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Anne Turner Packard

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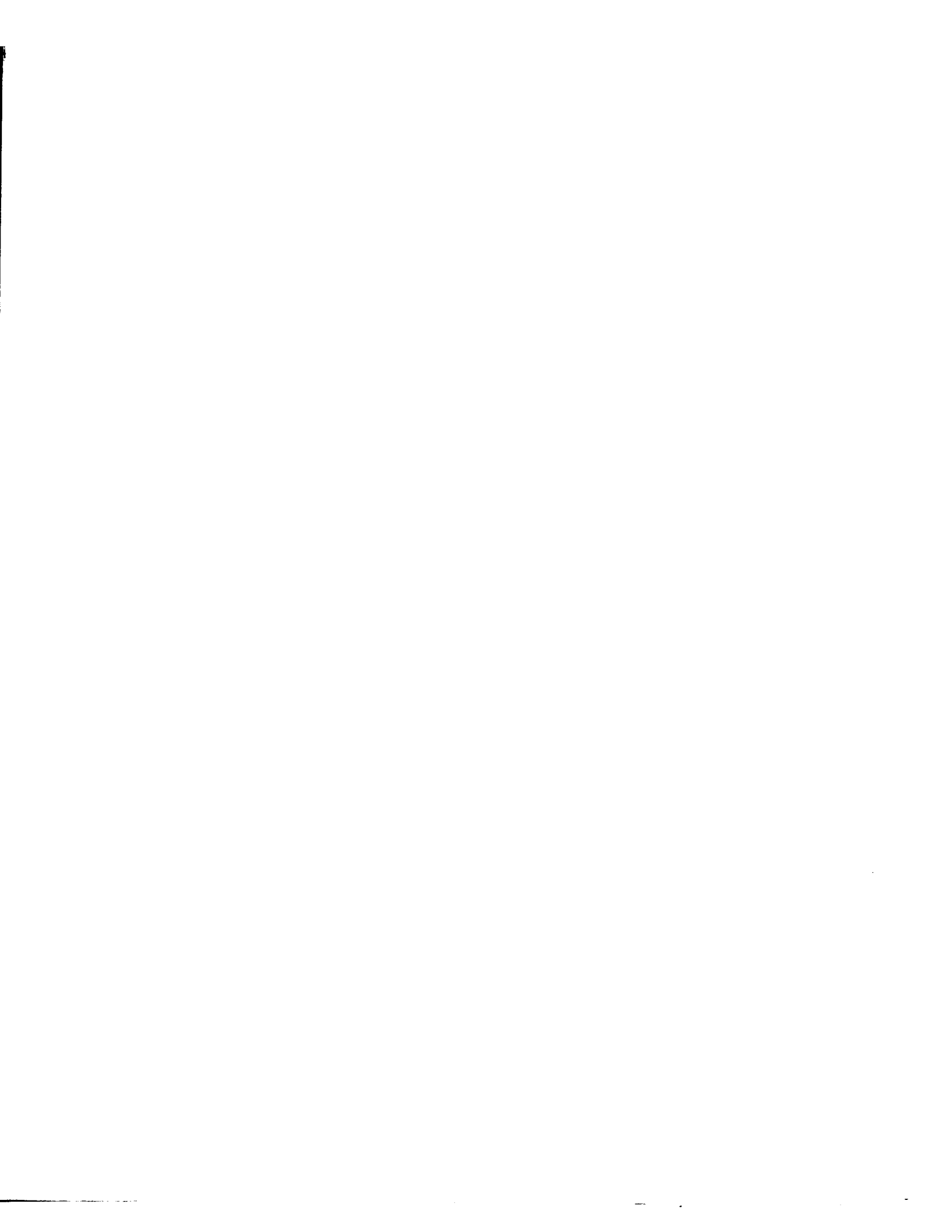
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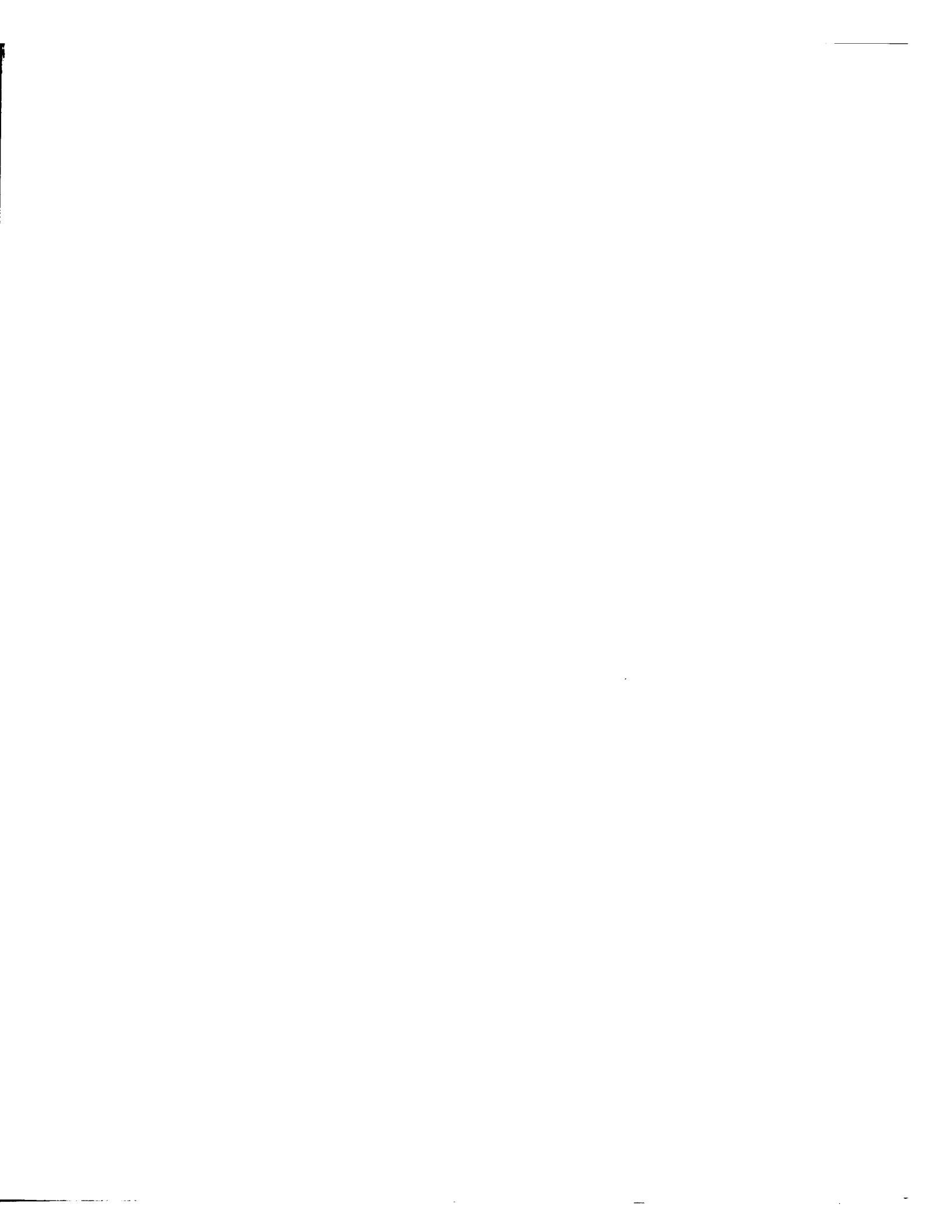
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**Horizontal distribution, feeding rates and prey selectivity of the  
littoral predator, *Polyphemus pediculus***

Packard, Anne Turner, Ph.D.

University of New Hampshire, 1992

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HORIZONTAL DISTRIBUTION, FEEDING RATES AND PREY  
SELECTIVITY OF THE LITTORAL PREDATOR,  
*POLYPHEMUS PEDICULUS*.

BY

ANNE T. PACKARD

BS, BATES COLLEGE, 1964  
MS, UNIVERSITY OF NEW HAMPSHIRE, 1966

DISSERTATION

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in Partial Fulfillment of  
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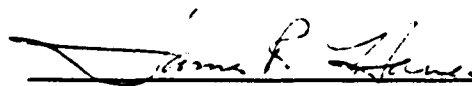
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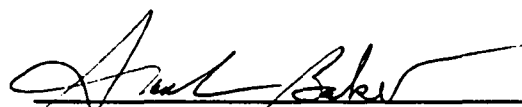
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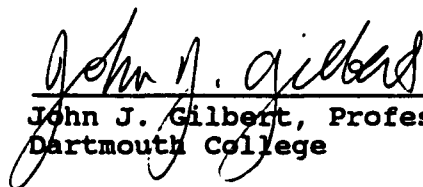
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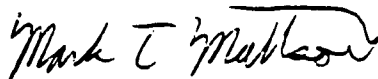
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---

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Sincere thanks to Jim Haney, my dissertation director, for introducing me to the world of zooplankton, more specifically to *Polyphemus pediculus*. His enthusiasm has been an inspiration, and is contagious.

Love and thanks to Roger Pedigo. With you, I did it.

**FOREWARD**

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86-0812  
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**HB 295**

**STATE OF NEW HAMPSHIRE**

**In the year of Our Lord one thousand  
nine hundred and eighty-six**

**AN ACT**

**relative to Mirror Lake in the town of Woodstock**

**Be it Enacted by the Senate and House of Representatives in General Court  
convened:**

**1 Mirror Lake.** Notwithstanding the provisions of RSA 486:11, for purposes of research of the polyphemus pediculus (sic) only, an exemption shall be granted until July 1, 1989, for the use of a boat powered by an electric motor on Mirror Lake in the town of Woodstock.

**2 Effective Date.** This act shall take effect upon its passage.

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ABSTRACT

HORIZONTAL DISTRIBUTION, FEEDING RATES AND PREY  
SELECTIVITY OF THE LITTORAL PREDATOR,  
*POLYPHEMUS PEDICULUS*.

by

Anne T. Packard

University of New Hampshire, May 1992

Littoral planktonic communities have rarely been included in food web dynamics and predator/prey behavior studies of planktonic communities of fresh water ecosystems. *Polyphemus pediculus*, a typically littoral predaceous cladoceran, is common in lakes and ponds throughout the northern temperate zone.

The patchy distribution of *Polyphemus* in littoral surface waters necessitates the use of a stratified random sampling regime to estimate and monitor *Polyphemus* populations. The population in Mirror Lake, NH, increased exponentially after the first appearance of parthenogenetic juveniles in late April. An abrupt decline in the population coincided with the movement of small *Micropterus dolomieu* fry into littoral areas in early June. Gut analyses indicated the small fry were eating *Polyphemus* but as they grew their diet changed to larger insect larvae and the *Polyphemus* population increased. Reproduction was entirely parthenogenetic until males appeared in late summer. Females carried resting eggs until the population disappeared in November.

Active aggregation behavior coincided with distinct horizontal movements toward shore over sunset, away from shore over sunrise. A comparison of diel movements of *Polyphemus* populations in two New Hampshire lakes supports the predator avoidance hypothesis.



Diel feeding rates of *Polyphemus* were studied in four-hour intervals with a differential count method. A multichambered predation trap accommodated three simultaneous feeding experiments and a control. Three different *Polyphemus* densities were used during each feeding experiment to represent the natural density range.

*Polyphemus* are diurnal feeders, more than 90% feeding occurring between sunrise and sunset. *Polyphemus* appear to select small, vulnerable prey (*Polyarthra* and individual *Conochilus*) over small prey with protective structures (*Kellicottia*). Feeding rates were highest for *Vorticella* that lived on *Anabena* colonies. *Polyarthra* and *Conochilus* constituted more than 70% of food ingested.

At patch densities feeding rates decreased and evidence of cannibalism was observed indicating that *Polyphemus*' aggregation behavior does not benefit feeding activities.

## SECTION I. GENERAL INTRODUCTION

Freshwater plankton communities contain complex mixtures of predaceous and herbivorous animals interacting with each other and their environment. Zooplankton interactions are most often described and measured by ingestion rates (Downing and Rigler 1984). Every level of the zooplankton community food web is also affected by changes in nutrient levels or vertebrate predators (Threlkeld *et al.* 1980). Zooplankton predation contributes to the stability of the planktonic community as the predators of smaller zooplankton are also prey for vertebrate predators (Levitan 1987). Most research efforts have examined suspension feeders such as calanoid copepods and cladocerans (Downing and Rigler 1984). Studies of predaceous zooplankton have concentrated primarily on *Chaoborus*, mysid shrimp and copepods (Kerfoot and Sih 1987). Methodologies similar to those used for feeding rates of filter feeding zooplankters have been used to estimate predation rates and ingestion rates whereby small animals such as nauplii, copepodites, rotifers or cladocerans replace algal or bacterial cells (Downing and Rigler 1984). Most zooplankton predation studies, however, have been limited to the limnetic zone of lake ecosystems. The littoral areas generally cover a small proportion of a lake and consequently have received proportionally less attention in limnological studies. As a result little is known about food web dynamics of littoral communities and predator/prey behavior of littoral zooplankton.

*Polyphemus pediculus* may be the only predaceous zooplankton that is typically littoral. Although *P. pediculus* is common in lakes, ponds and marshes throughout the northern hemisphere (Gurney 1923; Pennak 1978), *in situ* feeding studies of *Polyphemus* have not been reported previously. *Polyphemus* is monospecific, and hereafter in the text, the species name is deleted. The cladoceran

has a unique physical appearance characterized by a large single eye, rounded brood pouch and a long slender caudal peduncle with two long setae. The length of *Polyphemus* collected in New Hampshire did not exceed 1 mm.

Whole lake population estimates or population densities are difficult to obtain because *Polyphemus* is not only typically littoral in habitat but also has a tendency to swarm in patches or aggregations with densities ranging from 200 to more than 10,000 individuals  $L^{-1}$  within the patch (Haney and Mattson 1980). There appears to be some question in the literature as to the exact spatial affinity of *Polyphemus* (Haney and Mattson 1980). Mattson (1979) observed seasonal and diel movement to limnetic regions. In Lake Michigan aggregations of *Polyphemus* have been observed more than 3 km from shore (Wells 1960).

Based on published observations and data, an overall evaluation of *Polyphemus* in the aquatic community is difficult. Variations in morphology (Ischreyt 1933), electron and light microscopic studies of the eye structures and functions (Odselius and Nilsson 1983; Nilsson and Odselius 1983), embryological development of parthenogenic eggs (Kuhn 1913) and life cycle laboratory observations (Butorina 1963, 1971) have been reported. Habitats range from small stagnant and murky ponds (Butorina 1986, Young and Taylor 1988) to wide expanses of the Great Lakes (Wells 1960); from flatland lakes (Ischreyt 1933) to high altitude ponds (Zacharias 1906). The ecological implications of *Polyphemus* morphology, life cycle and behavior have not been thoroughly considered.

This *in situ* study of a littoral predator addresses several aspects of predation (Holling 1959). Is the predator affected by light, i.e. time of day or time of year? Is the feeding behavior affected by increases of prey density? Is the aggregation behavior of *Polyphemus* related to feeding behavior and do feeding rates increase within an aggregation? Do morphological characteristics of the prey affect selectivity of one prey over another? What attributes do *Polyphemus* exhibit to

make them successful predators. An overall understanding of the ecology of an individual *Polyphemus* population could reveal how this species has created such a successful niche.

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## SECTION II. ESTIMATES OF ABUNDANCE AND LIFE CYCLE PATTERN OF *POLYPHEMUS PEDICULUS* IN MIRROR LAKE

### Introduction

The patchy distribution and aggregation behavior of *Polyphemus pediculus* make it difficult to sample (Butorina 1963, 1969; Hutchinson 1967). It is generally considered to be a littoral species and its affinity for the shore area has been well documented (Axelson 1961; Heal 1962; Butorina 1963, 1969; Hutchinson 1967; Lindstrom 1952). In some lakes, however, *Polyphemus* occurs in the limnetic zone (Kikuchi 1930, 1937; McNaught 1966). An extensive study of *Polyphemus* distribution in a small New Hampshire lake, Stonehouse Pond, demonstrated that the populations move between the littoral and limnetic areas directed by wind action and time of day (Mattson 1979), and in Lake Michigan a patch of *Polyphemus* was reported > 3 km off shore (Wells 1960). Some *Polyphemus* population estimates and descriptions of vertical movements have been based solely on limnetic individuals (Kikuchi 1930, 1937; Djokosetiyanto and Lair 1983).

Little is known about littoral zooplankton communities, not only in this study site, Mirror Lake (Makarewicz 1985), but throughout the lakes of the world. Although the littoral areas are relatively small by surface area and percent volume, they are heterogeneous, with a variety of habitats and species. Less attention has been given to this region than the limnetic because accurate quantitative studies are time consuming and labor intensive (Daggett and Davis 1974). The few quantitative studies that have been reported involved benthic chydorids (Daggett and Davis 1974; Keen 1973; Whiteside 1974). Although *Polyphemus* was reported in some of

these studies, population densities were not quantified (Smirnov and Davis 1973).

### Location

Mirror Lake is located in the town of Woodstock (Grafton County) New Hampshire (43° 56.5'N, 71° 41.5'W) at an altitude of 213 m. The glacially formed lake covers an area of 15 ha, has a maximum depth of 11.0 m and an average depth of 5.7 m. The water is slightly acidic, nutrient poor with summer Secchi disk readings from 5 to 7 m. Mirror Lake lies within the Hubbard Brook Experimental Forest, a principal research area for watershed management. The physical characteristics and ecology of the lake have been well documented (Likens 1985).

The lake is asymmetrical with its deepest part near the north shore (Figure II.1). The northern and eastern shores have numerous boulders while the south shore is generally sand with areas of cobble (Figure II.2).

Macrophyte colonization extends to 7.2 m (Moeller 1975) (Figure II.3). This contour is considered to be the outer boundary of the littoral zone (Moeller 1985). Emergent vegetation is scarce. Floating-leaved nymphaeids are established over areas covered by mud or organic debris (Figures II.2 and II.3). Submerged vegetation, however, is extensive. Except for the waterlilies, most of the macrophytes are within 10 cm of the lake bottom, none are higher than 60 cm. Based on the types of submerged vegetation the littoral zone can be divided into three, almost distinct, bands (Moeller 1985). The upper band, to 3.0 m, is primarily colonized by submergent macrophytes with flowering stalks. The transition band (3.0-5.0 m) is characterized only by dense summer growths of bladderwort. The deeper band (5.0-7.2 m) is colonized by submergent pondweeds and *Nitella*.

Zooplankton populations differ between littoral and limnetic zones. Makarewicz (1985) lists *Polyphemus pediculus* as one of six species from Mirror Lake which are typically littoral. *Polyphemus* was generally found within the 4 m



depth contour by Makarewicz (1985). Comparable distributions were observed during the pilot studies for this research. Based on these observations and the lake morphometry, the littoral zone was defined as the area of the lake < 4 m depth. This corresponds to the midpoint of Moeller's intermediate vegetational littoral band.

### Methods and materials

#### Sampling Design

Total Population Estimations. To estimate the total population of a randomly distributed plankter, the number of organisms in one unit volume are simply extrapolated to the total lake volume. This method could greatly exaggerate or underestimate the population estimates of nonrandom species. A stratified random sampling design was used for *Polyphemus* because of the patchy occurrence and aggregation behavior (Cassie 1971). The strategy of a stratified random sampling design is to divide the heterogeneous system into homogeneous subpopulations or sampling strata (Cassie 1971; Barrett and Nutt 1979). The density of each subpopulation is first estimated from a pilot field study. By weighting the sample of each stratum by the relative abundance of its subpopulations and the volume of each stratum relative to the entire lake, the mean density in the lake can be most accurately estimated. The partitioning procedure is therefore very important to the overall success of the method. The more homogeneous each section is, the more precise the overall estimate will be.

Partitioning of Sampling Strata. Pilot study estimates of *Polyphemus* abundance around the lake, sediment maps and morphometric information (Likens 1985) were considered in the partitioning procedure. The pilot study density estimates were obtained from horizontal tows taken just below the surface at midday with a 151  $\mu\text{m}$  simple conical plankton net. Length of sample tows were estimated. The relative *Polyphemus* abundance in each tow was characterized by

high (mostly *Polyphemus*), medium (*Polyphemus* present in equal numbers with other species) or low (few, if any, *Polyphemus*) ratings. High densities of *Polyphemus pediculus* were collected along the southwest shore and in areas around the three inlets. All of these areas have sandy areas and are free of submergent vegetation. Low densities were identified along the northern shores and in the outflow area.

The entire lake was divided into seven horizontal strata (Table II.1), six in the littoral zone, and one in the limnetic or open water zone (Figure II.4). The surface area of the lake was measured by polar planimetry. Surface areas between depth contour lines were measured by superimposing a scale contour map of Mirror Lake on graph paper. The area was determined from the number of graph squares counted between depth contour lines. The area of each stratum was the sum of contour areas within the stratum boundary. Volumes were calculated from depth and contour area measurements (Lind 1979) (Table II.2). To estimate vertical distributions each horizontal stratum was divided into the following five depth intervals: 0-0.25 m, 0.25-0.75 m, 0.75-1.25 m, 1.25-1.75 m and 1.75-2.25 m.

Sample Allocation for population estimates. *Polyphemus* was sampled once a month during the summer 1986 with three 20 m horizontal surface tows from each stratum. The proportion of samples to be taken from each stratum for population estimations was determined by the relative density of *Polyphemus* in each stratum. For allocation of samples by depth *Polyphemus* was sampled from two littoral strata (2 and 4) and the limnetic stratum (7) from the surface (0.0-0.25 m) and 0.5-m depth intervals. Shallow ( $Z_{\max} = 1.0$  m) littoral samples were taken 8 m from shore from the surface and 0.5 m. Deeper littoral samples were taken down to 2.25 m. Limnetic samples were taken down to 2.25 m, 12 - 20 m from shore and oblique tows were taken from 8.0 m (Mattson 1979). The pilot study indicated approximately 80% of the *Polyphemus* inhabited shallow littoral areas and, 80% of

these were at the 0-0.25 m depth (Table II.3).

To minimize variation caused by swarming behavior and horizontal and/or vertical migrations observed during early morning and late afternoon, the length of the sampling period was limited to 4 h during midday. During the pilot study each sample was completed in approximately 7 min, and up to 34 samples could be taken in 4 h. These 34 samples were then distributed among the 7 lake strata with the Neyman allocation calculation (Barrett and Nutt 1975):

$$n_i = n \frac{N_i s_i}{\sum_{i=1}^L N_i s_i} = n \frac{N_i s_i}{N_1 s_1 + N_2 s_2 + \dots + N_L s_L}$$

where:

$n$  = total number of sample units selected

$n_i$  = number of units selected in stratum  $i$

$N_i$  = number of units in stratum  $i$

$s_i$  = estimate of the population standard deviation in stratum  $i$

A total of 34 samples, 31 from the littoral zone and 3 from the limnetic, were taken for each sampling period. Since just one individual was collected from the limnetic zone in both the horizontal and vertical sampling, stratum 7 was not included in the allocation calculations and 3 oblique tows were arbitrarily taken from the limnetic zone for the population sampling. Strata 1, 3 and 5 had the greatest number of *Polyphemus pediculus* and most of the samples (7 each) were distributed to these areas (Table II.4).

The Neyman calculations allocated samples only to the surface depth (0.0-0.25 m) although some *Polyphemus* were collected in the 0.25-0.75 m depths. If total abundance were calculated based on the entire population inhabiting just the top 0.25 m, the population would be underestimated by approximately 20%. If the numbers were extrapolated to the upper 1 m representing the deeper range of

habitat the population would be greatly overestimated. The depth to which surface densities should be extrapolated was determined by using all population counts from the 0.0-0.25 and 0.25-0.75 m samples ( $n=76$ ). The numbers collected in deeper samples,  $> 0.75$  m depth, comprised 1.3% of the total and were considered insignificant. The percentages collected from each depth (0-0.25 m and 0.25-0.75 m) for each transect were regressed with depth. The regression intercept, 0.6 m, ( $r^2=0.67$ ,  $p < 0.01$ ) was considered, for the purpose of population estimates, the lowest depth range for *Polyphemus pediculus* in Mirror Lake during midday.

The transect areas to be used for the abundance study were first selected on the bathymetric map and then located on site by permanent landmarks to insure that the tows would always be taken from the same points. Each littoral sample consisted of an oblique transect from shore with the exception of stratum 1, the stratum where the highest densities of *Polyphemus* were collected in the pilot study. Here some of the transects were set in a grid pattern to provide information of horizontal behavior parallel to the shore line. The limnetic samples were taken from a buoy over the deepest point in the lake as oblique tows from 8 m depth towed toward different points on shore around the lake (Figure II.4).

#### Sampling Apparatus

Samples were taken with a 12.5 cm diameter Clarke-Bumpus (CB) metered plankton net with a 151  $\mu\text{m}$  mesh Nitex net. All *Polyphemus* could be collected with this size mesh and allow smaller plankton to pass through to prevent clogging. The sampling procedure and equipment modifications were described by Mattson (1979). The CB unit was mounted on a 2.5 m aluminum pole with holes at 0.5 m intervals (Figure II.5). Samples could be taken down to 2.0 m depth by removing the pin holding the pole into the pivotal mechanism. This mechanism allowed the net to be raised or lowered in the water or maintained in a horizontal position for rinsing. The pivotal unit was mounted on the front of a 3.0 m aluminum Jon boat.

This placement minimized avoidance reactions by the zooplankton to the boat's shadow (Clutter and Anraku 1968). A stern-mounted electric motor was used to drive the boat at a constant speed. Two CB units were used interchangeably for the sampling regimes. Calibrations made in the Johns Hopkins University Flumes determined that one revolution of the metered sampler represented 4.8 and 3.9 liter samples for the two CB units respectively.

### Field Sampling

A "sample unit" consisted of a 20 m tow. Each tow was taken at a constant speed for a measured period of time. Before each sampling period the time for the boat to travel 20 m between 2 fixed points with the sampling net deployed was measured several times. The average time was used for all the sample tows for that day. The average sample volume (+/- S.D.) was 155.2 L (21.12).

Prior to sampling the net shutter was opened and held in this sampling position with a cotter pin placed through a hole near the mouth of the meter unit. When the boat was at sampling speed (approximately 1 m/sec) at the tow location the net was pivoted down into the water. After completion of the 20 m tow the cotter pin was pulled closing the shutter. The pole was pivoted up to a horizontal position. The plankton bucket was rinsed from the outside with lake water and emptied into a 151  $\mu\text{m}$  ring net. Organisms in the ring net were backwashed into a sample vial and preserved in 4 % sucrose formalin (Haney and Hall 1973). The net was reopened and pinned for the next tow.

The stratified random sampling design was implemented in 1987 biweekly from 11 May through 16 Nov. All collections were made in random sequence between 1000 and 1500 h.

### Laboratory Analyses

Samples were counted in the laboratory with a dissecting scope and channeled counting chambers. Each sample was counted in its entirety avoiding

subsampling error. Premature embryos released when preservative was added were not counted. Body lengths (from eye to the base of the caudal peduncle) of 25-75 *Polyphemus* from each sampling date were measured, gender and number of embryos or resting eggs were recorded.

### Calculations of Population Abundance

Estimations of total lake population abundance of *Polyphemus* were based on the mean number collected per sampling unit (20-m tow) in each stratum (h) and weighting the mean ( $\bar{Y}_h$ ) by the proportion of the volume sampled in the stratum ( $n_h$ ) to the total stratum volume ( $N_h$ ). The sum of the weighted mean densities represented the total stratified mean per sample unit ( $\bar{Y}_{st}$ ) in the entire sampling area (Cochran 1977):

$$\bar{Y}_{st} = \frac{\sum_{h=1} N_h \bar{Y}_h}{N_h} = \sum_{h=1} W_h \bar{Y}_h$$

where:  $N_h$  = total number of units in stratum h

$n_h$  = number of units sampled in stratum h

$$\bar{Y}_h = \frac{\sum_{i=1}^{n_h} y_h}{n_h} = \text{sample mean}$$

$$W_h = \frac{N_h}{N} = \text{sample weight of stratum h to sum of all strata}$$

If the estimated variance for simple random sampling is:

$$S_h^2 = \frac{1}{n_h - 1} \sum_{i=1}^{n_h} (Y_{hi} - \bar{Y}_h)^2$$

then unbiased estimates of variance of stratified means

within each stratum is (Cochran 1977):

$$S^2(\bar{y}_{st}) = \sum_{h=1} \frac{W_h^2 S_h^2}{n_h} - \sum_{h=1} \frac{W_h S_h^2}{N}$$

The estimated variance for each stratum was calculated and then values were totaled for each sampling date. The total population of *Polyphemus* in Mirror Lake on each sampling date was estimated by summing the volume weighted stratum mean densities as follows (Cochran 1977):

$$\text{Total Population} = N \bar{Y}_{st} \pm tNs(\bar{Y}_{st})$$

## Results

### Total Population Estimations

Juvenile *Polyphemus* were first noted in the water column of Mirror Lake in 1987 on 20 April. By 11 May, the population had increased to more than 70 million individuals (Figure II.6). The population had two periods of relatively high abundance. The maximum size population in May averaged  $6.50 \times 10^7$  individuals. By 14 June the population had decreased to a mid-season minimum of  $6.50 \times 10^5$  individuals. The second increase was smaller and averaged  $3.65 \times 10^7$  individuals. The high population level persisted through July and August. The population decreased in September and by mid-November *Polyphemus* was not detected in the water column.

### Population Composition

Juvenile *Polyphemus* appeared before mature females in early spring and were assumed to have developed from resting eggs. Resting eggs had been collected in benthic samples during the winter. Reproduction in Mirror Lake was entirely parthenogenetic through late summer (Figure II.7). Gametogenetic females first appeared in late August and males appeared in late September. By the end of October 75-85% of the population was gametogenetic with 40% males.

## Discussion

### Total Population Estimations

Two general seasonal trends of population abundance have been reported for *Polyphemus*. Most populations have a large spring maximum followed by a rapid decline with a smaller second increase or even a third later in the summer (Mattson 1979; Ischreyt 1933; Butorina 1963). Single population maximums have been reported specifically in high altitude lakes (Zacharias 1906). Mirror Lake had more than one population maximum, but it is difficult to compare total population estimates with most abundance estimates in the literature, other than Mattson (1979). Butorina (1963) reported spring densities in a reservoir reaching 2,173 individuals  $L^{-1}$ , while in the next year during low water levels, only 806 individuals  $L^{-1}$  were observed. Ischreyt (1933) sampled densities up to 51  $L^{-1}$  during the spring maximum and 27  $L^{-1}$  later in the season during the second increase in abundance. The sampling methods used in both studies did not take into account a patchy distribution and total population figures cannot be extrapolated from these data. Populations of *Polyphemus* in Mirror Lake and Stonehouse Pond (Mattson 1979) were estimated on a lake-wide basis. Although Mirror Lake is almost three times as large as Stonehouse Pond the total population of Stonehouse Pond during the spring maximum was almost three times greater in 1975 and two times greater in 1976 (Figure II.8). Total abundance in both lakes was similar during August and September. The number of embryos carried by a mature parthenogenetic female, the brood size, contributed to the size of the spring population maximum. Brood sizes averaged six *Polyphemus*<sup>-1</sup> in Mirror Lake during mid-May, the maximum was nine. Brood sizes had decreased to 3 or 4 by the end of May. Larger brood sizes (20-30) have been reported (Strohl 1907). Brood sizes up to 29 embryos were reported in Stonehouse Pond (Mattson 1979) which could account for the greater



population abundance when compared to Mirror Lake. Embryo production averaged between 2.0 and 3.0 per brood from July to October in both lakes.

#### Population Composition

Dicyclic reproduction patterns with two periods of sexual reproduction in a season have been reported for several cladoceran species (Green 1966; Stross 1969; Lampert and Krause 1976). In most cases, the first sexual reproductive period occurs during the spring population maximum. Dicyclic reproductive patterns have been reported for *Polyphemus* in European Lakes (Kielhach 1906; Strohl 1907; Ischreyt 1933; Green 1966). Mattson (1979) observed that the spring maximum and the first appearance of gametogenetic individuals occurred before the spring maximum of prey species on which *Polyphemus* feeds and suggested that lack of food stimulated formation of sexual individuals. A monocyclic pattern (single reproductive period) and low population densities occurred during a year of severe drought in an otherwise dicyclic population (Butorina 1963). In a high altitude lake (1200 m) monocyclic patterns and no spring population maxima were observed where colder temperatures inhibited the first reproductive pulse (Zacharias 1906) indicating that geographical location, higher latitudes and elevations can control the *Polyphemus* life cycle.

The total population of *Polyphemus* in Mirror Lake decreased from more than 70 million to less than 1 million individuals with no sexual reproduction observed. The rapid decline in total population abundance during periods of sexual reproduction can be attributed to the production of resting eggs which would not develop until later in the season in dicyclic populations or until the next season in monocyclic populations (Lampert and Krause 1976). The decrease in the average brood size after the spring maximum could maintain the population at a lower abundance level. The environmental factors generally believed to initiate sexual reproduction, such as extreme changes of water temperature or food availability, did

not occur in Mirror Lake in either 1986 or 1987.

Since the decrease in the *Polyphemus* population cannot be attributed to the production of resting eggs by sexual reproduction, other external stresses on the population should be examined as possible explanations. Predators could decrease the abundance of a fecund population. Smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*) are two of five fish species in Mirror Lake (Helfman 1985). Fry of both species were sighted in the shore area of Mirror Lake during the rapid decline of the *Polyphemus* population (Fig II.6). The average length of *M. dolomieu* fry collected on 2 June was 11.4 mm. Feeding studies of *M. dolomieu* reported that fry up to 15 mm in length feed on copepods and cladocerans, selecting insect larvae as they get larger (Wilkliff 1920 in Tester 1932). *Polyphemus* was reported to be selectively eaten by young of the year *P. flavescens* (Keast 1985). On one occasion after a feeding experiment had begun many young *M. dolomieu* encircled the relatively transparent apparatus, suggesting the bass were visually attracted to *Polyphemus*.

Gut analyses of 122 *M. dolomieu* fry (8-29 mm) and 57 *P. flavescens* (13-34 mm) collected at 4 m from shore at different time periods 4-24 June 1991 indicated that *M. dolomieu* were feeding on *Polyphemus* (Table II.5). No *Polyphemus* were found, however, in the guts of *P. flavescens*. Most of the *Polyphemus* consumed (94 %) were obtained from guts of fry 8-16 mm in length. The *P. flavescens* fry were generally larger, but consumed large numbers of other cladoceran species similar in size to *Polyphemus*. The smaller *M. dolomieu* fry appear to be the more important predator on *Polyphemus*. The smallmouth fry can consume large numbers of *Polyphemus*. Up to 70 individuals were found in one gut of a 16 mm fry. Four fry caught in the chambers during feeding studies had an average of 195 *Polyphemus* in each gut. The average length (+/- S.D.) of *M. dolomieu* fry collected after 18 June in 1987 and 1991 was 21.5 mm (2.1), n=32.

*Polyphemus* was not detected in any gut contents. The fry were feeding on Diptera, Trichoptera and Ephemeroptera larvae.

*M. dolomieu* are crepuscular feeders (Helfman 1980). Although all the *Polyphemus* found in gut contents were from fry collected before or after sunset, the data are inadequate to form any hypothesis of diel feeding activity of *M. dolomieu* fry on *Polyphemus*. Consecutive studies of fish size, gut analyses and diel migrations with *Polyphemus* horizontal movements and population abundance would provide a better understanding of this predator/prey interaction.

The most recent survey in 1973 of the population of *M. dolomieu* in Mirror Lake was reported to be 600-700 individuals, not including young of the year (Helfman 1985). If a conservative estimate of 100,000 fry were to feed on littoral zooplankton during early growth and each ate 20 *Polyphemus* in one day,  $2.00 \times 10^7$  individuals could be removed from the population each day. Over a two week period, more than one third of the population could be consumed by *M. dolomieu*. The fish predation is probably important in causing the first major decline in the population. The decrease in population caused by fish predation also reduces other environmental stress e.g. food availability and competition which could otherwise have stimulated sexual reproduction and formation of resting eggs.

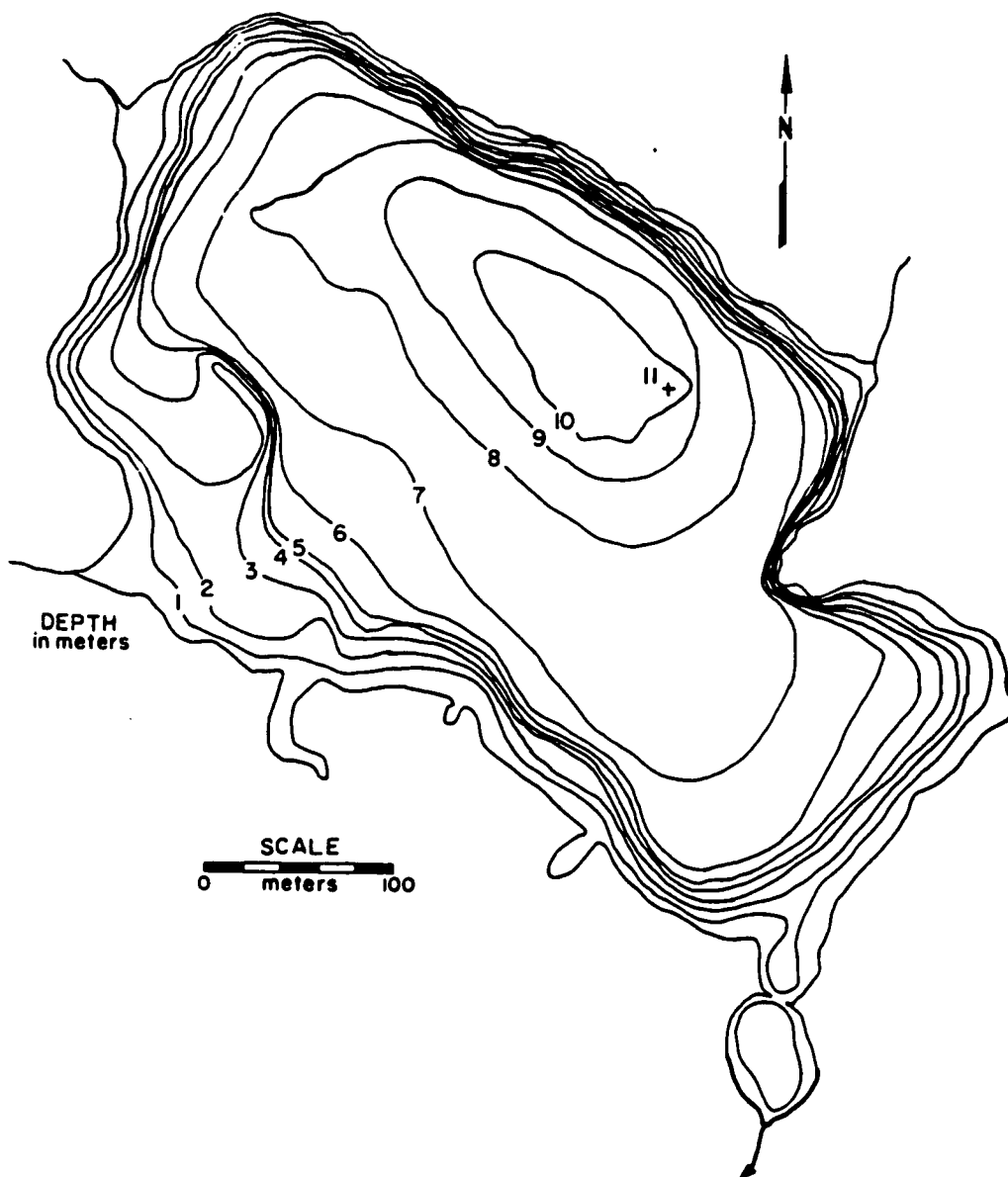


Figure II.1 Depth-contour map. Mirror Lake, Woodstock, New Hampshire.  
Redrawn from Likens (1985).

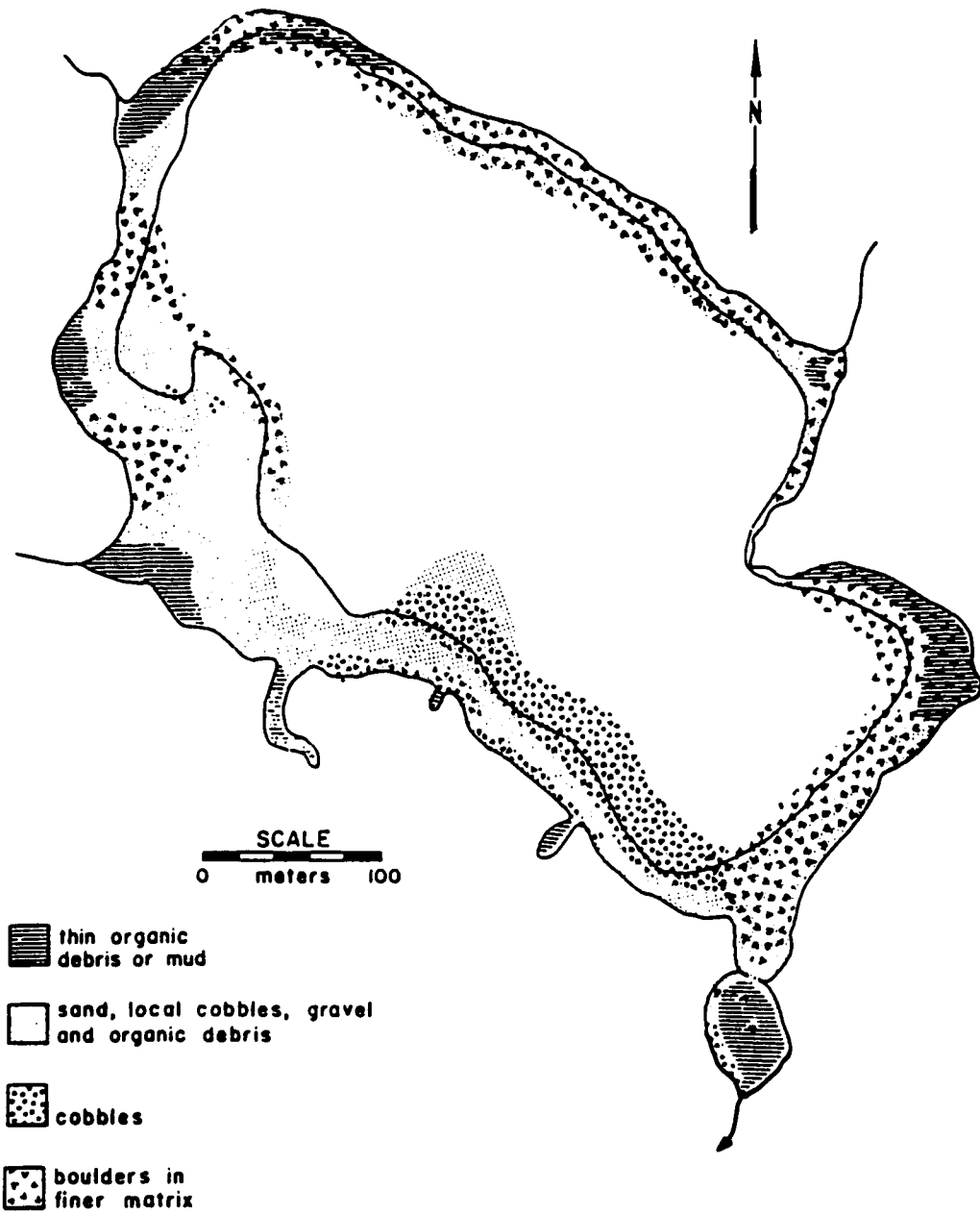


Figure II.2 Surficial sediments in Mirror Lake. Redrawn from Moeller (1978).

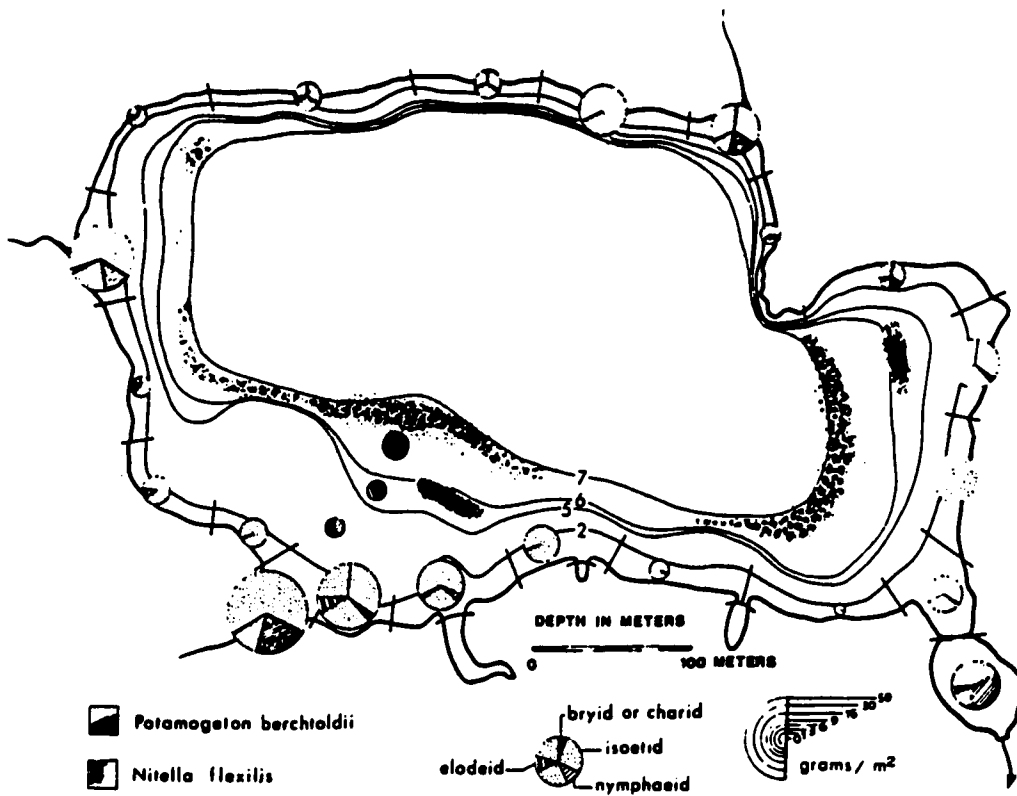


Figure II.3 Map of Mirror Lake portraying depth contours and spatial distribution of aquatic macrophyte biomass. (Moeller 1975, used with permission)

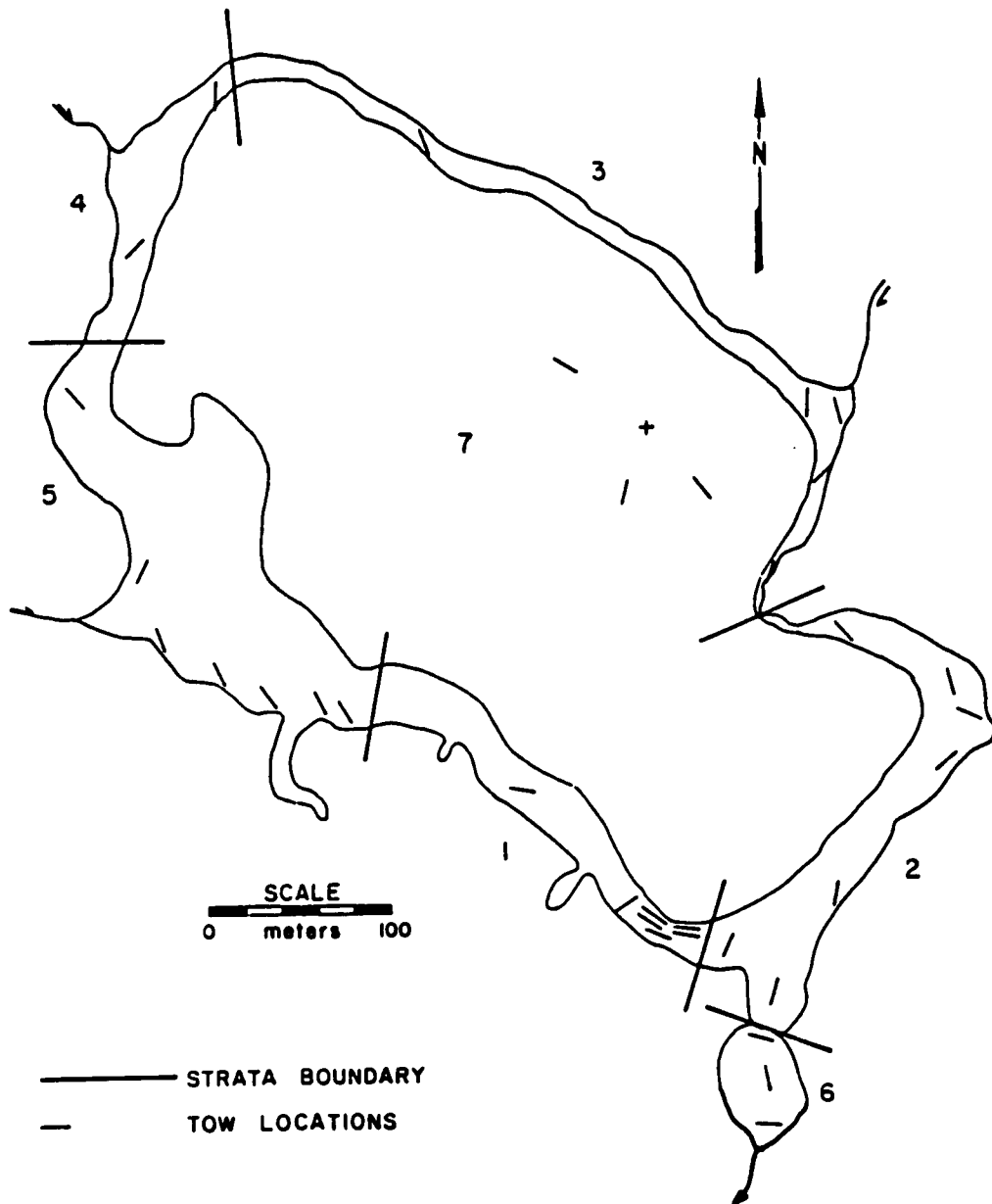


Figure II.4 Boundaries of strata and location of tows for estimation of total *Polyphemus* abundance in Mirror Lake, 1987. Tow locations are drawn to 20 m scale.

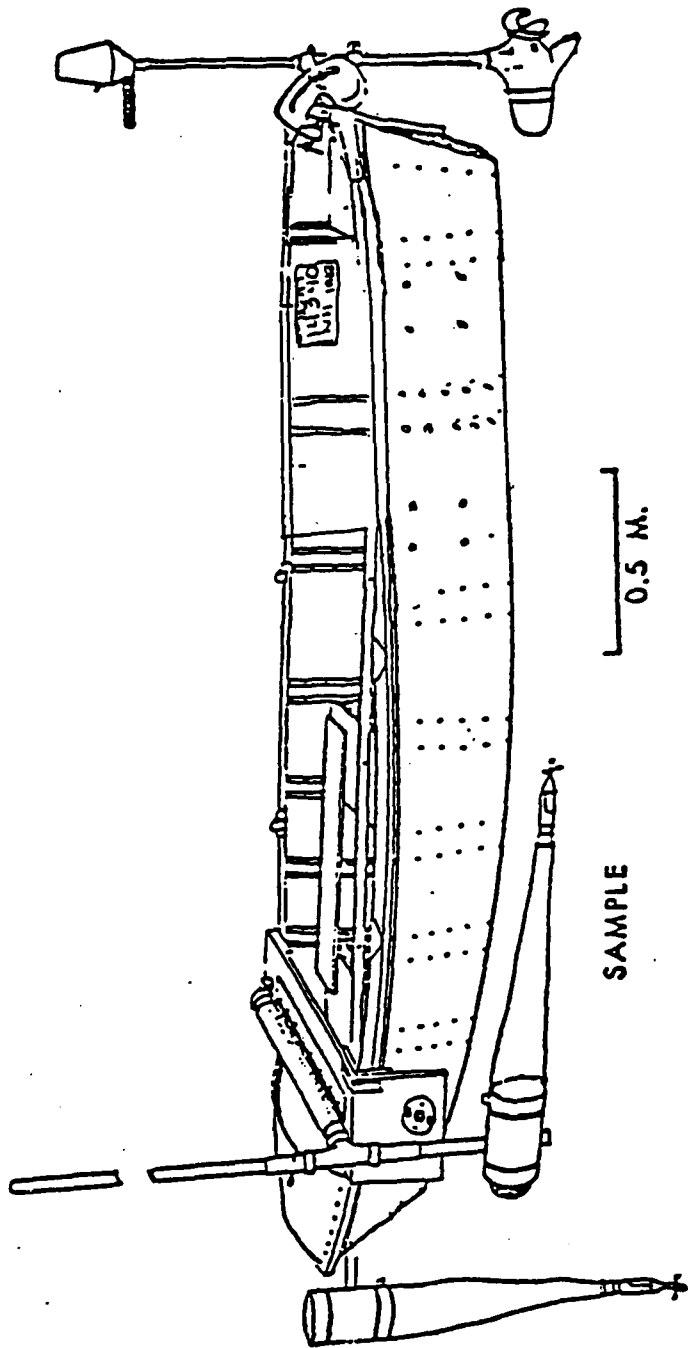


Figure II.5 Modifications of Clark Bumpus net and boat for stratified sampling (after Mattson 1979).



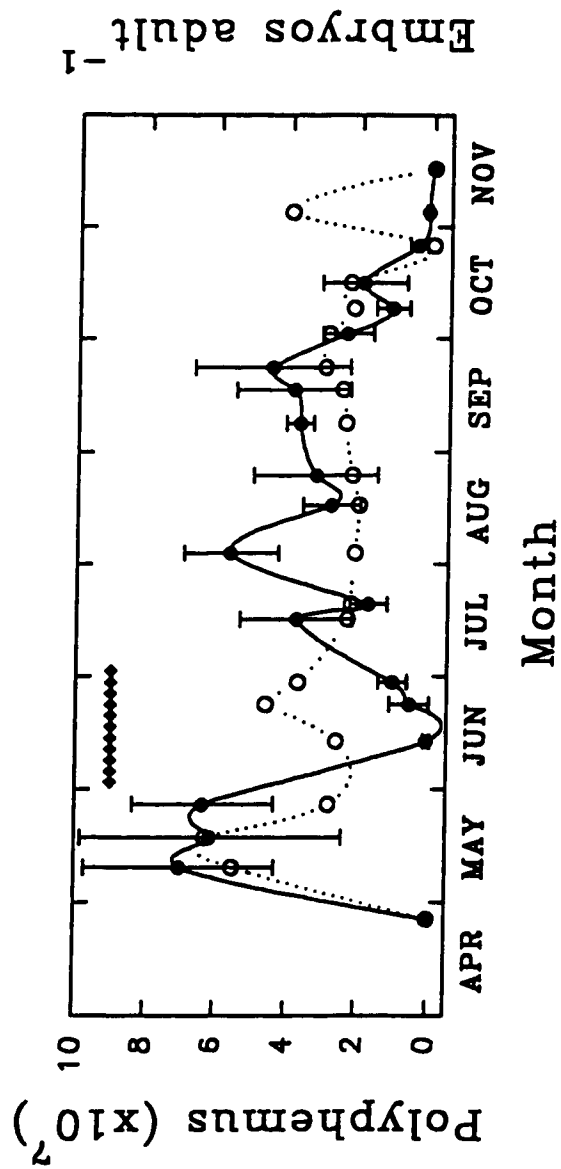


Figure II.6 Total *Polyphemus* population estimates (●) and average brood size (○), Mirror Lake 1987. Error bars indicate 95 % confidence intervals. ◆◆◆ indicate presence of *M. dolomeiui* in shore.

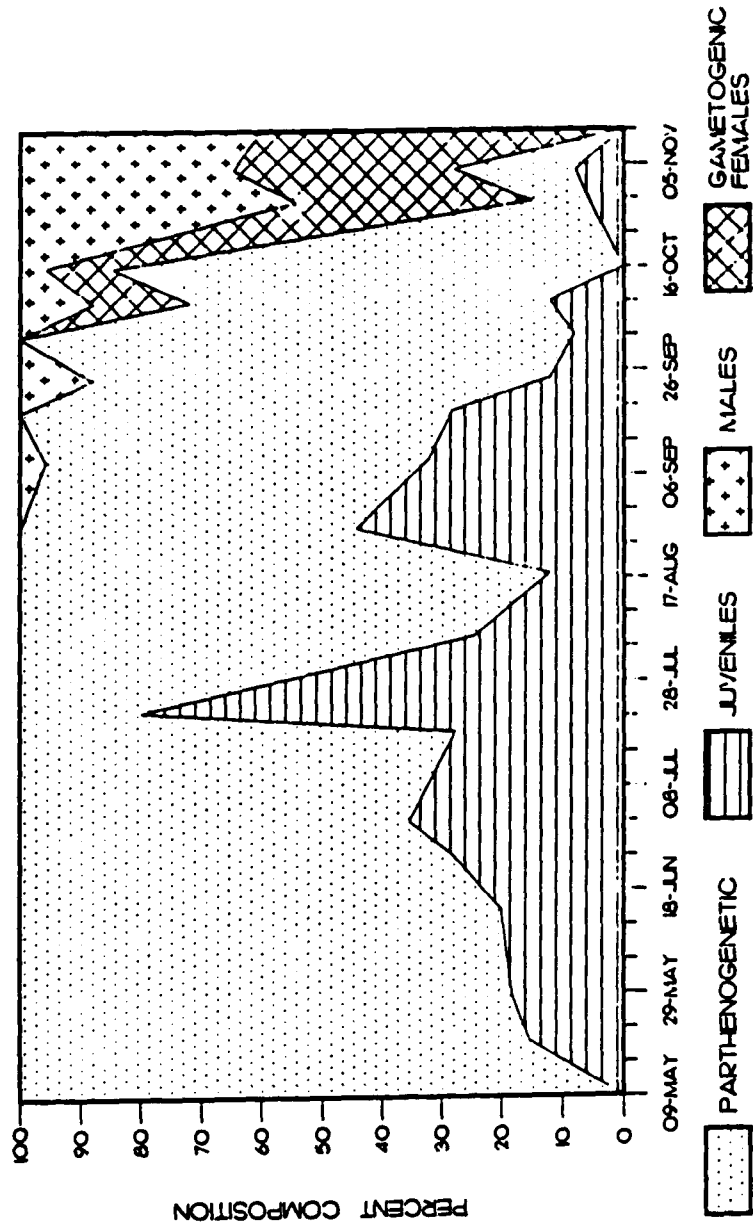


Figure II.7 Percent composition of *Polyphemus* population in Mirror Lake 1987.

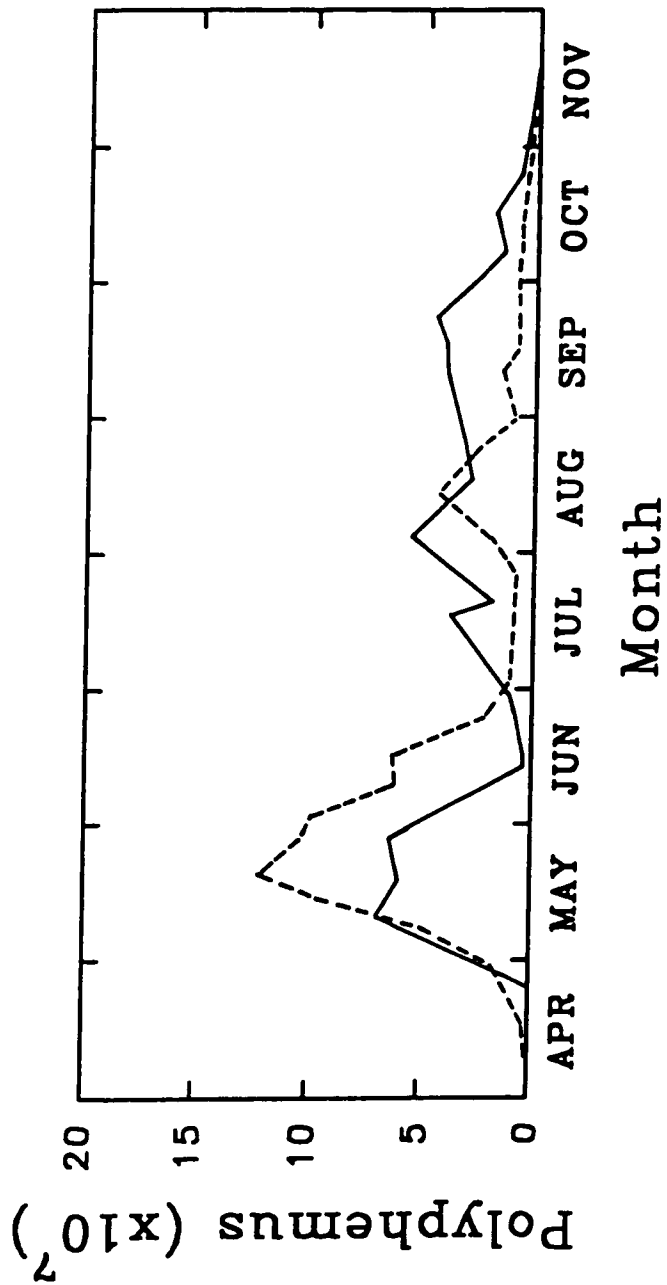


Figure II.8 Comparison of *Polyphemus* populations in Mirror Lake 1987 (---), and Stonehouse Pond 1976 (—). Stonehouse Pond data redrawn from Mattson (1979).

<u>Stratum</u>	<u>Description</u>
1	<u>Public beach</u> : Sandy, SSW exposure, high densities
2	<u>Outlet</u> : Boulders, organic debris, mud or sand, NNE exposure, low to medium densities
3	<u>Inlet</u> : Organic debris, boulders and steep slope, NE and SE exposures, low to medium densities
4	<u>Inlet</u> : Organic debris and mud, vegetation, WNW exposure, high densities
5	<u>Inlet</u> : Shallow organic debris and mud, emergent and floating vegetation, sandy beach area in front of private cabins, WSW exposure, medium to high densities
6	<u>Pool</u> : Between old (N) and new (S) dam, shallow organic debris over mud and sand, emergent and floating vegetation, low to medium densities
7	<u>Open water</u> : Beyond the 4 m contour

**Table II.1 Descriptions of major features of lake strata.**

<b>Littoral Stratum</b>	<b>Stratum Surface Area (M<sup>2</sup>)</b>	<b>Total Stratum Volume (M<sup>3</sup>)</b>	<b><i>Polyphemus</i> Habitat Volume (M<sup>3</sup>)</b>	<b>Habitat/ Total Ratio</b>
1	6224	10024	2976	.297
2	7312	11160	3437	.308
3	4712	7532	2285	.303
4	3552	5824	1762	.302
5	14480	31600	7668	.243
6	2256	2360	1046	.433
<b>Littoral Total</b>	<b>38536</b>	<b>68500</b>	<b>19174</b>	<b>.280</b>
<b>Limnetic Stratum</b>	<b>85452</b>	<b>341808</b>	<b>51271</b>	<b>14.99</b>

**Table II.2 Strata morphometric data for stratified sampling design.**

	Inner Littoral 8 m from shore $Z_{\max} = 1.0$ m	Outer Littoral 20 m from shore $Z_{\max} = 4.0$ m	Limnetic
Surface	2.1 (1.0)	0.5 (0.7)	0
0.5 m	0.5 (0.4)	0.2 (0.1)	0
1.0 m	*	<0.1 (<0.1)	<0.1 (<0.1)
1.5 m	*	<0.1 (<0.1)	0
2.0 m	*	0	0
0 - 8.0 m	OBLIQUE LIMNETIC TOWS		0

Table II.3 Pilot study to establish vertical distribution. Average number *Polyphemus* L<sup>-1</sup> (+/- S.D.).  
\* indicates no sample taken

Littoral Stratum	Mean No. <i>Polyphemus</i> L <sup>-1</sup> (+/- S.D.)	Allocated Sample Tows
1	6.2 (0.8)	7
2	7.4 (3.9)	7
3	6.4 (3.5)	5
4	3.5 (0.9)	2
5	2.9 (1.3)	7
6	6.2 (1.9)	3
7	<0.1 (<0.1)	3

Table II.4 Sample Allocation for Stratified Sampling Design.

Time Period	Size Range (mm)	<i>M. dolomieu</i> n	<i>Polyphemus</i> eaten
<b>SUNRISE</b>			
0500 - 0700	< 10	0	
	10-14	11	0
	15-19	0	
	20-24	0	
	> 25	0	
<b>BEFORE SUNSET</b>			
1700-1930	< 10	9	7.4 (9.8)
	10-14	10	1.5 (1.8)
	15-19	2	0
	20-24	0	
	> 25	0	
<b>AFTER SUNSET</b>			
2015-2350	< 10	2	5.5 (3.5)
	10-14	53	0.8 (3.0)
	15-19	20	6.9 (19.3)*
	20-24	10	0
	> 25	2	0

Table II.5 Relationship of average number *Polyphemus* eaten (+/- S.D.) per fish, size range of fish and time of day. \*Three guts contained *Polyphemus*; two, more than 50.



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### SECTION III. SPATIAL DISTRIBUTION AND DIEL MOVEMENTS OF *POLYPHEMUS PEDICULUS*

#### Introduction

*Polyphemus* typically occurs in aggregations or patches in shallow littoral areas. The patches range in size from a few centimeters to several meters in diameter, and most are limited to 0-0.5 m depth (Butorina 1986). Formation of patches has been associated with diel changes of light intensity (Mattson 1979). Aggregations reportedly lose integrity at sunset as individuals disperse in response to decreased light intensity (Butorina 1969, 1986). Aggregations reach highest densities as they reform in the morning (0400-0900 hours) (Butorina 1986). Although some aggregations are fixed in location (Butorina 1986), horizontal diel and seasonal movements between the littoral and limnetic zone have been reported in Stonehouse Pond, NH (Mattson 1979). Horizontal movements into the limnetic zone occurred at night, often succeeded by an inward movement to the littoral during the day. The diel movements were directed by changes in light intensity affecting visually mediated swimming behavior and by wind induced water currents (Mattson 1979).

Functions attributed to aggregation behavior include reproduction, feeding and protection (Butorina 1986). Aggregation behavior, however, has been observed in both parthenogenic populations and mixed gamogenetic (sexual) and parthenogenic populations. Changes of light conditions initiate patch formation. The aggregation behavior could also be an adaptation response to a selective force such as fish predation. Horizontal distribution and movements of the *Polyphemus* population in Mirror Lake were studied to observe possible diel patterns.

## Methods and Materials

### Location

Mirror Lake is located in the town of Woodstock (Grafton County) New Hampshire (43<sup>0</sup> 56.5'N, 71<sup>0</sup> 41.5'W) at an altitude of 213 m. The glacially formed lake covers an area of 15.0 ha, has a maximum depth of 11.0 m and an average depth of 5.75 m. Located within the Hubbard Brook drainage basin Mirror Lake has been included in the Hubbard Brook Ecosystem Study and the limnology has been well documented (Likens 1985). The lake is oriented on a NW-SE axis. The deepest part is closest to the north side creating steeper slopes which contain numerous boulders. The south side of the lake is more gently sloped and is sandy. The outflow of Mirror Lake drains from the SE end of the lake into the Hubbard Brook which is a tributary to the Pemigewasset River.

### Diel Studies

Two studies were designed to examine diel distributions and movements of *Polyphemus* throughout the entire littoral zone. The first study was conducted 17-18 August 1987 to observe diel horizontal movement of *Polyphemus* indicated by density changes between stations. Twenty sites were selected and marked at 100-m intervals around the lake. From these sites 20-m tows were taken perpendicular to the shoreline (Figure III.1). The entire sampling scheme was conducted five times beginning at 1500, 1930, 2200, 0530 and 1100 in random sequence and took two hours to complete.

A second diel study, conducted 18-19 August 1987, followed horizontal and vertical distributions and movements toward and away from the southwestern shore (south station). In each sampling period a series of 20-m tows was taken parallel to the shore; at 0.1 m, 4 m, 8 m, 12 m, and 20 m from shore. Buoys marked the location for each tow (Figure III.1). Samples were taken at surface (0.0-0.25 m) and 0.5-m depth intervals to the bottom along each transect at mid-day, during sunset,

mid-night and during sunrise. From 26 July-16 August 1990 the same sampling procedure was repeated three times at three locations, the southwest, north and east shores (south (1), north (2) and east (3) stations) (Figure III.1). Sampling frequency was increased and samples were taken one hour before, during and after sunset and sunrise at all stations. After the first diel sampling period in 1990 only surface samples were taken because in 1987 and in 1990 91-99 % of *Polyphemus* collected were from the surface sample (0.0-0.25 m). The sampling sequence was followed for three consecutive 24-h periods and two stations were sampled simultaneously.

Aggregation or patch densities of *Polyphemus* change seasonally with total lake abundance. For my study a *Polyphemus* aggregation was defined as a group with a density three or more times the average lake density of *Polyphemus* at that sampling period (Mattson 1979). The average *Polyphemus* density during the diel studies in August 1987 was  $1.4 \text{ L}^{-1}$ .

A 12.5 cm diameter Clarke-Bumpus (CB) metered plankton net with a  $151 \mu\text{m}$  mesh Nitex net was used for the diel studies following the procedure described elsewhere (Section II). Organisms collected were preserved in 4 % sucrose formalin (Haney and Hall 1973). In the laboratory the entire sample was examined and *Polyphemus* was enumerated with a dissecting microscope and channeled counting chamber. The proportion of the population collected at each distance from shore during a time period was weighted by that distance from shore to describe the position of the population in weighted mean distance (WMD).

### Results

Diel changes in *Polyphemus* densities and horizontal distribution were observed throughout the littoral zone in the first diel study (Figure III.2). The highest average densities occurred at sunset and sunrise ( $2.24$  and  $3.48 \text{ L}^{-1}$ ), and the lowest occurred at night ( $1.14 \text{ L}^{-1}$ ).

During mid-day sampling periods (1500 h, 17 August and 1100 h, 18 August),

average *Polyphemus* densities (1.6 and 1.8 L<sup>-1</sup>) were higher than the average density calculated from the total abundance estimate, 1.4 L<sup>-1</sup> (Section II). Patches were observed only at site 18 on the south shore. The highest number of patches were observed at sunrise (8) and sunset (4), all but one along the south and southwest shores. At night a total of 3645 *Polyphemus* were collected, half (.51) the number collected during sunset (7167). Highest night densities, including one patch, were found along the west shore. The changes in *Polyphemus* densities indicate a general movement from the north and south shores around to the west shore at night. No *Polyphemus* were collected in limnetic samples taken during the diel study. The sky was overcast and windspeeds decreased from 4.0 kph during the first sampling at 1500 h to < 1.0 kph from sunset to sunrise. Wind speeds increased to 15 kph out of the northwest during the 1100 h sampling (Hubbard Brook Experimental Forest weather data).

The second diel study, 18-19 August 1987, at the south station (station 1) revealed dynamic horizontal movement. At mid-day the population was dispersed in the outer littoral area, 8 - 20 m from shore (Figure III.3). At night 97% had moved within 8 m of shore. By sunrise 60% of the population had moved out to 8 - 20 m from shore. *Polyphemus* also exhibited short distance vertical movements. At midday most of the population was just below the surface, (0.0-0.25 m), although 14% had moved down to 0.5 m and 0.5% to 1.0 m. The deeper individuals moved up before sunset and 97% were at the surface as the population moved inward. The direction of movement in Mirror Lake was opposite to the diel movement observed in Stonehouse Pond (Mattson 1979).

*Polyphemus* moved away from shore during sunrise and toward shore during sunset at three stations in 1990 (Figures III.3 and III.4). Average weighted mean distances (WMD) after sunset were closer to shore than before sunset at the north (2) and east (3) stations (Table III.1). At the south (1) station, however, an outward

movement during sunset is indicated (Figure III.4). The south station was at the public beach and during all sunset sampling periods there was swimming activity within the buoys. The outward movement was likely a physical interference with the typical inward movement. An hour after sunset the swimmers had left and *Polyphemus* had moved into shore (WMD = 0.62 m).

*Polyphemus* appeared to have retained the post-sunset horizontal distributions throughout the night. An hour before sunrise, 75 - 95% of the *Polyphemus* collected at all three stations were still between the shoreline and 4 m (Figure III.5)(average WMD = 0.91 m). Movement away from shore before sunrise was rapid and an hour after sunrise only 10 % of the *Polyphemus* collected remained between the shore and the 4 m depth.

Changes in weighted mean distances were significantly affected by time of day and not by station orientation (2 way ANOVA,  $F=5.37$ ,  $p<0.05$ ). Weighted mean distances were significantly different before sunrise and after sunset (Duncan's multiple range test,  $p<0.05$ ). Only a small proportion of the population (< 15%) exhibited vertical movements, up before sunset and down after sunrise, not exceeding 1 m.

### Discussion

Horizontal movements of *Polyphemus* were very pronounced in Mirror Lake; most of the population moved distances up to 20 m within two hour periods. Swimming speeds from 11.2 to 57.2 m sec<sup>-1</sup> have been video-recorded in the laboratory (Young and Taylor 1988). Butorina (1986) reported rapid long distance movements by *Polyphemus* of 25 m in two hours. These swimming speeds could account for the diel changes of density distribution throughout the littoral area and the dynamic diel patterns of horizontal movement from the outer regions of the littoral area into shore during sunset and back out before sunrise.



Most patches were observed during sunset (1730 samples) and sunrise (0530 samples) concentrated along the SSW shore (Figure III.2). The absence of patches throughout the littoral areas except at station 18 during daylight hours and formation of patches along the west shore and not the SSW shore at night suggest some type of diel movement. If there was diel movement of *Polyphemus* in the littoral area, where were the large numbers collected at sunrise during the night? They did not move out into deeper limnetic water. *Polyphemus* was not collected in limnetic tows taken beyond 8 m from shore. The relatively low numbers of *Polyphemus* first sampled at night in the perpendicular tows can be explained. Most likely *Polyphemus* moved into shore at night as observed in the second diel study. If *Polyphemus* had moved to within 2-m from shore they could not be collected with the methodology used and described elsewhere (Section II). In the second diel study > 50% of the *Polyphemus* collected at night were 0.1 m from shore. *Polyphemus* must have been in the inshore shallow areas of the lake and during the first diel study the shallow areas were not sampled.

Although the methodology explains the low densities at night it does not explain the unusually high densities along the west shore (Figure III.2). There was a flood light at site 4, which illuminated the entire sampling area and four other sites where the high *Polyphemus* densities occurred. Between site 4 and both adjacent sites (3 and 5) there were large boulders extending into the water and large trees at the shoreline which blocked the light from the surface of the water at the two sites. *Polyphemus* densities at sites 3 and 5 were similar to densities along the eastern shore,  $< 1 L^{-1}$ . Light levels at all sites were below the sensitivity of the Whitney Photometer used to measure light intensity, as were light levels before sunrise and after sunset. The artificial light source could have simulated sunrise or sunset light conditions and *Polyphemus* responded by moving out from shore and/or aggregating.

The prevailing winds on Mirror Lake are usually from the northwest (Hubbard Brook Experimental Forest weather data) which could explain high densities of *Polyphemus* along the south shore. Mattson (1979) found a strong correlation between patch location and wind direction during the summer months. Patches formed on the downwind side of Stonehouse Pond during strong winds.

The formation and function of zooplankton patch densities or aggregations has often been associated with social activity or sexual reproduction (Colebrook 1960), increased feeding rates and predator avoidance (Folt 1987). Sexual activity has also been suggested as a function of *Polyphemus* aggregations (Butorina 1986). Active aggregations of parthenogenetic individuals were observed throughout the season before gamogenetic individuals appeared in the population. Feeding rates of *Polyphemus* have been reported to increase with predator density (Butorina 1986). Most feeding activity in Mirror Lake, however, occurred during the daylight hours (Section V), when *Polyphemus* densities approximated the average lake-wide littoral density.

Crepuscular aggregations in Mirror Lake were associated with an upward movement by a small proportion of the population. More pronounced than the diel vertical movement was the diel horizontal movement. The co-occurrence of aggregation and diel movements suggests there is a relationship between the two events. In Stonehouse Pond, a lake morphologically similar to Mirror Lake, Mattson (1979) observed significant horizontal movement of *Polyphemus* opposite of that observed in Mirror Lake; away from shore at night into the limnetic zone and, in varying degrees, inward during the day. His observed horizontal movement also coincided with vertical movement, downward at night, upward during the day. Absence of wind at night facilitated dissipation of patches and population shift into the limnetic zone. Similar diel behavior has been reported in the Rybinsk Reservoir (Butorina 1969).

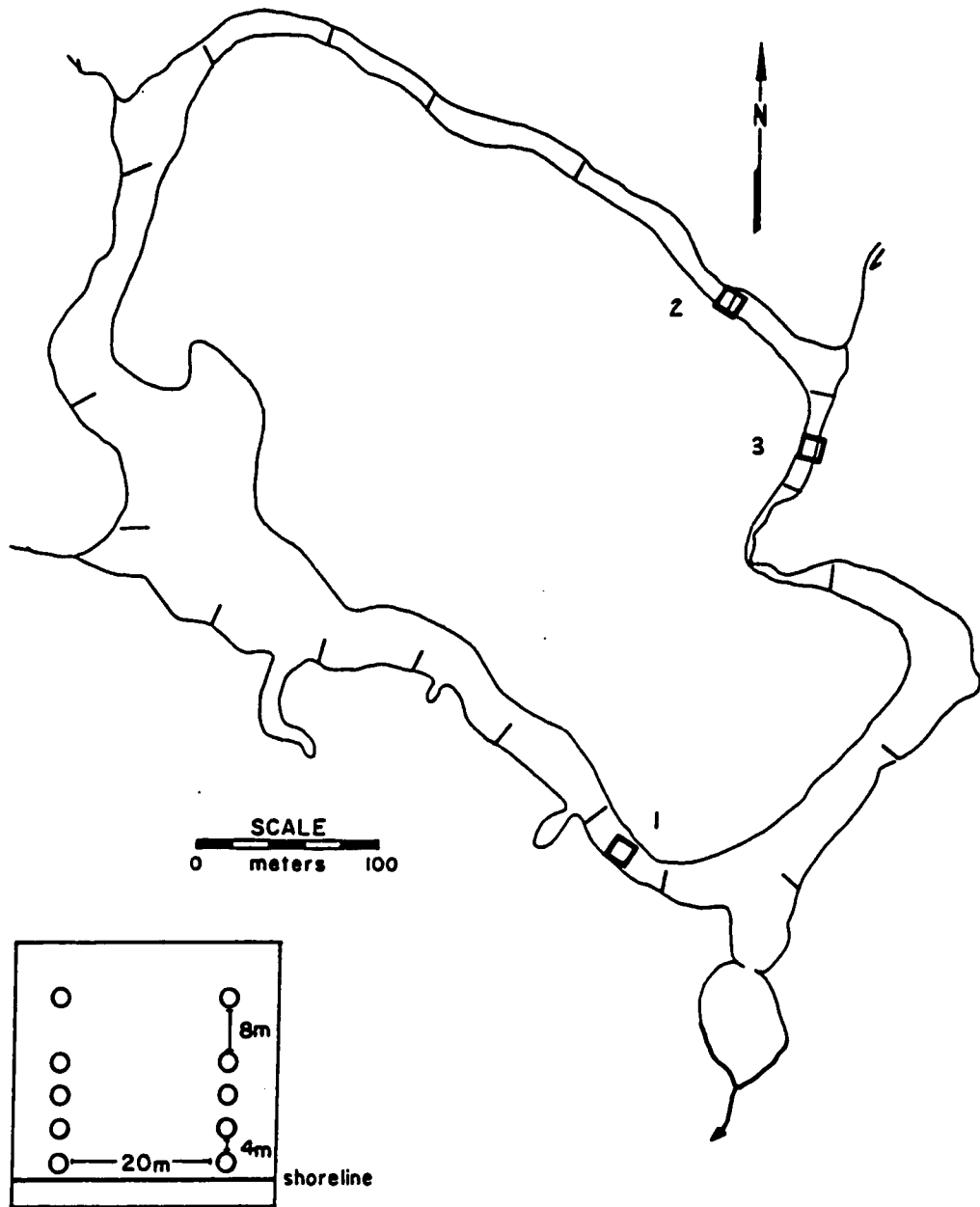
During the 17-18 August 1987 diel studies wind speed did not exceed 5 kph except at mid-day on 18 August when speeds to 18 kph were recorded. The diel horizontal patterns occurred consistently throughout the study. Inward horizontal movements were observed during calm, rain and storm conditions, while outward movements were observed against high wind. In Mirror Lake it is doubtful that this diel horizontal behavior can be correlated with wind.

A likely stimulus for this horizontal movement in Mirror Lake is light. Light intensity changes during sunset and sunrise are common cues for vertical and horizontal movements of many zooplankters (Haney 1988). *Polyphemus* is able to detect refracted or reflected light from particles under the water surface. The large compound eye of *Polyphemus* comprises 25 % of the body length and contains 130 facets (ommatidia). The photoreceptor within each ommatidium is a light sensitive rhabdom. There are 4 types of rhabdoms, regionally arranged, in the *Polyphemus* eye (Nilsson and Odselius 1983). One type of rhabdom causes *Polyphemus* to be more sensitive to vertically polarized light than to horizontally polarized light (Odselius and Nilsson 1983). This sensitivity is maximized when the angle between the sun's rays and a line drawn perpendicular to the surface is between  $42^{\circ}$  and  $64^{\circ}$ . At Mirror Lake this angle at which *Polyphemus* best detects other plankters and particles occurs in late morning, 0830 - 1030 hours, and late afternoon, 1530 - 1730 hours (Anderson 1977). These two periods of optimum vision for detecting particles coincide with maximum *Polyphemus* feeding but not with horizontal movements. Feeding activity and horizontal movements as affected by light are independent of each other and perhaps the relationship of light and diel movements can be explained with descriptive functions of the other rhabdom types.

The different patterns of diel movement in two physically similar New Hampshire lakes, Mirror Lake and Stonehouse Pond, suggest different selective forces. Predators can often affect behavior and abundance of prey populations

(Hall *et al.* 1970). The invertebrate predator species of both lakes was *Chaoborus*. *Chaoborus* exhibits pronounced vertical migrations after sunset and did not appear near the surface of Mirror Lake until after *Polyphemus* had moved into shore. The vertebrate predators, however, were different in the two lakes. *Micropterus dolomieu* (smallmouth bass) fry have been identified as a predator in Mirror Lake for the first few weeks after hatching (Section II). Several studies have reported increased feeding activity of *M. dolomieu* during crepuscular periods (Helfman 1981) followed by cessation of feeding and offshore migrations (Munther 1970; Emery 1973). The activities of *M. dolomieu* coincide with the aggregation and inshore movement of *Polyphemus*. The outward movement of *Polyphemus* during sunrise occurs just before or simultaneously with the inward movement and first feeding activity of the predators. *Polyphemus* aggregation and diel movements could have evolved as a predator avoidance behavior which decreased the chances of an individual being eaten and diminished the probability of encounter with a predator.

In Stonehouse Pond the vertebrate predators were limited to an introduced population of brook trout (*Salvelinus fontinalis*). As a part of New Hampshire's reclamation program Stonehouse Pond was treated regularly with rotenone, most recently in 1970. *S. fontinalis* were stocked as fall fingerlings, 10 - 15 cm long, and spring yearlings, 20 - 25 cm long, and were larger than fish fry which select *Polyphemus* size prey. If *S. fontinalis* were to swim into an aggregation, feeding did occur (Haney and Mattson 1980). Several years after Mattson's study of *Polyphemus* in Stonehouse Pond, another vertebrate predator, *Lepomis gibbosus* (common sunfish) was introduced. *L. gibbosus* exhibit feeding behavior similar to *M. dolomieu* and were very efficient predators on a *Polyphemus* population which did not exhibit a predator avoidance behavior. *Polyphemus* has not been in Stonehouse Pond since 1985. It appears that aggregation behavior did not prevent predators from decimating this population.



**Figure III.1 Location of sample tows for diel studies on 17-18 August 1987, 18-19 August 1987 and 26 July-18 August 1990. Inset shows detail of marker locations for horizontal movement studies.**

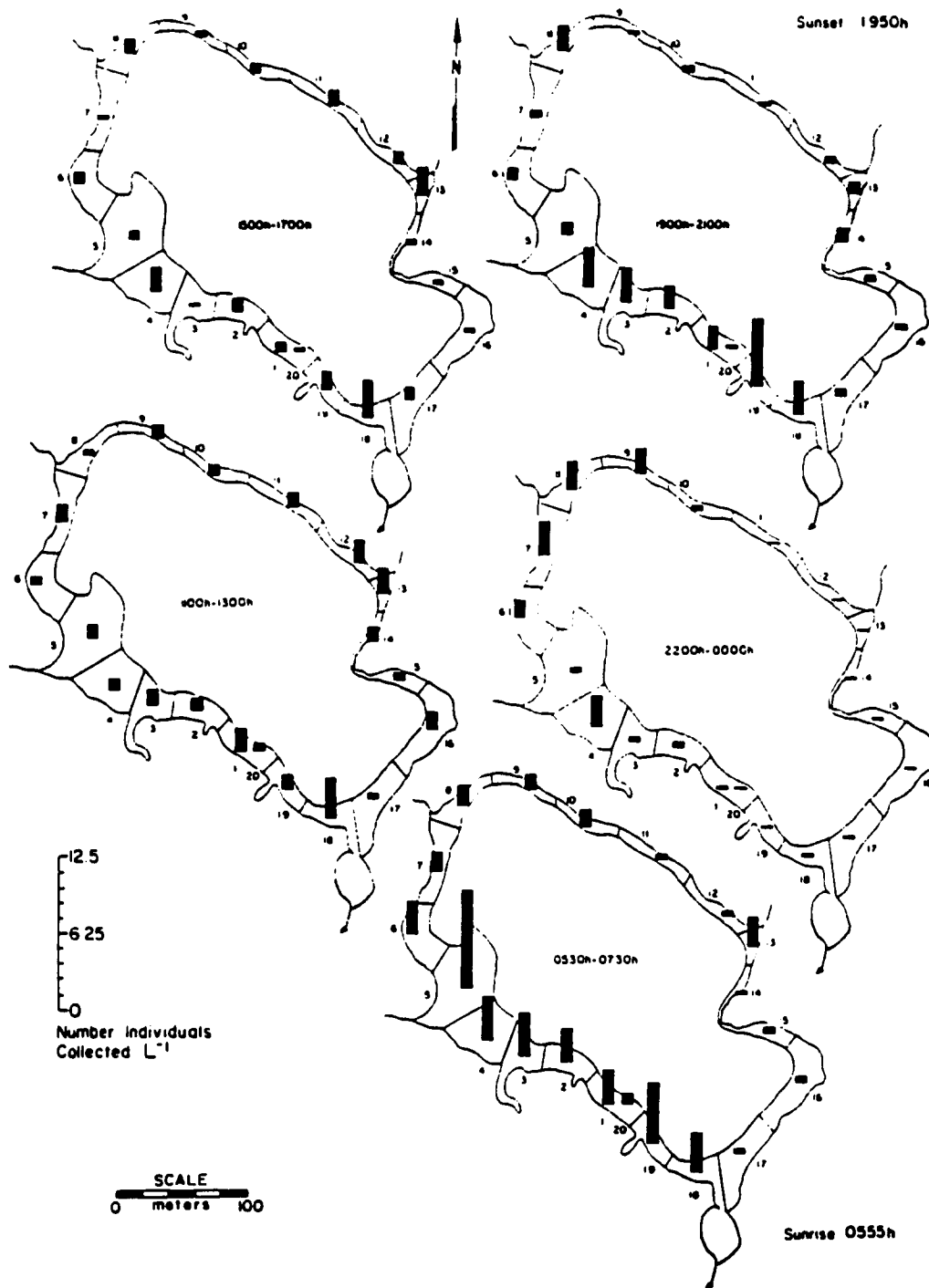


Figure III.2 Total diel densities and horizontal distribution of *Polyphemus*, Mirror Lake, 17-18 August 1987. (Clockwise, from upper left)

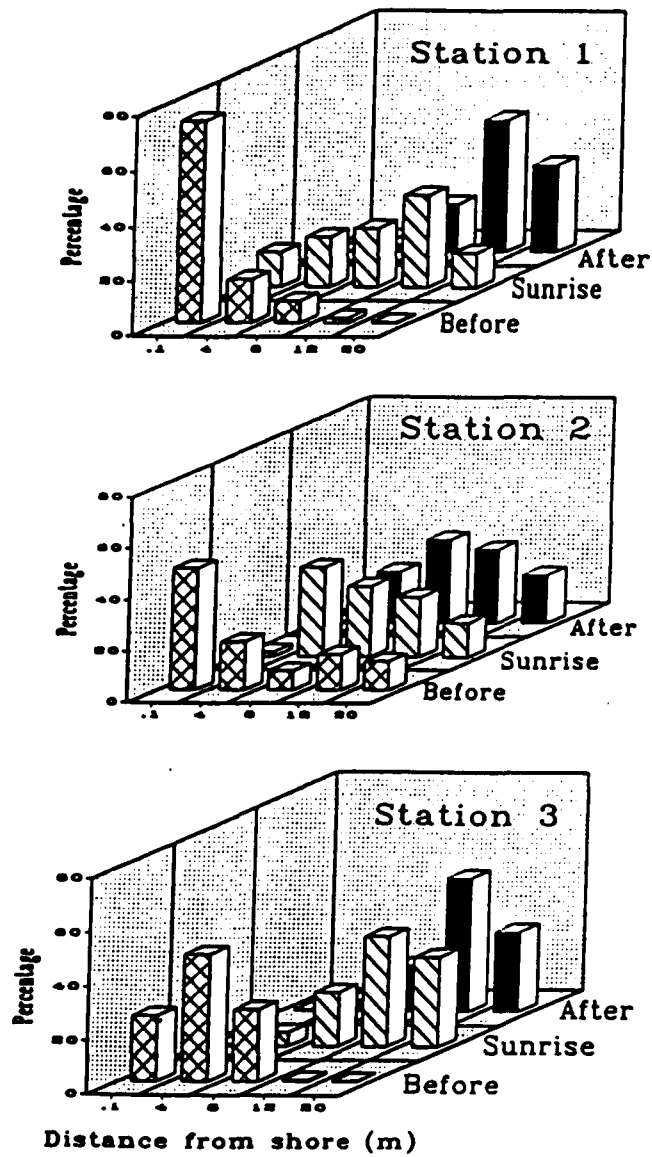


Figure III.3 Horizontal distribution of *Polyphemus* during sunrise (18-19 August 1987 and 26 July-16 August 1990) at the south (1), north (2) and east (3) stations. Bars represent average percent collected at each distance from shore relative to total number collected at that time period. Before sunrise  $n=21,106$ ; sunrise  $n=22,556$ ; after sunrise  $n=16,375$ .

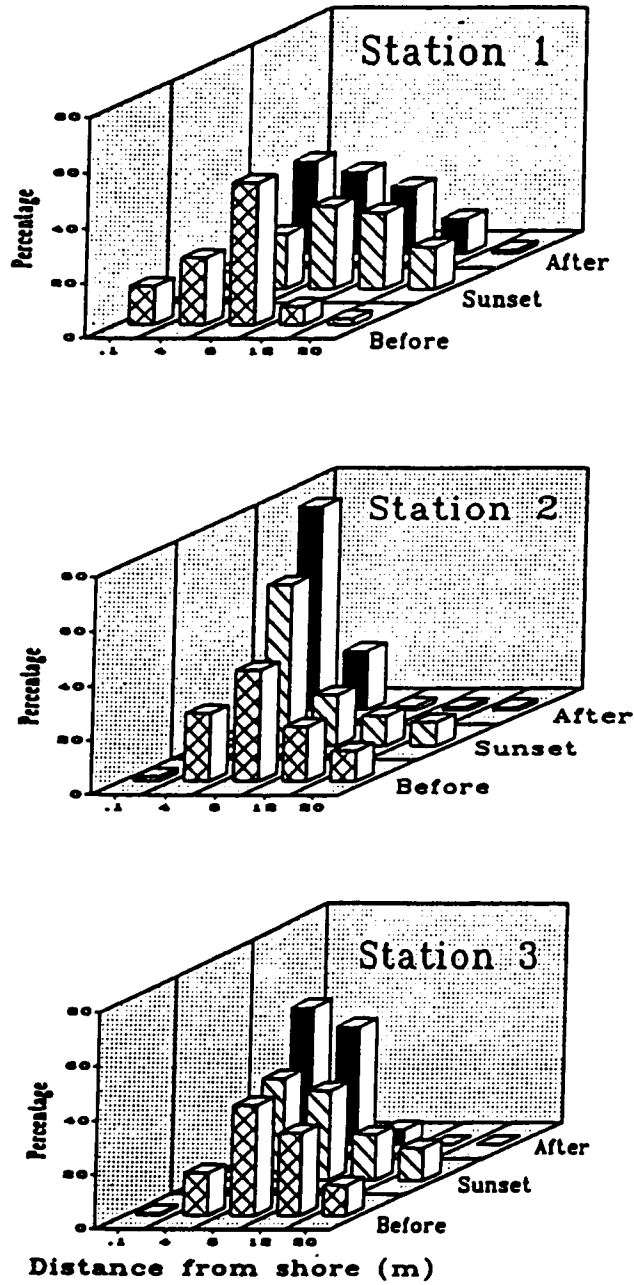


Figure III.4 Horizontal distribution of *Polyphemus* during sunset (18-19 August 1987 and 26 Jul - 16 August 1990) at the south (1), north (2) and east (3) stations. Bars represent average percent collected at each distance from shore relative to total number collected at that time period. Before sunset n = 30,127; sunset n = 32,073; after sunset n = 36,552.



Station	SUNSET			
	Before	During	After	Difference
South	1.29(1.46)	1.44(1.19)	0.61(0.53)	+0.67
North	1.81(1.16)	1.40(0.78)	0.29(0.29)	+1.52
East	1.98(1.44)	1.56(0.85)	0.46(0.65)	+1.52

	SUNRISE			
	Before	During	After	Difference
South	0.33(0.26)	2.03(1.69)	2.88(3.18)	-2.55
North	1.56(1.01)	1.59(0.87)	2.07(1.42)	-0.51
East	0.84(0.96)	1.45(1.21)	2.35(2.10)	-1.51

**Table III.1 Average weighted mean distances (m) (+/-S.D.) from shore during sunset and sunrise 18-19 August 1987 and 26 July-16 August 1990).**

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## SECTION IV. METHODOLOGIES DEVELOPED TO STUDY FEEDING RATES AND SELECTIVITY OF *POLYPHEMUS PEDICULUS*

### Introduction

Predation rates of zooplankton are generally estimated by one of three experimental approaches; gut content analyses (Gliwicz 1969; Confer 1971; Infante 1973; Swift and Federenko 1973; Brandl and Fernando 1975; Murtaugh 1981; Downing and Rigler 1984), isotope food labeling (Haney 1971, 1973; Peters 1975; Lane et al. 1976; Downing and Rigler 1984) and differential counts (Gliwicz 1968; Downing and Rigler 1984). The method I chose for estimating ingestion rates of *Polyphemus* was differential counts. Although this method is time consuming and labor intensive it has several advantages. Feeding rates on different prey can be estimated simultaneously. Experiments can be allowed to continue for long periods of time, thus compensating for variations caused by discontinuous feeding and undetected diel feeding patterns (Downing and Rigler 1984). Incompletely eaten prey cannot be identified in gut content analyses, but can be counted as such using the direct count method. Predaceous cladocerans tear prey with their mandibles and then suck the body contents in, rendering gut contents to a homogenous mass (Mordukhai-Boltovskaya 1960; Monokov 1972). Feeding rates and prey selectivity of predaceous cladocerans, therefore, cannot be established with gut content analyses. Predation studies with labeled food requires radioactive cultures of bacteria or algae which are first fed to the prey, and in turn are fed to the predators. Feeding studies have to be brief, ending before the labeled cells can pass through the gut of the prey or the prey through the gut of the predator. Butorina and Sorokin (1970) used 14-Carbon labeled *Chlorella* to label *Bosmina* and *Keratella*

which were offered to *Polyphemus* in unusually high densities. In high prey densities, gut passage of *Polyphemus* was as short as 10 minutes. Loss of the radioactive material through manipulation, incomplete ingestion, egestion, respiration or egg development, if the experiments were allowed to last too long, could result in underestimates of feeding rates (Peters 1975).

Feeding rates of the zooplankton community are affected by many factors. Light conditions, temperature, time of day, duration of the study, animal size, size and concentration of food particles, container size and volume per animal influence grazing and feeding by zooplankton in varying degrees (general literature review by Peters 1985). Peters and Downing (1984) surveyed the literature and collected feeding data from a broad range of experimental conditions and performed multiple regression analyses to describe the significance of these factors on feeding rates. Ingestion rates of herbivorous cladocerans are affected most significantly by food concentration, followed by animal size, water volume per animal, food size and temperature. In the laboratory, predation rates by the differential count or radioactive labeling method are typically estimated from experiments conducted in small vessels containing mixtures of plankton concentrated from net tows (e.g. Murtaugh 1981; Ramcharan and Sprules 1986; Matveeva 1989; Grossnickle 1978) or cultured prey (Butorina 1986). Duplicating *in situ* conditions and natural predator and prey densities and composition is very difficult. In addition, the handling required to set up feeding experiments could injure the predators or the prey or affect their behavior and physiology (Chow-Fraser 1986). *In situ* feeding experiments are not as convenient as those conducted in the laboratory but can provide a more accurate indication of what kind of prey and how many prey the predators are actually eating under virtually natural conditions.

The first *in situ* feeding studies were conducted by Gliwicz (1968) who used two 3 L. capacity experimental chambers. Both chambers trapped zooplankton and

lake water. A narcotic was released into one chamber to stop feeding activity. Zooplankton counts from this chamber were used as the control. Feeding rates of the zooplankton community were estimated by the differential count method. Hillbricht-Ilkowska and Karabin (1970) modified the method to study feeding rates of the predaceous cladoceran *Leptodora kindtii*. Vanderploeg *et al.* (1982) modified and enlarged the traps (30 L.) to study feeding rates and prey selectivity of *Mysis relicta*. In both studies traps were used to collect water containing natural zooplankton assemblages, predators were added to one chamber and the other chamber served as the control.

To ensure measurable feeding rates, predator densities used in the *Leptodora* experiments were 2-10 times ambient densities ( $350 \text{ m}^{-3}$ ). Bowers and Vanderploeg (1982) chose a predator density of  $166 \text{ mysids m}^{-3}$ , only slightly above the natural observed range of  $30\text{-}140 \text{ m}^{-3}$  (Grossnickle 1978; Beeton 1960) as a compromise between two conflicting requirements; sufficient numbers to obtain measurable feeding, while minimizing density induced stress. *In situ Polyphemus* densities are more variable than *Leptodora* and *Mysis*. Non-aggregation densities are less than  $1 \times 10^3 \text{ m}^{-3}$ , whereas densities within aggregations have been reported up to  $1.5 \times 10^7$  individuals  $\text{m}^{-3}$  (Mattson 1979). This broad range indicates the potential importance of predator density. The relationship of predator density and feeding rates could be demonstrated with manipulated feeding studies at several natural predator densities. A manipulative experiment by definition always involves two or more treatments and has as its goal one or more comparisons (Hurlbert 1984). Predator manipulated studies, especially *in situ* plankton feeding, are rare in the literature (Sih *et al.* 1985). Several predator densities used in a single experiment representing the range of natural densities would permit estimates of predator density effects on feeding rates. It is assumed that any changes occurring in the control chamber during the experiment also occur in the other chambers

(Hillbricht-Ilkowska and Karabin 1970; Vanderploeg *et al.* 1982; Hart and Christmas 1984; Nero and Sprules 1984).

The variability of natural prey densities between control and experimental chambers affects the sensitivity of an *in situ* differential count method of estimating predation rates. Vanderploeg *et al.* (1982) demonstrated that distribution of prey populations in control and experimental chambers were random. Cassie (1959), however, observed small scale patchiness in samples taken on a horizontal plane at 10 cm spatial intervals.

## Methods and Materials

### Feeding Chamber Design

A multichambered transparent plankton feeding trap was constructed to accommodate multiple predator densities in a single feeding experiment. Each chamber was designed to meet several criteria for an acceptable plankton trap. First, the chamber must move through lake water with minimal turbulence and close quickly at the selected depth to eliminate or minimize possible plankton avoidance responses (Smyly 1968). The chamber must be transparent to reduce visual avoidance (Schindler 1969, Hodgkiss 1977). The chamber must be large enough to collect a number of prey individuals adequate for statistical evaluation.

The multiple unit apparatus collects water with a Schindler trap-type closing mechanism and a remote predator introduction system modified after Haney (1971). Each chamber of the four-chambered trap was fabricated from 0.635 cm Plexiglas (21 x 21 x 61 cm outside diameter) with a capacity of 21.15 liters (Figure IV.1). The two end lids are hinged by pieces of rubber tubing and connected by a stainless steel tie rod causing the lids to work simultaneously. Self-adhesive foam gasket tape was applied to the contact area of the back and side edges of the lids as well as the

corresponding areas of the rims to prevent leakage. Magnetic tape on the front edges of the lids and rims kept the traps from opening under water. Holes (3 cm) were drilled in the center of each top lid to allow air to escape when closing on surface waters and to permit water to drain out as the assembly is raised. Rubber stoppers were placed into the holes during the feeding experiments to prevent exchange of water. On the bottom end of the front surface of each chamber is a 2.9 cm hole with a 3 cm neck. A ring net assembly is attached to the neck. A ring net assembly consisted of a 10 cm long tapered net with a Plexiglas plankton bucket (10 cm long, 8.5 cm diameter, 10  $\mu$ m mesh) attached to the narrow end.

*Polyphemus* are automatically released from a small cylinder in the corner of each chamber when the trap is closed. Each predator-release cylinder is constructed of Plexiglas tubing, rubber stoppers connected by a black wire strand leader to close off the ends of the cylinder and a second leader connecting the bottom stopper with an eyelet screw in the bottom lid (Figure IV.1).

This plankton trap/feeding chamber assembly was specifically designed for the surface waters of littoral areas typically inhabited by *Polyphemus*. The assembly of four chambers was set in a stainless steel frame and was raised and lowered by a winch mounted on a small permanent platform (Figure IV.2). The chambers are held open while being lowered by monofilament lines attached to the top lid and hooked to the top of the steel frame. *Polyphemus* were put into the release cylinders and the assembly was quickly lowered into the water. The lids were manually closed, releasing the predators. As an alternative, *Polyphemus* were added through the hole in the top lid. The procedure was reversed at the termination of the feeding experiments. The stoppers were removed from the top lids and the assembly was slowly raised allowing the water in each trap to filter through the ring nets. Plankton collected on the nets was backwashed into sample vials for preservation and subsequent laboratory analyses.



### Equipment and Assumptions Tested

Two assumptions of the differential count feeding method were tested before the experiments were begun. The first assumption was all individuals introduced or collected in the chambers are recovered. Second, prey distribution among the four replicate chambers is uniform, i.e. the number of each prey taxon in each of the three experimental chambers and the control chamber is not statistically different.

To test the first assumption, I examined the recovery rate of *Polyphemus* from the chambers. A known number of *Polyphemus* was added to each chamber as the assembly was deployed. After four hours the assembly was raised and all individuals in the chambers were collected on ring nets. The chambers were not rinsed. The individuals recovered were counted and the recovery rate for each chamber was calculated (Table IV.1A). The average recovery rate was 82.28% (+/- 7.29 S.D. n=28).

Possible physical entrapment of *Polyphemus* in the chambers was examined by a series of rinses. By rinsing each chamber with four liters of filtered water an average of more than 95% of the *Polyphemus* was recovered (Table IV.1B).

To test whether leakage from the chambers could account for any loss of *Polyphemus* the opening for the plankton bucket at the bottom of each chamber was covered and the chamber was filled with well water. An average of 522.1 mL (S.D. = 286.2, n = 11) leaked between the gaskets of the bottom lids in 4 minutes, the maximum time to raise the assembly at the end of a feeding experiment. This is an overestimation of water loss because the openings for the plankton buckets had been covered for the tests and the water pressure within the chambers exceeded that which existed during normal use. In practice, as the chambers were raised from the lake the water flowed out through the plankton buckets and the water levels in the chambers remain close to the lake level.

The 2.5% water loss could explain 2.5% of *Polyphemus* not recovered (six out

of an original concentration of 250 *Polyphemus*). The remaining proportion of *Polyphemus* not recovered (2.5%) was probably either still trapped in the chamber or cannibalized by other individuals. The rinse procedure was followed for all feeding experiments to insure high recovery rates of both predators and prey.

The second assumption of the differential count feeding method is uniform distribution of prey. Prey distribution in limnetic predation studies, however, has been reported as random (Vanderploeg *et al.* 1982), and small scale patchiness of zooplankton has been reported within small surface areas as sampled by the trap ( $< 1 \text{ m}^2$ ) (Cassie 1959). Larger scale ( $> 1 \text{ m}^2$ ) random distribution has been reported for some rotifer species in Mirror Lake (*Keratella* and *Kellicottia*) while the distribution of the other prey species was patchy (Makarewicz 1974). Small scale distribution studies of plankton in Mirror Lake have not been reported.

Since the control was not replicated during each *in situ* feeding experiment, *Polyphemus* predation rates were estimated by subtracting the single control chamber count of each prey item from the final count in each experimental chamber with *Polyphemus*. Lower than actual feeding rates would be obtained from experimental chambers with prey densities higher than the control at the beginning of the feeding period. Conversely, higher feeding rates would be obtained in experimental chambers with lower densities than the control chamber. The magnitude of the prey variation can determine the threshold sensitivity for the differential count method.

To determine whether variability between chambers was random I took ten multiple samples with the predation trap on seven separate dates. Two multiple samples were taken on two of these dates, three samples on one. Seven prey taxa were enumerated from each chamber.

A nested analysis of variance (ANOVA) model was developed to classify and compare three levels of variation in these data:

**DATE** - representing day to day variation among the seven days.

**WITHIN DATE** - representing variation among the replicate sets of counts taken on the same day.

**REPLICATE** - representing within date variation among the four chambers of one multiple sample.

The results demonstrate that all models were highly significant with R-squares of between 0.87 and 0.997 (Table IV.4). Within date, replicate variation was only 0.3% to 14.8% of the variation explained by the model, depending on the taxon. Based on the magnitude of date to date (12.0 - 99.7%) and within date (4.7 - 96.7%) variations, within chamber, or replicate variation cannot be pooled across these time frames. Differential counts were, therefore, derived by subtracting the single control chamber density from the three feeding chambers of the same feeding period.

Negative predation rates obtained from experimental chambers were not set to zero prior to computing mean predation rates since negative feeding rates reflect random, within chamber variation with equal probability of being positive or negative. If negative feeding rates, calculated from feeding chambers with more prey than the control chamber at the end of the feeding period, were set to zero, calculated mean feeding rates would be overestimated.

Density variation of copepod nauplii was the highest of all prey taxa examined. Nauplii were the largest of the prey taxa and also the fastest swimming. Patchy distribution of this group has been reported in Mirror Lake (Makarewicz and Likens, 1979)

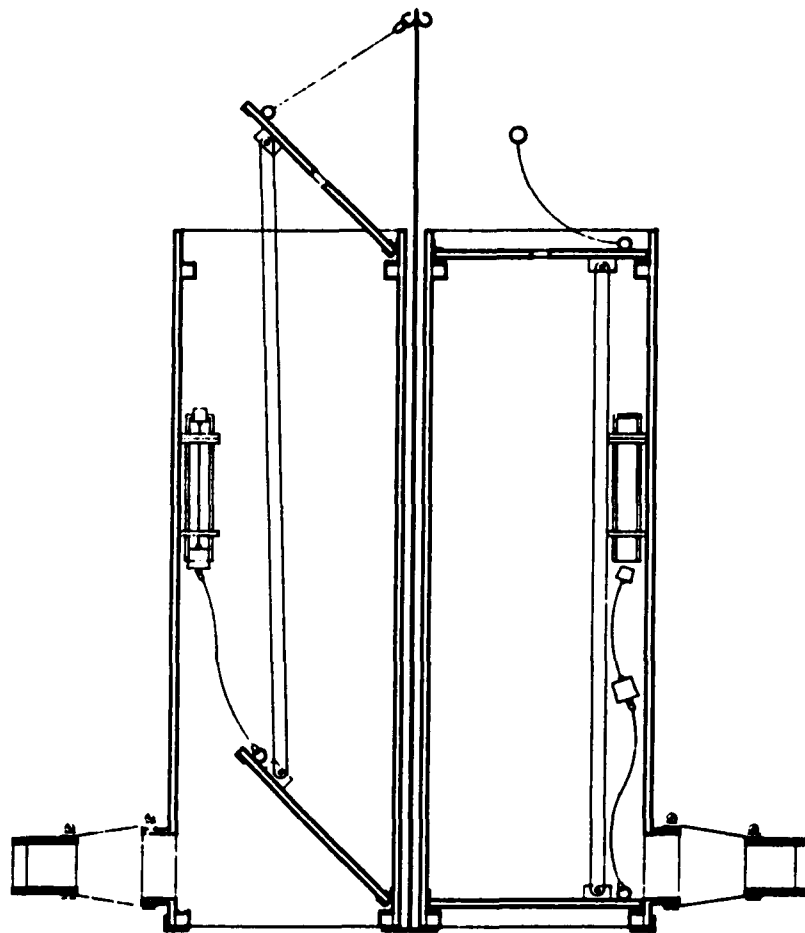
Density variation of colonial forms can be exaggerated when individuals are enumerated and not the colonies. The number of *Conochilus* in a live colony ranged from 12 - 50 individuals, the average was 30 (n = 140). Most *Conochilus* colonies

lost their integrity when placed in preservative which made individual enumeration necessary.

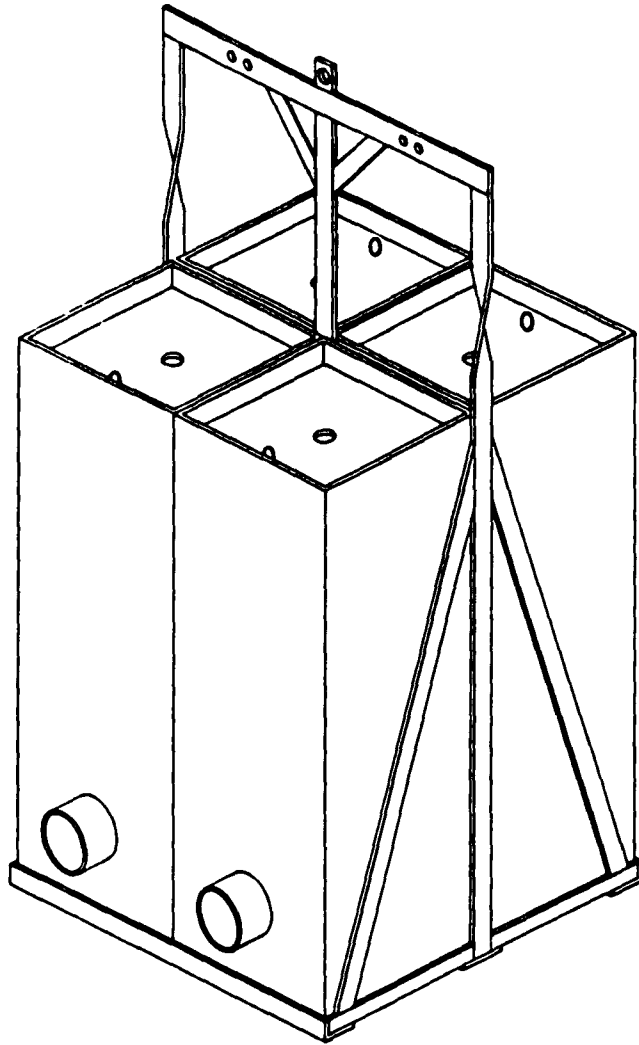
*Vorticella*, a large ciliate, was physically attached to *Anabena* colonies in Mirror Lake. More than 100 *Vorticella* were often counted on one colony. *Vorticella* was not, however, found on all *Anabena* colonies and the average number of *Vorticella* per *Anabena* colony ranged from 2 - 10. The number of individuals per colony was not correlated with total number counted chamber<sup>-1</sup> (*Conochilus*,  $R^2 = 0.05$ ,  $n = 10$ ; *Vorticella*  $R^2 = 0.05$ ,  $n = 9$ ).

To demonstrate the differential count method, three sets of data from feeding experiments conducted 1986-1987 are presented (Table IV.2). Prey density differences between the control and each of the experimental chambers indicate the number of each prey taxon eaten. Feeding rates can be calculated from these data (Section V) (Table IV.3).

The primary advantages of this *in situ* methodology for studying zooplankton predation are simplicity, dependability and accuracy. In addition, multiple samples can be obtained simultaneously for repetitions of predator/prey manipulations. Handling of manipulated organisms is kept to a minimum. The major limitation of this *in situ* feeding methodology is the lack of within test replicate variation of zooplankton among the single control and multiple experimental chambers.



**Figure IV.1 Section of chambers showing undeployed and deployed chamber.**



**Figure IV.2 Configuration of four chambers in stainless steel frame.**

**A. Initial Recovery Rates**

<u>Replicate</u>	<u>Average Recovery Rates (%)</u>	<u>n</u>
1	83.4	6
2	87.1	4
3	78.7	4
4	78.0	4
Overall rate	81.3 ± 7.3 (SE)	

**B. Rinse Treatments**

<u>Replicate</u>	<u>No Rinse</u>	<u>2L</u>	<u>4L</u>	<u>6L</u>
1	79.2	81.2	93.2	96.8
2	82.0	86.8	100.0	99.6
3	87.2	86.0	94.8	96.0
4	69.6	79.2	94.4	89.6
Overall Rate	79.5 ± 6.4	83.3 ± 3.2	95.6 ± 2.6	95.5 ± 3.7

**Table IV.1.**

**A. Percentages of *Polyphemus* recovered from chambers (250 individuals per chamber).**

**B. Percentages of *Polyphemus* recovered from chambers with increasing volumes of rinse water (250 individuals in each chamber), n = 16.**

<u>Date</u>	<u>Polyphemus</u>	<u>Prey species</u>							
	<u>NAU</u>	<u>KER</u>	<u>KEL</u>	<u>POL</u>	<u>CON</u>	<u>VOR</u>	<u>RHZ</u>	<u>ROT</u>	
28 May 86	0	319	58	5436	1684	1183	117	0	337
	1995	270	67	3248	1005	412	165	9	119
	6088	196	17	1471	544	110	17	0	76
	7984	255	9	1095	383	210	73	0	154
24 Jun 86	0	412	231	2613	8163	5825	55	165	1668
	866	298	137	2137	4502	4625	62	103	1176
	1162	248	101	1729	3124	5147	8	54	783
	4421	216	48	894	1416	3905	0	6	108
21 Sep 87	0	425	87	383	383	1242	1179	683	177
	1087	284*	81	216	270	1256	338	554	104
	2429	491	78	185	299	627	221	385	106
	5236	218	75	120	09	390	173	97	45

Table IV.2 Examples of total populations of *Polyphemus* and prey after feeding experiments.  
 (NAU nauplii; KER *Keratella*; KEL *Kellicottia*;  
 POL *Polyarthra*; CON *Conochilus*; VOR *Vorticella*;  
 RHZ rhizopods; ROT, other rotifers.)



<u>Date</u>	<i>Polyphemus</i>		Prey species						
	<u>L<sup>-1</sup></u>	<u>NAU</u>	<u>KER</u>	<u>KEL</u>	<u>POL</u>	<u>CON</u>	<u>VOR</u>	<u>RHZ</u>	<u>ROT</u>
28 May 86	94	0.01	0.00*	0.37	0.11	0.21	0.00*	0.00	0.03
	288	0.03	0.00*	0.30	0.08	0.06	0.01	0.00	0.03
	378	0.00*	0.00*	0.28	0.08	0.04	0.00*	0.00	0.01
24 Jun 86	42	0.04	0.06	0.15	1.69	0.35	0.00*	0.02	0.17
	55	0.05	0.03	0.23	1.70	0.15	0.00*	0.03	0.27
	209	0.02	0.01	0.16	0.81	0.11	0.00*	0.02	0.26
21 Sep 87	51	0.03	0.00*	0.04	0.03	0.00*	0.24	0.03	0.02
	115	0.00*	0.00*	0.02	0.01	0.07	0.12	0.01	0.02
	248	0.01	0.00*	0.01	0.02	0.05	0.06	0.04	0.00*

\* < 0.005

Table IV.3 Examples of predator densities (individuals L<sup>-1</sup>) and calculated feeding rates (prey *Polyphemus*<sup>-1</sup> h<sup>-1</sup>) on prey species from feeding experiments in a multichambered feeding/trap assembly. See Table IV.2 for explanation of designations for prey species.

R <sup>2</sup>	Taxon	Date		Within Date		Replicate		Total
		Variance	Percent	Variance	Percent	Variance	Percent	Variance
0.87	NAU	461	18.5%	1,663	66.7%	368	14.8%	2,493
0.99	KER	41,088	29.5%	95,996	69.0%	1,941	1.4%	139,025
0.98	KEL	684	44.7%	792	51.8%	53	3.5%	1,530
0.98	CON	—	0.0%	1,637,593	97.4%	43,120	2.6%	1,680,713
0.91	VOR	44,710	92.1%	—	0.0%	3841	7.9%	48,551
0.95	ROT	6,537	56.6%	4,451	38.5%	563	4.9%	11,551
0.98	POL	18,029	38.8%	27,296	58.7%	1,174	2.5%	46,499
0.99	Total	1,070,045	26.9%	2,860,352	72.0%	41,135	1.0%	3,971,532

**Table IV.4 ANOVA data; DATE, WITHIN DATE and REPLICATION variation.**

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## SECTION V. FEEDING RATES AND PREY SELECTIVITY OF THE PREDACEOUS CLADOCERAN *POLYPHEMUS PEDICULUS*

### Introduction

There has been an increasing awareness in recent years of the important role of predators in an aquatic ecosystem (Kerfoot and Sih 1987). Vertebrate predators, particularly fish, can affect species composition and size frequency distributions of the entire zooplankton community (Brooks and Dodson 1965). Predaceous zooplankton can similarly affect the plankton community (Confer 1971; Kerfoot 1977). Where predation is intense, more vulnerable prey species are limited in numbers or excluded from the system (Williamson *et al.* 1989). Often predaceous zooplankton play dual roles in the structure and function of the planktonic community by selectively feeding on smaller zooplankton and as preferred prey to larger zooplankton (Bowers and Vanderploeg 1982).

Of the three predaceous cladocerans, *Leptodora*, *Bythotrephes* and *Polyphemus*, *Polyphemus pediculus* is the smallest. It is typically littoral and ubiquitous throughout the northern temperate zone (Gurney 1923; Pennak 1978). Because of its patchy distribution, however, *Polyphemus* is seldom collected with traditional sampling methods and thus is overlooked in most studies. Its role in the food web of a fresh water ecosystem is not understood.

This field study is the first to measure feeding rates and prey preference of *Polyphemus* on natural zooplankton assemblages at ambient densities. Most feeding studies with *Polyphemus* were conducted under laboratory conditions with varied numbers of predators and prey counted into small containers (Butorina and Sorokin 1968, 1970; Matveeva 1989). *In situ* feeding studies have been limited to adding

selected numbers of *Polyphemus* to containers with single prey species (Haney and Mattson 1980). Because there was no precedence for prey preference by *Polyphemus*, all species were initially considered potential prey.

### Methods and Materials

#### Location

Mirror Lake is located in the town of Woodstock (Grafton County) New Hampshire (43°56.5'N-71°41.5'W) at an altitude of 213 m. The lake covers an area of 15.0 ha, has a maximum depth of 11.0 m and an average depth of 5.75 m. The water is slightly acidic and has a well established population of *Polyphemus pediculus*. Mirror Lake lies within the Hubbard Brook Experimental Forest and is a principal research area for watershed management. The limnology of the lake has been well documented (Likens 1985).

#### Field Procedures

A four chambered Plexiglas trap was designed and fabricated to collect water and ambient zooplankton populations for the feeding experiments (Section IV). The *in situ* studies were conducted from a platform supported by a wooden stilt frame 8 m from shore at a depth of 1.5 m. The platform was equipped with a winch for deploying and retrieving the feeding chambers.

*Polyphemus* to be added to the chambers for the feeding experiments were collected with a 151  $\mu\text{m}$  plankton net from horizontal tows in littoral areas of the lake. They were separated from the other plankton in the tows by attracting them towards a light at the end of a long aquarium. Fractions representing 1/2, 1/4 and 1/8 of *Polyphemus* separated were placed into the release cylinders in each of the three experimental chambers. *Polyphemus* densities added to the feeding chambers (7-550  $\text{L}^{-1}$ ) represented ambient densities (Mattson 1979). To expedite the predator release process and avoid overcrowding, *Polyphemus* was often poured directly into the chambers after deployment. The remaining 1/8 fraction of

*Polyphemus* was examined to detect any evidence of cannibalism or other mortality which could have occurred during collection, separation and introduction procedures, preserved in sucrose formalin and enumerated.

Each feeding experiment lasted 4 hours, after which the assembly was raised, and the water was drained at a constant rate through the 30  $\mu\text{m}$  mesh ring nets attached to the outlet of each chamber. As the bottom of the assembly reached the surface each chamber was rinsed thoroughly with 4 L. of filtered lake water. Soda water (250 mL) was added to each chamber to stop feeding activity (Gannon and Gannon 1975). The organisms collected in the ring nets were preserved in sucrose formalin (Haney and Hall 1973).

A total of 96 feeding experiments (four chambers for four hours) were conducted from May 1986 to October 1987 with a frequency of 1-6 experiments per week. In 1986 daytime feeding experiments were run from 1000-1400 hours. In 1987 diel feeding studies were run at 4-h intervals over 24 h periods.

#### Laboratory Analyses

*Polyphemus* and all prey species; crustaceans, rotifers and large protozoans, were identified and enumerated. Subsamples of at least 10% of each sample were taken with a Hensen Stemple pipette (Edmondson and Winberg 1971), placed in sedimentation chambers and allowed to settle at least 1 h  $\text{mL}^{-1}$ . The entire chamber was counted with an inverted microscope to avoid possible error caused by uneven distribution of the organisms in the chamber.

The difference between the number of each prey taxon in the control chamber, the chamber to which no *Polyphemus* were added, and the numbers in the experimental chambers, to which *Polyphemus* were added, represented the number of prey consumed by *Polyphemus* during the 4-h feeding period. Clearance rates (the volume of water from which the predator removed prey per unit time) were calculated from Gauld (1951) for each prey species and the total prey community:



$$C = V (\ln C_0 - \ln C_t) / tN$$

where C = clearance rate in mL per *Polyphemus* per hour

C<sub>0</sub> = number prey in control chamber

C<sub>t</sub> = number prey in experimental chamber

t = time in hours

N = number predators

V = Volume of water in each chamber

Feeding rates (f), the number of prey eaten h<sup>-1</sup> *Polyphemus*<sup>-1</sup>, were estimated for each species according to Frost (1972):

$$f = C \times C'$$

where C' is the arithmetic mean of the number of prey mL<sup>-1</sup> counted in the control and experimental chambers.

To compare the relative contribution of each prey type to the total consumption by *Polyphemus*, the numerical abundance was converted to biomass. Average dimensions of 25-50 individuals for each prey group, measured at 60 or 150x, were used to calculate biovolume (Downing and Rigler 1984). Dry weights were estimated from these biovolumes by assuming a specific gravity of 1.0 and a dry weight to wet weight ratio of 10% (Pace and Orcutt 1981)(Table V.1). Dry weights of *Polyphemus* were calculated from length and dry weight relationships (Rosen 1981).

Absolute and relative prey abundance varied considerably between *in situ* experiments. Selectivity Coefficient (W') was chosen to estimate prey preference because it is not biased by varying relative abundances of prey, amount of prey consumed or number of prey categories (Vanderploeg and Scavia 1979a). Coefficients were calculated by dividing the clearance rate for each prey species by the highest clearance rate calculated for that feeding period from each experimental chamber. W' is defined between 0 and 1. If a prey species was not consumed the

selectivity was 0 and the selectivity of the prey with the highest clearance rate, the most preferred, was 1.

Data analysis computed by regression or analysis of variance are presented at a significance level of  $p < 0.05$  unless otherwise indicated.

### Results

Table V.1 lists the zooplankton species eaten by *Polyphemus* in this study among all other zooplankton species present in Mirror Lake (Table V.2). The three letter designation for each prey group is used in some figures. The grouping, 'Other Rotifers' (ROT), includes the rotifer genera *Ascomorpha*, *Gastropus*, *Pleosoma*, *Rotaria* and *Trichocerca* which individually were too rare to be enumerated with the differential count method, but collectively numbers were high enough to insure accurate counts. This group includes both loricated and unloricated species with a length of 75 - 150  $\mu\text{m}$ .

#### Clearance Rates

Highest clearance rates  $Polyphemus^{-1} \text{ h}^{-1}$  (+/- .95 C.I.) were for *Vorticella* (4.5 +/- 1.4 mL), 'Other Rotifers' (4.6 +/- 1.2 mL) and *Keratella* (4.2 +/- 1.9 mL) (Figure V.1). The lowest clearance rates were for *Kellicottia* (0.9 +/- 0.5 mL) and nauplii (0.8 +/- 0.3 mL). Clearance rates for *Conochilus*, *Diffugia* and *Polyarthra* were significantly higher than for *Kellicottia* and nauplii ( $F = 7.59$ ).

Clearance rates of *Polyphemus* were not significantly correlated with individual or total prey densities. Clearance rates  $Polyphemus^{-1}$  on the total prey community decreased exponentially with increased density of *Polyphemus* (Figure V.2). The highest clearance rates ( $> 20 \text{ mL h}^{-1} Polyphemus^{-1}$ ) occurred in densities less than  $62 \text{ L}^{-1}$ . Although there were also several low clearance rates obtained in low predator densities, there were no high clearance rates at high predator densities.

Body size of *Polyphemus* was not significantly correlated with clearance rates. The lack of significance of body size on clearance rates in Mirror Lake is probably

attributed to the small size range. Body lengths of *Polyphemus* in Mirror Lake, including brood pouch, ranged from 0.45-0.94 mm. Body lengths of *Polyphemus* in other lakes ranged from 0.74-2.0 mm (Scourfield and Harding 1941; Brooks 1959; Balcer, Korda and Dodson 1984).

### Feeding Rates

Feeding rates on the total prey community averaged 0.37 prey *Polyphemus*<sup>-1</sup> h<sup>-1</sup> between sunrise and sunset. The feeding rates varied considerably on different prey. The highest average feeding rates, 0.20 *Vorticella* + /- 0.11 *Polyphemus*<sup>-1</sup> h<sup>-1</sup> were ten times higher than for nauplii (0.02 + /- 0.01 *Polyphemus*<sup>-1</sup> h<sup>-1</sup>) (Figure V.3). Feeding rates on other prey species ranged from 0.05 (+ /-.01) *Polyphemus*<sup>-1</sup> h<sup>-1</sup> on *Diffugia* to 0.11 (+ /-.05) h<sup>-1</sup> on *Polyarthra*. Feeding rates on *Vorticella* were significantly higher than other prey taxa except *Keratella*. Although feeding rates on all prey species were significantly higher than feeding rates on nauplii, there were no significant differences among feeding rates on the other six prey taxa (F=4.74). Dry weight conversions of prey allows comparisons of prey biomass ingested. For example, the dry weight biomass of one *Polyarthra* equals that of 36 *Vorticella*. Dry weight ingestion rates, based on dry weight conversions of total feeding rates, averaged 108 + /- 47 ng *Polyphemus*<sup>-1</sup> h<sup>-1</sup>. Most of the dry weight consumed *Polyphemus*<sup>-1</sup> h<sup>-1</sup> was *Polyarthra* (56 + /-24 ng), nauplii (16 + /- 5 ng) and *Conochilus* (13 + /- 6 ng) (Figure V.3). Biomass consumption of prey increased exponentially with increased prey biomass (Figure V.4). There appeared to be a tendency of decreased biomass consumption with increased predator densities but the decrease was not significant (Figure V.5).

*Polyphemus* ingested 6.67 (+ /- 10.5)% of its body weight h<sup>-1</sup> of daylight throughout the season (Table V.4). Most of the dry weight (% body weight *Polyphemus*<sup>-1</sup> h<sup>-1</sup>) ingested was *Polyarthra* (2.53), *Conochilus* (1.73) and *Vorticella* (0.74).

Evidence of cannibalism was most often observed when *Polyphemus* densities were greater than  $90 \text{ L}^{-1}$  in the feeding chambers (Figure V.6). Cannibalism was presumed because no evidence of cannibalism had been observed before *Polyphemus* were added to the chambers and no other predators which could prey on *Polyphemus* were collected from the chambers after the feeding experiments. Evidence of cannibalism included pieces of an individual *Polyphemus*; single antenna, jaw, caudal peduncle or the eye. Often the major portion of the body was intact with just a piece removed, from the brood pouch or just behind the eye.

#### Prey Selectivity

Selectivity coefficients ( $W'$ ) indicate *Polyphemus* prefers small prey or prey that have little or no protective structures (Figure V.7). Selectivity for *Kellicottia*, *Polyarthra* and rhizopods were significantly higher than for nauplii ( $F = 7.16$ ). *Vorticella*, was most preferred by *Polyphemus* with an average  $W'$  (+/- C.I.) of  $0.74 \pm 0.09$  which was significantly higher than for all other prey except for *Keratella*, the smallest, ( $0.51 \pm 0.14$ ) and the 'Other Rotifers', ( $0.67 \pm 0.09$ ). However, in the case of *Vorticella* selection may not be strictly on size as they live on *Anabena* colonies and may therefore be considered colonial like *Conochilus*.

Prey density and relative abundance of prey were not significantly correlated with the  $W'$  of any species. A single comparison of density effect with all prey species was not made since at no one time were all of the prey species present together in Mirror Lake. To detect if the presence or absence of one species could affect selectivity of *Polyphemus* for another species, a comparison of all selectivity coefficients among species present together was made. Whenever two species co-occurred the species with the higher  $W'$  was considered to be the preferred prey (Table V.3). Frequency of preference is the proportion of times a prey species had a higher  $W'$  with a co-occurring prey species. The colonial *Vorticella* had a 0.90 frequency of preference with nauplii, 0.81 with *Kellicottia*, 0.87 with *Polyarthra*, 0.83

with the colonial *Conochilus* and 0.84 with *Diffugia*. With *Keratella* and the 'Other Rotifers', however, the frequencies were close to even, 0.54 and 0.52 respectively, indicating very little or no preference of one over the other. Nauplii had preference frequencies of  $< 0.50$  with all other prey taxa suggesting selection against the larger prey. The frequencies of preference exhibit almost the same pattern as average W's when compared to prey size. Both are higher for smaller prey with two exceptions. *Kellicottia* are smaller than nauplii, *Polyarthra* and *Conochilus*, but had lower preference frequencies and selectivity coefficients than *Polyarthra* or *Conochilus*. *Conochilus* is ten times, by dry weight, the size of *Keratella*, *Polyphemus* did not exhibit preference for the smaller when the two prey co-occurred (Table V.3).

#### Diel Clearance and Feeding Rates

Clearance rates, feeding rates and biomass consumed were highest from sunrise through sunset (0530-1930 hours). Clearance rates on the total prey community during midday averaged between 8.8 and 12.9 mL *Polyphemus*<sup>-1</sup> h<sup>-1</sup> and decreased significantly after sunset (Figure V.8). Lowest clearance rates occurred at night (0.8 mL *Polyphemus*<sup>-1</sup> h<sup>-1</sup>). Before sunrise total clearance rates averaged 3.5 mL *Polyphemus*<sup>-1</sup> h<sup>-1</sup> and increased to 6.7 mL h<sup>-1</sup> during sunrise. Although clearance rates indicate vulnerability of prey to predation these data can also demonstrate the diel pattern of feeding activity. Feeding rates averaged 0.12 to 0.78 prey *Polyphemus*<sup>-1</sup> h<sup>-1</sup> during the daylight hours and decreased to 0.09 prey h<sup>-1</sup> after sunset (Figure V.9). *Polyphemus* can be considered a diurnal feeder since the average feeding rate at night was 0.05 prey h<sup>-1</sup>, and was not significantly different from zero ( $p > 0.05$ ). Although diel dry weight ingestion rates followed a similar pattern to feeding rates on prey individuals, there was a shift in the prey species eaten with time of day. Highest dry weight ingestion rates of *Polyarthra* occurred during the four hours after midday; second highest of *Polyarthra* and highest of *Kellicottia* and *Vorticella*, during sunset (Figure V.10). The high ingestion rate of

*Polyarthra* dry weight reflected increased available prey during these feeding periods (Figure V.9) since W' values were low. Both abundances and W' values were high for *Kellicottia* and *Vorticella* over sunset.

## Discussion

### Feeding Behavior

This study clearly demonstrates, as Haney and Mattson (1980) first speculated, that *Polyphemus* is a daytime predator. This supports the possibility of visual prey detection. Young and Taylor (1988) demonstrated that *Polyphemus* visually sight, chase and catch prey. The basic features of the *Polyphemus* compound eye are similar to other cladoceran eyes. The unusual foveal rhabdom of *Polyphemus*, however, may depress sensitivity to vertically polarized light (Nilsson and Odselius 1983; Odselius and Nilsson 1983), allowing *Polyphemus* to detect contrasts created when light is reflected or refracted off the prey. These structural components and their arrangement in the eye suggest that *Polyphemus* visually hunt their prey which appear as light particles against a dark background (Odselius and Nilsson 1983).

The aggregation behavior of *Polyphemus* does not enhance the feeding activity as suggested by Butorina (1986). Instead, feeding efficiency decreased at high *Polyphemus* densities. Visual or mechanical interference is highly probable in aggregations. The number of prey sightings could be decreased by one *Polyphemus* obstructing the visual field of another *Polyphemus* and a possible prey. An intervenient *Polyphemus* could also mechanically interrupt a chase path of another or be detected as prey and attacked. With increasing *Polyphemus* densities, the rate of encounter with another *Polyphemus*, and the likelihood of cannibalism, increases (Figure V.6). Cannibalism for lack of other prey could be considered an alternative hypothesis. If the density of prey were reduced by *Polyphemus* during a feeding experiment so encounters with available prey were decreased, would *Polyphemus*

feed on other *Polyphemus*? The proportion of available prey eaten was not correlated with predator density, suggesting that cannibalism occurred independently of prey density.

Although Butorina (1986) reported increased feeding rates with increased predator densities the correlation was not significant ( $p < 0.05$ ). The number of predators used in her feeding studies ranged from 1 to 1000 *Polyphemus*, but densities could not be determined because the volume of the containers used was not given.

The maximum *Polyphemus* density used in the feeding experiments for this study was  $550 \text{ L}^{-1}$ . The maximum density sampled in Mirror Lake during this study was  $46 \text{ L}^{-1}$  from a 20-m horizontal tow during a diel study (Section III). The density could be underestimated if the sample were taken through an aggregation. Densities of *Polyphemus* to  $806 \text{ L}^{-1}$  have been reported in the Rybinsk reservoir (Butorina 1986) and aggregations have been reported to reach  $15000 \text{ L}^{-1}$  in Stonehouse Pond, NH (Haney and Mattson 1980). While aggregation behavior has been reported throughout the day (Mattson 1979; Butorina 1986) it is most pronounced in Mirror Lake during dusk and pre-dawn (Section IV). Clearance rates and prey consumption, after dusk, were significantly lower than during mid-day suggesting that, although both feeding and aggregation activities are visually stimulated, the responses differ.

#### Feeding Rate Responses to Changes of Prey Densities

*Polyphemus* feeding rates increased as functions of density of the total prey. Maximum densities of individual species ranged from  $53 \text{ L}^{-1}$  (*Diffugia*) to  $375 \text{ L}^{-1}$  (*Polyarthra*),  $473 \text{ L}^{-1}$  (*Vorticella*) and  $495 \text{ L}^{-1}$  (*Conochilus* individuals in colonies). The feeding rate response to increased densities was significant for *Vorticella* and *Polyarthra* (Figure V.11). Similar increases of feeding rates on *Kellicottia* and *Polyarthra* have been observed in laboratory studies (Fuhlendorf, unpublished

data). Matveeva (1989) reported a significant increase in feeding rates as a function of prey density for *Synchaeta pectinata* and solitary *Conochilus unicornis*, reaching a saturation plateau at densities of 800 L<sup>-1</sup> and 300 L<sup>-1</sup> respectively. Butorina (1971) observed increased feeding rates on different prey types with increased densities up to 20 - 40 x 10<sup>3</sup> L<sup>-1</sup> and an abrupt decrease at higher prey densities. The laboratory studies demonstrated that there is a feeding saturation plateau for *Polyphemus* and indicate a type III feeding curve. The prey densities at which maximum feeding rates occurred, however, did not exist in Mirror Lake. The laboratory data suggest that *Polyphemus* did not reach maximum feeding potential during the *in situ* studies. The *Conochilus* density at which feeding saturation occurred in Matveeva's study was lower than natural *Conochilus* densities in Mirror Lake but, unlike the colonial nature of most *Conochilus*, only single individuals were used in the laboratory study.

#### Prey Selectivity

*Polyphemus* and the other predatory cladocerans, *Bythotrephes* and *Leptodora*, have been reported to be size-dependent predators (Zaret 1980). In addition to size, the presence or absence of protective morphological structures or predator avoidance behavior affects prey selection as indicated by the selectivity coefficients. *Vorticella* are picked off *Anabena* colonies by *Polyphemus* along with a few *Anabena* cells as evidenced by the intact cells in the gut. If *Polyphemus* were a visual feeder the *Anabena* colony would provide a larger target than an individual *Vorticella* and be selected as prey. As a colony, *Conochilus* could be considered a visual target but it is too large for *Polyphemus* to manipulate, while small colonies and solitary individuals are easily consumed (Haney and Mattson 1980; Matveeva 1989; Fuhlendorf, unpublished). The spined loricas of *Keratella* and *Kellicottia* could negatively affect selectivity. Although *Keratella* is smaller than *Vorticella*, and moves slowly (0.2-0.5 mm s<sup>-1</sup>) (Gilbert 1987) the many short spines probably compensate for the vulnerability of its size. The spines of *Kellicottia* triple the length of the body,



making it too long for *Polyphemus* to manipulate with the thoracic appendages. Lorica remains from the feeding chambers had large gashes in the main part of the bodies which were bent into right angles. This evidence indicates that *Polyphemus* grabbed the body, used the jaws to make holes in the loricas and removed the contents by suction (Monakov 1972).

Rapid movement of the paddles of *Polyarthra* mediate an escape response; short, quick jumps (about 2 mm or 15 body lengths, average velocity  $36 \text{ mm s}^{-1}$ ) (Gilbert 1985). In laboratory studies *Polyarthra* escape responses have been very effective against other invertebrate predators; *Asplanchna*, *Diacyclops* and first instar *Chaoborus* larvae. The escape response was often initiated by direct contact with a slow moving predator (*Asplanchna*) (Gilbert 1985). Stimulation of the escape response by acceleration of water has been observed in the inhalent current of filter feeding *Daphnia* (Gilbert 1987). The average swimming speed of *Polyarthra* is  $0.3 \text{ mm s}^{-1}$  (Gilbert 1985). The swimming speed of *Polyphemus* chasing a prey, however, has been recorded at  $15.4 \text{ mm s}^{-1}$  (Young and Taylor 1990). *Polyphemus* is an active predator and therefore does not create a water current for feeding. *Polyphemus* moves faster and may catch *Polyarthra* before the escape mechanism is engaged. The muscles which control the paddles are well developed and result in a higher than average dry weight/wet weight ratio (Dumont *et al.* 1975) which increases the food value of this prey.

#### Biomass ingested and relative ingestion rates.

Although selectivity coefficients and feeding rates indicate *Polyphemus* preferred and consumed high numbers of small prey, *Vorticella* and *Keratella*, the smallest of the eight prey taxa, averaged less than 5% of the total ingested dry weight during the 1987 season while the major bulk of the diet (average, 67%) was nauplii and *Polyarthra*, the largest prey taxa. From early August through mid-September, however, more than 50% of the biomass consumed by *Polyphemus* was

small prey although the larger prey were available. There is no indication from total population estimates or the average number of embryos carried by *Polyphemus* that the population was starving as both remained essentially unchanged over this time (Section II). This selectivity indicates that small prey can fulfill a large proportion of the energy requirements of *Polyphemus*.

Relative ingestion rates (% body dry weight ingested *Polyphemus*<sup>-1</sup> h<sup>-1</sup>) were calculated (Haney and Trout 1985) to compare biomass intake of *Polyphemus* at different times of the season. The average relative ingestion rate *Polyphemus*<sup>-1</sup> was 6.6% h<sup>-1</sup> (Table V.4). Haney and Trout (1985) reported lower rates for larger filter feeders e.g., *Daphnia pulex*, 2.3% h<sup>-1</sup> and *Ceriodaphnia quadrangula*, 2.1% h<sup>-1</sup>. Monakov (1963 in Monakov 1972) in 24-h studies reported 86.0% relative ingestion rates per day for the predator *Macrocyclops albidis* comparable to an average of 91.8% for *Polyphemus* during a 14-h feeding period (sunrise to sunset) observed in this study. Relative ingestion rates ranged from 0.01 - 31.1% h<sup>-1</sup> (Figure V.12) and were not correlated with predator size ( $p < 0.01$ ) or with prey density ( $p < 0.01$ ). Highest average relative ingestion rates occurred in late June and late July when increases in population estimations were observed. *Polyarthra*, the high food value prey (Dumont *et al.* 1975), contributed 75% of the dry weight ingested in late June when the *Polyphemus* population was increasing at an exponential rate after an abrupt decline in early June.

In summary, *Polyphemus* is a diurnal feeder with more than 90% of its feeding between sunrise and sunset. Feeding rates and selectivity were highest for *Vorticella* and other small species, indicating that *Polyphemus* is a size selective predator. *Polyphemus* selects larger, more vulnerable prey (*Polyarthra* and individual *Conochilus*) over smaller prey with protective structures (*Kellicottia*). Larger prey, *Polyarthra* and *Conochilus* and nauplii, however, constituted more than 70% of the biomass ingested as indicated by

**relative ingestion rates.**

**Although biomass ingestion rates increased with increased densities of preferred prey, saturated feeding levels were not attained during the *in situ* studies. Patch formation does not benefit feeding as feeding rates decreased with increased predator densities and cannibalism was observed at aggregation densities.**

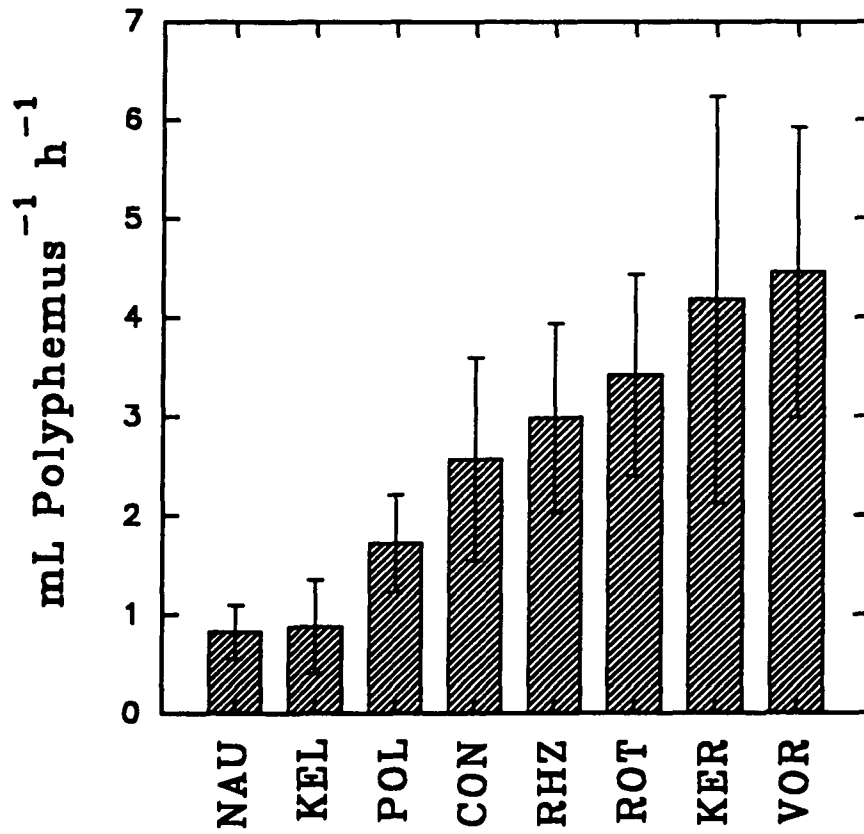


Figure V.1 Average clearance rates of *Polyphemus* on prey species, sunrise to sunset, 1987. (Error bars indicate 95% Confidence Intervals)

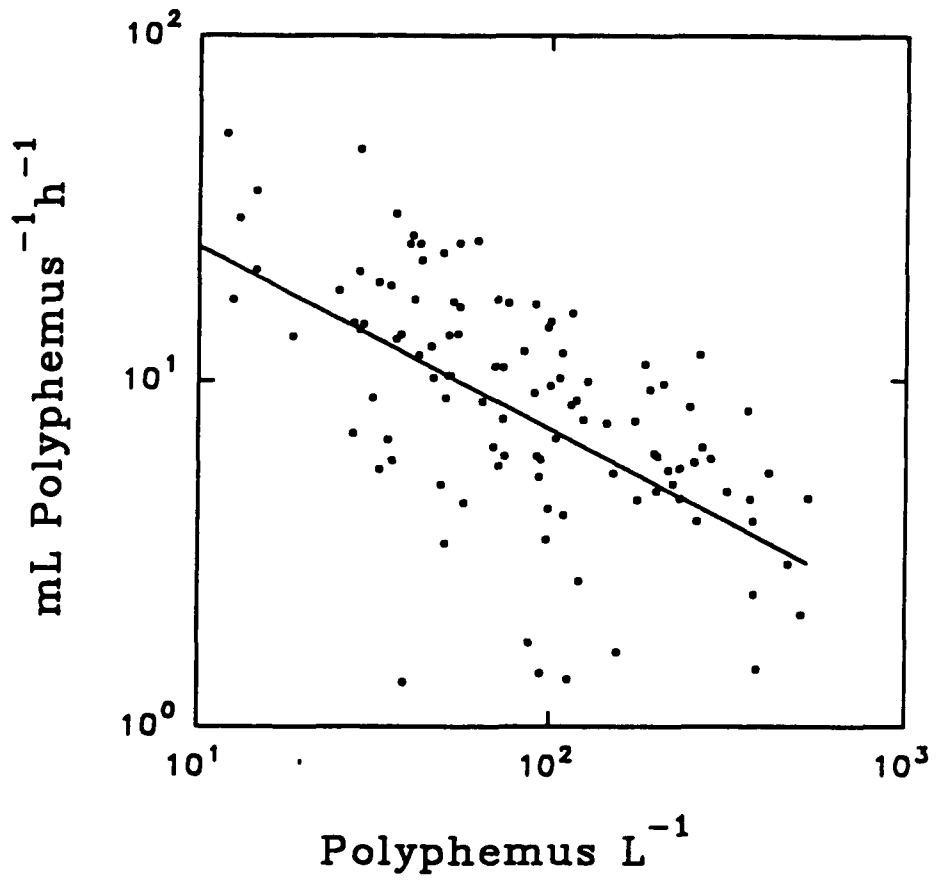


Figure V.2 Clearance rates by *Polyphemus* on total prey community vs density of *Polyphemus*.  $\log_{10} Y = 1.88 + 0.51 \log_{10} X$ ; ( $r^2=0.27$ ,  $n=113$ ).

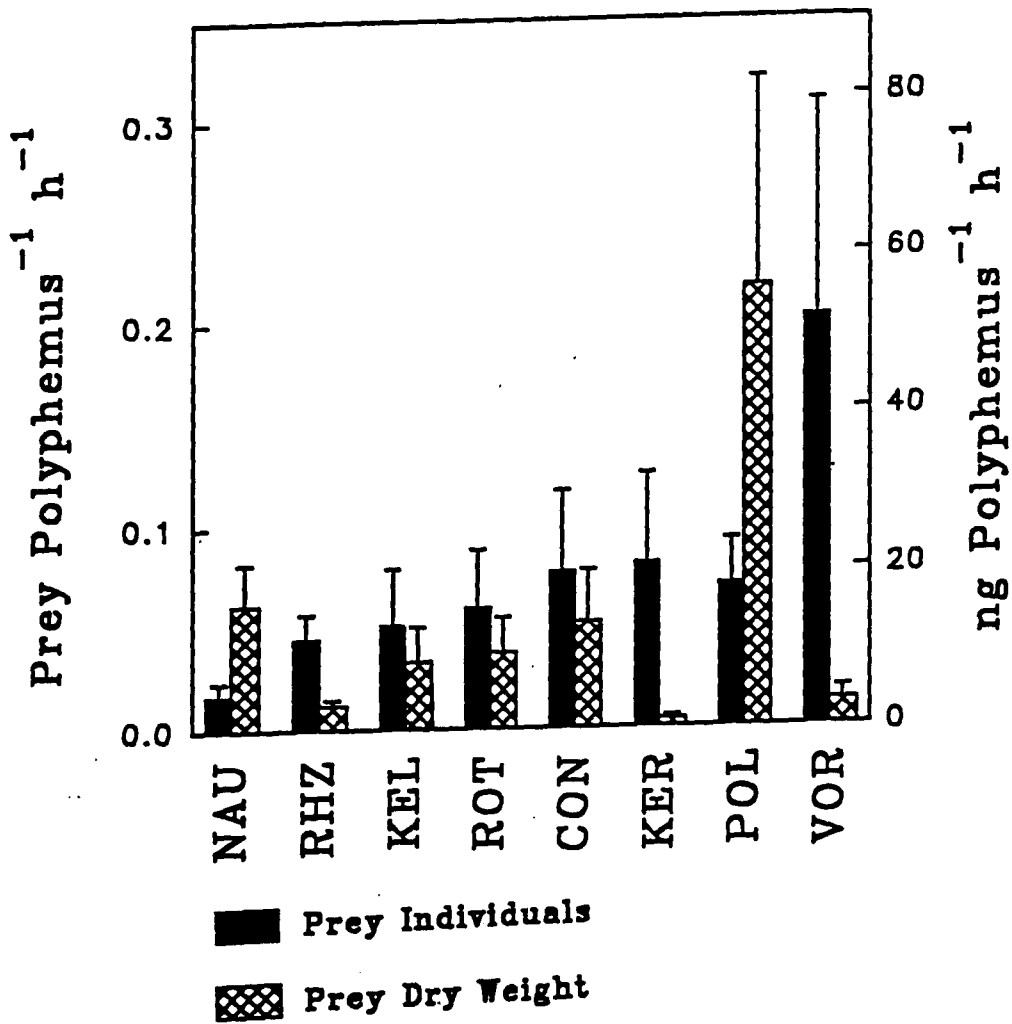


Figure V.3 Average diurnal feeding rates and dry weight consumption on prey species, 1987. (Error bars indicate 95% Confidence Intervals)

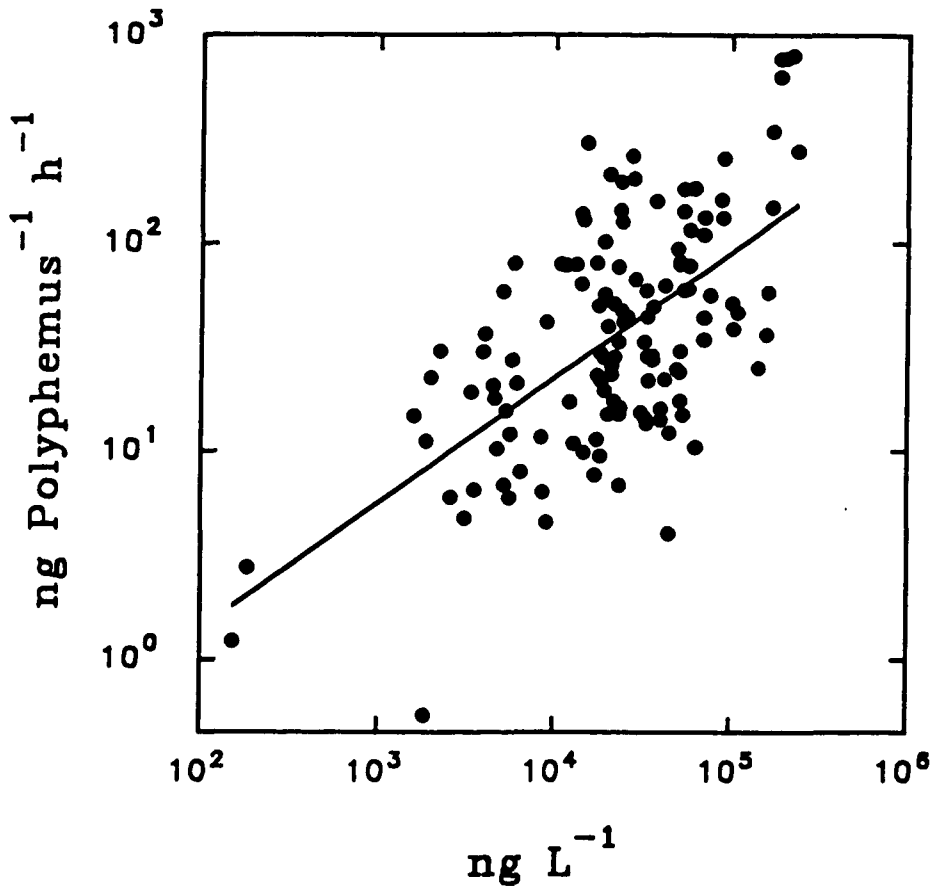


Figure V.4 Log comparison of feeding rates (biomass consumed  $\text{Polyphemus}^{-1} \text{ h}^{-1}$ ) vs prey density (biomass  $\text{L}^{-1}$ ). Mirror Lake 1987.  $\text{Log}_{10} Y = -1.55 + 0.01 \text{ log}_{10} X$ ; ( $r^2 = 0.24$ ,  $n = 113$ ,  $p = 0.05$ )

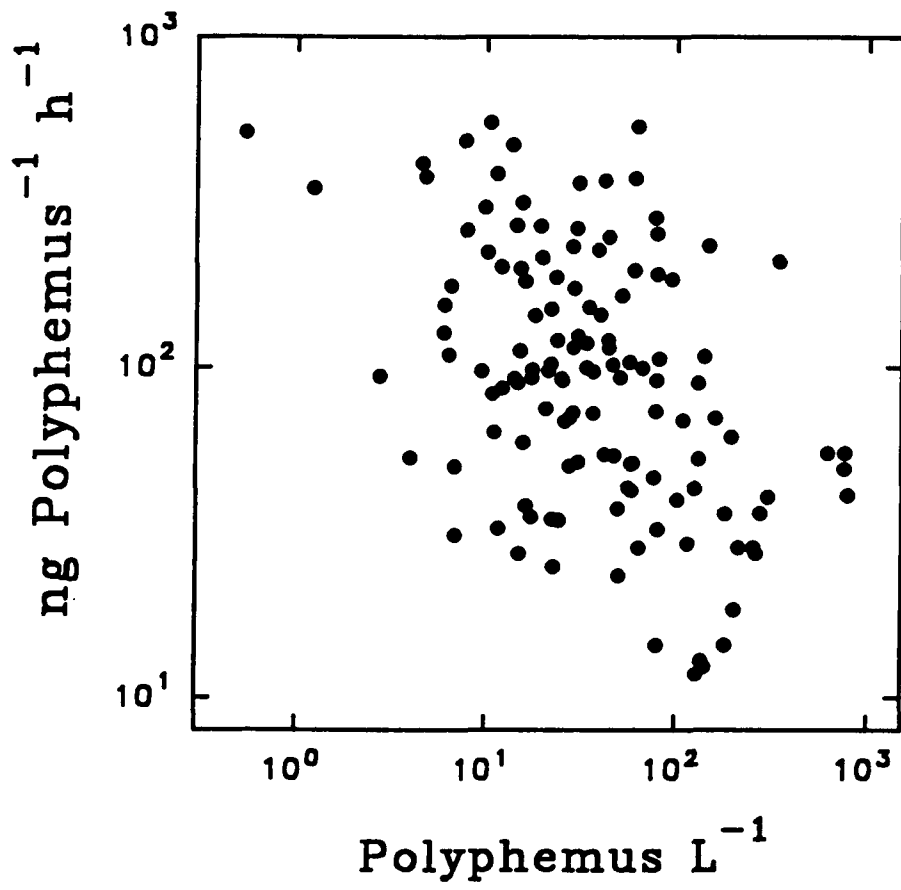


Figure V.5 Log comparison of feeding rates (biomass consumed  $Polyphemus^{-1} h^{-1}$ ) vs  $Polyphemus$  density ( $L^{-1}$ ).



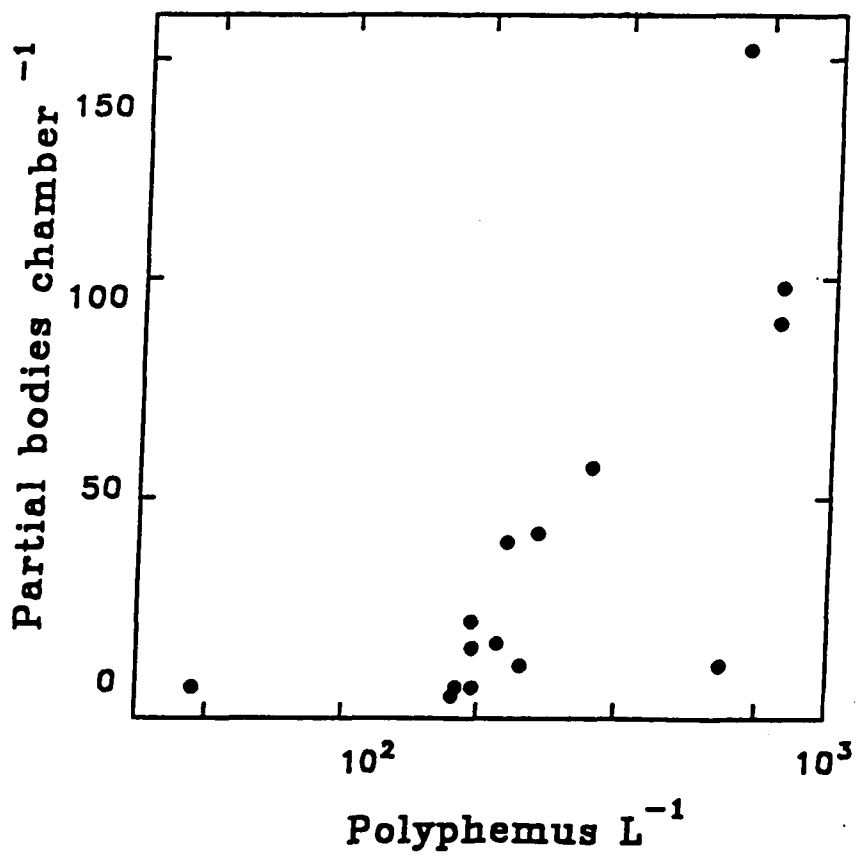
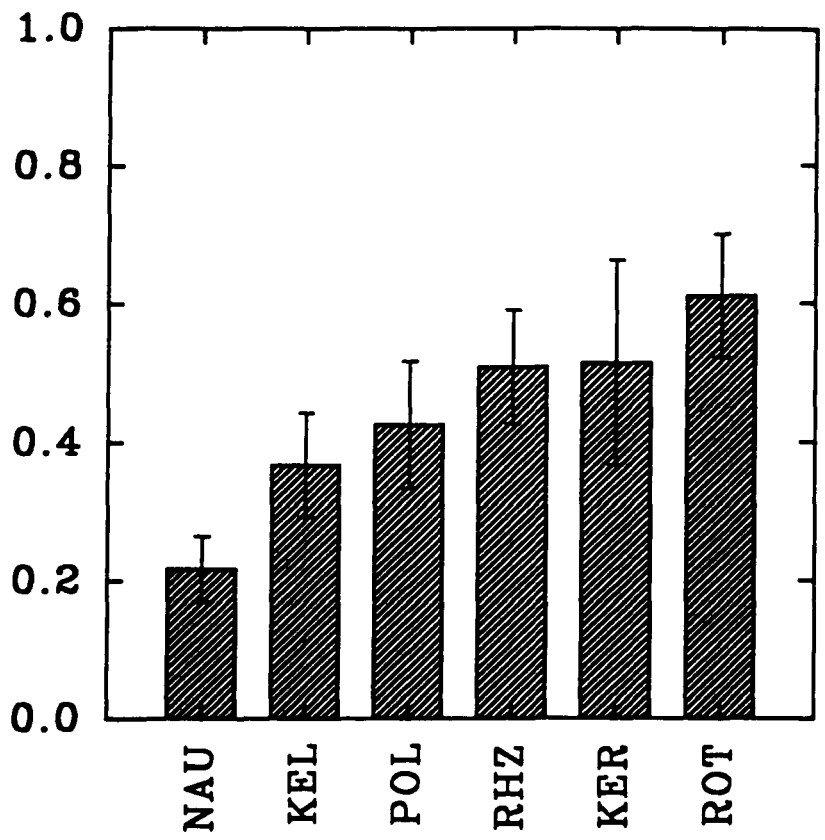


Figure V.6 Occurrences of cannibalism as function of predator density (Log<sub>10</sub> *Polyphemus* L<sup>-1</sup>).



**Figure V.7 Average selectivity coefficients (W') for prey species in Mirror Lake 1987. (Error bars indicate 95% Confidence Intervals)**

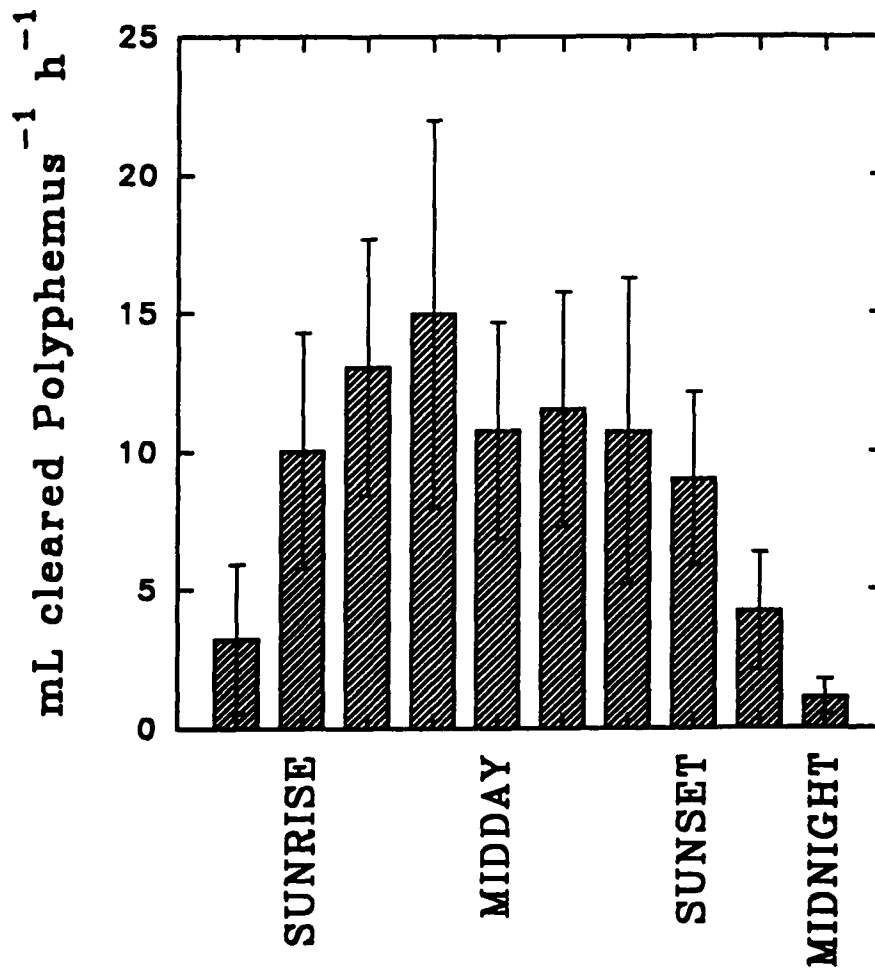


Figure V.8 Diel clearance rates on prey community. Average clearance rates (mL *Polyphemus*<sup>-1</sup> h<sup>-1</sup>) during 4-h experiments at intervals before, during and after sunrise, midday and sunset. (Error bars indicate 95% Confidence Intervals)

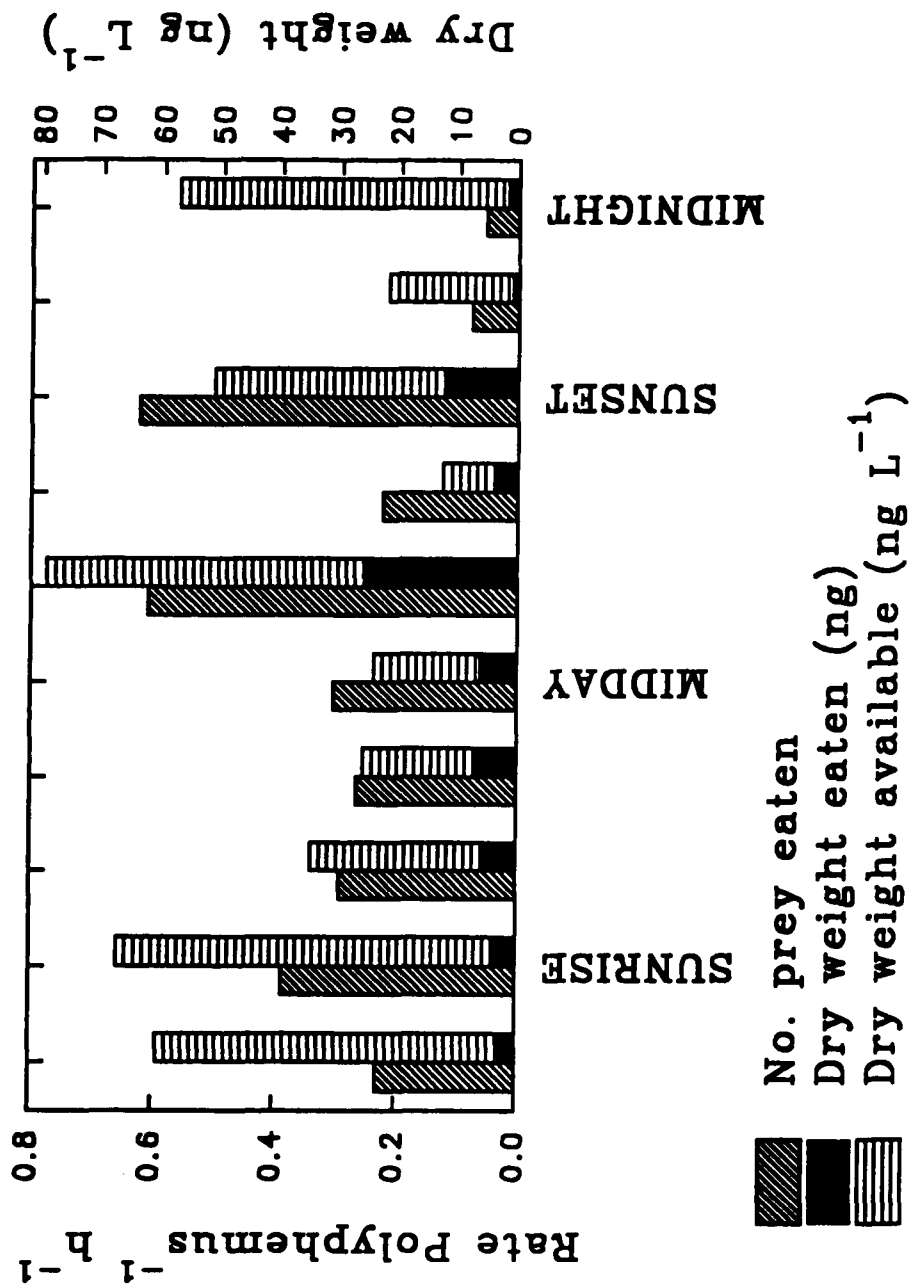


Figure V.9 Diel feeding rates and dry weight consumption compared to biomass of prey.

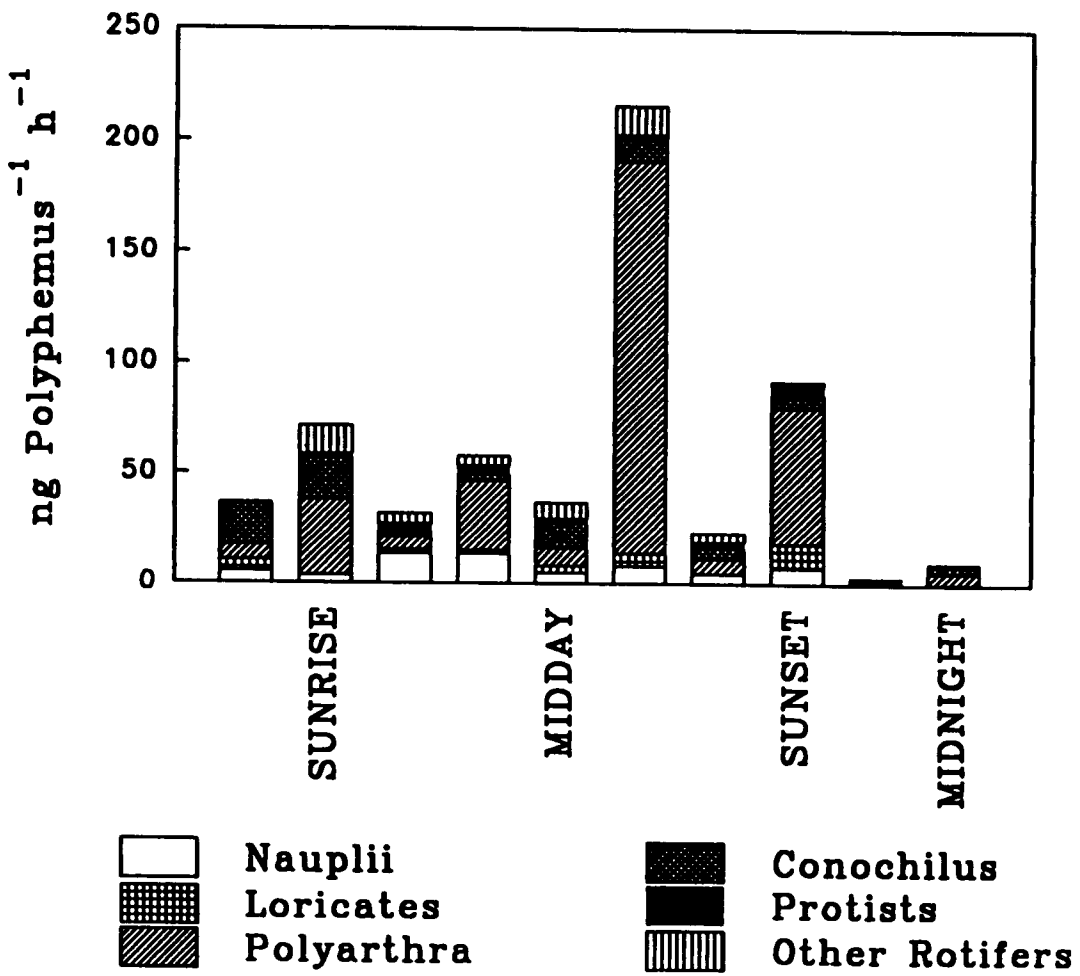


Figure V.10 Diel dry weight ingestion of prey species. Dry weights of *Keratella* and *Kellicottia* are combined as Loricates; *Vorticella* and rhizopods, as Protists.

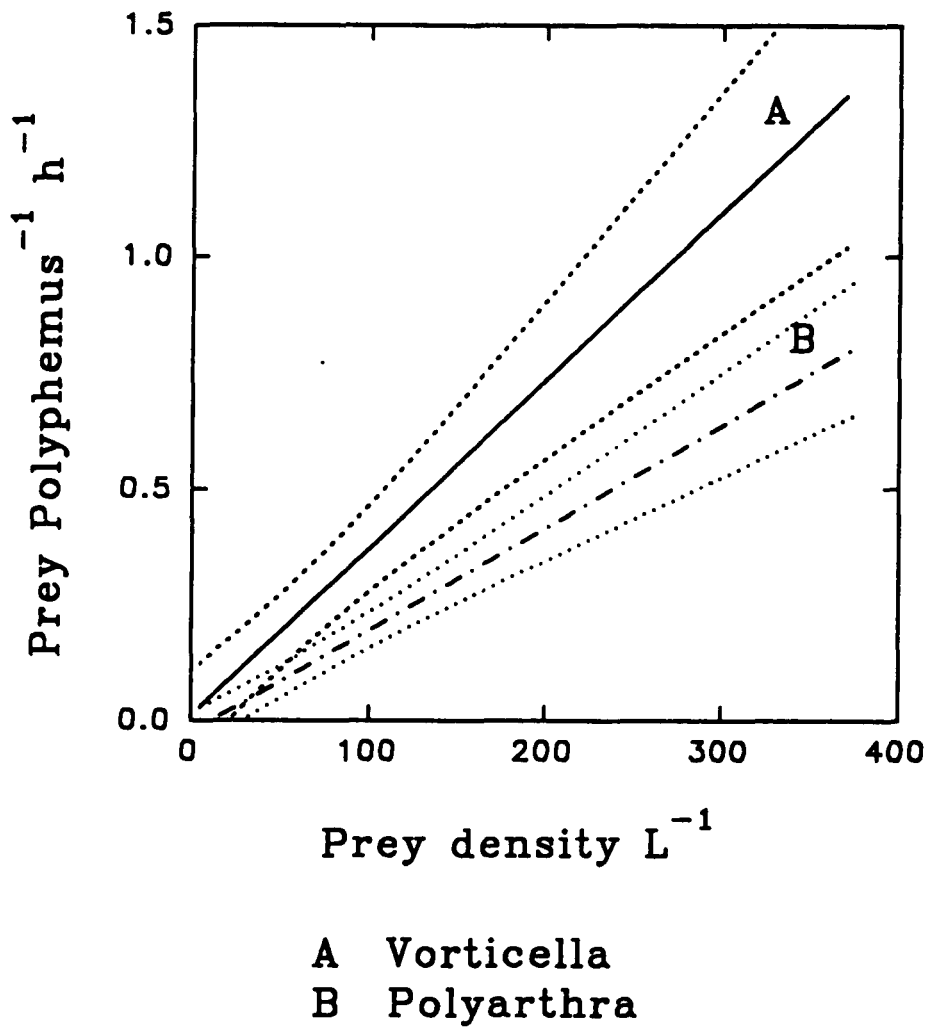


Figure V.11 Feeding rates by *Polyphemus* on two prey species increased as a function of density,  $p < 0.01$ . Broken lines indicated 95% Confidence Intervals

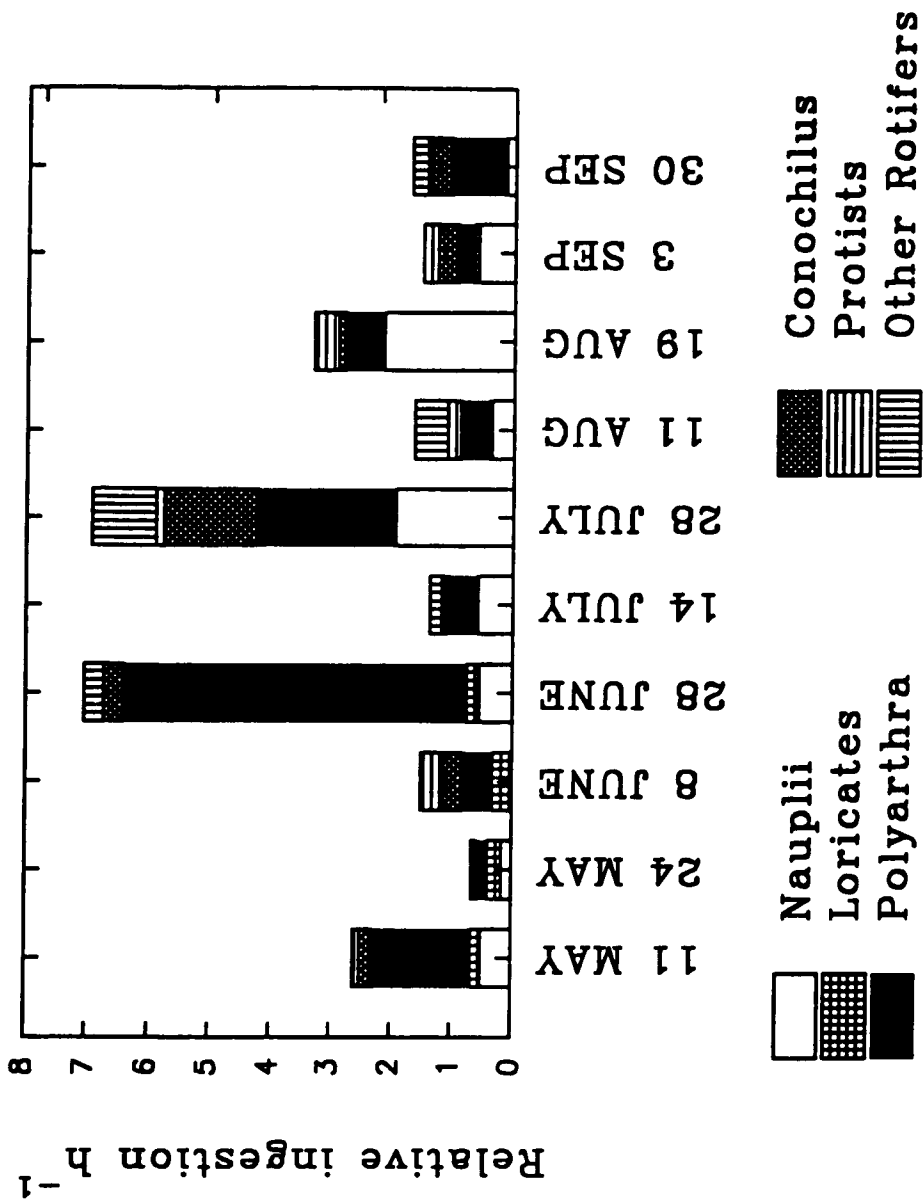


Figure V.12 Average relative ingestion rates of prey species during two week intervals around dates indicated. Rates of *Keratella* and *Kellicottia* are combined as Loricates; *Vorticella* and rhizopods, as Protists.









Species	Average Volume Individual <sup>-1</sup> ( $\mu\text{m} \times 10^3$ )	Morphological/ Behavioral Comments
<b>PROTOZOANS</b>		
<i>Vorticella</i> sp. (VOR) 	14.0	Colonial living in <i>Anabena circinalis</i>
<i>Diffugia</i> sp. (RHZ) 	63.0	Spherical granulated test
<b>ROTIFERA</b>		
<i>Polyarthra</i> spp. (POL) 	506.0	Bladelike paddles cause erratic jumps
<i>Conochilus</i> sp. (CON) 	140.0	5-60 indiv. held in gelatinous sheath, large, slow moving
<i>Kellicottia</i> sp. (KEL) 	101.5	Loricated with long anterior and posterior spines
<i>Keratella</i> spp. (KER) 	10.2	Loricated with several short anterior and one posterior spines
Other Rotifers (ROT) 	150.0	See Text
<b>COPEPODA</b>		
Nauplii (NAU) 	800.0	Large, fast moving

Table V.1 Prey in Mirror Lake eaten by *Polyphemus pediculus*.



Herbivores	Omnivores/Predators
<b>Cladocera</b>	
<i>Alonella excisa</i>	<i>Leptodora kindtii</i>
<i>Bosmina longirostris</i>	<i>Polyphemus pediculus</i>
<i>Chydorus</i> spp.	
<i>Daphnia ambigua</i>	
<i>Daphnia catawba</i>	
<i>Holopedium gibberum</i>	
<i>Hyaella azteca</i>	
<i>Latona setifera</i>	
<i>Ophryoxus gracilis</i>	
<i>Scapholeberis kingi</i>	
<i>Sida crystallina</i>	
<b>Copepoda</b>	
<i>Diaptomus minutus</i>	<i>Cyclops scutifer</i>
<i>Epischura lacustris</i>	<i>Cyclops vernalis</i>
	<i>Macrocyclus albidus</i>
	<i>Mesocyclops edax</i>
	<i>Tropocyclops prasinus</i>
<b>Rotifera</b>	
<i>Ascomorpha ecaudis</i>	<i>Asplanchna priodonta</i>
<i>Ascomorpha ovalis</i>	
<i>Ascomorpha saltans</i>	
<i>Ascomorpha</i> sp.	
<i>Conochiloides dossuarius</i>	
<i>Conochilus unicornis</i>	
<i>Gastropus stylifer</i>	
<i>Kellicottia bostoniensis</i>	
<i>Kellicottia longispina</i>	
<i>Keratella cochlearis</i>	
<i>Keratella crassa</i>	
<i>Keratella quadrata</i>	
<i>Keratella taurocephala</i>	
<i>Lecane</i> sp.	
<i>Pleosoma lenticulare</i>	
<i>Polyarthra dolichoptera</i>	
<i>Polyarthra vulgaris</i>	
<i>Polyarthra</i> sp.	
<i>Rotaria rotatoria</i>	
<i>Trichocerca</i> spp.	
<b>Protozoa</b>	
<i>Diffugia</i> sp.	
<i>Vorticella</i> sp.	

Table V.2 Zooplankton species of Mirror Lake

	<u>NAU</u>	<u>KEL</u>	<u>POL</u>	<u>CON</u>	<u>RHZ</u>	<u>KER</u>	<u>ROT</u>	<u>VOR</u>
NAU	\	.71	.73	.58	.83	.82	.91	.90
KEL	.29	\	.77	.58	.86	.88	.79	.81
POL	.27	.23	\	.60	.79	.81	.78	.87
CON	.42	.42	.40	\	.71	.45	.69	.83
RHZ	.17	.14	.21	.29	\	.50	.69	.84
KER	.18	.12	.19	.55	.50	\	.70	.54
ROT	.09	.21	.22	.31	.31	.30	\	.52
VOR	.10	.19	.13	.17	.16	.46	.48	\

**Table V.3** Frequency of preference of co-occurring species. The figures represent a matrix of the proportion of times the species group listed along the top had a higher  $W'$  when present with each of the species listed on the side.

Prey Taxon	Prey Dry Weight (ng individual <sup>-1</sup> )	Feeding Rate (ng h <sup>-1</sup> )	Relative Ingestion Rate (% h <sup>-1</sup> )
NAU	800	12.0 (4.0)	0.63 (0.11)
POL	506	53.6 (25.7)	2.51 (1.12)
ROT	150	10.9 (4.6)	0.54 (0.27)
CON	140	10.4 (4.2)	1.60 (0.94)
KEL	101	6.7 (2.5)	0.22 (0.07)
RHZ	63	3.7 (0.9)	0.24 (0.06)
VOR	14	3.3 (1.6)	0.70 (0.30)
KER	10	0.8 (0.4)	0.11 (0.06)
TOTAL		83.8 (26.3)	6.56 (3.03)

**Table V.4 Average feeding rates and relative ingestion rates of prey species by *Polyphemus* (+/- 95% Confidence Intervals), 05 May - 06 October 1987**

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