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FACTORS REGULATING INTRAZOOPLANKTON PREDATION

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TECHNICAL COMPLETION REPORT

Project Number A-041-NH

Water Resource Research Center
University of New Hampshire
Durham, New Hampshire

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ABSTRACT

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. This whole-lake stratified design was more accurate and precise in quantifying seasonal abundance than a conventional design, and best revealed changes in horizontal distribution.

Using this stratified design, the Polyphemus population of Stonehouse Pond, Barrington, New Hampshire 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, and a final decline to zero in late fall. The population over-wintered in the lake sediments as resting eggs. Changes in seasonal abundance resulted primarily from variation in natality rates of the Polyphemus population associated with alternation between parthenogenetic and gamogenetic reproductive modes.

In the spring and fall, the total Polyphemus population was primarily littoral, and in the summer it was also limnetic in distribution, although mean density was always greatest in the littoral. Diel changes in population distribution also occurred, and the population was aggregated at the lake surface in the day and dispersed horizontally and vertically in the epilimnion at night. Day-time patch location was highly correlated with wind direction, and patch configuration was dependent on the type of Polyphemus (sexual or asexual) present. A compartment model is proposed to explain the relationship between patch formation and biological and environmental factors.

A deterministic computer model was used to estimate the predation impact of the Polyphemus population on nauplii and Chonochilus. Maximum spring mortality rates for these prey were 8-11% day^{-1}.

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I. GENERAL INTRODUCTION

Heavy reliance of most larval fish as well as some mature forms on zooplankton as a food source establishes an important trophic link between the zooplankton community and fish in a lake. Fluctuations in the abundance and composition of the zooplankton can therefore influence the survival and productivity of such planktivorous fish.

Early studies were largely unsuccessful in attempts to relate changes in abiotic factors such as water temperature and chemistry to differences in abundance and composition of the zooplankton. A recent review of the literature suggests biotic factors such as predation and competition may play a decisive role (Hall et al., 1976).

Visual-feeding fish such as sunfish and trout selectively feed on the large-sized zooplankton, reducing the abundance of large species and confering a competitive advantage to the smaller forms. The response to high predation pressure from fish is a shift of the size structure of the zooplankton community to dominance by smaller zooplankton species. This "size-efficiency hypothesis" has found wide support in temperate (e.g. Brooks and Dodson, 1965), tropical (Zaret, 1972) and arctic lakes (O'Brien, 1975).

More recent research indicates the importance of size-selective predation by invertebrates as a force structuring the zooplankton community (Hall et al., 1976). Invertebrates such as predatory cladocera and copepods, in contrast to fish, generally select small prey, thereby reducing the small species and enhancing the survival of the larger zooplankton forms. Heavy predation by invertebrates leads to dominance of large zooplankton. Thus, to predict the size structure of a zooplankton community in nature, the relative strength of each predation pressure must be known.

Few quantitative studies have been carried out on the role of invertebrate predation in nature. McQueen (1969) demonstrated that cylcopoid copepods consumed 31% of their own young and 30% of the young of the dominant zooplankton grazer in one summer. Cummins et al. (1969) estimated that the predaceous cladoceran Leptodora removed

from 6.3 to 43.1% of the entire zooplankton grazer population. Because of spatial patchiness of zooplankton, serious problems in such studies dealing with natural populations has been the accurate estimation of the population of predator and prey species.

Despite its cosmopolitan distribution (Pennak, 1953) and abundance in many lakes, the cladoceran Polyphemus pediculus is probably the least studied of the predatory zooplankton. Laboratory feeding experiments by Butorina (1965, 1970, 1971b, 1971c; Butorina and Sorokin, 1971) have limited application to a natural system, since these experiments were often run at prey concentrations an order of magnitude or more greater than would be found in nature. The purpose of this study is to quantify the predatory pressure of Polyphemus pediculus on a natural zooplankton community.

To quantify the predation impact of Polyphemus in a lake, three fundamental questions were first posed: 1) What is the abundance of Polyphemus in the lake at any point in time? 2) Where are these Polyphemus located with respect to their prey? 3) What are the feeding rates and factors regulating the feeding rates of Polyphemus?

A major effort of this research was the field study designed to provide accurate and reliable estimates of the spatial and temporal distribution of the Polyphemus population in the lake. Controlled feeding experiments were conducted in the laboratory and in situ in the field to determine the feeding rate relationships of Polyphemus. Further direct observations were made in situ on the swimming and feeding behavior. These empirically-derived population abundance and distribution data were applied as state variables in a mechanistic feeding model. Model predictions of Polyphemus predation rates and their potential impact were evaluated.

There are several advantages to this modeling approach. First, a predictive model provides a conceptual framework in which experiments can be designed and evaluated. Secondly, it simplifies a complex, mechanistic relationship. Once the mechanisms regulating the components are identified and experimentally derived, it may be possible to measure the critical factors such as predator and prey

densities and use this information in the model to obtain an accurate prediction of the predation effect. Finally, organization of the results of feeding experiments in a mechanistic sub-model allows for future interface of this model with population dynamics and distribution sub-models. This work can be thought of as a first step in the creation of a realistic model of intrazooplankton predation, which will allow a quantitative comparison of the relative importance of invertebrate and vertebrate predation in aquatic communities.

II. EVALUATION OF SAMPLING DESIGN

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., 1978). 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, 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 size, or are they due to 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., 1978; 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 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). Stratified sampling provides a design by which one can simultaneously obtain population abundance estimates and study the distribution of the sampled organisms. The logic of this design is to utilize information about a heterogeneous population to divide

it into internally homogeneous subpopulations. Estimates of the total number (or mean density) of organisms in each subpopulation or stratum are then weighted by their representative proportion or 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 is rewarded with an increase in precision of the estimate over a corresponding estimate from randomly located samples (Cochran, 1977). Even arbitrary stratification will generally give a more precise estimate of population total or mean density than an estimate from a comparable design without stratification (Barrett and Nutt, 1975; Cochran, 1977). This characteristic of stratified sampling is particularly appealing since horizontal delimitation of a lake water mass can be somewhat arbitrary. Even if part of the same patch lay in two adjacent strata, a precise estimate of population size could be obtained because the greatest sampling variability would be contained within a small portion of the lake.

Stratified sampling has considerable intuitive appeal to aquatic ecologists. 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. By coding sample and stratum locations, the whole-lake spatial distribution pattern can be reconstructed. In addition to providing an estimate of the total population size with confidence limits for the whole lake, it is possible to statistically compare subpopulations within the lake. Using various sample allocation methods (Barrett and Nutt, 1975; Cochran, 1977) and pilot survey information, it is possible to estimate the precision that can be expected for a specified sampling effort and stratification scheme. Conversely, it is possible to determine the number of samples and effort needed for a pre-specified confidence limit width. Despite these advantages, stratified sampling has had only limited application in limnological studies (e.g. George, 1974; Marzolf and Osborne, 1972; Rigler and Cooley, 1974).

This study was undertaken for several reasons. Initially, it

provides a basis for evaluating the performance of stratified random sampling with respect to "conventional" sampling schemes in their ability to quantify seasonal population abundance of the predatory cladoceran, Polyphemus pediculus (L.). Polyphemus was selected as the study zooplankter in part because its distribution and aggregation behavior (Butorina, 1963, 1969; Hutchinson, 1967) make it a difficult organism to sample effectively. 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; Heal, 1962; Hutchinson, 1967; Lindstorm, 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 exact importance of these two lake regions can be determined using a whole lake stratified sampling design. Finally, this work provides the basis for a comprehensive study of the predation impact and aggregation behavior of the Polyphemus population.

MATERIALS AND METHODS

Study Site

Stonehouse Pond in southeastern New Hampshire, USA, was selected as the study site, primarily because information existed on its zooplankton which indicated a relatively large Polyphemus pediculus population, and for logistics such as lake morphometry and proximity. It is a slightly dystrophic glacial kettle lake, with a small watershed of mixed deciduous and conifer forest. Figure 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).

Pilot Survey

On three occations in late summer and early fall, 1974, Stonehouse Pond was sampled 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.

Implementing the Stratified Design - Spatial Aspects

The minimum information required to implement a stratified random sampling design is: 1) The population being sampled is finite, and 2) Some measure exists of the total number of sample units in each section or stratum and in the entire lake. Since a lake is conveniently a finite unit, the first requirement is satisfied. With regard to the second requirement, visual observations, pilot survey information, and morphometric data were used to stratify Stonehouse Pond. The 3-meter depth contour (Figure 1) was used to partition the lake horizontally into littoral and limnetic sections.

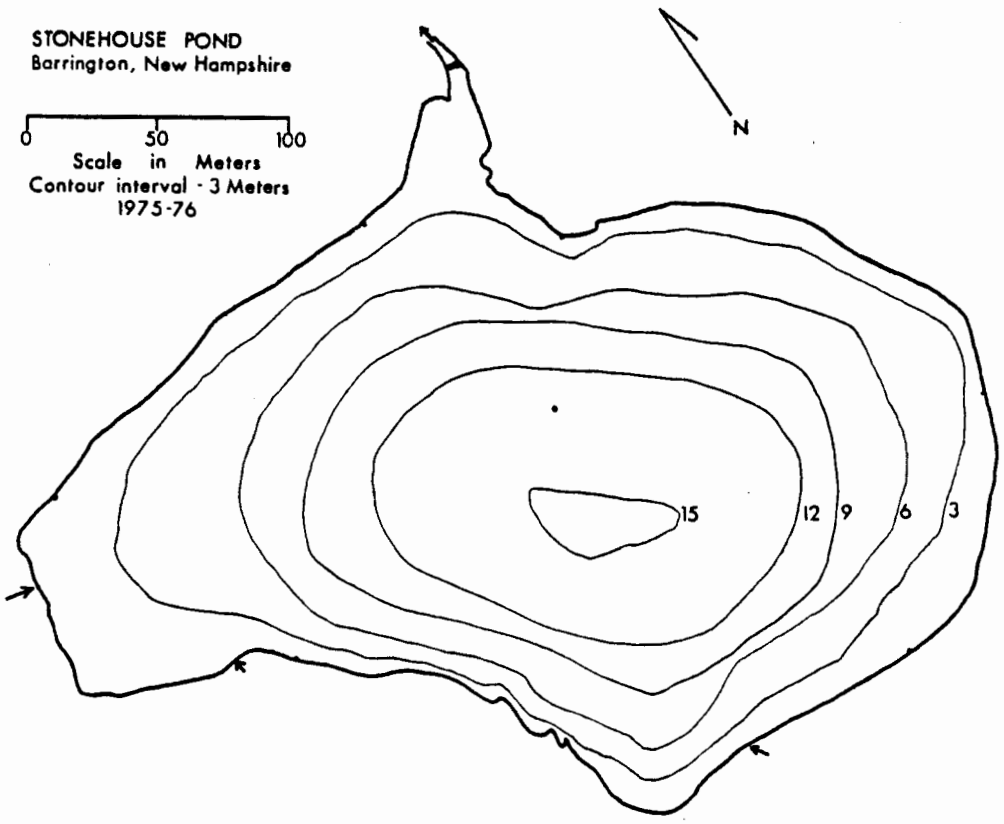


Figure 1. Bathymetric map of Stonehouse Pond, Barrington, New Hampshire, USA, based on a survey and sounding in May, 1975.

Although this devision 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. Stakes were used to divide the littoral region into six horizontal sections, based on compass points, bottom morphometry, and shoreline features (Figure 2). These stakes also served as visual reference points when sampling. Section areas and volumes were determined from a survey map by planimetry (Lind, 1974). Table 1 summarizes the physical properties of these lake sections. Since the entire littoral region is only 4.3% of the total lake volume, and only 11.8% of the epilimnetic volume (Table 1), it would normally not be necessary to partition the littoral zone. 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 behavior warranted subdivision of the littoral. Increasing the number of sections can increase precision (Cochran, 1977), but there is also a gain in ability to describe distribution. Using this same reasoning, each horizontal lake section (Figure 2) was divided into three vertical strata. Tow locations within each section were fixed by shoreline markers and buoys. All littoral tows were taken at an oblique angle to shore 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 (Figure 2).

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 (ten littoral and two 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 1700 DST.

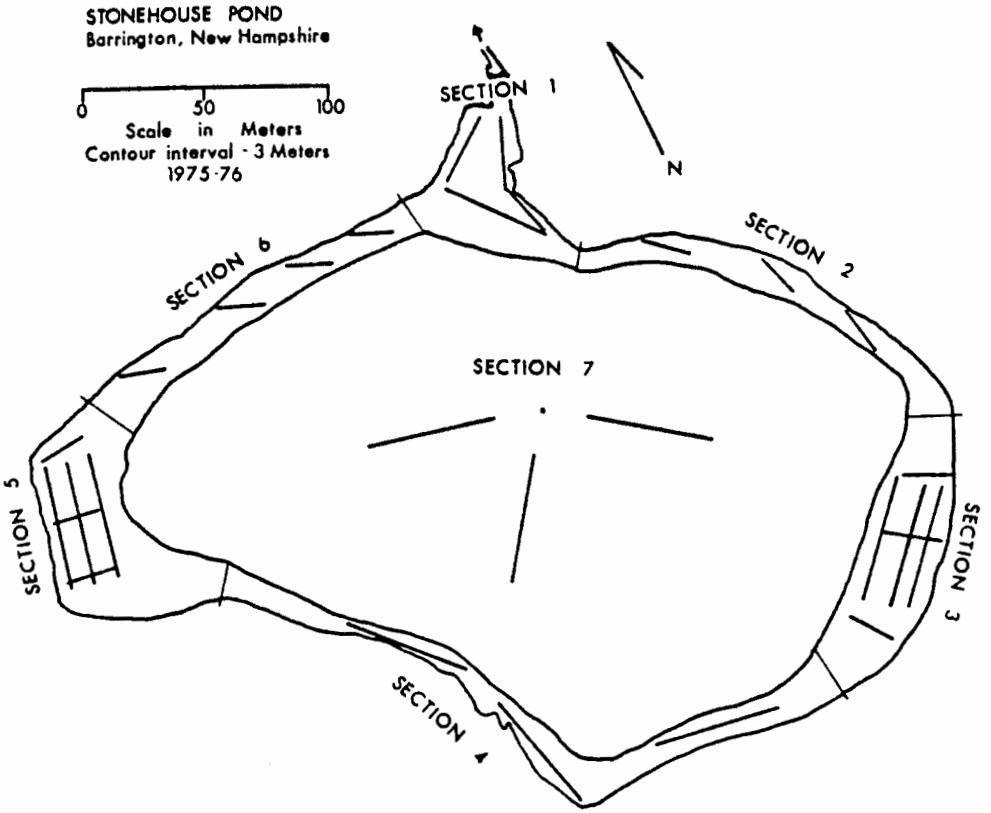


Figure 2. Lake sections and tow locations for stratified sampling of Stonehouse Pond.

Table 1.

Morphometric data on sections of Stonehouse Pond.

Littoral Section	Volume (M^3)	Surface Area (M^2)	Percent of Total Volume
1	2450	1860	
2	2175	1650	
3	2080	1750	
4	2990	2200	
5	5620	3400	
6	3255	2100	
Littoral Total	18570	12960	4.3 %
Limnetic Section			
0 to 3 M.	138800	46000	32.4 %
Below 3 M.	271500	46000	63.3 %
Limnetic Total	410300	46000	95.7 %
Lake Total	428870	58960	100.0 %

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

Littoral = 11.8 % of Epilimnetic volume.

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 (Figure 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.

Sample Allocation

Table 2 summarizes sample allocation for this design using a Neyman Allocation Method (Barrett and Nutt, 1975), and the estimated time required to collect these samples. 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. 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. Cost in terms of handling time for one sample was approximately five minutes, and included tow time, rinsing and preservation, and positioning to take the next sample. The estimated overall sampling time was seven hours and fifteen minutes, but in practice the entire lake could be sampled in six hours. Back calculation using the sample size formula of Barrett and Nutt (1975) provided an estimate of the expected 95% confidence interval (CI) width with this design. This value was an indication of the expected precision and was compared to the observed precision as a means for evaluating the sampling program.

Sampling Apparatus

Two Clarke-Bumpus (CB) metered plankton nets (Clarke and Bumpus,

Table 2.

Sample allocation for stratified sampling of Stonehouse Pond 1975-1976.

Littoral Section	Depth Slice	Number of Tows	Time Required (@ 5 min./tow)
1	0 - .25 M.	3	15 min.
	.25 - 1.0 M.	3	15 min.
	1.0 - 3.0 M.	2	10 min.
		8	40 min.
2	0 - .25 M.	3	15 min.
	.25 - 1.0 M.	3	15 min.
	1.0 - 3.0 M.	2	10 min.
		8	40 min.
3	0 - .25 M.	6	30 min.
	.25 - 1.0 M.	6	30 min.
	1.0 - 3.0 M.	6	30 min.
		18	90 min.
4	0 - .25 M.	3	15 min.
	.25 - 1.0 M.	3	15 min.
	1.0 - 3.0 M.	2	10 min.
		8	40 min.
5	0 - .25 M.	6	30 min.
	.25 - 1.0 M.	6	30 min.
	1.0 - 3.0 M.	4	20 min.
		16	80 min.
6	0 - .25 M.	3	15 min.
	.25 - 1.0 M.	3	15 min.
	1.0 - 3.0 M.	2	10 min.
		8	40 min.
Littoral Subtotal---------		66 tows -----	330 min.
Limnetic Section			
	0 - .25 M.	3	15 min.
	.25 - 1.0 M.	3	15 min.
	1.0 - 3.0 M.	12	60 min.
	Below 3.0 M.	3	15 min.
		21	105 min.
Lake Total ----------		87 tows -----	435 min. or 7 hours and 15 min.

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. Figure 3 summarizes these modifications.

Since virtually all samples were allocated to the upper 3 meters of the lake (Table 2), both CB meter units were mounted .5 meters apart on a 2.5 cm. diameter, 3.5 meter-long, aluminum pole. This pole was attached to a pivotal mechanism which allowed the nets to be raised or lowered in the water, or held along side the boat for rinsing. The pivotal mechanism was mounted in the bow of the boat to minimize possible avoidance reactions to the boat shadow by zooplankton in the surface waters (Clutter and Anraku, 1968; Fleminger and Clutter, 1965). A stern-mounted, electric-powered motor was used to propel the boat at a constant rate of 1 meter/second, with 120 CB meter revolutions/minute. This tow rate was well situated in the optimum towing velocity range of 80 to 145 revs./minute (Yentsch and Duxbury, 1956).

CB meter units were calibrated by towing this tandem mount without nets attached between stakes 50 meters apart in the lake littoral section 3. Calibration values by this method were 4.87 liters/rev. for the top net, and 5.11 liters/rev. for the bottom net. When the 151 μm nets were added to the meter units, 86-92% of the water in a 50-meter tow was accepted, which is in close agreement with Yentsch and Duxbury (1956). Net calibration values were checked at the start of each sampling date, and results were consistent with a variation in volume of less than 2% for a 50-meter tow.

To minimize the possibility of clogging, the standard sampling unit was a 20-meter tow, which was measured as 20 seconds on a stopwatch at a rate of 1 meter/second. Since sample volumes varied slightly by this method (range 199-225 liters) due to varying particulate concentrations in the water, and since the CB meter units were not modified to accept a fixed volume (Comita and Comita, 1957), all sample counts were scaled to a 200 liter sample.

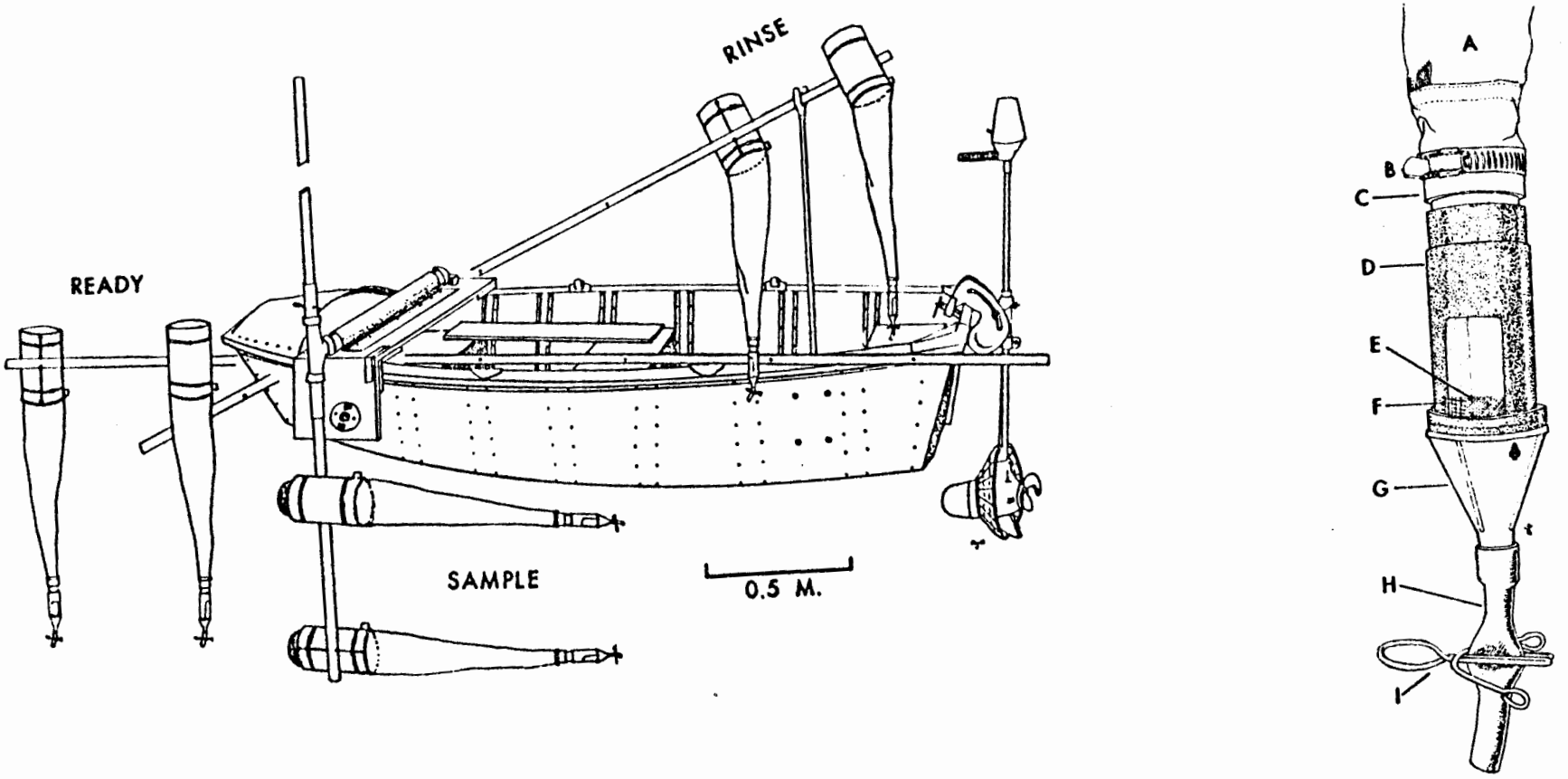


Figure 3. Modifications of Clarke-Bumpus nets and boat for stratified sampling. See text for further explanation.

A typical tow sequence was as follows. Net shutters were held open by cotter pins placed through holes near the mouth of the meter unit. These cotter pins were attached to a cord which, when pulled, would simultaneously close both units. Holes at .5 meter intervals in the net pole lined up with a hole in the pivotal mechanism. Nets were held at sampling depth by a pin placed through these holes. Once the net shutters were pinned open and the sampling depth was set, they were held in READY position (Figure 3). The boat then approached the tow location at a rate of 1 meter/second. When this location was reached, the nets were released and allowed to pivot into the SAMPLE position (Figure 3) as the boat continued to move. The nets were then towed for 20 seconds and closed by pulling the cord attached to the cotter pins. Care was taken to avoid sampling water disturbed by boat passage. The motor was turned off, the depth pin was removed, and the net pole was pivoted to the RINSE position (Figure 3). Nets were rinsed from the outside three times with lakewater, and their contents emptied from quick-drain buckets into sample vials of 4% formalin-sucrose (Haney and Hall, 1973). Nets were then pivoted around to the READY position and the process was repeated for the next tow sequence. In this manner, two depths at a fixed location could be sampled simultaneously with a total sample handling time of five minutes or less per sample.

The potential existed to capture surface organisms in the bottom net as it was lowered open to the sampling depth. This source of error was evaluated by lowering the open nets to the SAMPLE position as described above, and closing them immediately. Meter revolutions and sample contents resulting from this test indicated that carry-over of zooplankton did not occur and water was not filtered until the nets were vertical in the SAMPLE position. Calibration of the net and bucket rinse procedure indicated that three rinses removed 100% of the Polyphemus and 99.7% of the other net zooplankton.

Comparison of Sampling Designs and Computational Procedure

The effectiveness of several methods was compared for 30 consecutive sampling dates to cover the range of variation encountered

in an entire season. In addition to the Stratified sampling design outlined above, from June 19, 1975 through June 9, 1976, four 150-meter long tandem CB tows were taken at the start of each sampling date. Three of these integrated tows were located in randomly selected littoral sections, and one tow in the limnetic section, summing to a total of eight tows/date. These integrated samples and samples from the stratified design provided data for two independent estimates of the Polyphemus population size for each date. From each of these two designs, weighted and unweighted estimates of population size were calculated using the formulae in Table 3. In addition, eight tows were selected from the stratified samples which corresponded to the location of the integrated samples. These data provided the basis for a split plot analysis of variance (ANOVA) comparison of sampling design, sample size, weighting, and number of samples and their effect on accuracy and precision of population estimates.

To eliminate subsampling error, each sample from the stratified design was counted in its entirety in a gridded petri dish on a Wilde dissecting scope. 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 contents of the large volume integrated tows were totally 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 and varied between 7 and 11% of the total sampling variance.

All data analysis was 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 log10 scale (Figure 4; and Figures 5 and 6, panel B), 1 was added to all values to eliminate zero and negative logarithms (Colebrook, 1977). Two-way and split-plot ANOVA were performed on untransformed data blocked by sampling date. Accuracy was compared by ANOVA and Duncan's Multiple Range Test for mean separation of population size estimates. Precision was compared by

Table 3.

Notation and formulae used to calculate total Polyphemus population size by stratified or integrated sampling designs. See text for additional information.

Design	Stratified (20 meter tows)		Integrated (150 meter tows)	
Weighting	Weighted	Unweighted	Weighted	Unweighted
Statistic				
n	8 ; 84	8 ; 84	8	8
mean	$\bar{Y}_{st} = \frac{1}{N}\sum_{i=1}^{L} N_i \bar{Y}_i$	$\bar{Y} = \frac{\sum_{j=1}^{n} Y_j}{n}$	$\bar{Y}_{st}$	$\bar{Y}$
Total	$T = N\bar{Y}_{st}$	$T_1 = N\bar{Y}$	T	T_1
Standard error of mean	$S_{\bar{Y}_{st}} = \frac{1}{N}\sqrt{\sum_{i=1}^{L}(N_i S_{\bar{Y}_i})^2}$	$S_{\bar{Y}} = \sqrt{\frac{\sum_{j=1}^{n}(Y_j-\bar{Y})^2}{n-1}\left(\frac{N-n}{Nn}\right)}$	$S_{\bar{Y}_{st}}$	$S_{\bar{Y}}$
Standard error of total	$S_T = NS_{\bar{Y}_{st}}$	$S_{T_1} = NS_{\bar{Y}}$	S_T	S_{T_1}
Degrees of Freedom	$n_e - 1$	$n - 1$	$n_e - 1$	$n - 1$
CI on mean (±)	$T_\alpha = .05\ S_{\bar{Y}_{st}}$	$T_\alpha = .05\ S_{\bar{Y}}$	$T_\alpha S_{\bar{Y}_{st}}$	$T_\alpha S_{\bar{Y}}$
CI on total (±)	$T_\alpha = .05\ S_T$	$T_\alpha = .05\ S_{T_1}$	$T_\alpha S_T$	$T_\alpha S_{T_1}$

Y_i, Y_j = number of animals per sample

N = total number of sampling units in lake
n = total number of sampling units selected
L = number of strata in lake
For stratum i,
N_i = number of sampling units in stratum
n_i = number of sampling units selected
$\bar{Y}_i$ = stratum mean
$S_{\bar{Y}_i}$ = stratum standard error of the mean

T_α = Student's t-value
Effective degrees of freedom, n_e

$$n_e = \frac{\left(\sum_{i=1}^{L} g_i s_i^2\right)^2}{\sum_{i=1}^{L} \frac{g_i^2 s_i^4}{n_i - 1}} \quad \text{where } g_i = \frac{N_i(N_i-n_i)}{n_i}$$

s_i = stratum standard deviation

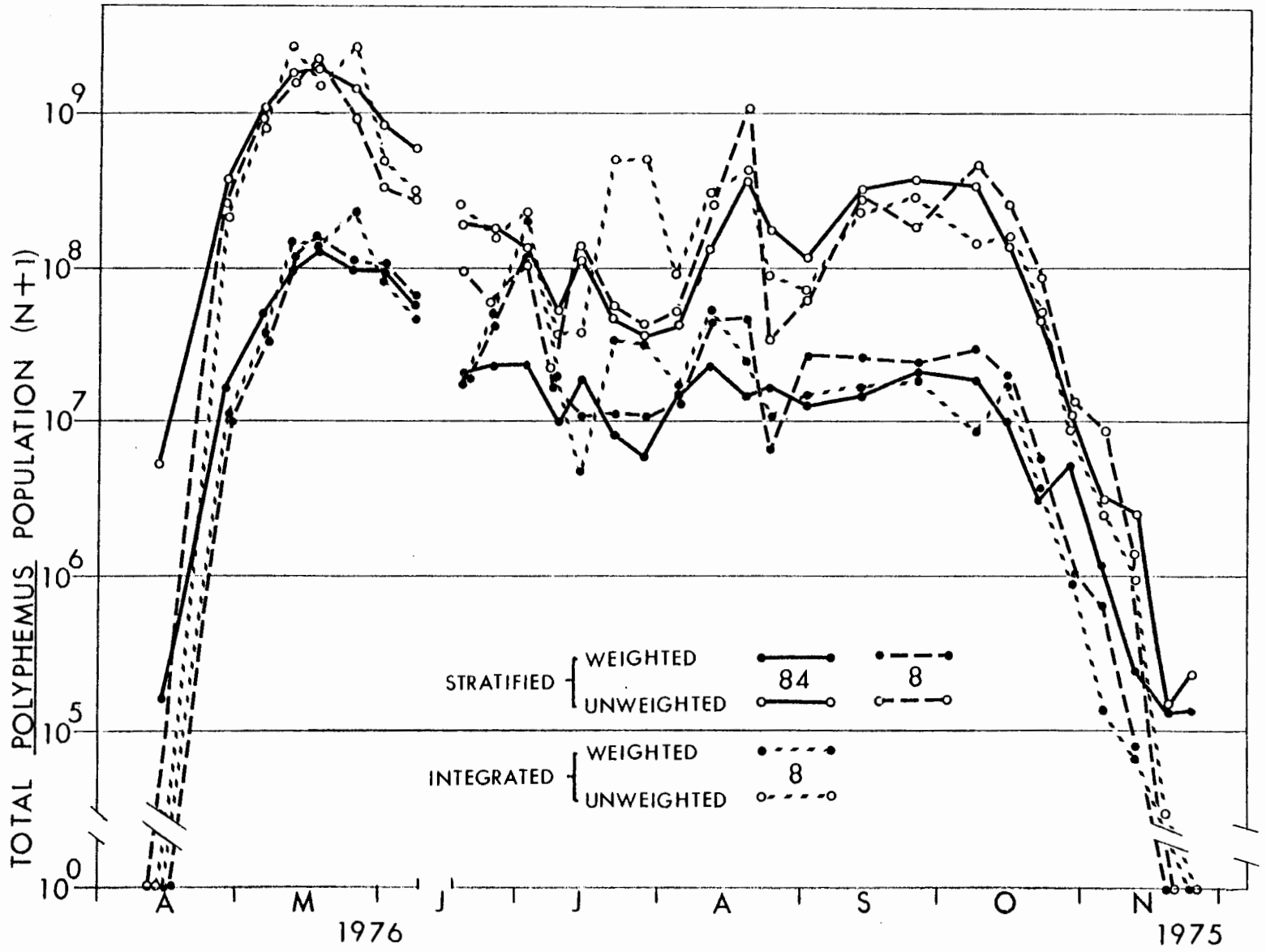


Figure 4. Comparison of six methods for calculating the total Polyphemus population in Stonehouse Pond for 30 consecutive sampling dates in 1975-1976. Note log10 scale. Formulae in Table 3.

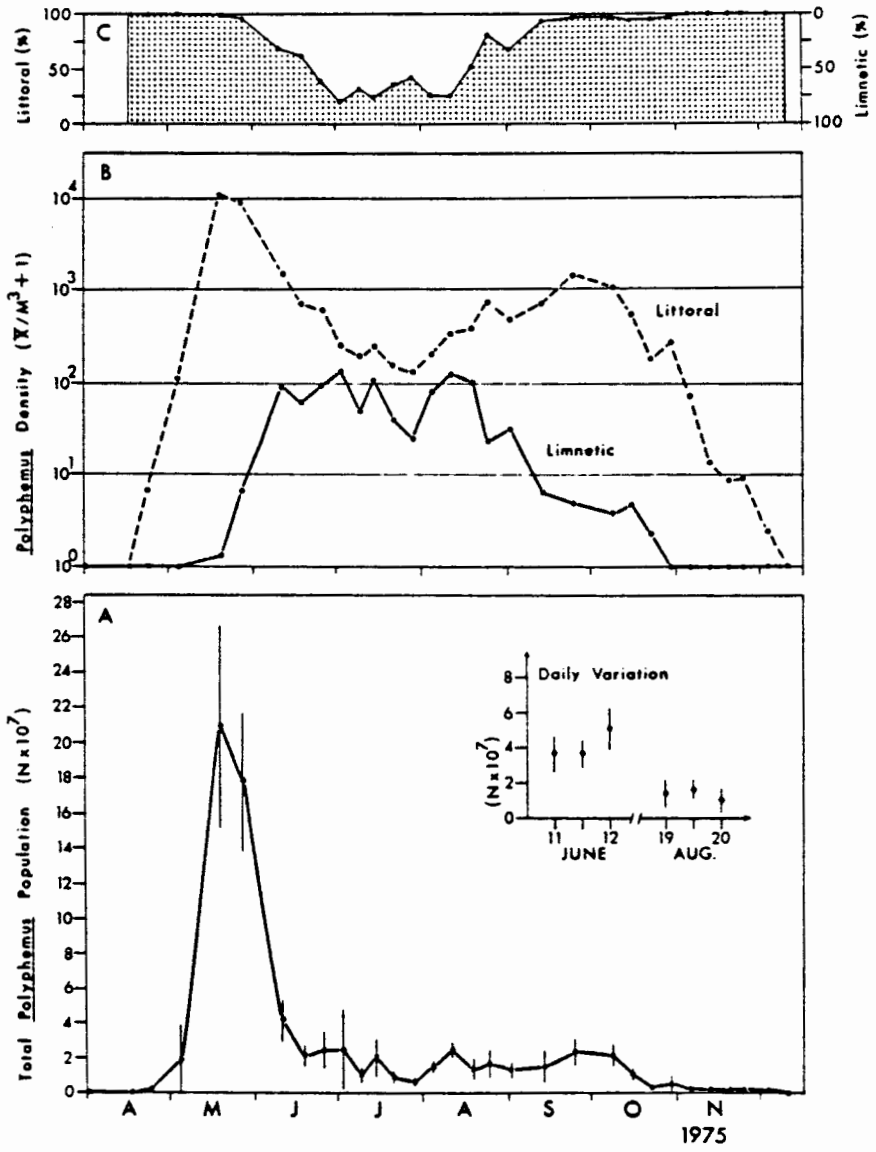


Figure 5. 1975 Seasonal abundance of Polyphemus pediculus in Stonehouse Pond based on weighted, stratified estimates.
Panel A: Seasonal and daily variation in total Polyphemus population. Vertical bars represent 95% confidence limits about total.
Panel B: Seasonal variation in Polyphemus density in the littoral and limnetic zones of Stonehouse Pond. Note log10 scale.
Panel C: Percent of total Polyphemus population partitioned between littoral and limnetic regions of Stonehouse Pond.

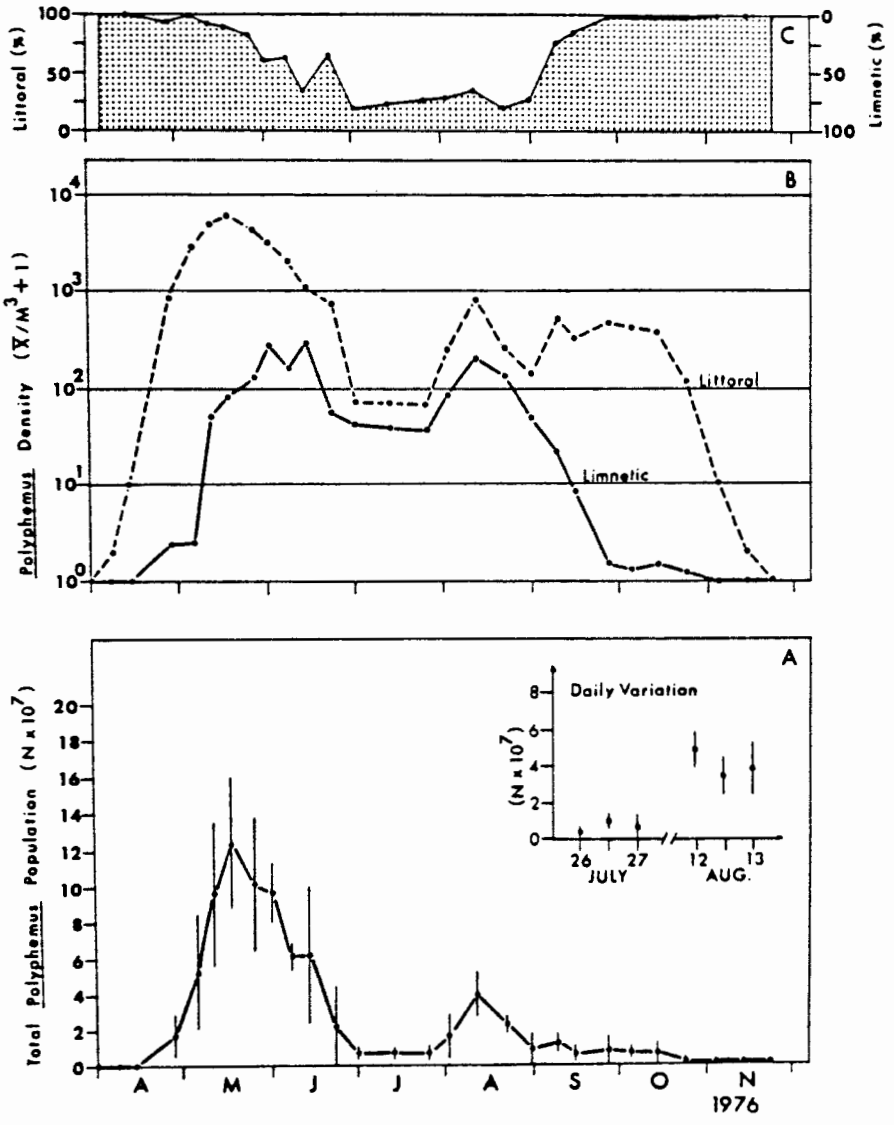


Figure 6. 1976 Seasonal abundance of Polyphemus pediculus in Stonehouse Pond based on weighted, stratified estimates.

Panels A, B, and C are the same as for Figure 5.

ANOVA and Duncan's Test on 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.

RESULTS AND DISCUSSION

Evaluation of Sampling Design

Figure 4 summarizes the comparison of six methods of estimating total Polyphemus population size. Confidence limits were not placed on this graph to avoid occlusion of the basic pattern. 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 by ANOVA methods indicated at $p = 0.05$ that curves based on weighted estimates were not significantly different from each other but were significantly lower than all three unweighted curves. Obviously, weighting was responsible for this order of magnitude difference.

More specifically, discrepancy between sample allocation method and weighting resulted in the observed difference. For weighted estimates, weighting is proportional only to the volume of each lake section (Table 3). If samples were allocated only in direct proportion to lake section volume, unweighted and weighted curves would be identical for the same sampling design because unweighted estimates of population size would in fact be "self-weighted" (Cochran, 1977). However, proportional allocation of samples would result in most tows being taken in the limnetic sections because of their proportionally large volume (Table 1). This allocation would not utilize pilot survey information which suggested the littoral and surface sections contained all of the Polyphemus population. 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. Estimates of population size, however, were weighted only in direct proportion to lake section volume. As a result, most samples were allocated to sections with high population density and low volume. 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. This problem elucidates a bias which can occur when seasonal abundance is quantified using unweighted mean densities of 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 arises. ANOVA methods applied to confidence interval width as a percent of the total population size revealed stratified estimates using 84 samples were significantly more precise ($p = 0.05$) than estimates based on 8 stratified or 8 integrated samples. A significant difference was not observed between the two 8-sample designs. This improvement in precision was observed even though CI widths were widened for weighted estimates by the effective degrees of freedom formula (Table 3) 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 (integrated) accepted only $4.8\% \pm 2.5\%$ (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 even after this error was factored out. The most probable reason for the observed difference in precision is an interaction between tow length and spatial scale of patchiness in the Polyphemus population.

Estimates from many small tows (84 stratified) were therefore more precise than those from few large tows (8 integrated) or few small tows (8 stratified). This observation is inconsistent with that of Wiebe, where he found an increase in tow length (volume) resulted in a dramatic increase in precision of estimates derived from a computer model (Wiebe, 1971) 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 seven hours to complete

a sampling date. The possibility existed that in this time the Polyphemus 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, 3 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 stratified section estimates failed to catch the integrated value. Out of these 44 values, 90% (40/44) occurred in the summer period June 15 to September 1. This result indicates that horizontal movement of the Polyphemus population across section boundaries had minimal effect on stratified sampling, and occurred primarily in the summer. This movement and its implications have been more thoroughly investigated by Mattson (1979).

A summary of the comparison of methods for estimating total Polyphemus population size revealed stratified sampling was the most accurate and precise method. However, other factors are usually considered in any sampling program, including time required to collect and process samples, manpower and equipment available, and the fact that a sampling design which is adequate for one species may not necessarily be adequate for a community of for other species. Using time as cost, and precision as benefit, a cost-benefit analysis revealed that, for 3.75 times the cost, the average increase in precision of stratified over integrated sampling was 7.30 ± 3.37 (95% CI; range 0 to 39.5). Stratified sampling, therefore, appears to be the optimum sampling strategy for whole lake quantification of zooplankton populations.

One final consideration concerns the observed versus expected confidence interval widths. The observed average CI width was

$\pm$ 10.1 x 10^6 for an estimate of the total Polyphemus population ($\pm$ 64 Polyphemus/Meter^3 for mean). This value was nearly three times wider than the expected CI width of $\pm$ 3.4 x 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 factored into the Neyman allocation method. As a result, expected precision was over-estimated. Pilot surveys for seasonal abundance studies should therefore encompass an entire year to closely approximate the expected precision for a stratified sampling design.

Changes in Seasonal Abundance and Distribution of Polyphemus pediculus as Influenced by Sampling Design

Figures 5 and 6 summarize the results of stratified sampling Stonehouse Pond for two years. Whole lake seasonal abundance (Figures 5 and 6, panel A) was typified as follows. After an absence of Polyphemus during the period of ice cover, a relatively synchronized hatching of individuals from resting eggs occurred when the littoral zone was free from ice. An exponential increase in population size ensued 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. A slight secondary peak (most noticeable in Figure 6, panel A) occurred in August of both years and was related to an increase in fecundity in the population. These curves (Figures 5 and 6, panel A) 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 Figures 5 and 6, panel A) 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. 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 3. Figures 5 and 6 (panel B) summarize changes in mean density of Polyphemus per meter^3. Density in the littoral was highest in the spring and fall of both years, and was nearly four orders of magnitude greater than limnetic density. Limnetic density was greatest in summer, and 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 (Figures 5 and 6, panel C) revealed quite a 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 (Figures 5 and 6, panel B), by virtue of its huge volume (Table 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 (Figures 5 and 6, panel B) while total population remained relatively constant (Figures 5 and 6, panel A), represented a shift in horizontal distribution of the Polyphemus population into the littoral zone.

Inadequate sampling design and differences in expression of seasonal abundance may therefore 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 or mean density) used to quantify abundance. Sampling limited to the limnetic zone of Lake Michigan (McNaught, 1966; Wells, 1960) and of several Japanese lakes (Kikuchi, 1930, 1937) typically observed Polyphemus only in the summer. Clearly this observation is consistent with the present study, but to characterize seasonal abundance of a Polyphemus population based only on limnetic samples 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 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 (Figures 5 and 6, panel C). Multinodal seasonal abundance curves (Butorina, 1963, 1971; Ischreyt, 1933) and the lack of error estimates make it difficult to interpret these peaks, but strongly suggested their sampling designs were inadequate to handle Polyphemus patchiness.

A stratified sampling design which employs varying time and space scales can be a means for accurate, precise, and efficient quantification of seasonal abundance and distribution of lake plankton. Its effectiveness in dealing with seasonal changes in horizontal distribution of the Polyphemus population in Stonehouse Pond provides evidence for the potential of stratified sampling as a tool for studying various biological attributes of lake systems.

MATERIALS AND METHODS

Study Site

Stonehouse Pond in southeastern New Hampshire (43° 12'N, 71° 06'W) was selected as the study site based on lake morphometry, proximity, and the presence of a large Polyphemus population. Briefly, 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 (Ferrante, 1974).

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 in 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, the samples were not used in subsequent calculations. On each sampling date, 84 200-liter Clarke-Bumpus net tows (151 μm mesh, 12.5 cm. diameter, 20-meter tow length) 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 to 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 at monthly intervals with a 30 cm. diameter, 151 μm 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 between several persons 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, 1974; Snedecor and Cochran, 1967).

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 length). These six horizontally integrated tows were from depths representative of greater than 90% of the Polyphemus population on each date, and were used to determine the size structure and percent composition of the population. All samples were preserved in 4% Formalin-Sucrose (Haney and Hall, 1973). A random subsample (Hensen-Stempel Piston Pipette method, Schwoerbel, 1970) from each tow was examined, and the first 50 Polyphemus were measured to the nearest occular micrometer unit on a Wilde dissecting microscope (1 occ. unit = 0.0182 mm). The entire subsample was examined for Polyphemus composition, and individuals were classified as juveniles, parthenogenetic females, gamogenetic females, or males (Table 4). If less than 50 Polyphemus were present in the first subsample, subsequent subsamples were examined as above until 50 Polyphemus were measured or the entire sample was seen. Average body length and percent composition were calculated by weighting the average at each depth by the corresponding percent of the total population.

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

Table 4.

Morphological characteristics used to distinguish embryonic developmental stages and to separate juvenile from mature Polyphemus.

Developmental stage	Morphological description	Development period (%)
early embryo	Oval to unpigmented embryos with limb buds present	86 %
middle embryo	Limbs with setae; compound eye with green pigment	9 %
late embryo	embryos with green pigment masked by black eye pigment; caudal setae not present	5 %
juvenile	newborn to sexual maturity; caudal setae present; immature gonads	
adult	parthenogenetic females, gamogenetic females, or males with mature ovaries or testes	

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 ratio of embryos per mature parthenogenetic female (redefined from here on as 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 body length measurements, and divided by the number of mature parthenogenetic females to provide a sample estimate of brood size. In addition, in 1976, mean brood size was determined for each date by examining the brood contents of 50 live parthogenetic females which were transported to the laboratory and narcotized in carbonate water. Brood size estimates by these two independent methods were nearly identical (T-test $p > 0.10$) indicating subsampling error and preservative effects (Prepas, 1978) were not serious in this study.

Duration of brood development (D), which was used to estimate B, was determined *in situ* at ambient food and temperature levels. The time between two successive broods was considered D, since mature *Polyphemus* females release new eggs into the brood pouch immediately following each moult and liberation of neonates (Butorina, 1971a). To determine D, 25 to 50 parthenogenetic females with mature embryos (Table 4) in their brood pouches were placed in a 4-liter glass container with a 202 μm NITEX cover, along with selected prey items at 2 to 4 times lake densities. These females with "synchronized" broods generally gave birth within six to twelve hours after isolation in the container. The time between hatching of this first brood and the next brood was D. Since these females were "synchronized", they required observation only once daily until mature embryos were seen, and were observed at six to twelve hour intervals from that time until hatching (depending on ambient temperature). Containers were cleaned and prey were added daily. Using this method, D was determined in each of four to five temperature periods in each year, representing a temperature range of 8° to 28°C. To account for diel variation in temperature, average median daily temperature for the duration of development was determined from a max-min thermometer attached to the *in situ* container, which was incubated in the littoral zone at 0.3 meters of depth.

Attempts to culture *Polyphemus* for several generations failed, so the number of instars and frequency of moulting was not determined. Short term observations and morphological examination provided the basis for classification of developmental stages found in Table 4.

All data analysis was performed on a Digital Electronics Corporation Model 1090 computer using programs written by the author. Regression analyses on duration of development and body size relationships were performed using the MINITAB statistical programs.

RESULTS

Seasonal Abundance and Composition

Figures 7 and 8 summarize seasonal changes in abundance, mean body size, and composition of the Polyphemus population for 1975 and 1976, respectively. 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 (Figures 7 and 8, panel A). 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.

Changes in population size structure reflected changes in composition. Smallest mean size was observed in early spring of both years (Figures 7 and 8, panel B), and was due to the presence of a large percentage of juveniles in the population (Figures 7 and 8, panel C). These juveniles were exephippial individuals, since they appeared before the presence of mature females and since littoral sediment samples taken just after ice-out revealed Polyphemus resting eggs with mature embryos. As this cohort of exephippial juveniles matured into parthenogenetic females, population mean body length increased sharply. It was the offspring of these exephippial individuals which contributed largely to the spring maximum in abundance. Hatching of Polyphemus resting eggs over a short period in the spring probably resulted in the relatively distinct peaks in seasonal abundance and population mean body length observed in 1975. Similarly, a relatively broad spring period of resting egg hatching probably resulted in broad abundance and body size peaks in 1976.

When the first brood of these exephippial Polyphemus hatched, population mean body size decreased (Figures 7 and 8, panel B) and the percent composition of juveniles increased (Figures 7 and 8, panel C). Oscillations in percent composition of juveniles continued

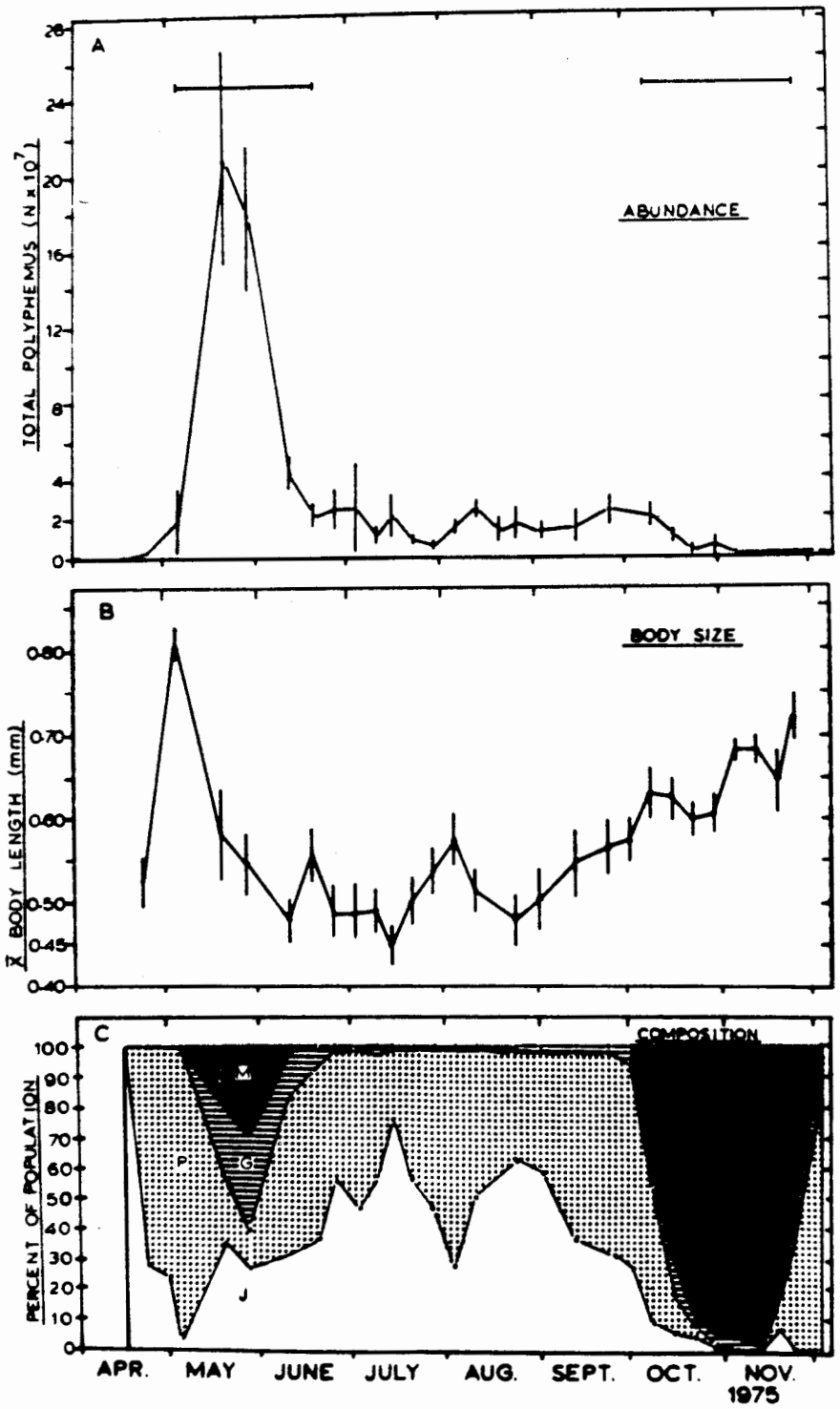


Figure 7. Seasonal abundance (Panel A), mean body length (Panel B), and percent composition (Panel C) of the 1975 Polyphemus population in Stonehouse Pond. Horizontal bars in Panel A represent periods of resting egg production. Vertical bars in Panels A and B represent 95% confidence intervals. In Panel C, dark shading (M) represents males, lines (G) represent gamogenetic females, dots (P) represent parthenogenetic females, and clear (J) represents juveniles.

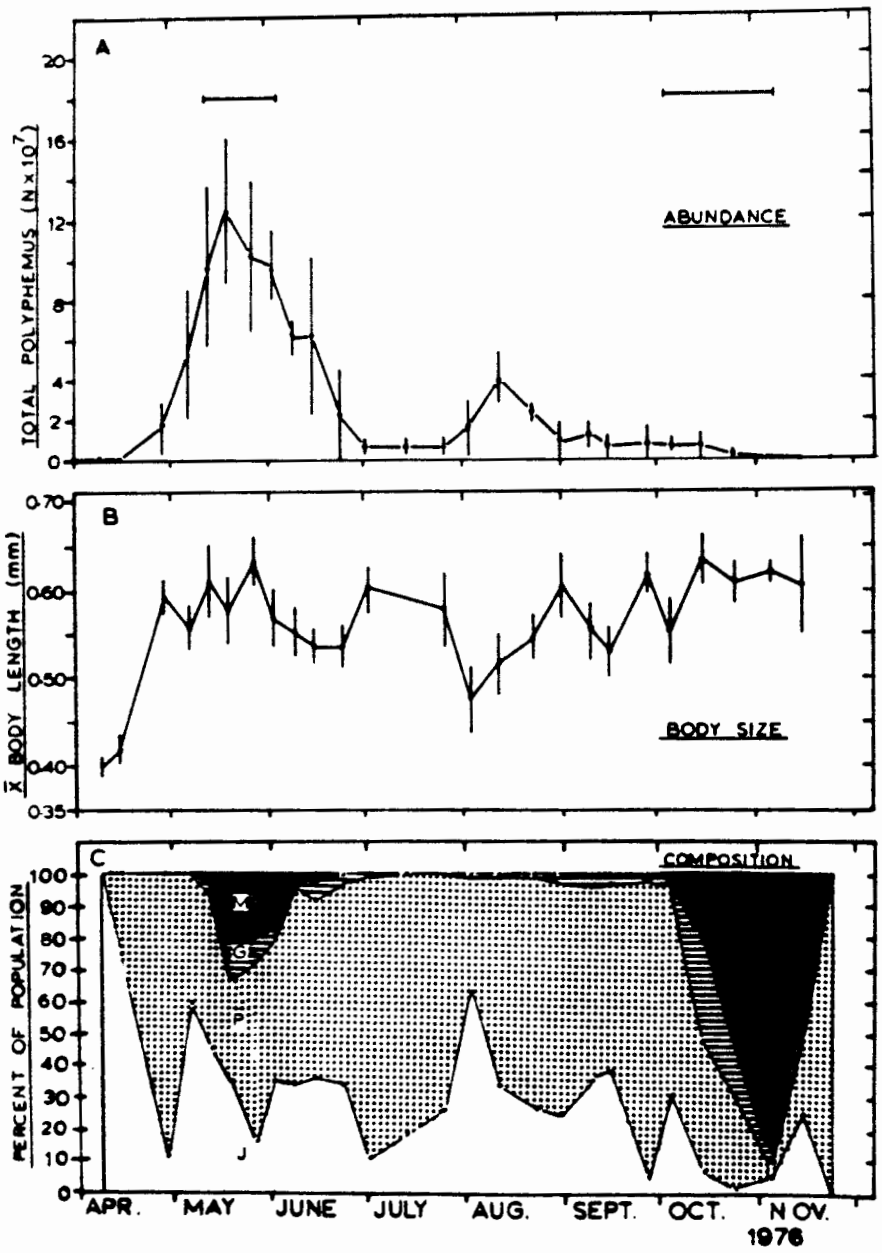


Figure 8. Seasonal abundance (Panel A), mean body length (Panel B), and percent composition (Panel C) of the 1976 Polyphemus population in Stonehouse Pond. Legend as in Figure 7.

to influence population mean size, with two to three peaks of juvenile composition and the corresponding depressions in body size occurring in the summer of each year.

In both years, following the spring maximum in abundance, sexual individuals appeared in the population (Figures 7 and 8, panel C). It is not known whether these sexual Polyphemus were third generation individuals or the second brood of exephippial animals. Resting eggs were produced by these sexual individuals. 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. Population mean body size increased in the fall as the percent of juveniles declined and the population was dominated by sexually mature individuals. In late fall, the population once more became dominated by parthenogenetic individuals, but total population size was extremely low.

Seasonal abundance curves for 1975 and 1976, therefore, were dominated by a spring maximum of four to five times greater than summer population levels. Population composition alternated between asexual (parthenogenetic) and sexual periods. Two periods of sexual reproduction (late spring and mid-fall) alternated with three asexual periods (early spring, a long period in the summer, and late fall). Changes in population mean body size were strongly influenced by parthenogenetic brood production and subsequent pulses of juveniles.

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 (Figure 9, panel B), and were characterized as three phases (spring, summer, and fall). The first broods in the spring from exephippial 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 two

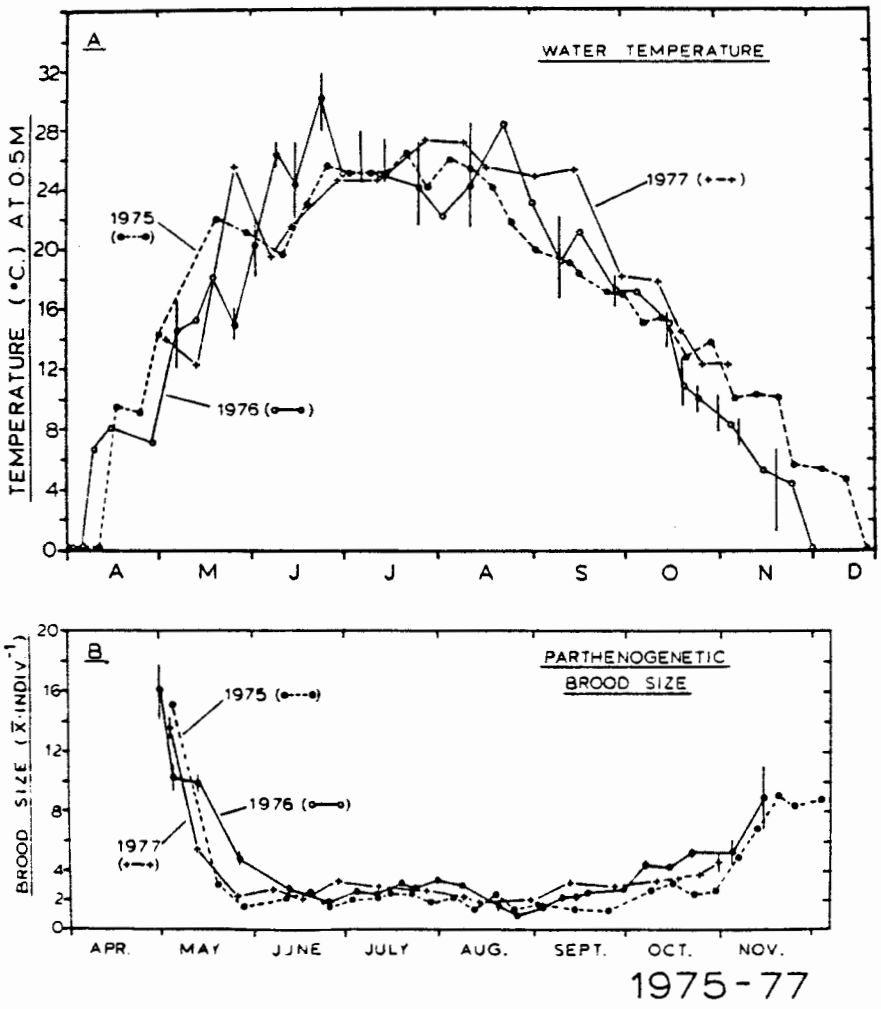


Figure 9. Seasonal change in median surface temperature (Panel A), and mean parthenogenetic brood size (Panel B) for Polyphemus in Stonehouse Pond. Vertical bars about the 1976-1977 temperature curves (Panel A) represent daily range in temperature. Vertical bars about the 1976-1977 mean brood size points (Panel B) represent 95% confidence intervals.

embryos per brood, and then increased in the fall.

In the spring and fall, brood size was inversely correlated with ambient water temperature (Figure 10). Linear regression equations best described this relationship and demonstrated a different response to temperature between seasons. Significant differences between the slopes ($p \leq 0.05$) 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.

The lack of correlation between brood size and temperature during the summer of all three years suggests 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 Chonochilus unicornis $r = -0.10$, $r = -0.20$; and Bosmina sp. $r = -0.29$, $r = -0.28$), and with total prey density calculated as volume (μ^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. Gamogenetic brood size was significantly smaller in spring than in fall, and averaged 2.17 resting eggs per brood ($\pm$ 95% C.I. = 0.46) for spring and 3.96 ($\pm$ 0.23 resting eggs per brood for fall. Butorina (1971a) also observed similar seasonal differences in gamogenetic brood size (2.5 eggs/brood, spring; 4.0 eggs/brood, fall).

When regressed against ambient water temperature, reciprocal

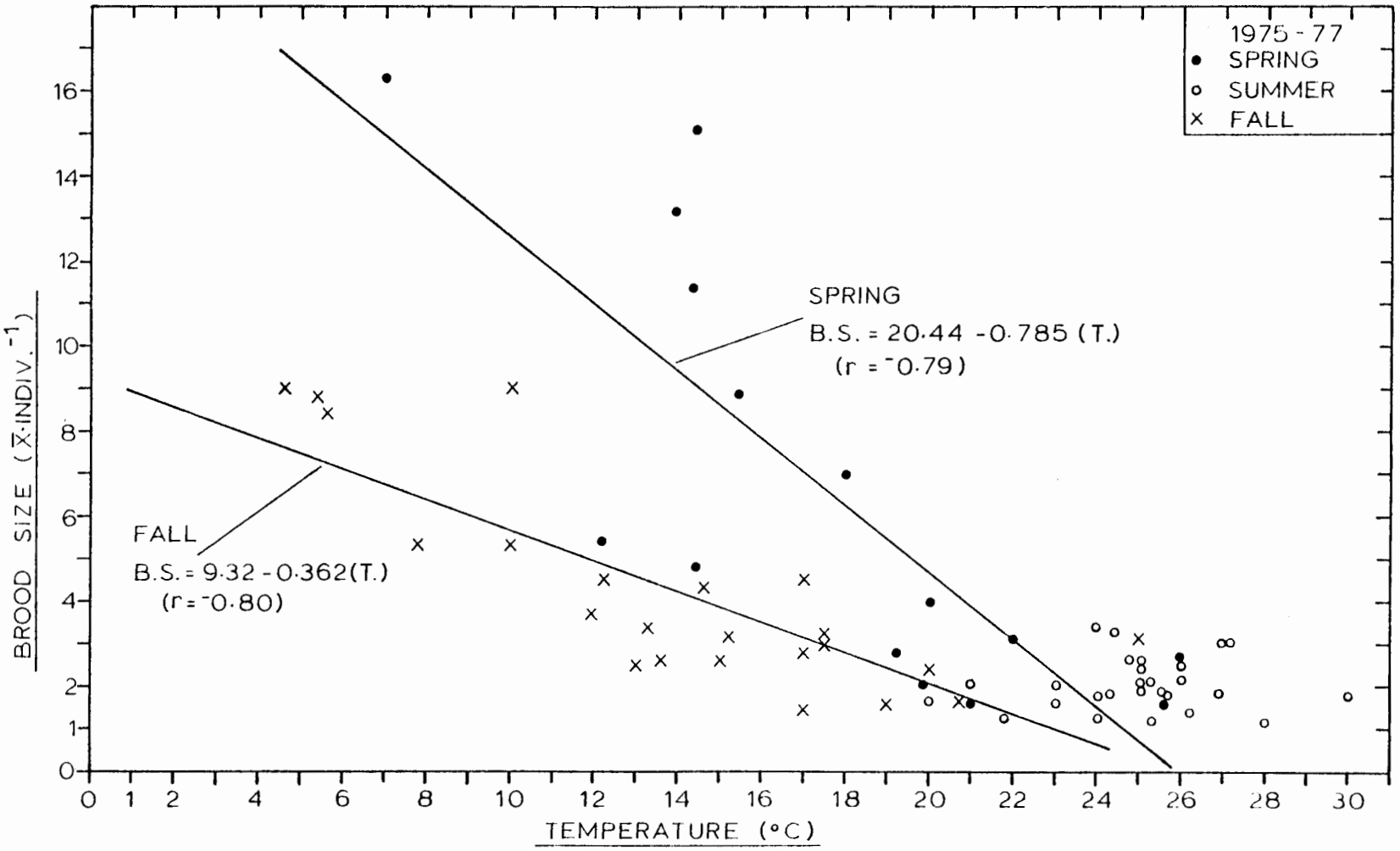


Figure 10. Scatter diagram of the seasonal relationships between parthenogenetic brood size and ambient water temperature for the 1975-1977 Polyphemus population in Stonehouse Pond. Regression lines are plotted and the relationship is given between brood size (B.S.) and temperature (T.) for spring and fall. The linear correlation coefficient, r, is also given. No correlation was found between temperature and brood size in the summer.

duration of brood development (1/D) exhibited a linear relationship. The equation was: $1/D = 0.0146$ (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 Q10 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.

Gamogenetic Versus Parthenogenetic Reproduction

The importance of gamogenetic and parthenogenetic reproduction at time of gamogenesis is quantified in Table 5. Parthenogenetic reproduction obviously accounted for the spring maximum in abundance observed in each year (Figures 7 and 8). However, the dominant period of resting egg production also occurred at the spring peak in abundance in both 1975 and 1976 (Table 5). This dominance was most striking in the spring of 1975, when the maximum number of resting eggs was 15 times greater than the fall maximum. 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 were lower in spring than in fall, the timing of gamogenesis with the spring maximum in abundance (horizontal bars, Figures 7 and 8, panel A) accounted for the greater numerical importance of this spring period of resting egg production.

On only one date in the spring and fall of 1975, resting eggs accounted for a greater percentage of the population reproductive output than parthenogenetic embryos (Table 5). 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 in the Polyphemus population throughout periods of resting egg production. 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 more important in 1975 than in 1976.

Table 5.

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.

Date	Total in Polyphemus population ($N \times 10^8$)	
	Parthenogenetic embryos	Resting eggs
20-V-75	1.3816 (54%)	1.1895 (46%)
28-V-75	0.3677 (28%)	0.9323 (72%)
11-VI-75	0.4118 (84%)	0.0796 (16%)
19-VI-75	0.2670 (89%)	0.0330 (11%)
2-X-75	0.2983 (87%)	0.0441 (13%)
9-X-75	0.2376 (75%)	0.0792 (25%)
16-X-75	0.0447 (48%)	0.0478 (52%)
23-X-75	0.0035 (48%)	0.0038 (52%)
30-X-75	0.0019 (20%)	0.0075 (80%)
19-V-76	2.8760 (87%)	0.4181 (13%)
27-V-76	2.7150 (94%)	0.1793 (6%)
2-VI-76	1.7169 (96%)	0.0632 (4%)
15-X-76	0.1309 (57%)	0.0968 (43%)
25-X-76	0.0354 (69%)	0.0157 (31%)
5-XI-76	0.0005 (55%)	0.0004 (45%)

Population Growth

Figures 11 and 12 summarize seasonal change in abundance, intrinsic rate of increase, natality, and mortality for 1975 and 1976, respectively. Seasonal abundance curves (Figures 11 and 12, panel A) were repeated from Figures 7 and 8 (panel A) for ease of comparison to population statistics. The range of r values (Figures 11 and 12, panel B) 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 (Figures 11 and 12, panel A).

Seasonal changes in r based on total population size reflected changes in seasonal abundance. Highest r values were observed in the spring of each year just prior to the spring maximum in abundance. 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.

Estimates of b using the formulae of Edmondson (1960), Caswell (1972), and Paloheimo (1974) were nearly identical throughout most of each year. In early spring and late fall, however, these estimates of b differed by as much as 58%. Cold water temperatures resulting in long duration of development (Edmondson, 1960; Paloheimo, 1974) and large brood sizes (Figure 9) 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 (Figures 11 and 12, panel C).

In early spring of both years, b was highest and was equal to r since d was zero (Figures 11 and 12, panel C). A sharp decrease in b immediately preceeded the spring maximum in abundance, and was probably due to declining brood size (Figure 9), and to a large percent of sexual individuals in the population (Figures 7 and 8, panel C) which produced resting eggs and, therefore, did not contribute to natality. The decrease in abundance following spring

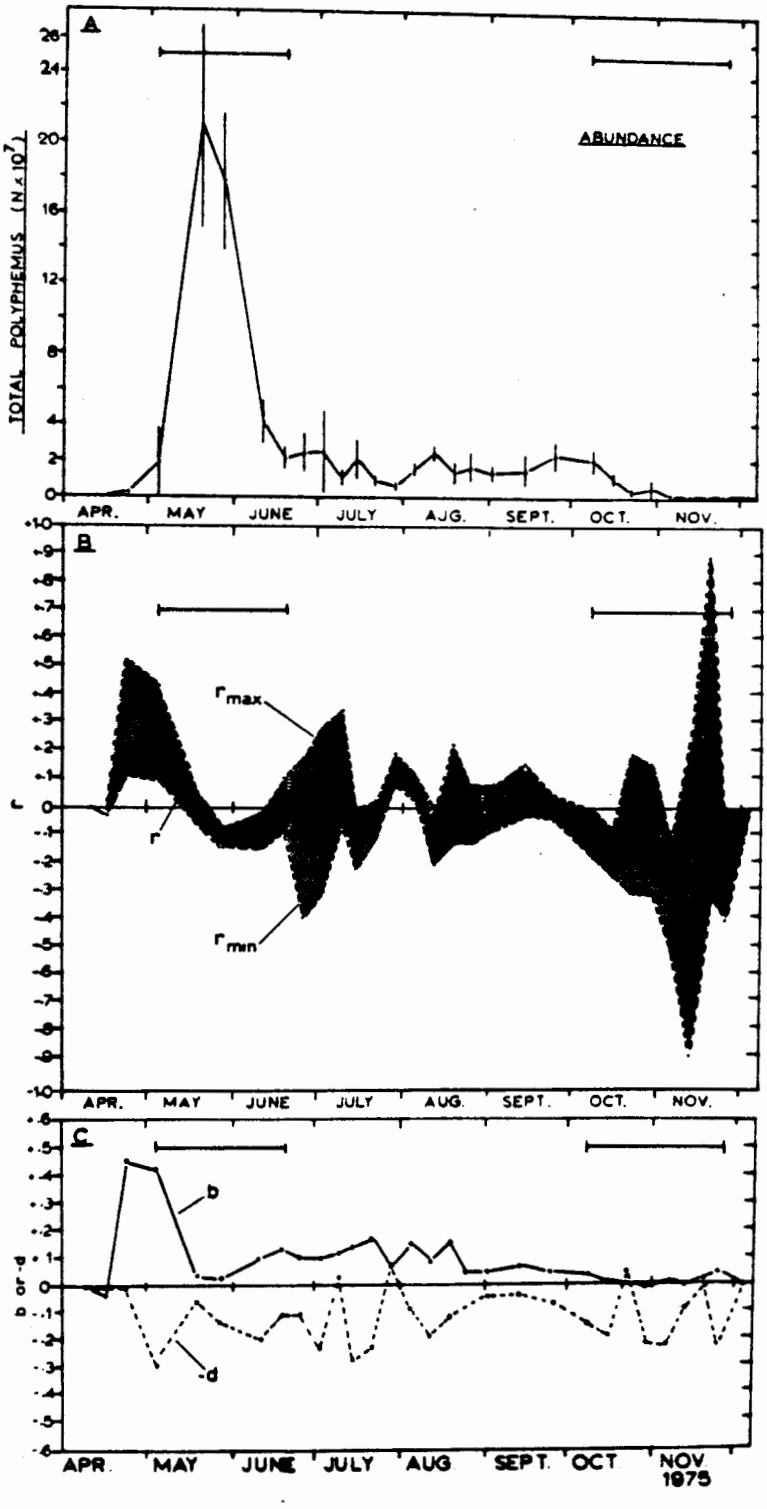


Figure 11. Seasonal change in population statistics for the 1975 Polyphemus population of Stonehouse Pond. Panel A is the seasonal abundance as in Figure 7. Panel B is the instantaneous rate of population increase (r) based on estimates of total population size (solid line). Dashed lines represent r based on 95% confidence limit extremes about population total (r_{max} and r_{min}). Shaded area between r_{max} and r_{min} represents the range of possible r values. Panel C shows 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.

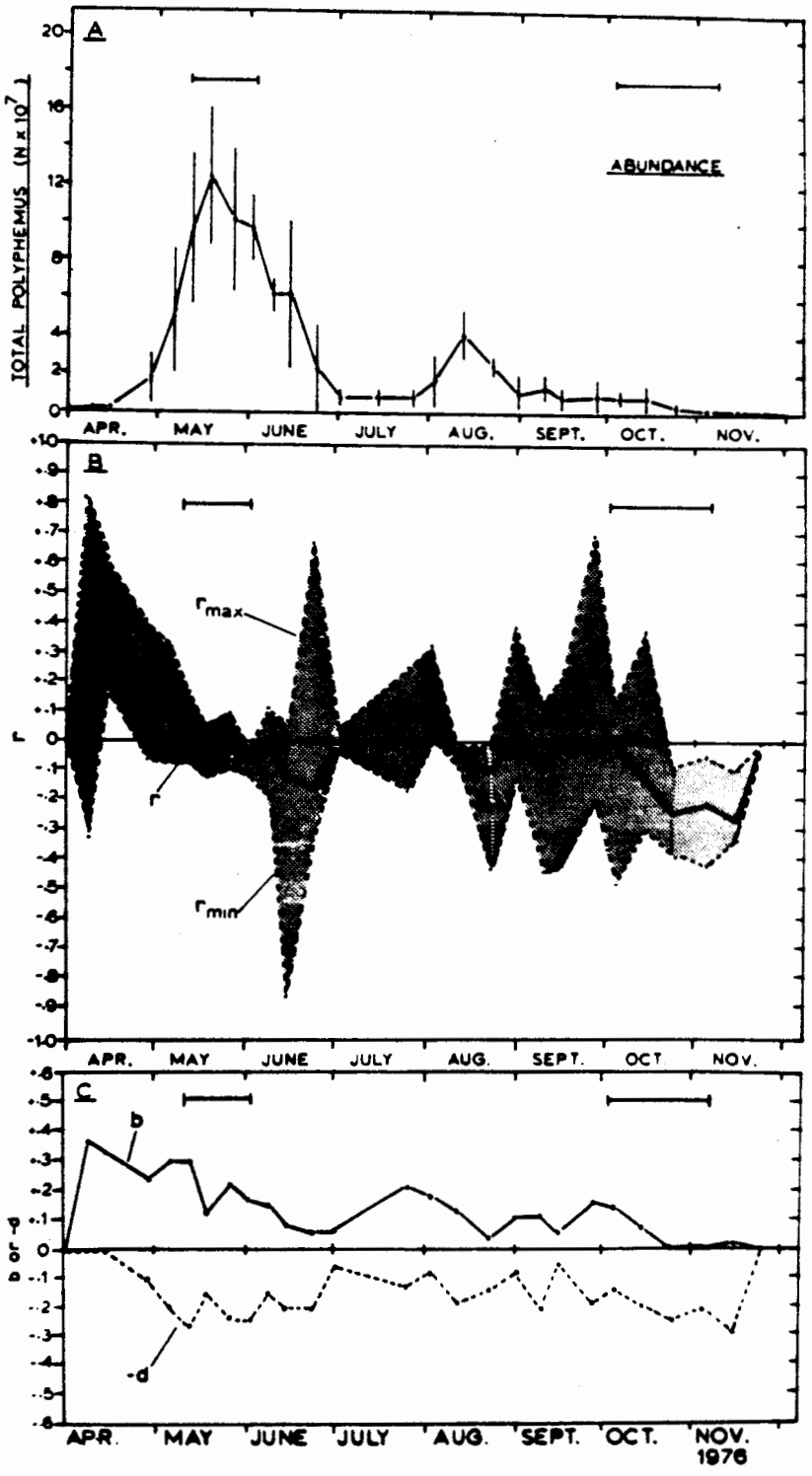


Figure 12. Seasonal change in population statistics for the 1976 Polyphemus population of Stonehouse Pond. Panel A shows the seasonal abundance as in Figure 8. Panel B shows the instantaneous rate of population increase - r. Panel C shows the instantaneous birth (b) and death (d) rates. Legend as in Figure 11.

maximum was primarily due to this change in b, since d was relatively constant at that time.

The increase in r associated with each secondary peak in abundance in early August resulted from different relationships between b and d. In 1975, the rise in r was associated with a decrease in d while b remained relatively unchanged. In 1976, an increase in r was due to a rise in b while d remained relatively constant.

Finally, negative r values observed in late fall were probably the result of an increase in d as sexual individuals died while per capita b was nearly zero.

Body Size

Seasonal abundance curves are often used to estimate zooplankton productivity, provided size-frequency and length-weight relationships are known. While the purpose of this study was not to estimate productivity, it was desirable to have a measure of body size independent of brood characteristics, which could be used to compare size differences between sexual and developmental stages of Polyphemus individuals and to identify size-related feeding classes. All reports of Polyphemus body size have been based on measurement from the anterior edge of the eye to the posterior edge of the brood pouch, hereafter referred to as brood length (BRL Table 6). This measure was correlated with dry weight (Dumont et al., 1975) and organic carbon content of Polyphemus (Butorina, 1973), but it may be influenced by brood size and/or developmental stage of embryos. BRL was, therefore, compared to a second measure of body size, body length (BRL Table 6), taken from the anterior edge of the eye to the base of the caudal pedicle.

Table 6 summarizes the relationship between BL, BRL, brood size and state of development for Polyphemus. In all cases, there was a significant linear relationship between BL and BRL, with all slope coefficients and intercepts significantly greater than zero ($p < 0.001$). Slope coefficients were also not significantly different

Table 6.

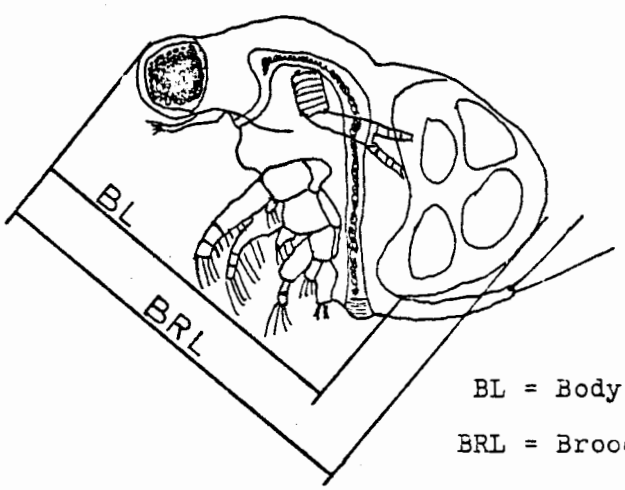
Summary of regression analysis of the relationship between brood size, state of brood development, and two measures of body size for parthenogenetic female Polyphemus. See text for additional information.

Brood information		Number	Regression equations		
number of embryos	state of develop.	observed	slope	intercept in mm.	r
1	clear	8	0.823	0.230	0.703
	mature	16	0.683	0.464	0.655
2	clear	51	0.809	0.260	0.912
	mature	51	0.811	0.349	0.858
3	clear	50	0.747	0.340	0.856
	mature	50	0.716	0.477	0.854
4	mature	50	0.477	0.750	0.624
5	mature	7	0.735	0.501	0.773

linear regression equations, $Y = mX + b$

Y = Brood length in milimeters; X = Body length in mm.

m = slope of regression line; b = Y axis intercept in mm.



BL = Body length

BRL = Brood length

from each other ($p > 0.05$) indicating the relationship between BL and BRL was similar regardless of brood size or state of development. However, Y intercepts were significantly different for each developmental state within a given brood size ($p < 0.01$), reflecting the larger BRL for each BL when mature embryos were found in the brood pouch. BRL was, therefore, not independent of brood development, and larger parthenogenetic females did not necessarily carry larger brood sizes.

Since isolated Polyphemus individuals were not observed to moult between the clear and black-eyed state, growth of the female cannot account for this difference in BRL. Also, BRL for broods with green-eyed embryos (Table 4) which were not reported in Table 6, were significantly greater than BRL for clear broods ($p < 0.01$), but indistinguishable from BRL for broods with black-eyed embryos ($p > 0.05$). These observations suggest the differences in BRL for different developmental stages may be due to growth of the embryos causing the carapace (which only covers the brood pouch and is moulted to liberate the brood) to balloon or pull away from the body in a posterior-lateral direction. BRL was, therefore, not independent of brood development, and BL was used to measure body size.

Seasonal Change in Body Length

Scatter diagrams in Figure 13 summarizes seasonal changes in maximum and minimum body length observed on each date for parthenogenetic females and juveniles. While juvenile size (Figure 13, panel C) and parthenogenetic female size (Figure 13, panel B) varied little throughout the year, the maximum body size of parthenogenetic females (Figure 13, panel A) was generally greatest in spring. The scatter of points about each mean body size line (Figure 13) suggests that body size may actually vary curvilinearly throughout the year, with largest body sizes occurring in the spring and fall. This was most noticeable for 1975, but was not tested statistically since curvilinearity was not apparent in both years.

Mean body length measurements for the two-year study period were, therefore, used to compare body size ranges between juvenile,

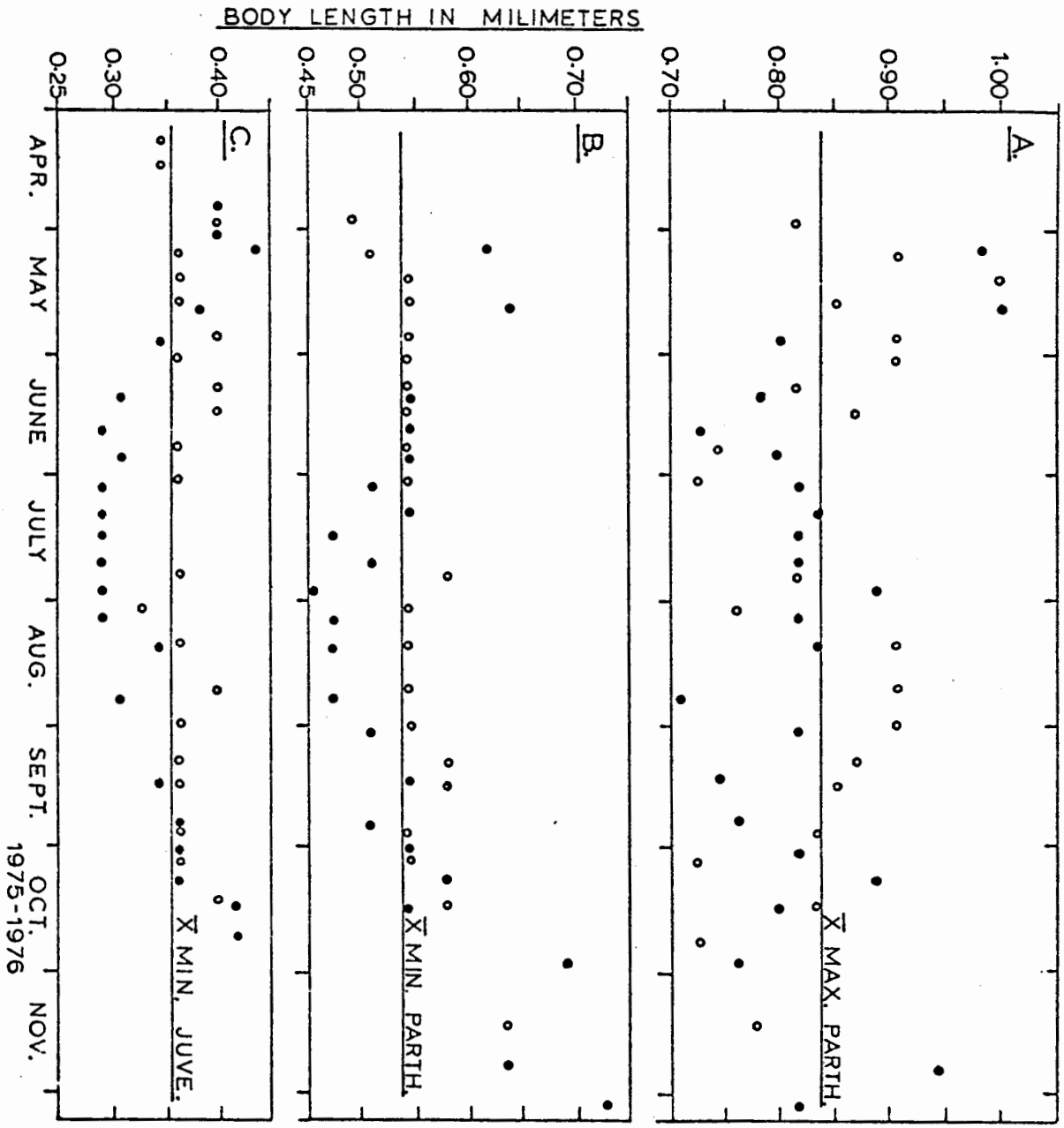


Figure 13. Scatter diagram of the size range of juvenile and parthenogenetic female Polyphemus in 1975 (solid circles) and 1976 (open circles).
Panel A is the maximum size of parthenogenetic females.
Panel B is the minimum size of parthenogenetic females.
Panel C is the minimum size of juvenile Polyphemus.
The horizontal line in each panel represents the mean for all points in each category.

parthenogenetic female, gamogenetic female, and male Polyphemus (Table 7). Parthenogenetic females ranged over a significantly greater body size than did gamogenetic females or males, and attained the largest body lengths. Gamogenetic females varied the least in size. Finally, males were generally smaller than gamogenetic females.

Table 7.

Comparison of range in body sizes for juveniles, and for male, parthenogenetic female, and gamogenetic female Polyphemus. Mean maximum and minimum body length (with confidence limits) and overall range in size were based on samples from Stonehouse Pond for 1975 and 1976.

Classification	Body length (mm) Mean ± 2*SE $\bar{X}$		Overall range in length (mm)
Juvenile			
Maximum	-	-	0.528
Minimum	0.357	0.012	0.291
Parthenogenetic			
Maximum	0.838	0.023	1.165
Minimum	0.539	0.012	0.455
Gamogenetic			
Maximum	0.761	0.034	1.092
Minimum	0.628	0.041	0.546
Males			
Maximum	0.728	0.011	0.764
Minimum	0.546	0.002	0.528
Resolution to nearest occular micrometer unit; 1 occular unit = 0.0182 mm.			

DISCUSSION

The population dynamics of Polyphemus were surprisingly similar to Holopedium gibberum (Lampert and Krause, 1976). Both Polyphemus and Holopedium had seasonal abundance cycles characterized by one relatively large spring maximum originating from resting eggs in the spring. Holopedium also had two periods of sexual reproduction and resting egg production (June and October). Finally, in both Polyphemus and Holopedium, the decline in population size following spring maximum was probably due to a decline in natality associated with the production of resting eggs.

In contrast to the Polyphemus in this study, few cladocerans have been reported to have two periods of sexual reproduction and resting egg production. 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 was also observed for Polyphemus by Butorina (1971a), and has occasionally been reported for Daphnia (e.g. Daphnia pulex, Stross, 1969).

Another aspect of Polyphemus population 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 (Figures 7 and 8, panel C). Although some cladoceran populations may at times have nearly 50% males (e.g. Leptodora kindtii, Cummins et al., 1969), values as high as 90 to 97% observed in this study appear unique.

With respect to the total Polyphemus population, the spring period of gamogenesis was most important (Table 5). 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). Spring production of resting eggs is generally considered an adaptation to life in ephemeral habitats such as shallow ponds which dry up in the summer (Hutchinson, 1967; Pennak, 1953). Flooding of these ponds in the fall results in hatching of the spring

resting eggs and eventually a fall period of resting eggs production. It may be possible, therefore, that the dicyclic pattern of resting egg production observed in the Polyphemus population was an adaptation to life in ephemeral habitats which was retained when this species inhabited larger and more "permanent" lacustrine habitats. It is also possible that this dicyclic pattern of gamogenesis may be quite common but reduced among other lacustrine cladocerans, and was rarely detected due to limited sampling designs. A comparison of Polyphemus population dynamics between ephemeral ponds and "permanent" lakes may shed some light on the role of alternation of reproductive modes in the life strategy of Polyphemus.

Exephippial Polyphemus in the spring of each year were more fecund and attained larger body sizes than individuals at any other time. Edmondson (1955) also observed larger body sizes associated with exephippial Daphnia in an arctic pond. Since the measure of body size used in this study was independent of brood size or development (Table 6), size differences must be the result of differential growth. The appearance of parthenogenetic females with large body and brood sizes in late fall, raises some interesting biological questions. Were these late fall animals exephippial Polyphemus? Do exephippial animals have intrinsically different growth rates than individuals from non-ephippial eggs, or is it some characteristic(s) of the nutrition and/or temperature environment which account for differential growth? Research has indicated the importance of temperature and food to cladoceran growth (e.g. Hall, 1964; Hutchinson, 1967), but clearly experimental work is needed on their relationship to the growth of exephippial animals.

The natality and mortality rates presented in this study were calculated using a per capita egg ratio (Paloheimo, 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-VII-75; 0.31, 2-VI-76; 0.37, 9-VI-76). In contrast, Hall (1964), Wright (1965), Applegate and Mullan (1969), and Prepas and Rigler (1978) all observed Daphnia mortalities in excess of 0.5 in the summer. In contrast to these Daphnia populations, a mid-summer peak in mortality (d) was not observed for Polyphemus and d rarely exceeded 0.2. Relatively low mortality rates of less than 0.2 were also observed for Holopedium (Lampert and Krause, 1976). The high mortality rates observed by Hall (1964) and Wright (1965) were probably due to Leptodora predation, while fish predation and possible Leptodora predation contributed to high Daphnia mortality in the study of Applegate and Mullan (1969). Death of neonates 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. trout predation (see Appendix 1), probably do not change significantly throughout the year, and were not as important to population dynamics as were changes in natality. 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 overall 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 to a summer plateau 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 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.

IV. PATCH STRUCTURE AND PATTERNS OF PATCHINESS IN A *POLYPHEMUS PEDICULUS* POPULATION

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.

In this section, the temporal and spatial patterns of patchiness in a population of the predatory cladoceran, *Polyphemus pediculus* (L.) are examined. 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.

MATERIALS AND METHODS

Terminology

It is 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.

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. 14). 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. 14). Additional physical, chemical, and biological information may be found in Ferrante (1974).

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 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 (Butorina, 1963; Hutchinson, 1967), Stonehouse Pond was divided horizontally into six major littoral sections and one limnetic section based on morphometric 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. 15). 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

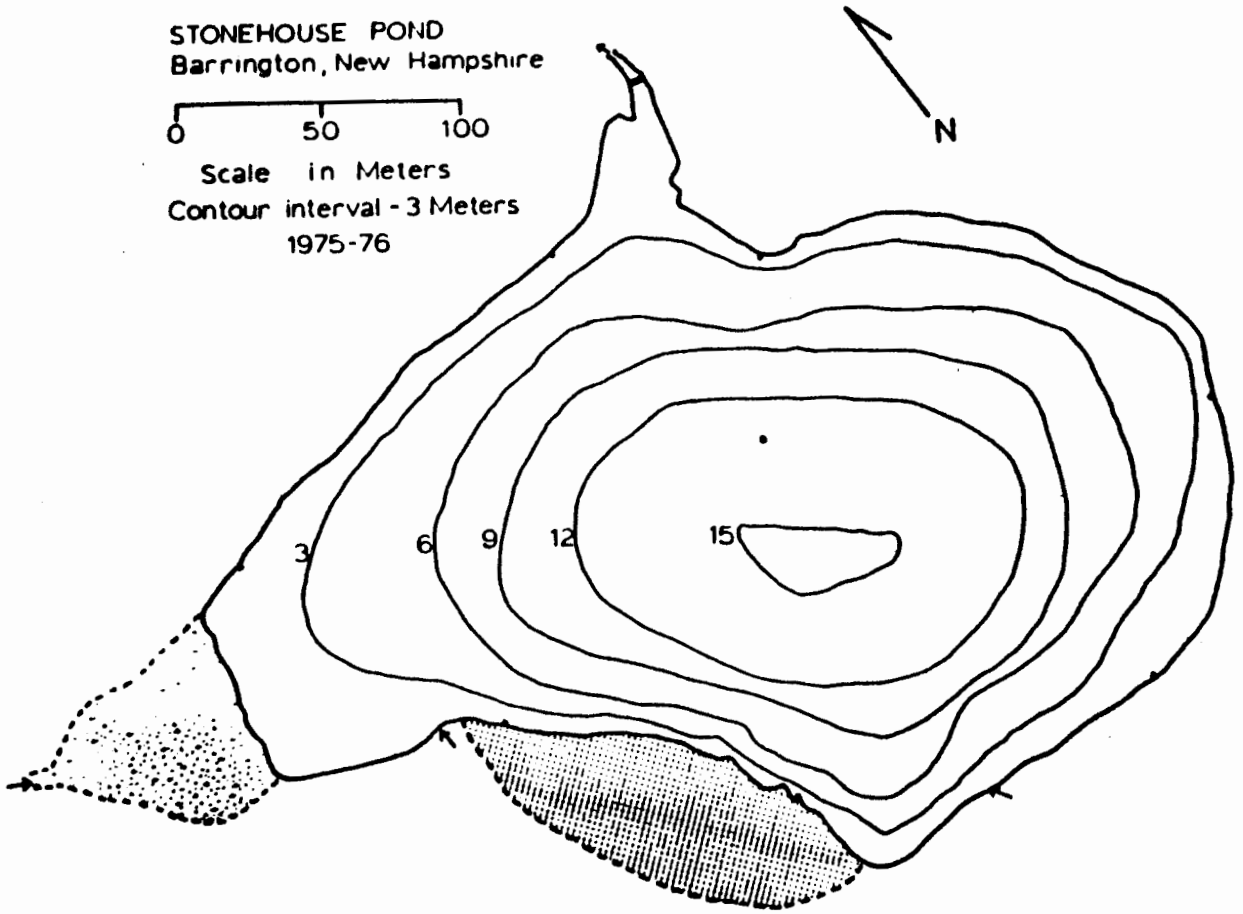


Figure 14. Morphometric map of Stonehouse Pond, Barrington, New Hampshire, U.S.A. The major inlet is through a stream which flows into a swamp on the west shore. The shaded area on the southwest shore is a granite cliff.

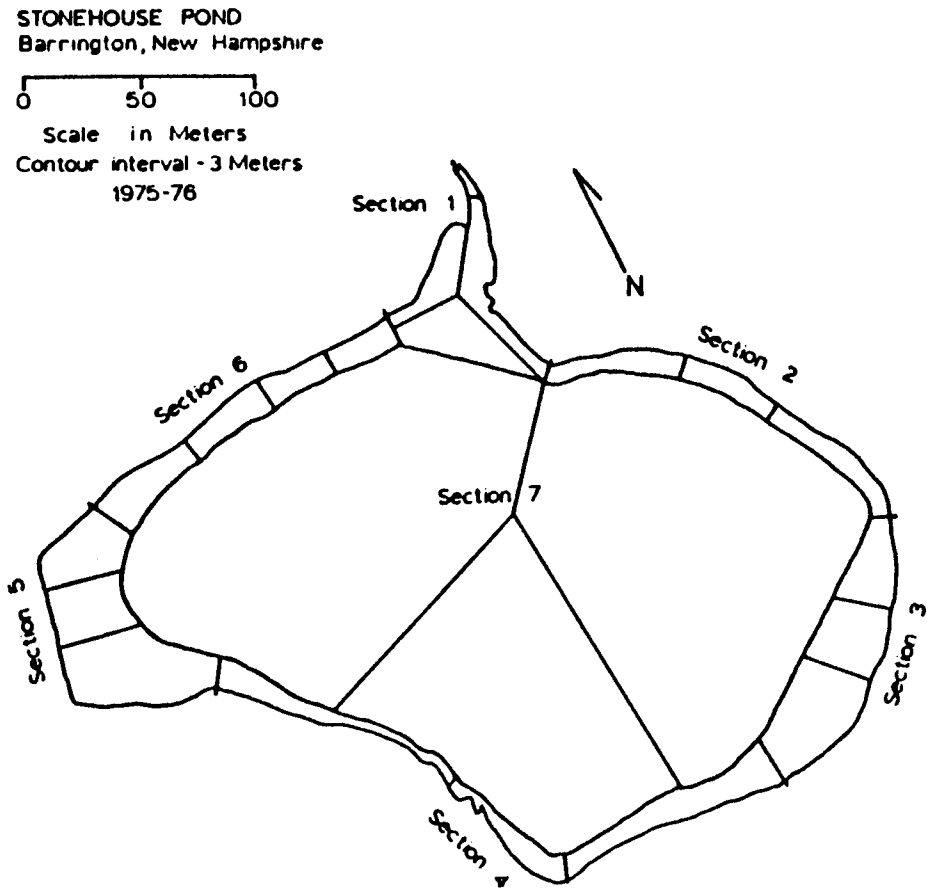


Figure 15. Stonehouse Pond sections and subsections which were used for stratified random sampling and spatial mapping.

occurred in these sections (Fig. 16). 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 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 meters long, 1500 liters). Subsamples from these integrated tows provided whole-lake estimates of Polyphemus population composition.

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.

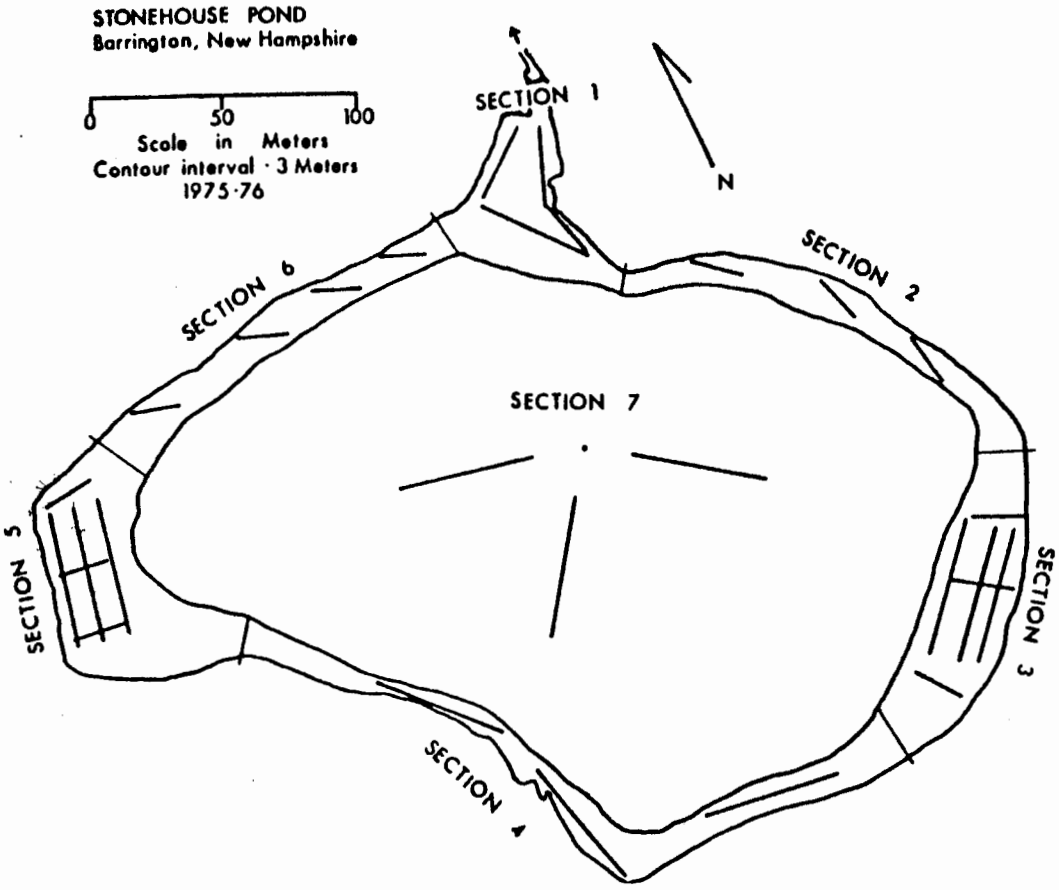


Figure 16. Location of Clarke-Bumpus net tows in relation to the major sections of Stonehouse Pond.

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.

Data Analysis

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 ($\overline{Z}$) 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 (Z90%), were calculated using a modification of the quartile method of Pennak (1943). This method involved computing the mean desnity of all samples at each 1/2 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 $\overline{Z}$ or Z90% was determined by linear extrapolation between depths. The difference between $\overline{Z}$ and Z90%, ΔZ, 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 $\overline{Z}$. 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.

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$\cdot M^{-2}$ for each of the 22 lake subsections (Fig. 15), and then divided by whole-lake mean density (indiv.$\cdot M^{-2}$) 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.

Aggregation indices

Variance to mean ratio ($V/\overline{X}$) and subsequent χ^2 Poisson variance test (George, 1974), and Lloyd's mean crowding ($\overset{*}{M}$) and patchiness ($\overset{*}{M}/\overline{X}$) indices (Lloyd, 1967) were used to describe statistical dispersion. Regression of log-transformed values of these parameters against the log of mean population density ($\overline{X}$) 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 require 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.

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 precipitation. 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 ($\chi^2 = 26.8$, $p < 0.001$), 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. 14) 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.

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.

RESULTS

Seasonal Abundance and Population Composition

Figs. 17 and 18 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 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.

Seasonal Horizontal Distribution

Figs. 19A and 19B 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. 17A-B, 18A-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. 19, 25 M). By early summer, the population

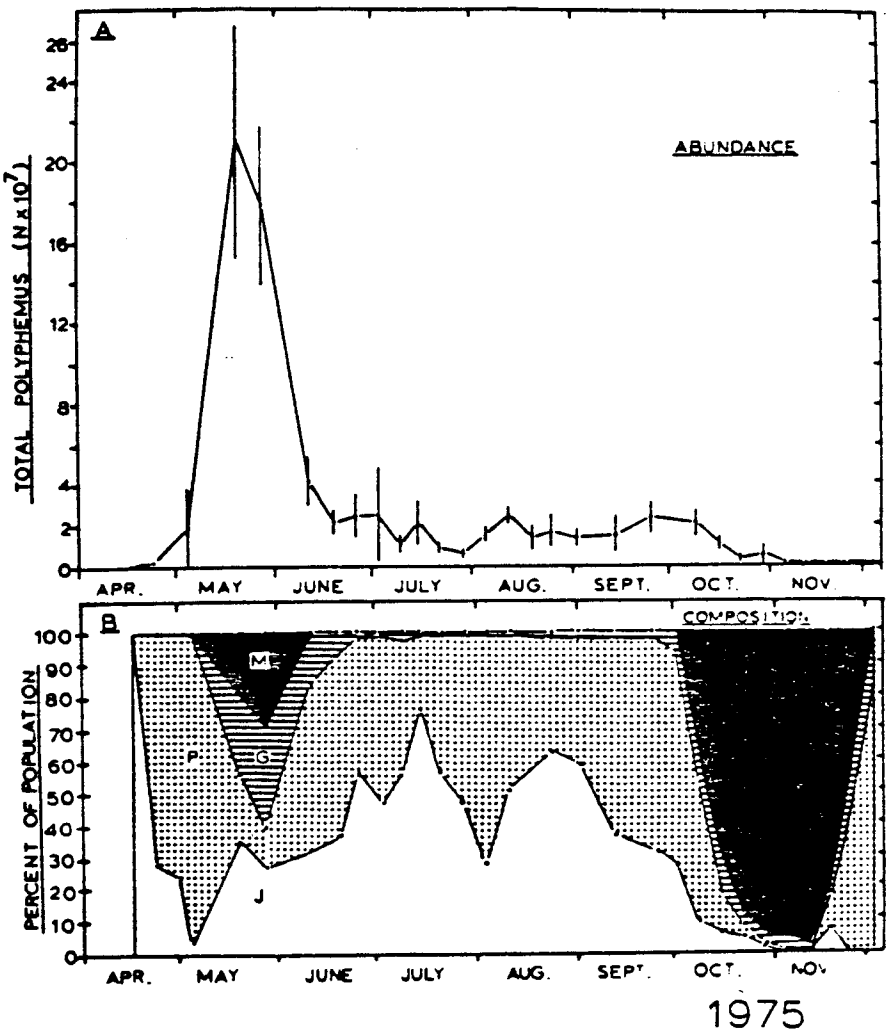


Figure 17. Whole-lake seasonal abundance (A) and composition (B) of the 1975 Polyphemus population in Stonehouse Pond. Vertical bars in 4A represent 95% confidence intervals. In 4B, dark shading (M) represents males, lines (G) - gamogenetic females, dots (P) - parthenogenetic females, and clear (J) - juveniles.

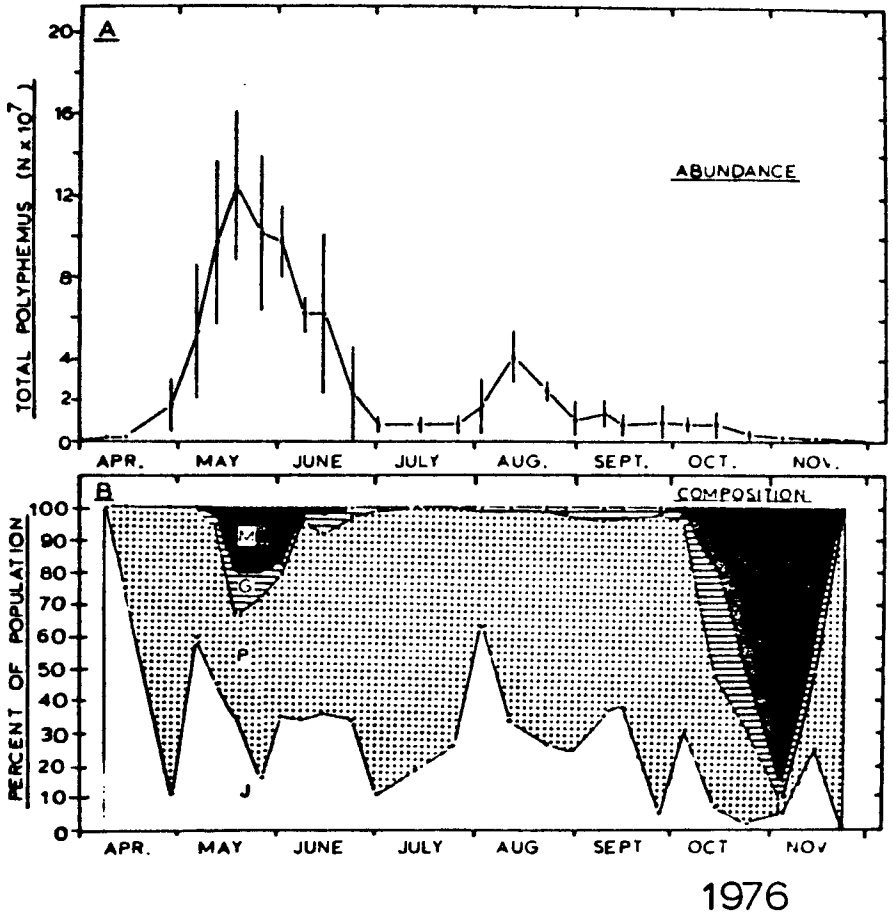


Figure 18. Whole-lake seasonal abundance (A) and composition (B) of the 1976 Polyphemus population in Stonehouse Pond. Legend as in Figure 17.

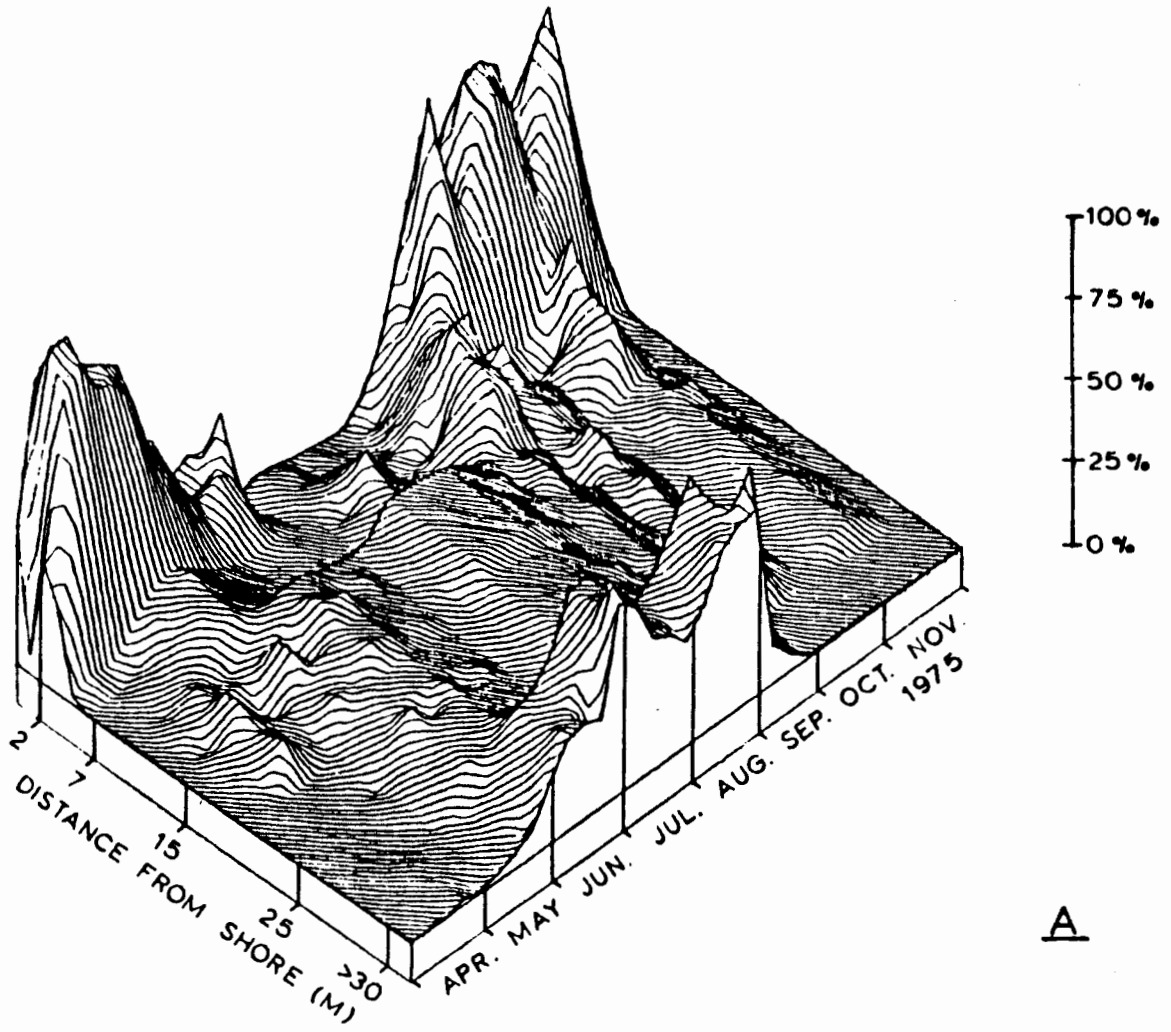
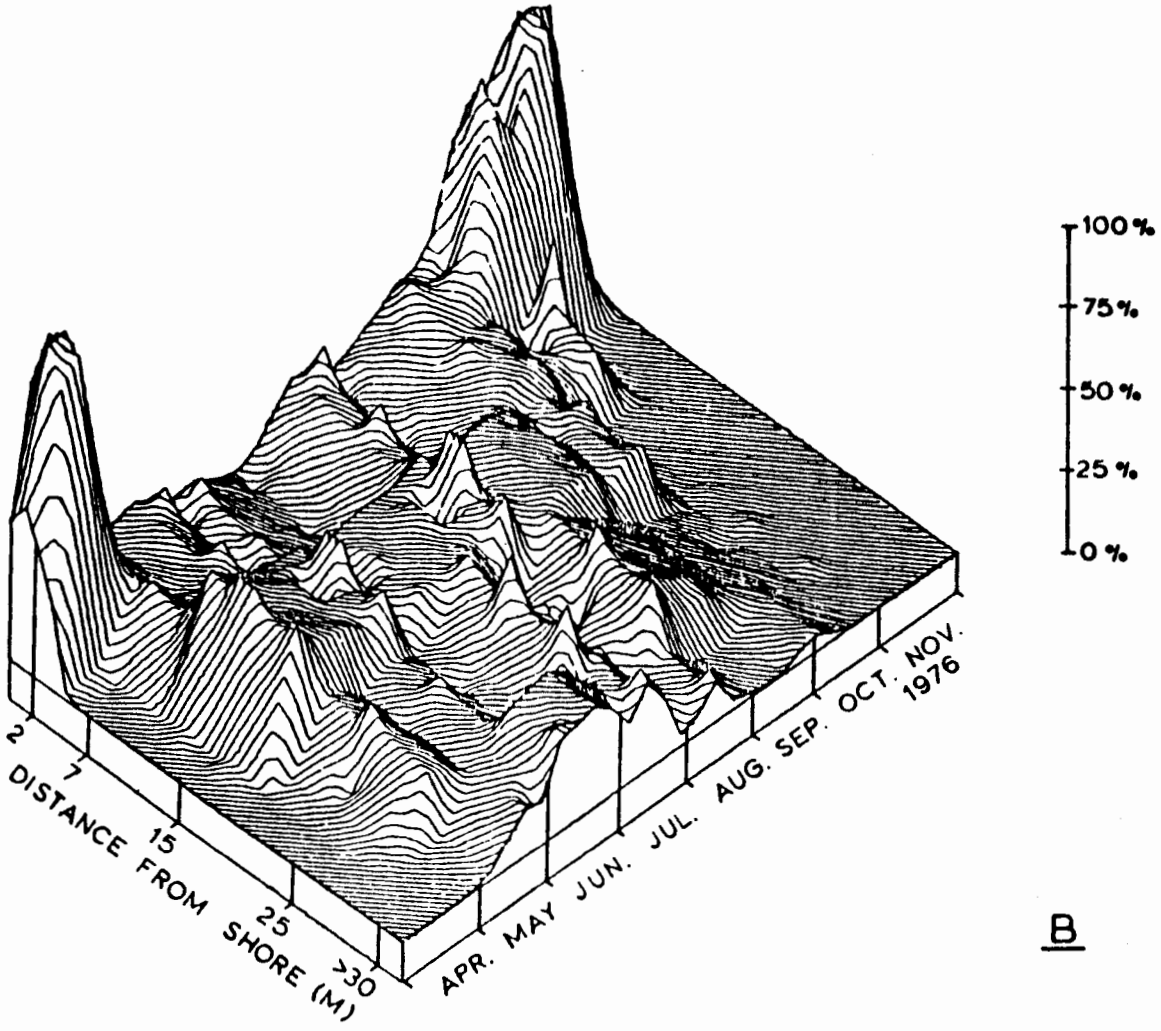


Figure 19. Three-dimensional representation of the seasonal change in horizontal distribution of the total Polyphemus population of Stonehouse Pond. A. 1975. B. 1976. X axis = date of year, Y axis = distance from shore in meters (note; Limnetic zone represented by > 30 meters from shore), Z axis = percent of total Polyphemus population.


100%
75%
50%
25%
0%
2
7
15
25
>30
DISTANCE FROM SHORE (M)
APR. MAY JUN. JUL. AUG. SEP. OCT. NOV.
1976

B

had declined to a summer plateau following a period of sexual reproduction, and it was beginning to appear in the limnetic zone (Fig. 19, > 30 M). Throughout the long summer period of parthenogenesis, the greatest proportion of the population was found in the limnetic zone. Small peaks and valleys in the summer period (Figs. 19A and 19B) 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.

Seasonal Vertical Distribution

The Polyphemus population was rarely found below 2 meters of depth (Fig. 20). Similarities between littoral (Fig. 20) or limnetic (Fig. 20) vertical profile and whole-lake profile (Fig. 20) reflected the changes in horizontal distribution observed in 1975 (Fig. 19). 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. 20D). 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).

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-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

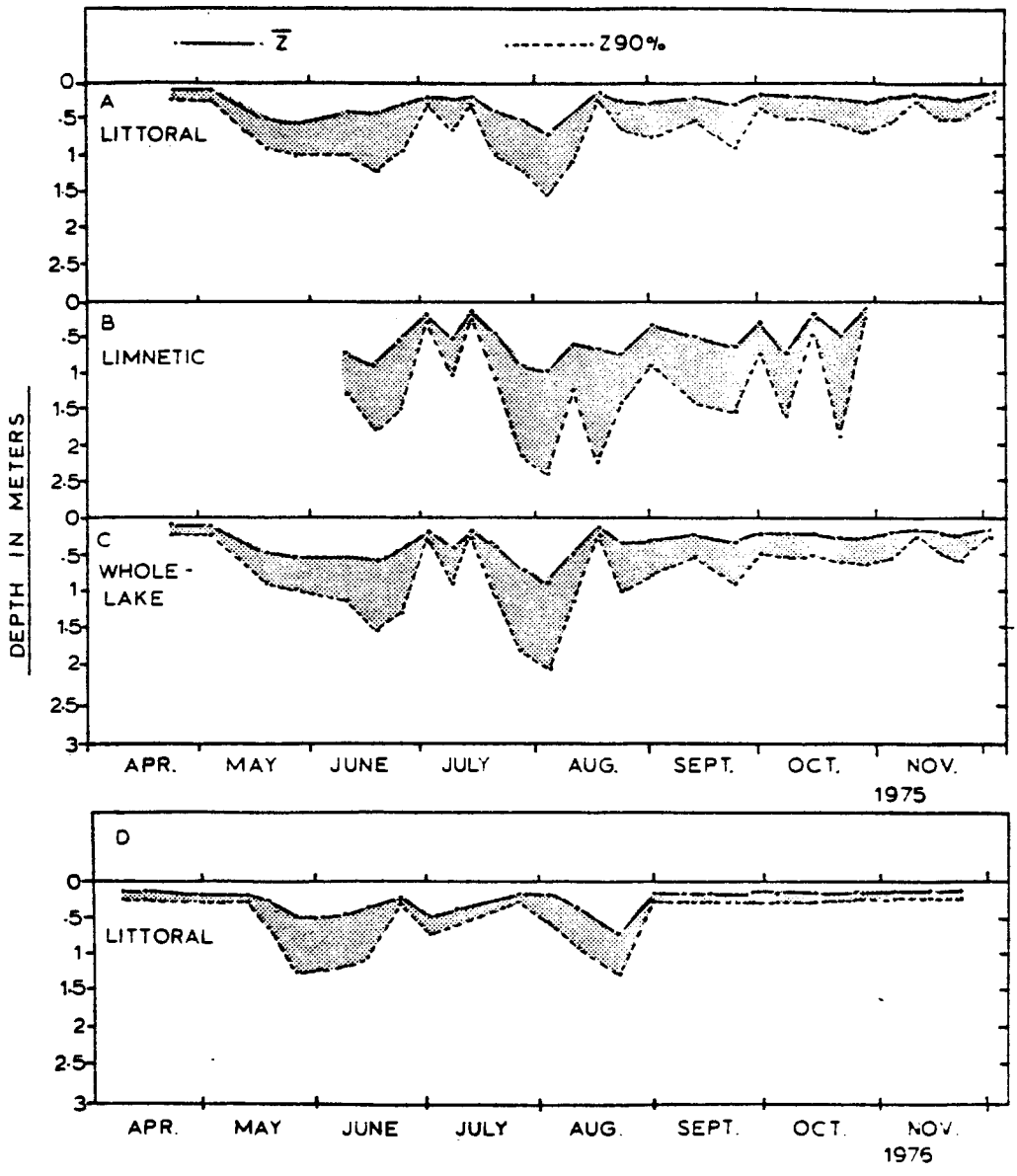


Figure 20. Seasonal variation in median depth ($\overline{Z}$) and Z90% of the total Polyphemus population in Stonehouse Pond. The width of the shaded area = ΔZ. A. 1975 littoral, B. 1975 limnetic, C. 1975 whole-lake, D. 1976 littoral. See text for additional explanation.

was limited to the littoral zone (Table 8). In the spring and fall, 2 - 3 Polyphemus patches were observed on each sampling date (Figs. 21A-D). In the summer, in contrast, typically one patch was found (Figs. 21E-G), and occasionally no patch at all was seen (Fig. 21H).

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 9. This 2 x 2 contingency table also revealed that wind direction was not differentially correlated with patch location between seasons (χ^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 in the upper left corner of each map in Figs. 21A-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. 21E-F. Examples of dates where no correlation was found between patch location and wind direction include Figs. 21G-H.

A significantly greater number of patches were observed in littoral section 3 ($\chi^2 = 14.11$, $p < 0.005$) than would be expected for the average littoral section (Table 8). 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

Table 8.

Classification of all Polyphemus patches observed in lake sections of Stonehouse Pond for 1975 and 1976. See text for definition of patch.

Patch location (lake section)	Number of patches observed			
	1975	1976	total	%
Littoral				
Section 1	3	6	9	14 %
Section 2	3	2	5	8 %
Section 3	16	5	21	33 %
Section 4	4	7	11	17 %
Section 5	8	6	14	22 %
Section 6	1	2	3	5 %
Littoral total	35	28	63	99 %
Limnetic				
Section 7	1	0	1	1 %
Grand totals	36	28	64	

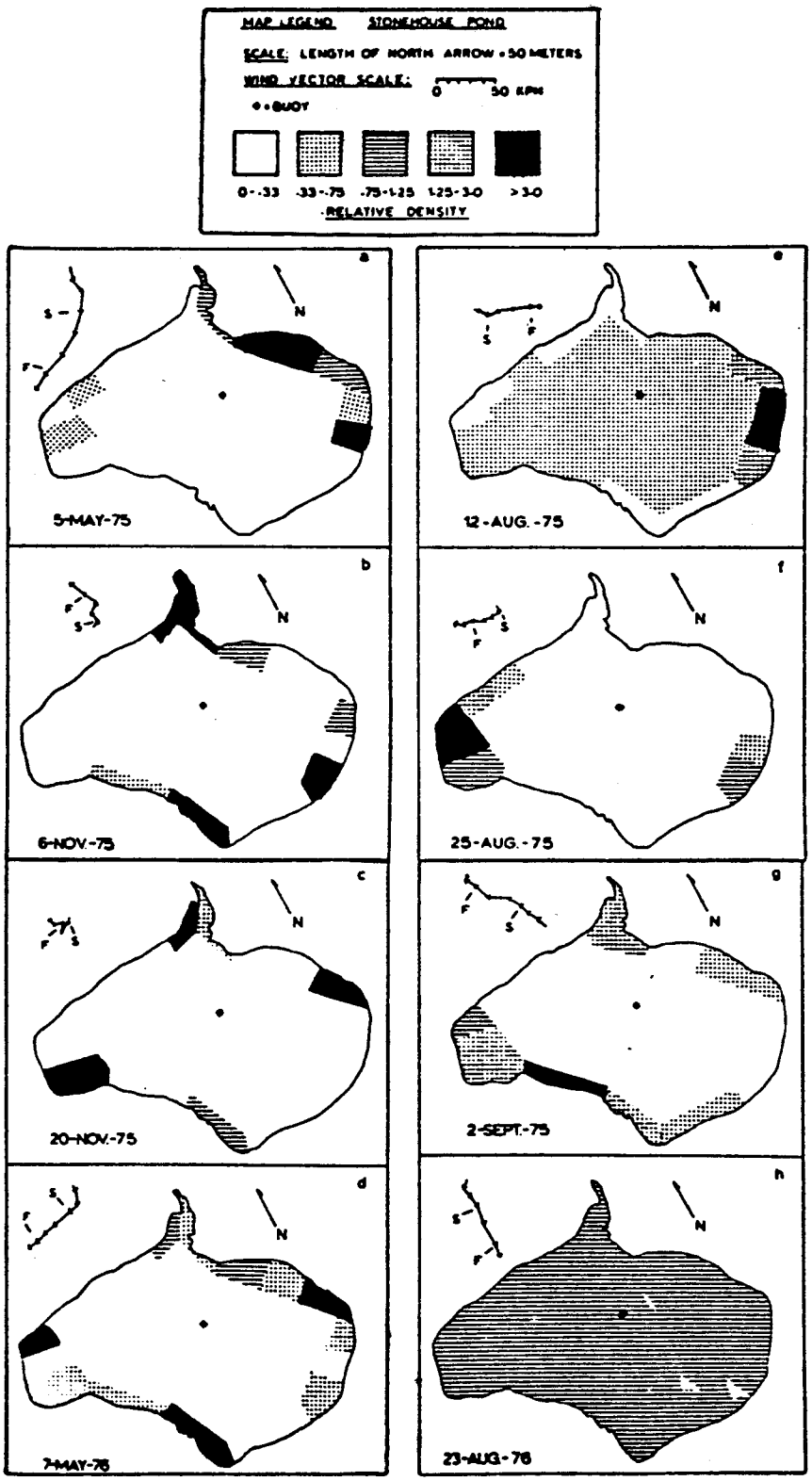


Figure 21. Seasonal variation of Polyphemus patch location in Stonehouse Pond for selected dates in 1975 and 1976. Wind vector diagrams represent wind speed (kilometers·hour^{-1}) and direction (from true north) taken at 3 hour intervals from 0100 to 2200 of the sampling date. Vectors applicable to the sampling period fall between S (start) and F (finish). See text for additional information.

Table 9.

2 X 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.

Correlation	Spring-Fall	Summer	n	Percent
Positive (+)	21	19	40	73 %
None(0 or -)	10	5	15	27 %
n	31	24	55	
Percent	68 %	79 %		
χ^2 for independence = 0.833, $0.25 < p < 0.50$				
χ^2 for wind correlation = 10.473, $p < 0.005$				

(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 8), but this number was not significantly different from average.

Seasonal Changes in Aggregation Indices

Tables 10 and 11 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 ($\overline{X}$), the variance to mean ratio ($V/\overline{X}$) and Lloyd's mean crowding index ($\overset{*}{M}$) had highly significant linear relationships (correlation coefficients in Tables 10 and 11) which indicated these indices were not independent of population size and, therefore, would not be useful in seasonal comparisons.

Lloyd's patchiness index ($\overset{*}{M}/\overline{X}$) was independent of population density (Tables 10 and 11) and, in general, reflected the seasonal changes in distribution presented graphically in Figs. 19-21. 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 popualtion 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 10 and 11). Patchiness was also generally lower in the limnetic than in the littoral zone.

Diel Patterns

Diel patterns of horizontal and vertical distribution appeared

Table 10.

1975 seasonal variation in selected aggregation indices for the Stonehouse Pond Polyphemus population. $\bar{X}/M^3$ - average Polyphemus density per cubic meter of lakewater, $V/\bar{X}$ - variance over mean ratio (Fisher's coefficient of dispersion), $\mathring{M}$ - Lloyd's mean crowding index, 2*SE $\mathring{M}$ - ± 95% confidence interval width for mean crowding, $\mathring{M}/\bar{X}$ - Lloyd's patchiness index for littoral and limnetic regions and for the whole lake, 2*SE $\mathring{M}/\bar{X}$ - ± 95% confidence interval width for whole-lake estimates of patchiness. See text for additional information.

			MEAN CROWDING		LLOYD'S PATCHINESS INDEX ($\mathring{M}/\bar{X}$)			
DATE	$\bar{X}/M^3$	$V/\bar{X}$	$\mathring{M}$	2*SE $\mathring{M}$	LITTORAL	LIMNETIC	WHOLE LAKE	2*SE $\mathring{M}/\bar{X}$
5-V-75	153	934	1254	1678	8.20 #	-	8.20 #	8.49
20-V-75	17510	26809	44913	19818	2.56 *	-	2.56 *	0.83
28-V-75	12472	15285	27990	10022	2.24 *	-	2.24 *	0.58
11-VI-75	1859	2923	4836	1967	2.38 *	1.58	2.60 *	0.78
19-VI-75	1310	4329	5822	3780	3.50 *	2.63	4.44 *	2.23
26-VI-75	1213	8222	10148	9683	6.72 *	3.63	8.36 *	6.27
3-VII-75	908	8772	10738	12113	10.55 *	12.86	11.83 *	10.51
10-VII-75	372	1767	2265	1944	4.77 *	2.65	6.09 *	4.08
15-VII-75	747	3289	4216	3166	4.94 *	7.63	5.64 *	3.31
22-VII-75	313	1098	1458	967	3.93 *	4.37	4.66 *	2.39
29-VII-75	240	1124	1429	1109	4.83 *	1.85 *	5.95 *	3.61
5-VIII-75	280	519	810	372	2.54 *	1.54 *	2.89 *	0.99
12-VIII-75	883	7675	9413	10195	8.84 *	2.43 *	10.66 #	9.09
19-VIII-75	2523	36875	47563	71495	13.70 #	3.74	18.85 #	22.10
25-VIII-75	1195	12440	15252	17850	10.00 #	2.50	12.76 #	11.76
2-IX-75	791	3657	4664	3640	4.67 *	7.05	5.90 *	3.60
14-IX-75	2109	33511	42275	60589	15.54 #	9.80	20.05 #	22.50
25-IX-75	2460	8108	10984	7845	3.20 *	2.85	4.47 *	2.46
9-X-75	2152	8296	10846	7574	3.90 *	3.70	5.04 *	2.74
16-X-75	958	5236	6565	5636	5.25 *	6.66	6.85 *	4.61
23-X-75	302	840	1171	681	3.00 *	6.44	3.87 *	1.73
30-X-75	77	635	796	946	9.39 #	2.70	10.40 #	9.68
6-XI-75	22	125	157	156	6.60 *	-	7.28 *	5.55
13-XI-75	17	141	178	220	9.27 *	-	10.40 #	10.06
20-XI-75	1	11	14	24	16.68 #	-	18.78 #	25.35
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 $\bar{X}/M^3$.

Table 11.

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.

DATE	$\bar{X}/M^3$	$V/\bar{X}$	MEAN CROWDING $\overset{*}{M}$	MEAN CROWDING 2*SE $\overset{*}{M}$	LLOYD'S PATCHINESS INDEX $(\overset{*}{M}/\bar{X})$ LITTORAL	LIMNETIC	WHOLE LAKE	2*SE $\overset{*}{M}/\bar{X}$
15-IV-76	36	578	799	1422	19.67 #	-	22.37 #	30.60
29-IV-76	2575	25777	32091	39472	11.38 #	-	12.46 #	12.04
7-V-76	7359	51263	63259	61602	7.92 *	5.35	8.60 *	6.58
13-V-76	11235	53860	68404	54423	5.62 *	8.32	6.09 *	3.79
19-V-76	12876	41236	55803	35599	4.00 *	1.14	4.33 *	2.14
27-V-76	9491	48968	61697	51049	6.01 *	1.75	6.50 *	4.21
2-VI-76	5381	18868	25095	16837	4.34 *	1.03	4.66 *	2.42
9-VI-76	3824	9958	14114	8009	3.43 *	1.02	3.69 *	1.60
15-VI-76	2206	7612	10473	9637	4.20 *	2.00	4.75 *	3.36
24-VI-76	1812	46974	79228	188595	37.67 #	1.73	43.72 #	76.66
2-VII-76	129	628	832	918	6.04	1.43	6.43	5.51
14-VII-76$	-	-	-	-	-	-	-	-
26-VII-76	280	1827	2272	2208	7.09 *	7.85	8.10 *	6.18
3-VIII-76	511	2722	3594	4160	6.30	2.55	7.03	6.32
12-VIII-76	1496	4268	5932	3688	3.67 *	3.23	3.97 *	1.89
23-VIII-76	248	177	427	154	1.69	1.05	1.71	0.72
1-IX-76	335	8808	14936	35772	40.48 #	2.81	44.63 #	78.63
10-IX-76	1141	6247	8242	9671	6.12	2.64	7.22	6.58
16-IX-76	779	7949	10754	17100	11.75 #	1.98	13.80 #	16.95
28-IX-76	1166	12063	16349	26171	11.90 #	9.60	14.03 #	17.33
6-X-76	1001	3937	5323	5257	4.51 *	2.28	5.32 *	4.06
15-X-76	979	9881	13553	22192	11.57 #	2.10	13.84 #	17.45
25-X-76	299	1762	2320	2826	6.57	-	7.75	7.32
5-XI-76	23	127	166	196	6.13	-	7.23	6.64
15-XI-76	3	39	54	101	16.85 #	-	19.85 #	28.41
corr. coef.¢	r =	+ 0.91	+ 0.92				+ 0.30	

* 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 $\bar{X}/M^3$.

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. 22-25).

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. 22, diel 4 Fig. 25). 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. 23D) and diel 4 day 1 (Fig. 25B). 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. 22, diel 4 day 2 Fig. 25B). If wind was light and its direction was variable, a patch was not formed (diel 3 day 2 Fig. 24D). 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. 23).

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. 26A-D. The daytime vertical distribution patterns for littoral and limnetic regions

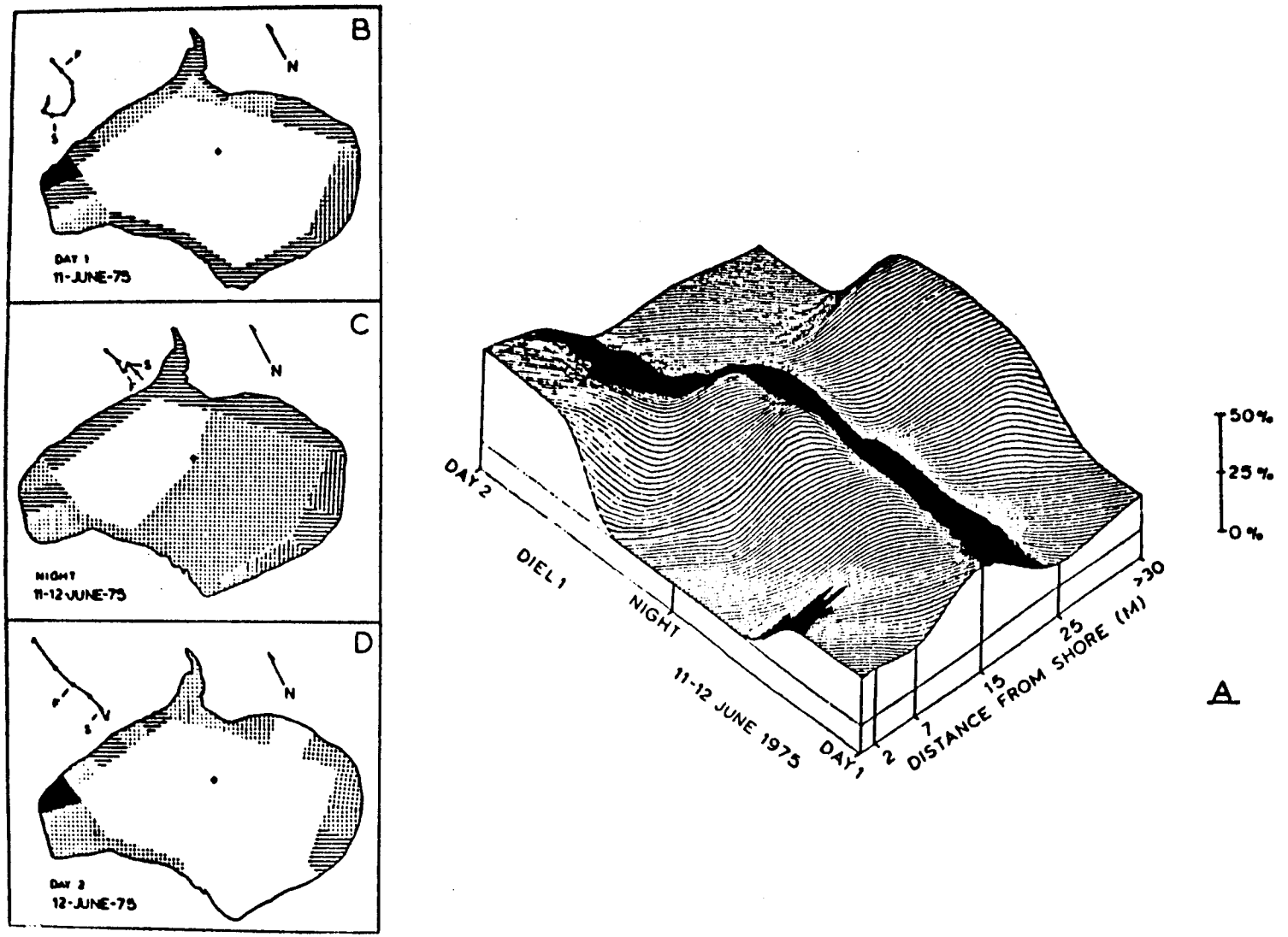


Figure 22. Diel change in horizontal distribution of the Polyphemus population in Stonehouse Pond for Diel 1, 11-12 June 1975. A. Three-dimensional representation, X, Y, and Z axes as in Figure 19. B-D. Spatial maps of patch location for day 1 (B), night (C), and day 2 (D), legend as in Figure 21.

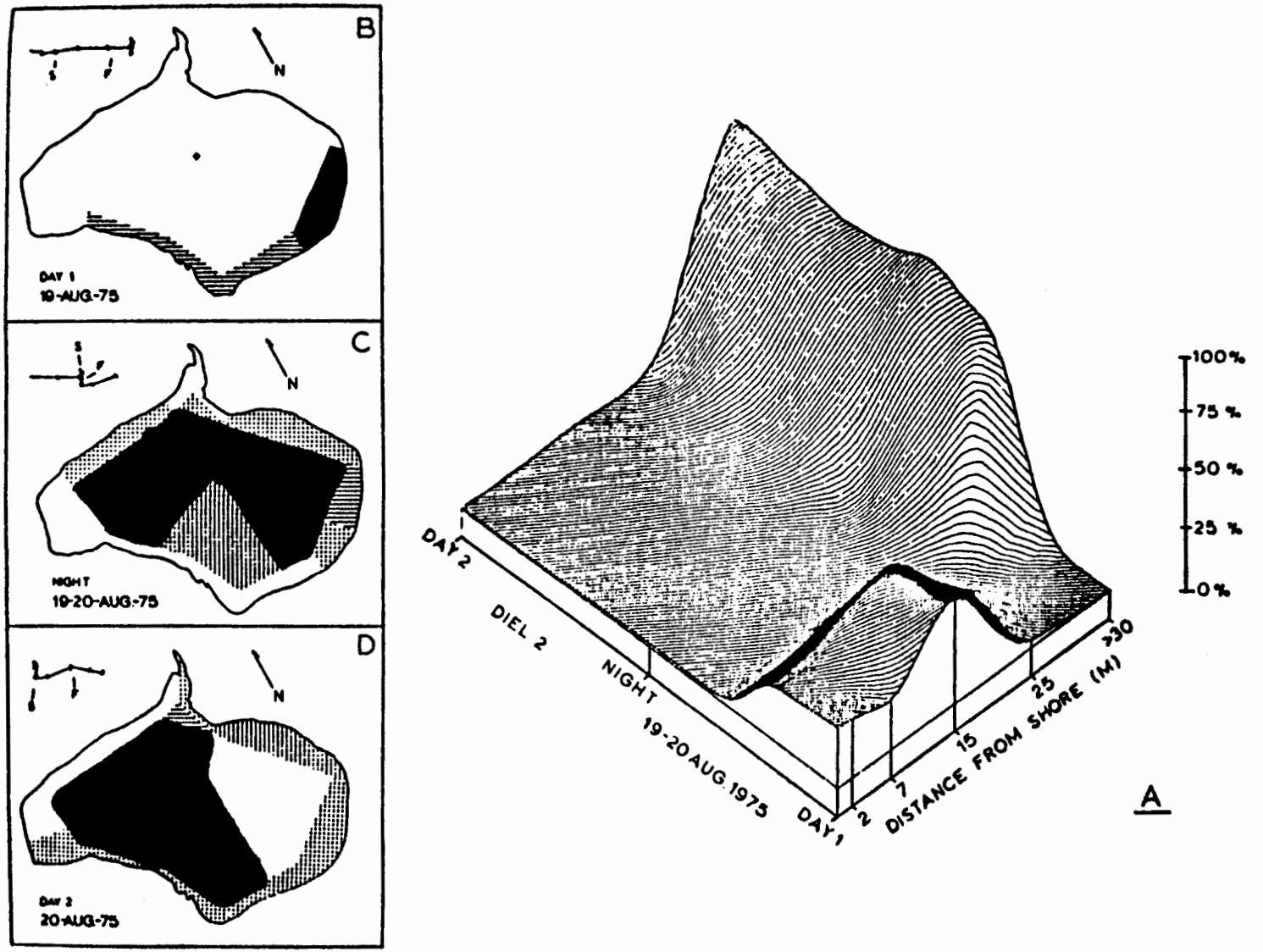


Figure 23. As Figure 22 for diel 2, 19-20 August, 1975.

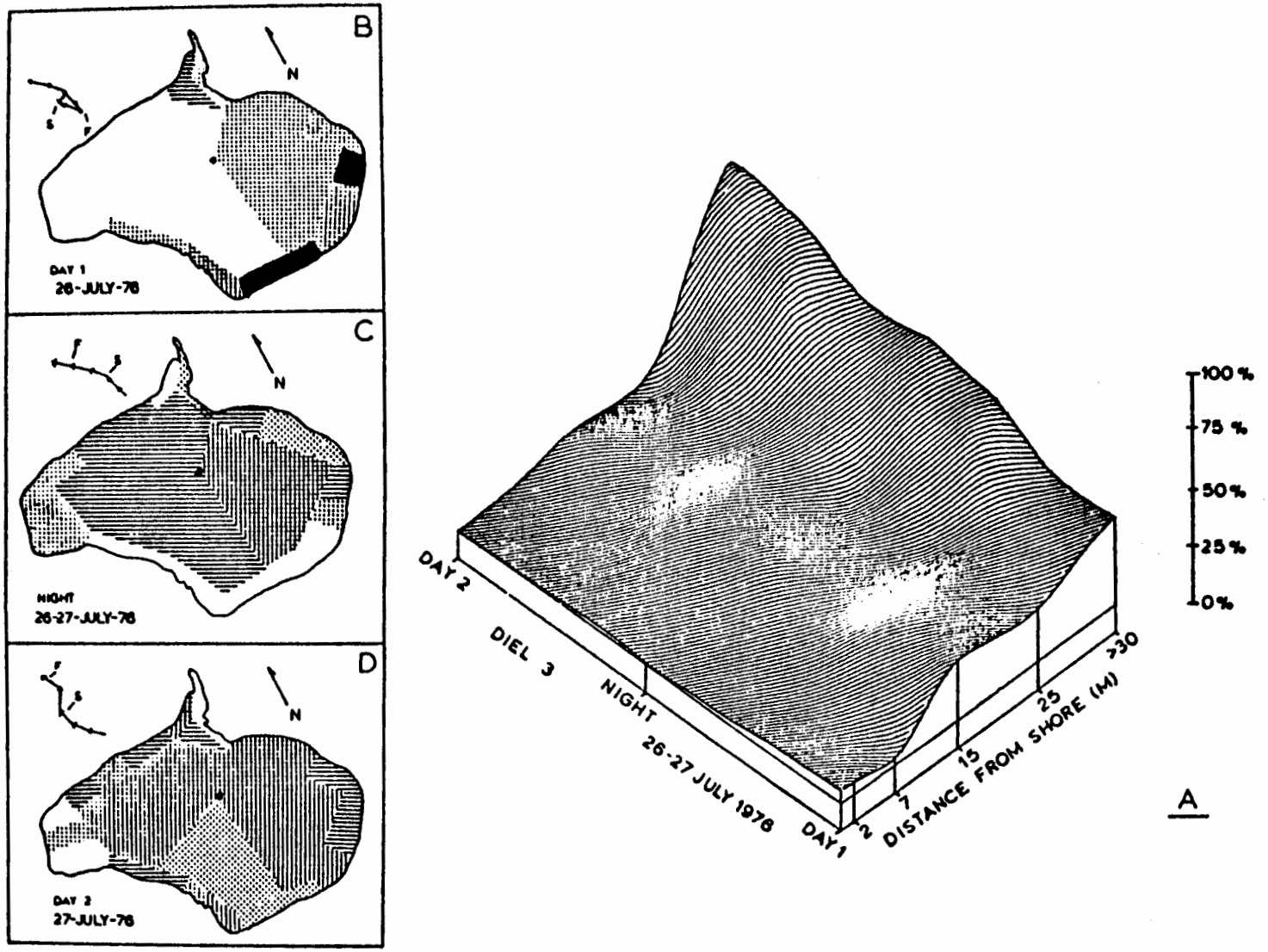


Figure 24. As Fig. 22 for diel 3, 26-27 July, 1976.

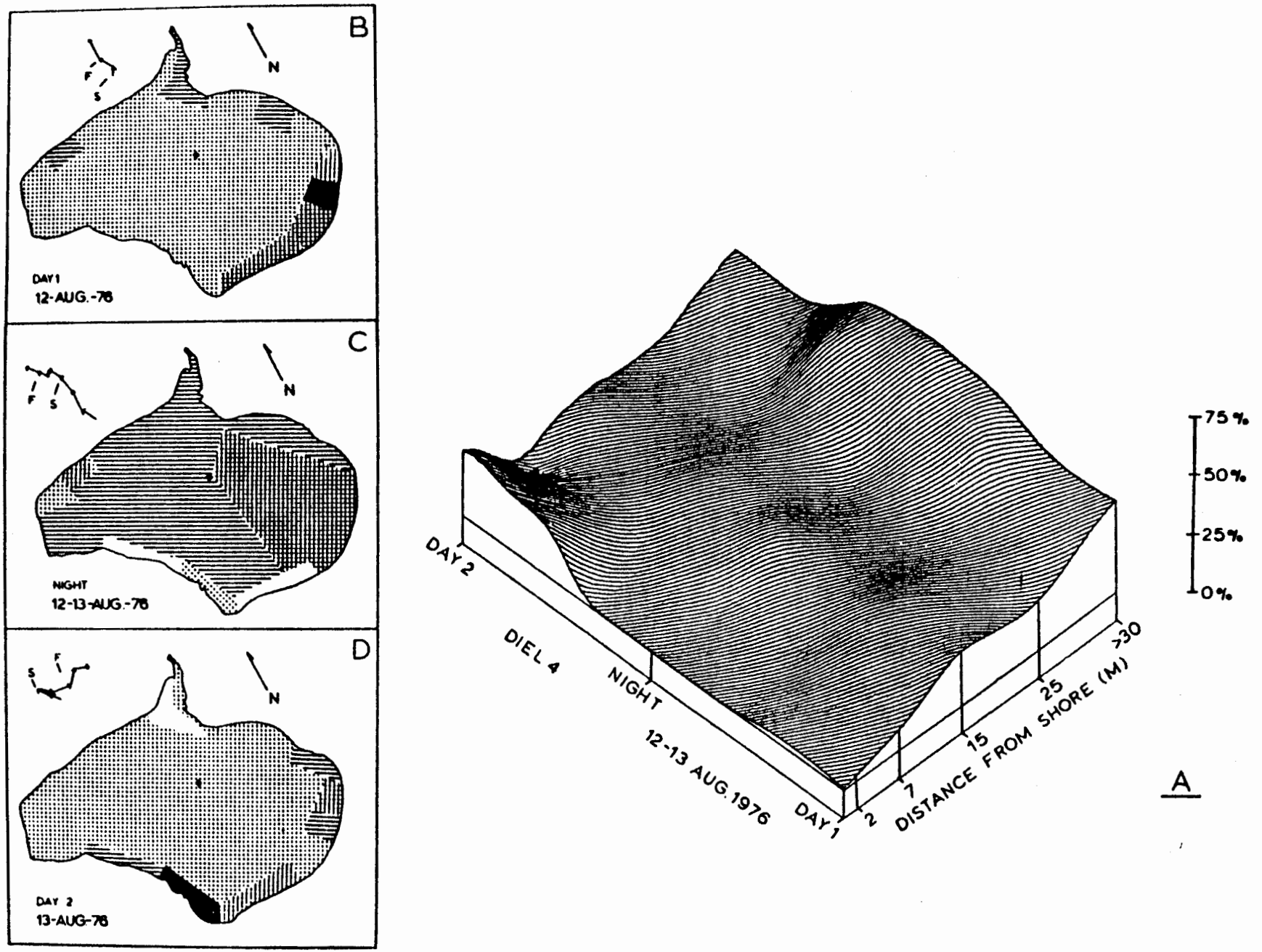


Figure 25. As Figure 22 for diel 4, 12-13 August, 1976.

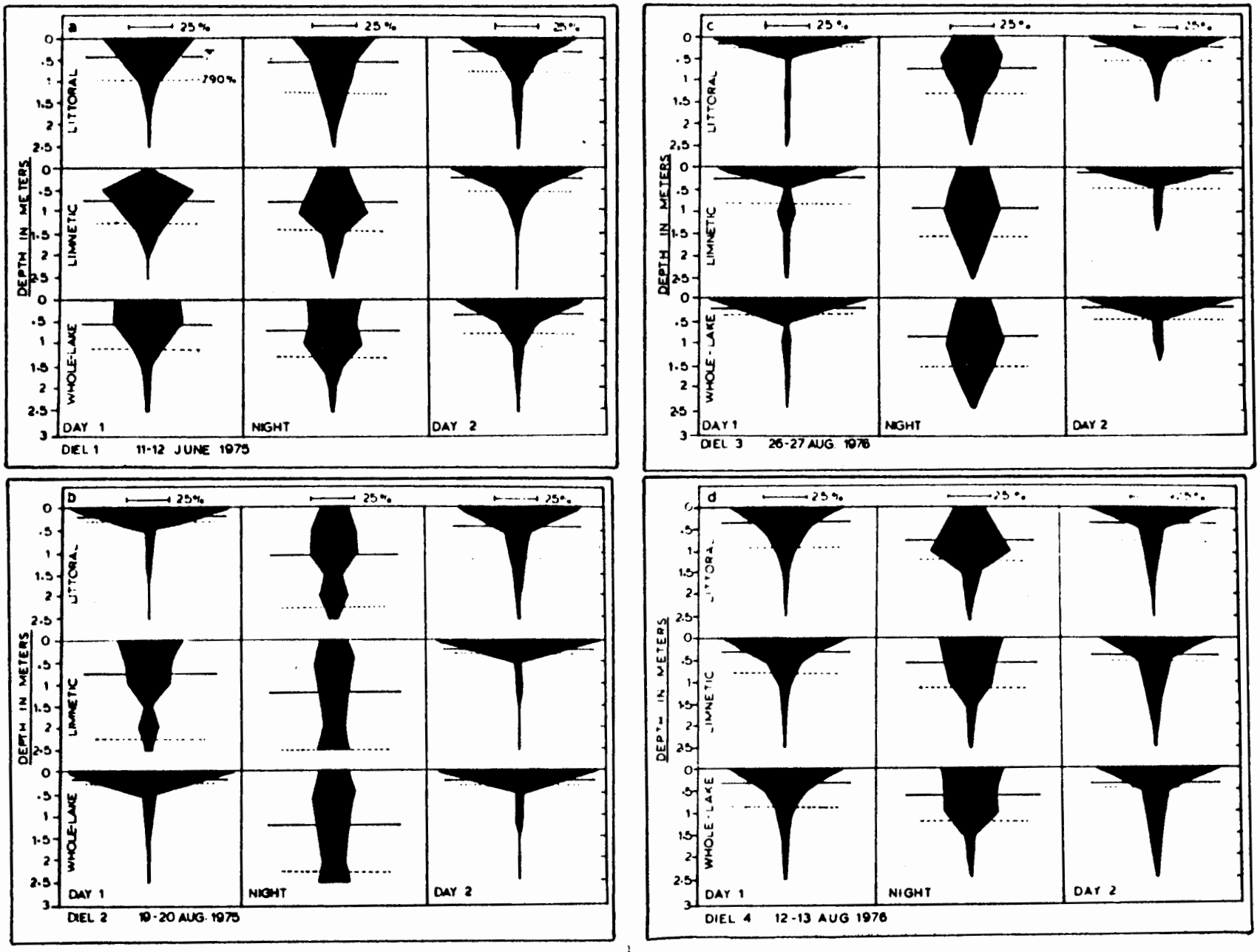


Figure 26. Diel variation in vertical distribution of the total Polyphemus population of Stonehouse Pond. A. diel 1, B. diel 2, C. diel 3, D. diel 4. Solid line - Z, Broken line - Z90%

and for the whole lake reflected the summer pattern described in Fig. 20. At night, however, the population was considerably more dispersed in the vertical plane than it was in corresponding locations in the day (Figs. 26A-D). $\bar{Z}$ and Z90% were significantly deeper at night than on either day, and ΔZ 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.

Diel Variation in Aggregation Indices

Table 12 summarizes aggregation indices calculated for each diel study. In general, aggregation indices reflected changes in spatial distribution which were graphically presented in Figs. 22-26. At night, when the population was spatially dispersed in horizontal and vertical planes, $V/\bar{X}$, $\overset{*}{M}$, and $\overset{*}{M}/\bar{X}$ 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 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 limits about aggregation indices were unusually wide for diel 2 day 1 and day 2, and for diel 4 day 2 (Table 12), because a large percent of the population was found in one patch. For diel studies 2 and 3, $V/\bar{X}$, $\overset{*}{M}$, and $\overset{*}{M}/\bar{X}$ were lower on day 2 than day 1 (Table 12), demonstrating that statistical dispersion was lower when a significant percent of the population remained in the limnetic zone.

Detailed Description of the Polyphemus Patch

Dimensions and internal structure

Sampling and in situ observations provided information on the dimensions, composition, and internal structure of Polyphemus patches.

Table 12.

Diel variation in selected aggregation indices for the Stonehouse Pond Polyphemus population. See legend of Table 10 for explanation of symbols and text for additional information.

Sampling period	$V/\overline{X}$	Mean Crowding $\overset{*}{M}$	Mean Crowding 95% CL	Patchiness $\overset{*}{M}/\overline{X}$	Patchiness 95% CL
Diel 1					
11-12 June 1975					
Day 1	2923	4836	1967	2.6	0.8
Night	2242	3200	2474	3.9	2.3
Day 2	7591	11942	6808	2.9	1.2
Diel 2					
19-20 Aug. 1975					
Day 1	36875	47563	71495	18.8	22.1
Night	178	290	137	2.7	0.9
Day 2	2048	2592	3574	15.4	16.6
Diel 3					
26-27 July 1976					
Day 1	1827	2272	2208	8.1	6.2
Night	114	216	78	2.1	0.2
Day 2	332	460	287	4.0	1.9
Diel 4					
12-13 Aug. 1976					
Day 1	4268	5932	3688	4.0	1.9
Night	181	505	116	1.5	0.2
Day 2	28544	36378	53133	19.0	21.7

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. 16) with resolution of 5-10 meters parallel to shore, 20-25 meters perpendicular 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 edge 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. 21E-G; 23B; 23D), the total number and percent of the total Polyphemus population contained in the one observed shoal on each date were as follows: 12 Aug. - 2.755×10^6 individuals, 11%; 19 Aug. - 1.301×10^7, 90%; 20 Aug. - 1.416×10^7, 98%; 25 Aug. - 7.823×10^6, 45%; 2 Sept. - 1.472×10^6, 11%; and 14 Sept. - 5.77×10^6, 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. 22-25), 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. 23B, 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. 23D, 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 13 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

Table 13.

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.

Date	n	Interanimal dist. (cm) Minimum	Mean	Polyphemus Density (cm^3)
3-May-77	33	0.2	0.5	6.9
Swarm	18	0.5	0.6	5.3
13-May-77	8	0.3	0.5	9.7
Swarm	4	0.4	0.5	10.7
	6	0.5	0.7	2.6
13-May-77	8	0.4	0.9	1.6
Swarm	6	0.9	1.6	0.2
	13	0.4	0.4	15.3
	10	0.4	0.4	11.6
25-May-77	19	0.4	0.7	3.0
Swarm	3	0.7	1.2	0.6
	20	0.4	0.7	2.9
	7	0.5	0.8	2.1
7-July-77	11	0.6	1.2	0.6
Shoal	18	0.6	0.7	3.0
	3	1.5	2.0	0.1
8-Aug.-77	7	0.8	1.2	0.5
Shoal	9	1.1	1.6	0.2
	47	0.3	0.4	13.8
	13	0.6	0.9	1.6
23-Sept.-77	6	0.5	1.5	0.3
Shoal	10	0.7	1.5	0.3
1-Nov.-77	15	0.4	0.8	1.6
Swarm	27	0.3	0.5	8.2
	3	0.5	0.6	3.7

(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 13) 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 13) 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.

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 27 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. 27 and ANOVA on log-transformed densities with block effects removed, Duncan's multiple range test

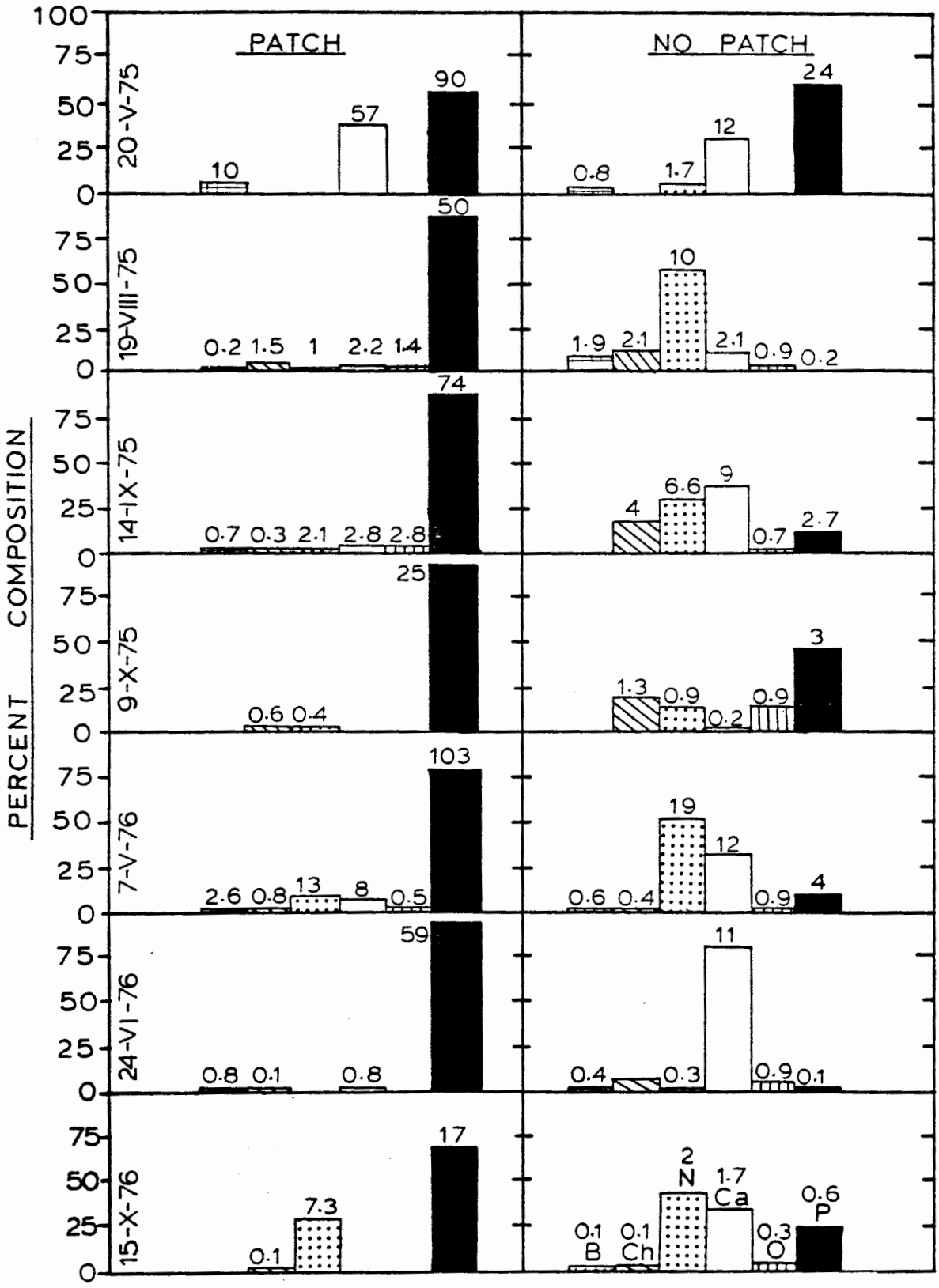


Figure 27. Zooplankton composition (% counted) inside selected Polyphemus patches and in adjacent non-patch areas of Stonehouse Pond. B - Bosmina sp., Ch - Chonochilus unicornis colonies (1 colony averaged 51 individuals), N - copepod nauplii, Ca - calanoid copepodites, O - other zooplankton species, primarily Holopedium gibberum and Daphnia sp., P - Polyphemus pediculus. The numbers written above the blocks for each species represent their density (indiv. liter^{-1}).

$p < 0.05$). 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. 28). In general, patch composition reflected the seasonal population dynamics of Polyphemus (Figs. 17 and 18). 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. 28). Significant differences in percent composition between patch and no patch areas were not observed (Fig. 28 and ANOVA as for Fig. 27). However, the averaging effect of 200 liter samples on the relatively small spring and fall 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. 20). 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.

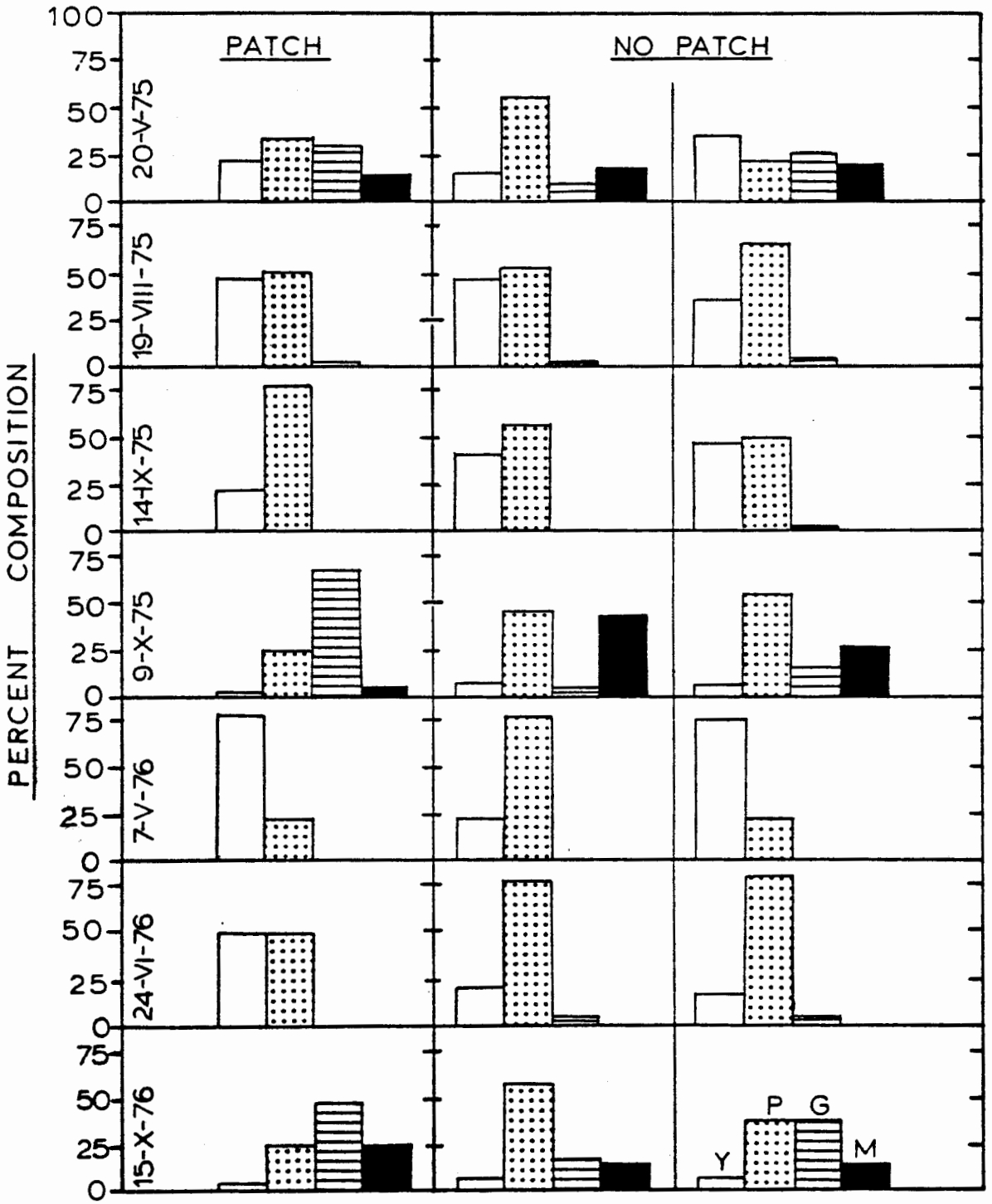


Figure 28. Polyphemus composition (% counted) inside selected Polyphemus patches and in two adjacent non-patch areas of Stonehouse Pond. Y - early instar Polyphemus, P - parthenogenetic females, G - gamogenetic females, M - males.

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.

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. 28), 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.

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.

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 observation, 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.

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. Axelson, 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. 29).

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 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

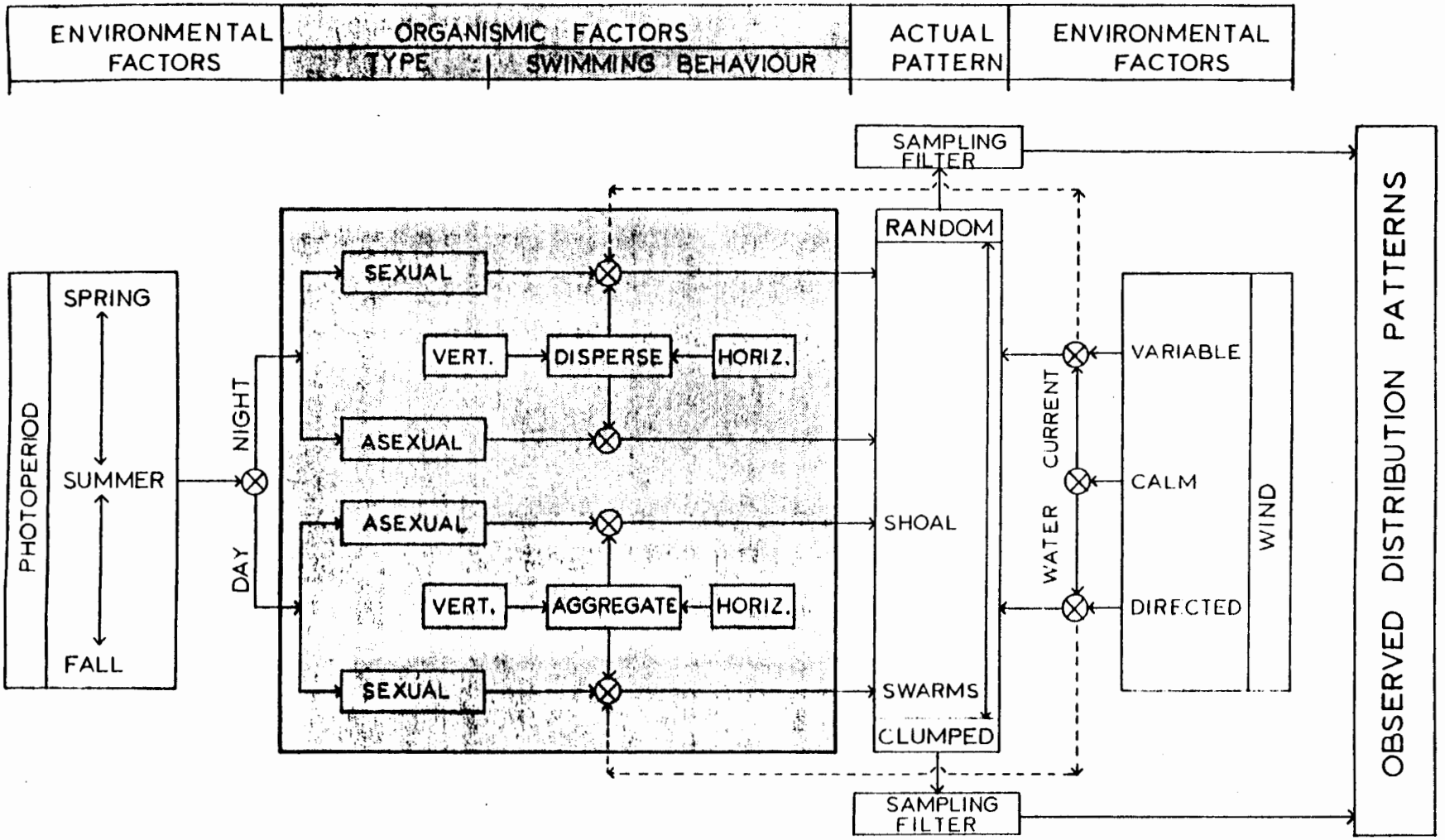


Figure 29. Compartment model of the proposed mechanism of patch formation delineating the interaction major environmental and biotic components to produce the observed distribution patterns. Components in the shaded area bounded by heavy lines represent biological factors related to the behaviour of individual zooplankters. Environmental components are outside of this shaded area. See text for a detailed description.

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.

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 in 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 reporduction, 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. 19) 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 copopods 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.

SUMMARY

Temporal and spatial patterns of patchiness were studied in a population of Polyphemus pediculus (L.) found in Stonehouse Pond, Barrington, New Hampshire (Fig. 14). 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. 15-16). 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. 17, 18) influenced patterns of horizontal and vertical distribution (Figs. 19, 20). The Polyphemus population was rarely found below 2 meters of depth (Fig. 20). In the spring and fall of both years, the population was found extremely close to shore (Fig. 19). 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 8). In the spring and fall, several patches were found on each date, while in the summer generally one patch was seen (Fig. 21). Patches were usually found on the downwind side of the lake (Fig. 21), and their location was highly correlated with wind direction at the time of sampling (Table 9).

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. 22-25). This horizontal dispersal was paralleled by vertical dispersal in the upper 3 meters of the water column (Fig. 26). 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 10-12) provided statistical support for seasonal and diel changes in Polyphemus population distribution which were graphically presented in Figs. 19-26.

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 13). Swarms were composed primarily of sexual individuals (Figs. 27, 28).

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 13). Shoals were composed primarily of juvenile Polyphemus (Figs. 27, 28).

A patch formation mechanism is proposed and summarized graphically (Fig. 29), 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.

V. FEEDING AND PREDATION IMPACT

INTRODUCTION

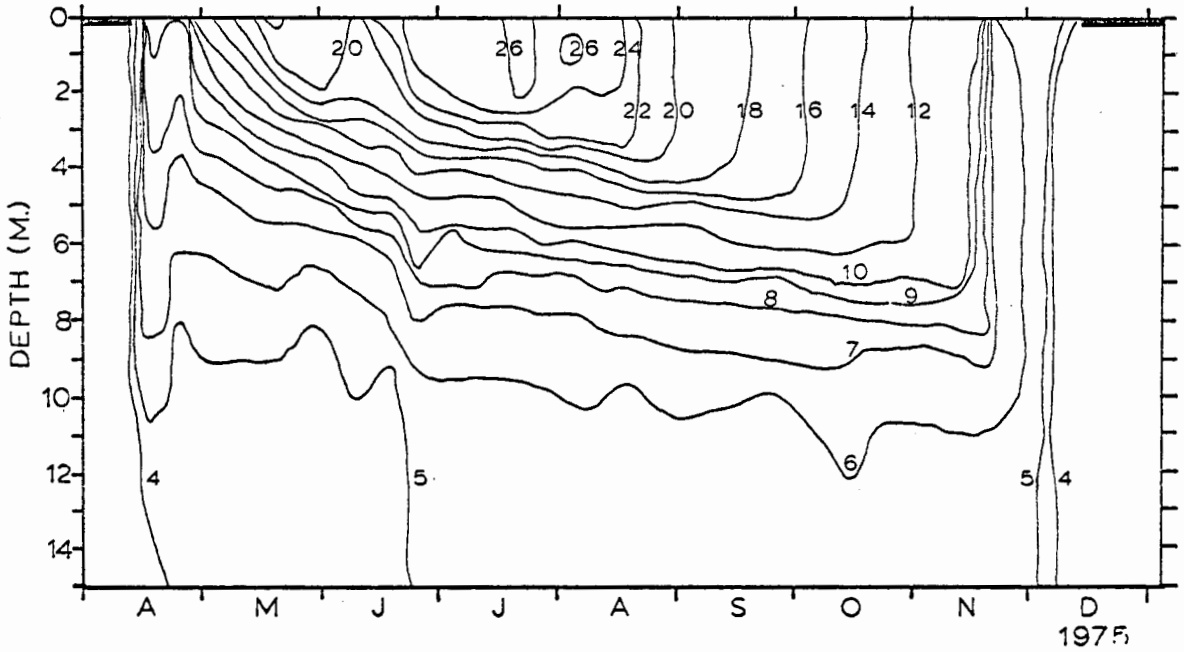
Study of the feeding habits of Polyphemus pediculus has been limited to the laboratory research of Butorina (1965, 1970, 1971b, 1971c; Butorina and Sorokin, 1969, 1971). This Russian researcher's results may have limited application to a natural system, since feeding experiments were often run at prey concentrations several times greater than would be found in nature (Butorina, 1971b, 1971c). The purpose of this section is threefold. First, techniques used to quantify Polyphemus feeding rates will be evaluated. Secondly, the factors influencing Polyphemus feeding rates will be identified and examined. Finally, the impact of Polyphemus predation on a natural zooplankton community will be quantified.

MATERIALS AND METHODS

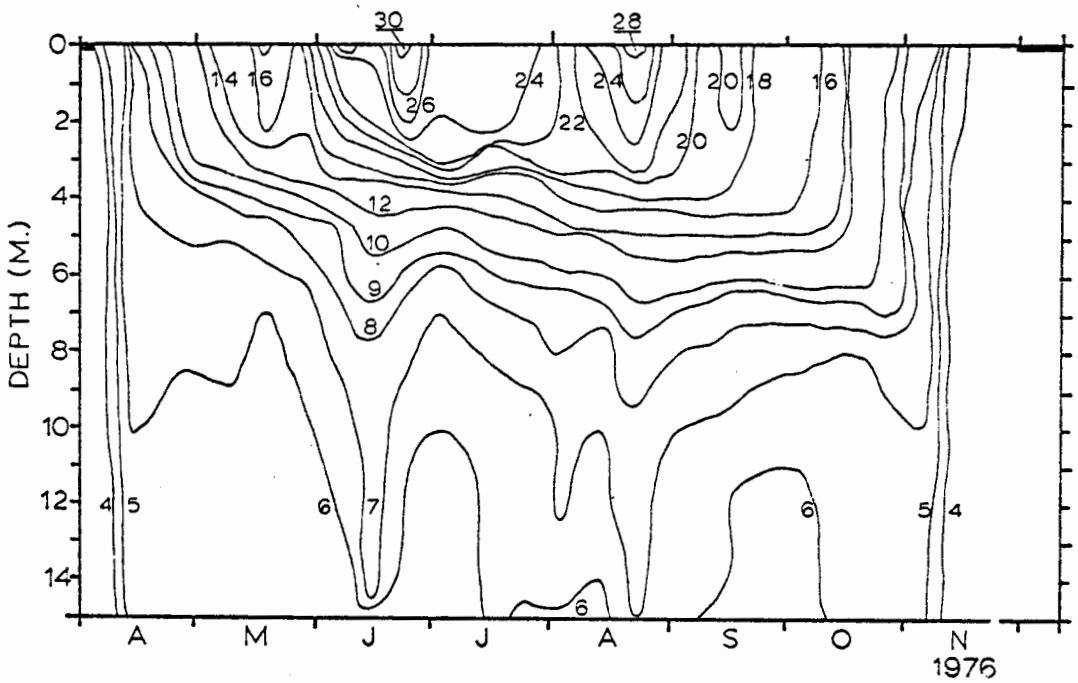
Study Site

Stonehouse Pond in Barrington, New Hampshire (43° 12'N, 71° 06'W) was selected as the study site based on lake morphometry, proximity, and the presence of a large Polyphemus population. It 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. Temperature isopleths for 1975 and 1976 (Figure 30, panels A and B) reveal short periods of spring and fall mixis and the formation of a thermocline between 3 and 7 meters of depth.

Stonehouse Pond 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. Natural reproduction of these trout does not occur (Mattson, pers. obs.), and at stocking size, these fish are primarily insectivorous (Appendix 1).



A



B

Figure 30. Thermal profile of Stonehouse Pond during 1975 (panel A) and 1976 (panel B) showing seasonal changes in the isopleths of temperature.

For comparison between different prey types, feeding rates were also expressed as μm^3 prey · Polyphemus^{-1} · Day^{-1} by multiplying the daily feeding rate times the prey mean body volume (NAWERK 1963). The following body volumes were used: 0.4×10^6 μm^3 for Chonochilus unicornis, 0.8×10^6 μm^3 for nauplii, and 55×10^6 μm^3 for Bosmina sp. Unless specified, all feeding rates are based on parthenogenetic female Polyphemus, 0.73 - 0.91 nm in body length.

Prey Population Sampling

A stratified random sampling design was used to quantify Polyphemus abundance in Stonehouse Pond in the ice-free periods of 1975-1976. This design provided abundance estimates with precision for a 95% confidence interval about the stratified mean Polyphemus density of ± 64 individuals per cubic meter. The design is described in detail in Section II of this report.

Sampling for prey species abundance was not as extensive as for Polyphemus, and was designed to describe seasonal change in patterns of abundance. In 1975, sampling was conducted with an 8.1 liter Van Dorn water sampler with contents filtered through a 48 µm Nitex net and preserved in 4% formalin-sucrose. In 1976, sampling for prey was part of the Polyphemus sampling program, and consisted of 20 meter long (200 liter) Clarke Bumpus net tows (151 µm netting). In both years, sampling for prey species was limited to littoral section 1 and limnetic section 7 (Fig. 2). In 1975, 7 Van Dorn (V.D.) samples were allocated to both section 1 and section 7. In the littoral section, 4 V.D. samples were collected just under the water surface at randomly assigned locations, and the remaining 3 V.D. samples were collected at 1.0 meters of depth. In the limnetic section, all V.D. samples were collected at a centrally located station buoy (Fig. 2) in a descending vertical series at 0, 1, 2, 3, 6, 7, and 8 meters of depth. In 1976, prey were enumerated from 4 net tows taken in littoral section 1 (0, 0.5, 1.0, and 1.5 m of depth) and from 3 oblique tows collected in limnetic section 7 (3 → 0 meters of depth). A 1/75 subsample of each tow or V.D. was selected by the

Hensen-Stempel pipette method (Schwoerbel 1970) for enumeration of the following prey categories:

The cladoceran, Bosmina sp.
A colonial rotifer, Chonochilus unicornis
Copepod nauplii
Diaptomus spp. copepodites, adults, eggs
Cyclops spp. copepodites, adults, eggs

All samples were enumerated on a Wild dissecting microscope at 25X magnification. Subsamples were generally combined from all samples within a lake section and a composite count was obtained. On selected dates, entire samples were enumerated to obtain information on the spatial variability and vertical distribution of prey.

Experimental Procedure

Radioisotope and differential count techniques were used to quantify Polyphemus predation and to examine various factors affecting predation rates. Table 14 summarizes the factors considered in this study and identifies the technique(s) used in their evaluation.

All feeding experiments were run in situ at ambient light and temperature conditions in Stonehouse Pond, Barrington, N.H. (located 24 km west of the laboratory at the University of New Hampshire). Polyphemus and all prey items were collected from this lake, except for Bosmina and Ceriodaphnia, which were not present in sufficient abundance to be used in feeding experiments. These prey were collected from a nearby impoundment on the Lamprey River, Newmarket, N.H. (located 4 km south of the laboratory at the University of New Hamsphire).

Figure 31 summarizes the experimental procedure for both isotope and differential count methods. Prey were collected by towing a 30 cm diameter 75 µm net. This plankton was resuspended in a 20-liter carboy of lakewater and transported to the laboratory. In the lab, five-liter aliquots of the carboy contents were gently filtered through a coarse net (505 µm or 363 µm depending on desired prey) and collected in a 48 µm net. This size sorted concentrate

Table 14

Variables (factors) and associated type of experimental procedure used to measure Polyphemus feeding rates.

FACTOR	FEEDING PROCEDURE (Diff. count)	(Isotope)
Container:		
tissue culture flasks - 40 ml.	X	X
- 64 ml.	X	X
Erlenmeyer flasks - 1100 ml.		X
Temperature range:		
11 °C - 28 °C	X	X
Photoperiod:		
day		X
night		X
24 hour	X	X
Prey:		
density range:		
50 - 10000/liter	X	X
type:		
Cladocera		
Bosmina sp.	X	X
Daphnia sp.	X	X
Ceriodaphnia sp.		X
first instar *P. pediculus*	X	X
Copepoda		
Diaptomus pygmaeus		
nauplii	X	X
copepodites 1 - 2	X	X
copepodites 3 - 6		X
Rotifera		
Keratella sp.	X	
Chonochilus unicornus		X
Predator (P. pediculus):		
body size:		
juvenile (0.36-0.55 mm)		X
adult - (0.55-0.73 mm)		X
- (0.73-0.91 mm)		X
type:		
juvenile		X
parthenogenetic female		
- immature brood	X	X
- mature brood		X
gamogenetic female		X
male		X

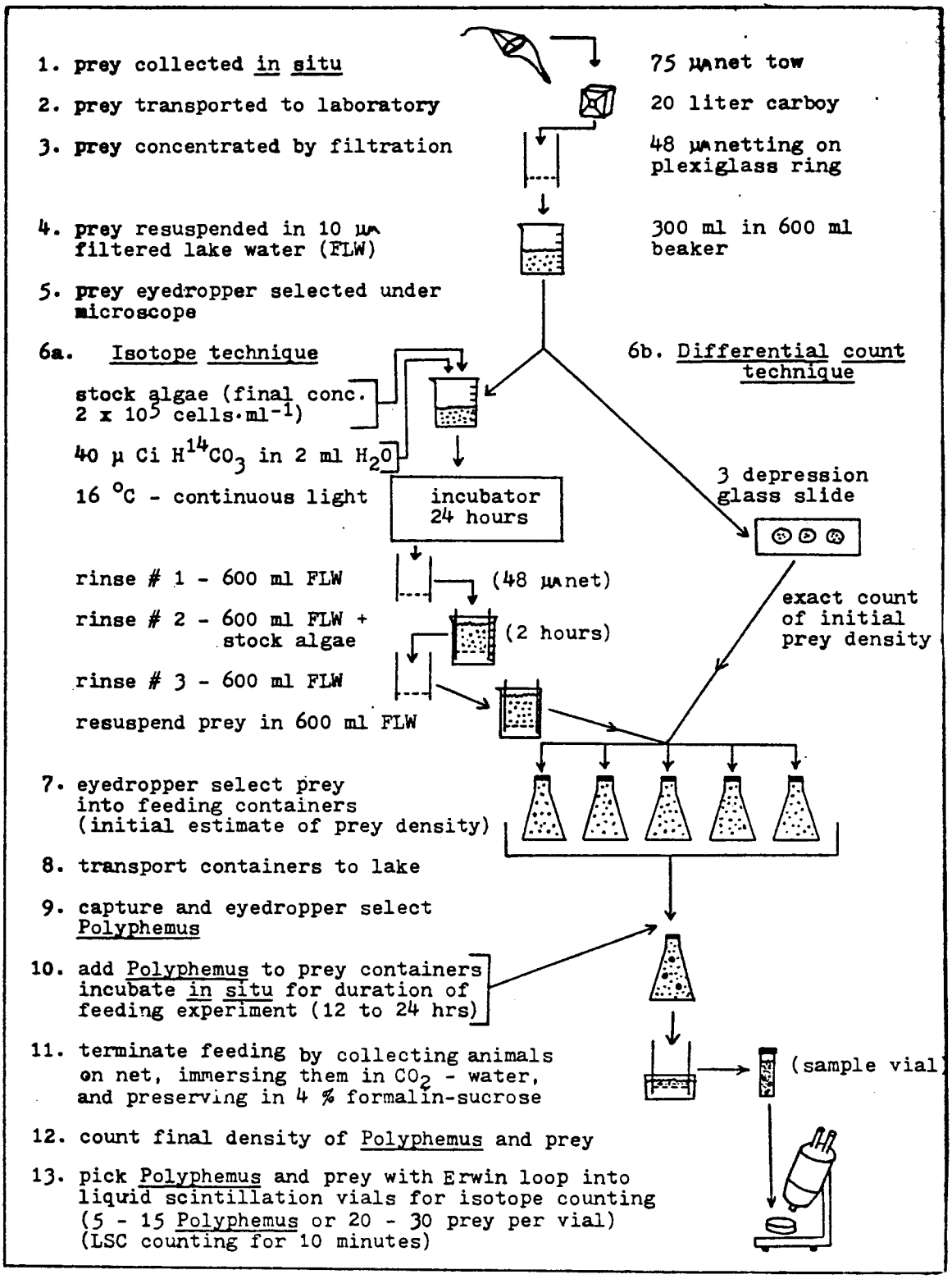


Figure 31. A flow diagram describing the two methods used to determine feeding rates of Polyphemus.

of plankton was resuspended in 10 µm filtered lake water (FLW) and the appropriate prey item was selected with an eyedropper using a dissecting microscope. Selected prey were placed in 300 ml of FLW in another beaker. The seemingly excessive number of eyedropper transfers of prey was necessary to eliminate accidental transfer of other zooplankton to the experimental chamber.

For differential count feeding experiments (right column of Figure 31, prey were eyedropper-transferred to a three depression glass microscope slide with approximately 7 to 10 animals per depression. The actual number of prey in each depression was then counted under the microscope and these prey were transferred to FLW in the experimental container. Care was taken to insure prey did not remain in the eyedropper or glass slide. Transfer in this manner allowed for virtually no counting error up to 150 prey counted. In all differential count experiments, an equal number of control and experimental containers was used, with the controls acting as a check on counting error and natural mortality of prey. Experimental and control containers were transported to the field immediately after prey were added. In the field, Polyphemus were captured and placed in the feeding flasks to initiate the feeding sequence. After the appropriate feeding period, the experiment was terminated by adding a formalin-sucrose mixture to a final concentration of 4% (Haney and Hall, 1973). The maximum-minimum temperature for the feeding period was recorded, and the containers were transported back to the laboratory where the entire contents of each container was counted. Only missing or partially consumed prey were considered eaten. The entire time required to run a differential count feeding experiment from collection of prey to enumeration of data was 36 hours (24 hour feeding exposure).

Differential count feeding experiments were run in tissue culture flasks of 40 and 64 mls in capacity. Five Polyphemus and from 5 to 100 prey were added per flask. Larger containers were not used in differential count experiments because of 1) increased counting error resulting from the number of prey required to maintain prey density, and 2) potential transfer error due to incomplete

rinsing of prey from the container following feeding exposure. Tissue culture flasks were examined under the microscope to insure all prey were removed for counting.

For isotope experiments (left column of Figure 31), stock algae consisting of a Chlorella pyrenoidosa and Dyctospherium sp. mixture was passed through a 10 µm net and added to the beaker of prey to adjust the food level to $2 * 10^5$ cells ml^{-1}. 14-carbon was then added in the quantity of 40 µCi $H^{14}CO_3$ in 2 ml of H_2O. Table 15 demonstrates the uptake of this isotope in the algae (particulate) and prey, which were all grazing zooplankton. From this table it was apparent that between 22 and 48 hours of feeding in this stock solution allowed for maximum uptake of isotope by the prey. It follows that a 24-hour feeding exposure to radioactivity labeled algae was used to label prey for all isotope feeding experiments. Prey to be labeled were incubated in continuous light (4-foot cool-white fluorescent light at 24 inches away) at 17°C with gentle agitation provided by a magnetic stirrer or air bubble through a drawn-out pipette. Following the exposure of prey to the algae-isotope solution, they were rinsed several times to remove loose isotope and any uneaten labeled algae. First they were passed through a 48 µm net to remove the feeding solution and then they were rinsed with 600 ml FLW. These labeled, rinsed prey were then selected by eyedropper into experimental containers or thoroughly mixed and equal portions of water were poured into the experimental containers to give the selected densities. These containers were transported to the lake, Polyphemus were captured and placed in the containers, and the feeding exposure began. Feeding experiments were terminated by pouring the container contents through a 48 µm net, immersing this net in soda water, and placing both Polyphemus and prey in a sample vial with 4% formalin-sucrose. These vials were transported to the lab and Polyphemus and prey items were immediately counted, measured and placed in a 10 ml liquid scintilation (LSC) vials (5-15 Polyphemus or 20-30 prey per vial). One-hundred Lambda of (0.1 ml) Protosol tissue solubilizer was added to each LSC vial and incubated for 24

Table 15

Accumulation of isotope in the particulate food <48 µm (algae) and in the prey items feeding on the 14-C labelled particulate.

	Elapsed time from addition of 20 µCi ^{14}C			
	4.5 hrs.	22.5 hrs.	48 hrs.	145 hrs.
Particulate (cpm/ml) (<48 µm > 0.45 µm)	1327	2932	2810	3242
Diaptomus (cpm/indiv.)	16.4	46.7	45.6	-
nauplii	16.4	46.7	45.6	-
copepodites 1 - 2	27.0	86.5	125.4	96.1
Particulate (cpm/ml) (<48 µm > 0.45 m)	6967	1709	1193	650
Diaptomus (cpm/indiv.)				
copepodites 3 - 6	3.2	40.3	79.2	71.3
Daphnia (cpm/indiv.)				
early instars	32.6	84.3	114.1	104.5

hours at room temperature. Following solubilization, 5 ml of Aquasol II fluor was added and the LSC vials were incubated for another 48 hours at room temperature. These vials were then cooled to 4°C and placed in a LSC counter and counted for 10 minutes each (3 replicate counts) with open window settings (6.8% gain, window settings 50 to 1000). Included in all isotope experiments were a small number of unlabeled Polyphemus and prey which were heat-killed, dyed with methylene-blue, and placed in the feeding chamber to act as a control for absorption of isotope by means other than feeding. These methylene-blue dyed control animals were never significantly above background (17-20 cpm). With this feeding method, LSC vials with Polyphemus averaged 50 to 75 times background CPM depending on experimental conditions. Standard deviation for counting was considerably less than 1% (Wang and Willis 1965).

Calculation of feeding rates: (number of prey per Polyphemus per day) = N

Differential count method:

$$N = \frac{\left[\begin{array}{l}(\text{number of prey at start of feeding period}) \\ - \\ (\text{number of intact prey at end of feeding period})\end{array}\right] \div \text{number of Polyphemus in container}}{\text{length of time in feeding period in decimal days}}$$

Isotope method#:

$$N = \frac{(\text{CPM/Polyphemus individual}) \div (\text{CPM/individual prey})}{\text{length of time in feeding period in decimal days}}$$

#All isotope counts are above background (17-20 CPM)

It is assumed that all the isotope contained in each prey is consumed by the Polyphemus when that prey is eaten. Otherwise CPM/prey would have to be multiplied by the percent of that prey eaten. This assumption was evaluated in combined isotope/differential count experiments.

RESULTS AND DISCUSSION

Evaluation of Methods

Differential count and isotope methods were compared to determine the need for a factor which would adjust isotope determined feeding rates for partial consumption of prey. In this comparison, nauplii were labeled with ^{14}C as in the isotope procedure, and used in differential count experiments. By the isotope method, Polyphemus were found to have an average feeding rate of 2.0 nauplii · Polyphemus^{-1} · day^{-1} (Table 16). These same Polyphemus were found to have an average feeding rate of 3.5 nauplii · Polyphemus^{-1} · day^{-1} by the differential count method, but this difference was not statistically significant ($X^2 = 7.819$, $0.25 \leq p \leq 0.50$). This observation suggested all of the isotope contained in a nauplius was ingested by Polyphemus and retained for 24 hours. This suggestion is supported by observations at the end of feeding experiments which revealed few partially consumed nauplii or Chonochilus in feeding containers. With relatively large prey (e.g. Bosmina or Ceriodaphnia), partially consumed prey were often found. Differential count-isotope experiments were not conducted with Chonochilus as prey, because then small size and colony structure prohibited accurate counting. It was assumed that Chonochilus, like nauplii, were totally ingested and an adjustment factor for partial consumption or isotope retention was not needed.

With a planktonic, raptorial predator like Polyphemus, the possibility existed that observed feeding rates were effected by the size of feeding containers. This effect was examined across three container sizes for nauplii and Chonochilus as prey. Container size was directly correlated with feeding rate (Table 17), and feeding rates in the relatively small tissue culture flasks were significantly lower than in large Erlenmeyer flasks (T test, $p < 0.05$). Small containers (64 ml) underestimated Polyphemus feeding rates by an average of 4.6111 times for

Table 16

Comparison of differential count and isotope feeding methods. Experimental conditions: 64 ml tissue culture flasks, prey density: 1125 nauplii per liter, temperature range 14 - 17°C, 24 hour feeding exposure.

Replicate Number	Feeding Rate (Nauplii · Polyphemus^{-1} · Day^{-1}) Diff. count Method	Isotope Method	Difference
1	4	3.7	+0.3
2	3	0.3	+2.7
3	7	3.9	+3.1
4	2	2.1	-0.1
5	5	0.9	+4.1
6	1	1.5	-0.5
7	2	0.1	+1.9
8	4	3.5	+0.5
Mean	3.5	2.0	1.5
Standard Error	±0.7	±0.5	±0.6

Table 17

Effect of container size on Polyphemus predation rate. Experimental conditions: Isotope experiments, in situ, temperature range - nauplii - 23-28°C, Chonochilus - 15-18°C. All feeding rates based on parthenogenetic female Polyphemus, with immature embryos in their brood pouches, 0.73-0.91 mm in body length. Feeding rate values represent the average 24 hour feeding rate for 15-30 Polyphemus individuals ± 2 * standard error of the mean.

Container type	Prey type and density	Feeding Rate: Prey·Polyphemus^{-1}·Day^{-1}	Feeding Rate: μm^3 prey·Polyphemus^{-1}·Day^{-1} * 10^6
40 ml tissue culture flask	nauplii 4800·liter^{-1}	2.4 ± 0.1	1.9 ± 0.1
64 ml tissue culture flask	nauplii 5000·liter^{-1}	2.7 ± 0.9	2.2 ± 0.7
1100 ml Erlenmeyer flask	nauplii 1500·liter^{-1}	12.5 ± 0.3	10.0 ± 0.3
64 ml tissue culture flask	#Chonochilus 2300·liter^{-1}	$18.0 ± 2.1	7.2 ± 0.8
1100 ml Erlenmeyer flask	#Chonochilus 2300·liter^{-1}	$73.0 ± 10.0	29.2 ± 4.0

Chonochilus colony density
1 Chonochilus colony ≃ 48 individuals
$ Chonochilus individuals

nauplii and 4.0556 times for Chonochilus when compared with 1100 ml Erlenmeyer flasks.

Factors Affecting Predation Rates

Abiotic and biotic factors which were identified to affect Polyphemus feeding rates included temperature, prey density and type, size and type of Polyphemus, and photoperiod. Figure 32 and 33 summarize the relationship between temperature and prey density for nauplii (Fig. 32) and Bosmina sp. (Fig. 33). For nauplii in 64 ml containers at spring-fall water temperatures (12-16°C), Polyphemus feeding rates increased linearly with increasing prey density to a plateau at 2.4 nauplii · Polyphemus · day^{-1} above a density of 781 nauplii · $liter^{-1}$. At summer temperatures, (26-27°C), feeding rates did not reach a plateau but increased linearly to a rate of 5.8 nauplii · Polyphemus · day^{-1} at the maximum prey density used (1563 nauplii · $liter^{-1}$). For Bosmina sp. in 64 ml containers at summer temperatures (24-27°C), feeding rates increased linearly to a plateau at 9 Bosmina · Polyphemus · day^{-1} above a density of 1250 Bosmina · $liter^{-1}$.

Table 18 presents a comparison of daily feeding rates for different sizes and types of Polyphemus. Small Polyphemus had lower feeding rates than large individuals of the same type. For parthenogenetic females, the state of brood development did not appear to influence feeding activity. Gamogenetic females had the highest feeding rates with Chonochilus as prey. Males had extremely low feeding rates for their size; these rates were lower than those observed for the much smaller juvenile Polyphemus.

Polyphemus feeding rates exhibited a strong diel periodicity; feeding occurred primarily in the daylight period (Table 19). Daytime feeding rates averaged 5-13 times greater than nighttime rates with nauplii as prey. In containers darkened for 24 hours (covered with foil), feeding rates were low and nearly identical to nighttime rates.

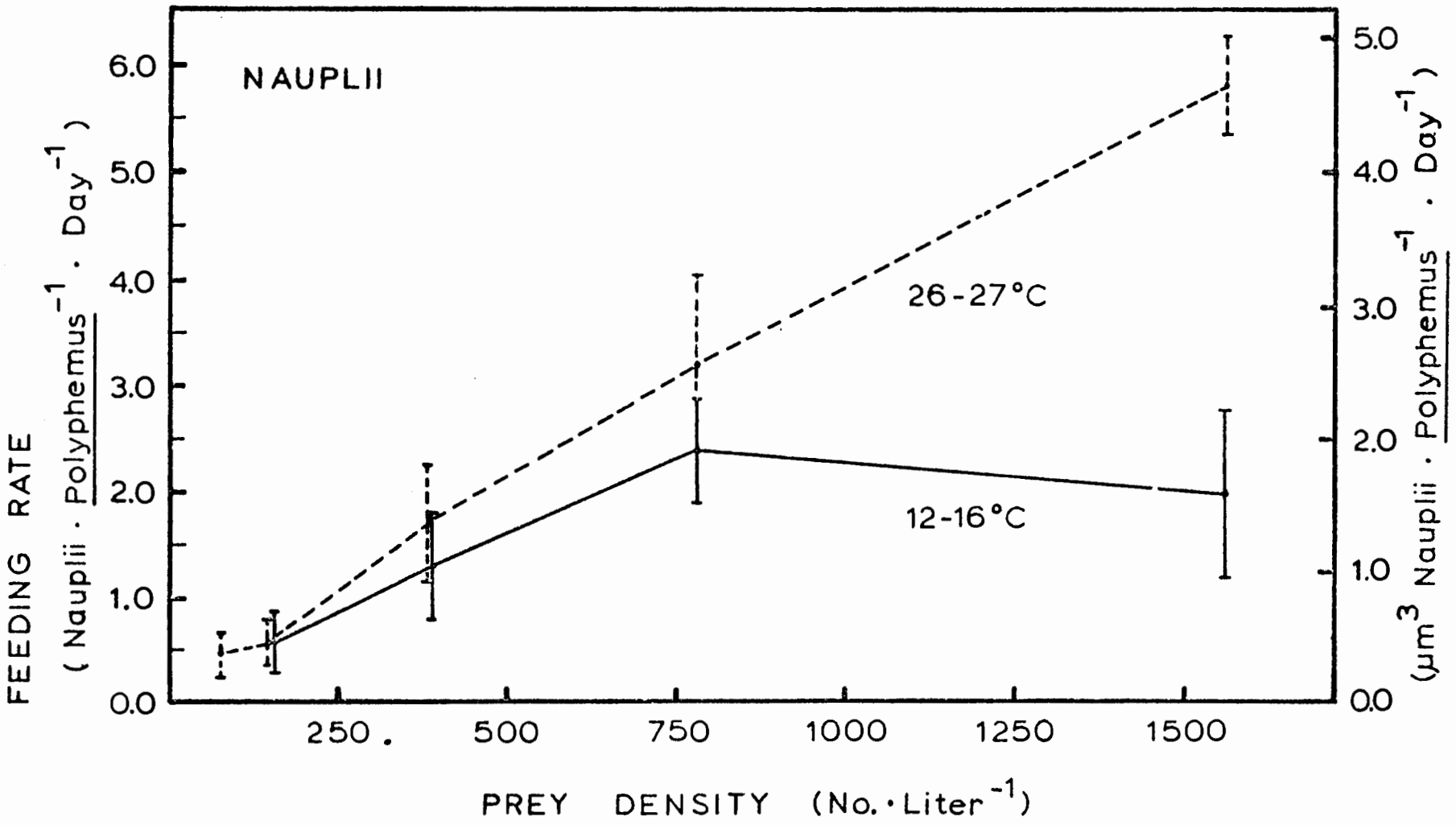


Figure 32. Effects of nauplii density and temperature on Polyphemus feeding with nauplii. Experimental conditions: differential count method, 64 ml tissue culture flasks, 24 hour in situ feeding exposure. Each point represents the mean feeding rate based on 7 to 10 replicate experiments. Vertical bars represent 2 * standard error of the mean feeding rate.

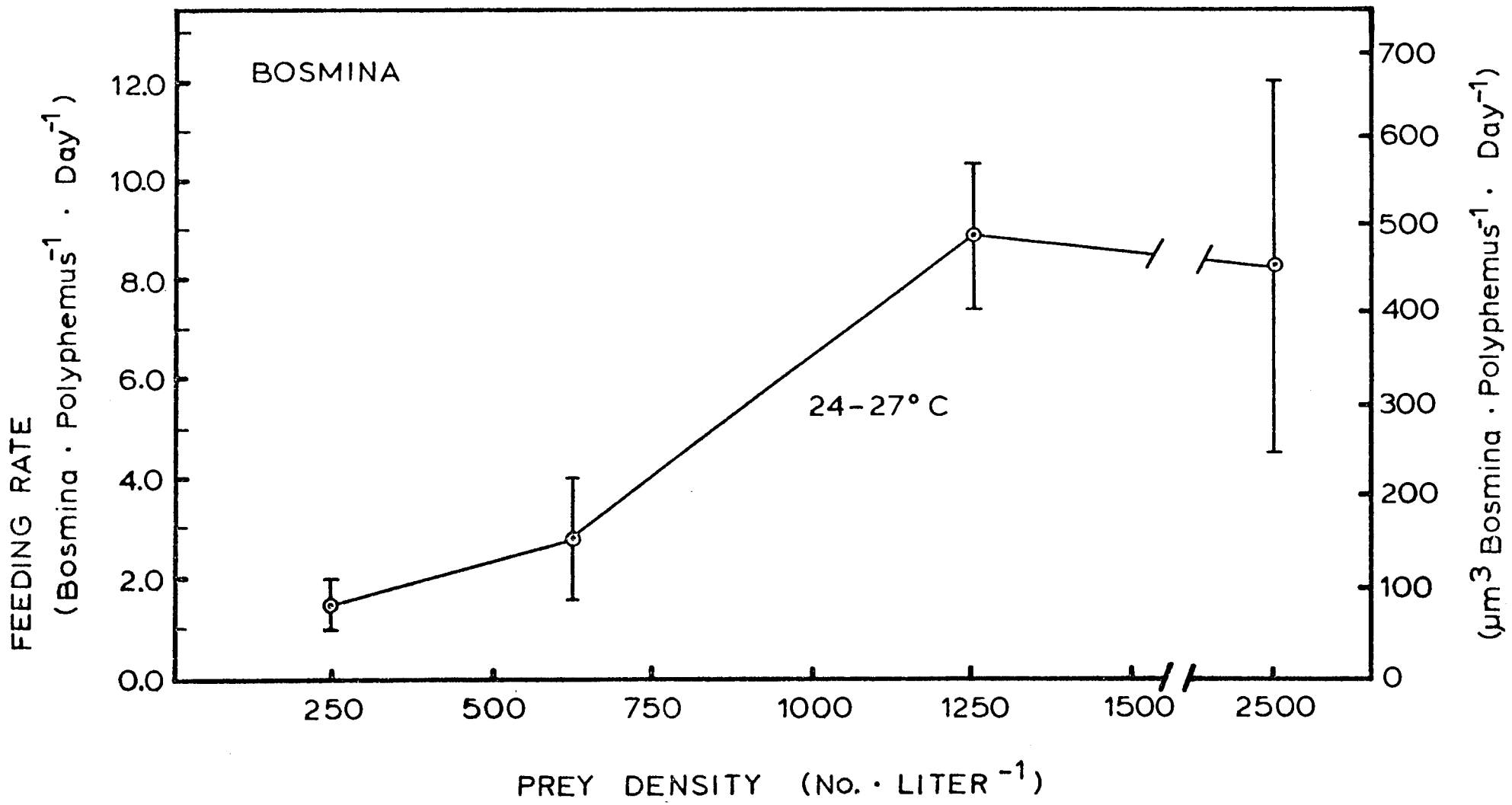


Figure 33. Effects of Bosmina prey density on Polyphemus feeding (see Figure 32 for explanation).

Table 18

24-Hour feeding rates for different sizes and types of Polyphemus. All feeding rates are the average of 15-30 Polyphemus individuals + 2 * standard error of the mean. Error estimates were not available for experiments with Chonochilus.

Polyphemus pediculus		Feeding Rate	
Type	body length (mm)	Prey·Polyphemus^{-1}·Day^{-1}	μm^3 Prey·Polyphemus^{-1}·Day^{-1}*10^6
Chonochilus as prey			
juvenile	0.36 - 0.55	9.8 (39.7)	3.9 (15.9)
parth. female			
immature brood	0.73 - 0.91	16.9 (68.5)	6.8 (27.4)
mature brood	0.73 - 0.91	18.1 (73.4)	7.2 (29.4)
gamog. female	0.73 - 0.91	22.5 (91.3)	9.0 (36.5)
experimental conditions: 64 ml tissue culture flask, 15 - 18°C; prey density - 2300 Chonochilus colonies per liter (1 colony = 48 individuals); isotope method, numbers in parentheses represent feeding rates scaled to a 1100 ml container by multiplying by 4.0556.			
Diapotomus pygmaeus nauplii as prey			
juvenile	0.36 - 0.55	16.6 ± 3.4	13.3 ± 2.7
parth. female			
immature brood	0.55 - 0.73	22.8 ± 1.5	18.2 ± 1.2
immature brood	0.73 - 0.91	51.6#	41.3#
experimental conditions: 1100 ml Erlenmeyer flask, 23 - 28°C; prey density - 1500 per liter; isotope method. # - based only on 2 Polyphemus individuals.			
Diaptomus pygmaeus nauplii as prey			
gamog. female	0.73 - 0.91	13.7 ± 4.3	10.9 ± 3.5
male	0.55 - 0.73	2.9 ± 0.7	2.3 ± 0.5
experimental conditions: 1100 ml Erlenmeyer flask, 11 - 15°C; prey density - 100 per liter; isotope method.			

Feeding rates determined by the isotope method appeared affected by the sequence of day and night periods. In experiments independent of the temporal sequence, the 24-hour rate should be comparable to the sum of the day and night half-day rates. This was only true for sunrise to sunrise experiments (sr-sr Table 19, expts. 2a, 2b). In sunset to sunset experiments (ss-ss Table 13, expts. 1a, 1b), the sum of the half-day rates was approximately one-half the 24-hour rate. This observed pattern may result from a diel periodicity in egestion of radioactive fecal material. Butorina and Sorokin (1971) demonstrated the existance for Polyphemus of a short term egestion periodicity (< 1 hour), and it is possible a diel pattern also exists. These differences may also reflect peak feeding activity at dawn and dusk which was differentially included in ss-ss and sr-sr experiments due to slight overlap of feeding periods. Data from short term feeding experiments is needed to definitely interpret this pattern.

Prey Population Dynamics

Figure 34 describes the daytime vertical distribution of prey on selected dates in 1975. Bosmina, Chonochilus and Diaptomus pygmaeus adults and copepodites were most abundant above the thermocline. Cyclopoid copepodites and adults were found in greatest abundance in and above the thermocline. Nauplii were generally most abundant below the thermocline. A pronounced hypolimnetic peak in nauplii abundance was observed in August 1975.

The seasonal patterns of abundance for Bosmina and Chonochilus (Fig. 35) varied between 1975 and 1976. For Bosmina, low abundance and sampling variability made it difficult to interpret seasonal trends. An abundance peak occurred in mid-summer in 1975, and in spring and possibly in mid-summer in 1976. Chonchilus exhibited a late summer abundance peak in 1975 and late spring, mid-summer and late-summer peaks in 1976.

Table 19

Diel variation in *Polyphemus* feeding rates, expressed as the number of *Diaptomus pygmaeus* nauplii consumed per *Polyphemus* per time period. Values represent the mean feeding rate based on 15-30 *Polyphemus* ± 2 * standard error of the mean. *In situ* isotope experiments in 1100 ml Erlenmeyer flasks.

Experiment # number	time period	temperature range (°C)	prey density (prey·liter^{-1})	feeding rate prey·Polyphemus^{-1}·period^{-1}	feeding rate 10^6 m^3 prey·Polyphemus^{-1}·period^{-1}
1a	day (12 hrs)	23 - 28	1500	8.4 ± 1.4	6.7 ± 1.1
	night (12 hrs)	23 - 25	1500	1.6 ± 0.3	1.3 ± 0.2
	24 hours (ss - ss)	23 - 28	1500	22.8 ± 1.5	18.2 ± 1.2
1b	day (12 hrs)	23 - 28	1500	12.5 ± 0.3	10.0 ± 0.2
	night (12 hrs)	23 - 25	1500	2.5 ± 0.9	2.0 ± 0.7
	24 hours (ss - ss)	23 - 28	1500	51.6@	41.3@
2a	day (12 hrs)	11 - 15	100	13.8 ± 1.9	11.1 ± 1.5
	night (12 hrs)	12 - 15	100	1.0 ± 1.0	0.8 ± 0.8
	24 hours of dark	11 - 15	100	1.1 ± 1.0	0.9 ± 0.8
	24 hours (sr - sr)	11 - 15	100	13.7 ± 4.3	10.9 ± 3.5
2b	day (12 hrs)	11 - 15	100	4.2 ± 1.8	3.3 ± 1.5
	night (12 hrs)	12 - 15	100	0.6 ± 0.3	0.5 ± 0.2
	24 hours of dark	11 - 15	100	0.5 ± 0.09	0.4 ± 0.07
	24 hours (sr - sr)	11 - 15	100	2.9 ± 0.7	2.3 ± 0.5

Legend: #1a = 0.55 - 0.73 mm parthenogenetic female *Polyphemus*
1b = 0.73 - 0.91 mm parthenogenetic female *Polyphemus*
2a = 0.73 - 0.91 mm gamogenetic female *Polyphemus*
2b = 0.55 - 0.73 mm male *Polyphemus*
@confidence limits not available; rate based on only 2 *Polyphemus*

ss - sunset
sr - sunrise

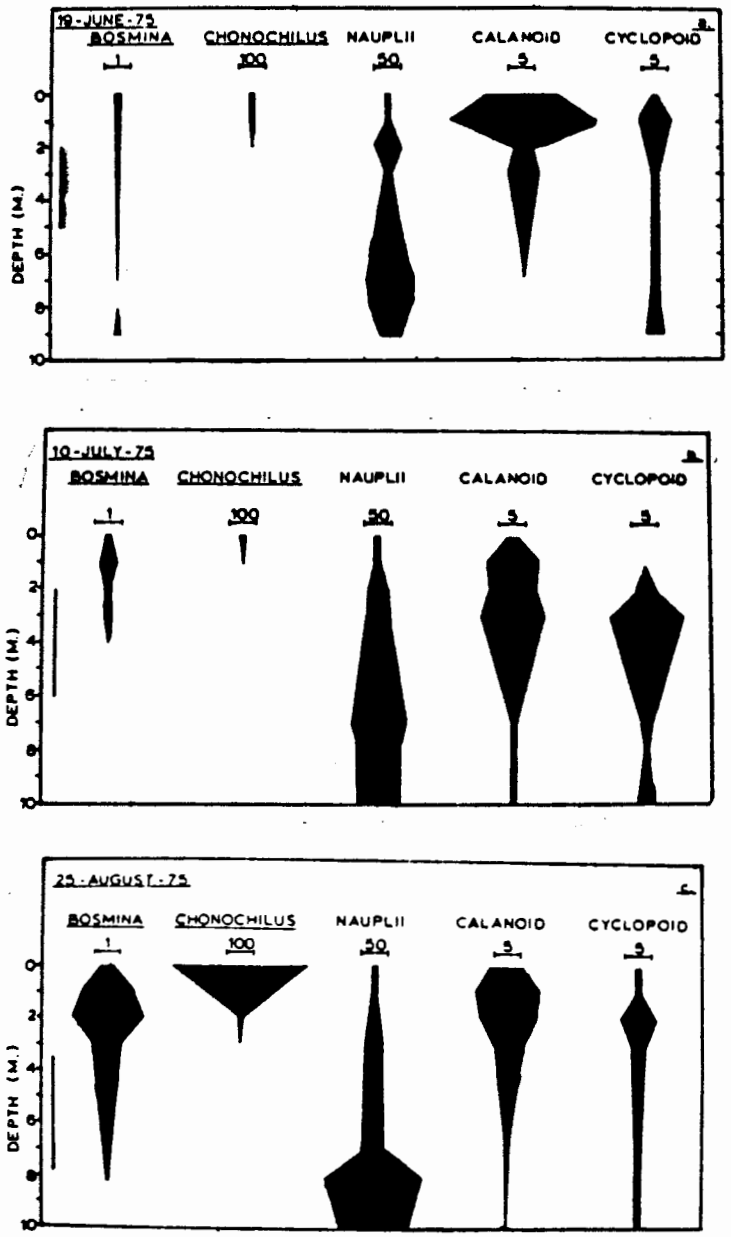


Figure 34. Kite diagrams of the daytime, limnetic, vertical distribution of Stonehouse Pond prey species for selected dates in 1975: a) 19 June 1975; b) 10 July 1975; c) 25 August 1975.

Legend: The horizontal bar above each diagram is proportional in length to the density of prey at a particular depth. The scale is the same for each species, but differs between species as follows: Bosmina sp. - 1 individual·liter^{-1}, Chonochilus unicornis - 100 individuals·liter^{-1}, copepod nauplii - 50 individuals·liter^{-1}, calanoid copepodites and adults - 5 individuals·liter^{-1}, and cyclopoid copepodites and adults - 5 individuals·liter^{-1}. The vertical bar at the left margin of each panel represents the location and thickness of the thermocline.

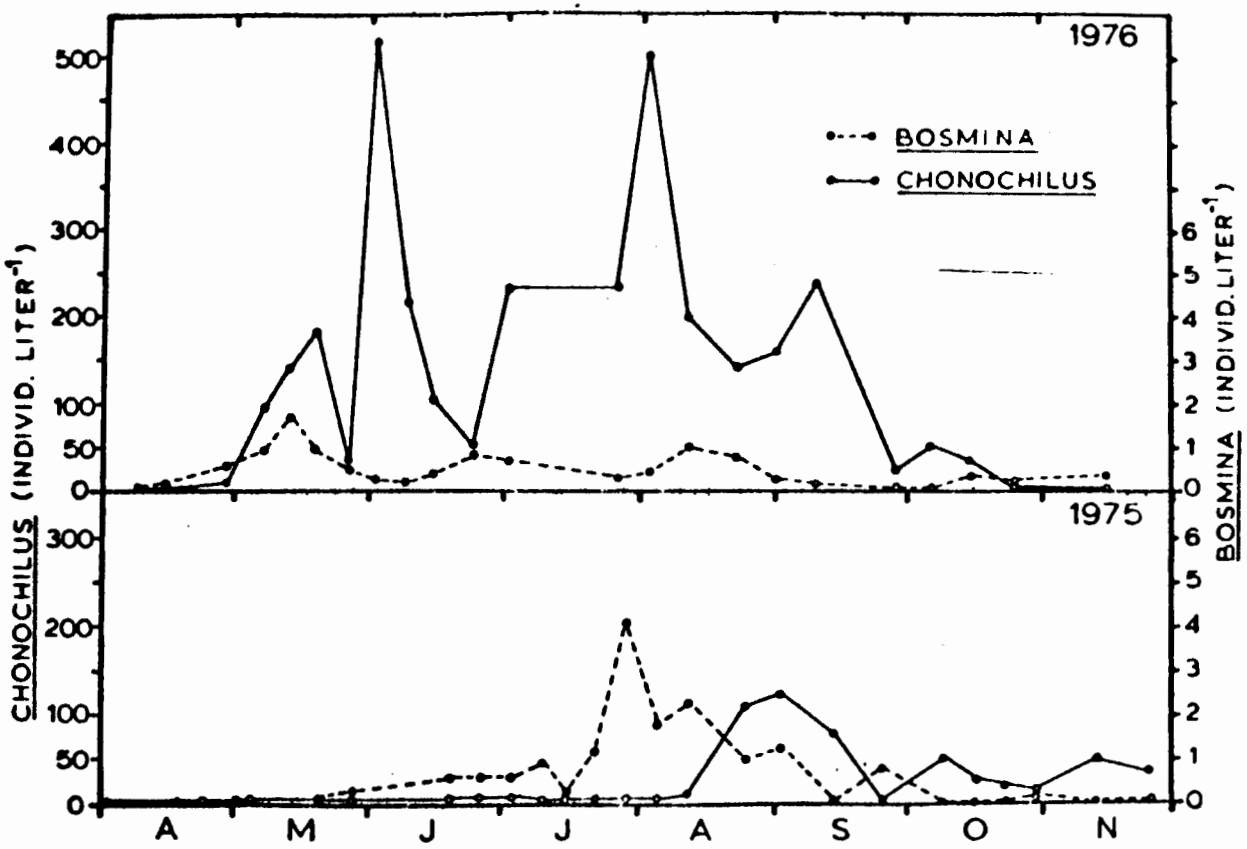


Figure 35. 1975 and 1976 seasonal changes in abundance for Bosmina sp. and Chonochilus unicornis in Stonehouse Pond. Numbers represent weighted whole lake densities as individuals·liter^{-1}. Note different scales for Bosmina (right margin) and Chonochilus (left margin).

The seasonal patterns of abundance of Stonehouse Pond copepod populations varied between 1975 and 1976, and were at least partially influenced by changes in sampling methods. In 1975, sampling was with an 8.1 liter Van Dorn water bottle with the contents filtered onto a 48 m net. In 1976, sampling was with 500 liter Clarke-Bumpus net tows with 153 μm netting. Also, 1975 sampling was in the littoral zone and in the limnetic both above and below the thermocline, while in 1976, samples were not taken in the hypolimnion. The influence of these methodological differences is best demonstrated by comparing the seasonal changes in densities (Figs. 36 and 37) with copepod vertical distributions (Fig. 33).

In 1975 (Fig 36a), sampling with the Van Dorn water bottle depicted high and variable numbers of copepod eggs in spring and early summer, and a decline in egg production in the fall. The early spring peak of eggs was almost exclusively produced by Diaptomus pygmaeus, while in late May and June cyclopoid copepods were primary contributors to egg production. A relatively small spring peak of nauplii abundance followed the Diaptomus egg peak, and a much larger peak of nauplii abundance occurred in mid-summer (Fig. 36b). This mid-summer nauplii peak occurred in the hypolimnion (Fig. 34c) and was composed primarily of cyclopoid nauplii (Mattson personal observation). The 1975 copepodite and adult copepod population (Fig 36c) was dominated by Diaptomus pygmaeus, and peaked coincident with the August nauplii peak. Otherwise, the population was low in early spring and fall and relatively constant at a density of 6-8 individuals · liter^{-1} from late May to September.

The 1976 copepod population was dominated almost exclusively by Diaptomus pygmaeus (Fig. 37). The absence of sampling in and below the thermocline apparently excluded most cyclopoid copepods from density estimates. The 1975, mid-summer, hypolimnetic peak in nauplii abundance was also apparently missed by epilimnetic sampling in 1976. Only an April peak in nauplii abundance was seen in 1976 (Fig. 37b), and this peak corresponded

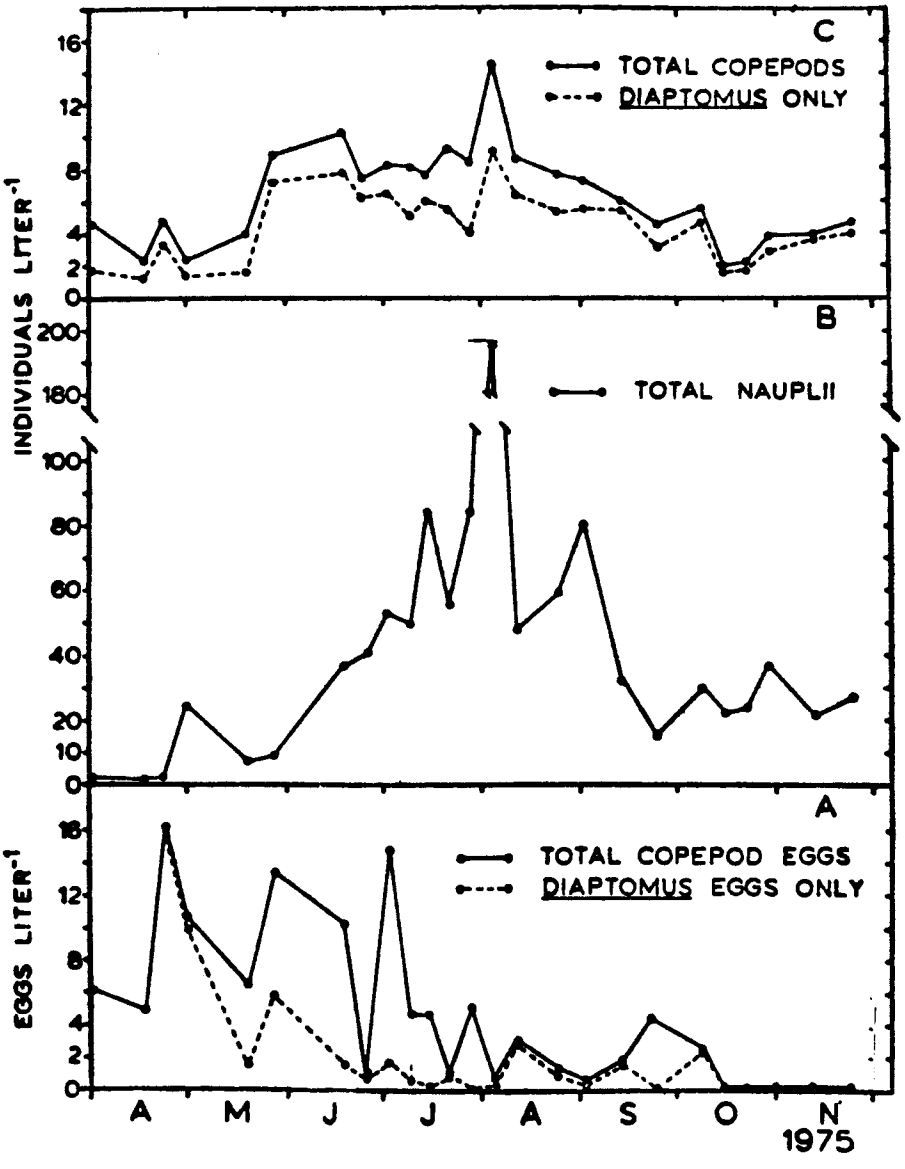


Figure 36. 1975 seasonal change in copepod abundance in Stonehouse Pond. A. copepod eggs; B. nauplii; C. copepodites and adults. Numbers represent weighted whole-lake densities as individuals·liter^{-1}. Dashed line - for Diaptomus only; solid line for all copepods including both Cyclopoid and Calanoid copepods. Calanoid and Cyclopoid nauplii were not distinguished.

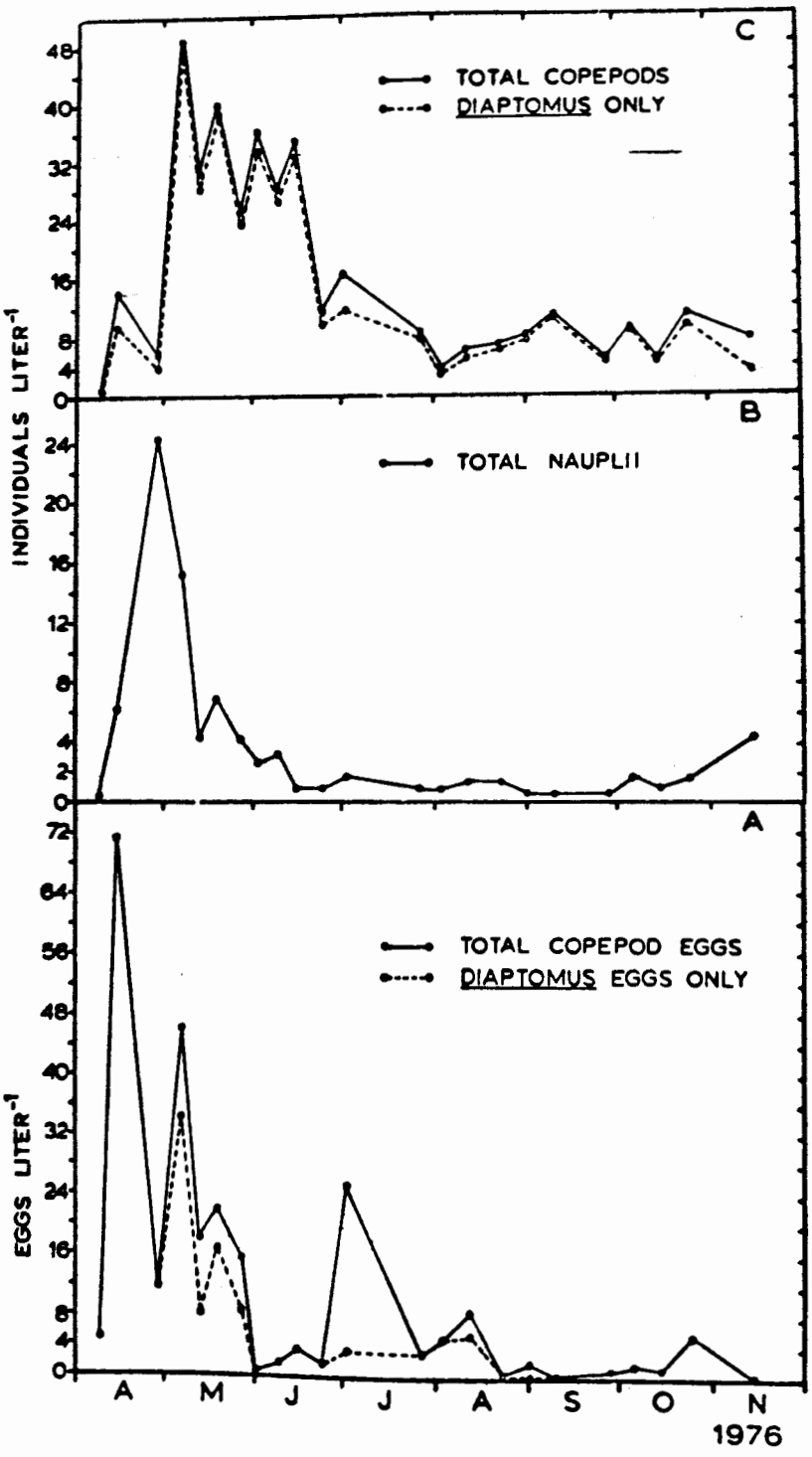


Figure 37. 1976 seasonal change in copepod abundance in Stonehouse Pond. Legend as in Figure 19. Note scale changes between 1975 and 1976.

in both timing and magnitude to the 1975 spring peak (Fig. 36b). The 1976 spring nauplii peak directly followed a peak in Diaptomus pygmaeus egg production (Fig. 37a) and in turn was followed by a peak in Diaptomus copepodites and adults (Fig. 37c).

Sampling in 1976 probably more closely reflected prey population exposure to Polyphemus predation than in 1975, since sampling was limited only to lake regions in which Polyphemus were found (littoral and epilimnion). These Clarke-Bumpus samples may underestimate nauplii and Chonochilus abundance due to loss of some individuals through the 153 μm mesh, but they would tend to be less sensitive to prey patchiness than the Van Dorn samples collected in 1975. Therefore, the 1976 samples would probably have less variation and more precisely describe changes in prey abundance than the 1975 samples.

Predation Impact

Figure 38 presents a block diagram of the deterministic computer model used to calculate predation impact (total number of prey that can be consumed by the Polyphemus population for a sampling date) by the Polyphemus population on nauplii and Chonochilus as prey. Predation impact was considered a function of several factors, namely: 1) temperature, 2) prey type and density 3) photoperiod, 4) type and size composition of Polyphemus population, 5) feeding container size. It works as follows:

The BASIC program has three nested looping sequences. Prey calculations are nested within a lake region loop which is nested in a date loop. For a given prey type and lake region, a multiple regression model relates water temperature and prey density to a daily feeding rate of one parthenogenetic female (PARTH 2) Polyphemus. This regression model had a correlation coefficient of $r^2 = 0.99$. This standard rate is then adjusted for a container effect and for the number of hours of daylight available for feeding. The Polyphemus composition is then used to adjust the adjusted

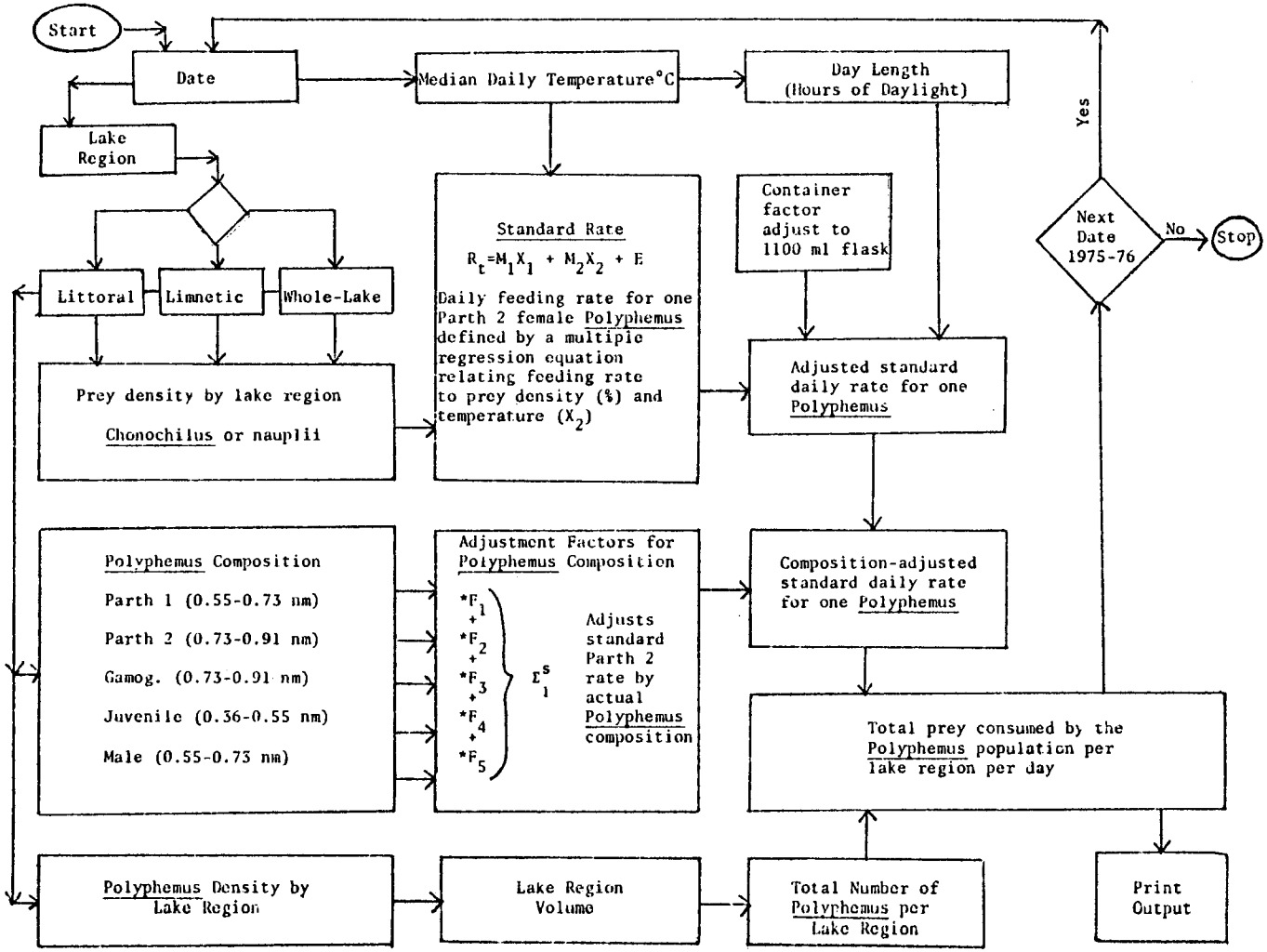


Figure 38. Flow diagram of the computer model used to calculate predation impact (total number of prey consumed per day per lake region) by the Polyphemus population of Stonehouse Pond. See text for a description of this model.

standard daily rate to a composition-adjusted standard daily rate for one Polyphemus. This composition adjustment accounts for different feeding rates by different size and type Polyphemus actually present in the lake region. If all of the Polyphemus were PARTH 2 females (0.73-0.91 nm body length), the adjusted standard daily rate would not change when adjusted for compostion. Finally, the Polyphemus density in a lake region is multiplied by the region volume to determine the total number of Polyphemus. This total is multiplied by the composition-adjusted standard daily rate for one individual to obtain an estimate of the daily total number of prey which could be consumed by the Polyphemus population of a lake region at that time.

The impact of the Polyphemus predation as total prey and percentage of prey population consumed was estimated using the BASIC model. Outputs of the model for two prey species examined, copepod nauplii and Chonochilus for 1975 and 1976 are presented in Tables 20 and 21. For both prey items highest mortalities due to Polyphemus predation took place in the littoral zone of the lake, where mortality rates were generally about 10-100 times greater. This reflects primarily the spatial aggregation of Polyphemus in the littoral region during their peak population densities in the spring and fall.

Maximum littoral mortality rates were similar for both nauplii and Chonochilus and were generally in the spring period of late May-June. The periods of highest mortality for nauplii occurred 20-28 May, 1975 (9-11% day^{-1}) and 7 May-15 June, 1976 (1-6% day^{-1}). Maximum Chonochilus mortality occurred in a brief peak on 28 May, 1975 (8% day^{-1}) and from late May - mid June, 1976 (1-5% day^{-1}). During other periods predation rates were generally <1% day^{-1}. Impact of Polyphemus predation in the open water of the lake was greatest during mid-summer when the population of Polyphemus was more dispersed horizontally. Maximum limnetic predation never exceeded 0.8% day^{-1} for either prey.

Thus, these estimates of prey mortality of up to 11% day^{-1}

Table 20

Nauplii mortality rates due to Polyphemus predation for 1975-76. Estimates calculated with the Basic Polyphemus feeding model. Mortalities are expressed as the total number of prey eaten in the entire lake as well as littoral and limnetic regions or as the proportion of the population consumed per day^{-1}, where, for example, 0.08 = 8% eaten day^{-1}.

	Total Number of Nauplii Consumed Per Region per Day					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
	Whole Lake Weighted						
Date 1975	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
24 April 75	-	18.9E2	-	20.2E1	0	6.01E-6	0
5 May 75	11.1E4	51.3E5	10.2E6	86.0E3	0	1.32E-3	0
20 May 75	11.2E6	15.4E6	19.7E6	35.4E5	34.4E3	1.14E-1	1.12E-5
28 May 75	11.5E6	14.7E6	17.9E6	10.3E5	47.0E4	8.80E-2	1.27E-4
11 June 75	10.4E5	13.8E5	17.3E5	74.8E3	55.5E4	9.83E-3	3.47E-4
19 June 75	63.9E5	86.3E5	10.9E6	90.6E4	33.9E5	7.95E-3	2.20E-4
26 June 75	62.7E5	10.6E6	11.9E6	12.4E5	57.0E5	6.74E-3	3.29E-4
3 July 75	11.3E5	13.7E6	26.2E6	10.4E5	11.1E6	2.89E-3	4.98E-4
10 July 75	29.2E5	52.3E5	75.3E5	57.3E4	36.6E5	2.08E-3	1.74E-4
15 July 75	84.2E5	17.0E6	25.6E6	72.0E4	13.4E6	2.63E-3	3.73E-4
22 July 75	37.2E5	48.6E5	60.1E5	29.3E4	32.0E5	1.10E-3	1.36E-4
29 July 75	39.3E5	49.4E5	59.5E5	17.9E4	29.1E5	1.37E-3	8.06E-5
5 Aug. 75	27.5E6	33.6E6	39.7E6	35.2E4	25.7E6	2.46E-3	3.07E-4
12 Aug. 75	95.9E5	11.5E6	13.3E6	66.1E4	87.9E5	3.37E-3	4.35E-4
19 Aug. 75	30.3E5	62.3E5	94.3E5	11.5E5	46.8E4	6.18E-3	2.07E-5
25 Aug. 75	45.9E5	85.3E5	12.5E6	11.1E5	16.6E5	6.31E-3	6.61E-5
2 Sept. 75	56.9E5	81.9E5	10.7E6	40.3E4	27.4E5	3.73E-3	8.04E-5

Table 20 (cont.'d)

	Total Number of Nauplii Consumed Per Region per Day Whole Lake Weighted					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
Date 1975	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
14 Sept. 75	15.5E5	38.4E5	61.4E5	72.8E4	20.8E4	5.92E^{-}3	1.54E^{-}5
25 Sept. 75	18.0E5	26.2E5	34.4E5	50.2E4	67.6E3	1.12E^{-}2	1.10E^{-}5
9 Oct. 75	30.0E5	42.5E5	55.0E5	12.2E4	96.0E3	7.48E^{-}3	7.50E^{-}6
16 Oct. 75	69.1E4	10.2E5	13.4E5	29.2E3	54.9E3	2.37E^{-}3	5.89E^{-}6
23 Oct. 75	19.4E4	26.0E4	32.5E4	46.1E2	14.5E3	5.64E^{-}4	1.45E^{-}6
30 Oct. 75	48.5E3	52.5E4	10.0E5	14.2E4	11.5E3	7.55E^{-}4	7.37E^{-}7
6 Nov. 75	77.7E3	88.6E3	99.4E3	30.4E3	0	1.62E^{-}4	0
13 Nov. 75	17.0E2	12.3E3	22.9E3	60.9E2	0	3.11E^{-}5	0
20 Nov. 75	12.1E1	11.0E3	21.9E3	59.2E2	0	2.46E^{-}5	0
25 Nov. 75	66.4E2	18.0E3	29.4E3	10.8E3	0	3.61E^{-}5	0
4 Dec. 75	13.0E2	61.8E2	11.1E3	36.8E2	0	1.23E^{-}5	0
Date 1976	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
9 April 76	6.7E0	40.4E0	74.1E0	40.4E0	0	2.35E^{-}7	0
15 April 76	18.0E1	61.9E2	12.2E3	24.5E1	0	5.28E^{-}5	0
29 April 76	72.8E4	35.0E5	62.7E5	60.5E5	19.8E4	7.24E^{-}3	6.60E^{-}5
7 May 76	21.1E5	57.2E5	93.3E5	61.3E4	27.5E3	2.30E^{-}2	1.33E^{-}5
13 May 76	21.8E5	37.4E5	53.0E5	30.3E4	32.3E4	4.41E^{-}2	4.92E^{-}4
19 May 76	58.9E5	83.6E5	10.8E6	44.0E3	88.1E4	5.92E^{-}2	8.08E^{-}4
27 May 76	24.1E5	38.8E5	53.4E5	89.6E3	77.7E4	4.02E^{-}2	1.16E^{-}3

Table 20 (cont.'d)

Date 1976	Total Number of Nauplii Consumed Per Region per Day Whole Lake Weighted					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
2 June 76	17.9E5	21.9E5	26.0E5	29.8E3	10.1E5	2.68E-2	2.46E-3
9 June 76	19.0E5	22.3E5	25.5E5	12.1E4	93.6E4	2.33E-2	1.87E-3
15 June 76	24.5E4	67.0E4	10.9E5	13.1E4	11.7E5	1.31E-2	8.36E-3
24 June 76	43.2E1	21.7E4	43.3E4	46.5E3	80.1E3	8.63E-3	5.93E-4
2 July 76	64.1E3	14.3E4	22.1E4	21.7E3	11.8E4	8.71E-4	4.84E-4
26 July 76	44.8E3	83.3E3	12.2E4	51.4E3	20.0E3	1.10E-3	1.87E-4
3 Aug. 76	22.0E3	13.2E4	24.3E4	46.8E3	91.2E3	2.29E-3	7.66E-4
12 Aug. 76	41.9E4	57.4E4	73.0E4	21.7E4	59.4E4	7.00E-3	3.02E-3
23 Aug. 76	29.7E4	36.9E4	44.2E4	96.4E3	28.4E4	2.51E-3	1.35E-3
1 Sept. 76	37.4E2	62.1E3	12.0E4	57.7E3	30.5E3	1.34E-3	4.78E-4
10 Sept. 76	28.2E3	59.7E3	91.3E3	97.4E3	11.8E3	4.09E-3	1.67E-4
16 Sept. 76	68.1E2	36.2E3	65.6E3	45.8E3	47.8E2	2.74E-3	6.04E-5
28 Sept. 76	46.4E1	48.6E3	96.8E3	36.5E3	47.0E1	3.93E-3	4.98E-6
5 Oct. 76	52.2E3	10.3E4	15.3E4	52.2E3	13.3E2	3.09E-3	5.08E-6
15 Oct. 76	71.6E1	53.8E3	10.7E4	10.9E4	54.6E1	2.98E-3	4.75E-6
25 Oct. 76	59.7E2	19.5E3	33.1E3	26.8E3	33.9E1	6.16E-4	1.55E-6
5 Nov. 76	52.8E1	15.0E2	24.7E2	11.5E2	0	2.69E-5	0
15 Nov. 76	91.8E0	39.8E1	70.4E1	21.5E1	0	4.82E-6	0

Table 21

Chonochilus mortality rates due to *Polyphemus* predation for 1975-76. See Table 20 for explanation.

	Total Number of *Chonochilus* Colonies Consumed per Region per Day					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
	Whole Lake Weighted						
Date 1975	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
24 April 75	0	0	0	0	0	0	0
5 May 75	0	0	0	0	0	0	0
20 May 75	0	0	0	0	0	0	0
28 May 75	72.6E1	93.0E1	11.3E2	18.9E3	0	7.75E-2	0
11 June 75	52.6E3	70.0E3	87.4E3	63.5E2	28.0E3	8.63E-3	3.05E-4
19 June 75	42.1E2	56.8E2	71.5E2	63.5E2	20.7E2	7.01E-3	1.94E-4
26 June 75	10.6E3	17.9E3	25.2E3	85.9E2	93.1E2	5.92E-3	2.90E-4
3 July 75	25.0E2	30.1E3	57.7E3	15.1E3	22.3E3	2.53E-3	4.39E-4
10 July 75	46.4E1	82.9E1	12.0E2	23.0E2	39.3E1	1.83E-3	1.53E-4
15 July 75	55.7E2	11.3E3	16.9E3	19.7E2	86.4E2	2.31E-3	3.27E-4
22 July 75	95.9E2	12.5E3	15.5E3	20.6E3	58.4E2	9.69E-4	1.19E-4
29 July 75	46.8E2	58.9E2	71.0E2	59.5E3	0	1.21E-3	0
5 Aug. 75	22.5E3	27.5E3	32.5E3	94.2E2	19.9E3	2.16E-3	2.71E-4
12 Aug. 75	45.8E3	54.8E3	63.7E3	14.4E4	23.8E3	2.95E-3	3.82E-4
19 Aug. 75	79.5E3	16.4E4	24.8E4	21.0E4	11.7E3	5.42E-3	1.82E-5
25 Aug. 75	16.3E4	30.2E4	44.1E4	18.5E4	57.2E3	5.58E-3	5.82E-5

Table 21 (cont.'d)

Date 1975	Total Number of *Chonochilus* Colonies Consumed per Region per Day: Whole Lake Weighted LL	Whole Lake Weighted $\bar{x}$	Whole Lake Weighted VL	Littoral	Limnetic	Decimal Proportion Prey Population Eaten/Day (x100=percent): Littoral	Limnetic
2 Sept. 75	16.9E4	24.4E4	31.8E4	77.6E4	65.2E3	3.30E-3	7.06E-5
14 Sept. 75	71.5E3	17.7E4	28.3E4	41.2E4	86.0E2	5.22E-3	1.35E-5
25 Sept. 75	64.9E2	94.5E2	12.4E3	54.5E3	19.2E1	9.83E-3	9.72E-6
9 Oct. 75	94.0E3	13.3E4	17.3E4	16.7E4	28.5E2	6.57E-3	6.58E-6
16 Oct. 75	16.0E3	23.5E3	31.0E3	84.0E3	10.6E2	2.10E-3	5.16E-6
23 Oct. 75	29.6E2	39.5E2	49.5E2	12.7E2	21.7E1	4.96E-4	1.27E-6
30 Oct. 75	36.9E1	39.9E2	76.1E2	39.5E1	87.9E0	6.63E-4	6.48E-7
6 Nov. 75	16.0E2	18.2E2	20.5E2	27.8E1	0	1.44E-4	0
13 Nov. 75	73.3E0	53.1E1	98.9E1	15.8E1	0	2.72E-5	0
20 Nov. 75	4.0E0	36.8E1	73.2E1	15.0E1	0	2.16E-5	0
25 Nov. 75	16.6E1	45.0E1	43.4E1	26.9E1	0	3.19E-5	0
4 Dec. 75	32.5E0	15.4E1	27.6E1	91.5E0	0	1.08E-5	0
Date 1976	**LL**	**$\bar{x}$**	**VL**	**Littoral**	**Limnetic**	**Littoral**	**Limnetic**
9 April 76	0.6E0	3.7E0	6.9E0	3.9E0	0	6.04E-7	0
15 April 76	1.0E0	33.3E0	65.7E0	9.3E0	0	4.62E-5	0
29 April 76	44.1E2	21.2E3	3.80E3	51.5E3	10.6E2	6.37E-3	5.78E-5
7 May 76	25.5E4	69.0E4	11.3E5	77.7E3	33.2E2	2.03E-2	1.17E-5

Table 21 (cont.'d)

Date 1976	Total Number of Chonochilus Colonies Consumed per Region per Day					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
	Whole Lake Weighted						
	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
13 May 76	13.4E5	23.0E5	32.6E5	38.0E5	15.9E4	3.87E-2	4.34E-4
19 May 76	28.7E5	40.7E5	52.7E5	89.7E5	30.6E4	5.21E-2	7.13E-4
27 May 76	25.4E4	40.7E4	56.1E4	44.7E4	69.1E3	3.53E-2	1.02E-3
2 June 76	65.0E5	79.8E5	94.5E5	26.5E5	34.4E5	2.36E-2	2.16E-3
9 June 76	24.1E5	28.2E5	32.3E5	63.7E4	11.5E5	2.05E-2	1.65E-3
15 June 76	48.9E4	13.4E5	21.9E5	42.0E4	22.2E5	1.15E-2	7.30E-3
24 June 76	46.9E1	23.5E4	47.0E4	13.5E4	81.2E3	7.61E-3	5.23E-4
2 July 76	16.0E4	35.6E4	55.3E4	45.2E3	30.0E4	7.67E-4	4.25E-4
26 July 76	19.5E4	36.2E4	53.0E4	10.2E3	12.4E4	9.64E-4	1.65E-4
3 Aug. 76	22.7E4	13.7E5	25.1E5	10.2E5	76.7E4	2.01E-3	6.72E-4
12 Aug. 76	10.5E5	14.4E5	18.3E5	20.6E4	16.4E5	6.14E-3	2.65E-3
23 Aug. 76	49.4E4	61.5E4	73.6E4	99.1E3	50.4E4	2.20E-3	1.19E-3
1 Sept. 76	16.1E3	26.8E4	51.9E4	99.2E2	21.7E4	1.18E-3	4.20E-4
10 Sept. 76	20.8E4	44.0E4	67.3E4	90.5E4	79.5E3	3.59E-3	1.47E-4
16 Sept. 76	22.3E3	11.8E4	21.5E4	23.3E4	13.8E3	2.40E-3	5.30E-5
28 Sept. 76	33.9E1	35.6E3	70.8E3	10.8E4	24.2E1	3.46E-3	4.38E-6
5 Oct. 76	28.6E3	56.2E3	83.8E3	75.2E2	75.9E1	2.71E-3	4.45E-6
15 Oct. 76	49.6E1	37.3E3	74.2E3	29.2E2	49.2E1	2.62E-3	4.17E-6

Table 21 (cont.'d)

Date 1976	Total Number of *Chonochilus* Colonies Consumed per Region per Day					Decimal Proportion Prey Population Eaten/Day (x100=percent)	
	Whole Lake Weighted						
	LL	$\bar{x}$	VL	Littoral	Limnetic	Littoral	Limnetic
25 Oct. 76	34.4E1	11.2E2	19.0E2	26.3E1	22.7E0	$5.44E^{-}4$	$1.36E^{-}6$
5 Nov. 76	8.9E0	25.2E0	41.5E0	9.1E0	0	$2.35E^{-}5$	0
15 Nov. 76	0.1E0	0.3E0	0.6E0	1.2E0	0	$4.30E^{-}6$	0

indicate that predation by Polyphemus can be an important factor in the regulation of prey species such as nauplii and Chonochilus, especially in the spring period. To further evaluate the influence of Polyphemus predation on these prey species population growth rates of the prey should also be examined and compared with mortality rates. Also, estimates of predation rates on larger, slower growing prey such as Bosmina should also be included to evaluate the total impact of Polyphemus predation on the zooplankton community.

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APPENDIX I

APPENDIX 1

Gut analysis of 81 brook trout, Salvelinus fontinalis, captured in Stonehouse Pond, Barrington, New Hampshire.

Summary

Total number of fish examined = 81

Length range of fish examined = 11 - 32 cm

Examination period = 24-IV-75 - 21-V-79

Capture methods = WF = Wet fly fishing (48 fish)
DF = Dry fly fishing (21 fish)
BS = 24-meter bag seine (12 fish)

Gut Contents	Percent	Number of fish	*Ranking (number of fish) 1	2	3	4
Zooplankton	56%	45	-	-	-	-
Polyphemus	17%	14	4	5	4	1
Other	48%	39	20	18	1	0
Insecta	97.5%	79	57	20	2	0
Other Invertebrates	11%	9	0	4	3	2

*Ranking of prey contribution to diet, as abundance (number) of prey in gut.

1 > 2 > 3 > 4

1 = most abundant prey in gut

4 = least abundant prey in gut

Summary

Frequency distribution of ranking of prey contribution to diet of 81 brook trout.

Prey	Ranking	# Fish	Frequency ⟶	
Polyphemus	1	4	XXXX	(X = 1 fish)
	2	5	XXXXX	
	3	4	XXXX	
	4	1	X	
Other Zooplankton	1	20	XXXXXXXXXXXXXXXXXXX	(X = 1 fish)
	2	18	XXXXXXXXXXXXXXXXX	
	3	1	X	
	4	0		
Insecta	1	57	XXXXXXXXXXXXXXXXXXXXXXXXXXX	
	2	20	XXXXXXXXXX	(X = 2 fish)
	3	2	X	
	4	0		
Other Invertebrates	1	0		(X = 1 fish)
	2	4	XXXX	
	3	3	XXX	
	4	2	XX	

				Gut Contents (stomach & esophagus only)			
				Zooplankton			
Fish #	Total Length(cm)	Capture Date	Capture Method	Polyphemus	Other	Class Insecta	Other
1	23	24-IV-75	WF	0	0	1	2
2	25	24-IV-75	WF	0	0	1	2
3	23	24-IV-75	WF	0	0	1	2
4	--	29-IV-76	WF	0	0	1	0
5	--	29-IV-76	WF	0	2	1	0
6	--	29-IV-76	WF	0	0	1	0
7	--	29-IV-76	WF	0	0	1	0
8	--	29-IV-76	WF	0	0	1	0
9	--	29-IV-76	WF	0	0	1	0
10	--	29-IV-76	WF	0	0	1	0
11	--	29-IV-76	WF	0	0	1	0
12	24	8-VI-76	WF	3	1	2	0
13	25	8-VI-76	WF	0	0	1	2
14	25	8-VI-76	WF	0	0	1	0
15	20	28-IX-76	WF	3	1	2	0
16	14	22-X-76	BS	0	0	1	0
17	14	22-X-76	BS	0	1	2	3
18	14	22-X-76	BS	1	2	3	4
19	14	22-X-76	BS	0	1	2	0
20	13	22-X-76	BS	2	0	1	0
21	13	22-X-76	BS	1	0	2	0
22	14	22-X-76	BS	0	1	2	0
23	15	22-X-76	BS	0	0	1	0
24	12	22-X-76	BS	4	1	2	3
25	11	22-X-76	BS	0	2	1	0

				Gut Contents (stomach & esophagus only)			
				Zooplankton			
Fish #	Total Length(cm)	Capture Date	Capture Method	Polyphemus	Other	Class Insecta	Other
26	13	22-X-76	BS	0	2	1	0
27	20	17-V-77	WF	0	1	2	0
28	22	17-V-77	WF	0	1	2	0
29	24	17-V-77	WF	0	1	2	0
30	22	17-V-77	WF	0	1	2	0
31	21	17-V-77	WF	0	2	1	0
32	24	17-V-77	WF	0	1	2	0
33	17	18-V-77	WF	1	0	2	0
34	21	18-V-77	WF	3	2	1	0
35	20	18-V-77	WF	0	1	2	0
36	19	18-V-77	WF	0	2	1	0
37	18	18-V-77	WF	0	1	2	0
38	19	18-V-77	BS	2	0	1	0
39	24	18-V-77	WF	2	0	1	0
40	20	18-V-77	WF	2	0	1	3
41	19	18-V-77	WF	0	1	2	0
42	32	24-V-77	WF	0	0	1	0
43	22	24-V-77	DF	0	2	1	0
44	22	24-V-77	WF	0	0	1	0
45	21	24-V-77	WF	0	0	1	0
46	22	24-V-77	WF	0	0	1	0
47	18	24-V-77	WF	0	0	1	0
48	20	24-V-77	WF	0	0	1	0
49	20	24-V-77	WF	0	0	1	0
50	21	24-V-77	WF	0	0	1	0
51	16	25-V-77	WF	1	2	3	0
52	22	31-V-77	WF	0	0	1	0
53	21	31-V-77	WF	0	1	2	0
54	24	31-V-77	WF	0	2	1	0
55	22	2-VI-77	DF	3	2	1	0

				Gut Contents (stomach & esophagus only)			
				Zooplankton			
Fish #	Total Length(cm)	Capture Date	Capture Method	Polyphemus	Other	Class Insecta	Other
56	23	2-VI-77	DF	0	1	2	0
57	22	6-VI-77	DF	0	0	1	0
58	19	6-VI-77	DF	2	3	1	4
59	24	7-VI-77	DF	0	2	1	0
60	19	7-VI-77	DF	0	0	1	0
61	20	7-VI-77	DF	0	0	1	0
62	20	7-VI-77	DF	0	0	1	0
63	24	7-VI-77	DF	0	0	1	0
64	21	7-VI-77	DF	0	2	1	0
65	24	7-VI-77	DF	0	2	1	0
66	19	11-V-78	WF	0	0	1	0
67	20	11-V-78	WF	0	0	1	0
68	21	11-V-78	WF	0	0	1	0
69	22	11-V-78	WF	0	0	1	0
70	25	18-V-78	DF	0	1	0	0
71	20	18-V-78	DF	0	0	1	0
72	21	18-V-78	DF	0	1	0	0
73	23	18-V-78	DF	0	0	1	0
74	20	18-V-78	DF	0	0	1	0
75	21	18-V-78	DF	0	1	2	0
76	19	18-V-78	DF	0	2	1	0
77	17	8-V-79	WF	0	1	2	0
78	21	21-V-79	WF	0	2	1	0
79	19	21-V-79	WF	0	2	1	0
80	22	21-V-79	DF	0	2	1	0
81	23	21-V-79	DF	0	0	1	0