DISTRIBUTION PATTERNS AND POPULATION DYNAMICS OF POLYPHEMUS PEDICULUS (L) (CRUSTACEA, CLADOCERA) IN A SMALL NEW ENGLAND LAKE

MARK THOMAS MATTSON
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Keywords
Biology, Limnology
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DISTRIBUTION PATTERNS AND POPULATION DYNAMICS
OF POLYPHEMUS PEDICULUS (L.) (CRUSTACEA, CLADOCERA) IN A SMALL NEW ENGLAND LAKE

by

MARK T. MATTSON
B.A., University of Connecticut, 1973
M.S., University of New Hampshire, 1975

A DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy
in
Zoology

May, 1979
This thesis has been examined and approved.

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James P. Barrett, Professor of Forest Biometrics, Institute of Natural and Environmental Resources

14-May-1979
Date
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My wife, Linda, has been an enduring source of love, support, and encouragement throughout this work. Her assistance in preparing figures and proofreading this manuscript is also greatly appreciated.
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ABSTRACT

DISTRIBUTION PATTERNS AND POPULATION DYNAMICS
OF POLYPHEMUS PEDICULUS (L.) (CRUSTACEA, CLADOCERA) IN A SMALL NEW ENGLAND LAKE

by
MARK T. MATTHSON
University of New Hampshire, May, 1979

A stratified random sampling design was evaluated in its ability to quantify spatial and seasonal changes in abundance of the predatory cladoceran, Polyphemus pediculus (L.). A whole-lake stratified design with sample units consisting of eighty-four 20 meter Clarke-Bumpus tows was more accurate and precise in quantifying seasonal abundance than a conventional design of eight 150 meter tows, and better revealed changes in horizontal distribution. Using this stratified design, the seasonal dynamics and patterns of patchiness of the Polyphemus population in Stonehouse Pond, Barrington, N. H., was examined for two years, 1975 and 1976.

Seasonal abundance was typified by an exponential rise to a spring maximum, followed by an exponential decline to a summer plateau. A slight secondary peak occurred in August of each year, and abundance declined to zero in late fall.

There were two sexual (at the spring abundance maximum and in mid-fall) and three parthenogenetic (early spring, a long summer period, and late fall) periods of reproduction.
Gamogenetic brood size was significantly smaller in the spring
(2.17 ± 0.46) than in the fall (3.96 ± 0.23). The first
parthenogenetic broods in the spring from exephippial Polyphemus
were the largest in each year. Parthenogenetic brood size
declined rapidly to a summer plateau, and increased again in
the fall. In the spring and fall, brood size was inversely
correlated with ambient water temperature, and was apparently
unrelated to prey densities. In the summer, brood size remained
relatively unchanged and was not correlated with changing
water temperatures or prey densities.

Population growth rates were characterized primarily
by changes in natality associated with these alternating
reproductive modes. The timing of gamogenesis with the spring
abundance maximum resulted in greater resting egg production
in the spring than in the fall. In both sexual periods, resting
egg production was large and occasionally the dominant mode
of reproduction.

In the spring and fall, the total Polyphemus population
was found extremely close to shore, while in the summer it was
primarily limnetic in distribution. However, mean densities
were usually greater and patches were typically found in the
littoral zone. In the spring and fall, several patches were
found on each date, while in the summer generally one littoral
patch was seen. Patches were usually found on the downwind
side of the lake and their location was highly correlated with
wind direction.

Results from four diel studies (day-night-day sampling)
revealed Polyphemus patches dissipated and the littoral
population dispersed horizontally into the limnetic zone at night. This horizontal dispersal was paralleled by vertical dispersal in the upper 3 meters of the water column.

In situ observation, microsampling, and photography indicated spring-fall patches were actually small, dense swarms of *Polyphemus* which were composed primarily of sexual individuals. Summer patches were more loosely organized shoals of *Polyphemus* and were composed primarily of juveniles. Swarm and shoal composition reflected whole-lake dynamics of the *Polyphemus* population. A mechanism is proposed which suggests how patch formation might be initiated by abiotic factors and maintained by visual cues.
SECTION I

GENERAL INTRODUCTION

It is not difficult to observe that terrestrial plants and animals are rarely randomly or uniformly distributed. Specific terminology exists to describe aggregations of these organisms. Groves of trees, flocks of birds, and swarms of bees are often easily seen. These clustered or patchy distributions often result from behavioural interactions and/or the response of these organisms to their environment. Aggregations may result from dispersal mechanisms, organisms clustering around a food source or an optimal substrate, or they may function for mating or defense.

In the aquatic environment, particularly for relatively small, planktonic organisms, sampling replaces sight as the means for describing distribution, and imposes certain biases and limitations referred to as the "sampling filter" (Haury et al., Manuscript). Conflicting viewpoints existed in the early literature concerning plankton distributions. Hensen (1887) believed plankton were relatively evenly distributed in the ocean, and when aggregations occurred they were the result of temporary or unusual environmental conditions. Haeckel (1890) suggested plankton were patchy. A review of the literature (Cassie, 1963) has resolved this conflict and demonstrated plankton patchiness is quite common in the aquatic environment.
Recent literature reviews reveal that statistical aspects of plankton patchiness have been thoroughly described, but there is little information on the patterns of patchiness or changes of these patterns in space and time (Fasham, 1978; Haury et al., Manuscript). Advances in sampling designs and equipment are necessary to provide this information. Continuous sampling devices and spectral analysis techniques have been particularly useful in describing patterns of phytoplankton distribution (chlorophyll) and their relationship with environmental factors such as water currents or thermal discontinuities (Fasham, 1978). These techniques have also been applied to zooplankton (Mackas and Boyd, 1979) but are limited since they cannot distinguish between species.

*Polyphemus pediculus* is a species of freshwater zooplankton considered to be patchy, but its distribution has not been quantitatively studied. In this thesis, a stratified random sampling design is applied to the study of a lake population of this predatory microcrustacean. This design, which utilizes information about population distribution to obtain precise estimates of its abundance, is compared in Section II to a more "conventional" sampling scheme in its ability to quantify seasonal changes in *Polyphemus* abundance and distribution. Section III describes seasonal changes in population abundance, composition, and growth statistics. In Section IV, sampling and *in situ* observations are used to examine temporal and spatial patterns of distribution in the *Polyphemus* population, and possible factors responsible for these patterns. Comparisons can be made between whole-lake
population events (Section III) and patch phenomena (Section IV). This description of *Polyphemus* distribution patterns and consideration of the functions of aggregations may be used for comparison with organisms in other systems.

1. Literature Cited


SECTION II

EFFECT OF SAMPLING DESIGN ON DETECTION OF SEASONAL
CHANGE IN HORIZONTAL DISTRIBUTION AND ABUNDANCE
ESTIMATES OF POLYPHEMUS PEDICULUS (L.)

1. Introduction

Zooplankton patchiness can be studied as both a phenomenon and a factor influencing the precision of population estimates. As a phenomenon, patchiness or over-dispersion of zooplankton populations is generally considered typical of plankton in a wide variety of time and space scales (Cassie, 1963; Haury et al., Manuscript). However, sampling programs for seasonal abundance and population dynamics are often more appropriate for uniform or under-dispersed populations than for the admittedly patchy zooplankton. Rarely are confidence limits placed about field population estimates, because of a lack of replicate sampling or perhaps because the computed variance generally exceeds the mean population density, which is itself a consequence of over-dispersion (Wiebe and Holland, 1968). Without confidence limits or some estimate of error, it becomes difficult to interpret seasonal abundance curves. Are the differences between sampling dates due to a real change in population numbers, or are they due to spatial changes in zooplankton distribution and their effect on sampling error?

Several references have described possible sources of error in plankton sampling (e.g. Cassie, 1971; Haury et al.,
Manuscript; UNESCO, 1968), including mechanical aspects of the sampling device, subsampling, data analysis, and sampling design. These sources of error must be evaluated before any attempt is made to identify and interpret the underlying biological pattern. Errors in sampling design are often the most difficult to evaluate, because generally no means of evaluating these errors are incorporated in the design.

A stratified random sampling design appears to be most directly applicable to the problems of sampling freshwater systems (Cassie, 1971) for it provides a design by which one can simultaneously obtain population abundance estimates and study the distribution of the sampled organisms. This work represents part of a study to examine feeding, patchiness, and population dynamics of the predatory cladoceran, Polyphemus pediculus (L.). The purpose of this section is to evaluate the performance of stratified random sampling with respect to "conventional" sampling schemes in their ability to quantify seasonal population abundance. Secondly, there is some question in the literature as to the exact spatial affinity of Polyphemus. Typically, the Polyphemus population is considered to be littoral in distribution (Axelson, 1961; Butorina, 1963, 1969; Hutchinson, 1967; Lindstrom, 1952). However, Polyphemus patches have been reported a great distance from shore, e.g. two miles from shore in Lake Michigan (Wells, 1960). Other investigators reporting the limnetic occurrence of Polyphemus include Kikuchi (1930, 1937) and McNaught (1966). The importance of these two lake regions was determined using a whole-lake stratified sampling design.
2. Material and Methods

A. Study Site

Stonehouse Pond in southeastern New Hampshire, U.S.A. (43°12' N, 71°06' W) was selected as the study site, primarily because information existed on its zooplankton (Ferrante, 1974) which indicated a relatively large Polyphemus pediculus population, and for logistics such as lake morphometry and proximity. It is a glacial kettle lake, with a small watershed of mixed deciduous and conifer forest, and is slightly dystrophic. Figure II-1 summarizes the results of a survey and sounding of Stonehouse Pond at the spring high water period in May, 1975. Additional physical, chemical, and biological information may be found in Ferrante (1974).

B. Pilot Survey

On three occasions in late summer and early fall, 1974, Stonehouse Pond was sampled using an unmetered net to obtain preliminary information on the distribution and density of Polyphemus for subsequent use in implementing a stratified random sampling design. This survey revealed the greatest densities of Polyphemus were in the top meter of water in the littoral region. No Polyphemus were collected below three meters of depth, and only a few individuals were collected in the center of the lake.

C. The Stratified Random Sampling Design

The logic of stratified random sampling is to utilize information about a heterogeneous population to divide it into internally homogeneous subpopulations. Estimates of the total
Fig. II-1. Bathymetric map of Stonehouse Pond, Barrington, New Hampshire, USA, based on a survey and sounding in May, 1975.
STONEHOUSE POND
Barrington, New Hampshire

Scale in Meters
Contour Interval: 3 Meters
1975-76
number (or mean density) of organisms in each subpopulation or stratum are then weighted by their representative proportion of the total system, and an estimate of the total population (or weighted mean density) can be quantified. Success at partitioning or stratifying the lake into homogeneous subpopulations results in an increase in precision of the estimate over a corresponding estimate from randomly located samples (Cochran, 1977). The existence of several natural strata can be used to partition a lake into potentially homogeneous sections, e.g. horizontally into littoral and limnetic, and vertically into the thermal strata. For the same number of samples, a stratified design will generally give a more precise estimate of population size than a random design, even if the strata are arbitrarily selected (Barrett and Nutt, 1975; Cochran, 1977). This characteristic of stratified sampling is particularly appealing since boundaries between lake regions can be somewhat arbitrary. In an extremely patchy population of zooplankton, if part of the same patch occupied two adjacent strata, a precise estimate of population size could be obtained if the greatest sampling variability was contained within a small portion of the lake.

D. Implementing the Stratified Design - Spatial aspects

Visual observations, pilot survey information, and morphometric data were used to stratify Stonehouse Pond. The three meter depth contour (Fig. II-1) was used to partition the lake horizontally into littoral and limnetic sections. Although this division is somewhat arbitrary, it corresponds
closely to several natural boundaries, including the top of
the thermocline (Ferrante, 1974), the depth to which littoral
macrophytes occur, and the depth above which all Polyphemus
were observed in the pilot survey. The littoral region was
divided into six horizontal sections, based on compass points,
bottom morphometry, and shoreline features (Fig. II-2).
Section areas and volumes were determined from a survey map
by planimetry (Lind, 1974). Table II-1 summarizes the physical
properties of these lake sections. Since the entire littoral
zone is only 4.3 % of the total lake volume, and only 11.8 %
of the epilimnetic volume (Table II-1), it would normally not
be necessary to partition it. However, pilot survey results
and a desire to use these data as a basis for a study of
temporal and spatial aspects of Polyphemus aggregation behaviour
warranted subdivision of the littoral. Increasing the number
of sections can increase precision (Cochran, 1977), and there
is a gain in ability to describe distribution. Using this
same reasoning, each horizontal lake section (Fig. II-2) was
divided into three vertical strata, 0 to 0.25 M., 0.25 M. to
1.0 M, and 1.0M. to 3.0M. All littoral tows were taken at an
oblique angle to the shoreline from the shore out, except in
sections 3 and 5 where sampling was on an overlapping grid.
Limnetic section 7 tows were taken from a central buoy towards
shore (Fig. II-2).
Fig. II-2. Lake sections and tow locations for stratified sampling of Stonehouse Pond.
STONEHOUSE POND
Barrington, New Hampshire

Scale: 1:500
Contour Interval: 3 Meters
1975-76
Table II-1. Morphometric data on sections of Stonehouse Pond.
<table>
<thead>
<tr>
<th>Littoral Section</th>
<th>Volume (M³)</th>
<th>Surface Area (M²)</th>
<th>Percent of Total Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2450</td>
<td>1860</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>2175</td>
<td>1650</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>2080</td>
<td>1750</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>2990</td>
<td>2200</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>5620</td>
<td>3400</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>3255</td>
<td>2100</td>
<td></td>
</tr>
<tr>
<td>Littoral Total</td>
<td>18570</td>
<td>12960</td>
<td>4.3 %</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Limnetic Section</th>
<th>Volume (M³)</th>
<th>Surface Area (M²)</th>
<th>Percent of Total Volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 to 3 M.</td>
<td>138800</td>
<td>46000</td>
<td>32.4 %</td>
</tr>
<tr>
<td>Below 3 M.</td>
<td>271500</td>
<td>46000</td>
<td>63.3 %</td>
</tr>
<tr>
<td>Limnetic Total</td>
<td>410300</td>
<td>46000</td>
<td>95.7 %</td>
</tr>
</tbody>
</table>

| Lake Total       | 428870      | 58960             | 100.0 %                |

Epilimnion (Above 3 M. depth) = 36.6 % of total lake volume.

Littoral = 11.8 % of Epilimnetic volume.
E. Implementing the Stratified Design - Temporal Aspects

Stonehouse Pond was sampled throughout 1975 and 1976. In the period of ice cover (December to April) 12 vertical hauls were taken at monthly intervals with a 30 cm. diameter 80 μ net (10 littoral and 2 limnetic samples). In the ice free period, the interval between sampling dates varied between 5 and 12 days, and was closest in periods of rapid population change (Spring and Fall). On a given sampling date, all samples were collected between 0900 and 1800 DST. Daily variation in population estimates was examined on two dates in each of the two years in this study. On these occasions, the lake was sampled during the first day, that night, and the following day. Within a sampling date, lake sections were sampled in a random sequence in time. Within each section, samples were collected from fixed locations (Fig. II-2) in a random sequence in time. All random sequences were computer generated. Thus, although this was a stratified random sampling design, samples were fixed or systematic in space and random in time. Fixed spatial locations were necessary to reconstruct patterns of zooplankton distribution.

F. Allocation of Stratified Samples

A Neyman Allocation method (Barrett and Nutt, 1975) was used to allocate samples to lake sections. Eighty-four samples were allocated throughout the lake in direct proportion to lake section volume and the corresponding standard deviation as estimated in the pilot survey. With this method, 2 - 6 samples were allocated to each lake section. Three additional
samples were collected on each sampling date in the limnetic zone below 3 meters of depth, although not required by Neyman Allocation. Since *Polyphemus* were never collected in these deep limnetic samples, they were not used in subsequent calculations. Processing time for one sample was approximately 5 minutes, and included towing time, rinsing and preservation, and positioning to take the next sample. The estimated sampling time was 7 hours and 15 minutes (@ 5 minutes/sample), but in practice the entire 87 stratified samples could be collected in 6 hours. The possibility that the population changed its distribution within this sampling period is evaluated below.

G. Sampling Apparatus

Two Clarke-Bumpus (CB) metered plankton nets (Clarke and Bumpus, 1950) with 12.5 cm. diameter openings and 151 μ Nitex nets were used for quantitative sampling. Several modifications of the basic CB system were used to increase sampling efficiency (Fig. II-3), and two depths at a fixed location could be sampled simultaneously. The pivotal mechanism (Fig. II-3) was mounted in the bow of the boat to minimize possible avoidance reactions to the boat shadow by zooplankton (Clutter and Anraku, 1968), and tows were made at a near maximum rate of 120 meter revolutions/minutes. Net meter units were calibrated according to the methods of Yentsch and Duxbury (1956) and accepted 86 - 92 % of the water in a 50 meter tow. Calibration values were checked in situ at the start of each sampling date and varied less
Fig. II-3. Clarke-Bumpus meter units and nets, 0.5 M. apart, attached to a 3.5 M. aluminum pole and mounted on a pivotal mechanism in the bow of boat. Tow sequence: 1. Prior to sampling, net shutters were opened and nets were held in READY position. 2. When boat moved into sampling location, nets were released and allowed to pivot into SAMPLE position. 3. Shutters were closed immediately upon completion of a tow and nets pivoted into RINSE position. Nets were rinsed from the outside with lakewater, and their contents emptied from quick-drain buckets into sample vials with preservative. 4. Nets were returned to READY position for next tow.
than 2 % between dates. The standard sampling unit was a 20 meter tow, which was measured as 20 seconds on a stopwatch at a towing rate of 1 meter/second, and varied in volume between 199 and 225 liters. All samples were preserved in 4 % formalin-sucrose (Haney and Hall, 1973).

Zooplankton could possibly be caught in the bottom net as it was lowered open to the sampling depth. This potential source of error was evaluated by lowering the open nets to the SAMPLE position (Fig. II-3) and closing them immediately. Meter revolutions and sample contents resulting from this test indicated that carryover of zooplankton did not occur and water was not filtered until the rod holding the nets was vertical in the SAMPLE position.

H. Comparison of Sampling Designs and Computational Procedure

The following sampling designs were compared for 30 consecutive sampling dates (June 19, 1975 - June 9, 1976) to cover the range of variation encountered in an entire season:

1. Strat 84 - The stratified random sampling design outlined above.

2. Integ 8 - Four 150 meter long tandem CB tows were taken in the first hour of each sampling date. Three of these integrated tows were located in randomly selected littoral sections, and one tow in the limnetic section, yielding eight samples per date.
3. Strat 8 - A subset of eight samples was selected from the Strat 84 samples which corresponded to the location of the Integ 8 samples. The Strat 84 and Integ 8 designs, therefore, provided two independent estimates of Polyphemus population size for each sampling date. From each of these three designs, weighted and unweighted estimates of population size were calculated according to the formulae of Barrett and Nutt (1975) and Cochran (1977). Unweighted estimates were based on the simple arithmetic mean density, \( \bar{X} = \frac{1}{n} \sum_{j=1}^{n} X_j \), where \( \bar{X} \) is the mean density, \( X_j \) is the Polyphemus density in the \( j \)th sample, and \( n \) is the total number of samples collected in the design. Weighted or stratified estimates were based on the stratified mean density, \( \bar{X}_{st} \), which is the sum of the arithmetic mean densities in each lake section (stratum) weighted by the proportion of the whole lake found in each section according to the formula \( \bar{X}_{st} = \sum_{i=1}^{l} \frac{N_i}{N} \bar{X}_i \), where \( N_i \) is the volume of the \( i \)th lake section, \( N \) is the volume of the whole lake, \( \bar{X}_i \) is the arithmetic mean density of Polyphemus in the \( i \)th lake section, and \( l \) is the number of sections in the lake. The total Polyphemus population size was then calculated by multiplying the weighted or unweighted mean density by \( N \).

These data provided the basis for a split-plot analysis of variance (ANOVA) comparison of weighting method (main plots), sampling design—volume and number of samples (subplots), and sampling date (blocks) and their effect on accuracy and precision of population estimates. Accuracy was compared by ANOVA and Duncan's Multiple Range Test for
mean separation on untransformed population size estimates. Precision was compared by ANOVA and Duncan's Test on 95% Confidence Interval (C.I.) width expressed as a percentage of the total population size. This measure of precision is commonly used in forestry (Freese, 1962) and was used here as a coefficient of variation.

To eliminate subsampling error, each sample from the stratified design (Strat 8 and Strat 84 samples) was counted in its entirety in a gridded petri dish under a dissecting microscope. Care was taken to count only individuals which were viable at the time of collection and not embryos which had been expelled from brood pouches. The entire contents of the Integ 8 samples were counted if numbers were less than 300, or subsampled using the Hensen-Stempel Piston Pipette method (Schwoerbel, 1970). Subsampling error by this method was random (Chi-Square test p > 0.1) and varied between 7 and 11% of the total sampling variance.

All data analyses were performed on a Digital Electronics Corporation DEC-10 computer system with BASIC programs written by the author or modified by the author from Barrett and Nutt (1975). In plotting graphs on a log_{10} scale (Figs. II-4, II-5B, II-6B), 1 was added to all values to eliminate zero and negative logarithms (Colebrook, 1977).

3. Results and Discussion

Figure II-4 summarizes the comparison of six methods of estimating total Polyphemus population size. For clarity of presentation confidence limits were not placed on this graph.
Fig. II-4. Comparison of six methods for calculating the total *Polyphemus* population in Stonehouse Pond, for 30 consecutive sampling dates 1975-1976. Note $\log_{10}$ scale. See text for additional explanation.
In general, curves for weighted estimates were an order of magnitude less than curves based on unweighted estimates of population size, regardless of sampling design. For the same design, curves based on unweighted estimates appeared to have a greater amplitude of variation than the corresponding curve from weighted estimates. Statistical comparison confirmed the importance of weighting method (F-value significant at $p < 0.005$) instead of sampling design (F-value significant at $p > 0.25$). Curves based on weighted estimates were not significantly different from each other ($p > 0.05$) but were significantly lower than all unweighted curves ($p < 0.01$). Obviously, weighting was responsible for this order of magnitude difference.

More specifically, discrepancy between sample allocation method and weighting resulted in the observed difference. Population size estimates based on unweighted formulae were unfairly biased and overestimated because they contained a large proportion of high density samples from a small proportion of the lake. For weighted estimates, weighting is proportional only to the volume of each lake section. Therefore, when calculating the weighted mean density, a sample from the relatively large limnetic surface section would carry approximately seven times more weight than a sample representative of the littoral zone because of the volume differential (Table II-1). If samples were allocated only in direct proportion to lake section volume, seven times more samples would be taken in this limnetic section than in the entire littoral zone, and both unweighted and weighted mean densities would
be identical. However, proportional allocation of samples would not utilize pilot survey information which found few Polyphemus in the limnetic zone. The Neyman method of sample allocation used in this study allocated samples in direct proportion to both lake section volume and pilot survey estimates of lake section standard deviation. As a result, most samples were allocated to littoral sections with high population density and low volume, at a ratio of 1:3 instead of 7:1 (limnetic:littoral). This problem elucidates a bias which can occur when seasonal abundance is quantified using unweighted mean densities or mean densities which are not from samples equally representative of the entire lake.

Having established for this study that weighted estimates were the only unbiased estimates of the total Polyphemus population, the question of precision was considered. ANOVA methods applied to confidence interval width as a percent of the total population revealed population estimates from the Strat 84 design were significantly more precise \((p<0.001)\) than estimates based on the Strat 8 or Integ 8 designs regardless of weighting method. A significant difference was not observed between the two eight sample designs. This improvement in precision was observed even though CI widths were widened for weighted estimates by the \(T\)-value based on effective degrees of freedom (Barrett and Nutt, 1975; Cochran, 1977) which is fairly conservative compared to the actual \(T\)-value used in unweighted calculations. The difference in precision is most likely not due to differential clogging of tows, because a 150 meter tow (Integ 8)
accepted only 4.8% ± 2.5% (95% CI) less water than a comparable tow calculated from the 50 meter calibration tows. It is also not due to subsampling error, because the differences in precision were statistically significant (p<0.001) after this error was factored out. The most probable reason for the observed differences in precision is an interaction between number of tows and spatial scale of patchiness in the Polypemus population.

Population abundance estimates from the design with many small tows (Strat 84) were therefore more precise than those from few large tows (Integ 8) or few small tows (Strat 8). This observation is inconsistent with Wiebe (1971), who found an increase in tow length (volume) resulted in a dramatic increase in precision of estimates derived from a computer model and from the open ocean (Wiebe, 1972). This inconsistency is probably due to differences in the scale of patchiness between freshwater and open ocean plankton.

In practice, it required approximately 7 hours to complete a sampling date (1 hour for the Integ 8 design and 6 hours for the Strat 84 design). The possibility existed that in this time the Polypemus population could change the configuration of its distribution, and portions could be sampled more than once or not at all thus biasing the estimate. This possibility was examined by comparing weighted estimates of section subpopulations from both integrated and stratified samples. Since integrated tows were taken in the first hour of the same sampling date as the stratified tows, there is little chance of a configuration change biasing the integrated
samples. For each of 30 sampling dates, two depths in each of three randomly selected littoral sections were compared individually to see if the 95% CI from the stratified weighted subpopulation estimates contained the corresponding integrated estimate. Out of 180 comparisons, 44 or 24.4% of the 95% C.I.'s for stratified section estimates failed to enclose the integrated value. Out of these 44 values, 90% (40/44) occurred in the summer period June 15 - September 14. This horizontal movement of the *Polyphemus* population across section boundaries was reflected in the variation of abundance estimates between Integ 8 and Strat 84 designs at this time (Fig. II-4), but these differences were not statistically significant (ANOVA, p > 0.05). This movement and its implications will be treated elsewhere (Section IV).

An additional means of evaluating the Strat 84 design required a comparison of the observed and expected average 95% C.I. Expected 95% C.I. was determined by back calculation from the sample size formula of Barrett and Nutt (1975). The observed average C.I. width was $\pm 10.1 \times 10^6$ for an estimate of the total *Polyphemus* population ($\pm 64$ *Polyphemus*/Meter$^3$ for weighted mean). This value was nearly three times wider than the expected CI width of $\pm 3.4 \times 10^6$ for the total ($\pm 21.5$ *Polyphemus*/Meter$^3$ for mean). This difference was due to underestimation of section variances in the pilot survey. Since the pilot survey did not encompass the entire range of seasonal variation, high spring variance was not calculated in the Neyman Allocation method and the expected precision was overestimated. Pilot surveys for seasonal abundance
studies should attempt to encompass maximum yearly variation to closely approximate the expected precision for a stratified sampling design.

A summary of the comparison of methods for estimating Polyphemus population size revealed the stratified design was the most accurate and precise method. By quadrupling the time required to collect and process samples, the average increase in precision of stratified over integrated sampling was eight times. A major hindrance of the stratified design employed in this study was the absolute amount of time required to obtain results. The investigator was somewhat removed in time from changes occurring in the zooplankton community due to a lengthy sample processing period. Quantitative factors such as time, manpower and equipment, and funding can be incorporated into a relative cost formula and used in various sample allocation methods (Barrett and Nutt, 1975; Cochran, 1977) to estimate the precision that can be expected for a specified sampling effort. Conversely, it is possible to determine the number of samples and cost required for a pre-specified C.I. width.

Qualitative factors also require consideration in any sampling program, including goals of the study and the fact that a sampling design for one species may not necessarily be adequate for another species or for a zooplankton community. For a single species of limnetic zooplankton, partitioning the lake into the three thermal strata would probably suffice, and most samples would be allocated to the epilimnion. To efficiently quantify a zooplankton community or a species
with an extremely patchy distribution (e.g. *Polyphemus*), horizontal lake sections are required in addition to the limnetic thermal strata. The exact number and location of these horizontal sections would depend largely on lake morphometry and goals of the study, but again the costs and benefits could be evaluated using pilot survey information.

The additional cost and effort of a detailed stratified design can often be justified by the information it provides on population spatial distribution. Its usefulness in describing changes in seasonal abundance and distribution of the *Polyphemus* population is demonstrated in Figs. II-5 and II-6, for 1975 and 1976, respectively. In both years, after an absence of *Polyphemus* in the period of ice cover, population size increased exponentially to a spring maximum, followed by a nearly exponential decline to a summer plateau, and a final decline to zero just prior to ice-on (Figs. II-5A, II-6A). A slight secondary peak (most noticeable in Fig. II-6A) occurred in August of both years and was related to an increase in fecundity in the population. These curves (Figs. II-5A, II-6A) were surprisingly similar from year to year, suggesting that perhaps with better sampling designs much of the variability associated with seasonal abundance curves could be eliminated. Daily variation (Insert Figs. II-5A, II-6A) was considerably less than weekly and seasonal variation, again supporting the adequacy of stratified sampling.

Considering the littoral and limnetic regions of Stonehouse Pond as two subpopulations, seasonal changes in horizontal distribution were examined. Figures II-5B and
Fig. II-5. 1975 seasonal abundance of *Polyphemus pediculus* in Stonehouse Pond based on weighted, stratified estimates. A. Seasonal and daily variation in total *Polyphemus* population size. Vertical bars represent 95% confidence limits about total. B. Seasonal variation in *Polyphemus* density in the littoral and limnetic zones of Stonehouse Pond. Note log scale. C. Percent of total *Polyphemus* population partitioned between littoral and limnetic regions of Stonehouse Pond.
Fig. II-6. As Figure II-5 for 1976 seasonal abundance of Polyphemus pediculus.
II-6B summarize changes in mean density of *Polyphemus* per meter$^3$. Mean density was calculated for the upper 3 meters of water in both the littoral and limnetic regions because *Polyphemus* were never collected below this layer. Expressing mean density for the entire water column would merely reduce limnetic densities by a factor of approximately three.

Density in the littoral was highest in the spring and fall of both years, and at those times was nearly four orders of magnitude greater than limnetic density. Limnetic density was greatest in summer, but *Polyphemus* individuals were virtually absent from this region in spring and fall. However, limnetic density never exceeded the corresponding littoral density.

Partitioning the total *Polyphemus* population into littoral and limnetic subpopulations (Figs. II-5C, II-6C) revealed a slightly different pattern. In spring and fall, virtually the entire population was contained in the littoral. In the summer, although limnetic density was lower than littoral density (Figs. II-5B, II-6B), by virtue of its greater volume (Table II-1) approximately 80% of the total population was limnetic. Therefore, in the fall of each year, the synchronized decline in limnetic density and rise in littoral density (Figs. II-5B, II-6B) while total population remained relatively constant (Figs. II-5A, II-6A), represented a shift in horizontal distribution of the *Polyphemus* population into the littoral zone. In the spring, a horizontal movement of the population from the littoral to the limnetic zone occurred but was not clearly demonstrated in these figures because of a rapid decline in population size.
Inadequate sampling designs and differences in expression of seasonal abundance may have resulted in the existing confusion in the literature regarding spatial affinity of the *Polyphemus* population. The exact affinity depends upon the time of year the lake was sampled, and the parameter (total number or mean density) used to quantify abundance. Results of sampling limited to the limnetic zone of Lake Michigan (McNaught, 1966; Wells, 1960) and of several Japanese lakes (Kikuchi, 1930, 1937) typically revealed *Polyphemus* only in the summer. This observation is consistent with the present study, but to characterize seasonal abundance of a *Polyphemus* population based only on limnetic sampling would be erroneous and misleading. A single midsummer peak in the limnetic zone observed in Stonehouse Pond reflected a change in horizontal distribution of the *Polyphemus* population and not a change in population size. Similarly, sampling limited to the littoral zone would also be biased by the seasonal change in horizontal distribution. Examination of *Polyphemus* mean density from littoral samples led Axelson (1961), Butorina (1971), and Lindstrom (1952) to consider *Polyphemus* to be primarily littoral in distribution. The present study, however, revealed that in the summer the population was primarily limnetic (Figs. II-5C, II-6C). Multinodal seasonal abundance curves (Butorina, 1963, 1971; Ischreyt, 1933) and the lack of error estimates make it difficult to interpret these peaks, but strongly suggest their sampling designs were inadequate to handle *Polyphemus* patchiness.

A stratified random sampling design which employs varying time and space scales can increase accuracy and precision.
of plankton population abundance estimates. Its resolution of seasonal changes in horizontal distribution of the Polyphemus population of Stonehouse Pond indicates the potential of stratified sampling as a tool for studying plankton patchiness in lake systems. Clearly, studies of plankton patchiness could be improved with appropriate sampling designs.

4. Summary

A stratified random sampling design was evaluated in its ability to quantify spatial and seasonal changes in the abundance of the predatory cladoceran, Polyphemus pediculus (L.). A whole-lake stratified design with sample units consisting of eighty-four 20 meter Clarke-Bumpus tows was more accurate and precise in quantifying seasonal abundance than a conventional design of eight 150 meter tows (Fig. II-4), and better revealed changes in horizontal distribution. Using this stratified design, the Polyphemus population of Stonehouse Pond, Barrington, N.H., was examined for two years, 1975 and 1976 (Figs. II-5, II-6). Seasonal abundance was typified by an exponential rise to a spring maximum, followed by an exponential decline to a summer plateau. A slight secondary peak occurred in August of each year, and abundance declines to zero in late fall. In spring and fall, the total population was primarily littoral, and in the summer it was limnetic in distribution, although mean density was always greater in the littoral. Sampling limited only to the littoral or limnetic zone would misrepresent seasonal abundance due to this seasonal change in horizontal distribution of the Polyphemus population.
5. Literature Cited


SECTION III

ALTERNATING REPRODUCTIVE MODES AND THE SEASONAL DYNAMICS OF POLYPHEMUS PEDICULUS (L.) IN A SMALL NEW ENGLAND LAKE

1. Introduction

In spite of the cosmopolitan distribution and abundance of *Polyphemus pediculus* in many lakes, there are few studies of this predaceous cladoceran. Butorina has described aspects of the morphology (Butorina, 1967, 1968, 1973), life cycle (Butorina, 1963, 1971a), feeding (Butorina, 1965, 1970, 1971b, 1971c; Butorina and Sorokin, 1966, 1970), and distribution (Butorina, 1969, 1971d) of *Polyphemus*. Virtually all other research has been limited to the taxonomy and morphology of *Polyphemus* (Dumont et al., 1975; Green, 1961; Hasler, 1937; Ischreyt, 1933a, 1933b; Makruschin, 1973; Mordukhai-Boltovskoi, 1968; Smirnov, 1960).

The extremely patchy distribution of *Polyphemus* has severely limited quantitative investigations of its population dynamics. Irregular fluctuations in seasonal abundance curves (Butorina, 1963, 1971a) suggest sampling variability may have obscured real population changes. Recently, Mattson described this patchiness (Section IV) and demonstrated that sampling variability could be reduced using a stratified random sampling design (Section II).
Recent research has demonstrated the importance of predation-induced mortality to zooplankton abundance and community size structure (reviewed in Hall et al., 1976). Since population growth results from differences between natality and mortality rates, changes in natality also influence seasonal dynamics. Butorina (1971a) suggested gamogenesis may be the dominant mode of reproduction at certain times in the *Polyphemus* population. Since resting eggs do not contribute immediately to natality, a dominant period of gamogenesis may cause a decrease in population growth and a concomitant decline in abundance. It is important, therefore, to investigate the seasonal dynamics of a zooplankton population which may be influenced by dominant periods of gamogenesis. The purpose of this study was to evaluate the contribution of parthenogenesis and gamogenesis to the seasonal dynamics of *Polyphemus* using stratified sampling. The effect of these reproductive modes was considered with respect to changes in abundance, composition, and population growth rates.

2. Materials and Methods
   
   A. Study site

   Stonehouse Pond in southeastern New Hampshire was selected as the study site based on lake morphometry, proximity, and the presence of a large *Polyphemus* population. Stonehouse Pond is a small, mesotrophic, glacial kettle lake, with a surface area of 5.7 hectares, a maximum depth of 17 meters, and a mean depth of 7.6 meters. It was last reclaimed in October, 1966, and a population of 20 - 30 cm brook trout,
Salvelinus fontinalis, is maintained by yearly stocking by the State of New Hampshire. This lake has been described in detail elsewhere (Section II; Section IV; Ferrante, 1974).

B. Sample collection and enumeration

The stratified random sampling design used to quantify seasonal abundance of the Polyphemus population in Stonehouse Pond has been described and evaluated previously (Section II), and will be only briefly outlined here. First, the entire lake surface was divided into six littoral sections and one limnetic section. Within each of these seven horizontal lake sections, samples were collected at 1/2 meter intervals from 0 - 3 meters of depth. In the limnetic section, three additional samples were taken as oblique tows from 11 meters to 3 meters of depth. Since Polyphemus were not captured in these deep limnetic samples, these samples were not used in subsequent calculations. On each sampling date, eighty-four 200 liter Clarke-Bumpus net tows (151 µ mesh, 12.5 cm. diameter, 20 meter long) were allocated throughout the lake using the spatial pattern described above. These samples were collected from fixed horizontal locations in a random sequence in time. Population sampling by this method was at 5 - 12 day intervals in the ice free periods of 1975 and 1976, and was closest at times of rapid population change. In the period of ice cover, sampling was performed at monthly intervals using a 30 cm. diameter, 151 µ plankton net, which was towed vertically from the bottom to the surface at two locations in each horizontal lake section. The total number of Polyphemus
in all stratified samples was counted on a dissecting microscope, and counting error varied between 0 % for small samples, to 6 % for relatively large samples. Total *Polyphemus* population size was estimated by weighting the average *Polyphemus* density in each section by the appropriate volume of water, and then summing these section totals to obtain a whole lake total (Barrett and Nutt, 1975; Cochran, 1977).

In addition to the stratified design outlined above, three randomly selected horizontal locations were sampled at 0 and 0.5 meters of depth with relatively large volume tows (1500 liters, 151 μ mesh, 12.5 cm diameter, 150 meter long). These six horizontally-integrated tows were from depths representative of greater than 90 % of the *Polyphemus* population on each date (Section IV), and were used to determine the percent composition of the population. All samples were preserved in 4 % Formalin-Sucrose (Haney and Hall, 1973). From each tow, a random subsample (Hensen-Stempel piston pipette method, Schwoerbel, 1970) of at least 50 *Polyphemus* was examined for population composition, and individuals were classified as juveniles, parthenogenetic females, gamogenetic females, or males (Table III-1). Percent composition was calculated by weighting the average at each depth by the corresponding percent of the total population.

C. *Duration of brood development*

Duration of brood development (D) was determined in situ as the time between two successive broods, since mature *Polyphemus* females release new eggs into the brood pouch.
Table III-1. Morphological characteristics used to distinguish embryonic developmental stages and to separate juvenile from mature *Polyphemus*.
<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>Morphological description</th>
<th>Development period (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>early embryo</td>
<td>Oval to unpigmented embryos with limb buds present</td>
<td>86 %</td>
</tr>
<tr>
<td>middle embryo</td>
<td>Limbs with setae; compound eye with green pigment</td>
<td>9 %</td>
</tr>
<tr>
<td>late embryo</td>
<td>embryos with green pigment masked by black eye pigment; caudal setae not present</td>
<td>5 %</td>
</tr>
<tr>
<td>juvenile</td>
<td>newborn to sexual maturity; caudal setae present; immature gonads</td>
<td></td>
</tr>
<tr>
<td>adult</td>
<td>parthenogenetic females, gamogenetic females, or males with mature ovaries or testes</td>
<td></td>
</tr>
</tbody>
</table>
immediately following each molt and liberation of neonates (Butorina, 1971a). Twenty-five to fifty parthenogenetic females with late stage embryos (Table III-1) along with selected prey items at two to four times lake densities were placed in a 4 liter glass container with a 202 μ NITEX cover. Containers were incubated in the littoral zone at 0.3 meters of depth. D was estimated as the time between hatching of the first broods (6 - 12 hours after isolation) and the next broods. These "synchronized" females required observation only once daily until the subsequent late stage embryos were seen and, depending on ambient temperature, were observed at 6 to 12 hour intervals thereafter. Containers were cleaned and prey were added daily. Using this method, D was determined at 4 or 5 temperatures in each year, representing range of 8 - 28°C. To account for diel variation in temperature, average median daily temperature for the duration of development was determined with a max-min thermometer. Seasonal and diel temperature range can be seen in Fig. III-1A.

D. Population growth statistics

Population growth statistics were calculated based on application of an exponential growth model (Edmondson, 1960; Hall, 1964). While the instantaneous rate of increase (r) was calculated from the change in total population size between successive sampling dates, the instantaneous birth rate (b) was estimated from finite birth rate (B) using the formula of Edmondson (1960 formula 9). Recent computational refinements of Edmondson's formula by Caswell (1972) and Paloheimo (1974)
were also compared. Since the *Polyphemus* population in this study was always found in relatively homeothermal epilimnetic water, estimation of \( b \) from \( B \) did not require depth-temperature weighting as proposed by Prepas and Rigler (1978). The instantaneous death rate (d) was estimated by difference from a rearrangement of the formula \( r = b - d \).

The *Polyphemus* population may be dominated at times by sexually reproducing individuals producing resting eggs, with the only contribution to population growth coming from parthenogenetic broods. In this case, \( B \) could be estimated using the ratio of eggs (embryos) per parthenogenetic female (egg ratio) per day, or using the ratio of eggs (embryos) per individual per day (per capita egg ratio, Paloheimo, 1974). To relate \( B \) to the total *Polyphemus* population, the above ratios could be multiplied respectively by the total number of mature parthenogenetic females or by the total population size. Since it may be difficult to distinguish between late instar juveniles and mature females, the per capita egg ratio was used and \( b \) was estimated from this ratio.

The number of embryos per mature parthenogenetic female, hereafter called "brood size", was of interest in this study since it reflected reproductive potential, and was calculated in two ways. In both 1975 and 1976, all *Polyphemus* embryos were counted in the same subsamples used for population composition, and divided by the number of mature parthenogenetic females to provide an estimate of brood size. In addition, in 1976, mean brood size was determined for each date by examining the brood contents of 50 live parthenogenetic females.
which were transported to the laboratory and narcotized in carbonate water. Brood size estimates by these two independent methods were nearly identical (paired t-test by date, p > 0.10) indicating subsampling error and preservation effects (Prepas, 1978) were not serious in this study. Brood size was also quantified in 1977 from live females.

3. Results

A. Brood size and duration of development

Seasonal curves for the change in mean parthenogenetic brood size were remarkably similar for the 1975 through 1977 period (Fig. III-1B), and were characterized as three phases (spring, summer, and fall). The first broods in the spring from exsheppial Polyphemus were the largest recorded in each year, and were occasionally as high as 29 embryos per brood. Brood size declined rapidly from this first brood to a summer plateau of approximately 2 embryos per brood, and then increased in the fall. This seasonal pattern was also observed by Butorina (1971a).

In the spring and fall, brood size was inversely correlated with ambient water temperature (Fig. III-2). Linear regression equations best described this relationship and demonstrated a different response to temperature between seasons. Significant differences between the slopes (p < 0.05) of these equations suggested brood size changed more slowly with changing temperature in the fall than in the spring. In the summer, brood size remained relatively unchanged and was not correlated with water temperature.
Fig. III-1. Seasonal change in median surface temperature (A) and mean parthenogenetic brood size (B) for *Polyphemus* in Stonehouse Pond. Vertical bars about the 1976 temperature curve (A) represent diel temperature range. Vertical bars about 1976 and 1977 mean brood size (B) represent 95% confidence intervals.
**TEMPERATURE**

**WATER TEMPERATURE**

- 1975
- 1976
- 1977

**PARTHENOGENETIC BROOD SIZE**

- 1975
- 1976
- 1977
Fig. III-2. Scatter diagram of the seasonal relationships between parthenogenetic brood size and ambient water temperature for the 1975-1977 Polyphemus population in Stonehouse Pond. Regression lines are plotted and the relationship is given between brood size (B.S.) and temperature (T.) for spring and fall. The linear correlation coefficient, r, is also given. No correlation was found between temperature and brood size in the summer.
**Temperature vs. Brood Size**

**SPRING**
- Brood Size (B.S.) = 20.44 - 0.785(T.
- Correlation coefficient (r) = -0.79

**FALL**
- Brood Size (B.S.) = 9.32 - 0.362(T.
- Correlation coefficient (r) = -0.80
The lack of correlation between brood size and temperature during the summer of all three years suggested other factors were important. Since food level has been directly correlated with brood size in Daphnia (Hall, 1964; Lampert, 1978), the relationships of brood size to food, temperature, and their interaction were examined in simple and multiple regression models. Brood size was poorly correlated with the density of several important prey species (copepod nauplii $r = +0.37$ linear, $r = +0.10$ log-linear; the colonial rotifer Chronochilus unicorns $r = -0.10$, $r = -0.20$; and Bosmina sp. $r = -0.29$, $r = -0.28$), and with total prey density calculated as volume ($\mu^3$ of prey) from the tables of Nauwerck (1963) ($r = -0.29$, $r = -0.34$). A time-lag correction of prey density based on the brood development time (Lampert, 1978) did not improve these relationships. As a result, the addition of food abundance and/or the interaction of food and temperature in a multiple regression model accounted for only $0.4\%$ of the total variation in the relationship of these factors to brood size (temperature alone accounted for $53.3\%$ of the total variation).

A dicyclic pattern of gamogenesis was observed. Average gamogenetic brood size was significantly smaller in spring ($2.17 \pm 95\%$ C.I. = 0.46) than in fall ($3.96 \pm 0.23$). Butorina (1971a) also observed seasonal differences in gamogenetic brood size ($2.5$ eggs/brood - spring, $4.0$ eggs/brood - fall).

When regressed against ambient water temperature, reciprocal duration of brood development ($1/D$) exhibited a
linear relationship. The equation was: \( \frac{1}{D} = 0.0146 \text{ (temp. } °C) - 0.0413, r = +0.927, \) for \( D \) in days, slope significantly greater than zero (\( p<0.001 \)). Although the biological relationship between development time and temperature may more closely approximate a \( Q_{10} \) response and, therefore, be curvilinear and a power function (Bottrell, 1975; Hall, 1964; Munro and White, 1975), for the resolution and range of field conditions in this study, a linear model was a good predictor of parthenogenetic brood development time.

**B. Seasonal abundance, composition, and population growth**

Seasonal abundance curves for 1975 (Fig. III-3A) and 1976 (Fig. III-4A) were dominated by a spring maximum of 4–5 times greater than summer population levels. In both years, the population was only present in the water column in the ice-free period. Following ice-out (early April), total population size grew exponentially to a spring maximum in late May. An exponential decline followed this spring maximum to a summer plateau. In early August of both years, a slight secondary peak in abundance occurred, and was most noticeable in 1976. After this secondary peak, population size declined linearly to zero just prior to ice-on in early December.

Population composition (Figs. III-3B, III-4B) changed between asexual (parthenogenetic) and sexual periods. Two periods of sexual reproduction (late spring at the abundance maximum and mid-fall) alternated with three asexual periods (early spring, a long summer period, and late fall). Juveniles were the first Polyphemus to appear in the spring of each year.
Fig. III-3. Seasonal change in population statistics for the 1975 Polyphemus population of Stonehouse Pond. 
A. Seasonal abundance - vertical bars represent 95% confidence intervals. B. Percent composition - dark shading (M) represents males, lines (G) - gamogenetic females, dots (P) - parthenogenetic females, and clear (J) - juveniles. C. Instantaneous rate of population increase (r) based on estimates of total population size (solid line) and based on 95% confidence limit extremes about the population total (dashed line - \( r_{\text{max}} \) and \( r_{\text{min}} \)). Shaded area between \( r_{\text{max}} \) and \( r_{\text{min}} \) represents the range of possible r values due to sampling variability. D. Instantaneous birth (b) and death (d) rates. Note: negative d values (-d) were used since mortality represents a loss from the population. Horizontal bars represent periods of resting egg production.
Fig. III-4. Seasonal change in population statistics for the 1976 Polyphemus population of Stonehouse Pond.
A. Seasonal abundance. B. Percent composition.
C. Instantaneous rate of population increase (r).
D. Instantaneous birth (b) and death (d) rates.
Legend as in Fig. III-3.
These juveniles were exphemial individuals, since 1) they appeared before the presence of mature females and 2) littoral sediment samples taken just after ice-out revealed Polyphemus resting eggs with late stage embryos. As this cohort of exphemial juveniles matured, population composition became dominated by parthenogenetic females. Oscillations in percent composition of juveniles and parthenogenetic females continued throughout the summer and 2 - 3 peaks occurred in each year.

In both years, sexual individuals appeared at the spring abundance maximum and produced resting eggs (Figs. III-3B, III-4B). A second period of sexual reproduction occurred in the fall of each year, and at that time the population was almost exclusively composed of males and gamogenetic females. While sex ratios were relatively even in the spring sexual period, a significantly larger percent of the population was males in the fall. In late fall, the population was once more dominated by parthenogenetic individuals but the total population size was extremely low.

Highest $r$ values were observed in the spring of each year just prior to the spring maximum in abundance (Figs. III-3C, III-4C). A rise in the $r$ value curves was also associated with the secondary peak in population abundance in early August of each year. In the fall of each year, $r$ was negative as the population declined to zero. Throughout the rest of each year, $r$ oscillated about zero. The range of $r$ values due to sampling variability generally varied between 0.2 and 0.4. Extreme range of $r$ was observed in the fall of both
years and in late June of 1976, and was due to relatively
wide confidence limits (Figs. III-3A, III-4A).

Estimates of \( b \) using the formulae of Edmondson (1960),
Caswell (1972), and Paloheimo (1974) were nearly identical
throughout most of each year except in early spring and late
fall when these estimates differed by as much as 58%. Cold
water temperatures resulting in long duration of development
(Edmondson, 1960; Paloheimo, 1974) and large brood size (Fig.
III-1B) at these times probably accentuated mathematical
differences in the above formulae. Paloheimo (1974) has
demonstrated convincingly that the formulae of Edmondson and
Caswell overestimate \( b \) as \( D \) increases. Therefore, Paloheimo's
formula was used to summarize seasonal changes in \( b \).

The only contribution to natality were from hatching
of resting eggs and parthenogenetic reproduction. As Polyphemus
hatched from resting eggs in early spring of both years, \( b \)
was highest and was equal to \( r \) since \( d \) was zero (Figs. III-3D,
III-4D). Large parthenogenetic broods (Fig. III-1B) and a
high percent of parthenogenetic females sustained natality
at a high level and contributed to the spring abundance maximum.
A sharp decrease in natality immediately preceded this maximum.
This was due to declining brood size and to a large percent
of sexual individuals in the population which produced resting
eggs and, therefore, did not immediately contribute to natality.
The decrease in abundance following the spring maximum was
primarily due to this change in natality, since mortality was
relatively constant at that time.
The increase in population growth rate associated with each secondary peak in abundance resulted from different relationships between natality and mortality (Figs. III-3, III-4). In 1975, the increase in $r$ was due to a decrease in mortality while natality and brood size (Fig. III-1B) remained relatively unchanged. In 1976, $r$ increased with an increase in natality which was associated with a slight rise in brood size while mortality was relatively constant.

Finally, negative $r$ values observed as population size declined in the fall were probably the result of an increase in mortality as sexual individuals died while per capita natality was nearly zero.

C. Gamogenetic vs Parthenogenetic reproduction

The contribution of gamogenetic and parthenogenetic reproduction at times of gamogenesis is quantified in Table III-2. The dominant period of resting egg production occurred at the spring peak in abundance in both 1975 and 1976. This dominance was most striking in the spring of 1975, when the maximum number of resting eggs was fifteen times greater than the fall maximum (Table III-2). In 1976, the spring maximum number of resting eggs exceeded the fall maximum by a factor of four. Although gamogenetic brood size and percent composition in the total population (Figs. III-3B, III-4B) were lower in spring than in fall, the timing of gamogenesis with the spring maximum in abundance (Figs. III-3A, III-4A) accounted for the greater numerical importance of this spring period of resting egg production.
Table III-2. The total number of parthenogenetic embryos and resting eggs which were observed in the Polyphemus population in each spring and fall period of gamogenesis (1975-1976). In parentheses: the relative importance (%) of gamogenetic and parthenogenetic reproduction on each date.
<table>
<thead>
<tr>
<th>Date</th>
<th>Total in Polyphemus population (N x 10^8)</th>
<th>Parthenogenetic embryos</th>
<th>Resting eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>20-V-75</td>
<td>1.3816 (54%)</td>
<td>1.1895 (46%)</td>
<td></td>
</tr>
<tr>
<td>28-V-75</td>
<td>0.3677 (28%)</td>
<td>0.9323 (72%)</td>
<td></td>
</tr>
<tr>
<td>11-VI-75</td>
<td>0.4118 (84%)</td>
<td>0.0796 (16%)</td>
<td></td>
</tr>
<tr>
<td>19-VI-75</td>
<td>0.2670 (89%)</td>
<td>0.0330 (11%)</td>
<td></td>
</tr>
<tr>
<td>2-X-75</td>
<td>0.2983 (87%)</td>
<td>0.0441 (13%)</td>
<td></td>
</tr>
<tr>
<td>9-X-75</td>
<td>0.2376 (75%)</td>
<td>0.0792 (25%)</td>
<td></td>
</tr>
<tr>
<td>16-X-75</td>
<td>0.0447 (48%)</td>
<td>0.0478 (52%)</td>
<td></td>
</tr>
<tr>
<td>23-X-75</td>
<td>0.0035 (48%)</td>
<td>0.0038 (52%)</td>
<td></td>
</tr>
<tr>
<td>30-X-75</td>
<td>0.0019 (20%)</td>
<td>0.0075 (80%)</td>
<td></td>
</tr>
<tr>
<td>19-V-76</td>
<td>2.8760 (87%)</td>
<td>0.4181 (13%)</td>
<td></td>
</tr>
<tr>
<td>27-V-76</td>
<td>2.7150 (94%)</td>
<td>0.1793 (6%)</td>
<td></td>
</tr>
<tr>
<td>2-VI-76</td>
<td>1.7169 (96%)</td>
<td>0.0632 (4%)</td>
<td></td>
</tr>
<tr>
<td>15-X-76</td>
<td>0.1309 (57%)</td>
<td>0.0968 (43%)</td>
<td></td>
</tr>
<tr>
<td>25-X-76</td>
<td>0.0354 (69%)</td>
<td>0.0157 (31%)</td>
<td></td>
</tr>
<tr>
<td>5-XI-76</td>
<td>0.0005 (55%)</td>
<td>0.0004 (45%)</td>
<td></td>
</tr>
</tbody>
</table>
On only one date in the spring and fall of 1975, resting eggs accounted for a greater percentage of the total population reproductive output than parthenogenetic embryos (Table III-2). On two additional dates in the fall of both 1975 and 1976, percentages of resting eggs and embryos were approximately equal. Otherwise, in 1975 and 1976, parthenogenesis was the dominant mode of reproduction. Gamogenesis accounted for a particularly low percentage of the population reproductive output in the spring of 1976. In general, it appeared that gamogenetic reproduction was numerically more important in 1975 than in 1976 (Table III-2).

4. Discussion

The seasonal pattern of change in parthenogenetic brood size exhibited two unusual features: 1. the largest broods were the first broods in the spring from exephippial Polyphemus and 2. the apparent lack of correlation between brood size and food level. Maximum brood size of cladocerans is often attained at larger body sizes associated with the fifth or sixth post-adult instars (Hutchinson, 1967). Large first broods cannot be attributed to large body sizes of these exephippial Polyphemus, since females with the largest broods had the smallest body size (spring first brood, $\bar{X}$ body length in mm = 0.70 ± 0.02 - 95% C.I.; ten days later, $\bar{X}$ = 0.81 ± 0.03; summer, $\bar{X}$ = 0.81 ± 0.02). This evidence suggests genetic differences in fecundity exist between exephippial and non-ephippial parthenogenetic females.
The observed lack of correlation between brood size and prey density does not preclude a causal relationship. In calanoid copepods, the seasonal pattern of change in clutch size is often similar to the pattern observed for *Polyphemus*, and has been related to changes in food supply (Hutchinson, 1951, 1967). Since *Polyphemus* provide some nutrition to their developing embryos through secretions into the brood pouch (Hutchinson, 1967), a link might be expected between brood size, embryo development, and food. However, the association between food and brood size is undoubtedly complex, particularly for predatory cladocerans. As a mobile raptor, *Polyphemus* select prey and may not feed only in response to food density. Therefore, density alone may not reflect food availability. Qualitative differences in food also may have confounded the brood size-prey density correlation since the primary food source for *Polyphemus* in early spring and late fall was copepod nauplii, while in the summer rotifers may have constituted a larger portion of their diet (Mattson and Haney, unpublished). The extreme difficulty in culturing *Polyphemus* in the laboratory also may reflect intricate food relationships for this predator.

Few lacustrine cladocerans have been reported to have dicyclic patterns of gamogenesis and resting egg production. In this study, *Polyphemus* had a spring period of sexual reproduction in late May-early June and a fall period in October-November, alternating with three periods of parthenogenetic reproduction. A similar dicyclic pattern of gamogenesis was suggested for *Polyphemus* by the observations of Butorina.
(1971a), and occasionally has been reported for Daphnia (e.g. D. longispina, Hutchinson, 1967).

Another aspect of Polyphemus seasonal dynamics which differed markedly from other cladocerans was the high percentage of males in the population at the time of sexual reproduction, particularly in the fall (Figs. III-3B, III-4B). Although some cladoceran populations may at times have nearly 50% males (e.g. Leptodora kindtii, Cummins et al., 1969), values as high as 90 - 97% observed in this study appear unique.

The seasonal dynamics of Polyphemus were remarkably similar to Holopedium gibberum (Lampert and Krause, 1976). Both populations had dicyclic sexual cycles (spring and fall). Both had a greater percent of males in the fall than in the spring sexual period, although for Holopedium males never exceeded 16% of the population composition. Finally, in both populations resting eggs comprised a large percent of the total reproductive output at times of gamogenesis.

For the total Polyphemus population, the spring period of gamogenesis was numerically most important (Table III-2). It is not known whether these spring resting eggs hatch in the fall, the following spring, or not at all (as suggested for Holopedium by Lampert and Krause, 1976). If this dicyclic pattern of resting egg production can be considered an adaptation life in ephemeral habitats (Hutchinson, 1967; Pennak, 1953) which was retained by Polyphemus when this species inhabited larger and more "permanent" bodies of water, then some of the spring resting eggs may indeed hatch in the fall. It is also possible that this dicyclic pattern of gamogenesis
may be quite common, but the spring period is reduced among other lacustrine cladocerans, and has been rarely detected due to limited sampling designs.

If dicyclic gamogenesis has been retained by lake populations, it undoubtedly has several adaptive advantages. In both years, spring and fall gamogenesis began within a week of each other, at the same water temperature (15°C), and at a similar daylength (spring - 14.0 hrs., fall - 11.5 hrs.). This suggested gamogenesis occurred in response to environmental conditions which predicated potentially adverse conditions (e.g. warm summer temperatures or cold winter temperatures). Two periods of gamogenesis cued to the same environmental conditions may provide a degree of redundancy which would increase the probability of population survival from year to year. However, both sexual periods need not arise from the same selective pressures. The spring period may be a response to crowded conditions and possible food limitation associated with the abundance maximum, as has been suggested for other cladocerans (Hutchinson, 1967). Spring gamogenesis may also provide a means for maximum survival at a time of intense predation by planktivorous fish larvae by allowing the primarily littoral Polypheus population to "escape" as resting eggs in the sediments.

The natality and mortality rates presented in this study were calculated using a per capita egg ratio (Palchheim 1974), and cannot be directly compared to rates derived from the ratio of embryos per parthenogenetic female. The former rates are sensitive to changes in population composition and
decrease as the percent of sexual individuals increases. Polyphemus mortality rates calculated for comparison with other studies \(d = b - r\), \(b\) based on parthenogenetic females only) were highest in the summer, but on only three occasions exceeded 0.3 \(d = 0.34, 22\text{-VII-75}; 0.31, 2\text{-VI-76}; 0.37, 9\text{-VI-76}\). In contrast, Hall (1964), Wright (1965), Applegate and Mullan (1969), and Prepas and Rigler (1978) all observed instantaneous mortality rates for Daphnia in excess of \(d = 0.5\) in the summer. Predation probably contributed to high Daphnia mortalities in the first three studies, while neonate death at the time of birth most likely resulted in high summer mortality in the study of Prepas and Rigler (1978).

For Polyphemus, external sources of mortality (e.g. predation) probably do not change significantly throughout the year. Since gamogenetic females die with the release of their only brood of resting eggs (Butorina, 1971a; Makrushin, 1973), their "natural" mortality contributed as much as 32% to the population mortality in the spring of 1975 (12% in 1976). In both Polyphemus and Holopedium (Lampert and Krause, 1976), the decline in population size following spring maximum was most likely due to a decline in natality associated with gamogenesis and the production of resting eggs. Since gamogenesis was numerically less important in 1976 than in 1975, the decline in population size following the spring abundance maximum was less precipitous and a broader peak was observed. More experimental research is needed on the life history and population biology of Polyphemus before additional attempts are made to interpret the details of its population dynamics.
5. **Summary**

The influence of parthenogenetic and gamogenetic reproduction was examined with respect to seasonal changes in abundance, composition, and population growth statistics of a *Polyphemus pediculus* (L.) population in Stonehouse Pond, Barrington, N. H., U.S.A. A stratified random sampling design was employed to accurately and precisely describe these characteristics of *Polyphemus* seasonal dynamics in 1975 and 1976.

Seasonal curves for change in parthenogenetic brood size had three distinct phases (spring, summer, fall) (Fig. II-1B). An unusual feature was that the first broods in the spring from exshepippial *Polyphemus* were the largest in each year. Brood size declined rapidly to a summer plateau and then increased in the fall. In the spring and fall, brood size was inversely correlated with ambient water temperature (Fig. III-2) and was apparently unrelated to prey densities. In the summer, brood size remained relatively unchanged and was not correlated with changing water temperature or prey densities.

A dicyclic pattern of gamogenesis was observed, and brood size was significantly smaller in the spring (2.17 ± 0.46) than in the fall (3.96 ± 0.23).

Seasonal abundance curves were dominated by a spring maximum of 4 - 5 times greater than summer population levels (Figs. III-3A, III-4A). A slight secondary peak in abundance occurred in August of both years. As evidence of the dicyclic gamogenesis, two sexual (at the spring abundance maximum and in mid-fall) and three parthenogenetic (early spring, a long
summer period, and late fall) periods of reproduction were observed in each year (Figs. III-3B, III-4B). Sex ratios were relatively even in the spring, but in the fall males comprised more than 90% of the population. Population growth was characterized primarily by changes in natality associated with these alternating reproductive modes (Figs. III-3C-D, III-4C-D).

The timing of spring gamogenesis with the abundance maximum resulted in greater resting egg production in the spring than in the fall (Table III-2). In both sexual periods, resting egg production was large and occasionally the dominant mode of reproduction. These results are discussed with respect to the predominance of dicyclic sexual cycles in the Cladocera, their adaptive advantages, and influence on population dynamics.
6. Literature Cited


SECTION IV

PATCH STRUCTURE AND PATTERNS OF PATCHINESS
IN A POLYHEMUS PEDICULUS POPULATION

1. Introduction

Many studies have demonstrated the existence of zooplankton patches but few describe the structure and pattern of patches or changes in these components in time and space (Haury, 1976). Recent research has emphasized a need for biological studies of zooplankton aggregations not only as an interesting phenomenon, but to evaluate their role in ecosystems (e.g. Clutter, 1969; Dumont, 1967, Emery, 1968; Hamner and Carleton, 1979; Haury, 1976; Steele, 1974). It appears from these studies that the structure and pattern of zooplankton patches results from the interaction of biological and environmental factors.

The purpose of this study was to examine in detail the temporal and spatial patterns of patchiness in a population of the predatory cladoceran, Polyphemus pediculus (L.). Patterns were compared on time scales varying from two years to hours and on space scales ranging from several hundred meters (whole-lake) to centimeters. Components of patch structure examined included horizontal and vertical dimensions, internal and external density and composition, and statistical dispersion. Attempts were also made to evaluate the causes
and function of Polyphemus patches, and their relationship to Polyphemus population dynamics.

2. Materials and Methods
   A. Terminology

   In this study it was necessary to distinguish between several terms used to describe the groups of zooplankton. Clutter (1969), Mauchline (1971), and Zelickman (1974) have reviewed this terminology, and their definitions were used to differentiate patch (or aggregation), shoal, school, and swarm.

   A patch or aggregation is a single or multispecies group statistically defined as over-dispersed (= supra-dispersed) making no inference to the factors responsible for this clumped or clustered distribution. The remaining three terms all imply some level of biological interaction. A shoal of zooplankton is a large, single species, aggregation ranging in size from a few meters to tens of meters across. Individuals within a shoal may be uniformly spaced or they may be composed of smaller cohesive groups (swarms or schools). A swarm of zooplankton is a small, single species aggregation often less than one meter across, and characterized by an interrelationship of individuals. This term implies greater cohesiveness than is found in a shoal, and swarm densities often exceed shoal densities by a factor of three or more. A school is a specialized swarm in which individuals are uniformly spaced, oriented parallel to each other (polarized), and swimming in the same direction. Zelickman (1974) extends
the definition of swarm to imply that the organisms in a swarm "recognize" each other and that the swarm is capable of integrated behaviour within larger groups. This concept of a swarm as a "super-organism" appears widely adhered to by the Russian workers (e.g. Darkov, 1975; Radakov, 1973; and Zelickman, 1974) but was not used in this study.

B. Study Site

Stonehouse Pond in southeastern New Hampshire, U.S.A. (43°12'N, 71°06'W), was selected as the study site primarily because it (1) contained large Polyphemus populations, (2) lake morphometry was conducive to sampling, and (3) it was easily accessible. It is a glacial kettle lake, with a small drainage basin of mixed deciduous and conifer forest, and is slightly dystrophic. The main water supply is from a small stream which flows into the lake through a swampy area on the west side of the lake, and from ground water and seasonal runoff on the southwest side (Fig. IV-1). An unusual morphometric feature of this lake is the granite cliff which rises vertically out of the water on the southwest shoreline to a height above the water of 35 meters (Fig. IV-1). Lake contours reflect the slope of the cliff in this region. Additional physical, chemical, and biological information may be found in Ferrante (1974).

C. Sampling Design

A stratified random sampling design (Barrett and Nutt, 1975; Cochran, 1977) was used to quantify seasonal abundance and to describe temporal patterns of whole-lake
Fig. IV-1. Morphometric map of Stonehouse Pond, Barrington, New Hampshire, U.S.A. The major inlet is through a stream which flows into a swamp on the west shore. The shaded area on the southwest shore is a granite cliff.
distribution of the Polyphemus population. This design is
described and evaluated in detail elsewhere (Section II),
but will be briefly outlined with reference to this study.

Since Polyphemus is generally considered to be a
littoral zooplankter (Boutouina, 1963; Hutchinson, 1967),
Stonehouse Pond was divided horizontally into six major
littoral sections and one limnetic section based on morpho-
metric and physiographic features such as bottom type, compass
orientation, and shoreline structures (e.g. cliff, swamp,
outlet). Each major section was then subdivided into three
subsections (four in section 6) for a total of 22 horizontal
lake regions (Fig. IV-2). At least two 200 liter samples
were collected within each subsection using a modified Clarke-
Bumpus apparatus (Section II), one sample just below the lake
surface (center of net at 10 cm of depth) and one at 0.5
meters of depth. An overlapping grid of tows in sections
3 and 5 provided information on horizontal zonation parallel
to shore and aided in describing the configuration of patches
which occurred in these sections (Fig. IV-3). Tows were also
taken at 0.5 meter intervals from 0 to 3 meters (depth
permitting) in at least one subsection of each major section
to provide information on vertical zonation. Finally, three
oblique tows were taken in the limnetic zone below 3 meters
of depth on each date. Since Polyphemus were never collected
in these deep tows, these samples were not used in this
analysis.

Once every 5 to 12 days in the ice free periods of
1975 and 1976, 84 samples from the above spatial arrangement
Fig. IV-2. Stonehouse Pond sections and subsections which were used for stratified random sampling and spatial mapping.
STONEHOUSE POND
Barrington, New Hampshire

Scale in Meters
Contour interval - 3 Meters
1975-76
Fig. IV-3. Location of Clarke-Bumpus net tows in relation to the major sections of Stonehouse Pond.
STONEHOUSE POND
Barrington, New Hampshire

Scale in Meters
Contour interval: 3 Meters
1975-76
were collected in a 6 hour midday period. Diel variation in patchiness was examined on two dates in each of the two years. On these occasions, the lake was sampled on the first day, that night, and the following day. Location and time of collection was recorded for each sample to reconstruct spatial distribution on each date and to examine temporal variation within the sampling date.

The total number of *Polyphemus* in all stratified samples was counted and used to provide estimates of seasonal abundance. Subsamples from stratified samples falling within selected *Polyphemus* patches and adjacent areas were examined for zooplankton and *Polyphemus* composition. *Polyphemus* were classified as juveniles, parthenogenetic females, gamogenetic females, or males. In addition, three randomly selected horizontal locations were sampled at 0 and 0.5 meters of depth with large volume (integrated) tows (151 μ mesh, 12.5 cm diameter, 150 meter long, 1500 liters). Subsamples from these integrated tows provided whole-lake estimates of *Polyphemus* population composition.

D. *In situ* Observations

In addition to the sampling design outlined above, 30 + hours of *in situ* observations were made in 1976 and 1977 to examine the internal structure and behaviour of *Polyphemus* individuals within patches. *In situ* sessions consisted of a diver or divers snorkeling parallel to shore in the littoral or swimming along the long axis of the lake in the limnetic zone and recording the location of observable patches, and
incidents of feeding, mating, etc. Events were recorded in writing, and, in 1977, with a Nikonos 35 mm camera with a 2:1 or 3:1 extension tube on a 35 mm lens and an electronic flash. Photographs were used to examine the orientation of Polyphemus with respect to each other and to measure inter-animal distances.

E. Data analysis

1. Percent of population in the vertical or horizontal plane

Data from the stratified sampling design were used to estimate the total Polyphemus population for each sampling date. Median depth ($Z$) or the fulcrum depth above and below which 50% of the population was found, and the depth above which 90% of the population was found ($Z_{90\%}$), were calculated using a modification of the quartile method of Pennak (1943). This method involved computing the mean density of all samples at each ½ meter interval from 0 to 3 meters of depth, and then weighting each mean density by the volume of water at that depth interval to determine the percent of the total population in each depth slice. Percentages of the population were then cumulated from the surface to 3 meters, and $Z$ or $Z_{90\%}$ was determined by linear extrapolation between depths. The difference between $Z$ and $Z_{90\%}$, $\Delta Z$, represented vertical dispersion in the population.

In the horizontal plane, the lake was divided, proceeding from the shoreline out, into concentric rings of 0 - 5, 5 - 10, 10 - 20, 20 - 30, and greater than 30 meters.
Percent of the population in each ring was calculated in a manner similar to that for Z. In presenting this data, population percent in each ring was plotted respectively at 2, 7, 15, 25 and >30 meters from shore. Greater than 30 meters from shore was considered to be limnetic, and less than 30 meters was considered littoral. Although somewhat arbitrary, this boundary corresponds closely with physical and biological features of the lake which are often used to distinguish the two zones, including the top of thermocline and the maximum distance from shore to which rooted macrophytes occur.

2. Spatial mapping

Spatial mapping was used to examine the details of whole-lake horizontal distribution patterns in the Polyphemus population. It was necessary to use relative density in mapping to isolate spatial pattern (grain) from changes in seasonal abundance (Pielou, 1974). On each date, Polyphemus density was expressed as individuals·M⁻² for each of the 22 lake subsections (Fig. IV-2), and then divided by whole-lake mean density (indiv·M⁻²) to give relative density values. Five classes of relative density were then selected based upon examination of a composite frequency histogram of all relative density values from 1975 and 1976. This composite histogram was bimodal, with the smaller upper mode centered above a relative density of 3 (3 times the average lake density), and with values ranging from 0 to 28. A relative density of greater than 3 was selected as indicating a patch of Polyphemus. This value also corresponds with other reports of within patch densities varying from 3-11 times that of adjacent waters.
(Smith et al., 1976; Wiebe, 1970). The lower mode of the composite frequency distribution was skewed to the left, and was divided into four proportional classes symmetric about 1 (relative density the same as average density), which normalized this portion of the distribution. Final relative density classes were as follows: 0 - 1/3, 1/3 - 3/4, 3/4 - 5/4, 5/4 - 3, and greater than 3.

3. Aggregation indices

Variance to mean ratio (V/X) and subsequent $\chi^2$ Poisson variance test (George, 1974), and Lloyd's mean crowding ($\bar{M}$) and patchiness ($\bar{M}/X$) indices (Lloyd, 1967) were used to describe statistical dispersion. Regression of log-transformed values of these parameters against the log of mean population density ($\bar{X}$) tested their usefulness for seasonal comparisons of population statistical dispersion (George, 1974). Several methods of computing Lloyd's indices were tested, including estimation of the negative binomial parameter $k$ by moments, by the number of samples with no Polyphemus, by maximum likelihood, and by using the truncated negative binomial distribution (Bliss and Fisher, 1953; Lloyd, 1967). The latter three methods although usually more precise (Bliss and Fisher, 1953) require classification of sample counts into equal interval frequency classes. For seasonal comparisons this was not practical since variation in seasonal abundance required wide frequency classes in the spring and relatively narrow classes in the remaining part of the year. Lloyd's indices reported in this paper, therefore, are based on estimates of $k$ by moments, which requires only information on
population mean, variance, and the number of samples. On
certain dates when wide confidence intervals about Lloyd's
indices suggested $k$ was imprecise, and when other evidence
indicated the population was highly aggregated, the maximum
likelihood method was used. However, since no significant
improvement in precision was observed these results were not
reported.

4. Ancillary data

Selected environmental and habitat parameters
were observed to examine their correlation with patch location.
Habitat survey maps were used to record the locations of
aquatic macrophyte beds and the pattern of shading in each
littoral section due to seasonal and daily changes in solar
altitude. On each sampling date, weather-related information
was recorded at a permanently fixed buoy in the center of the
lake, including wind direction and speed (hand-held anemometer),
air and water temperature, percent cloud cover, and precipita-
tion. This information was supplemented with continuously
recorded weather data summarized in Local Climatological Data –
Monthly Data Sheets from the U.S. National Weather Service
Bureau, Concord, N.H. (35 km due west of Stonehouse Pond).
These two sets of observations agreed closely ($X^2 = 26.8,$
$p<0.001$), with only one consistent disagreement. When Concord
reported wind out of the NE, it was recorded as variable on
the lake surface, probably due to the influence of the cliff
on the SW shore (Fig. IV-1) deflecting air currents. Due to
this inconsistency, correlations of patch location and wind
direction were made using data recorded at the lake at the
time of sampling. Wind vector diagrams on spatial maps were based on U.S. National Weather Service observations recorded at 3 hour intervals from 0100 to 2200 on each day.

5. Computation and graphics

All data analyses were performed on a Digital Electronics Corp. Model 1090 computer using programs written by the author. Two and three-dimensional maps and graphs were drawn by a Calcomp plotter using SYMAP and SYMVU computer-graphic programs (Dougenik and Sheehan, 1977). Split-plot analysis of variance (ANOVA) was used to compare sample composition between areas of high and low Polyphemus density. In selected samples blocked by date, the main plot factor was the presence or absence of a high density of Polyphemus (patch or no patch), and the subplots were log-transformed densities representing species composition. Main plot and subplot means were compared by Duncan's multiple range test.

3. Results

A. Seasonal abundance and population composition

Figs. IV-4 and IV-5 summarize seasonal, whole-lake changes in abundance and composition of the Polyphemus population for 1975 and 1976, respectively, and are presented to provide a basis for comparison with patch phenomena. In both years, the population was only present in the water column in the ice-free period. Following ice-out (early April), total population size grew through parthenogenetic reproduction to a spring maximum in late May. A period of sexual reproduction coincided with this spring maximum, followed by a decline in
Fig. IV-4. Whole-lake seasonal abundance (A) and composition (B) of the 1975 *Polyphemus* population in Stonehouse Pond. Vertical bars in 4A represent 95% confidence intervals. In 4B, dark shading (M) represents males, lines (G) - gamogenetic females, dots (P) - parthenogenetic females, and clear (J) - juveniles.
AFLUNDANCE.

COMPOSITION

TOTAL POLYPHEMUS (N=10^7)

PERCENT OF POPULATION

APR. MAY JUNE JULY AUG. SEPT. OCT. NOV.

1975
Fig. IV-5. Whole-lake seasonal abundance (A) and composition (B) of the 1976 Polyphemus population in Stonehouse Pond. Legend as in Fig. IV-4.
abundance to a summer plateau dominated once again by parthenogenetic individuals. In early August of both years, a slight secondary peak in abundance occurred, and was most noticeable in 1976. After this secondary peak, a fall period of sexual reproduction occurred, and population size declined to zero just prior to ice-on in early December. Since Polyphemus population events were closely related to the seasons, changes in composition were used to delimit seasons in 1975 and 1976. In 1975, spring referred to sampling dates between 17 April and 28 May, summer - 11 June to 14 September, and fall - 25 September to 12 December. The 1976 seasons were as follows: spring - 9 April to 9 June, summer - 15 June to 28 September, and fall - 6 October to 24 November.

B. Seasonal Horizontal Distribution

Figs. IV-6A and IV-6B summarize seasonal changes in whole-lake horizontal distribution for 1975 and 1976, respectively. The patterns were quite similar in both years, and were influenced by changes in Polyphemus abundance and population composition (Figs. IV-4A-B, IV-5A-B). In early spring, Polyphemus individuals appeared in the littoral zone extremely close to shore. As population size increased in the spring, it extended horizontally to the outer edge of the littoral (Figs. IV-6, 25 M). By early summer, the population had declined to a summer plateau following a period of sexual reproduction, and it was beginning to appear in the limnetic zone (Fig. IV-6, >30 M). Throughout the long summer period of parthenogenesis, the greatest proportion of the population
Fig. IV-6. Three-dimensional representation of the seasonal change in horizontal distribution of the total Polyphemus population of Stonehouse Pond. A. 1975. B. 1976. X axis = date of year, Y axis = distance from shore in meters (note: Limnetic zone represented by >30 meters from shore), Z axis = percent of total Polyphemus population.
was found in the limnetic zone. Small peaks and valleys in the summer period (Figs. IV-6A and IV-6B) reflected horizontal variability in the population distribution and the presence of patches. As fall approached and sexual individuals became abundant, the population returned to the extremely near-shore littoral region where it remained until the lake was completely frozen.

C. Seasonal Vertical Distribution

The Polyphemus population was rarely found below 2 meters of depth (Fig. IV-7). Similarities between littoral (Fig. IV-7A) or limnetic (Fig. IV-7B) vertical profile and whole-lake profile (Fig. IV-7C) reflected the changes in horizontal distribution observed in 1975 (Fig. IV-6A). When found in the limnetic zone (summer), the population was deeper and was more dispersed in the upper 2 meters of the water column than when it occupied the littoral zone (spring and fall) (paired t-test by date, p<0.01).

The 1976 littoral pattern of vertical distribution was similar to 1975 (Fig. IV-7D). Limnetic and whole-lake comparisons could not be made in 1976 because limnetic samples were collected by integrating the upper 3 meters in the water column to facilitate counting (except for diel studies).

D. Abiotic Factors Influencing Patch Location and Formation

A total of 64 relative density maps were prepared for the 1975-1976 sampling period to examine the details of seasonal horizontal variability in this essentially two
Fig. IV-7. Seasonal variation in median depth ($\bar{Z}$) and Z90% of the total Polyphemus population in Stonehouse Pond. The width of the shaded area = $\Delta Z$. A. 1975 littoral, B. 1975 limnetic, C. 1975 whole-lake, D. 1976 littoral. See text for additional explanation.
dimensional population distribution. From these maps, several were selected which represented characteristics of the seasonal distribution patterns. With one exception (20 August 1975), daytime patch location was limited to the littoral zone (Table IV-1). In the spring and fall, 2–3 Polyphemus patches were observed on each sampling date (Figs. IV-8A-D). In the summer, in contrast, typically one patch was found (Figs. IV-8E-G), and occasionally no patch at all was seen (Fig. IV-8H).

The relationship of patch location with selected environmental and habitat characteristics was examined to suggest possible abiotic factors influencing patch formation. No relationship was found between habitat factors such as the location of aquatic macrophyte beds, shading or direct sunlight, surface temperature irregularities (e.g. at springs, outflow, inflow) or time of day and the location of Polyphemus patches. No correlation was found between atmospheric conditions such as percent cloud cover or precipitation and the presence of patches in a particular location. A strong correlation was found between wind direction at the time of sampling and patch location as indicated in Table IV-2. This 2 X 2 contingency table also revealed that wind direction was not differentially correlated with patch location between seasons ($X^2$ for independence), which implied that patches reacted to wind-induced water currents in a similar manner regardless of season. However, in the spring and fall the presence of several patches, only one of which was correlated with wind direction (as indicated by the wind vector diagrams
Table IV-1. Classification of all Polyphemus patches observed in lake sections of Stonehouse Pond for 1975 and 1976. See text for definition of patch.
<table>
<thead>
<tr>
<th>Patch location (lake section)</th>
<th>Number of patches observed</th>
<th>1975</th>
<th>1976</th>
<th>total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Littoral Section 1</td>
<td></td>
<td>3</td>
<td>6</td>
<td>9</td>
<td>14 %</td>
</tr>
<tr>
<td>Section 2</td>
<td></td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>8 %</td>
</tr>
<tr>
<td>Section 3</td>
<td></td>
<td>16</td>
<td>5</td>
<td>21</td>
<td>33 %</td>
</tr>
<tr>
<td>Section 4</td>
<td></td>
<td>4</td>
<td>7</td>
<td>11</td>
<td>17 %</td>
</tr>
<tr>
<td>Section 5</td>
<td></td>
<td>8</td>
<td>6</td>
<td>14</td>
<td>22 %</td>
</tr>
<tr>
<td>Section 6</td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>5 %</td>
</tr>
<tr>
<td>Littoral total</td>
<td></td>
<td>35</td>
<td>28</td>
<td>63</td>
<td>99 %</td>
</tr>
<tr>
<td>Limnetic Section 7</td>
<td></td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1 %</td>
</tr>
<tr>
<td>Grand totals</td>
<td></td>
<td>36</td>
<td>28</td>
<td>64</td>
<td></td>
</tr>
</tbody>
</table>
Fig. IV-8. Seasonal variation of *Polyphemus* patch location in Stonehouse Pond for selected dates in 1975 and 1976. Wind vector diagrams represent wind speed (kilometers·hour$^{-1}$) and direction (from true north) taken at 3 hour intervals from 0100 to 2200 of the sampling date. Vectors applicable to the sampling period fall between S (start) and F (finish). See text for additional information.
Table IV-2. 2 \times 2 Chi-square contingency table demonstrating the positive correlation between wind direction at the time of sampling and the location of Polyphemus patches, and the independence of this correlation with season. A positive correlation was assigned when a patch was found in the downwind section of the lake. No correlation was assigned if 1. a patch was not found in the downwind lake section but in another section, 2. a patch was found when wind direction was variable, or 3. a patch was found when it was calm. 9/64 sampling dates could not be classified because no patch was observed and wind direction was variable or calm.
<table>
<thead>
<tr>
<th>Correlation</th>
<th>Spring-Fall</th>
<th>Summer</th>
<th>n</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Positive (+)</td>
<td>21</td>
<td>19</td>
<td>40</td>
<td>73 %</td>
</tr>
<tr>
<td>None (0 or -)</td>
<td>10</td>
<td>5</td>
<td>15</td>
<td>27 %</td>
</tr>
<tr>
<td>n</td>
<td>31</td>
<td>24</td>
<td>55</td>
<td></td>
</tr>
<tr>
<td>Percent (+)</td>
<td>68 %</td>
<td>79 %</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

χ² for independence = 0.833, 0.25 < p < 0.50
χ² for wind correlation = 10.473, p < 0.005
in the upper left corner of each map in Figs. IV-8A-D), suggested other factors may be more important than wind in regulating patch formation and location at these times. Examples of dates where wind direction was positively correlated with patch location include Figs. IV-8E-F. Examples of dates where no correlation was found between patch location and wind direction include Figs. IV-8G-H.

A significantly greater number of patches were observed in littoral section 3 ($X^2 = 14.11, p < 0.005$) than would be expected for the average littoral section (Table IV-1). This observation provided additional support to the importance of wind direction as an abiotic factor regulating patch location in Stonehouse Pond, since section 3 was downwind of the prevailing wind direction for this geographic area (as supported by the data of this study and of the U.S. National Weather Service). The next greatest number of patches was observed in littoral section 5 (Table IV-1), but this number was not significantly different from average.

E. Seasonal Changes in Aggregation Indices

Tables IV-3 and IV-4 summarize statistical attributes of the seasonal change in *Polyphemus* population dispersion for 1975 and 1976, respectively. For all dates in both years, the population was statistically overdispersed, regardless of the index used. However, when regressed against mean density ($\bar{X}$), the variance to mean ratio ($V/\bar{X}$) and Lloyd's mean crowding index ($\bar{M}$) had highly significant linear relationships (correlation coefficients in Tables IV-3 and IV-4) which
Table IV-3. 1975 seasonal variation in selected aggregation indices for the Stonehouse Pond Polyphemus population. $\bar{X}/M^2$ - average Polyphemus density per cubic meter of lakewater, $\bar{V}/\bar{X}$ - variance over mean ratio (Fisher's coefficient of dispersion), $\bar{M}$ - Lloyd's mean crowding index, $2\text{SE} \bar{M} = \pm 95\%$ confidence interval width for mean crowding, $\bar{M}/\bar{X}$ - Lloyd's patchiness index for littoral and limnetic regions and for the whole lake, $2\text{SE} \bar{M}/\bar{X} = \pm 95\%$ confidence interval width for whole-lake estimates of patchiness. See text for additional information.
<table>
<thead>
<tr>
<th>DATE</th>
<th>X/(X^2)</th>
<th>(\bar{V}/X)</th>
<th>(\bar{X}^2)</th>
<th>(2*SE\ \bar{X}^2)</th>
<th>LITTORAL</th>
<th>LIMNETIC</th>
<th>WHOLE LAKE</th>
<th>2*SE (\bar{X}/X)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5-V-75</td>
<td>153</td>
<td>934</td>
<td>1254</td>
<td>1678</td>
<td>6.20</td>
<td>-</td>
<td>8.20</td>
<td>3.49</td>
</tr>
<tr>
<td>20-V-75</td>
<td>21710</td>
<td>26809</td>
<td>44913</td>
<td>19818</td>
<td>2.56</td>
<td>-</td>
<td>2.56</td>
<td>0.83</td>
</tr>
<tr>
<td>28-V-75</td>
<td>12972</td>
<td>15285</td>
<td>27990</td>
<td>10022</td>
<td>2.26</td>
<td>-</td>
<td>2.24</td>
<td>0.58</td>
</tr>
<tr>
<td>11-VI-75</td>
<td>1859</td>
<td>2923</td>
<td>4836</td>
<td>1967</td>
<td>2.39</td>
<td>1.15</td>
<td>2.60</td>
<td>0.78</td>
</tr>
<tr>
<td>19-VI-75</td>
<td>1310</td>
<td>4329</td>
<td>5822</td>
<td>3780</td>
<td>3.50</td>
<td>2.63</td>
<td>4.44</td>
<td>2.23</td>
</tr>
<tr>
<td>26-VI-75</td>
<td>1213</td>
<td>8222</td>
<td>10148</td>
<td>9883</td>
<td>6.72</td>
<td>3.63</td>
<td>8.36</td>
<td>6.27</td>
</tr>
<tr>
<td>3-VII-75</td>
<td>908</td>
<td>5772</td>
<td>10773</td>
<td>12113</td>
<td>10.55</td>
<td>12.86</td>
<td>11.63</td>
<td>10.51</td>
</tr>
<tr>
<td>10-VII-75</td>
<td>372</td>
<td>1767</td>
<td>2265</td>
<td>1944</td>
<td>4.77</td>
<td>2.65</td>
<td>6.09</td>
<td>4.08</td>
</tr>
<tr>
<td>15-VII-75</td>
<td>747</td>
<td>3289</td>
<td>4216</td>
<td>3166</td>
<td>4.94</td>
<td>7.63</td>
<td>5.64</td>
<td>3.31</td>
</tr>
<tr>
<td>22-VII-75</td>
<td>313</td>
<td>1098</td>
<td>1458</td>
<td>967</td>
<td>3.93</td>
<td>4.37</td>
<td>4.66</td>
<td>2.39</td>
</tr>
<tr>
<td>29-VII-75</td>
<td>240</td>
<td>1124</td>
<td>1489</td>
<td>1109</td>
<td>4.85</td>
<td>1.85</td>
<td>5.95</td>
<td>3.61</td>
</tr>
<tr>
<td>5-VIII-75</td>
<td>280</td>
<td>519</td>
<td>810</td>
<td>372</td>
<td>2.54</td>
<td>1.54</td>
<td>2.89</td>
<td>0.99</td>
</tr>
<tr>
<td>12-VIII-75</td>
<td>883</td>
<td>7675</td>
<td>9413</td>
<td>10195</td>
<td>8.84</td>
<td>2.43</td>
<td>10.66</td>
<td>9.09</td>
</tr>
<tr>
<td>19-VIII-75</td>
<td>2523</td>
<td>36875</td>
<td>47563</td>
<td>71495</td>
<td>13.70</td>
<td>3.74</td>
<td>18.85</td>
<td>22.10</td>
</tr>
<tr>
<td>25-VIII-75</td>
<td>1195</td>
<td>12840</td>
<td>15252</td>
<td>17850</td>
<td>10.00</td>
<td>2.50</td>
<td>12.76</td>
<td>11.76</td>
</tr>
<tr>
<td>2-IX-75</td>
<td>791</td>
<td>3657</td>
<td>4664</td>
<td>3640</td>
<td>4.67</td>
<td>7.05</td>
<td>5.00</td>
<td>3.60</td>
</tr>
<tr>
<td>14-IX-75</td>
<td>2109</td>
<td>33511</td>
<td>42275</td>
<td>60589</td>
<td>15.54</td>
<td>9.80</td>
<td>20.05</td>
<td>22.50</td>
</tr>
<tr>
<td>25-IX-75</td>
<td>2660</td>
<td>8108</td>
<td>10864</td>
<td>7845</td>
<td>3.20</td>
<td>2.85</td>
<td>4.47</td>
<td>2.96</td>
</tr>
<tr>
<td>9-X-75</td>
<td>2152</td>
<td>8296</td>
<td>10846</td>
<td>7574</td>
<td>3.90</td>
<td>3.70</td>
<td>5.04</td>
<td>2.74</td>
</tr>
<tr>
<td>16-X-75</td>
<td>958</td>
<td>5236</td>
<td>6565</td>
<td>5636</td>
<td>5.25</td>
<td>6.66</td>
<td>6.85</td>
<td>4.61</td>
</tr>
<tr>
<td>23-X-75</td>
<td>302</td>
<td>840</td>
<td>1171</td>
<td>681</td>
<td>3.00</td>
<td>6.44</td>
<td>3.87</td>
<td>1.73</td>
</tr>
<tr>
<td>30-X-75</td>
<td>77</td>
<td>635</td>
<td>796</td>
<td>946</td>
<td>9.39</td>
<td>2.70</td>
<td>10.40</td>
<td>9.68</td>
</tr>
<tr>
<td>6-XI-75</td>
<td>22</td>
<td>125</td>
<td>157</td>
<td>156</td>
<td>6.60</td>
<td>-</td>
<td>7.28</td>
<td>5.55</td>
</tr>
<tr>
<td>13-XI-75</td>
<td>17</td>
<td>161</td>
<td>178</td>
<td>220</td>
<td>9.27</td>
<td>-</td>
<td>10.40</td>
<td>10.06</td>
</tr>
<tr>
<td>20-XI-75</td>
<td>1</td>
<td>11</td>
<td>14</td>
<td>24</td>
<td>16.68</td>
<td>-</td>
<td>18.78</td>
<td>25.35</td>
</tr>
</tbody>
</table>

corr. coef. \(r\) = + 0.93, + 0.94, + 0.44

* Significantly greater than 1.00 (Random) with 95% Confidence.

# Not significantly greater than 1.00, but other evidence suggests the population was extremely aggregated.

# Correlation coefficient for linear regression of index against \(X/\bar{X}^2\).
Table IV-4. 1976 seasonal variation in selected aggregation indices for the Stonehouse Pond Polyphemus population. See legend of Table IV-3 for explanation of symbols and text for additional information.
<table>
<thead>
<tr>
<th>DATE</th>
<th>X/A²</th>
<th>V/X</th>
<th>MEAN CROWDING</th>
<th>LLOYD'S PATCHINESS INDEX (W/X)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>LITTORAL</td>
<td>WHOLE LAKE</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>LIMNETIC</td>
<td></td>
</tr>
<tr>
<td>15-IV-76</td>
<td>35</td>
<td>176</td>
<td>1922</td>
<td>12.67 # -</td>
</tr>
<tr>
<td>29-IV-76</td>
<td>257</td>
<td>579</td>
<td>39472</td>
<td>11.38 # -</td>
</tr>
<tr>
<td>7-V-76</td>
<td>7355</td>
<td>512</td>
<td>63259</td>
<td>2.92 * 5.35</td>
</tr>
<tr>
<td>13-V-76</td>
<td>11233</td>
<td>5800</td>
<td>59423</td>
<td>5.62 * 8.32</td>
</tr>
<tr>
<td>19-V-76</td>
<td>12876</td>
<td>1226</td>
<td>35599</td>
<td>4.00 * 1.14</td>
</tr>
<tr>
<td>27-V-76</td>
<td>9491</td>
<td>4896</td>
<td>61697</td>
<td>6.01 * 1.75</td>
</tr>
<tr>
<td>2-VI-76</td>
<td>5381</td>
<td>1886</td>
<td>16837</td>
<td>4.34 * 1.03</td>
</tr>
<tr>
<td>9-VI-76</td>
<td>3824</td>
<td>9958</td>
<td>8009</td>
<td>3.43 * 1.02</td>
</tr>
<tr>
<td>15-VI-76</td>
<td>2206</td>
<td>7612</td>
<td>9637</td>
<td>4.00 * 2.00</td>
</tr>
<tr>
<td>24-VI-76</td>
<td>1812</td>
<td>4604</td>
<td>188595</td>
<td>37.67 # 1.73</td>
</tr>
<tr>
<td>2-VII-76</td>
<td>129</td>
<td>628</td>
<td>918</td>
<td>6.04 * 1.43</td>
</tr>
<tr>
<td>14-VII-76</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>26-VII-76</td>
<td>280</td>
<td>1827</td>
<td>2206</td>
<td>7.09 * 7.85</td>
</tr>
<tr>
<td>3-VIII-76</td>
<td>511</td>
<td>2722</td>
<td>4160</td>
<td>6.30 * 2.55</td>
</tr>
<tr>
<td>12-VIII-76</td>
<td>1496</td>
<td>4268</td>
<td>3688</td>
<td>3.67 * 3.23</td>
</tr>
<tr>
<td>23-VIII-76</td>
<td>246</td>
<td>177</td>
<td>154</td>
<td>1.69 * 1.05</td>
</tr>
<tr>
<td>1-IX-76</td>
<td>335</td>
<td>8080</td>
<td>35772</td>
<td>40.48 # 2.81</td>
</tr>
<tr>
<td>10-IX-76</td>
<td>1141</td>
<td>6240</td>
<td>9671</td>
<td>6.12 * 2.64</td>
</tr>
<tr>
<td>16-IX-76</td>
<td>779</td>
<td>7949</td>
<td>17100</td>
<td>11.75 # 1.98</td>
</tr>
<tr>
<td>28-IX-76</td>
<td>1166</td>
<td>12063</td>
<td>26171</td>
<td>11.90 # 9.60</td>
</tr>
<tr>
<td>6-X-76</td>
<td>1001</td>
<td>5937</td>
<td>5323</td>
<td>4.51 * 2.28</td>
</tr>
<tr>
<td>15-X-76</td>
<td>979</td>
<td>9881</td>
<td>2192</td>
<td>11.57 # 2.10</td>
</tr>
<tr>
<td>25-X-76</td>
<td>299</td>
<td>1762</td>
<td>2826</td>
<td>6.57 -</td>
</tr>
<tr>
<td>5-XI-76</td>
<td>23</td>
<td>127</td>
<td>196</td>
<td>6.13 -</td>
</tr>
<tr>
<td>15-XI-76</td>
<td>3</td>
<td>39</td>
<td>101</td>
<td>16.85 # -</td>
</tr>
</tbody>
</table>

corr. coef.² r = + 0.91 + 0.32 + 0.70

* Significantly greater than 1.00 (Random) with 95% Confidence.
# Not significantly greater than 1.00, but other evidence suggests the population was extremely aggregated.
$ Incomplete data. Some of the samples on this date were lost.
∂ Correlation coefficient for linear regression of index against X/A².
indicated these indices were not independent of population size and, therefore, would not be useful in seasonal comparisons.

Lloyd's patchiness index \( \frac{M}{X} \) was independent of population density (Tables IV-3 and IV-4) and, in general, reflected the seasonal changes in distribution presented graphically in Figs. IV6-8. Although independent of density, this index was often not estimated with enough precision to allow date by date statistical comparisons of the degree of patchiness in the Polyphemus population. This was unfortunate, since on dates when mapping suggested the population was extremely aggregated, patchiness was also high but 95% confidence limits about this index were often so wide it was not significantly different from random expectation. With the exception of spring 1975, early spring and late fall patchiness averaged higher than in summer. However, when large patches were present, summer patchiness equalled or even exceeded spring-fall values (e.g. 12-25 Aug. 1975, 1 Sept. 76, Tables IV-3 and IV-4). Patchiness was also generally lower in the limnetic than in the littoral zone.

F. Diel Patterns

Diel patterns of horizontal and vertical distribution appeared to result from the interaction of diel changes in visually-mediated swimming behaviour of Polyphemus with wind-induced water currents. Diel changes in whole-lake horizontal distribution are best examined in conjunction with relative density maps to illustrate this interaction (Figs. IV-9-12).
Fig. IV-9. Diel change in horizontal distribution of the Polyphemus population in Stonehouse Pond for Diel 1, 11-12 June 1975. A. Three-dimensional representation, X, Y, and Z axes as in Fig. IV-6. B-D. Spatial maps of patch location for day 1 (B), night (C), and day 2 (D), legend as in Fig. IV-8.
Fig. IV-10. As Fig. IV-9 for diel 2, 19-20 August, 1975.
Fig. IV-11. As Fig. IV-9 for die1 3, 26-27 July, 1976.
Fig. IV-12. As Fig. IV-9 for diel 4, 12-13 August, 1976.
Although differences existed, the main consistencies in all four diel studies were the dissipation of patches and the dispersal of littoral Polyphemus into the limnetic zone at night. In each diel, the limnetic subpopulation was significantly larger at night than it was on day 1 (t-test, p<0.05). Correspondingly, the littoral subpopulation was significantly smaller at night than on day 1. Limnetic subpopulations were also significantly larger at night than on day 2, but only when the population moved back into the littoral zone (diel 1 Fig. IV-9, diel 4 Fig. IV-12). The absence of wind at night probably facilitated patch dissipation and the population shift into the limnetic zone, and suggested this shift was related to a diel change in swimming behaviour. The daytime patch location was downwind in all diels except diel 2 day 2 (Fig. IV-10D) and diel 4 day 1 (Fig. IV-12B). The daytime establishment of patches in the littoral following the nightly dispersal into the limnetic was closely related to the constancy of wind direction and the magnitude of its speed. With strong winds from a constant direction, a patch formed on the downwind side of the lake (diel 1 day 2 Fig. IV-9D, diel 4 day 2 Fig. IV-12B). If wind was light and its direction was variable, a patch was not formed (diel 3 day 2 Fig. IV-11D). Diel 2 was unusual in that a large portion of the population was found in one huge patch which maintained its integrity when it moved into the limnetic zone at night and remained there on day 2 despite strong NW winds (Fig. IV-10).
Horizontal dispersal of the *Polyphemus* population at night was paralleled by dispersal in the vertical plane.

Diel variation in whole-lake, limnetic, and littoral vertical distribution were summarized in the kite diagrams of Figs. IV-13A-D. The daytime vertical distribution patterns for littoral and limnetic regions and for the whole lake reflected the summer pattern described in Fig. IV-7. At night, however, the population was considerably more dispersed in the vertical plane than it was in corresponding locations in the day (Figs. IV-13A-D). $\bar{Z}$ and $Z_{90\%}$ were significantly deeper at night than on either day, and $\Delta Z$ was significantly greater at night (paired t-test, $p < 0.001$), thus statistically supporting the observation that the population was vertically more dispersed at night.

G. Diel Variation in Aggregation Indices

Table IV-5 summarizes aggregation indices calculated for each diel study. In general, aggregation indices reflected changes in spatial distribution which were graphically presented in Figs. IV-9-13. At night, when the population was spatially dispersed in horizontal and vertical planes, $V/X$, $\hat{M}$, and $\hat{M}/\bar{X}$ each averaged significantly lower than for day 1 or day 2 (ANOVA and Duncan's test, $p < 0.05$). The only exception was on diel 1 night, where patchiness was greater than on either day, but this difference was not significant ($p > 0.05$). Confidence limit comparison of patchiness against random expectation demonstrated that regardless of time of day, the *Polyphemus* population was significantly aggregated. Confidence
Fig. IV-13. Diel variation in vertical distribution of the total Polyphemus population of Stonehouse Pond. A. diel 1, B. diel 2, C. diel 3, D. diel 4. Solid line – Z, Broken line – 290%.
Table IV-5: Diel variation in selected aggregation indices for the Stonehouse Pond Polyphemus population. See legend of Table IV-3 for explanation of symbols and text for additional information.
<table>
<thead>
<tr>
<th>Sampling period</th>
<th>V/X</th>
<th>Mean Crowding</th>
<th>Patchiness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>95% CL</td>
</tr>
<tr>
<td><strong>Diel 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11-12 June 1975</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 1</td>
<td>2923</td>
<td>4836</td>
<td>1967</td>
</tr>
<tr>
<td>Night</td>
<td>2242</td>
<td>3200</td>
<td>2474</td>
</tr>
<tr>
<td>Day 2</td>
<td>7591</td>
<td>11942</td>
<td>6808</td>
</tr>
<tr>
<td><strong>Diel 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19-20 Aug. 1975</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 1</td>
<td>36875</td>
<td>47563</td>
<td>71495</td>
</tr>
<tr>
<td>Night</td>
<td>178</td>
<td>290</td>
<td>137</td>
</tr>
<tr>
<td>Day 2</td>
<td>2048</td>
<td>2592</td>
<td>3574</td>
</tr>
<tr>
<td><strong>Diel 3</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>26-27 July 1976</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 1</td>
<td>1827</td>
<td>2272</td>
<td>2208</td>
</tr>
<tr>
<td>Night</td>
<td>114</td>
<td>216</td>
<td>78</td>
</tr>
<tr>
<td>Day 2</td>
<td>332</td>
<td>460</td>
<td>287</td>
</tr>
<tr>
<td><strong>Diel 4</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12-13 Aug. 1976</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Day 1</td>
<td>4268</td>
<td>5932</td>
<td>3688</td>
</tr>
<tr>
<td>Night</td>
<td>181</td>
<td>505</td>
<td>116</td>
</tr>
<tr>
<td>Day 2</td>
<td>28544</td>
<td>36378</td>
<td>53133</td>
</tr>
</tbody>
</table>
limits about aggregation indices were unusually wide for
diel 2 day 1 and day 2, and for diel 4 day 2 (Table IV-5),
because a large percent of the population was found in one
patch. For diel studies 2 and 3, $\sqrt{\bar{X}}$, $\bar{M}$, and $\bar{M}/\bar{X}$ were lower
on day 2 than day 1 (Table IV-5), demonstrating that
statistical dispersion was lower when a significant percent
of the population remained in the limnetic zone.

H. Detailed Description of the Polyphemus Patch

1. Dimensions and internal structure

Sampling and in situ observations provided
information on the dimensions, composition, and internal
structure of Polyphemus patches. When a patch was situated
in littoral section 3 or 5, its approximate shape and size
could be defined by a grid of samples (Fig. IV-3) with reso-
lution of 5-10 meters parallel to shore, 20-25 meters perpen-
dicular to shore, and 0.5 meters vertically. Using this
sampling grid, 35 patches were examined in the two year
sampling period.

Spring and fall patches were defined as narrow bands,
less than 5 meters wide, with their long axes parallel to
shore. Their exact length was difficult to determine because
they were found less than 7 meters from shore at the inner
dge of the sampling grid. In situ observations, however,
revealed these nearshore bands of Polyphemus were actually
small, dense swarms, oval to circular in shape, within 10 cm
of the water surface. They varied in diameter from 0.5 to 5
meters. As many as eight of these swarms were observed in
section 3 at one time. Sampling with 20 meter long tows was obviously too coarse to distinguish these swarms, which, consequently, appeared as a continuous band. Micro-sampling within these swarms revealed internal densities as high as 492 Polyphemus·liter⁻¹ (4 liter sample - 29 April 1976). The corresponding 200 liter sample (20 meter long tow) estimated Polyphemus density as 35 individuals·liter⁻¹, indicating several relatively large interswarm gaps were sampled with this tow in addition to one or more swarms.

In the summer, Polyphemus patches were defined by the sampling grid as most often oval or rectangular in shape, and were centered at 15 meters from shore, with their long axes parallel to shore. Their dimensions varied between 20-50+ meters long and 10-15 meters maximum width. Summer patches, like the spring and fall swarms, were found within 10-20 cm of the surface. In situ observations and photography suggested these summer patches were, by definition, shoals of Polyphemus. Internal density of these shoals varied from 8 - 58 Polyphemus·liter⁻¹ with an average density of 15 individuals·liter⁻¹. Shoal densities were 3 - 12 times higher than whole-lake average densities.

Because of their relatively large size and high internal density, summer shoals often contained a significant proportion of the total Polyphemus population. For example, in the weekly series 12 August - 14 September 1975 (12 Aug. - 2 Sept. mapped in Figs. IV-8E-G; IV-10B; IV-10D), the total number and percent of the total Polyphemus population contained in the one observed shoal on each date were as
follows: 12 Aug. - $2.755 \times 10^6$ individuals, 11%; 19 Aug. - $1.301 \times 10^7$, 90%; 20 Aug. - $1.416 \times 10^7$, 98%; 25 Aug. - $7.823 \times 10^6$, 45%; 2 Sept. - $1.472 \times 10^6$, 11%; and 14 Sept. - $5.77 \times 10^6$, 39%.

The weekly series 12 Aug. - 14 Sept. 1975 also provided some interesting observations on shoal integrity and structure. Integrity was obviously maintained in the one shoal observed throughout the diel 2 period (19-20 Aug.) since it contained virtually all of the Polyphemus population. The high percent of the population found in the one shoal on 25 Aug. suggested this shoal may have maintained its integrity for as long as a week. However, since patches usually dissipated at night (Figs. IV-9-12), maintenance of patch integrity for longer than one day appeared unlikely for Polyphemus.

In situ observations on the diel 2 shoal and other shoals revealed limnetic shoals were more diffuse than their littoral counterparts. When found in the littoral zone, the diel 2 shoal (Fig. IV-10B, day 1) had a configuration typical of summer shoals, with a mean internal density of $50660 \pm 1711$ Polyphemus $M^{-3}$. In the limnetic zone (Fig. IV-10D, day 2), this shoal was found at the surface (0 - 25 cm) as it was in the littoral location, but was widespread horizontally and had an internal density of only $3251 \pm 1432$ indiv. $M^{-3}$.

In situ close-up photography in 1977 confirmed visual observations of Polyphemus orientation within swarms and shoals, and suggested that internal density may occasionally be much higher than was estimated by sampling. Table IV-6
Table IV-6. Minimum and mean interanimal distance and internal density of shoals and swarms of Polyphemus determined photographically, in situ in Stonehouse Pond. See text for additional information.
<table>
<thead>
<tr>
<th>Date</th>
<th>n</th>
<th>Minimum</th>
<th>Mean</th>
<th>Polyphemus Density (cm(^3))</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-May-77</td>
<td>33</td>
<td>0.2</td>
<td>0.5</td>
<td>6.9</td>
</tr>
<tr>
<td>Swarm</td>
<td>18</td>
<td>0.5</td>
<td>0.6</td>
<td>5.3</td>
</tr>
<tr>
<td>13-May-77</td>
<td>8</td>
<td>0.3</td>
<td>0.5</td>
<td>9.7</td>
</tr>
<tr>
<td>Swarm</td>
<td>4</td>
<td>0.4</td>
<td>0.5</td>
<td>10.7</td>
</tr>
<tr>
<td>13-May-77</td>
<td>6</td>
<td>0.5</td>
<td>0.7</td>
<td>2.6</td>
</tr>
<tr>
<td>13-May-77</td>
<td>8</td>
<td>0.4</td>
<td>0.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Swarm</td>
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<td>0.4</td>
<td>0.4</td>
<td>15.3</td>
</tr>
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<td>13-May-77</td>
<td>10</td>
<td>0.4</td>
<td>0.4</td>
<td>11.6</td>
</tr>
<tr>
<td>25-May-77</td>
<td>19</td>
<td>0.4</td>
<td>0.7</td>
<td>3.0</td>
</tr>
<tr>
<td>Swarm</td>
<td>3</td>
<td>0.7</td>
<td>1.2</td>
<td>0.6</td>
</tr>
<tr>
<td>25-May-77</td>
<td>20</td>
<td>0.4</td>
<td>0.7</td>
<td>2.9</td>
</tr>
<tr>
<td>7-July-77</td>
<td>7</td>
<td>0.5</td>
<td>0.8</td>
<td>2.1</td>
</tr>
<tr>
<td>Shoal</td>
<td>11</td>
<td>0.6</td>
<td>1.2</td>
<td>0.6</td>
</tr>
<tr>
<td>7-July-77</td>
<td>18</td>
<td>0.6</td>
<td>0.7</td>
<td>3.0</td>
</tr>
<tr>
<td>8-Aug.-77</td>
<td>3</td>
<td>1.5</td>
<td>2.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Shoal</td>
<td>7</td>
<td>0.8</td>
<td>1.2</td>
<td>0.5</td>
</tr>
<tr>
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<td>1.1</td>
<td>1.6</td>
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<td>8-Aug.-77</td>
<td>47</td>
<td>0.3</td>
<td>0.4</td>
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<tr>
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<td>0.6</td>
<td>0.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Shoal</td>
<td>6</td>
<td>0.5</td>
<td>1.5</td>
<td>0.3</td>
</tr>
<tr>
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<td>10</td>
<td>0.7</td>
<td>1.5</td>
<td>0.3</td>
</tr>
<tr>
<td>1-Nov.-77</td>
<td>15</td>
<td>0.4</td>
<td>0.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Swarm</td>
<td>27</td>
<td>0.3</td>
<td>0.5</td>
<td>8.2</td>
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<td>3</td>
<td>0.5</td>
<td>0.6</td>
<td>3.7</td>
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</table>
summarizes estimates of internal density and inter-animal spacing based on photographs taken within the densest part of selected shoals and swarms. These photographs "sampled" a volume of 16.8 cm$^3$ at 2:1 magnification (1 cm. depth of field) and 25.2 cm$^3$ at 3:1. Unfortunately, net tows were not taken at the same time as the photographs to permit direct comparison of density estimates by both methods. Minimum inter-animal distance (Table IV-6) represents the average shortest linear distance between two adjacent individuals in a photograph, and indicated that Polyphemus in swarms "tolerated" closer distances to nearest neighbors than in shoals. Mean inter-animal distance (Table IV-6) represents the average distance between a randomly located individual and its six nearest neighbors (Clutter, 1969), and was also shortest in swarms. The cube of mean inter-animal distance was taken as the volume of water per individual, and the reciprocal of this volume was used as an estimate of internal density. Swarm and shoal densities estimated in this manner were often more than an order of magnitude higher than densities estimated by stratified sampling. In situ observations and photography, therefore, suggested that net tows were too large to accurately describe swarm dimensions, and that they may have underestimated maximum densities in swarms and shoals by more than an order of magnitude.

2. Swarm and shoal composition

To accurately fit the definition of swarm or shoal, the aggregate in its unit of habitat must be composed
primarily of individuals of the same species. Seven Polyphemus patches were selected for detailed composition analysis. These patches were chosen from each season in the study period and had the highest relative densities, as defined by spatial mapping. Figure IV-14 revealed the percent composition and density of Polyphemus and other zooplankton in 200 liter tows taken within patches or adjacent to them. As can be seen from this figure, samples within a patch were almost exclusively composed of Polyphemus individuals. In nearby areas, Polyphemus had a significantly lower percent composition and density (Fig. IV-14 and ANOVA on log-transformed densities with block effects removed, Duncan's multiple range test p < 0.05). There were also significantly more nauplii and calanoid copepodites in non-patch areas than within patches (ANOVA as above).

In these same seven patches and adjacent areas, the composition of the types of individuals within the Polyphemus population was also examined (Fig. IV-15). In general, patch composition reflected the seasonal population dynamics of Polyphemus (Figs. IV-4 and IV-5). Patch and no patch areas in late spring (20-V-75) and fall (9-X-75, 15-X-76) were composed of both parthenogenetic and sexual Polyphemus, while in early spring (7-V-76) and summer (19-VII-75, 14-IX-75, 24-VI-76) they were almost exclusively parthenogenetic (Fig. IV-15). Significant differences in percent composition between patch and no patch areas were not observed (Fig. IV-15 and ANOVA as for Fig. IV-14). However, the averaging effect of 200 liter samples on the relatively small spring and fall
Fig. IV-14. Zooplankton composition (% counted) inside selected *Polyphemus* patches and in adjacent non-patch areas of Stonehouse Pond. B - *Bosmina* sp., Ch - *Chonochilus* unicornis colonies (1 colony averaged 51 individuals), N - copepod nauplii, Ca - calanoid copepodites, O - other zooplankton species, primarily *Holopedium gibberum* and *Daphnia* sp., P - *Polyphemus pediculus*. The numbers written above the blocks for each species represent their density (indiv. liter⁻¹).
Fig. IV-15. *Polyphemus* composition (% counted) inside selected *Polyphemus* patches and in two adjacent non-patch areas of Stonehouse Pond. Y - early instar *Polyphemus*, P - parthenogenetic females, G - gamogenetic females, M - males.
swarms may have masked real, but small-scale (in centimeters) differences in composition. For example, micro-samples from an early spring swarm reported earlier to have a density of 492 Polyphemus·liter⁻¹ (29 April 1976) also revealed this swarm was composed exclusively of parthenogenetic females with huge broods of mature embryos (e.g. 24 embryos·female⁻¹). 200 liter samples may also have obscured small-scale differences in Polyphemus composition within shoals. For example, four micro-samples taken within a shoal on 17 August 1976 revealed 99.8% of the individuals were early instar Polyphemus.

Seasonal changes in age-depth stratification in the Polyphemus population were examined using the ratio of juveniles to mature individuals in selected surface tows and the corresponding tows from 0.5 meters of depth. In the spring and fall, age-depth stratification was not observed because of the limited vertical distribution in the population (Fig. IV-7). In the summer, proportionally more young were found at the surface and more parthenogenetic females were found at 0.5 meters of depth (paired t-test, p<0.01). A significantly greater proportion of parthenogenetic females was also observed below shoals of Polyphemus than within shoals. Age-depth stratification disappeared at night when the population dispersed.

Averaging by 200 liter samples may have obscured small-scale differences between composition of shoals and swarms and adjacent areas, particularly in the spring and fall. However, examination of the dimensions, orientation, and composition of Polyphemus aggregates using a combination of sampling,
photography, and in situ observation unequivocally support the use of the term swarm to describe spring and fall aggregates of Polyphemus and shoal to describe summer groups.

I. Function of Shoaling and Swarming
One of the primary purposes of in situ observation was to attempt to assess the possible function of swarms and shoals of Polyphemus. Approximately 12 hours were spent observing in situ swarms of Polyphemus in the spring and fall, and 18 hours were spent observing shoals. Since the late spring and fall population was often composed of equal sex ratios of sexually reproductive individuals (Fig. IV-15), it was reasonable to assume that swarms might represent mating aggregations. Of the countless number of individuals observed at these times, only five mating pairs were seen, four pairs on 26 May 1977 and one on 1 November 1977. Sexual identity was determined by capturing these mating pairs in an eyedropper and examining them under a microscope in the laboratory. When observed in situ, these pairs were in similar positions as were mating individuals observed in the laboratory, with the smaller male posterior and slightly ventral to the gamogenetic female and clasping her caudal pedicle with his thoracic appendages. Laboratory observations were also made of live plankton samples captured from Polyphemus swarms in 4 liter glass jars and transferred in toto to a windowsill location. Little mating was observed in these jars in the mid-day period. At sunset, however, as many as 7 - 12 mated pairs were observed simultaneously in the same jar, with
coupling lasting from 15 to 20 minutes. These crude laboratory observations suggest that mating occurred at twilight and/or in evening periods when it could not effectively be observed. Clutter (1969) observed a similar temporal pattern of mating in marine mysid shrimp. Spring and fall swarms may, therefore, function as mating aggregations. Mating was not a factor contributing to summer shoaling, since the population was exclusively parthenogenetic at that time.

Laboratory and field feeding experiments suggest Polyphemus feed exclusively in the daylight period (Mattson and Haney, Unpub.). Several in situ observations were made of Polyphemus individuals feeding in shoals and swarms, however, these observations were biased towards large prey such as colonies of the rotifer Chonochilus unicornis. In one hour, typically 2 - 3 Polyphemus individuals were observed feeding on Chonochilus colonies. Direct observation of Polyphemus predation on small prey species such as Bosmina sp. and copepod nauplii was not possible by the methods of this study. Polyphemus captured in eyedroppers after altering their swimming to what appeared to be an attack behaviour, occasionally were found upon microscopic examination to be grasping prey. For example, five Polyphemus captured from a swarm on 2 June 1976 each carried a partially eaten Bosmina. Mass feedings were never observed. However, the limitations of direct in situ observations did not permit conclusions to be made about the function of shoals or swarms as feeding aggregations.
4. Discussion

The results of this study described clearly seasonal and diel patterns of patchiness in a population of *Polyphemus pediculus*. Several questions arise concerning the underlying processes operating to produce these patterns, such as the mechanism of patch formation, the function of swarms and shoals, and the possible adaptive significance of the observed patterns. However, before these questions can be addressed, an attempt should be made to evaluate effects of the "sampling filter" (Haury et al., Manuscript) on the described patterns.

A. Evaluation of Methods

The effectiveness of each sampling technique employed in this study depended largely on the temporal and spatial scale examined. The stratified design with its relatively large samples (200 liter) and coded locations described whole-lake seasonal and diel changes in abundance and composition with a high degree of precision. This precision was gained in part by the design, but also because these samples obscured patterns at smaller spatial and temporal scales. Imprecise estimates of aggregation indices demonstrated the problems of applying samples relevant to relatively large-scales to a small-scale phenomenon.

It was evident in this study that, in the spring and fall, several swarms and gaps were sampled with each 200 liter sample (20 meter long tow). Averaging, therefore, occurred and aggregation was most probably underestimated. In the summer, when shoal dimensions were similar to sample unit
size, averaging was probably less important. Even when averaging occurred, the degree of patchiness in the Polyphemus population was often several times greater than literature values reported for other freshwater zooplankton (e.g. Dumont, 1967; George, 1974). Indeed the Polyphemus population probably represents an extreme case of aggregation in freshwater zooplankton.

Wide confidence limits about Lloyd's mean crowding and patchiness indices probably resulted from this extreme aggregation. Since several methods of estimating negative binomial parameters failed to improve the precision of Lloyd's indices, it was likely that another compound frequency distribution may have better described the Polyphemus population. As noted by Anscombe (1950), it is quite unlikely in populations with mobile fauna which aggregate for reproduction, defense, or other social functions that any of the common compound frequency distributions will describe such populations adequately. Attempts to develop statistical frequency distributions more applicable to plankton have met with some success (Cassie, 1962; Sandusky and Horne, 1978), and this is an area for additional research which should be approached using the smallest volume samples appropriate for the size and characteristics of the species.

An implicit assumption when samples from the stratified design were used for spatial mapping was that population distribution did not change in the sampling period (6 hours). Evidence has already been presented which suggested this was not a serious problem, based on a comparison of within date
and between date variation in abundance estimates (Section II). Additional support for this contention is found in the spatial maps. Since lake sections were sampled in a random sequence in time, if patches moved within a sampling date or dissolved in one location and formed in another, this change would appear as several patches on the spatial maps. This might be particularly important if a patch straddled the arbitrary boundary between adjacent lake sections, which would result in overestimation of patch size. However, patches were rarely mapped across section boundaries, and in the summer only one patch was found on most sampling dates. Several patches were observed on each date in spring and fall, which might suggest patch movement was occurring at that time. However, the separation of these patches in distance and time make it highly unlikely that one rapidly moving patch could account for the observed pattern. Also, in situ observations indicated the spring-fall population was actually distributed as many small, dense swarms which would appear as a few patches when mapped due to their small size relative to sample unit volume.

The whole-lake sampling design best revealed patterns which resulted from the Polyphemus population's response to environmental factors such as photoperiod or wind-induced water currents. Photography, microsampling, and in situ observation complemented this whole-lake design by providing information on small-scale phenomena and the biological interactions of individuals. Photography and microsampling probably best described swarm and shoal densities. However, an impractical large number of these samples would be needed
to describe whole-lake patterns and seasonal abundance with
the same precision as large volume samples. In situ observa-
tion, although largely qualitative, provided the best insight
into the behavioural basis for the observed patterns. Clearly
several sampling techniques are required to describe and
interpret patterns of patchiness on several space and time
scales.

B. Proposed Mechanism of Patch Formation

Patch formation appeared to be initiated by abiotic
factors and maintained by visual cues. Diel and seasonal
changes in Polyphemus distribution suggested the importance
of light-related behaviour, visual stimuli, and wind-induced
water currents to patch formation, although other factors
may also be involved. In this study, patches and the entire
Polyphemus population were observed to disperse vertically
and horizontally at night. This observed dispersion supported
the importance of light and vision in maintaining patch
integrity and daytime distribution. Butorina (1971b) observed
similar diel changes in the vertical dispersion of Polyphemus.
Also, swarms of marine copepods (Hamner and Carleton, 1979)
and mysid shrimp (Clutter, 1969; Zelickman, 1974) were
observed to disperse at night or when visual stimuli from
other individuals were absent.

Seasonal differences in the configuration of Polyphemus
aggregates were also observed in this study, and in situ
observations suggested visually-mediated behaviour and type
of individual were related to these differences. Spring-fall
swarms of sexual individuals were found close to shore, maintained short inter-animal distances, and responded to external visual stimuli (diver's hand) as a cohesive unit. Summer shoals were found farther from shore, were composed primarily of juvenile Polyphemus, and were larger and more loosely organized than swarms. Individuals in shoals reacted to a swimming diver by scattering horizontally in different directions, but rejoined the shoal when the disturbance subsided. Regular spacing and occasional parallel orientation also suggested these individuals were interacting visually. Butorina (1963) and Heal (1962) also observed summer shoals of juvenile Polyphemus. Observations on a wide variety of zooplankton suggest sexual individuals form swarms while shoals are frequently formed by one sex or age class (e.g. Brandl and Fernando, 1971; Clutter, 1969; Colebrook, 1960b; Klemetsen, 1970). Differences in the eye structure between parthenogenetic and sexual Polyphemus may help explain the apparent differences in light-related behaviour, since sexual individuals, particularly males, have larger eyes than parthenogenetic females (Butorina, 1968).

Observations of this study also suggest that wind-induced surface water currents may influence Polyphemus patch location and formation. Good evidence exists to support the importance of wind-driven water currents to patch location and formation for several zooplankton species (e.g. Axelton, 1961; Colebrook, 1960a; Langford and Jermolajev, 1966; Ragotzkie and Bryson, 1953; Stavin, 1971). Colebrook (1960a) developed a theoretical model which demonstrated how zooplankton
patches could form on the downwind side of a lake as the result of an interaction between zooplankton diel vertical migration and wind-driven surface currents and resulting internal seiche. His model was based partly on the observations of Ragotzkie and Bryson (1953), which clearly demonstrated the formation of Daphnia patches by horizontally converging, wind-induced, surface water currents. More recently, Kamaykowski (1978) using a computer model approach, had results which compared favorably with the observations of Colebrook (1960a). In the present study, however, vertical migration and an internal seiche did not exist, and the observations of Ragotzkie and Bryson (1953) appear most applicable.

The patch formation mechanism proposed in this study can be divided into several components. The two principal components are: 1) wind-induced surface water currents and 2) light-oriented swimming behaviour of Polyphemus. The swimming behaviour can be divided into horizontal and vertical spatial components, and a biological interaction component which depends on the type of Polyphemus present (sexual or parthenogenetic, adult or juvenile). These components interact on diel and seasonal time scales to produce distribution patterns similar to those found in this study (Fig. IV-16).

Laboratory studies by Kikuchi (1938) and Butorina (1969) suggest that in low to middle light intensities Polyphemus are positively phototactic and swim vertically in the water column, while in high light intensities kinetic swimming behaviour occurs in the horizontal plane. In extremely
Fig. IV-16. Compartment model of the proposed mechanism of patch formation delineating the interaction among major environmental and biotic components to produce the observed distribution patterns. Components in the shaded area bounded by heavy lines represent biological factors related to the behaviour of individual zooplankters. Environmental components are outside of this shaded area. See text for a detailed description.
PHOTOPERIOD

ENVIRONMENTAL FACTORS

<table>
<thead>
<tr>
<th>ENVIRONMENTAL FACTORS</th>
<th>ORGANISMIC FACTORS</th>
<th>ACTUAL PATTERN</th>
<th>ENVIRONMENTAL FACTORS</th>
</tr>
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<tbody>
<tr>
<td>TYPE</td>
<td>SWIMMING BEHAVIOUR</td>
<td></td>
<td></td>
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</tbody>
</table>

SAMPLING FILTER

RANDOM

SEXUAL

VERT.

DISPERSE

HORIZ.

ASEXUAL

VERT.

AGGREGATE

HORIZ.

ASEXUAL

CLUMPED

SEXUAL

SWARMS

OBSERVED DISTRIBUTION PATTERNS

WIND

CURRENT

WATER CALM VARIABLE

DIRECTED

DAY NIGHT

SPRING SUMMER FALL

150
low light conditions, or in diffuse light, swimming was random. This photic behaviour would cause Polyphemus to swim to the surface at sunrise and sunset, swim horizontally in the day, and disperse horizontally and vertically at night. These laboratory observations are supported by field observations of Butorina (1971b) which suggest a sunrise and sunset ascent of the Polyphemus population, and by the observations of this study which demonstrated daytime swimming was primarily in the horizontal plane and dispersal of the population occurred at night. If this daytime horizontal swimming was regulated by a shoreline attraction mechanism as opposed to the shoreline avoidance mechanism proposed by Siebeck and Ringelberg (1969), Polyphemus would tend to aggregate in near-shore regions in the day. The configuration of these near-shore aggregations would depend on the type of individuals in the population. Sexual individuals would tend to form swarms, while early instar and parthenogenetic individuals would form surface shoals. Surface water currents generated by wind action would concentrate these "shoreline-attracted" Polyphemus on the downwind side of the lake. Polyphemus swimming behaviour, although kinetic in the horizontal plane, would be directed towards the downwind side of the lake by wind blowing from a relatively constant direction, and appear undirected when it was relatively calm or when wind direction was variable or deflected by shoreline structures.

Observations exist, therefore, which support many of the assumptions of this patch formation mechanism. However, this does not rule out other equally attractive hypotheses.
Future research on the spatial orientation and swimming behaviour of *Polyphemus* and other zooplankton will be most useful in evaluating the assumptions of this proposed mechanism.

### C. Possible Adaptive Significance and Function of the Observed Patterns of Patchiness

Observations of this study suggest spring and fall swarming was linked with sexual reproduction. Clutter (1969), Brandl and Fernando (1971) and others have also suggested zooplankton may swarm to facilitate mating. Even without swarming, the limited nearshore distribution of the *Polyphemus* population in the spring and fall would increase density and consequently the probability of finding a mate. In addition to increased copulation success, this nearshore distribution may increase the hatching success of resting eggs which result from mating. *Polyphemus* resting eggs, unlike ephippia of most Cladocera, sink and are encased in a sticky, gelatinous envelope. If these resting eggs require a hatching stimulus which is found only in the littoral, e.g. dessication or freezing and thawing, then eggs dropped in nearshore regions would remain there by adhering to vegetation and sediments and have a greater hatching success than eggs in anaerobic limnetic sediments.

Population self-regulation may be an important function of swarming and shoaling (Clutter, 1969). For *Polyphemus*, the concurrence of these aggregations with population events suggests they may provide information to individuals on population density or related factors (Hutchinson, 1967) which
helps stimulate the onset of sexual reproduction. *Polyphemus* in shoals and swarms experience population densities at least an order of magnitude more than if they were randomly dispersed. Since these aggregations occur primarily in the daytime when *Polyphemus* does most of its feeding (Mattson and Haney, Unpubl.), localized food limitation may occur. This food limitation might stimulate sexual reproduction, which does not contribute immediately to population growth since only resting eggs are produced. Therefore, population growth would be effectively limited before the food supply was totally depleted. The one large shoal observed for several weeks in late summer of 1975 (and 1976) may have helped stimulate the onset of sexual reproduction and swarming in the fall, either as the sole stimulus or acting in conjunction with environmental factors such as photoperiod and/or declining water temperatures. Similarly, the nearshore spring distribution (Fig. IV-6) may have functioned as a large shoal and helped stimulate sexual reproduction and swarming.

Cannibalism has also been suggested as a means of population self-regulation which could occur in swarms and shoals (Clutter, 1969). Although cannibalism on young has been reported for *Polyphemus* (Butorina, 1971a), it was most likely an artifact of crowded laboratory conditions since it was observed in this study in laboratory containers but not *in situ*. Also, separation of young from adults in summer shoals and by depth stratification would preclude cannibalism.

Swarming and shoaling may function to reduce predation by decreasing the frequency of encounter between predator and
prey. This idea appears widely accepted in the fisheries literature (e.g. Brock and Riffenburg, 1960; Colgan, 1974; Cushing and Jones, 1968; Seghers, 1974; Shaw, 1978; and Vine, 1971) and has been extended to zooplankton populations (Clutter, 1969; Hamner and Carleton, 1979). By occupying surface and littoral waters, Polyphemus individuals are extremely vulnerable to visual predation. Swarming or shoaling would appear to be most useful in reducing predation. In Stonehouse Pond, however, visual predation by vertebrates is probably not as important as it may be in other lakes, since larval fish are not present because the lake is reclaimed, only artificial bait is allowed, and a brook trout (Salvelinus fontinalis) population is maintained exclusively by stocking. A suggestion that swarming by Polyphemus may be effective in reducing trout predation is provided by gut analyses of 58 trout collected in near-shore littoral regions in the spring and fall (Mattson and Haney, Unpubl.). Eleven of these fish had Polyphemus in their guts, but only four trout had more than four Polyphemus. However, guts of these four trout were completely packed with Polyphemus suggesting that only a few fish find swarms, but when they do they feed intensively.

The overall distribution of the Polyphemus population may function to minimize invertebrate predation effects by spatially separating predator and prey. For example, cyclopoid copepods have high predation rates on Polyphemus (e.g. 2 Polyphemus per cyclopoid per day, Mattson and Haney, Unpubl.) but were found primarily below the thermocline in Stonehouse Pond. However, predatory insects like backswimmers and
dyticids were often found in the same samples as were *Polyphemus*. Dispersing into the limnetic at night would also subject the population to predation by *Chaoborus* (Fedorenko, 1975), which were regularly observed in surface samples at night. The relative importance of these predators should be assessed before the advantages of swarming and shoaling with respect to predation can be evaluated.

The patterns of distribution observed in this study probably confer a combination of the above advantages to individuals and to the *Polyphemus* population. Swarming appeared to result from the interaction of sexual individuals and may facilitate copulation success and/or survival of resting eggs. Shoaling was related to the interaction of the *Polyphemus* population with its environment, and may be a precondition to the onset of sexual reproduction and swarming. Future research should continue to emphasize the biological aspects of zooplankton aggregations, and to investigate processes important to their formation and function.

5. **Summary**

Temporal and spatial patterns of patchiness were studied in a population of *Polyphemus pediculus* (L.) found in Stonehouse Pond, Barrington, New Hampshire (Fig. IV-1). Whole-lake seasonal and diel patterns were best revealed using a stratified random sampling design with 200 liter samples collected from fixed locations in the lake (Figs. IV-2-3). In both 1975 and 1976 these samples were used to reconstruct horizontal and vertical distribution patterns. **In situ**
observations, microsamples (4 liter), and photography complemented the whole-lake design and were used to describe the internal structure and behaviour of *Polyphemus* within patches.

Whole-lake changes in seasonal abundance and population composition (Figs. IV-4, IV-5) influenced patterns of horizontal and vertical distribution (Figs. IV-6, IV-7). The *Polyphemus* population was rarely found below 2 meters of depth (Fig. IV-7). In the spring and fall of both years, the population was found extremely close to shore (Fig. IV-6). In the summer, most of the population was found in the limnetic zone. This horizontal shift into the limnetic zone directly followed a period of sexual reproduction which occurred at a spring abundance maximum. The shift back into the littoral zone preceded a fall period of gamogenesis.

*Polyphemus* patches were typically found in the littoral zone (Table IV-1). In the spring and fall, several patches were found on each date, while in the summer generally one patch was seen (Fig. IV-8). Patches were usually found on the downwind side of the lake (Fig. IV-8), and their location was highly correlated with wind direction at the time of sampling (Table IV-2).

Results from four diel studies (day-night-day sampling) revealed *Polyphemus* patches dissipated and the littoral population dispersed horizontally into the limnetic zone at night (Figs. IV-9-12). This horizontal dispersal was paralleled by vertical dispersal in the upper 3 meters of the water column (Fig. IV-13). Apparently this pattern resulted from the
interaction of diel changes in Polyphemus swimming behaviour with diel changes in wind-induced water currents.

Aggregation indices (Tables IV-3-5) provided statistical support for seasonal and diel changes in Polyphemus population distribution which were graphically presented in Figs. IV-6-13.

In situ observations revealed spring-fall patches were actually several dense swarms of Polyphemus, oval to circular in shape, and 0.5 - 5 meters in diameter, which were found within 10 cm of the lake surface and within 2 meters of the shore. These swarms had internal densities as high as 15300 Polyphemus•liter⁻¹ (Table IV-6). Swarms were composed primarily of sexual individuals (Figs. IV-14, IV-15).

Summer patches were shoals of Polyphemus, oval to rectangular in shape, parallel to shore, 20 - 50 meters long and 10 - 15 meters wide, and were found within 10-20 cm of the lake surface and between 15 - 25 meters from shore. These shoals had internal densities varying between 8 - 58 indiv.·liter⁻¹, and occasionally as high as 13800 indiv.·liter⁻¹ (Table IV-6). Shoals were composed primarily of juvenile Polyphemus (Figs. IV-14, IV-15).

A patch formation mechanism is proposed and summarized graphically (Fig. IV-16), and suggested how the seasonal and diel patterns of patchiness described in this study might result from the interaction of wind-induced surface water currents and light-oriented swimming behaviour of Polyphemus.
individuals. This mechanism is supported by the observations of this study and by those found in the literature.

Finally, possible functions and adaptive advantages of the observed patterns of patchiness are considered. Swarms may facilitate copulation success and/or survival of resting eggs. Shoals may provide information to Polyphemus individuals on population density or related factors which helps stimulate the onset of sexual reproduction and swarming. Swarming and shoaling may also function to reduce vertebrate and invertebrate predation by spatially or temporally separating predator and prey. These aggregations probably confer a combination of advantages upon the Polyphemus population.
6. Literature Cited


