two sampling occasions at the shortest distance classes and implies that the average patch size was < 2 - 4m on those times. The lack of significant autocorrelations in more sampling times may be due to the removal of variability by trend surface analysis or by the fact that patches that are present are of varying size and uneven spacing. In such cases. the autocorrelation coefficients may cancel each other or reduce the respective significances. If the patches are unevenly spaced, they could produce autocorrelograms with the same significant structure in the small distance classes but with no other significant values afterwards. Autocorrelation requires the assumption of isotropy in the data (i.e. the autocorrelation function is the same in all directions or there is one generating process responsible for the autocorrelation function (Legendre and Legendre. 1998)). Therefore. autocorrelograms can also be found insignificant if the generating process of the aggregations is not the same for the full pond scale. No differences in patterns were observed between the midday. afternoon and night sampling efforts. This might be due to the small size of the pond and few variable microhabitats available.

In pond 8. large surface trends were found on both cloudy. sunny and rainy days with no consistent patterns throughout the time of day in the sampling season (Table 5). The most widespread trend encountered was an offshore gradient with higher copepod densities along the western and eastern shores with decreasing copepod numbers towards the midpond areas (Fig 7). This result contradicts the general shore avoidance hypothesis found (Johannsson *et. al.*. 1991) but would indicate the presence of a shoreline effect in the distribution of *H. shoshone*. Wicklum (1999) found that *H. shoshone* in high altitude fishless lakes of Montana exhibited similar trends during the day but not during the night

Although identified only on one occasion. strong winds originating from the north-west were most likely responsible for downwind accumulation of *H. shoshone* on the midday sample of July 16th (Fig 7). Pond 8 is positioned in a sheltered area and generally does not experience high wind velocities. thus wind can be considered an occasional factor structuring the distribution of *H. shoshone* in this pond. Thus, these whole pond patterns are probably generated by a variety of interacting processes. From the significant autocorrelograms in pond 8 the patch size for shallow samples was found to be from 1.6 or less to 7m in size, and in the deep samples 2.0 or less to 7m in size (Fig 9). Dividing the trend and autocorrelation analyses by depth has been generally unsuccessful at identifying differences between the shallow horizontal samples and the shallow shore samples combined with deep midpond samples. Although no emergent patterns were found in comparing trends from shallow and deep samples, autocorrelograms were significant more often in the deep than shallow samples. This finding indicates that the littoral/midpond deep samples are more spatially structured at smaller scales. These results are also consistent with the paired t-tests performed by depth in pond 8 (Table 6) which demonstrated the presence of differences in densities of copepods at different depths when time of day was considered (Fig 10). Typically, large crustacean zooplankton avoid the photic zone by remaining in deep waters and migrate towards the surface at night when visual predators are inactive (White, 1998). These findings suggest the presence of vertical migration of *H. shoshone* in pond 8, but further investigation should be performed before such a conclusion is made. Vertical migration is extremely widespread among freshwater zooplankton (Hutchinson, 1967) and a general tendency toward upward movement such as that indicated in Fig 10 is by far the most common pattern.

Partial regression analyses

The third objective of this study was to identify predictors that might explain the observed *H. shoshone* distribution patterns. Partial regression analysis is a way of estimating how much of the variation of the response variable can be attributed exclusively to one set of factors. once the effect of the other set has been taken into account (Legendre and Legendre. 1998). Furthermore. this technique can be used in circumstances where the data shows evidence of spatial dependence (Legendre and Legendre, 1998). Studies using this technique have been performed on a community of fish inhabiting a littoral rocky reef (Garcia-Charton and Perez-Ruzafa. 2001). density of holy leaf miners (Brewer and Gaston. 2002) and a macrozooplankton assemblage found in Lake of Geneva (Pinel-Alloul *et al.*. 1999). Legendre and Legendre (1998) have pointed out two major incentives for analysing data in this manner. First. spatial structuring can be a major source of false correlations. In fact. interactions between ecological variables can appear strong and causal. but may be overestimated if both variables follow a common spatial gradient (Bocard *et. al.*, 1992). For example. the relationship between distance to logs and light intensity with zooplankton density from the July 30th midday sample taken in pond 11 might lead one to conclude that copepod density is largely dependent on these variables with $R^2 = 79\%$. However. the amount of variation in copepod density. after controlling for the effects of space was only 47%. Secondly. both the spatial and the non-spatial components of the environmental variation (Fraction a and b) may be causal and the magnitude of the spatially structured environmental effect or some other component of the variation in the response variable may be of interest in itself.

Partial regression analysis yielded different results in the two ponds studied and it is interesting to note that two ponds that are so close together could have such different physical factors influencing the distribution of a single species. During the summer of 2001, the horizontal spatial distribution of *H. shoshone* in pond 11 was driven by light intensity and distance to logs. This is the first freshwater study that has established a relationship between light intensity and copepod density in the field. Most of the significant partial regressions were found on sunny midday samples. Pond 11 is surrounded by trees and the shadows cast on the water create a mosaic of light and shadowed areas. Phototaxis is a directional response to a light stimulus (Rudin, 1997) and given a defined light source, positively phototactic animals will be attracted and aggregations will form (Yen and Bundock, 1997) in the most suitable areas. Phototaxis has been established in the marine copepods *Dioithona oculata* (Ambler et al., 1991) and in *Coullana canadensis* (Yen and Bundock, 1997) but not in the species studied but could be a mode of aggregation. Although significant predictors were found on the midday July 27th sample one should be cautious in interpreting this date due to the passing clouds that could possibly be a source of false correlations. Additionally, the midday July 5th and night July 19th samples should be also interpreted with caution due to the presence of autocorrelations on those two sampling times.

Previous studies indicated that water temperature may be a proximate control variable for zooplankton abundance in alpine lakes (Sommer, 1989; Pinel-Alloul *et al.*, 1999). It has been proposed that the direct influence of temperature could affect temperature-dependent metabolism and development in some species of copepods (McLaren and Crokett, 1981). Temperature was not a factor retained in the partial regression analysis in pond 11 and this might be due to the low variability of temperature on a horizontal scale in such a small pond. Similarly, Byron *et al.* (1983) found that aggregations of *Diaptomus tyrrelli* from Lake Tahoe were not influenced by microscale temperature differences. Alternatively, but less likely, *H. shoshone* metabolism could be more temperature independent. Pinel-Alloul *et al.* (1999) found that different crustacean species responded to temperature in different ways and this might be due to different thermal requirements of the different species. Could light intensity serve a similar role to that of temperature? Pigmentation could be adaptive to cold water copepods by providing warmth through absorption of solar radiation (Byron, 1982). A study by Byron (1981) has shown that pigmented copepods undergo metabolic facilitation when exposed to light and would experience faster average growth rates than unpigmented copepods under identical water temperature regimes. Actually, some copepods appear to seek light, particularly at low water temperatures (Byron, 1982). For example, *Calanus finmarchicus* is photonegative at temperatures above 13°C and becomes photopositive at temperatures above 13°C (Byron, 1982). Thus, metabolic facilitation of the pigmented *H. shoshone* could act to enhance competitive ability and could be adaptive for copepods inhabiting cold water and temporary-ponds since they must fit development times in the short growing season found in the Colorado Rocky Mountains (Byron, 1982).

Partial regression analysis pointed to the presence of logs as a proximate factor influencing the distribution of *H. shoshone* in pond 11. These results support the findings from the trend analyses, where higher densities of copepods were found in close proximity of the logs. As previously discussed, such structures can provide hiding places from visual predators. Alternatively, logs protruding out of the water could create an edge effect to which copepods could be attracted. Anecdotal evidence provided by Byron *et al.* (1983) concurs with these findings; *Diaptomus tyrrelli* occurred in higher numbers immediately adjacent to rocks protruding above the water surface in Lake Tahoe. The unexplained spatial variation (Fraction c) was relatively small in the significant midday and afternoon samples of pond 11. Thus, spatially structured environmental variables or biotic factors that were not measured in this study had little influence in explaining the distribution of *H. shoshone* in pond 11 during midday and afternoon samples. This fraction was relatively large in the night samples and indicates that other spatially structured variables not included in the analysis could explain the distribution of *H. shoshone* at night. This result is not surprising due to the fact that light measurements were not taken during the night due to the low sensitivity of the light meter used. Additionally, different factors might influence the distribution patterns at night. In the significant partial regressions analyses, the amount of unexplained variation (Fraction d) is fairly high, and reflects the influence of nonspatially structured (at this sampling scale) environmental factors that were not assessed during the study.

In pond 8, the environmental predictors were found to vary with sampling time and day and probably reflect the increased complexity of this pond compared to pond 11. The environmental predictors retained by the regressions explained a small amount of the variability in copepod density numbers suggesting that the main environmental or biotic factors were not included in the analysis. The amount of unexplained variation was extremely high (51-80%) and could not be explained solely by nondeterministic fluctuations and could reflect the action of some other variables at different scales. Partial regression analysis was only performed on a horizontal scale. The vertical aspect of *H.*

shsohone distribution was not included in the analyses, thus, the environmental variables measured and retained by partial regressions could have been inadequate in explaining the spatial distribution of *H. shoshone* due to greater depth of this pond. Additionally, the presence of autocorrelations on many sampling efforts could have also influenced the obtained results.

Pond 11 and pond 8 experience different densities of the tiger salamander *Ambystoma tigrinum nebulosum*, a keystone predator occurring at the Mexican Cut watershed. Wissinger *et al.* (1999) found that salamander larvae hatchlings that feed primarily on copepods and cladocerans were found at higher densities in pond 8 than 11. In 1990, the highest number of hatchling larvae found at the Mexican cut were found in pond 8, where 450 individuals were tagged compared to 40 larvae in pond 11. Although pond 8 is twice as large as pond 11, the predation pressure in pond 8 was still more intense than in pond 11. The high number of salamander larvae potentially exhibiting high predation pressure and the small number of hiding places in pond 8 could account for the inconsistent spatial patterns found in the distribution of *H. shoshone*. The importance of salamanders as predators has been found to shape the patterns of zooplankton distribution and abundance among ponds encountered in these wetlands (Dodson, 1970; Sprules, 1972). Future studies on the spatial distribution of *H. shoshone* should take into account a combination of both abiotic and biotic explanatory variables and establish the dynamics of spatial distribution of salamanders and other predators within both ponds. Predation can be viewed as a proximate factor of patchiness in two ways. Aggregations can be induced by chemical cues that are released by predators (Dawidowicz, 1999). For example, Pijanowska and Kowalczewski (1997) found that the exposure of *Daphnia magna* to chemical cues released by fish induced a tendency to form and maintain aggregations in *Daphnia* clones originating from habitats inhabited by fish. Bollens and Frost (1989) found that the marine copepod *Acartia hudsonica* changed its vertical distribution and migration behaviour depending on the presence or absence of its natural predator, the three spined stickleback (*Gasterosteus aculeatus*), through the exposure of these copepods to the chemicals released by the fish had no effect on their distribution. A second mechanism in which predators can create patchiness is by physically removing prey and thus creating heterogeneity (Sarnelle *et al.*, 1993).

Role of background markers

The fourth objective of this study was to examine the role that white and black background markers play on the formation of copepod aggregations in *Hesperodiaptomus shoshone*. In both ponds, (U2 and U6) significant differences in the number of copepods sampled above the control, and black and white markers were found. Consistently, in the two ponds, significantly more copepods were found above white than black markers. On average, 4x more copepods were found above the white than black markers in pond U2 and 3x more often in pond U6. These findings are consistent with Herbert *et al.*'s (1980) study, which found the predatory copepod *Heterocope septentrionalis* to aggregate above areas of pale substrate. Unlike this study, Herbert *et al.* (1980) found swarms greater than 300x the ambient density.

Although in both ponds significantly more copepods were found above the white than black markers, comparisons of both markers with the controls did not yield consistent results. In pond U6, copepods preferred white markers to controls but no such differences were established in pond U2 (Fig 11 and Fig 12). This difference in results between ponds might be due to much higher copepod densities encountered in pond U2 than U6 or to slightly different colourations of the pond substrate. According to Herbert et al. (1980), aggregations can enhance mating success by increasing the number of female-male encounters, especially when mating success is limited by population density. Thus, in pond U2 there might be no advantage of preferentially choosing white background markers because an optimal patch size or density was already attained. Similar observations were made by De Meester et al. (1993) where the degree of patchiness in the cladoceran *Scapholeberis mucorata* was found to decrease in ponds with increased zooplankton density. If photic stimuli draw copepods together locally as an aggregate there must be some mechanism that also keeps them apart. Understanding the mechanisms which maintain spacing between individuals in an aggregation should also allow the calculation of maximum aggregation densities.

In pond U2, significantly fewer copepods were found above the black markers than the controls, similar but not significant trends were observed in pond U6 (Fig 11 and Fig 12). If copepods do orient themselves by reflected light then they should avoid non-reflective surfaces and choose higher contrast ones. Copepods are probably incapable of vision in terms of image formation (Buskey and Peterson, 1996), but use their abilities for phototaxis behaviour to hold their position within a range of light intensity. The repeated measures ANOVA on light intensity showed that light intensity was always highest above the white than black and control treatments in both ponds and suggests a similar trend as copepod abundance. Temperature above the markers and controls had no effect on the number of copepods found and was not correlated with copepod numbers. This result is consistent with the findings from the partial regression analyses in pond 11 where temperature was not selected as a predictor in explaining *H. shoshone* distribution.

FUTURE STUDIES

Due to budget limitations, light measurements throughout this study were taken in the photometric system of units, which only takes into consideration the visible wavelengths of the light spectrum. Thus wavelengths below 400nm (UV) or above 700nm (IR) were not considered. This might be a drawback especially due to the established importance of UV radiation in high altitude lakes and ponds (Vinebrooke and Leavitt, 1999; Sommargua, 2001) and to the fact that UV vision has been previously established in some copepods (Johnsen, 2001). Although, UV light has not been found damaging to *H. shoshone* (Byron, 1982), behavioural regulation of UV exposure might contribute to the observed spatial distribution patterns. Additionally, light has a range of attributes, varying in time and space, such as spectral quality or directionality of polarized light. These signals must be discerned above the ambient noise of the aquatic environment. (Yen and Bundock, 1997). Future studies should integrate all these aspects of light and an underwater spectrophotometer should be employed in order to include a wider range of wavelengths. Perhaps if such attributes of light could be included in the analysis, more accurate models could be developed to predict spatial heterogeneity. Although the results are convincing that light plays an important role in *H. shoshone* heterogeneity, future studies should establish the formation of aggregations in *H. shoshone* under laboratory conditions. Additionally, upcoming studies should employ light meters that are more sensitive in order to evaluate the possible impact of moonlight on the distribution of *H. shoshone*. Buskey and Peterson (1996) showed that the aggregations of *Dioithona oculata* a marine copepod could actually be induced to form aggregations under low light intensity comparable to that of moonlight. In addition, Gliwicz (1986) observed cycles in zooplankton densities that fluctuated in phase with the moon

Further studies should additionally examine differences in individual behaviour within aggregations. Gulbrandsen (2001) found that in *Artemia* no exchange occurred between individuals found in light induced aggregations and individuals outside aggregations. Individuals would either be engaged in aggregations or they would apparently lead a solitary life. De Meester and Dumont (1998) found similar behaviours in *Daphnia* and explained them in terms of varying genotypes. They propose the existence of three distinct genotypes that are either positively phototactic, negatively phototactic or so called "gypsies". The gypsies are able to migrate between light and dark conditions. It would be interesting to find out if such differences exist in the aggregative behaviours of copepods.

A recently growing problem in the western Rockies is the introduction (via helicopters and fixed-wing aircraft) of trout into high alpine lakes for recreational fishing (Wissinger *et al.*, 1999). Many of these lakes and ponds were historically fishless and such introductions could lead to changes in invertebrate community composition. Liss *et al.* (1998) showed that introduced trout can reduce or eliminate larger, more visible diaptomids from lakes. In order to establish the importance of such impacts on *H. shoshone*, sampling programs and possible outcomes of such introductions can only be established in light of spatial structures of both predator and prey.

CONCLUSIONS

Our environment is spatially and temporally structured. The many ecological studies involving spatial structure have played a significant role in attempts to better understand ecological processes. In fact, spatial analysis has recently become one of the most rapidly growing fields in ecology (Fortin, 2002). This popularity is directly related to a growing awareness among ecologists of the importance of spatial structure to understand ecological processes.

This is the first study that has examined the relationships between the horizontal distribution of copepods and environmental factors in small alpine ponds related to sampling time of day. Intensity of aggregation was found to be largest during the midday samples and decreased in the afternoon and night samples. This study has provided evidence that the diaptomid copepod *H. shoshone* exhibits small and large-scale pond patterns. In pond 11, the large-scale spatial patterns remained relatively constant irrespective of the sampling time of day, while in pond 8 no constant patterns were identified. Size and distance between aggregations varied in both ponds studied and the observed patch size was anywhere from <2m to 7m in length. Additionally, the presence of non-significant autocorrelograms suggests that aggregations occur at different sizes and distances from each other. Although the results were mixed between ponds, light and physical structures such as logs play an important role in determining spatial distribution of *H. shoshone* pond 11. In pond 8, the environmental factors chosen in the partial regression analysis poorly explained the spatial heterogeneity of *H. shoshone*. Results also indicate the possibility of vertical migrations in pond 8. Substrate colouration was also found to play an important role in the spatial distribution of *H. shoshone*. Higher densities of copepods were found above lighter than darker introduced panels in both study ponds. Neither physical nor biological drivers alone can explain the complexity of zooplankton spatial heterogeneity, and future studies should include more comprehensive sampling programs that take into consideration both physical and biological factors.

Figure 1: Mexican Cut Nature Preserve Watershed (Figure modified from Wissinger *et al.*, 1999).

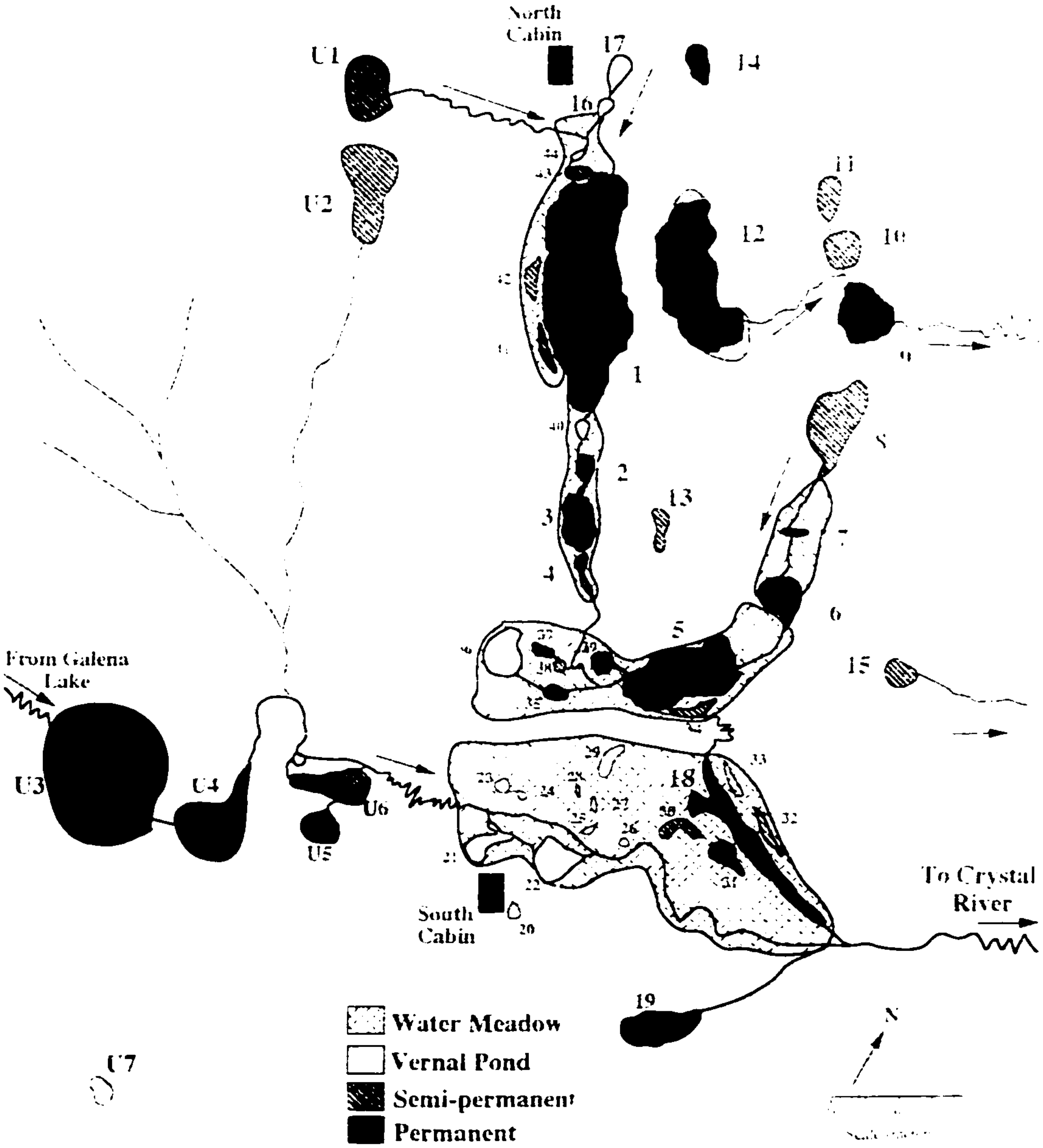

North Cabin
17
14
U1
16
44
43
U2
11
12
10
42
41
1
9
40
8
2
13
3
7
4
6
5
37
39
36
35
From Galena Lake
15
U3
U4
U6
U5
29
33
23
24
28
27
18
32
25
26
30
31
21
22
South Cabin
20
To Crystal River
19
N
U7
Water Meadow
Vernal Pond
Semi-permanent
Permanent

Figure 2: Pond 8 modified from S. Horn (unpublished). The sampling locations are indicated by dots on the pond. The open rectangles show the position of the logs within the pond.

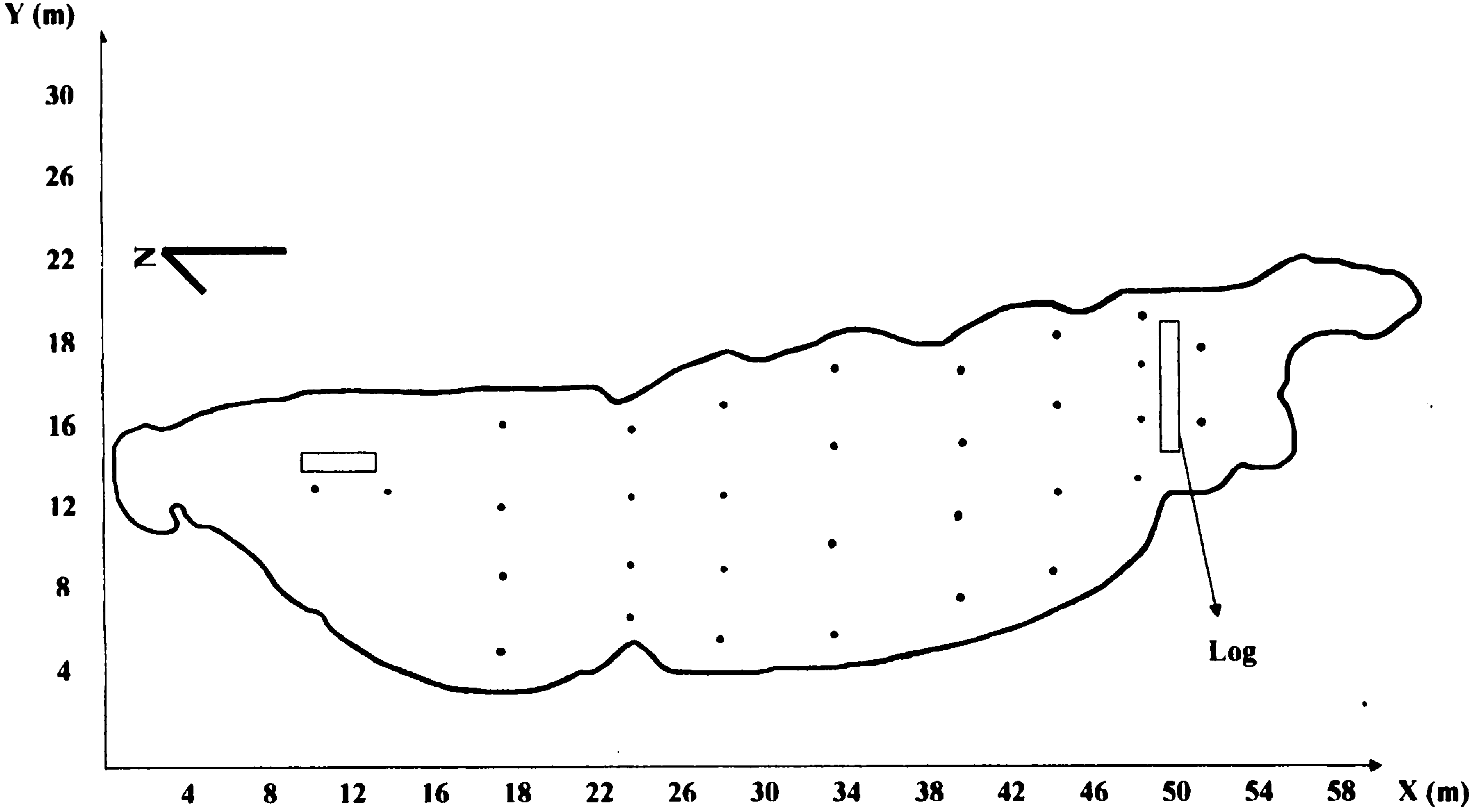

Y (m)
30
26
22
18
16
12
8
4
N
Log
4
8
12
16
18
22
26
30
34
38
42
46
50
54
58
X (m)

Figure 3: Pond 11 modified from S. Horn (unpublished). The sampling locations are indicated by dots on the pond. The open rectangles show the position of the logs within the pond.

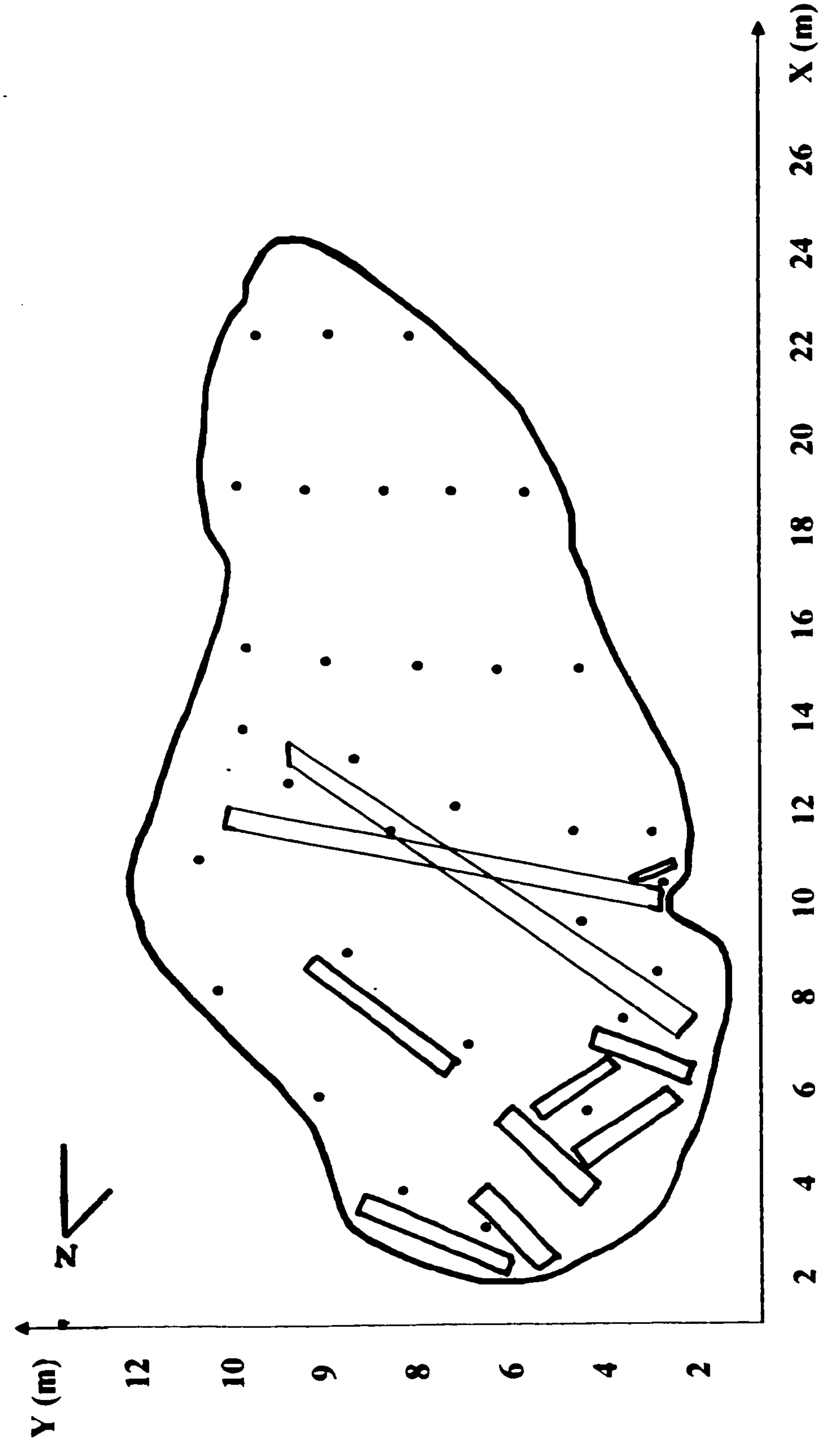

Y (m)
12
10
9
8
6
4
2
N
2
4
6
8
10
12
14
16
18
20
22
24
26
X (m)

Figure 4: Morisita's I_d values for pond 11 by sampling date and time. The filled in circles represent midday samples, the open circles; afternoon samples and the filled in triangles night samples.

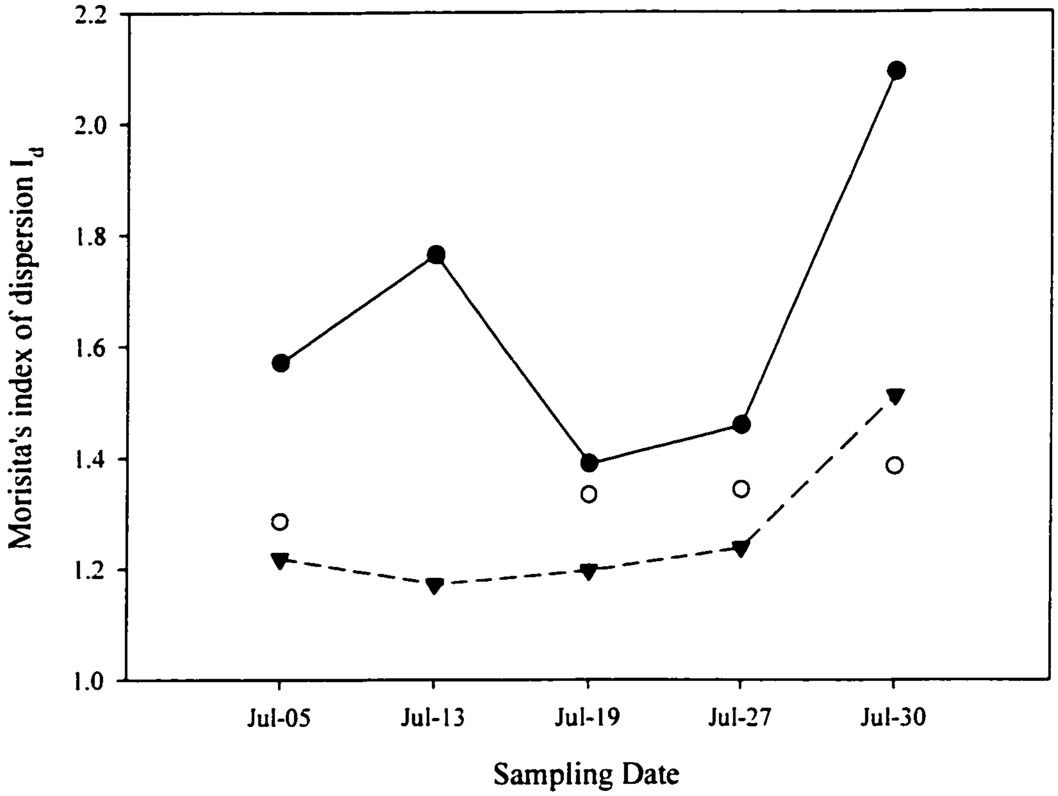

Morisita's index of dispersion I_d
2.2
2.0
1.8
1.6
1.4
1.2
1.0
Jul-05
Jul-13
Jul-19
Jul-27
Jul-30
Sampling Date

Figure 5: Morisita's I_d values for pond 8 by sampling date and time. The filled in circles represent midday samples; the open circles, afternoon samples; the filled in triangles night samples and the open triangles morning samples.

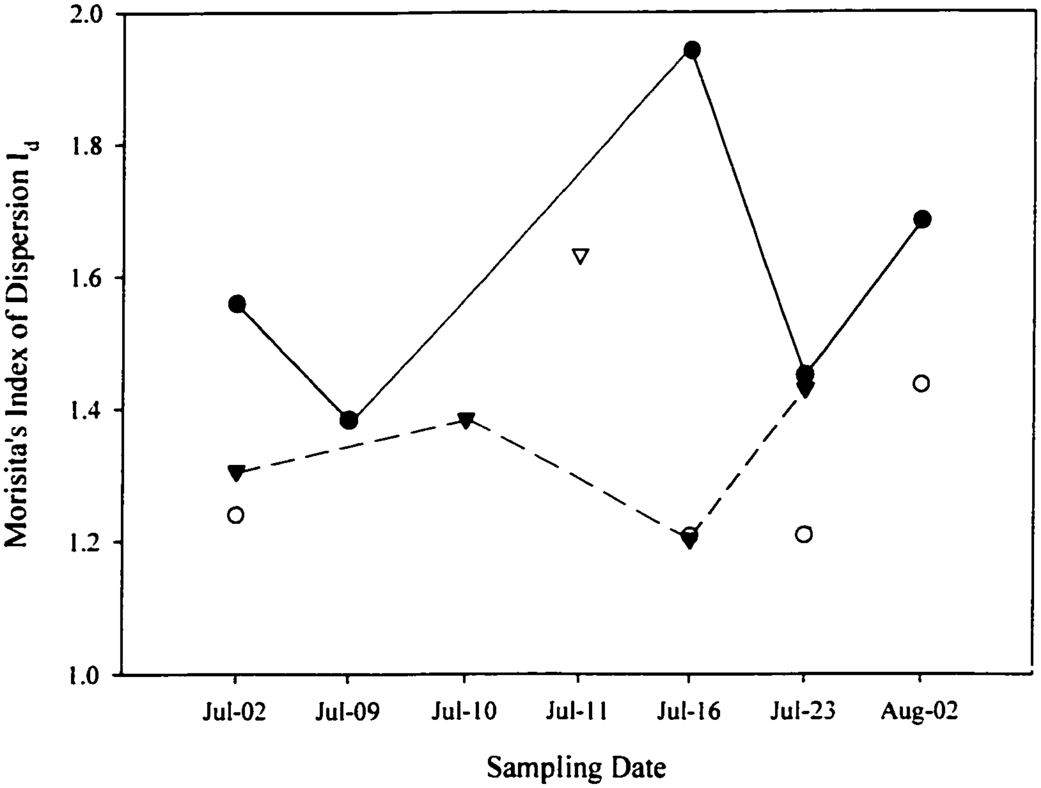

2.0
1.8
1.6
1.4
1.2
1.0
Morisita's Index of Dispersion I_d
Jul-02
Jul-09
Jul-10
Jul-11
Jul-16
Jul-23
Aug-02
Sampling Date

Figure 6: The contoured linear and quadratic trend-surfaces fitted to *H.shoshone* density data, for pond 11 for each significant sampling time (refer to Fig 2). Trends near the corners should not be interpreted, since they are outside the pond sampling range.

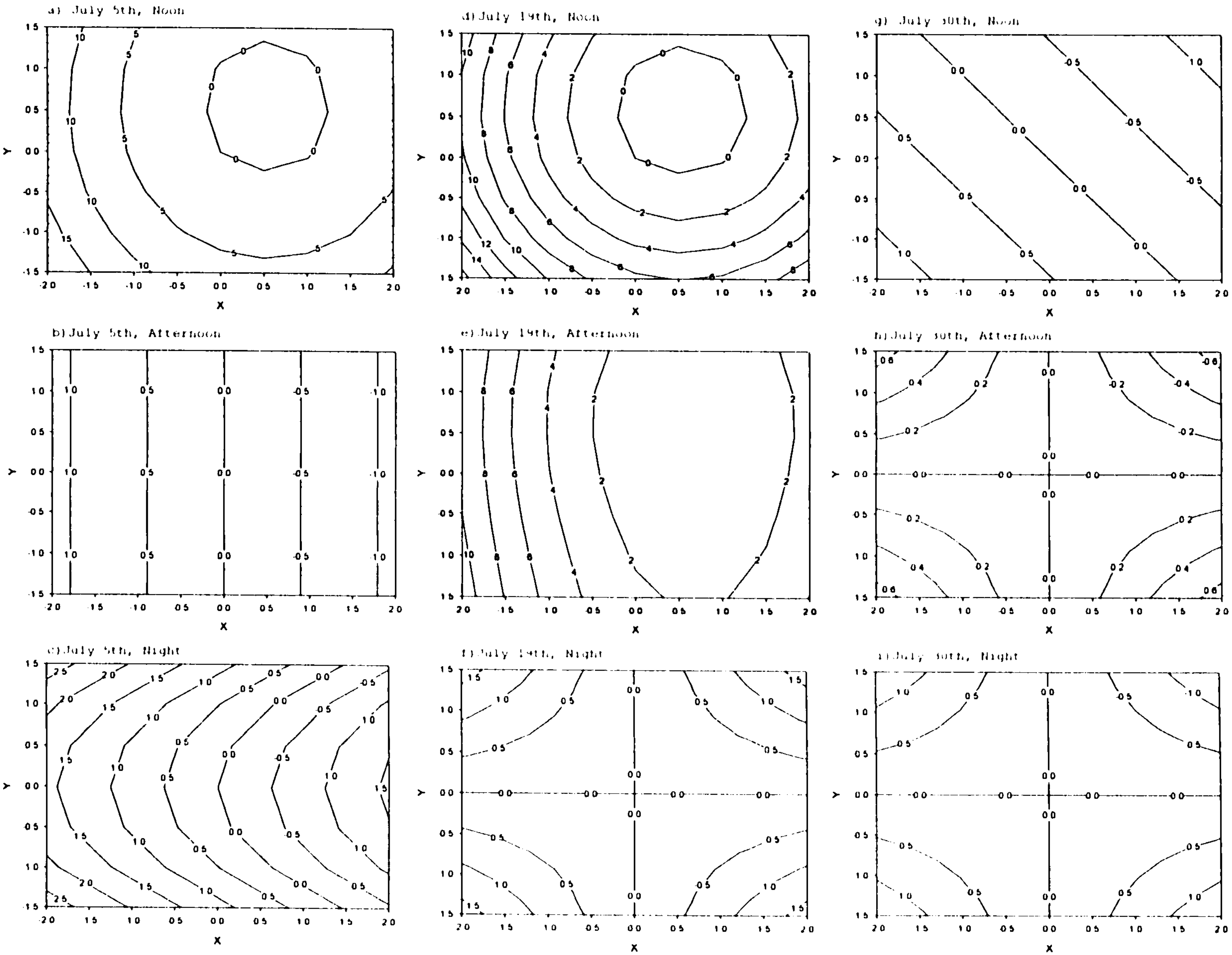
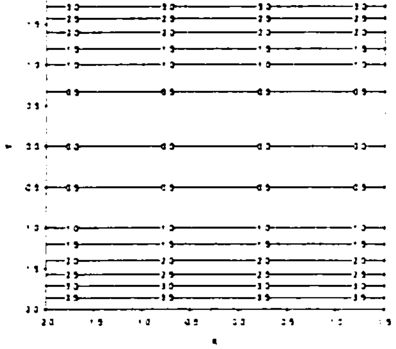
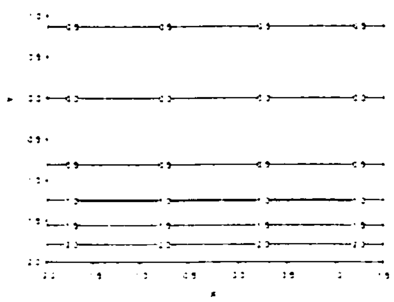

a) July 5th, Noon
b) July 5th, Afternoon
c) July 5th, Night
d) July 19th, Noon
e) July 19th, Afternoon
f) July 19th, Night
g) July 30th, Noon
h) July 30th, Afternoon
i) July 30th, Night
X
Y
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0

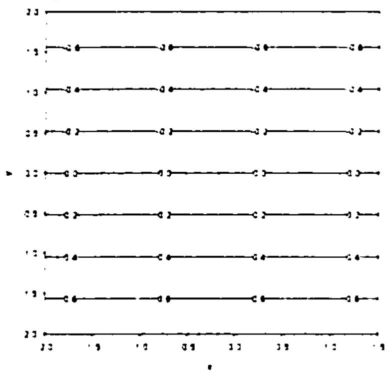
Figure 7: The contoured linear and quadratic trend-surfaces fitted to *H.shoshone* density data, for pond 8 for each significant sampling time and for deep and shallow samples. Trends near the corners should not be interpreted, since they are outside the pond sampling range.



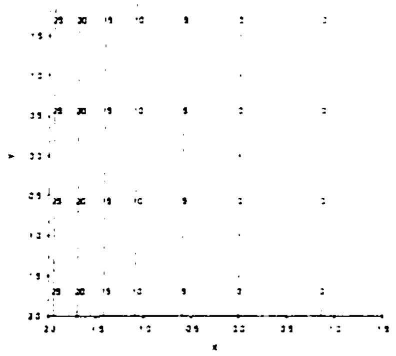
July 2nd, Noon (shallow)



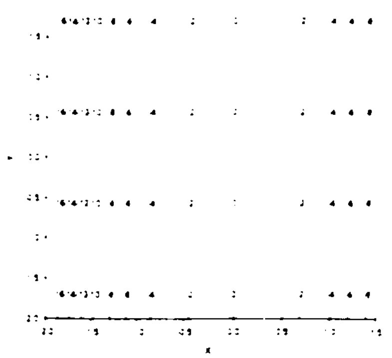
July 2nd, Noon (Deep)



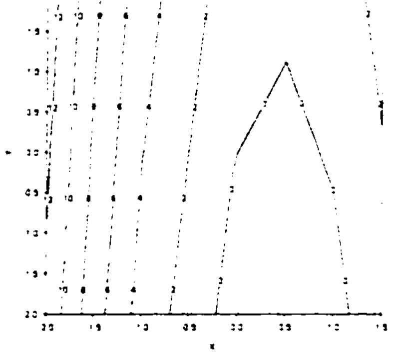
July 2, Afternoon



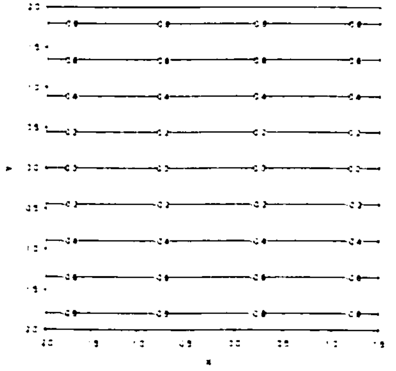
July 2nd, Night (shallow)



July 2nd, Night Deep

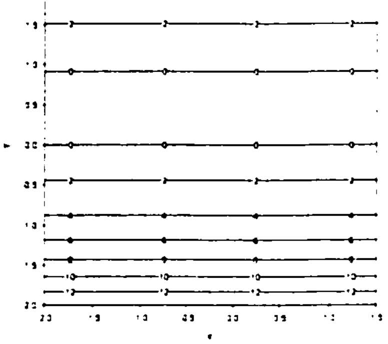


July 9th, Noon (shallow)

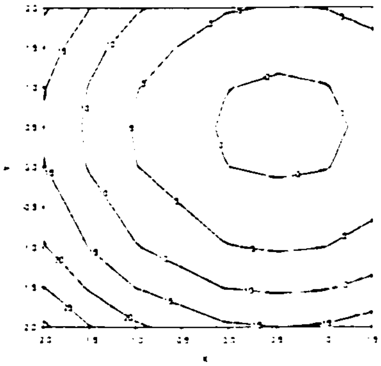


July 9th, Noon (Deep)

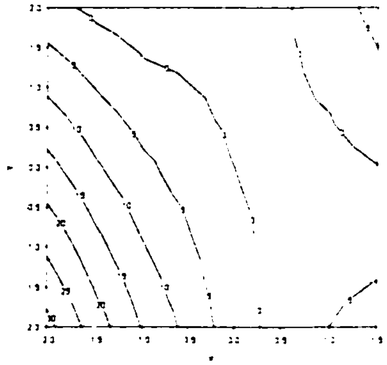
July 10th, Night (shallow)



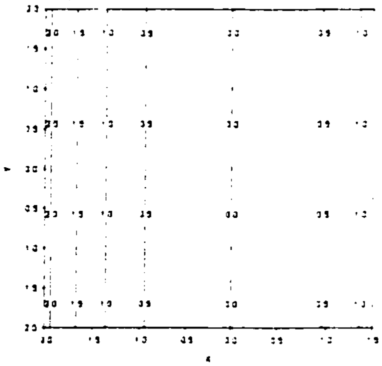
July 10th, Night (Deep)



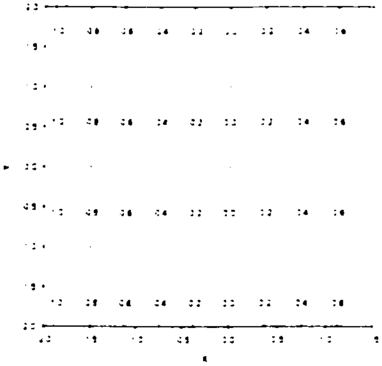
July 16th, Noon (shallow)



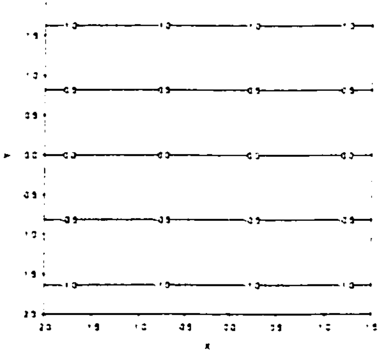
July 23rd, Afternoon (shallow)



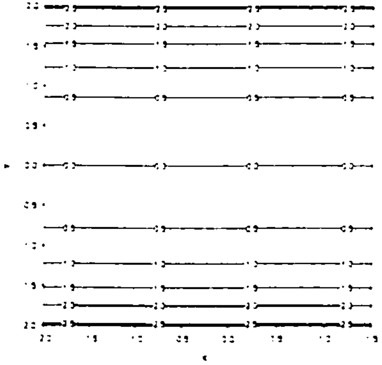
July 23rd, Afternoon (Deep)

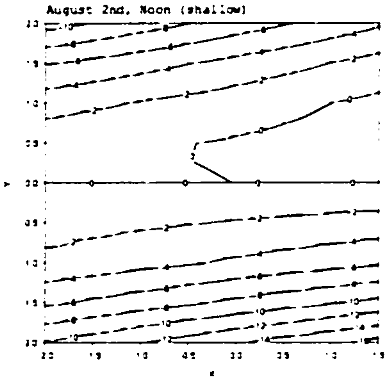


July 23rd, Night (shallow)

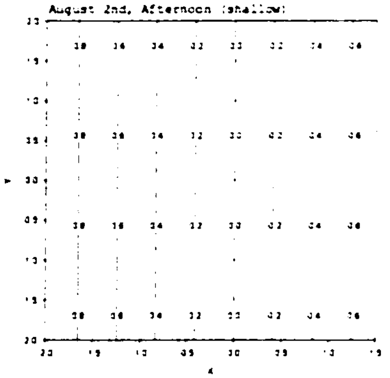


July 23rd, Night (Deep)

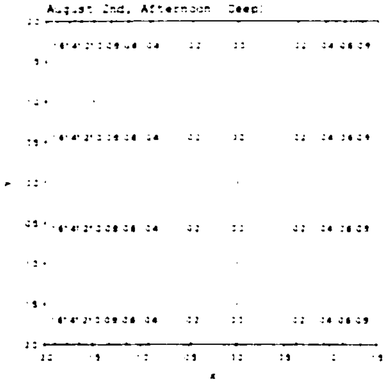




August 2nd, Noon (shallow)

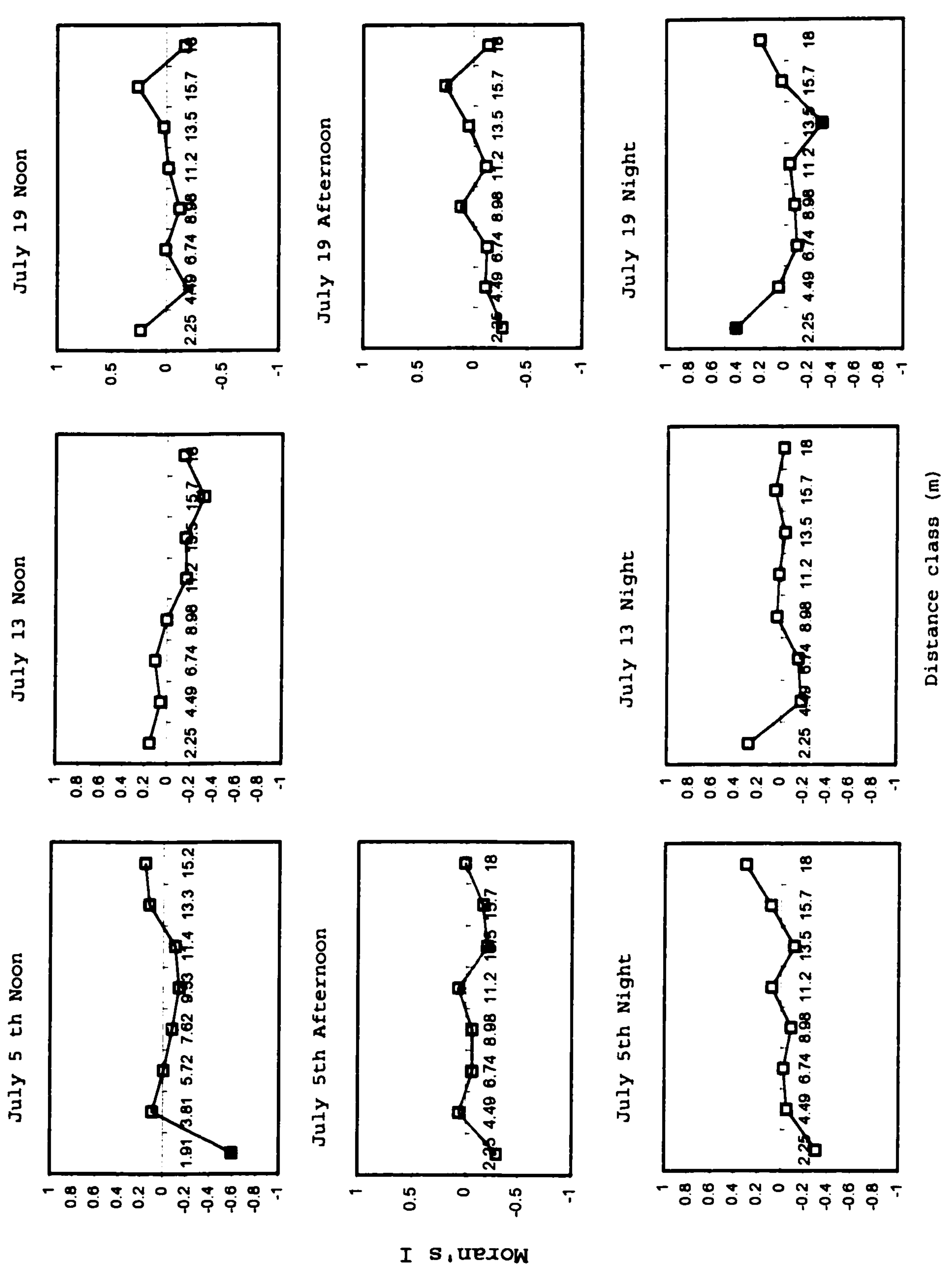


August 2nd, Afternoon (shallow)



August 2nd, Afternoon (Deep)

Figure 8: Autocorrelograms of *H. shoshone* densities in pond 11 through the summer of 2001. Vertical axis: Moran's I autocorrelation coefficients: horizontal axis: upper limits of distance classes expressed in meters. Solid squares are values significant at a progressive bonferonni corrected level, and white squares are non significant values. Moran's I coefficients >0 indicate positive autocorrelations and values < 0 indicate negative autocorrelations.


July 5 th Noon
1.91 3.81 5.72 7.62 9.53 11.4 13.3 15.2
July 13 Noon
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 19 Noon
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 5th Afternoon
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 19 Afternoon
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 5th Night
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 13 Night
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
July 19 Night
2.25 4.49 6.74 8.98 11.2 13.5 15.7 18
1 0.8 0.6 0.4 0.2 0 -0.2 -0.4 -0.6 -0.8 -1
1 0.5 0 -0.5 -1
Moran's I
Distance class (m)

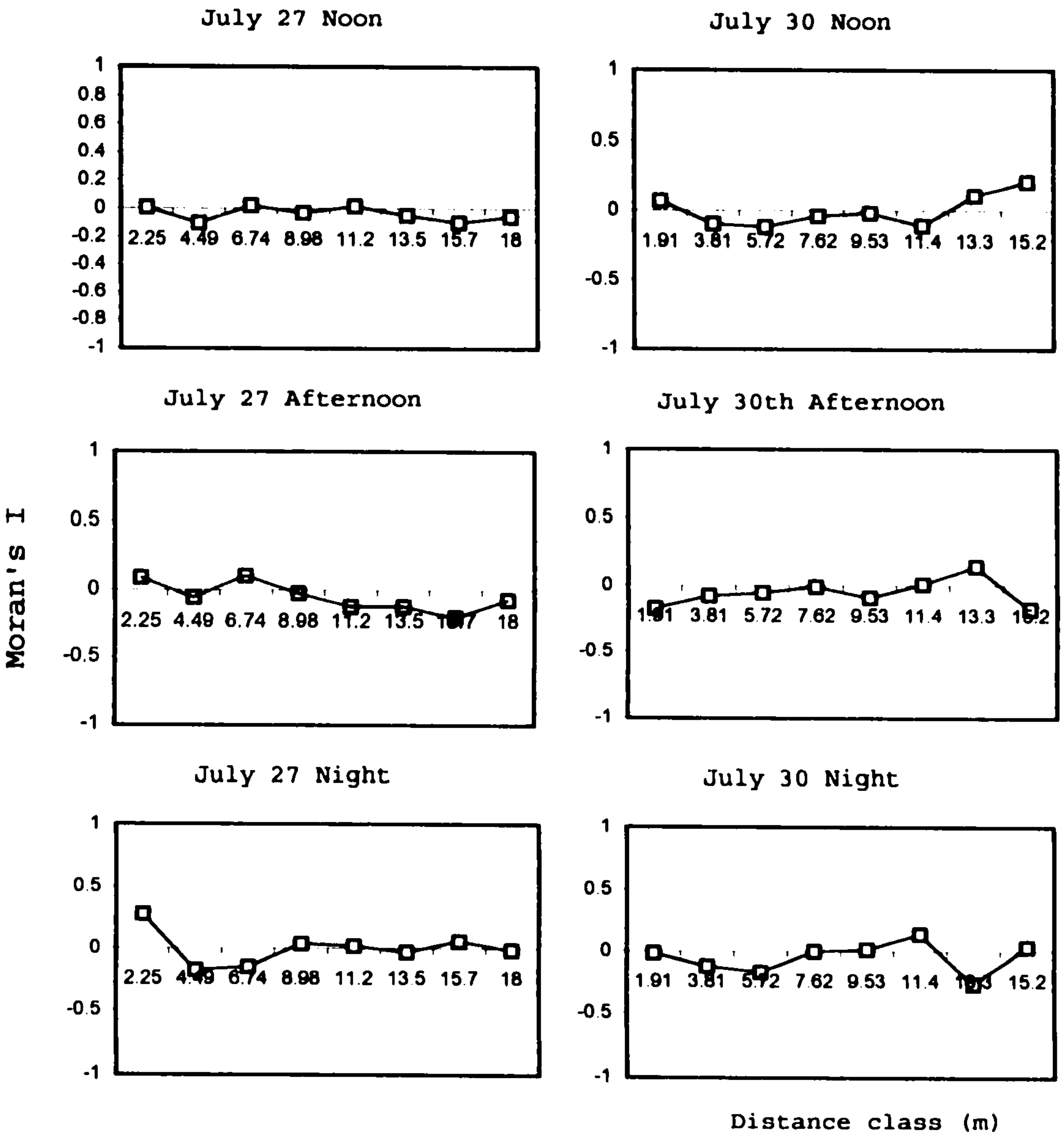
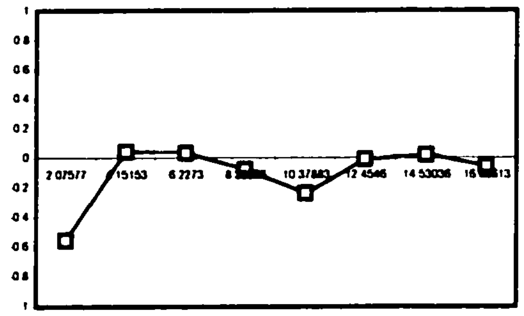
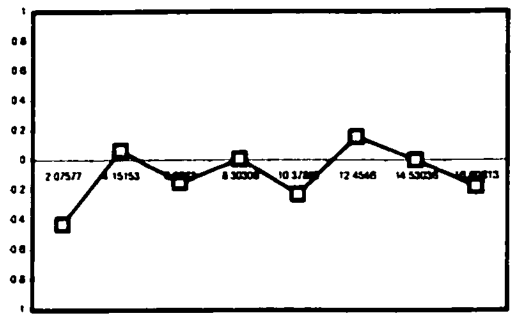
July 27 Noon
July 30 Noon
July 27 Afternoon
July 30th Afternoon
July 27 Night
July 30 Night
Moran's I
Distance class (m)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
0.5
-0.5
2.25
4.49
6.74
8.98
11.2
13.5
15.7
18
1.91
3.81
5.72
7.62
9.53
11.4
13.3
15.2

Figure 9: Deep and shallow autocorrelograms of *H. shoshone* densities in pond 8 through the summer of 2001. Vertical axis: Moran's I autocorrelation coefficients; horizontal axis: upper limits of distance classes expressed in meters. Solid squares are values significant at a progressive bonferonni corrected level, and white squares are non significant values. Moran's I coefficients >0 indicate positive autocorrelations and values < 0 indicate negative autocorrelations.

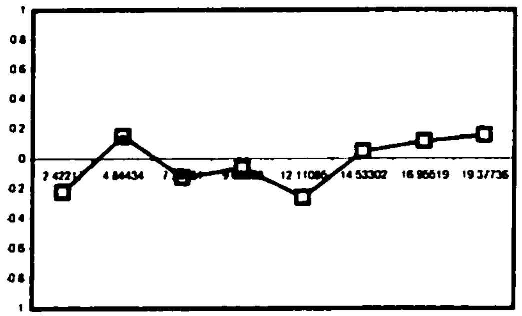
July 2nd, Noon (Shallow)



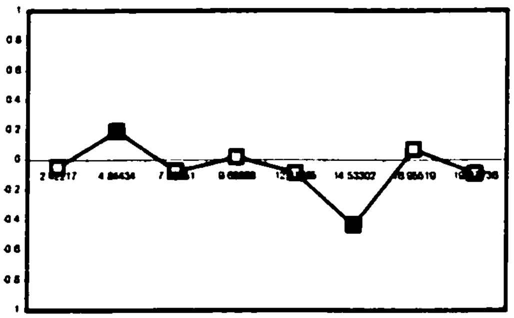
July 2nd, Noon (Deep)



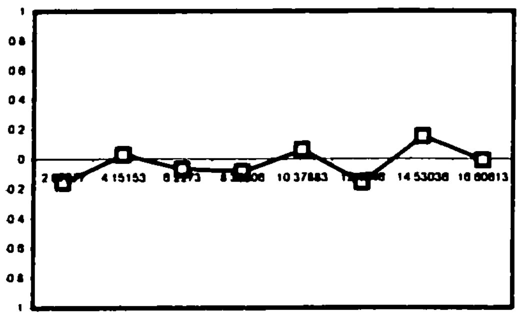
July 2nd, Afternoon (Shallow)



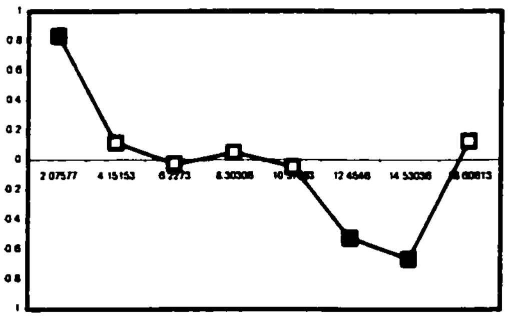
July 2nd, Afternoon (Deep)

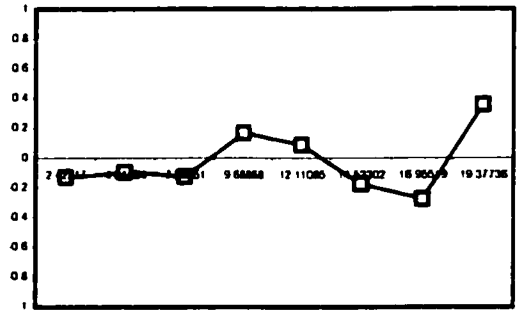


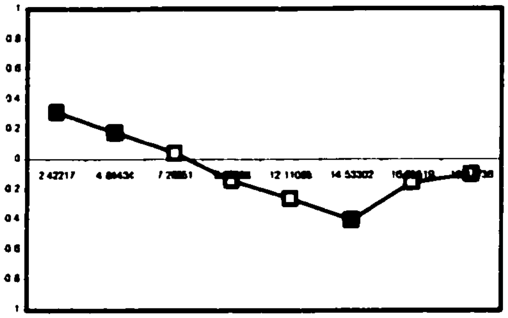
July 2nd, Night (Shallow)

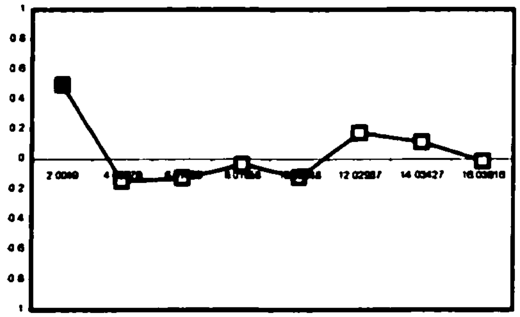


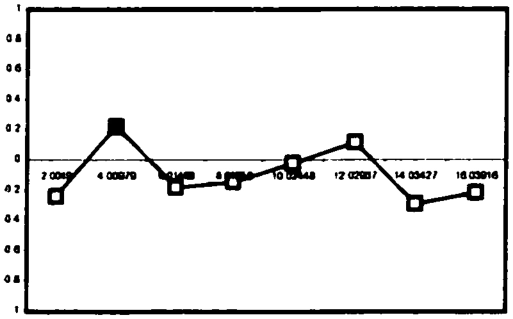
July 2nd, Night (Deep)

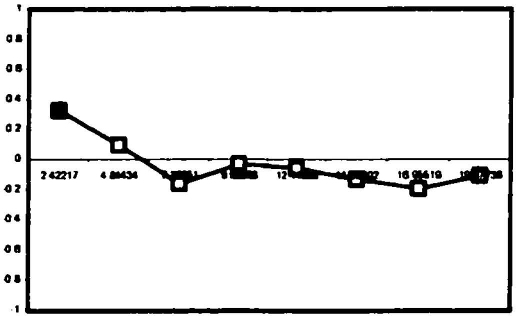


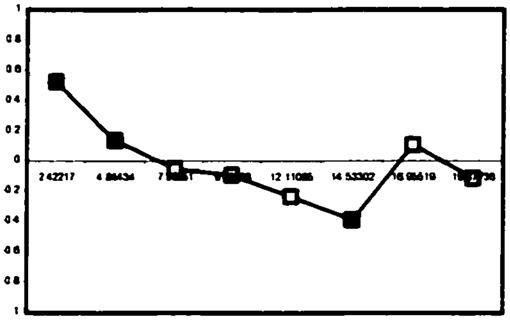

July 9th, Noon (Shallow)


July 9th, Noon (Deep)

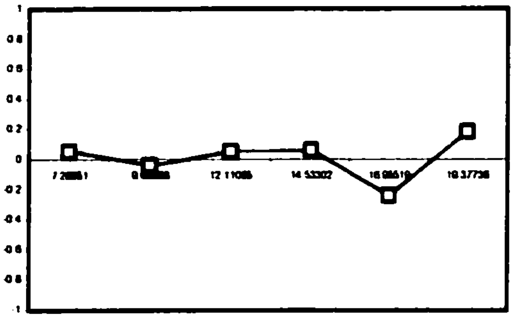

July 10th, Night (Shallow)


July 10th, Night (Deep)

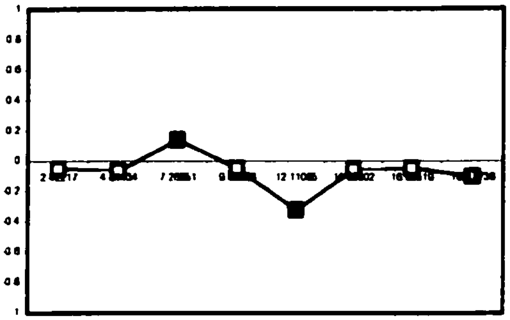

July 11th, Morning (Shallow)


July 11th, Morning (Deep)

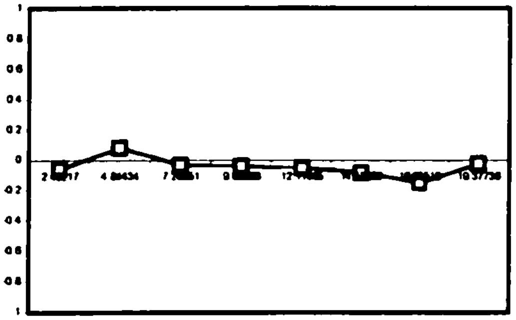
July 16th, Noon (Shallow)



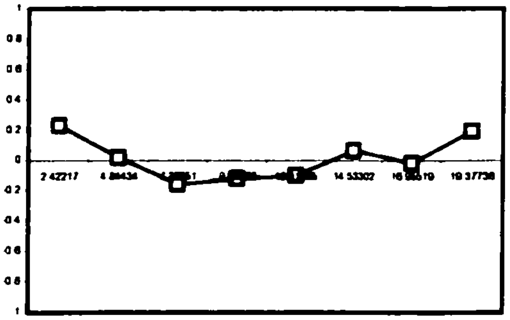
July 16th, Noon (Deep)



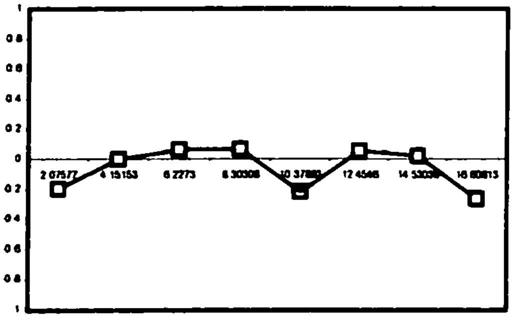
July 16th, Afternoon (Shallow)



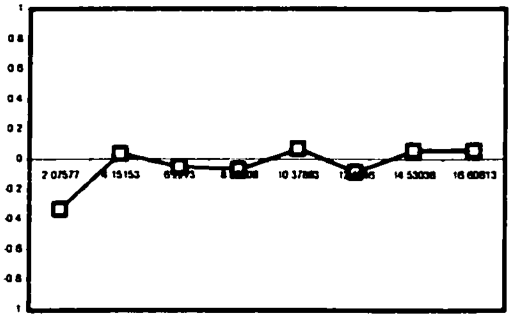
July 16th, Afternoon (Deep)



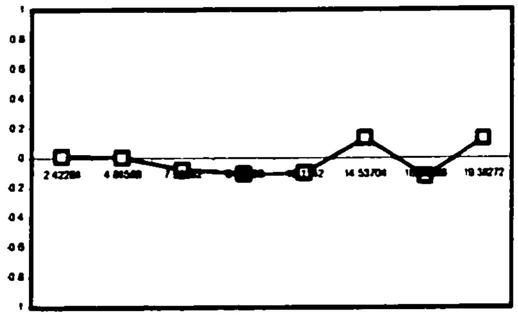
July 16th, Night (Shallow)



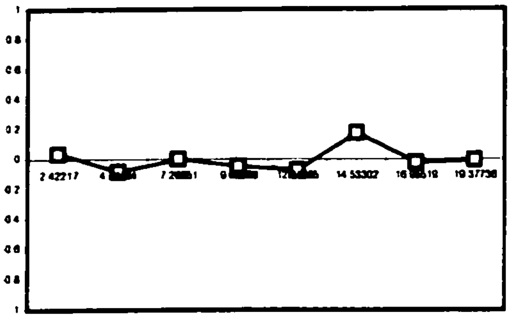
July 16th, Night (Deep)



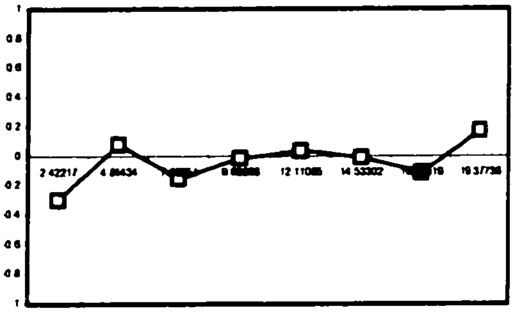
July 23rd, Noon (Shallow)



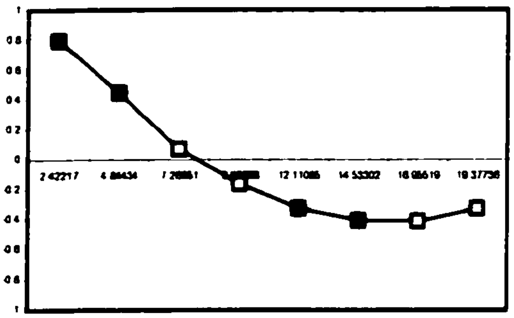
July 23rd, Noon (Deep)



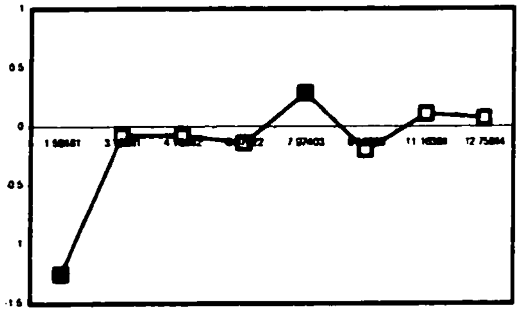
July 23rd, Afternoon (Shallow)



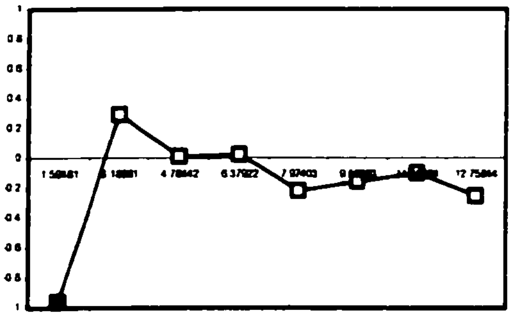
July 23rd, Afternoon (Deep)

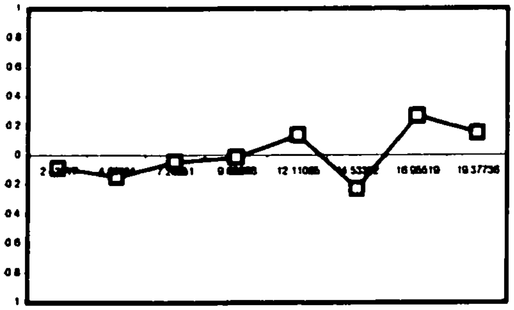


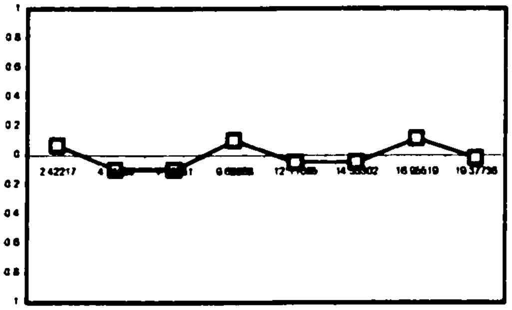
July 23rd, Night (Shallow)

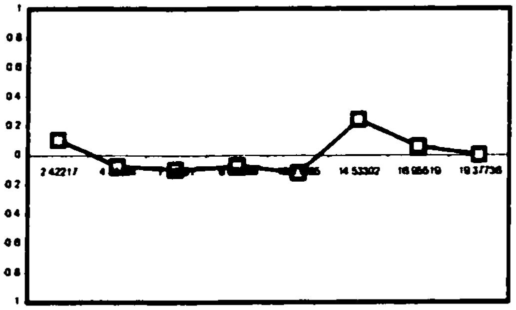


July 23rd, Night (Deep)




August 2nd, Noon (Shallow)


August 2nd, Noon (Deep)


August 2nd, Afternoon (Shallow)

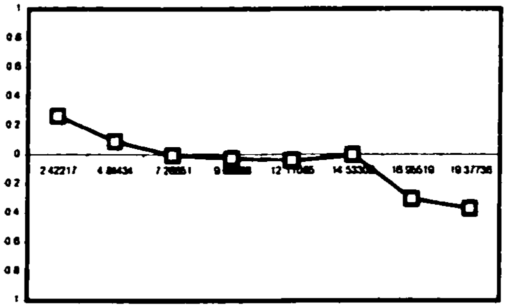

August 2nd, Afternoon (Deep)

Figure 10: Mean paired differences between shallow and deep midpond samples of *H. shoshone* for four sampling times of the day: morning, midday, afternoon and night, with respective p values. Positive differences indicate more individuals in the shallow samples while negative differences more individuals in the deep samples.

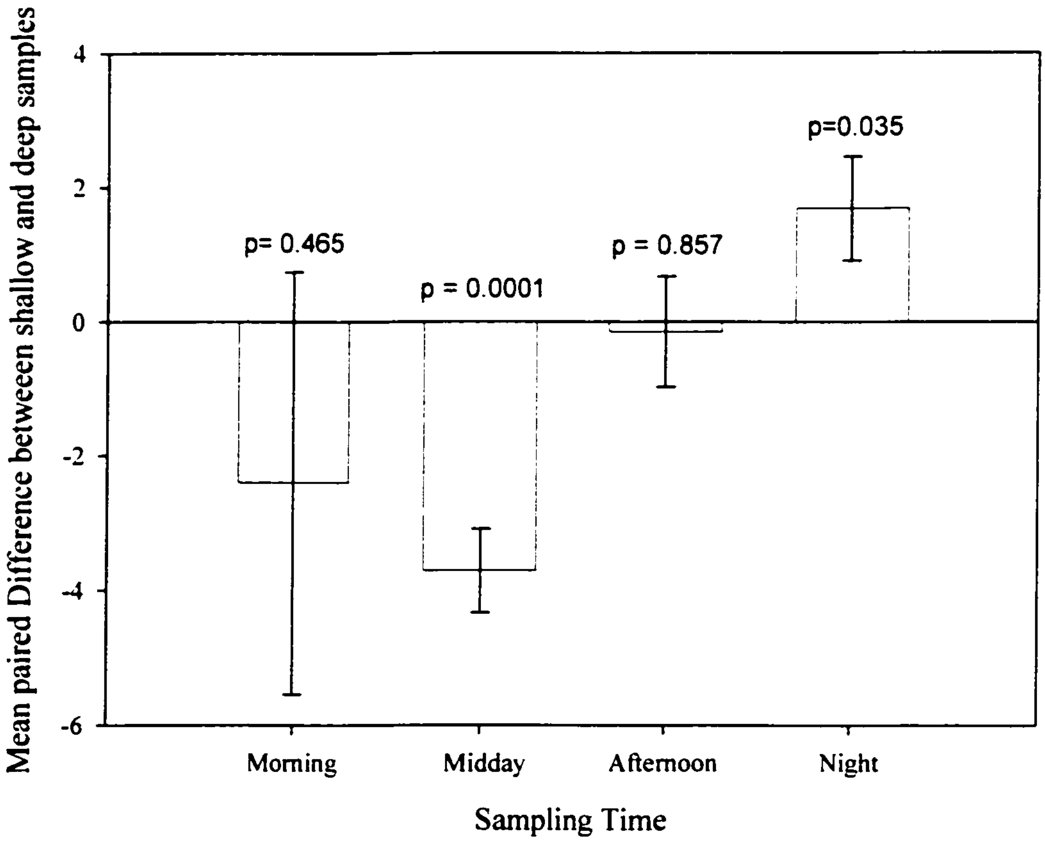
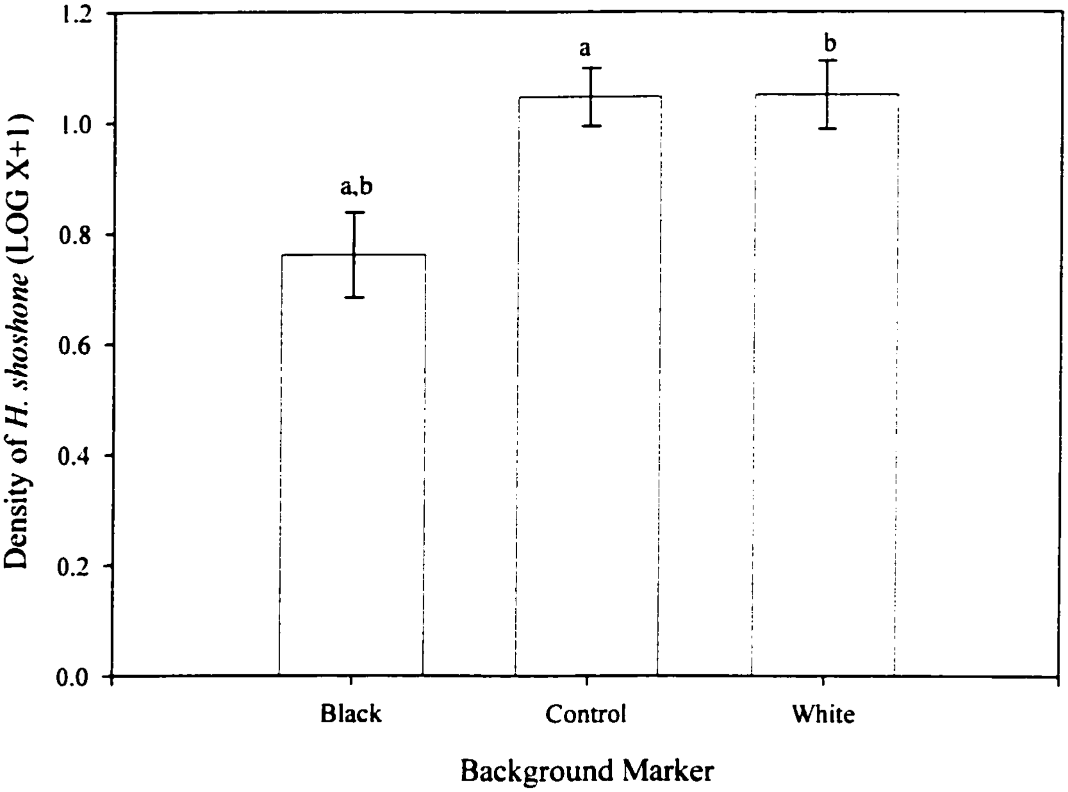

Mean paired Difference betweeen shallow and deep samples
4
2
0
-2
-4
-6
p= 0.465
p = 0.0001
p = 0.857
p=0.035
Morning
Midday
Afternoon
Night
Sampling Time

Figure 11: Pond U2. Mean densities of *H. shoshone* found above the background markers, with the standard error of the mean. Significant, differences ($\propto$=0.05) between treatments are labelled by letters, refer to text for exact significance and statistics values.



1.2
1.0
0.8
0.6
0.4
0.2
0.0
Density of *H. shoshone* (LOG X+1)
a,b
a
b
Black
Control
White
Background Marker

Figure 12: Pond U6. Mean densities of *H. shoshone* sampled above the background markers, with the standard error of the mean. Significant, differences ($\propto$=0.05) between treatments are labelled by letters, refer to text for exact significance and statistics values.

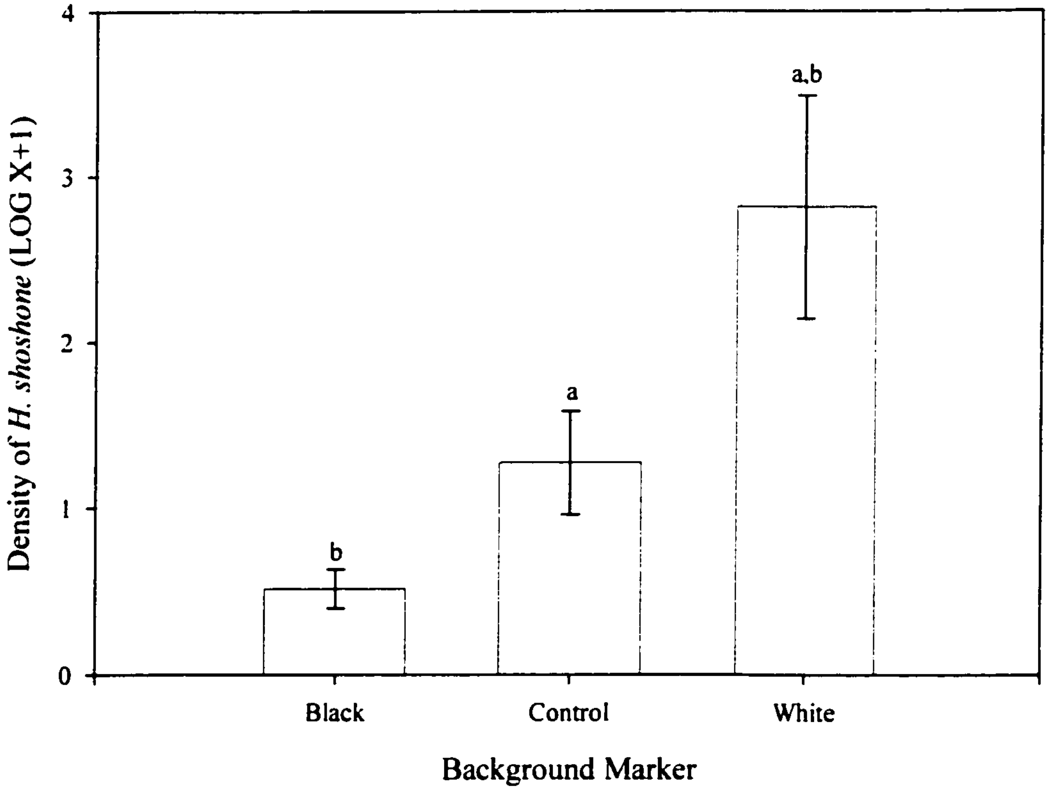

4
3
2
1
0
Density of *H. shoshone* (LOG X+1)
a,b
a
b
Black
Control
White
Background Marker

Table 1: Spatial trends of *H. shoshone* densities in pond 11 during summer of 2001. Sign (s) of relationship indicates direction (linear; x, y) or shape (second order: x2,y2,xy) of copepod densities in pond 11 with standardized regression coefficients. Missing coefficients indicate that the variables were not included in the model. Dates marked with an asterisk indicate that the dependent variable was subjected to a log transformation.

Date	**Time**	**Trend**	**x**	**y**	**x^2**	**y^2**	**xy**	**r^2**	**P**	**F**
Jul-05	Noon *	2nd order	-2.29	-1.915	2.096	1.72		0.441	0.003	5.321
Jul-05	Afternoon *	Linear	-0.559					0.313	0.001	13.207
Jul-05	Night *	2nd order	-0.797			0.286		0.394	0.0001	19.433
Jul-19	Noon *	2nd order	-1.792	-1.87	1.659	1.598		0.352	0.016	3.67
Jul-19	Afternoon *	2nd order	-1.743	-1.374	1.293	1.492		0.376	0.01	4.067
Jul-19	Night *	2nd order					0.57	0.325	0.001	14.44
Jul-30	Noon *	Linear	-0.351	-0.347				0.305	0.009	5.711
Jul-30	Afternoon	2nd order					-0.229	0.342	0.001	13.536
Jul-30	Night *	2nd order					-0.472	0.223	0.01	7.735

Table 2: Spatial trends of shallow *H. shoshone* densities in pond 8 during summer of 2001, Sign (s) of relationship indicates directio (linear; x, y) or shape (second order: x2,y2,xy) of copepod densities in pond 8 with standardized regression coefficients. Missing coefficients indicate that the variables were not included in the model. Dates marked with an asterisk indicate that the dependent variable was subjected to a log transformation.

Date	**Time**	**Trend**	**x**	**y**	**x^2**	**y^2**	**xy**	**r^2**	**p**	**F**
Jul-02	Noon *	2nd order				0.545		0.297	0.006	9.308
Jul-02	Afternoon*	Linear		-0.384				0.148	0.03	5.197
Jul-02	Night*	2nd order	4.13		-4.482			0.422	0.001	9.785
Jul-09	Noon*	2nd order	-1.931	0.388	2.122			0.414	0.003	6.126
Jul-10	Night	2nd order		-2.218		2.325		0.22	0.045	3.521
Jul-16	Noon*	2nd order	-3.604	-1.244	2.354		2.133	0.422	0.004	4.93
Jul-23	Afternoonn	2nd order			0.53			0.281	0.002	11.739
Jul-23	Night	Linear		0.613				0.376	0.001	13.236
Aug-02	Noon*	2nd order		1.698		-2.615	0.928	0.279	0.025	3.608
Aug-02	Afternoonn*	Linear	-0.482					0.233	0.005	9.096

Table 3: Spatial trends of deep *H. shoshone* densities in pond 8 during summer of 2001, Sign (s) of relationship indicates direction (linear; x, y) or shape (second order: x2,y2,xy) of copepod densities in pond 8 with standardized regression coefficients. Missing coefficients indicate that the variables were not included in the model. Dates marked with an asterisk indicate that the dependent variable was subjected to a log transformation.

Date	**Time**	**Trend**	**x**	**y**	**x^2**	**y^2**	**xy**	**r^2**	**p**	**F**
Jul-02	Noon*	2nd order				0.618		0.382	0.001	13.573
Jul-02	Night*	2nd order	3.955		-4.3			0.392	0.001	8.687
Jul-09	Noon*	Linear		0.446				0.199	0.013	6.959
Jul-10	Night	2nd order	-2.655	-2.578	2.462	2.632		0.399	0.016	3.819
Jul-23	Afternoon*	Linear	0.532					0.283	0.002	11.816
Jul-23	Night	2nd order				0.639		0.408	0.001	15.146
Aug-02	Afternoon*	2nd order			-0.44			0.193	0.012	7.196

Table 4: Summary of spatial statistic results for pond 11 with comments regarding to environmental conditions encountered at the Mexican Cut at the time of sampling.

Date	**Sampling time**		**Morisita**	**Trend analysis**	**Autocorrelation**	**Comments**
Jul-05	Noon	12:30 - 13:30	1.57	yes	yes	Sunny
	Afternoon	16:45 - 17:30	1.28	yes		Sunny
	Night	22:45 - 0:00	1.21	yes		Full moon
Jul-13	Noon	12:00 - 13:15	1.76			Cloudy for sampling, rain 15:00-18:00
	Night	18:00 - 19:15	1.17			Cloudy for sampling
Jul-19	Noon	12:00 - 13:00	1.39	yes		Sunny
	Afternoon	17:00 - 18:00	1.33	yes		Sunny
	Night	23:00 - 0:00	1.23	yes	yes	Full moon
Jul-27	Noon	12:00 - 13:00	1.45			Partially cloudy
	Afternoon	17:30 - 18:30	1.34			Cloudy, rain last 20min of sampling
	Night	23:00 - 0:00	1.23			Half moon
Jul-30	Noon	12:30 - 13:45	2.09	yes		Sunny
	Afternoon	17:50 - 18:20	1.38	yes		Rain throughout sampling
	Night	22:45 - 0:00	1.51	yes		Fog and rain, 1/4 moon

Table 5: Summary of spatial statistic results for pond 8 with comments regarding to environmental conditions encountered at the Mexican Cut at the time of sampling.

Date	**Sampling time**		**Morisita**	**Trend Analysis**		**Autocorrelation**		**Comments**
				Shallow	Deep	Shallow	Deep	
Jul-02	Noon	11:45-13:00	1.56	yes	yes			Last 15min. of sampling rain/hail/snow
	Afternoon	17:00-18:00	1.23	yes			yes	cloudy
	Night	23:0-0:30	1.3	yes	yes		yes	3/4 moon
Jul-09	Noon	12:00-13:15	1.38	yes			yes	Partially cloudy for sampling, rain rest of day
Jul-10	Night	23:00-0:15	1.38	yes		yes	yes	Thunderstorms from 16:00-22:00. No rain for sampling
Jul-11	Morning	7:15-8:30	1.63			yes	yes	Sunny
Jul-16	Noon	13:00-14:15	1.94	yes			yes	Sunny, Strong wind from North West
	Afternoon	17:30-18:45	1.2					Sunny
	Night	22:00-23:30	1.2					1/4 moon
Jul-23	Noon	12:00-13:15	1.45					Cloudy
	Afternoon	17:15-18:45	1.21	yes	yes		yes	Sunny
	Night	23:00-24:00	1.43	yes	yes	yes	yes	1/4 moon
Aug-02	Noon	12:00-13:00	1.68	yes				Cloudy
	Afternoon	17:00-18:00	1.44	yes	yes			Partially cloudy, full moon

Table 6: Results of partial regression analysis in pond 11 on *H. shoshone* densities constrained by matrices of environmental and spatial variables. The meaning of the fractions are the following: a, nonspatially structured environmental component (local effects); b, spatially structured component (gradients); c, residual spatial component; d, undetermined (nonspatial) variation.

Date	Sampling Time	Environmental variables measured	Environmental variables retained by forward selection	Spatial variables	% variance explained by each fraction	Fraction (a+b+c)
Jul-05	Midday	Light intensity	Water depth	x	a: 3.9	
		Water depth	Distance to logs	y	b: 26	F= 3.8
		Distance to logs		x^2	c: 17	p = 0.008
		Temperature		y^2	d: 53.1	
Jul-05	Afternoon	Light intensity	Distance to logs	x	a: 4.3	
		Water depth	Light intensity		b: 29.2	F=5.018
		Distance to logs			c: 2.3	p = 0.007
		Temperature			d: 64.2	
Jul-05	Night	Water depth	Distance to logs	x	a: 10.6	
		Distance to logs		y^2	b: 23.8	F = 14.487
		Temperature			c: 15.6	p = 0.0001
					d: 50	
Jul-13	Midday	Light intensity			a:	
		Water depth	n.s	n.s.	b: n.s.	
		Distance to logs			c:	
		Temperature			d:	
Jul-13	Night	Water depth			a:	
		Distance to logs	n.s.	n.s.	b: n.s.	
		Temperature			c:	
					d:	
Jul-19	Midday	Light intensity	Light intensity	x	a: 37.4	
		Water depth		y	b: 10.1	F=13.8
		Distance to logs		x^2	c: 25.1	p= 0.0001
		Temperature		y^2	d: 27.4	

Table 6 continued…

Date	Sampling Time	Environmental variables measured	Environmental variables retained by forward selection	Spatial variables	% Variance explained by each Fraction	Fraction (a+b+c)
Jul-19	Afternoon	Light intensity	Water depth	x	a: 38.4	
		Water depth	Light intensity	y	b: 22.8	F= 13.168
		Distance to logs		x^2	c: 14.8	p = 0.0001
		Temperature		y^2	d: 24	
Jul-19	Night	Water depth		xy	a: 0	
		Distance to logs			b: 0	F=14.54
		Temperature			c: 32.5	p= 0.001
					d: 67.5	
Jul-27	Midday	Light intensity	Distance to logs		a: 65.3	
		Water depth	Light intensity		b: 0	F=27.236
		Distance to logs			c: 0	p= 0.0001
		Temperature			d: 34.7	
Jul-27	Afternoon	Water depth			a:	
		Distance to logs	n.s	n.s.	b: n.s.	
		Temperature			c:	
					d:	
Jul-27	Night	Water depth			a:	
		Distance to logs	n.s.	n.s.	b: n.s.	
		Temperature			c:	
					d:	
Jul-30	Midday	Light intensity	Distance to logs	x	a: 47.5	
		Water depth	Light intensity	y	b: 31.9	F=50.194
		Distance to logs			c: 2.3	p = 0.0001
		Temperature			d: 18.3	
Jul-30	Afternoon	Water depth		xy	a: 0	
		Distance to logs			b: 0	F= 13.537
					c: 34.2	p = 0.001
					d: 65.8	
Jul-30	Night	Water depth		xy	a: 0	
		Distance to logs			b: 0	F= 7.704
					c: 22.3	p = 0.01
					d: 77.7	

Table 7: Results of partial regression analysis in pond 8 on *H. shoshone* densities constrained by matrices of environmental and spatial variables. The meaning of the fractions are the following: a, nonspatially structured environmental component (local effects); b, spatially structured component (gradients); c, residual spatial component; d, undetermined (nonspatial) variation.

Date	**Sampling Time**	**Environmental variables measured**	**Environmental variables retained by forward selection**	**Spatial variables**	**% variance explained by Fraction**	**Fraction (a+b+c)**
Jul-02	Midday	Pond depth	Distance to edge	y^2	a: 12	
		Distance to logs			b: 9	F=7.5
		Distance to edge			c: 20.7	p=0.003
		Rocks			d: 58.3	
Jul-02	Afternoon	Pond depth		y	a: 0	
		Distance to logs			b: 0	F=5.1
		Distance to edge			c: 14.8	p=0.03
		Rocks			d: 85.2	
Jul-02	Night	Pond depth	Distance to logs	x	a: 0	
		Distance to logs		x^2	b: 29.5	F=6.3
		Distance to edge			c: 12.7	p=0.002
		Rocks			d: 57.8	
Jul-09	Midday	Pond depth	Distance to logs			
		Distance to logs		x	a: 2.4	
		Distance to edge		x^2	b: 32.9	F=4.6
		Rocks		y^2	c: 8.5	p=0.006
		Temperature			d: 56.2	
		Light intensity				
Jul-10	Night	Pond depth			a: 0	
		Distance to logs		y^2	b: 0	F=3.5
		Distance to edge		y^2	c: 22	p=0.045
		Rocks			d: 78	

Table 7 continued...

Date	Sampling Time	Environmental variables measured	Environmental variables retained by forward selection	Spatial variables	% variance explained by Fraction	Fraction (a+b+c)
Jul-11	Morning	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	Temperature		a: 18.5 b: 0 c: 0 d: 81.5	F=6.7 p=0.014
Jul-16	Midday	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	Distance to logs	x y x^2 xy	a: 7 b: 14.1 c: 28.1 d: 50.8	F=3.9 p=0.009
Jul-16	Afternoon	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	n.s.	n.s	a: b: c: d: n.s.	
Jul-16	Night	Water depth Distance to logs Distance to edge Rocks	n.s.	n.s.	a: b: c: d: n.s.	
Jul-23	Midday	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	Water depth		a: 25.2 b: 0 c: 0 d: 74.8	F=10.113 p=0.003

Table 7 continued...

Date	Sampling Time	Environmental variables measured	Environmental variables retained by forward selection	Spatial variables	% variance explained by Fraction	Fraction (a+b+c)
Jul-23	Afternoon	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	Light intensity	x^2	a: 10 b: 26.7 c: 1.4 d: 61.9	F=8,9 p=0.001
Jul-23	Night	Water depth Distance to logs Distance to edge Rocks		y	a: 0 b: 0 c: 37.6 d: 62.4	F=13.236 p=0.001
Aug-02	Midday	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity		y y2 xy	a: 0 b: 0 c: 27.9 d: 72.1	F=3.608 p=0.025
Aug-02	Afternoon	Water depth Distance to logs Distance to edge Rocks Temperature Light intensity	Temperature	x	a: 3 b: 23.2 c: 0.1 d: 73.7	F=5.175 p=0.012

BIBLIOGRAPHY

Aguilera, M.P. 2002. Distribution pattern of *Hesperodiaptomus shoshone* and *Leptodiaptomus coloradensis* and it's effect their mating and reproductive success. MSc. Thesis. Concordia University.

Ambler, J. W., F. D. Ferrari, and J. A. Fornshell. 1991. Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays. *Journal of Plankton Research* . 13: 1257-1272.

Andrew, N.L., and B.D. Mapstone. 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology* 24: 39-90.

Avois, C., P. Legendre, S. Masson, and B. Pinel-Alloul. 2000. Is the sampling strategy interfering with the study of spatial variability of zooplankton communities? *Canadian Journal of Fisheries and Aquatic Science* 57: 1940-1956.

Badgley, C., and D. L. Fox. 2000. Ecological biogeography of North American mammals: Species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* 27: 1437-1467.

Betsill, R., and A.M.van den Avyle. 1994. Spatial heterogeneity of reservoir zooplankton: a matter of timing? *Hydrobiologia* 277: 63-70.

Bocard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1945-1055.

Bocard, D., and P. Legendre. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environmental Ecology and Statistics* 1: 37-53.

Bollens, S. M., and B. W. Frost. 1989. Predator-induced diel vertical migration in a planktonic copepod. *Journal of Plankton Research* 11: 1047-1065.

Brewer, A. M., and K. J. Gaston. 2002. The geographical range structure of the holly leaf-miner. I. Population density. *Journal of Animal Ecology* 71: 99-111.

Buskey, E. J. 1998. Energetic costs of swarming behavior for the copepod *Dioithona oculata*. *Marine Biology* 130: 425-431.

Buskey, E. J., and Peterson, J.O. 1996. The swarming behavior of the copepod *Dioithona oculata*: in situ and laboratory studies. *Limnology and Oceanography* 41: 513-521.

Buskey, E. J., J. O. Peterson, and J. W. Ambler. 1995. The role of photoreception in the swarming behaviour of the copepod *Dioithona oculata*. *Marine and Freshwater Behaviour and Physiology* 26: 273-285.

Byron, E. R. 1981. Metabolic stimulation by light in a pigmented freshwater invertebrate. *Proceedings of the National Academy of Sciences* 78: 1765-1767.

Byron, E. R. 1982. The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. *Ecology* 63: 1871-1886.

Byron, E. R., P. T. Whitman, and C. R. Goldman. 1983. Observations of copepod swarms in lake Tahoe. *Limnology and Oceanography* 28: 378-382.

Cliff, A. D., and J. K. Ord. 1981. Spatial Processes: Models & Applications. Pion, London.

Colebrook, J. M. 1960. Some observations of zooplankton swarms in Windermere. *Journal of Animal Ecology* 29: 241-242.

Davidowicz, P. 1999. Koszty behawioralnej obrony przed drapieGnictwem: model dobowych migracji pionowych zwierz"t planktonowych. *Widadomo;ci Ekologiczne* XLV: 1-15.

Davis, C. C. 1969. Seasonal distribution, constitution and abundance of zooplankton in Lake Erie. *Journal of Fisheries and Research Board of Canada* 26: 2429-2476.

De Meester, L., and H. J. Dumont. 1998. The genetics of phototaxis in *Daphnia magna*: Existence of three phenotypes for vertical migration among parthogenetic females. *Hydrobiologia* 162: 47-55.

De Meester, L., S. Maas, K. Dierckens, and H. J. Dumont. 1993. Habitat selection and patchiness in *Scapholeberis*: horizontal distribution and migration of *S.mucoranta* in a small pond. *Journal of Plankton Research* 15: 1129-1139.

de Nie, H. W., H. J. Bromley, and J. Vijverberg. 1980. Distribution patterns of zooplankton in Tjeukemeer, The Netherlands. *Journal of Plankton Research* 2: 317-334.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography* 15: 131-137.

Folt, C. 1987. An experimental analysis of costs and benefits of zooplankton aggregation. Pages 300-314 in C. Kerfoot and A. Sih., ed. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hannover and London.

Folt, C., and P. C. Schulze. 1993. Spatial patchiness, individual performance and predator impacts. *Oikos* 68: 560-566.

Folt, C. L., and C. W. Burns. 1999. Biological drivers of plankton patchiness. *Trends in Ecology and Evolution* 14: 300-305.

Fortin, M. J. 2002. Introductory remarks. Spatial analyses in ecology: statistical and landscape issues. *Ecoscience* 9: iii-v.

Fortin, M. J. 1999. Effects of sampling unit resolution on the estimation of spatial autocorrelation. *Ecoscience* 6: 636-641.

Garcia-Charton, J., and A. Perez-Ruzafa. 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. *Marine Biology* 138: 917-934.

Gittins, R. 1968. Trend surface analysis of ecological data. *Journal of Ecology* 56: 845-869.

Gliwicz, Z. M. 1986. A lunar cycle in zooplankton. *Ecology* 67: 883-897.

Gliwicz, Z. M., and A. Rykowska. 1992. "Shore avoidance" in zooplankton: a predator-induced behavior or predator-induced mortality? *Journal of Plankton Research* 14: 1331-1342.

Gulbrandsen, J. 2001. *Artemia* swarming - Mechanisms and suggested reasons. *Journal of Plankton Research* 23: 659-669.

Hamner, W. M. 1988. Behaviour of plankton and patch formation in pelagic ecosystems. *Bulletin of Marine Science* 43.

Hamner, W. M., and J. H. Carleton. 1979. Copepod swarms: Attributes and role in coral reef ecosystems. *Limnology and Oceanography.* 24: 1-14.

Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277-327. in J. H. Steele, ed. *Spatial Patterns in Plankton Communities*. Plenum Press, New York.

Haury, L. R., and H. Yamazaki. 1995. The dichotomy of scales in the perception and aggregation behavior of zooplankton. *Journal of Plankton Research* 17: 191-197.

Herbert, P. D. N., A. G. Good, and M. A. Mort. 1980. Induced swarming in the predatory copepod *Heterocope septentrionalis. Limnology and Oceanography.* 25: 747-750.

Horne, J. K., and D. C. Schneider. 1995. Spatial variance in ecology. *Oikos* 74: 18-26.

Hurlbert, S. H. 1990. Spatial distribution of montane unicorn. *Oikos* 58: 257-271.

Hutchinson, G. E. 1967. A Treatsie on Limnology. John Wiley, New York.

Irvine. 2000. Macrodistribution, swarming behaviour and production estimates of the lakefly *Chaoborus edulis* (Diptera:Chaoboridae) in Lake Malawi. *Advances in Ecological Research* 31: 431-447.

Jensen, K. H., O. T. Kleiven, and P. J. Jakobsen. 1999. How important is light in the aggregation behaviour of *Daphnia pulex* (Cladocera: Crustacea)? *Hydrobiologia* 411: 13-18.

Jimenez, J. J., J. P. Rossi, and P. Lavelle. 2001. Spatial distribution of earthworms in acid-soil savannas of the eastern plains of Colombia. *Applied soil ecology* 17: 267-278.

Johannsson, O. E., M. E.L., and R. O'Gorman. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Science* 48: 1546-1557.

Johnsen, S. 2001. Hidden in plain sight: The ecology and physiology of organismal transparency. *Biological Bulletin* 201: 301-318.

Krebs, C. J. 1989. Ecological Methodology. Harper & Row, New York.

Larsson, P. 1997. Ideal free distribution in *Daphnia*? Are daphnids able to consider both the food patch quality and the position of competitors? *Hydrobiologia.* 360: 143-152.

Legendre, P., and M. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80.

Legendre, P., and L. Legendre. 1998. Numerical Ecology. Elsevier Science BV, Amsterdam, The Netherlands.

Legendre, P., and A. Vaudor. 1991. The R package: multidimensional analysis, spatial analysis. Département de Sciences Biologiques, Université de Montréal, Montréal, Québec.

Leising, A. W., and J. Yen. 1997. Spacing mechanisms within light-induced copepod swarms. *Marine Ecology Progress Series* 155: 127-135.

Lewis, J. B., and J. J. Boers. 1991. Patchiness and composition of coral reef demersal zooplankton. *Journal of Plankton Research* 13: 1273-1289.

Liss, W. J., G. L. Larson, E. K. Deimling, R. L. Ganio, R. Hoffman, and G. Lomnicky. 1998. Ecological effects of stocked trout in naturally fishless high mountain lakes: North Cascades National Park Service Complex, WA, USA. *Hydrobiologia* 379: 63-75.

Macas, D. L., K. L. Denman, and M. R. Abott. 1985. Plankton patchiness: Biology in the physical vernacular. *Bulletin of Marine Science* 37: 652-674.

MacCord, F. S., and L. F. L. Duarte. 2002. Dispersion in Populations of *Tropiometra carinata* (Crinoidea : Comatulida) in the Sao Sebastiao Channel, Sao Paulo State, Brazil. *Estuarine coastal and shelf science* 54: 219-225.

Malone, B. J., and D. J. McQueen. 1983. Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. *Hydrobiologia* 99: 101-124.

Maly, E. J., and M. P. Maly. 1974. Dietary differences between two co-occurring calanoid copepod species. *Oecologia* 17: 325-333.

Mauchline, J. 1998. The Biology of Calanoid Copepods. Academic Press, San Diego.

McLaren, I. A., and C. J. Corkett. 1981. Temperature dependent growth and production by a marine copepod. *Canadian Journal of Fisheries and Aquatic Science* 38: 77-83.

Megard, R. O., M. M. Kuns, M. C. Whiteside, and J. A. Downing. 1997. Spatial distributions of zooplankton during coastal upwelling in western Lake Superior. *Limnology and Oceanography* 42: 827-840.

Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37: 17-23.

Niemiela, J., Y. Haila, E. Halme, T. Pajunen, and P. Punttila. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. *Journal of Biogeography* 19.

Omori, M., and W. M. Hammer. 1982. Patchy distribution of zooplankton: behavior, population assessment and sampling problems. *Marine Biology* 72: 193-200.

Parrish, J. K., and L. Edelstein-Keshet. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* 284: 99-101.

Passy, S. I. 2001. Spatial paradigms of lotic diatom distribution: A landscape ecology perspective. *Journal of Phycology* 37: 370-378.

Patalas, K. 1969. Composition and horizontal distribution of crustacean plankton in lake Ontario. *Journal Fish. Res. Bd Can.* 26: 2135-2164.

Pijanowska, J., and A. Kowalczewski. 1997. Predators can induce swarming behaviour and locomotory responses in *Daphnia*. *Freshwater Biology* 37: 649-656.

Pinnel-Alloul, B. 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300/301: 17-42.

Pinnel-Alloul, B., C. Guay, N. Angeli, P. Legendre, P. Dutilleul, G. Balvay, D. Gerdeaux, and J. Guillard. 1999. Large scale spatial heterogeneity of macrozooplankton in Lake Geneva. *Canadian Journal of Fisheries and Aquatic Science*. 56: 1437-1451.

Pinnel-Alloul, B., G. Methot, G. Verrault, and Y. Vigneault. 1990. Zooplankton species associations in Quebec lakes: variation with abiotic factors, including natural and anthropogenic acidification. *Canadian Journal of Fisheries and Aquatic Science* 47: 110-121.

Pinnel-Alloul, B., T. Niyonsenga, and P. Legendre. 1995. Spatial and environmental components of freshwater zooplankton. *Ecoscience* 2: 1-19.

Pinnel-Alloul, B., and D. Pont. 1991. Spatial distribution patterns in freshwater macrozooplankton: variation with scale. *Canadian Journal of Zoology* 69: 15567-1570.

Riley, G. A. 1976. A model of plankton patchiness. *Limnology and Oceanography* 21: 873-880.

Ringelberg, J. 1969. Spatial orientation of planktonic crustaceans 1. The swimming behaviour on a vertical plane. *Verhandlungen (Internationale Vereinigung fur Theoretische und Angewandte Limnologie)* 17: 841-847.

Ritz, D. A. 1994. Social aggregations in pelagic invertebrates. *Advances in Marine Biology* 30: 156-213.

Rudin, N. 1997. Dictionary of Modern Biology. Barron's Educational Series, Inc., Hauppauge, NY

Sarnelle, O., K. W. Kratz, and S. D. Cooper. 1993. Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. *Oecologia* 96: 208-218.

Siebeck, O. 1968. Spatial orientation of planktonc crustaceans1. The swimming behaviour in a horizontal plane. *Verhandlungen (Internationale Vereinigung fur Theoretische und Angewandte Limnologie)* 17: 831-840.

Sokal, R. R. 1979. Ecological parameters inferred from spatial correlograms. Pages 167-176 in G. P. Patil and M. L. Rosenzweig, eds. Contemporary Quantitative Ecology and Related Ecometrics. International Co-operative Publ. House, Fairland, Maryland.

Sommaruga, R. 2001. The role of solar UV radiation in the ecology of alpine lakes. *Journal of Photochemistry and Photobiology B-Biology*. 62: 35-42.

Sommer, U. 1989. Plankton Ecology: Succession In Plankton Communities. Springler-Verlag, Berlin.

Southwood, C. 1971. Ecological Methods With Particular Reference To The Study Of Insect Populations. Chapman and all eds, London.

Sprules, W. G. 1972. Effects of size selective predation and food competition on high altitude zooplankton communities. *Ecology* 53: 375-386.

Stockwell, J. D. 1996. Spatial Distribution of Zooplankton Biomass in Lake Erie. PhD. Thesis. University of Toronto.

Thomson, J. D., G. Weiblen, B. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: lilies, gophers and rocks. *Ecology* 77: 1698-1715.

Thrush, S. F. 1991. Spatial patterns in soft-bottom communities. *Trends in Ecology and Evolution* 6: 75-79.

Ueda, H., A. Kuwahara, M. Tanaka, and A. M. 1983. Underwater observations on copepod swarms in temperate and subtropical waters. *Marine Ecology Progress Series* 11: 165-171.

Underwood, A. J. 1996. Scales of spatial pattern of distribution of intertidal invertebrates. *Oecologia* 107: 212-224.

Vinebrooke, R., and P. Leavitt. 1999. Differential responses of littoral communities to ultraviolet radiation in an alpine lake. *Ecology* 80: 223-237.

Ward, H. B., and G. C. Whipple. 1959. Fresh Water Biology. Wiley, New York.

White, M. D. 1998. Horizontal distribution of pelagic zooplankton in relation to predation gradients. *Ecography* 21: 44-62.

Wicklum, D. 1999. Variation in horizontal zooplankton abundance in mountain lakes: shore avoidance or fish predation? *Journal of Plankton Research* 21: 1957-1975.

Wissinger, S. A., A. J. Bohonak, H. H. Whiteman, and W. S. Brown. 1999. Subalpine wetlands in Colorado. Habitat permanence, salamander predation, and invertebrate communities. in D. P. Batzer, R. B. Rader, and S. A. Wissinger, eds. Invertebrates In Freshwater Wetlands Of North America: Ecology And Managment. John Wiley & Sons Inc.

Wissinger, S. A., and H. H. Whiteman. 1992. Fluctuations in a Rocky Mountain population of Salamanders: Anthropogenic Acidification and Natural Variation? *Journal of Herpertology* 26: 377-391.

Yen, J., and E. A. Bundock. 1997. Aggregate behavior in zooplankton: Phototactic swarming in four developmental stages of *Coullana canadensis* (Copepoda, Harpacticoida). Pages 143-162 in J. K. Parrish and W. Hamner, eds. Animal Groups In Three Dimensions. Cambridge University Press, Cambridge, U.K.; New York.

Zar, J. H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey.