Distribution pattern of *Hesperodiaptomus shoshone* and *Leptodiaptomus coloradensis* and its effects on their mating and reproductive potential.

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ABSTRACT

Distribution pattern of *Hesperodiaptomus shoshone* and *Leptodiaptomus coloradensis* and its effect on their mating and reproductive potential.

Maria Pia Aguilera Salas

The main objective of this study was to describe the spatial distribution of *Hesperodiaptomus shoshone* (Forbes SA, 1893) and *Leptodiaptomus coloradensis* (Marsh, 1911). I then attempted to determine whether mating and reproductive potential (proportion of females carrying spermatophores, the proportion of females carrying clutches and the proportion of males attaching spermatophores) were affected by spatial distribution. The final goal was to determine whether there was a size difference between individuals inside and outside aggregations and a corresponding clutch size difference. Samples were taken from four ponds located at Mexican Cut, Colorado. Results indicated that *H. shoshone* had a patchy distribution while *L. coloradensis* showed a random pattern in its dispersion. Further analyses were only performed on H. *shoshone*. Mating potential was higher for both males and females within aggregations. However females within aggregations did not carry clutches more often than females outside aggregations. Females within aggregations were significantly larger, but no difference was observed among males and clutch size was significantly larger for females within aggregations. The distribution of *H. shoshone* may in part be attributed to physical processes and local pressures such as predation and food allocation. From an

adaptive standpoint, their distribution patterns seem to increase the frequency of mating encounters, thereby enhancing the mating potential of individuals found within these patches.

ACKNOWLEDGEMENTS

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Finally I would like to dedicate my work to Manuel. Words can't describe what your undying love and support have meant to me all this years. Thanks for not letting me give up, but most of all, thanks for always being there when I needed you.

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INTRODUCTION:

'Spatial heterogeneity' is what results from interactions between the spatial distribution of environmental constraints and the differential responses of organisms to these constraints (Milne 1991). Ecologists now recognise that spatial heterogeneity is a major factor involved in the regulation of the structure and dynamics of ecological entities (Levin 1992, Pinel-Alloul 1995, Megard *et al.* 1997). High spatial heterogeneity disturbs competition while at the same time causing an increase in habitat diversity, which in turn means an increase in species diversity (Williams 1988), it also reduces the impact of predation, and increases population stability (Neill 1990).

An aggregation, which is a major form of spatial heterogeneity (Hamner and Carleton 1979, Anderson *et al.* 1982), may serve several adaptive functions including food exploitation, mating encounters and protection from predators (Haury and Yamazaki 1995, Leising and Yen 1997).

Loosely defined, an aggregation is a clumping or clustering of individuals in a population with a non-random and non-uniform distribution. Aggregations have been identified in many terrestrial, oceanic and large scale freshwater environments (Legendre & Fortin 1989, Bernstein *et al.* 1991, Buskey & Peterson 1996). Zooplankton are but one of many organisms affected by spatial heterogeneity. The first goal of this study was to identify the distribution pattern of two calanoid copepods, *Hesperodiaptomus shoshone* (Forbes SA., 1893) and *Leptodiaptomus coloradensis* (Marsh, 1911) found in small high altitude ponds. Secondly I attempted to establish whether or not there is a connection between distribution patterns and fecundity or overall mating success in the populations being studied.

Aggregations can result from sorting by physical forces such as water, wind and currents. Animals that are passively transported via these physical processes form "passive aggregations". Different types of medusae (*Aequorea forskalea, Aurelia aurita, and Cyanea capillata*), which are often found in dense aggregations associated with localized physical phenomena (Hamner & Schneider 1986), are good examples of this type of aggregation.

Another type of aggregation is found around an attractive source (food, nesting territory, presence of mates). Under these conditions members of the aggregation actively seek specific locations (Cuddington &. McCauley 1994). These types of aggregations are referred to as "active aggregations". In these situations the aggregation is apt to disappear if the source of attraction wanes. Also individuals may constantly join and leave the aggregation and, of course, many animal aggregations are formed and maintained by the mutual attraction of members ((Parrish and Hamner, 1997). Active aggregations have been observed in a variety of organisms, e.g. the antelope *Saiga tatarica* (Bekenov *et al.* 1998), tadpoles of the toad *Bufo maculates* (Spieler & Linsenmair 1999), the dance fly *Rhamphomyia marginata* (Svensson 1997), the midge *Chironomus plumosus* (Neems *et al.* 1998), and the copepod *Dioithona oculata* (Buskey 1998).

Ecological phenomena such as aggregations can be studied from a proximate or an ultimate behaviour point of view.

A proximate analysis is intended to reveal the underlying mechanisms and the environmental factors that cause the phenomenon to occur. Proximate factors are the structural and mechanical influences that directly produce and control behaviour (i.e. the immediate conditions that cause the organism to respond in a particular way). Such factors that may cause spatial heterogeneity (i.e. aggregative behaviour) in natural populations of zooplankton include the presence of predators or competitors (Boikova 1986, Folt *et al.*1993, Folt & Schulze 1993), local food abundance (Larsson 1997), light intensity and illumination factors (Jensen *et al.* 1999) and temperature and salinity gradients (Omori & Hamner 1982, Betsill & Van den Avyle 1994).

An ultimate analysis provides functional explanations from an evolutionary perspective. Ultimate factors are the direct, evolutionary factors that produce behaviour. Ultimate factors may include enhanced mating success, increased protection from visual predators and adaptation to seasonality (Zaret 1975, Hamner & Carlton 1979, Hebert *et al.* 1980, Folt *et al.* 1993, Buskey & Peterson 1996, Folt & Burns 1999).

More specifically aggregations may enhance mating success by increasing the number of male-female encounters, especially when mating success is limited by population density (Hebert *et al.* 1980). Low population densities diminish the chances of encountering a mate, resulting in lower birth rates and population growth rates (Andrewartha & Birch 1954). Therefore, adaptations that increase the probability of mating encounters should be favoured because they keep the local population density above a critical level below which the population cannot increase (Gerritsen 1980). Aggregations of organisms may also enhance mating success by making mate-finding easier (Watras 1983). For example, female bullfrogs searching for mates are more likely to hear the mating calls of aggregated males than those of a solitary individual (Bourne 1993). A large group of female copepods is likely to exude higher concentrations of pheromones, thus attracting a larger number of males, or simply making it easier for potential mates to find them (Snell & Morris 1993, Van Duren & Videler 1996). In turn aggregated males may be more readily located by females, since they can be more easily found (de Nie *et al.* 1980). The increase in mating success in aggregations has been reported in a variety of arthropods ranging from midges and gnats to mosquitoes (Byron *et al.* 1983). However, it is a general consensus that ultimate causes responsible for the observed spatial distribution in nature are poorly understood (Taylor 1984, Vodopich & Cowell 1984, Megard *et al.* 1997, Wicklum 1999).

Aggregations and Zooplankton:

Most zooplankton are distributed in clumps, swarms, aggregations or patches. All these terms refer to a discontinuity in plankton density associated with environmental and biological factors (Cryer & Townsend 1988). The variety of terms used when referring to a patch of zooplankton creates ambiguity when defining this phenomenon. Zooplankton aggregations have been defined as horizontal or vertical regions of the distribution of a population of zooplankton that contain densities of individuals (usually) 3 to 5 times the mean density of the population (Mackas *et al.* 1985). Another well known definition is that given forth by Hamner (1988) which states that an aggregation is 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. Discrepancies found between definitions generally reflect the statistical analysis used in each study and the same basis has been used to determine which definition is most appropriate for this study. Although not ideal, Hamner's definition was chosen. The terms aggregation, patch and clump are used interchangeably in the literature and will be employed in this manner throughout this study.

Zooplankton aggregations are thought to influence predation, mortality rates, reproduction, feeding and species diversity (Megard *et al.* 1997). The environmental factors that explain the spatial structure of zooplankton communities depend on the scale of the observations (Avois *et al.* 2000). Aggregations occur on scales ranging from centimetres to meters and greater (Byron *et al.* 1983, Haury & Yamasaki 1995). Zooplankton patches found over large scales (>1km) are reported to be mainly caused by current patterns (Patalas & Salki 1969) or by seasonal variables such as temperature and day length (Urabe 1989). On smaller scales (10-1000m), wind induced currents (Riley 1976) and Langmuir circulation patterns (de Nie *et al.* 1980) may be responsible for the observed patchiness. On even smaller scales (1-10m), the scale of interest for this study, physical gradients (Pinel-Alloul & Pont 1991) and biological interactions might be of greater importance (Folt & Burns 1999).

Zooplankton heterogeneity at spatial and temporal scales of ecological interest such as seasonality and depth are an important focus of aquatic ecology research because of their importance for models of productivity, herbivory, nutrient cycling and trophic interactions in planktonic ecosystems. Within-lake zooplankton spatial heterogeneity represents another type of stochastic variation, being produced by biotic components of the ecosystem not related to the other spatial and temporal gradients (Downing 1991). Even though spatial distribution is a major factor affecting the ecology of zooplankton, we know very little about the mechanisms that produce and maintain zooplankton spatial heterogeneity created by these biotic components (Megard *et al.*, 1997).

Objectives:

The first objective of this research is to test the hypothesis that *Hesperodiaptomus shoshone* and *Leptodiaptomus coloradensis* copepods have a clumped spatial distribution (i.e. they aggregate). The second objective is to determine whether mating and reproductive potential (ability to mate and carry/produce a spermatophore/clutch) within an aggregation is greater than mating and reproductive potential outside it. If being within an aggregation increases reproductive potential in any way, then the proportion of females carrying spermatophores or clutches and the proportion of males fertilizing females should be higher within aggregations. Byron *et al.* (1983) offers an excellent example in this area where a similar study was performed using *Diaptomus tyrrelli* but in their case reproduction associated with the aggregations was of minimal importance to the total population reproduction, since most of the population did not form aggregations. If distribution has no effect on reproduction and the population conforms to the ideal free distribution (Giske *et al.* 1997) and they distribute themselves in proportion to the profitabilities of different patches (Begon et al. 1996), or if aggregations are short-lived, then the number of females carrying spermatophores and/or clutches and the number of males fertilizing females should not be significantly different within or outside aggregations.

The final objective of this study is to determine the variation in individual size with respect to spatial distribution. According to Pinel-Alloul (1995) zooplankton patchiness is a species- and size-specific property. Piontkovski and Williams (1995) reported that the spatio-temporal variability of biomass of organisms increases in higher trophic levels, from phytoplankton through microzooplankton to macrozooplankton, i.e. with the increase in size of the organisms. These authors concluded that the lower energy flow of higher trophic levels is accompanied by increased fluctuations in time and space. In marine environments, heterogeneity of the spatial distribution increases with the size of organisms, from phytoplankton through microzooplankton to macrozooplankton (Piontkovski *et al.* 1995). The increase in spatial heterogeneity means that relatively heterogeneous patterns of predators exist on more uniformly distributed patterns of their prey (Mackas and Boyd 1979, Mackas *et al.* 1985). However Pinel-Alloul *et al.* (1988) indicated that larger freshwater zooplankters seem to be less heterogeneously distributed than small zooplankters. Possible explanations put forth by these authors suggested that greater spatial aggregation might allow small zooplankters to avoid predators and locate mates, whereas reduced spatial heterogeneity in large species may decrease competition.

It has already been established that larger females are preferred by males searching for a potential mate (Marszalek, unpublished). If aggregations have a positive influence on the mating success of individuals then large females in turn can maximise their chance of reproducing by actively seeking an aggregation were males can more readily find them. Large females might be able to travel farther and may maintain their positions with greater ease. In turn I expect to see a higher number of eggs per clutch. Males do not necessarily benefit from a larger size. According to Grad & Maly (1988) there seems to be an optimal sex size ratio making males that are smaller than their mates (and also smaller than other males) more successful when attempting to mate. Since males are the ones who actively seek a mate and they are most successful when they are small I expect to see slightly larger males within aggregations (owing to optimal sex size ratio).

MATERIALS AND METHODS:

Study Organisms:

The species chosen for this study are the calanoid copepods, *Hesperodiaptomus shoshone* and *Leptodiaptomus coloradensis*. Both copepod species reproduce sexually, and females must copulate before a clutch of eggs can be extruded (Watras & Haney 1980). Their life cycle includes six naupliar stages and five copepodid stages before the final moult into adulthood, after which growth stops (Ward & Whipple 1959). *Hesperodiaptomus shoshone* is found in British Columbia, Illinois, Alaska and the Rocky Mountains. This species is univoltine and matures early in the spring (Maly & Maly 1974). According to earlier observations by E. Maly (personal communication) *H. shoshone* males seem to be patchily distributed, while females distributed themselves more evenly horizontally and vertically in small ponds. *L. coloradensis* is found exclusively in the state of Colorado, USA. This species is multivoltine and usually produces two generations yearly in many ponds (Maly & Maly 1974). These species coexist in all four ponds studied. Both species are highly visible due to their pigmentation, thus facilitating visual location for mapping, identification, and sorting once in the lab.

Study Site:

The study was conducted at the Mexican Cut Nature Preserve, a protected area under the jurisdiction of the Nature Conservancy in the state of Colorado in Gunnison County. The reserve contains several subalpine (3400-3600m elevation) 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.* 1999a). Basins can be categorized as permanent, semi-permanent (they may or may not dry in a given year during late autumn), or vernal (they dry each year during summer). The reserve is composed of two "shelves". The "lower shelf" of the reserve has 19 ponds (L1-L19) all situated very close to one another but differing in hydroperiod, acid neutralizing capacity (ANC), and community composition (Wissinger *et al.* 1999b). Samples were obtained from four lower shelf semi-permanent ponds L6, L8, L10, and L11 (Figure 1). These four ponds are all under 0.2 ha in area and 0.2-1.3m. deep (Maly 1970). They are located at altitudes of approximately 3230m. These ponds were chosen because they offer a wide range of population densities of both *H. shoshone* and *L. coloradensis*.

Sampling technique and schedule:

Ponds were sampled between June 11th and August 1st, 2000 inclusively. Ponds L6, L8 and L11 were sampled a total of eight times and pond L10 a total of nine times. Sampling locations were first selected by establishing a set of transects (between 6-8 transects per pond) covering all regions of each pond. Within these transects a set of 3-5 sampling locations were established at approximately equal intervals.

Pond L6: transects separated by 2.5 – 4.0m apart
sampling locations at 2.5 – 3.5m apart
Pond L8: transects separated by 5.0 – 7.5m apart
sampling locations at 3.5 – 5.0m apart
Pond L10: transects separated by 2.5 – 4.0m apart
sampling locations at 2.5 – 3.5m apart

Pond L11: transects separated by 2.5 – 3.5m apart

sampling locations at 2.0 – 3.0m apart

All sampling for the remainder of the season was performed in the same locations chosen during the first sampling week (Figure 2). Sampling was done between 11:00 AM and 13:00 PM. All ponds were sampled on a biweekly basis. Two ponds were sampled each day (sampling days were chosen on the basis of weather, trying to keep conditions similar at all times). Sampling was done from aboard a rubber dinghy from which a 4L Schindler-Patalas plexiglas trap was dropped into the water (depth of samples varied between 0.5-1.0m). Data recorded included date and time of sampling, density of males and females present in the sample, whether or not females carried clutches and/or spermatophores.

Samples were preserved in plastic vial containers (volume: 72ml) to which I added 15 to 20 drops of ethanol (80%) immediately after collection in order to minimize predation by *H. shoshone* on *L. coloradensis* (vials were never filled to more than ¾ their volume and never less than ½). All sorting and scoring for all experiments was done the day after sampling and required at least a day for every sampling day. Samples were then filtered and condensed into glass vials (8.0ml) and five to ten drops of formalin solution (5%) were added to all samples, which were then sent to Concordia University.

Identification of aggregations:

Population densities (mean number of individuals per sampling date) were estimated for each sex, for each species, throughout the summer across all ponds. The degree of aggregation for each sex and both sexes combined was determined using the un-standardized Morisita's index of dispersion (I_d) for each sampling date (Appendix I).

According to this index:

$I_d > 1$ Aggregated distribution

$I_d = 1$ Random distribution

$I_d < 1$ Uniform distribution

All sampling dates showing a significantly aggregated distribution (determined using I_d) for each sex and both sexes combined were then examined and samples having densities of copepods one standard deviation above the mean were arbitrarily chosen as aggregations, based on Hamner's (1988) definition, and used to compare mating and reproductive potential within and outside aggregations.

Evaluation of female mating potential:

Female mating potential was determined by counting the number of females carrying spermatophores in each sample. Female mating potential within aggregations was determined by calculating the proportion of females carrying spermatophores within a male aggregation. Female mating potential outside aggregations was determined by calculating the proportion of females carrying spermatophores in samples outside any aggregations. Data recorded to determine female mating potential included proportion of females carrying spermatophores per Schindler sample, and whether these females were found within a male aggregation or not.

Evaluation of female reproductive potential:

Reproductive potential was determined by calculating the number of females carrying clutches within each sample. Female reproductive potential within aggregations was determined by calculating the proportion of females carrying a clutch within a male aggregation. Female reproductive potential outside aggregations was determined by calculating the proportion of females carrying clutches in samples outside any aggregations. Data recorded included proportion of females carrying egg clutches per sample and whether these females were found within an aggregation or not.

Evaluation of average male mating potential:

Although it is well known that males contribute unequal numbers of spermatophores (i.e. some males are more successful at mating than others) (Gerritsen 1980, Grad & Maly 1988, Grad & Maly 1992, Neems *et al.* 1998, Michalska 2000) it is impossible under field conditions, where individuals roam freely, to determine the number of matings of each male captured. Therefore in this study I have determined the average mating potential, which is the potential for an average male to mate.

The number of spermatophores deposited per sample was used to measure male mating potential and samples considered to be from aggregations were then compared to the rest of the samples. Mating potential of males within aggregations was determined by calculating the proportion of males having potentially attached spermatophores within a female aggregation. Male mating potential outside aggregations was determined by calculating the proportion of males having potentially attached spermatophores in samples outside aggregations. Data recorded included proportion of males per sample having potentially deposited spermatophores and whether males were found within a female aggregation or not.

Evaluation of size difference between individuals found within and outside aggregations:

Samples from the 2000 field study were inadequately preserved making accurate measurement impossible. Due to this unforeseen effect, prosome length of males and females was determined from samples taken during the summer of 2001 from ponds L8 and L11.

The sampling technique used during the summer of 2001 was virtually identical to that used during the previous summer. Changes included three sampling efforts per sampling date (midday, afternoon and night). Ponds were sampled six times, pond L8 from July 2nd to August 2nd inclusively and pond L11 from July 5th to July 30th inclusively. Only midday samples were used for this analysis so as to most closely resemble the sampling regime during the previous summer. Only samples having both male and female aggregations were used to obtain the individuals that were to represent "aggregations".

Females and males within and outside aggregations were measured under a Wild inverted microscope at 30X magnification. The measurement taken was the prosomal length which is the distance from the tip of the head to the notch of the furcal rami (Figure 3). All lengths were recorded to the nearest ±0.01mm. Sixty females from aggregations and sixty-six females found outside aggregations were measured in pond L8. Seventy-eight females from aggregations and eighty-eight found outside aggregations were measured from pond L11. The number of males measured in pond L8 included eighty-one males from aggregations and seventy-two males found outside aggregations.

In the case of pond L11, fifty-nine males from aggregations and seventy-one males found outside aggregations were measured.

Evaluation of clutch size difference between females found within and outside aggregations:

Clutches used for the analysis came from all four ponds studied and were obtained during the first field season (summer 2000). Clutch size of females found within and outside aggregations (of males and females combined) was estimated by counting the number of eggs within an egg sac (i.e. clutch). Clutch size was determined under a Wild inverted microscope at 30X magnification. Ninety-two clutches from aggregations and one hundred and four found outside aggregations were examined for pond L6. One hundred and thirty-five clutches found within and one hundred and twenty-two found outside aggregations from pond L8 were examined. In the case of pond L10, one hundred and fifty-three clutches found within and one hundred and sixty-nine found outside aggregations were examined. Finally one hundred and forty-eight clutches found within aggregations and one hundred and fifty-nine found outside aggregations were examined from pond L11.

DATA ANALYSIS:

Determining the presence of aggregations:

Distribution patterns of *H. shoshone* and *L. coloradensis* were determined by the use of the un-standardized Morisita's Index of dispersion (I_d) (Appendix I) for all sampling times for each sampling date, as outlined in Krebs (1989). In order to test its significance a null hypothesis of randomness is tested by:

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

where χ^2= Tests statistic with a chi-square distribution

(Krebs 1989)

It was assumed that there was no change in spatial patterns during the time required to sample a pond. Each sample obtained provided a snapshot of *H. shoshone* and *L. coloradensis* numbers in a 2hr. time interval. Student's paired-sample *t* test was used to test whether there was a significant difference between I_d values across sexes (male, female) for both species.

All analyses of mating and reproductive potential as well as size difference were performed only on *H. shoshone* observations. Data points were separated into two groups (outside aggregation = Non, within aggregation = Aggr) for each pond.

Mating and reproductive potential:

Mating and reproductive potential were tested by performing paired *t*-tests and Sign tests (whenever data was not normal and could not be transformed) (data highly skewed). These tests were performed on the median, comparing samples found within and outside aggregations per date. A sampling date was considered a datum. Fisher's method for combining probabilities (Sokal & Rohlf 1995) was used then to combine all ponds for each analysis.

Size difference between aggregated and non-aggregated individuals:

Data was transformed using the Box-Cox transformation. Independent samples *t*-tests (Zar, 1996) were used to test whether individuals within aggregations were significantly larger than individuals outside aggregations. Each sampling effort was considered a datum in these analyses. Samples are believed to be sufficiently far apart both in space and time to be considered independent.

Difference between clutch size of aggregated and non-aggregated females:

Independent samples *t*-tests or Mann-Whitney U (Zar, 1996) were used to test whether clutches from females within aggregations were significantly larger (i.e. more eggs per clutch) than clutches from females outside aggregations. Each sampling effort was considered a datum in these analyses. Samples are believed to be sufficiently far apart both in space and time to be considered independent.

Figure 1. Map of ponds sampled during summer 2000 and 2001. Ponds sampled are labelled L6, L8, L10, and L11. Ponds are located in the "lower shelf" of the Mexican Cut Nature Preserve, Colorado, USA. (Figure modified from Wissinger and Whiteman 1992) Acid neutralizing capacity (ANC) refers to the ability to maintain the water pH.

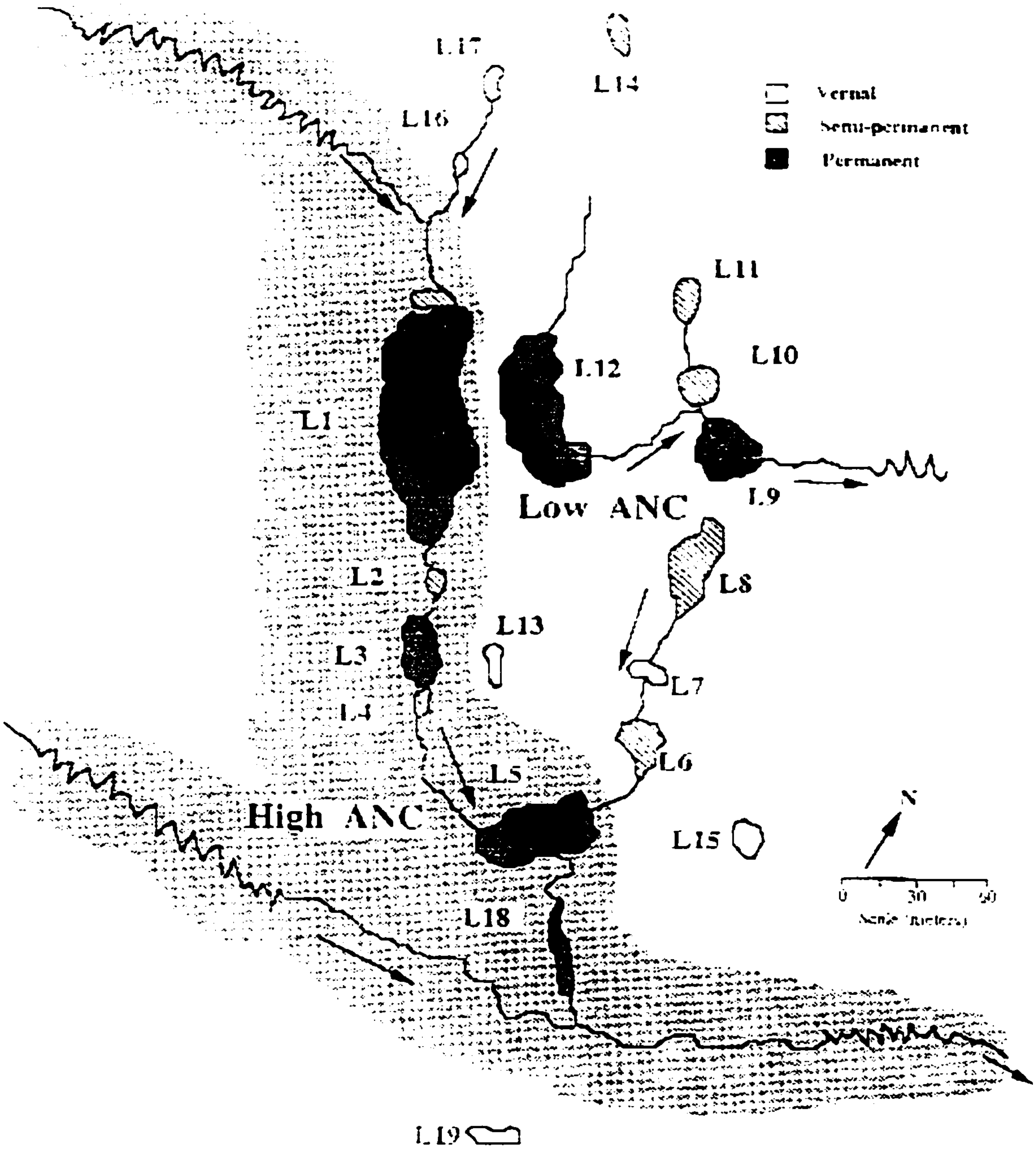
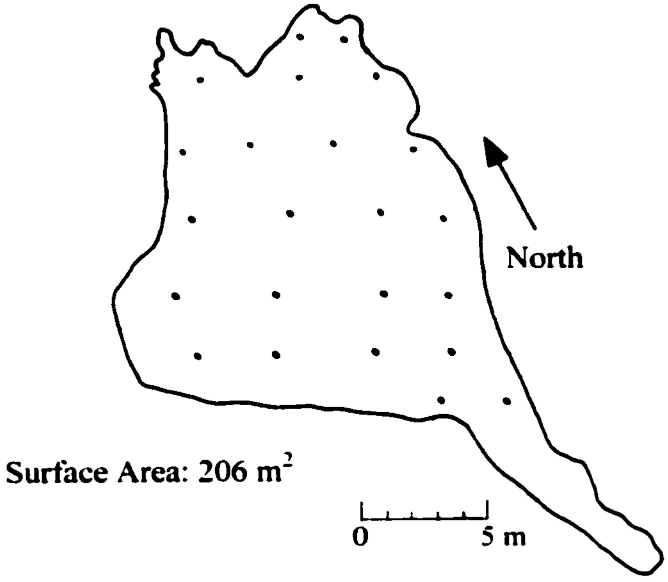
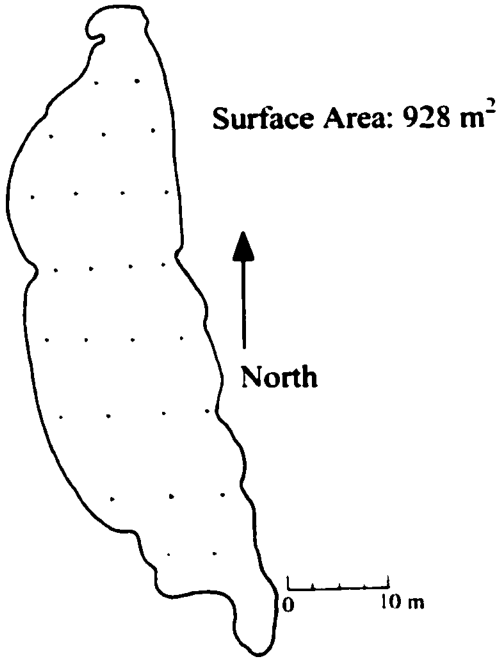

L17
L14
L16
Vernal
Semi-permanent
Permanent
L11
L10
L12
L1
L9
Low ANC
L2
L8
L13
L3
L7
L4
L6
L5
High ANC
L15
N
0
30
60
Scale (meters)
L18
L19

Figure 2. Diagram of each pond containing sampling grid. Each dot represents a sample location. Relative size of ponds is not representative of real dimensions. (Figures modified from S. Horn, unpublished)

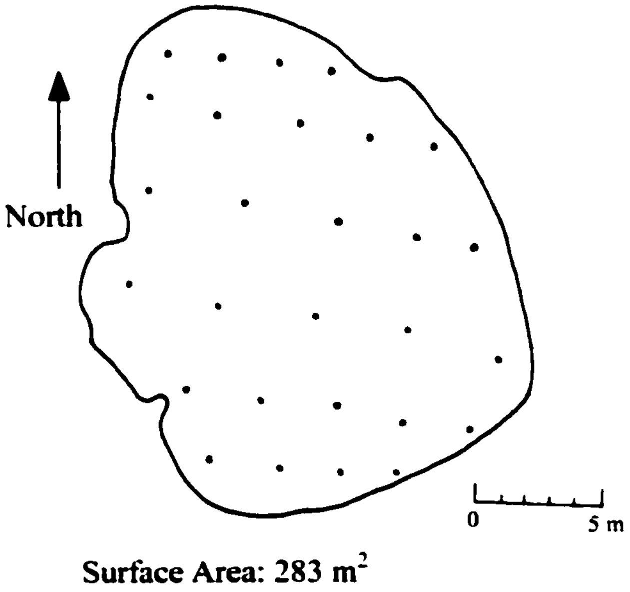
a) Pond L6



b) Pond L8



c) Pond L10



d) Pond L11

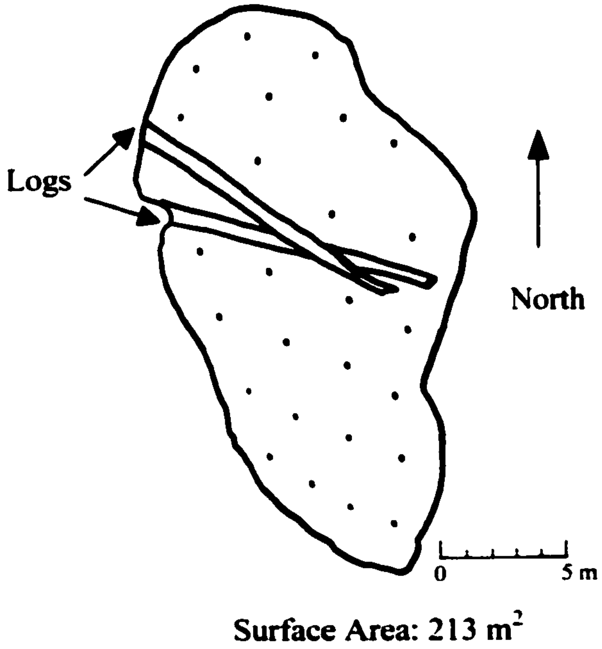
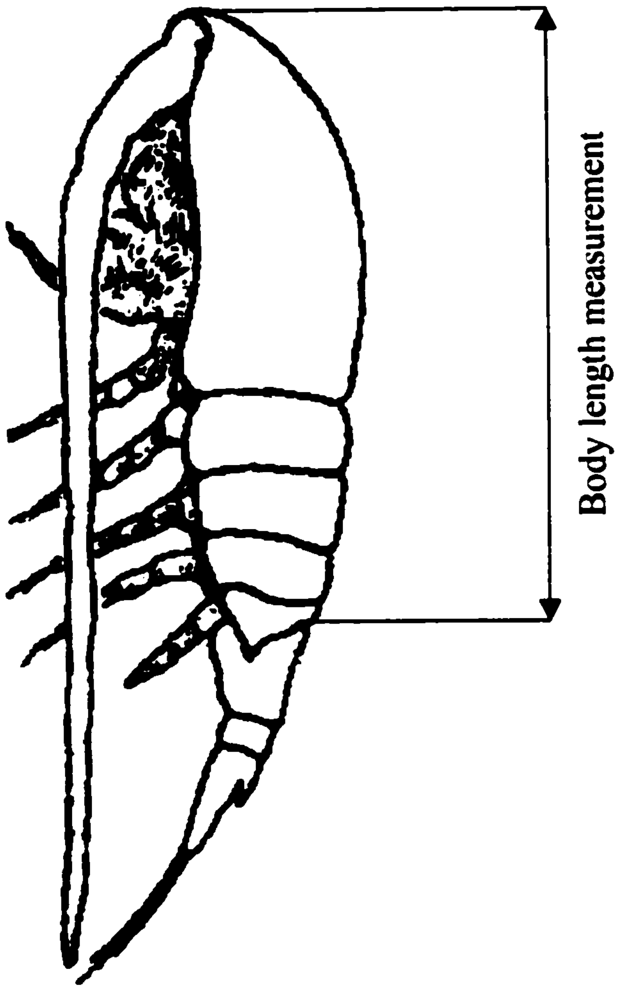


Figure 3. Schematic diagram of body length measurement taken on male and female *Hesperodiaptomus shoshone*.


Body length measurement

RESULTS:

Overall density, range and sampling variability for all 4 ponds and both species are compiled on Tables A and B, Appendix II.

Morisita's index of dispersion (I_d) results for *H. shoshone* are shown in Table 1. All I_d values obtained for ponds L6, L8 and L11 are significant across all dates, samples and sexes. Pond L10 I_d values are also significant for all dates with the exception of the June 26th female sample, which had an I_d value of 0.637 ($p > 0.05$). (Figure 4)

Morisita's index results for *L. coloradensis* are shown in Table 2. I_d values for pond L6, and L11 are not significant. Pond L8 I_d values were not significant across all samples except for the July 27th male ($0.005 < p < 0.05$) and both sexes ($p < 0.001$). Pond L10 I_d values were not significant for all male and female samples. Pond L10 both sexes samples were not significant except for July 17th ($p < 0.001$), July 25th ($0.005 < p < 0.050$) and July 29th ($p < 0.001$). (Figure 5)

Differences among Morisita's Index of Dispersion values:

Student's t test performed on *H. shoshone* values indicated no significant difference between sexes (male vs. female) for pond L6 ($t = -0.598$, d.f.= 14, $p = 0.560$), pond L8 ($t = -1.71$, d.f.= 14, $p = 0.190$), pond L10 ($t = 1.14$, d.f.= 16, $p = 0.270$), and pond L11 ($t = -0.926$, d.f.= 14, $p = 0.370$) (Figure 6).

Student's t test performed on *L. coloradensis* values indicated no significant difference between sexes (male vs. female) for pond L6 ($t = 0.744$, d.f.= 10, $p = 0.474$), pond L8 ($t = -1.385$, d.f.= 10, $p = 0.196$), pond L10 ($t = -0.326$, d.f.= 8, $p = 0.753$) and pond L11 ($t = 0.328$, d.f.= 12, $p = 0.748$) (Figure 7).

Female mating potential:

Comparison of medians per date in ponds L6 and L8 indicated that there is a significant difference between the proportion of *H. shoshone* females carrying spermatophores within male aggregations and those outside aggregations (Pond L6: t= 3.41, d.f.= 7, p= 0.011; L8: t= 3.10, d.f.= 7, p= 0.017). Ponds L10 and L11 analysis showed no significant difference but followed the same trend as the other two ponds (Pond L10: Sign test, p= 0.063; Pond L11: Sign test, p= 0.125) (Figure 8).

Combined Fisher's probability results indicated that overall the proportion of *H. shoshone* females carrying spermatophores within male aggregations was significantly higher than the proportion of females outside aggregations carrying spermatophores (χ^2= 26.86, p= 0.0007).

Average male mating potential:

Comparison of medians per date across all ponds indicated that the average mating potential of *H. shoshone* males within female aggregations was significantly higher than the average mating potential of males outside aggregations (Pond L6: t= 2.96, d.f.= 7, p= 0.021; Pond L8: t= 3.23, d.f.= 7, p= 0.014; Pond L10: t=2.88, d.f.= 8, p= 0.020; Pond L11: t= 2.80, d.f.= 7, p= 0.027). (Figure 9)

Combined Fisher's probability results indicated that overall the average mating potential of *H. shoshone* males within female aggregations was significantly higher than the average mating potential of males outside aggregations (χ^2= 31.31, p= 0.0001)

Female reproductive potential:

Comparison of medians per date across all ponds indicated that the proportion of clutched *H. shoshone* females within male aggregations was not significantly higher than the proportion of clutched *H. shoshone* females outside aggregations (Pond L6: t= 0.144, d.f.= 7, p= 0.890; Pond L8: t= 0.970, d.f.= 7, p= 0.365; Pond L10: t= -0.008, d.f.= 8, p= 0.994; Pond L11: t= 0.508, d.f.= 7, p= 0.627). (Figure 10)

Combined Fisher's probability results indicated that overall the proportion of clutched *H. shoshone* females within male aggregations was not significantly higher than the proportion of clutched *H. shoshone* females outside aggregations (χ^2= 3.194, p= 0.922).

Size difference between aggregated and non-aggregated individuals' results:

In pond L8 *H. shoshone* female size within and outside aggregations differed significantly (t=2.46, n_{Aggr}=60, n_{Non}=66, p=0.017) with females within "male/female" aggregations being significantly larger than females outside aggregations. Pond L11 *H. shoshone* female size t-test results were also significant with females within aggregations being significantly larger than females outside aggregations (t=2.72, n_{Aggr}=78, n_{Non}=88, p=0.008). Figure 11 is a graphical representation of the size difference between aggregated and non-aggregated females for ponds L8 and L11.

Male size did not differ significantly in either pond (pond L8: t=-1.44, n_{Aggr}=81, n_{Non}=72, p= 0.153; pond L11: Mann-Whitney U= 202.500, n_{Aggr}=59, n_{Non}=71, p= 0.796). Furthermore in pond L8 males outside aggregations were overall larger than males within 'male/female" aggregations. Figure 12 is a graphical representation of the size difference between aggregated and non-aggregated males for ponds L8 and L11.

Difference between clutch size of aggregated and non-aggregated females:

In pond L6 females within aggregations had clutches that were significantly larger (i.e. more eggs per clutch) than females outside aggregations ($t=2.317$, $n_{Aggr}=92$, $n_{Non}=104$, $p=0.022$). The same was true for pond L8 (Mann-Whitney U= 5262, $n_{Aggr}=135$, $n_{Non}=122$, p= 3.489e-007), pond L10 (Mann-Whitney U= 10733, $n_{Aggr}=153$, $n_{Non}=169$, p= 0.0067) and pond L11 ($t=5.880$, $n_{Aggr}=148$, $n_{Non}=159$, p= 1.075e-008). (Figure 13)

Table 1. Morisita's Index of Dispersion values (I_d) for *H. shoshone* for all four ponds across all sampling dates. P values calculated using X^2 distribution table (Zar, 1996)

Pond	Date	Male		Female		Both	
		I_d	(p)	I_d	(p)	I_d	(p)
L6	27-Jun	1.4576	$p < 0.001$	1.9683	$p < 0.001$	1.5373	$p < 0.001$
	30-Jun	1.2954	$p < 0.001$	1.4994	$p < 0.001$	1.1960	$p < 0.001$
	5-Jul	1.4703	$p < 0.001$	1.7276	$p < 0.001$	1.4315	$p < 0.001$
	8-Jul	1.2714	$p < 0.001$	1.2649	$p < 0.001$	1.2840	$p < 0.001$
	15-Jul	1.7279	$p < 0.001$	2.2529	$p < 0.001$	1.5863	$p < 0.001$
	19-Jul	1.7052	$p < 0.001$	1.5883	$p < 0.001$	1.3296	$p < 0.001$
	22-Jul	1.6965	$p < 0.001$	1.5883	$p < 0.001$	1.4040	$p < 0.001$
	27-Jul	1.7611	$p < 0.001$	1.1799	$p < 0.001$	1.5002	$0.025<p<0.05$
L8	21-Jun	1.6981	$p < 0.001$	1.2248	$0.01<p<0.05$	1.4120	$p < 0.001$
	29-Jun	1.5750	$p < 0.001$	1.6915	$p < 0.001$	1.6299	$p < 0.001$
	5-Jul	1.1578	$p < 0.001$	1.4540	$p < 0.001$	1.1014	$p < 0.001$
	8-Jul	1.4124	$p < 0.001$	2.3178	$p < 0.001$	1.3461	$p < 0.001$
	15-Jul	1.7113	$p < 0.001$	2.1808	$p < 0.001$	1.8110	$p < 0.001$
	19-Jul	1.8189	$p < 0.001$	2.6203	$p < 0.001$	1.7004	$p < 0.001$
	22-Jul	1.1384	$0.01<p<0.05$	1.7920	$p < 0.001$	1.1661	$p < 0.001$
	27-Jul	1.4978	$p < 0.001$	1.4045	$p < 0.001$	1.3486	$p < 0.001$
L10	26-Jun	1.2299	$0.025<p<0.05$	0.6369	$P > 0.999$	1.4865	$p < 0.001$
	29-Jun	1.8358	$p < 0.001$	2.2438	$p < 0.001$	1.5169	$p < 0.001$
	01-Jul	1.3986	$p < 0.001$	1.9547	$p < 0.001$	1.4987	$p < 0.001$
	06-Jul	1.4749	$p < 0.001$	1.5000	$p < 0.001$	1.4779	$p < 0.001$
	13-Jul	2.0206	$p < 0.001$	1.7813	$p < 0.001$	1.7461	$p < 0.001$
	17-Jul	2.7543	$p < 0.001$	1.6490	$p < 0.001$	1.9928	$p < 0.001$
	20-Jul	1.7395	$p < 0.001$	1.2959	$p < 0.001$	1.5142	$p < 0.001$
	25-Jul	1.4935	$p < 0.001$	1.3784	$p < 0.001$	1.3835	$p < 0.001$
	29-Jul	2.0357	$p < 0.001$	1.3115	$p < 0.001$	1.6746	$p < 0.001$
L11	27-Jun	1.1743	$p < 0.001$	1.1421	$0.005<p<0.05$	1.1142	$p < 0.001$
	1-Jul	1.2275	$p < 0.001$	1.3478	$p < 0.001$	1.2291	$p < 0.001$
	6-Jul	1.3156	$p < 0.001$	1.4932	$p < 0.001$	1.2951	$p < 0.001$
	13-Jul	1.6238	$p < 0.001$	1.5321	$p < 0.001$	1.5235	$p < 0.001$
	17-Jul	1.3174	$p < 0.001$	1.2819	$p < 0.001$	1.3182	$p < 0.001$
	20-Jul	1.3563	$p < 0.001$	1.2620	$p < 0.001$	1.2929	$p < 0.001$
	25-Jul	1.7228	$0.005<p<0.05$	1.4916	$p < 0.001$	1.4624	$p < 0.001$
	29-Jul	1.2789	$p < 0.001$	3.8352	$p < 0.001$	1.3351	$p < 0.001$

Figure 4. Plots of the Morisita's index of dispersion values for *H. shoshone* across all dates. Solid circles # represent male values, open circles) represent female values and inversed triangles &represent both sexes combined. Dotted line delimits areas of different distribution: values greater than 1 = aggregated, values less than or equal to 1 = uniform or random distributions.

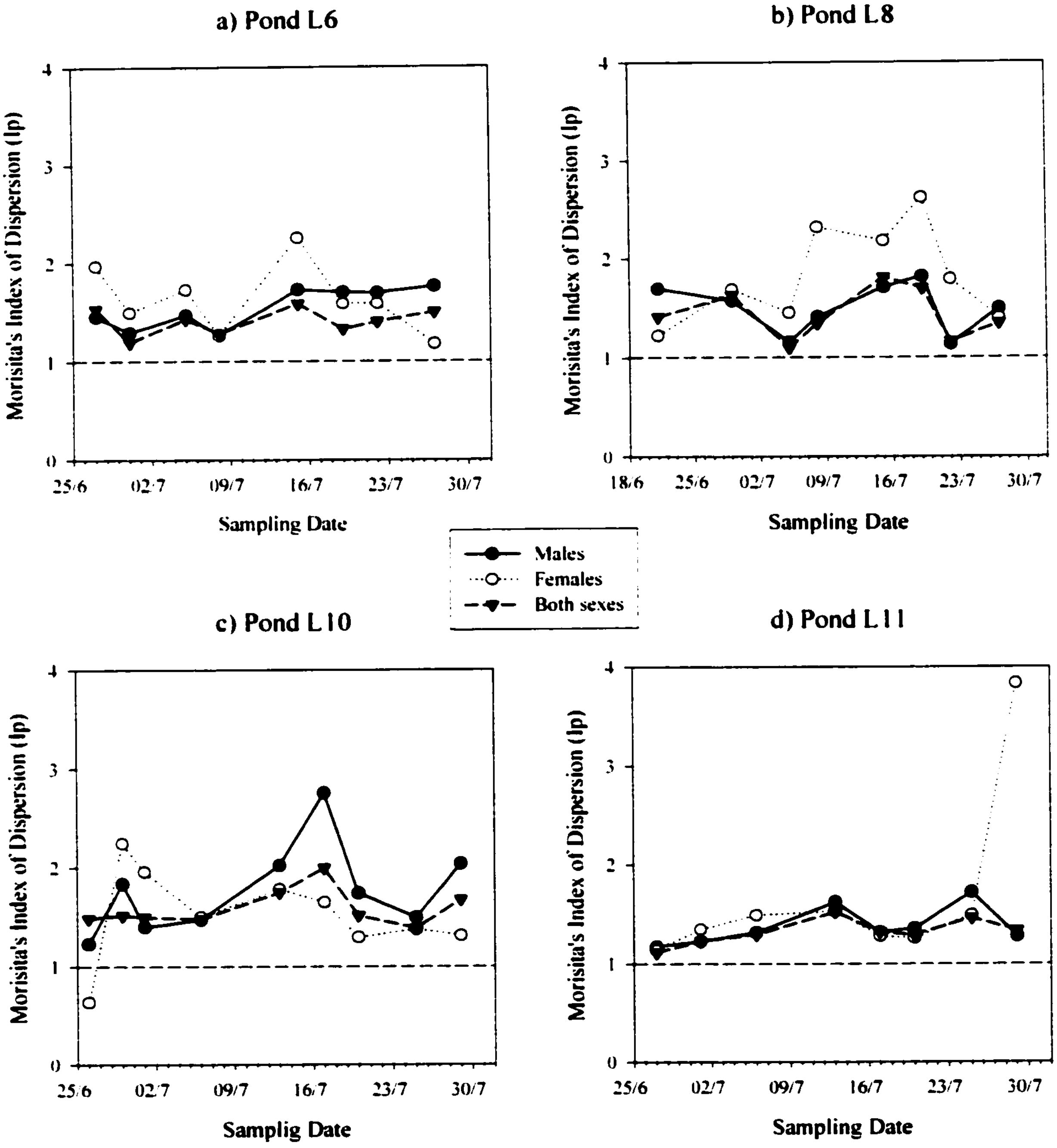

a) Pond L6
b) Pond L8
c) Pond L10
d) Pond L11
Morisita's Index of Dispersion (Ip)
0
1
2
3
4
25/6
02/7
09/7
16/7
23/7
30/7
18/6
Sampling Date
Samplig Date
Males
Females
Both sexes

Table 2. Morisita's Index of Dispersion values (I_d) for *L. coloradensis* for all four ponds for all sampling dates. Significance was calculated using Chi-square critical values table. (Zar 1996)

Pond	Date	Male		Female		Both	
		I_d	(p)	I_d	(p)	I_d	(p)
L6	27-Jun	-	-	-	-	-	-
	30-Jun	-	-	-	-	-	-
	5-Jul	1.0771	$0.5>p >0.25$	1.1756	$0.10 >p >0.05$	1.0265	$0.25 >p >0.10$
	8-Jul	1.0881	$0.10 >p >0.05$	0.8861	$0.75 >p >0.50$	1.0335	$0.25 >p >0.10$
	15-Jul	1.0021	$0.25 >p >0.25$	0.9226	$0.5 >p >0.25$	0.9824	$0.5 >p >0.25$
	19-Jul	1.0076	$0.25 >p >0.25$	0.9601	$0.95 >p >0.90$	0.9965	$0.5 >p >0.25$
	22-Jul	0.9759	$0.975 >p >0.95$	0.9852	$0.75 >p >0.50$	0.9967	$0.5 >p >0.25$
	27-Jul	0.9942	$0.5 >p >0.25$	1.0123	$0.5 >p >0.25$	1.0016	$0.5 >p >0.25$
L8	21-Jun	-	-	-	-	-	-
	29-Jun	-	-	-	-	-	-
	5-Jul	0	$0.95 >p >0.90$	1.3333	$0.5 >p >0.25$	1.2987	$0.25 >p >0.10$
	8-Jul	0.9115	$0.975 >p >0.95$	1.0891	$0.25 >p >0.10$	0.9999	$0.50 >p >0.25$
	15-Jul	1.0036	$0.50 >p >0.25$	1.0255	$0.25 >p >0.10$	1.0079	$0.25 >p >0.10$
	19-Jul	1.0134	$0.25 >p >0.10$	0.9531	$0.975 >p >0.95$	1.0048	$0.25 >p >0.10$
	22-Jul	1.0209	$0.1 >p >0.05$	1.0239	$0.05 >p > 0.025$	1.0052	$0.05 >p > 0.025$
	27-Jul	1.0199	$0.05 >p > 0.005$	1.0021	$0.50 >p >0.25$	1.0368	$p < 0.001$
L10	26-Jun	-	-	-	-	-	-
	29-Jun	-	-	-	-	-	-
	01-Jul	-	-	-	-	-	-
	06-Jul	-	-	-	-	-	-
	13-Jul	1.0807	$0.1 >p >0.05$	1.0585	$0.5 >p >025$	1.0480	$0.25 >p >0.10$
	17-Jul	1.0443	$0.1 >p >0.05$	1.0389	$0.25 >p >0.10$	1.0660	$p < 0.001$
	20-Jul	1.0224	$0.25 >p >0.10$	1.0781	$0.25 >p >0.10$	1.0269	$0.1 >p >0.05$
	25-Jul	1.0156	$0.1 >p >0.055$	1.0171	$0.25 >p >0.10$	1.0174	$0.05 >p > 0.005$
	29-Jul	1.0102	$0.1 >p >0.0505$	1.0101	$0.1 >p >0.05$	1.0128	$p < 0.001$
L11	27-Jun	-	-	-	-	-	-
	1-Jul	1.0104	$0.25 >p > 0.10$	1.0269	$0.5 >p > 0.25$	1.0019	$0.5 >p > 0.25$
	6-Jul	1.0020	$0.5 >p > 0.25$	0.9571	$0.90 >p > 0.75$	1.0058	$0.5 >p > 0.25$
	13-Jul	0.9774	$0.75 >p > 0.5$	1.0119	$0.5 >p > 0.25$	0.9999	$0.5 >p > 0.25$
	17-Jul	1.0497	$0.25 >p > 0.10$	1.0070	$0.5 >p > 0.25$	1.0198	$0.25 >p > 0.10$
	20-Jul	1.0600	$0.10 >p > 0.05$	1.0833	$0.25 >p > 0.10$	1.0460	$0.10 >p > 0.05$
	25-Jul	1.1073	$0.10 >p > 0.05$	1.0064	$0.5 >p > 0.25$	1.0467	$0.25 >p > 0.10$
	29-Jul	1.0044	$0.5 >p > 0.25$	1.0656	$0.5 >p > 0.25$	1.0361	$0.25 >p > 0.10$

Figure 5. Plots of the Morisita's index of dispersion for *L. coloradensis* across all dates. Solid circles # represent male values, open circles) represent female values and inversed triangles & represent both sexes combined. Dotted line delimits areas of different distribution: values greater than 1 = aggregated, values less than or equal to 1 = uniform or random distributions. Asterisks (*) indicate dates during which no adults were present in the samples.

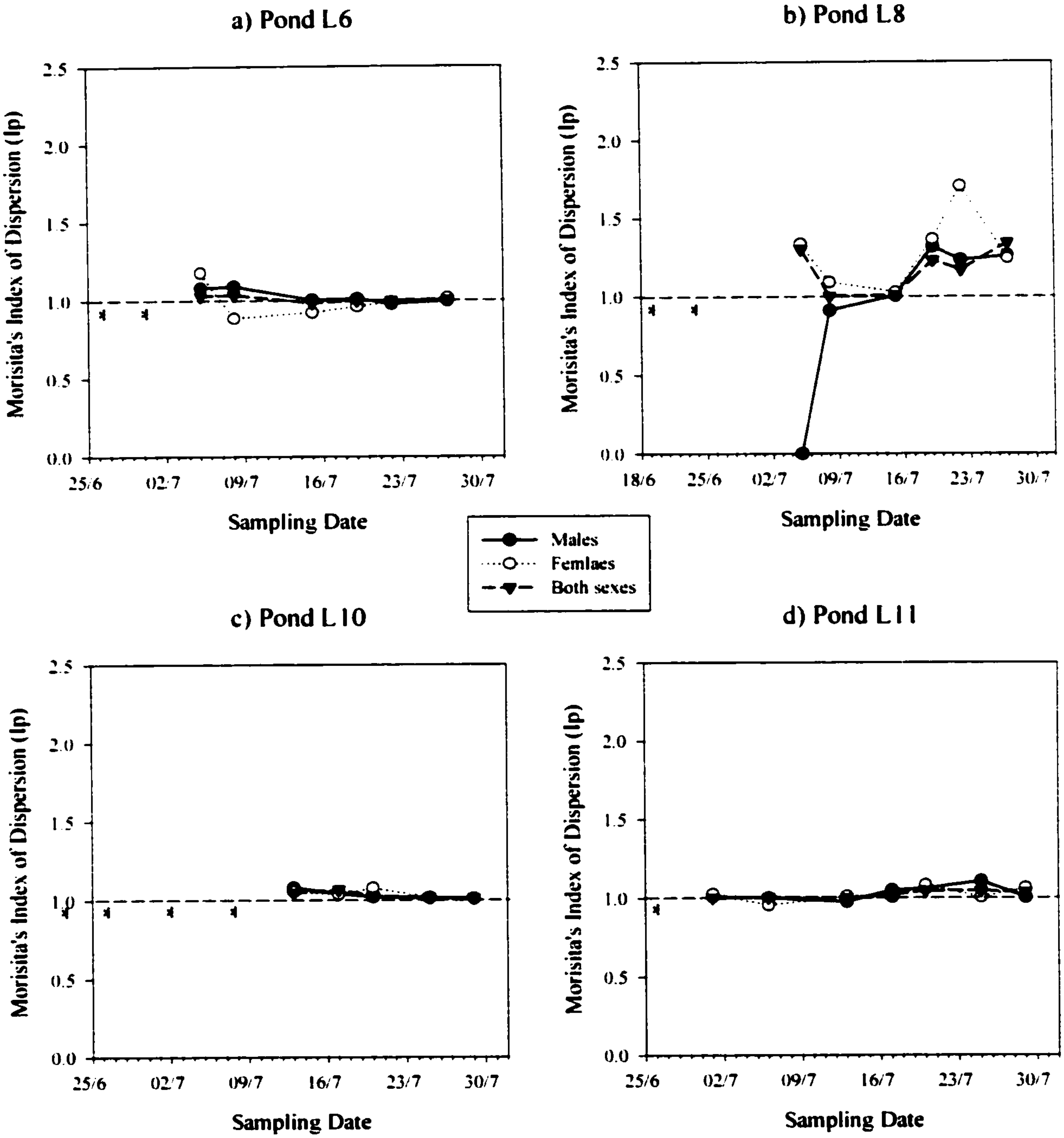
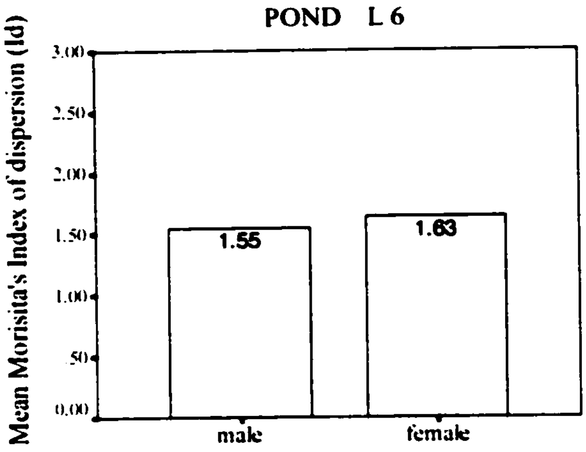
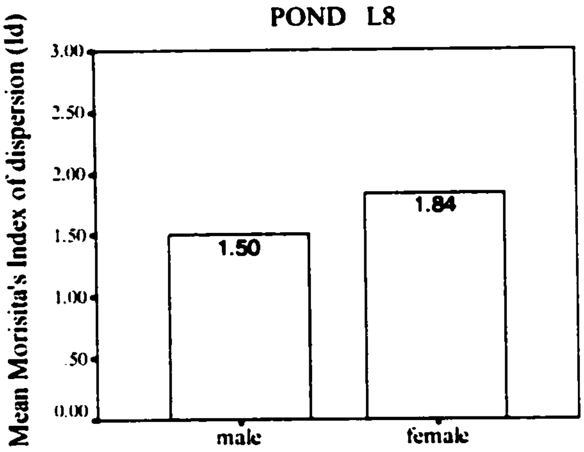

a) Pond L6
b) Pond L8
c) Pond L10
d) Pond L11
Morisita's Index of Dispersion (Ip)
2.5
2.0
1.5
1.0
0.5
0.0
18/6
25/6
02/7
09/7
16/7
23/7
30/7
Sampling Date
Males
Femlaes
Both sexes

Figure 6. Bar diagrams comparing mean Morisita's index of dispersion values between sexes for every pond for *H. shoshone*. Value within each bar is the exact mean I_d for each sex for each pond.

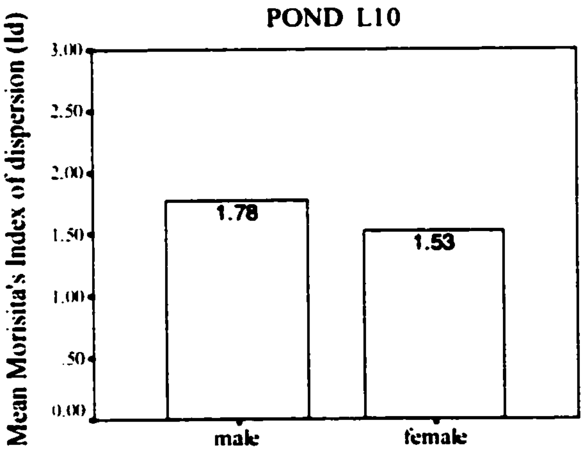
a)


POND L 6
Mean Morisita's Index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.55
1.63
male
female

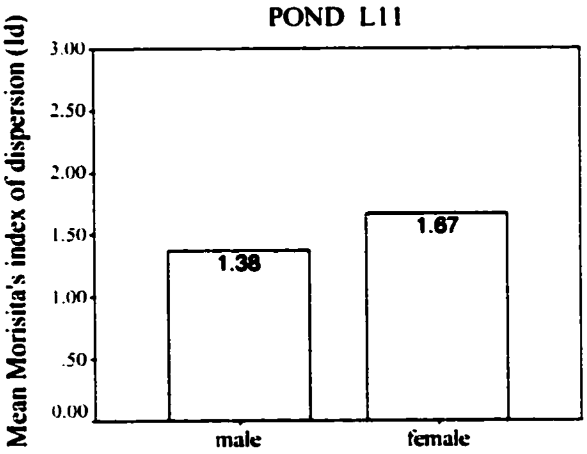
b)


POND L8
Mean Morisita's Index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.50
1.84
male
female

c)

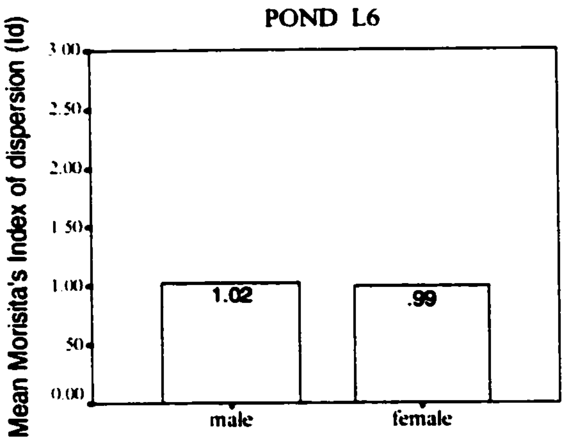

POND L10
Mean Morisita's Index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.78
1.53
male
female

d)

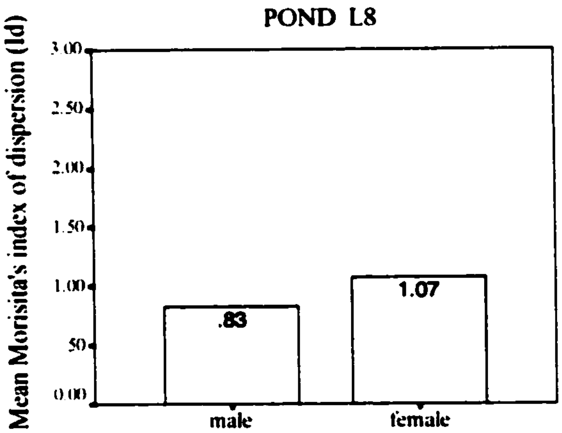

POND L11
Mean Morisita's index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.38
1.67
male
female

Figures 7. Bar diagrams comparing mean Morisita's index of dispersion values between sexes for every pond for *L coloradensis*. Value within each bar is the exact mean Id for each sex for each pond.

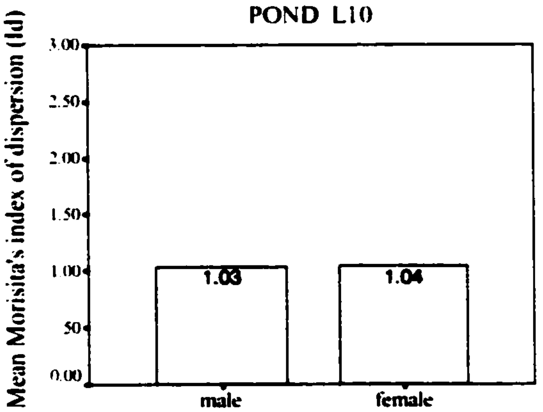
a)


POND L6
Mean Morisita's Index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.02
.99
male
female

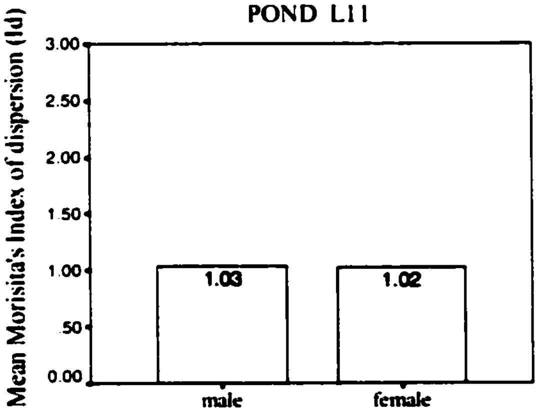
b)


POND L8
Mean Morisita's index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
.83
1.07
male
female

c)


POND L10
Mean Morisita's index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.03
1.04
male
female

d)


POND L11
Mean Morisita's Index of dispersion (Id)
3.00
2.50
2.00
1.50
1.00
.50
0.00
1.03
1.02
male
female

Figures 8. Median of proportion females with attached spermatophores for all ponds across all dates within aggregations versus outside aggregations (Aggr. vs. Non)

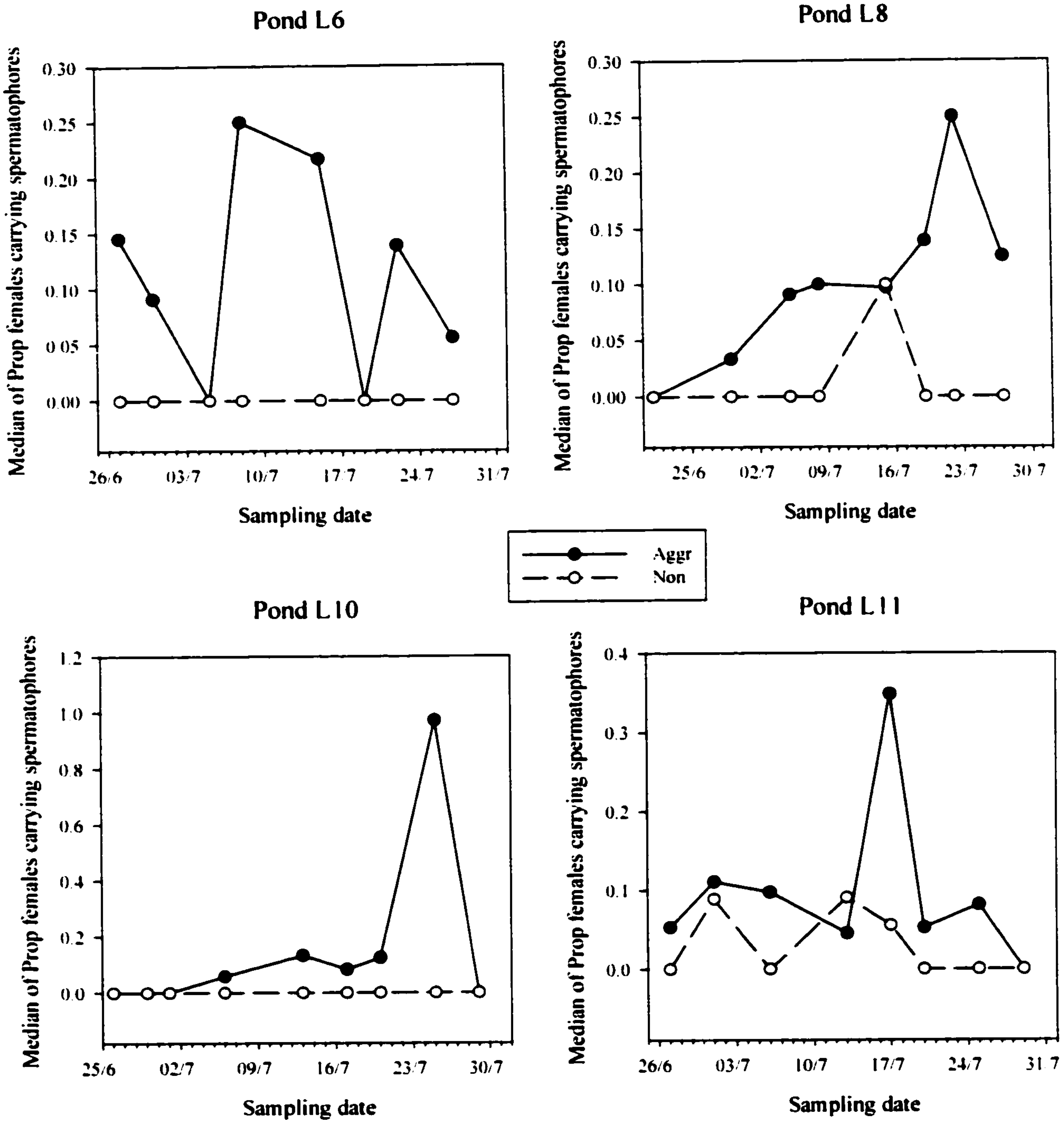

Pond L6
Median of Prop females carrying spermatophores
0.30
0.25
0.20
0.15
0.10
0.05
0.00
26/6
03/7
10/7
17/7
24/7
31/7
Sampling date
Pond L8
Median of Prop females carrying spermatophores
0.30
0.25
0.20
0.15
0.10
0.05
0.00
25/6
02/7
09/7
16/7
23/7
30/7
Sampling date
Aggr
Non
Pond L10
Median of Prop females carrying spermatophores
1.2
1.0
0.8
0.6
0.4
0.2
0.0
25/6
02/7
09/7
16/7
23/7
30/7
Sampling date
Pond L11
Median of Prop females carrying spermatophores
0.4
0.3
0.2
0.1
0.0
26/6
03/7
10/7
17/7
24/7
31/7
Sampling date

Figure 9. Median of average male mating potential for all ponds across all dates within aggregations versus outside aggregations (Aggr. vs. Non)

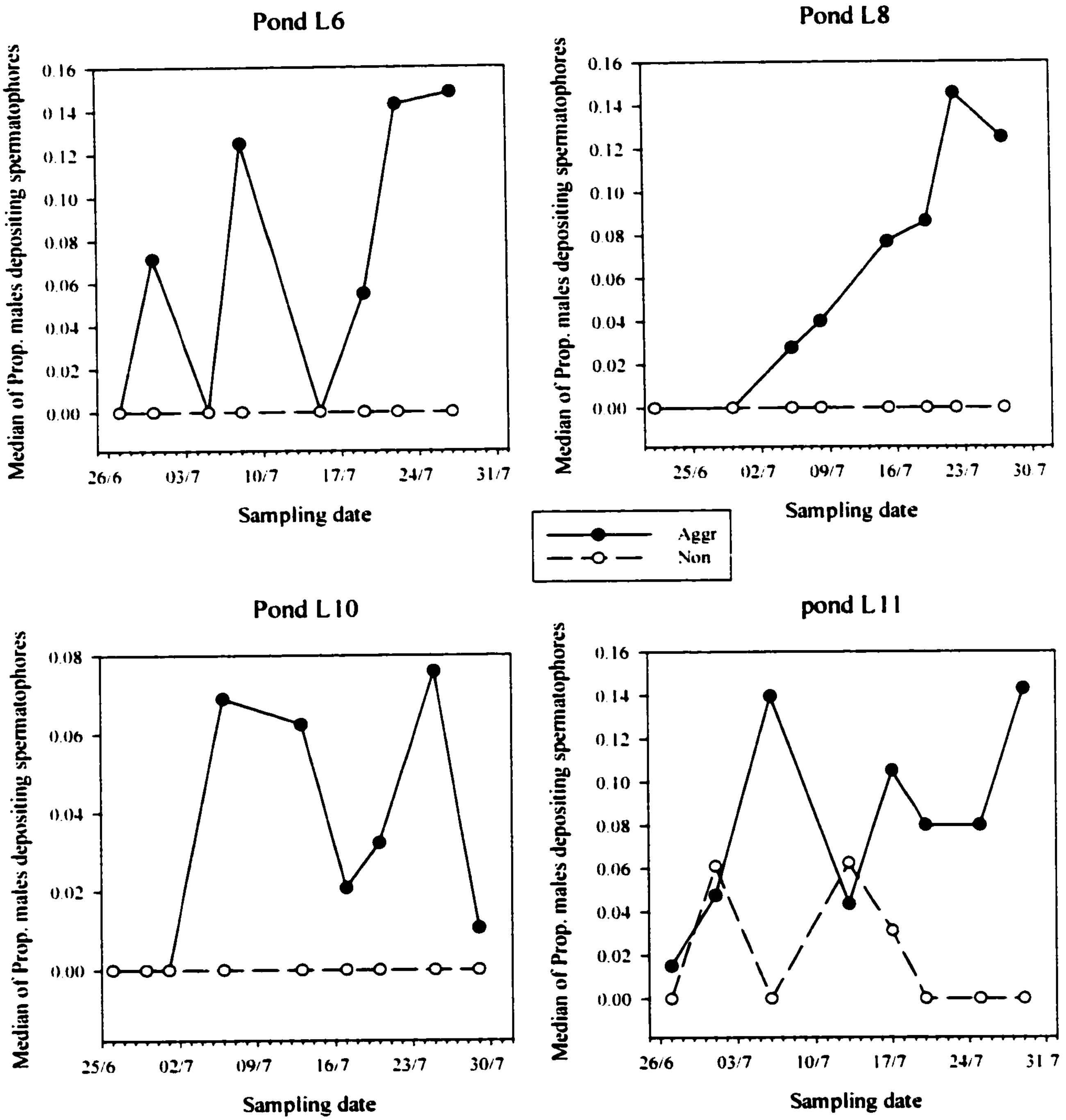

Pond L6
Median of Prop. males depositing spermatophores
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
26/6
03/7
10/7
17/7
24/7
31/7
Sampling date
Pond L8
Median of Prop. males depositing spermatophores
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
25/6
02/7
09/7
16/7
23/7
30/7
Sampling date
Aggr
Non
Pond L10
Median of Prop. males depositing spermatophores
0.08
0.06
0.04
0.02
0.00
25/6
02/7
09/7
16/7
23/7
30/7
Sampling date
pond L11
Median of Prop. males depositing spermatophores
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
26/6
03/7
10/7
17/7
24/7
31/7
Sampling date

Figure 10. Median of proportion females carrying clutches for all ponds across all dates within aggregations versus outside aggregations (Aggr. vs. Non)

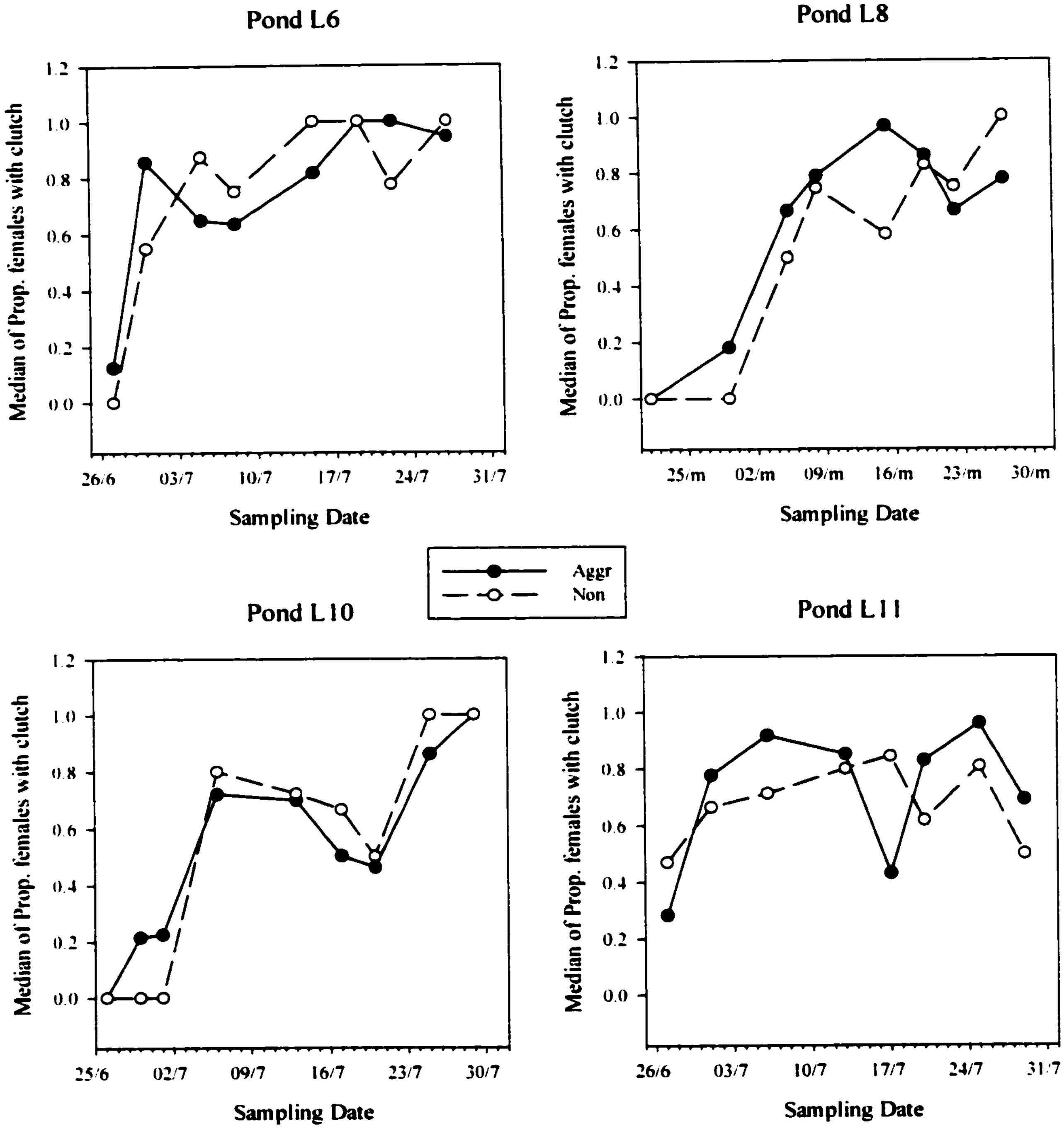

Pond L6
Pond L8
Pond L10
Pond L11
Median of Prop. females with clutch
1.2
1.0
0.8
0.6
0.4
0.2
0.0
26/6
03/7
10/7
17/7
24/7
31/7
25/m
02/m
09/m
16/m
23/m
30/m
25/6
02/7
09/7
16/7
23/7
30/7
Sampling Date
Aggr
Non

Figure 11. Female size difference between individuals found within and outside aggregations for ponds L8 and L11. The Y-axis indicates female size (mm) and the X-axis indicates whether individuals belong to an aggregation or not. The box represents the interquartile range which contains the 50% of values. The lines extend from the box to the highest and lowest values and the line across the box indicates the median.

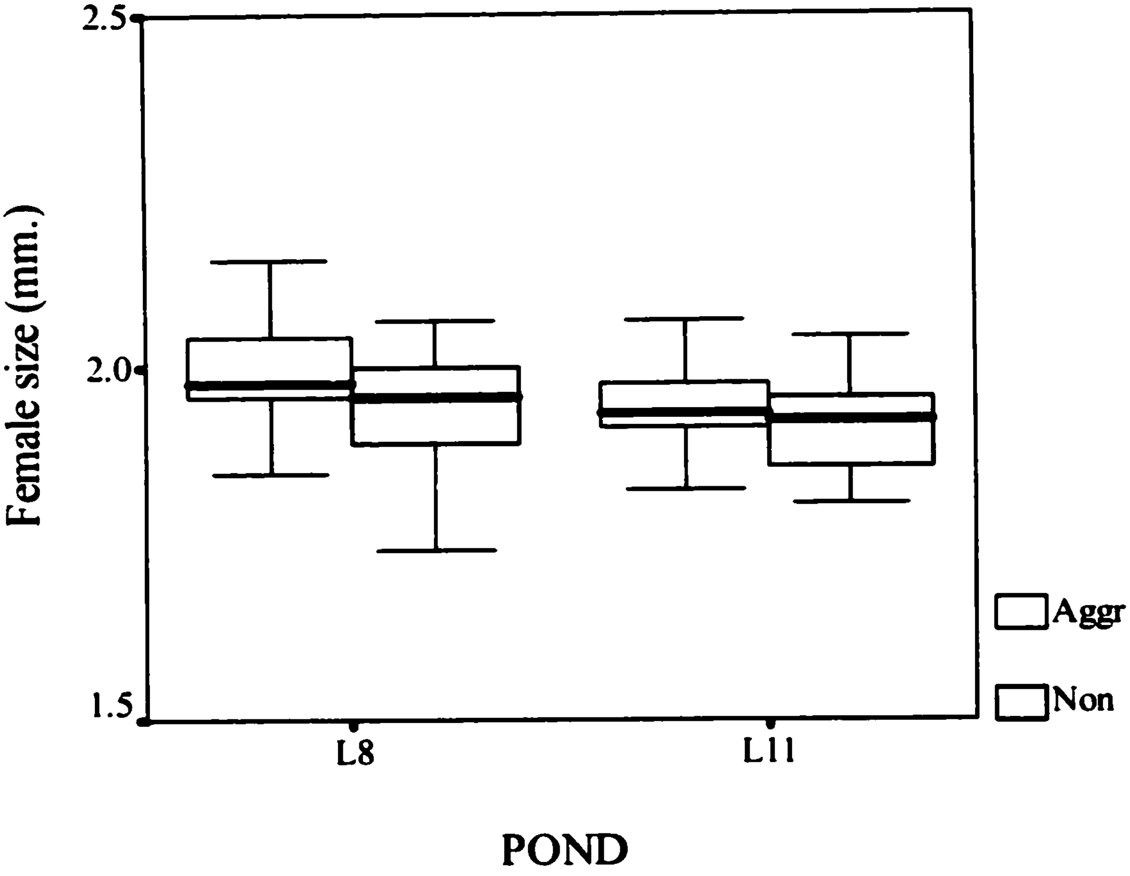

2.5
2.0
1.5
Female size (mm.)
L8
L11
POND
Aggr
Non

Figure 12. Male size difference between individuals found within and outside aggregations for ponds L8 and L11. The Y-axis indicates male size (mm) and the X-axis indicates whether individuals belong to an aggregation or not. The box represents the interquartile range which contains the 50% of values. The lines extend from the box to the highest and lowest values and the line across the box indicates the median.

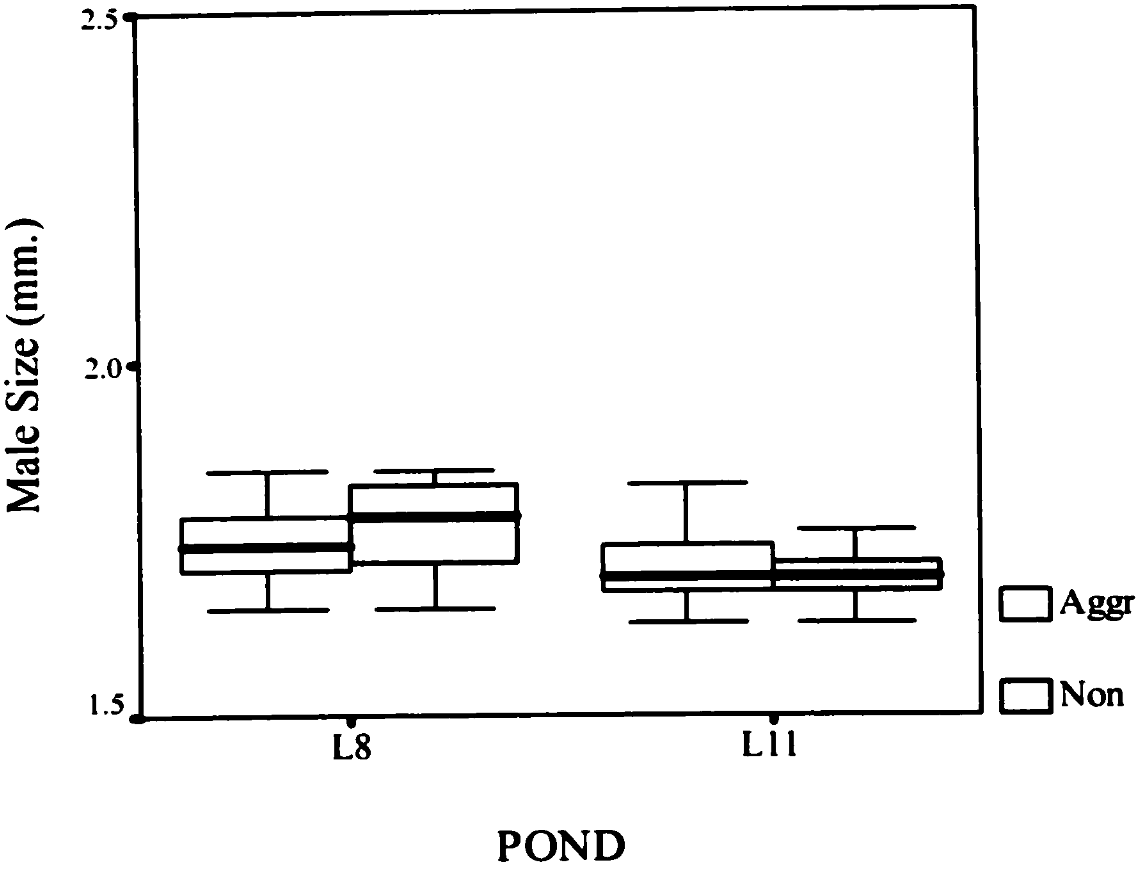
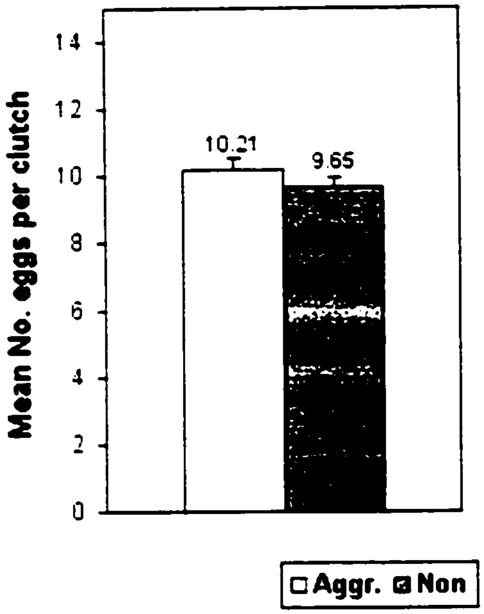
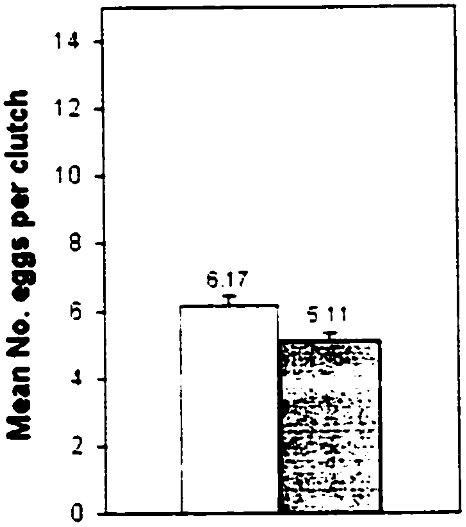

2.5
2.0
1.5
Male Size (mm.)
L8
L11
POND
☐ Aggr
☐ Non

Figure 13. Number of eggs per clutch for ponds L6, L8, L10 and L11. The X-axis indicates the number of eggs per clutch and Y-axis whether the clutches came from females found within or outside aggregations. Error bars represent 95% confidence limit of the means.

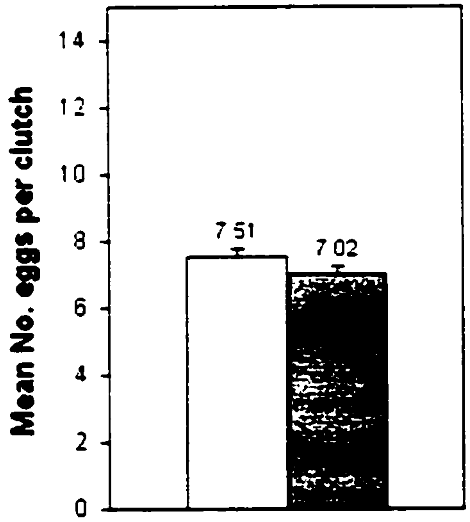
a) Pond L6:



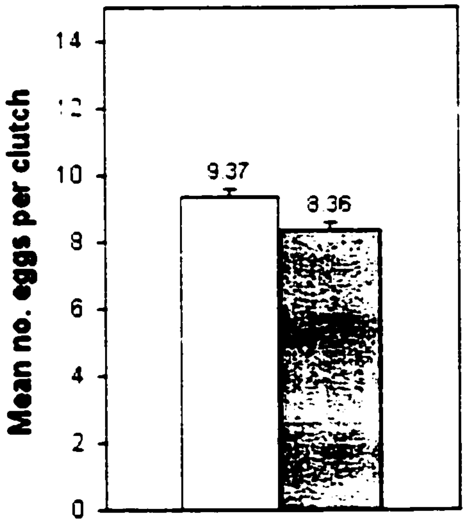
b) Pond L8:



c) Pond L10:



d) Pond L11:



DISCUSSION:

Objective I:

The first goal of this research was to test whether *H. shoshone* and *L. coloradensis* had patchy distributions by means of the commonly used Morisita's Index of dispersion (Hurlbert 1990, Gonzáles *et al.* 1999, Xavier & Suesdek Rocha 2001).

Results indicated that *H. shoshone* indeed had overall a significantly patchy distribution across all ponds. On the other hand *L. coloradensis* I_d values were overall not significant indicating that its distribution resembled more closely that of a random pattern regardless of sex or date. Several possible hypotheses can explain the discrepancy observed between the distributions of *H. shoshone* and *L. coloradensis*.

Although attraction to a common source may be responsible for the creation of the aggregation, repulsion also plays a crucial role in determining group structure (Parrish & Hamner 1980). Uncontrolled attraction would end up in an aggregation so dense that the costs to individual members would quickly outweigh the benefits. As density increases, basic resources such as food are depleted faster than they can be replenished. At the same time other repulsion forces such as increased risk of predation also affect the group structure. Thus it is the combination of attractive and repulsive forces that should define the physical attributes of the group and in turn give shape to the spatial pattern being observed.

In this study the marked difference in distribution between the two species may be the result of marked differences in the strength/influence of the attractive (mates, food) and repulsive (predators, food depletion) forces shaping their spatial distribution (Jakobsen & Johnsen 1988). In a laboratory evaluation of costs and benefits of aggregative behaviour in terms of feeding rates in two species of copepods from Lake Tahoe, Folt (1987) concluded that although aggregation was costly, it was also beneficial in terms of avoiding predation (Parrish & Hamner 1980)

Leptodiaptomus coloradensis main predators are *H. shoshone* and the tiger salamander *Ambystoma tigrinum* to a much lesser degree (Wissinger & Whiteman 1992, Wissinger *et al.* 1999b). The main source of nutrients for *L. coloradensis* is phytoplankton, and to a lesser extent pollen and spores found in water column in these ponds (Sprules 1972, Maly & Maly 1974). Since *L. coloradensis* is multivoltine in the populations being studied its density remains high throughout the summer (Maly and Maly 1974). These high densities were observed across the ponds surfaces sampled indicating a more or less uniform distribution of *L. coloradensis*. Personal observations made by Wissinger and Whiteman indicate that the distribution of phytoplankton in the ponds is not overly patchy with densities considered low to intermediate (water clarity high). It may be possible that low food conditions affect the distribution of *L. coloradensis*. According to Jakobsen & Johnsen (1988) *Daphnia sp.* tend to disperse in low food conditions and same response has been reported by several other authors studying fish (Hunter 1966, Robinson & Pitcher 1989). The fact that aggregations tend to diffuse when food resources are limited may indicate that there is a sort of threshold bellow which aggregating is not beneficial and therefore that tactic is abandoned. And although predation pressure may be high the need to feed overrides the need for safety. Therefore, in this case predation pressure may be lower compared to the feeding needs of each individual and as a result *L. coloradensis* distribution resembles more the distribution of its food source, phytoplankton.

On the other hand the food sources for *H. shoshone* are varied and abundant. They include all phytoplankton species, *L. coloradensis* adults and *H. shoshone* nauplii among others (Wong 1983). These prey species are present throughout the summer and are quite abundant except for *H. shoshone* nauplii which disappear early in the summer. While the predatory nature of *H. shoshone* makes nutrition an important driver in their distribution. and although individuals in smaller groups should achieve satiation more quickly than those in large aggregations, when a predator threatens, the per capita risk in small aggregations is high relative to individuals in larger groups (Parrish & Hamner 1980). *Ambystoma tigrinum* hatchlings and one to two year larvae feed heavily on *H. shoshone* (Batzer *et al.* 1999) making predation a very important factor controlling both density and distribution of *H. shoshone*. *Hesperodiaptomus shoshone* is a univoltine species producing only a single generation each summer and the reduction in numbers caused by predation could affect significantly the overall density of the populations and their overall reproductive success. They are also brightly coloured (Byron 1982) and therefore highly visible to predators such as *A. tigrinum* salamanders, which are known as keystone predators on this species of zooplankton and undoubtedly affect significantly the distribution and abundance of *H. shoshone* (Dobson 1970, 1974). In a study by Parrish & Hamner (1980) mysid swarms tended to rapidly become more compact after feeding and similar results were observed in other experimental studies with fish (Hunter 1966, Robinson & Pitcher 1989) indicating that there may be a trade-off between maximising inter-individual spacing for foraging versus anti-predation. At the same time the stability of predator-prey interactions may be affected by the patchy distribution of prey (*H. shoshone*) with predators concentrating their attack where the prey is abundant (Turchin 1989). Consequently in the case of *H. shoshone* predation pressure may be a more important factor than food dispersion and consumption, and therefore may strongly influence their distribution (i.e. patchy).

Another interesting hypothesis that may explain the difference in the distribution patterns between *H. shoshone* and *L. coloradensis* is that proposed by Young *et al.* (1994) in their study with *Daphnia longispina* and *Daphnia magna*. In that study relatedness was investigated as a cue for aggregative behaviour. Their survey found that the majority of individual *Daphnia* sampled from a swarm shared the same esterase band pattern. Their laboratory study showed that the swarm formation is facilitated by the presence of clone-mates and, since swarms can occur in the dark, it may involve own–clone recognition cues, most likely semiochemical (chemical signalling or recognition of specific compounds). In the case of copepods the tendency to form aggregations may also be genetic (as seen in *Daphnia*), with some species genetically predisposed to aggregate while others are not.

Even in a homogeneous environment where no other extrinsic factors affect the distribution, complex interactions between different species can result in spontaneous pattern formation. The study by Young *et al.* (2001) suggests that this is certainly possible. Young *et al.* (2001) showed that clusters form out of spatially uniform initial conditions without environmental variability, predator-prey interactions, kinesis or taxis. According to Young *et al.* (2001) the aggregative mechanism is reproductively driven; births must always be adjacent to a living organism. It seems then that this clustering can overcome diffusion and create non-poissonian correlations between pairs or organisms, leading to the emergence of aggregated patterns in their distribution.

The Ideal Free Distribution (IFD) might offer an explanation to the patchy distribution observed in *H. shoshone* and the random or uniform distribution seen in *L.*

coloradensis. The IFD model is a theoretical model for studying density-dependent effects on the spatial distribution of optimal individuals in a group. Density dependency relates to resources and predators and their efficiencies. While density-dependent effects on resources in most situations yield diminishing return with increased competition, this may be compensated by reduction in predation risk (Milinsky 1977, Jakobsen *et al.* 1994). The IFD model presented by Giske *et al.* (1997) includes density dependent predation risk and the possibility of density-independent regulation of the feeding rate in the profitability function. Such a model yields the following prediction: if competitor density is very low or almost absent, individuals should join groups to avoid predation instead of spreading out to match the resource input.

According to the IFD model, predators should distribute themselves so each obtains the same food intake (i.e. equal fitness). However two opposing adaptive responses shape the distribution of predators. At high prey densities food should be easier to find so predators should spend more time where the prey is located, but interference will be greater at high predator densities so predators may try to avoid it by moving away (Sutherland 1983). The resulting predator distribution pattern should show that predators while still concentrating on the prey location may have a more diffused pattern than that of the prey in order to balance the opposing forces pushing their distribution. This situation allows the prey to remain clumped without being completely wiped out (Fields & Yen 1997). At the same time the prey may be benefiting from the dilution effect in which a predator is confused by a large mass of individuals and therefore have a lower rate of predation (Hamner & Carleton 1979). This hypothesis can then explain the distributions of *H. shoshone* and *L. coloradensis* as different outcomes to the same set of adaptive responses, where importance of resources, predators and competitors varies to create unique conditions that give rise to unique distribution patterns.

Another possible factor affecting the distribution of *H. shoshone* and *L. coloradensis* is the difference in size between the two species, *H. shoshone* being almost twice the size of *L. coloradensis* (unpublished data). Zooplankton patchiness is a species- and size-specific property (Pinel-Alloul 1995). According to Piontkovski and Williams (1995) the spatio-temporal variability of biomass of organisms increases in higher trophic levels, from phytoplankton through microzooplankton to macrozooplankton, i.e. with the increase in size of the organisms. These authors concluded that the lower energy flow of higher trophic levels is accompanied by increased fluctuations in time and space. Organisms acting as predators should be more sensitive to spatio-temporal variability in the abundance and biomass of their prey over these trophic levels.

Another possible explanation may be found within the rate of locomotion of zooplankton (Siebeck 1969). Larger zooplankton species have a greater rate of locomotion than their smaller counterparts (Peters 1983, Cuddington & McCauley 1994). A higher rate of locomotion allows an individual to be more efficient at maintaining its position within the aggregation whenever environmental changes occur (wind, rain, water disturbance by scientists). Therefore it is possible that the smaller *L. coloradensis* simply may not be able to counteract the effects of wind, rain and other disturbances and therefore be constantly dispersed.

Objective II:

The second goal of this project was to determine whether mating (% of females carrying spermatophores and average male mating potential) and reproductive potential (% of females carrying clutches) was positively correlated with aggregative behaviour. Male and female mating potential was significantly higher for individuals within aggregations in all ponds studied.

These results suggest that the aggregations observed may have a positive effect on mating and ultimately overall reproduction rates as seen in other copepod species such as *Heterocope septentrionalis* (Hebert *et al.* 1980) and *Diaptomus tyrrelli* (Byron *et al.* 1983). The patchy distribution observed in this study may be analogous to insect mating swarms, serving to bring males and females together (Young *et al.* 1994) by the use of pheromones. A study done by Poulet and Ouellet (1982) demonstrated the importance of chemosensory detection of dissolved amino acids in stimulating aggregation and feeding in copepods. However it may be expected that any attractive substance, either released during feeding or emitted by mature individuals of either sex, would be rapidly dispersed and diluted in water reducing the potential value of this signaling system unless all individuals within the aggregation secrete the substance at the same time. Also, no study has yet quantified copepod pheromone levels within and outside aggregations in order to confirm this hypothesis. Furthermore, the study by Crease and Hebert (1983) focusing on a common zooplankton species (*Daphnia magna)* failed to detect the presence of pheromones within *Daphnia magna* aggregations.

Changes in the physical properties of the environment may serve as important proximate cues for initiating biological and ecological processes that result in zooplankton aggregation. Physical cues (e.g. light, pond morphology) could provide the primary, proximal information for movements of individuals within an aggregation, as well as for movement of the entire aggregation (Marszalek 2002). Some zooplankton actively change their swimming behaviour in response to food patches or odours (attractants- Hamner & Hamner 1977, Folt & Goldman 1981, Poulet & Ouellet 1982) for example they swim shorter distances and turn more frequently inside favourable patches compared to their behaviour outside of patches.

Active responses to physical cues can also facilitate aggregation through the interplay between local circulation and the directed movements of the animals; these in turn produce ultimately favourable conditions for reproduction, resulting in population changes that then culminate in locally high densities of plankton (Graham *et al.* 2001). It may also be a response to variable light intensity, spectral quality or directionality of polarized light which may be serving as an aid to increase the metabolism of *H. shoshone* (Jensen *et al.* 1999)

There was no significant difference in the reproductive success (as measured by the proportion of females carrying clutches) of females within and outside aggregations across all ponds. Although it appears contradictory to have significantly higher mating potential while reproductive potential does not seem to be affected, this can be explained by mutual interference caused by the high densities of conspecifics, which may be the basis for reductions in per capita feeding rates and subsequent reductions in fecundity (Folt *et al.* 1993). Therefore although the higher encounter rate may be causing an increase in mating potential it may also be causing a decrease in reproductive potential by decreasing the overall per capita food intake.

However the number of eggs per clutch was influenced by distribution with females within aggregations showing larger clutches. These results are discussed in the next objective.

Objective III:

The third and final objective of this project was to determine whether size of individuals was significantly greater within aggregations than outside of them, and to establish if there was a corresponding difference in number of eggs per clutch.

Hesperodiaptomus shoshone female size within aggregations was significantly greater than outside aggregations. However male size was not significantly different. In the case of females there appears to be to be an advantage to large size, since larger females produce larger clutches and may produce the first clutches in the season. First clutches may be found on larger females because they developed faster due to higher food intake or because they hatched earlier (Maly 1973).

Another factor influencing the higher proportion of large females within aggregations may be mobility. According to Pinel-Alloul *et al.* (1988) larger zooplankton are more heterogeneously distributed than smaller ones. This observation may be explained by the rates of locomotion of larger zooplankton, which are greater (Peters 1983, Cuddington & McCauley 1994) and thus allows them to be more efficient at maintaining their position within the aggregations whenever environmental changes occur (wind, rain, water disturbance by scientists).

Males on the other hand don't require a large size to have a higher mating potential. For males it is important to mate as often as possible and being larger requires spending more time feeding (time not spent mating) and it delays maturation time (McLaren &

Corkett 1981), therefore smaller males that reach adulthood sooner should be able to mate more in their lifetime than larger males. However larger males may have a higher stamina and longevity, which in turn results in a longer period to mate. As a consequence of the interaction between these two opposing forces, male size is highly variable and is considered a stable trait (Neems *et al.* 1998). It is unknown at the moment whether this is what is occurring in the case of *H. shoshone* and the ideas above stated are but a sample of possibilities affecting the size of the males in this study.

Sex size ratio may also influence the size of males. According to Grad and Maly (1992) the size ratio at which copulation and clutch formation are most successful is influenced by the size of female genital segment width and the male right fifth claw length. Therefore manoeuvrability of the male is highly important, and keeping in mind that females always try to escape copulation, smaller males may more successfully control the female therefore facilitating the deposition of the spermatophore.

Clutch size was significantly larger (higher number of eggs per clutch) in aggregated females than in non-aggregated ones across all ponds. This finding is in agreement with earlier studies that established that food availability and prosome length are known determinants of clutch size (Maly 1974, 1983, Elmore 1983, Chow-Fraser & Maly 1991, 1992). As mentioned before significantly larger females were found within the aggregations and so it follows that the clutches they carried were in turn significantly larger.

CONCLUSION:

In this study I have found evidence that *H. shoshone* has an aggregative distribution while *L. coloradensis* shows a random distribution pattern most of the time. The distribution of *H. shoshone* may in part be attributed to physical processes (proximate causes) and local pressures (ultimate causes) such as light, water currents, predation and food allocation. I have also established that mating potential is significantly higher for males and females within aggregations for most ponds. Female reproductive potential however is not significantly different. *Hesperodiaptomus shoshone* female size within aggregations was significantly greater than outside aggregations, but male size was not significantly different. A corresponding significant difference in clutch size was observed between egg sacs found in aggregated and non-aggregated individuals.

I have found evidence of a possible positive relationship between the pattern of distribution and the overall reproductive success of *H. shoshone* in this study, that is patches with high number of individuals (i.e. aggregations) seem to have an overall higher reproductive success. The production of larger clutches (within aggregations) may in turn enhance this possible effect, which translates into more potential offspring, and therefore a possible higher survival rate for the populations studied. However it is also clear that overall reproductive success is not the only major driver of aggregative behaviour in these ponds.

Other factors (both proximate and ultimate) unknown at this time seem to contribute largely to the dispersion patterns observed and must be identified in order to have a more clear understanding of the cues and forces structuring the distribution of *H. shoshone*. The random distribution patterns of *L. coloradensis* need to be explained. Factors influencing these patterns may be size, predation pressure and resource availability to name a few.

Spatial heterogeneity plays a central role in the structure and dynamics of zooplankton communities. Most zooplankters are distributed in swarms or aggregates. Therefore understanding the spatial heterogeneity of zooplankton will have a profound effect on our understanding of the populations being affected by this phenomenon, their interactions with others species, and the consequences of these interactions on community properties and functions.

Future work in this area should focus on determining the relative importance of predation and food resource allocation with respect to the spatial distribution of these copepod species.

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APPENDIX I:

Morisita developed the Morisita's index of dispersion in 1962.

Morisita's index of dispersion formulae:

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

I_d= Morisita's index of dispersion

η = Sample size

$\sum x$ = Sum of the quadrat counts = $x_1 + x_2 + x_3 + \ldots$

$\sum x^2$ = Sum of quadrat counts squared = $x_1^2 + x_2^2 + x_3^2 + \ldots$

This Index of dispersion is relatively independent of population density, and it has a known sampling distribution. Morisita indicated that one could test the null hypothesis of randomness by

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

Where χ^2 = Test statistic with a chi-square distribution

APPENDIX II:

Table A. Mean density, standard deviation variance and range of values observed for males and females per date for *H. shoshone*.

POND	DATE	MALE				FEMALE			
		$\overline{X}$	Std. Dev.	Variance	Min-Max	$\overline{X}$	Std. Dev.	Variance	Min-Max
L6	27-Jun	2.35	2.143	4.591	0-8	1.79	2.194	4.813	0-11
	30-Jun	5.33	3.742	14.000	0-14	2.63	2.483	6.165	0-11
	5-Jul	3.74	3.241	10.507	0-13	2.30	2.493	6.216	0-12
	8-Jul	6.20	4.12	17.000	0-16	4.16	2.982	8.890	1-12
	15-Jul	6.68	6.349	40.310	0-29	2.52	3.267	10.677	0-12
	19-Jul	5.27	5.048	25.485	0-26	2.85	2.781	7.735	0-11
	22-Jul	5.23	4.990	24.905	0-20	2.85	2.782	7.782	0-10
	27-Jul	5.92	5.789	33.514	0-21	2.77	2.046	4.184	0-9
L8	21-Jun	3.00	3.087	9.529	0-10	3.78	2.669	7.124	0-9
	29-Jun	5.53	4.862	23.636	0-16	4.50	4.345	18.879	0-15
	5-Jul	8.47	4.485	20.119	2-18	4.83	3.966	15.729	0-14
	8-Jul	10.81	7.773	60.428	2-36	7.64	9.322	86.903	0-50
	15-Jul	7.32	6.823	46.559	0-26	6.26	7.335	46.559	0-31
	19-Jul	7.22	7.147	51.079	0-26	4.87	6.661	51.079	0-36
	22-Jul	6.06	3.359	11.286	1-16	3.94	4.063	16.512	0-20
	27-Jul	9.19	7.239	52.415	0-29	4.22	3.405	11.596	0-13
L10	26-Jun	2.38	2.111	4.458	0-8	1.76	2.214	4.904	0-11
	29-Jun	4.14	4.357	18.980	0-18	3.21	3.931	15.456	0-17
	01-Jul	5.69	4.252	18.079	0-16	4.21	4.601	21.170	0-17
	06-Jul	7.40	5.917	35.007	1-29	5.33	4.589	21.057	0-17
	13-Jul	11.86	12.539	157.238	1-48	6.86	6.358	40.423	0-23
	17-Jul	12.90	17.719	313.956	0-96	6.87	6.065	36.783	0-20
	20-Jul	15.16	13.820	191.006	0-58	6.23	4.507	20.313	0-16
	25-Jul	12.74	9.811	96.264	1-54	6.42	4.958	24.584	0-18
	29-Jul	12.06	12.976	168.383	0-57	5.47	4.024	16.193	0-16
L11	27-Jun	15.24	7.590	57.590	7-33	8.33	4.317	18.633	4-21
	1-Jul	12.43	7.005	49.075	2-33	10.56	7.140	50.984	2-34
	6-Jul	15.96	9.980	99.607	3-44	13.79	10.554	111.389	1-37
	13-Jul	15.87	13.404	179.664	3-60	13.52	10.720	114.897	2-41
	17-Jul	11.42	7.377	54.427	37-1	6.167	4.156	17.275	0-13
	20-Jul	8.21	5.756	33.128	2-41	5.87	3.904	15.244	0-19
	25-Jul	9.54	8.827	77.911	0-29	7.167	5.776	33.362	0-23
	29-Jul	4.00	2.934	8.609	1-25	4.21	3.730	13.911	0-13

Table B. Mean density, standard deviation variance and range of values observed for males and females per date for *L. Coloradensis*.

POND	DATE	MALE				FEMALE			
		$\overline{X}$	Std. Dev.	Variance	Min-Max	$\overline{X}$	Std. Dev.	Variance	Min-Max
L6	27-Jun	0.00	-	-	-	0.00	-	-	-
	30-Jun	0.04	-	-	-	0.00	-	-	-
	5-Jul	1.78	1.423	2.026	0-5	1.96	1.628	2.652	0-7
	8-Jul	2.52	1.759	3.093	0-7	2.08	1.256	1.577	0-5
	15-Jul	4.88	2.211	4.890	0-8	2.32	1.376	1.893	0-5
	19-Jul	14.15	3.967	15.735	9-23	10.04	2.425	5.878	3-14
	22-Jul	18.54	3.153	9.938	13-24	13.81	3.298	10.882	8-19
	27-Jul	18.73	4.075	16.605	11-27	12.19	3.753	14.082	6-18
L8	21-Jun	0.00	-	-	-	0.00	-	-	-
	29-Jun	0.00	-	-	-	0.00	-	-	-
	5-Jul	0.4	0.498	0.248	0-1	0.33	0.6065	0.368	0-2
	8-Jul	5.77	1.655	2.740	2-7	3.58	2.143	4.591	0-9
	15-Jul	18.55	4.513	20.365	11-26	12.52	3.773	14.232	3-19
	19-Jul	16.12	5.041	21.415	11-27	10.41	2.223	4.968	5-12
	22-Jul	23.56	5.403	29.190	12-33	15.87	4.895	23.951	11-30
	27-Jul	38.78	7.799	30.839	21-48	48.78	11.6394	35.475	17-48
L10	26-Jun	0.00	-	-	-	0.00	-	-	-
	29-Jun	0.00	-	-	-	0.00	-	-	-
	01-Jul	0.00	-	-	-	0.00	-	-	-
	06-Jul	0.00	-	-	-	0.00	-	-	-
	13-Jul	2.71	1.825	3.333	1-6	1.46	1.252	1.567	0-5
	17-Jul	8.29	3.327	11.068	3-13	6.55	3.023	9.137	2-13
	20-Jul	10.13	3.524	12.420	3-16	3.67	2.175	4.731	1-9
	25-Jul	24.87	5.994	15.926	15-24	15.61	4.359	19.007	8-21
	29-Jul	40.03	7.342	23.903	27-43	38.06	7.231	22.290	26-44
L11	27-Jun	0.00	-	-	-	0.00	-	-	-
	1-Jul	4.91	21.275	5.174	1-9	5.35	2.4792	6.146	1-9
	6-Jul	8.46	2.948	8.692	0-11	7.50	2.841	8.075	2-13
	13-Jul	7.43	2.352	8.132	2-11	7.56	3.596	12.929	2-15
	17-Jul	7.58	3.579	12.806	2-15	3.25	1.864	3.474	1-8
	20-Jul	7.21	3.367	11.340	1-11	2.67	1.849	3.419	0-7
	25-Jul	3.96	2.430	5.909	0-8	4.25	2.080	4.328	0-8
	29-Jul	2.96	1.758	3.091	0-6	1.96	2.142	4.589	0-7