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Life Cycles, Biomass and Production of Copepods in Lake Memphremagog

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A Thesis

in

The Department

of

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ABSTRACT

Life Cycles, Biomass and Production of Copepods in Lake Memphremagog

Vahé Sarafian

Production and biomass of the 4 most abundant copepod species in the central basin of Lake Memphremagog, Québec (Canada) - Vermont (U.S.A.), were estimated from weekly or bimonthly samples collected from mid-May to mid-November 1976.

The life cycles of the 4 species were described from instar analysis. Three cyclopoid species, Cyclops bicuspidatus thomasi, C. vernalis and Mesocyclops edax, each produced 4 or 5 generations during the ice-free period, while the calanoid, Diaptomus sicilis was univoltine.

Production was estimated with the increment-summation method (Winberg, 1971). Generation lengths were deduced from the population curves, and instar durations were calculated with Ivanova's (1973) method or from the abundance curves.

Total production of the 4 species during the 187 day period was 11.24g.m^{-2}(dry), of which half was attributed to C.b. thomasi. D. sicilis produced 2.18g.m^{-2} and C. vernalis and M. edax produced 1.5g.m^{-2} each. Total egg production amounted to 3.7g.m^{-2}.

Mean monthly biomass added up to 1.36g.m^{-2}. C.b. thomasi contributed 0.675g.m^{-2} and C. vernalis, M. edax and D. sicilis had mean monthly standing stocks of 0.07g.m^{-2}, 0.175g.m^{-2} and 0.44g.m^{-2} respectively. These production and biomass figures, when compared to published values, indicate that the central basin of Lake Memphremagog would be in the mesotrophic to eutrophic range.

Two indirect methods for estimating secondary production were tested for their accuracy in predicting copepod production in Lake Memphremagog. These were the production/biomass ratio (P/B) using adult body mass as a scaling factor (Banse and Mosher, 1980) and primary production, which has been shown (Brylinsky, 1980) to explain up to 50% of the variability in carnivorous zooplankton production (CZP). These methods predicted P/B and CZP values that were approximately 50% of the calculated amounts. It was concluded that although indirect methods could, at present, be useful in limited situations, their predictive power can be improved only if a more accurate data base, obtained directly, is available.

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INTRODUCTION

The importance of studying biological productivity in freshwaters was recognized some time ago by Welch (1935) who defined limnology as the study of productivity in inland waters. Since then, a lot of knowledge has been gained on primary production but relatively few studies of secondary production have been forthcoming.

The reason for the slower progress in secondary production studies is that contrary to primary production, which can be measured directly as the uptake rate of one element (e.g. ^{14}C), no single method exists yet which can estimate the production of the very complex and varied groups that make up secondary producers. Freshwater ecologists have not yet agreed as to which organisms belong to this group. Secondary producers have been defined as all heterotrophic organisms exploiting the aquatic environment (Waters, 1977) including fish, reptiles, birds and mammals; Morgan (1980) has included in this categoty the zooplankton, zoobenthos and fish, although he acknowledged the presence of tertiary producers in each of the three groups. More recently, Downing (1984) restricted the range of organisms considered secondary producers to freshwater invertebrates.

Thus, although by a strict definition, the term secondary producer should apply only to herbivores, separating groups according to their diets is, in practice, very difficult since many freshwater species are omnivores, detritivores or may change diets during their development from larval to adult stage. There is general agreement, however, that

if not strictly true, a functional definition of secondary producers in freshwaters includes at least the invertebrates, irrespective of their diets. Of course, if the diets are known, then a subdivision into herbivore and carnivore production improves the accuracy of the data.

A generally accepted definition of secondary production (Clarke, 1946; Waters, 1977; Parsons 1980) is "that amount of tissue elaborated per unit time, per unit area, regardless of its fate". Contrary to primary production which is divided into net and gross production, the usual convention (Odum, 1959) is not to include respiratory energy in the calculation of secondary production which is therefore analogous to net primary production.

It can be deduced from the above that measuring the productivity of such a wide range of organisms is not an easy task. No single method can be applied to all of them since they represent many different life histories. A complete analysis requires the collection of large numbers of samples to overcome heterogeneous distributions and the sorting and analysis of samples can be overwhelming. This may have been an important factor contributing to the large number of publications related to methodology rather than to the actual measurement of secondary production (e.g.; Winberg, 1971; Edmondson, 1974; Rigler and Downing, 1984).

Since this study is concerned with the production of a group of secondary producers, the copepods, it would be useful to review some of the theoretical reasons for studying secondary production.

In the 2nd edition of the IBP Handbook on secondary productivity, Downing (1984) lists four theoretical justifications for undertaking

research on secondary production. These are: a) Energy or material transfer within ecosystems. b) Management of aquatic resources. c) Detection of pollution. d) Formation of general theories of biological production. The following paragraphs, condensed and modified from Downing (1984) summarize his justifications for these categories.

a) Energy or material transfer within ecosystems

Lindeman (1942) proposed that organisms be ranked by their mode of obtaining energy, i.e. primary producers, secondary producers, etc. The trophic dynamic concept established a link between organisms based on a common currency, energy, which they fix to form their own tissue which then becomes available to the next trophic level. Lindeman explained the shaping of communities by the relative success with which organisms exploit the available energy.

This concept has attracted much attention. Many research projects such as the International Biological Program (IBP) have been inspired by it and relationships between the various production levels have been explored (Hall et al., 1970; Makarewicz and Likens, 1979; Brylinsky, 1980).

Although the trophic-dynamic approach to ecosystems analysis is still very popular among ecologists, the complexity of the interactions among organisms, which form an intricate food web, has hindered the verification of the theory. Peters (1977) suggested that the theory is non-operational and therefore not very useful because of the near impossibility of assigning to a particular trophic level organisms such as omnivores, detritivores or animals that change diets during different stages of their development.

b) Management of aquatic resources

Many studies have shown the importance of invertebrates in the diet of fish (Nakashima and Leggett, 1975; Zwanenburg, 1981) and since fish are usually considered the most useful aquatic resource to man, it has been suggested (e.g. Waters, 1977) that a better understanding of secondary production will improve fish management.

c) Detection and treatment of pollution

Production can be enhanced near areas of human activity (Mikulski et al., 1975 cited in Downing, 1984) or decreased, if the pollutants are toxic (Zelinka, 1977 cited in Downing, 1984). Patalas (1970, cited in Waters, 1977) monitored the effect of thermal effluents on zooplankton production to measure the possible detrimental effects of heated water. Waters (1977) suggests that secondary producers could be used in sewage treatment.

d) Formation of general theories of biological production

General theories are useful when they are testable and can make measurable predictions on the outcome of events (Peters, 1983). Factors that affect secondary production, both biotic and abiotic, are being examined through multivariate analysis (e.g. Brylinsky, 1980) in order to enable ecologists to predict events affecting production. Improved predictive ability could lead to manipulation of factors affecting production to our advantage (e.g. in resource management) and future studies will undoubtedly concentrate on this area.

The above justifications bring into perspective the importance of undertaking goal oriented studies which could result in improved

predictive ability in both theoretical ecology or environmental planning. The accumulation of unrelated facts and data that are not comparable hinders the elaboration of empirically derived generalizations from which predictions can be made. The complex nature of secondary producers makes it very difficult to collect accurate data on all the representative groups of this trophic level even in one location unless such projects are undertaken by large teams working simultaneously on the same water body. It is usually necessary, in order to obtain usable data, to study secondary producers in small groups of related organisms or even in individual species.

This study attempts to obtain data on one group of secondary producers, the copepods and its goal is twofold: a) to provide production data which will complement simultaneous production studies of other producer groups in the same lake (Lake Memphremagog) and b) to compare the data obtained with a direct method of measuring production to other indirect methods and discuss the merits of both approaches.

The organisms I studied are the pelagic (open water) copepods which together with the cladocerans and rotifers make up the bulk of the zooplankton biomass in freshwater lakes (Nauwerck et al., 1980), although protozoans have been shown to occasionally represent an important planktonic fraction (Rigler et al., 1974, Pace and Orcutt, 1981).

Copepods and cladocerans are the major representatives of the Crustacea in lakes. Their numbers are comparable reaching as many as 1000/liter but generally less than 100/liter (Nauwerck et al., 1980).

The highest numbers are recorded in "summer-warm" eutrophic lakes. Rotifers, on the other hand, may reach numbers as high as 10,000/liter, and their favored habitat is more often the oligotrophic lake (Nauwerck et al., 1980). These numbers are averages obtained from surveys of large numbers of lakes in all parts of the world for the International Biological Program. On a local scale, the numbers of individuals contributed by each major group can show considerable variation. For example, cladocerans are almost nonexistent in the oligotrophic Great Bear Lake (Patalas, 1975) and rotifers are exclusively present in Mowich lake (Larson, 1973).

In terms of their contributions to production, copepods and cladocerans appear to be comparable, as evidenced by a literature survey of production data by Waters (1977), where the bulk of total cladoceran and copepod annual productions ranged from 1 to 50g(dry weight)/m^2. Among individual species, cladocerans and especially Daphnia are the most productive. The copepod Epischura reached 28.7g/m^2/yr in lake Baikal (Moskalenko, 1971 cited in Waters, 1977) but in Sanctuary lake (Cummins et al., 1969, cited in Waters, 1977) Daphnia galeata mendotae was estimated to have produced 110g/m^2/yr. Rotifers, as a group, do not produce as much as the crustaceans. The data surveyed by Waters (1977) show rotifer production on average more than an order of magnitude lower than either of the crustaceans.

The fraction of the zooplankton production attributed to copepods is highly variable from one locality to another. Estimates vary from 19% of the total zooplankton (mean of 3 years) in Mirror Lake

(Makarewicz and Likens, 1979) to 41% in Severson Lake (Comita, 1972) to over 85% in Lake Erken (Nauwerck, 1963). These large variations in productivities stress the importance of learning more about the factors affecting production so that we can develop the predictive theories we need. McLaren (1969) pointed out the importance of knowing the life histories of zooplankters when attempting to estimate their productivity, and this is particularly true for copepods.

Life cycle of copepods

The free-living copepods (some are parasitic) are represented by 3 suborders: the Calanoida, the Cyclopoida and the Harpacticoida, the latter group being extremely littoral (Wilson and Yeatman, 1959). Studies of pelagic copepods, therefore, usually concentrate on the first two suborders. Copepods reproduce only sexually and females usually carry one or two egg sacs externally. After hatching, the young (called nauplii and designated with a capital N) undergo a series of molts (6 for calanoids, 5 or 6 for cyclopoids, designated by Arabic numerals, e.g. N1, N2 etc.). to reach the copepodid stage where the molting process continues until the sixth copepodid stage which is the adult. Copepodids are designated by a capital C followed by Roman numerals, e.g. CI, CII, etc. The 11 or 12 stages are also known as instars.

Conceptually, the calculation of production is very simple. It consists of adding up the growth increments of the population until all surviving members reach the adult stage (assuming adults do not grow). In practice, however, growth and mortality do not occur at constant rates, with some of the earlier naupliar stages lasting only a day or

two making it very difficult to obtain representative numbers with sampling frequencies of a week or more. The estimation of production requires some knowledge of the time spent by the animals in each instar and methods for obtaining estimates of the instar durations will be presented later.

Many direct methods for the measurement of secondary production have been developed. They all make use (to varying degrees) of the actual population numbers and distribution parameters to arrive at an estimate of production. Several reviews cover these methods extensively (Winberg, 1971; Edmondson, 1974; Waters, 1977; Nauwerck et al., 1980; Rigler and Downing, 1984). The scope of the present study does not allow a discussion on all the methods available but I have chosen three methods that can be applied to copepod populations and which make use of field data in different ways.

Methods for estimating zooplankton production

a) Increment-summation

This is the most "direct" method because it requires the least number of inherent assumptions to calculate production. Samples are collected throughout the growing season and the number of individuals in each developmental stage is multiplied by the increase in weight from the previous stage. In this procedure the mean time taken for an individual to pass through each stage must be known as well, since as mentioned earlier, the growth rate from egg to adult is not constant. Because of the importance of the instar duration, a separate section has been devoted to it in this study after the production methods have been presented (page 13).

The increment-summation method is probably the most accurate but it requires the most detailed population parameters which are tedious to obtain (relatively frequent sampling and identification of all stages). Less accurate but faster methods have also been sought as exemplified by the graphical or "Soviet" (Cooley, 1973) method.

b) Graphical

Introduced by Winberg (1971), this method can be useful when information is only available in subdivisions of eggs, nauplii (grouped) and copepodids (grouped) but not in individual instars. It is based on the generalized formula presented by Winberg et al. (1965) and Pechen and Shushkina (1964) (cited in Winberg, 1971).

$$P = \frac{N_e \cdot W_e}{T_e} + \frac{N_n \cdot \Delta W_n}{T_n} + \frac{N_c \cdot \Delta W_c}{T_c}$$

where P = production per unit time

e, n, c = egg, nauplius and copepodid respectively

N = number of individuals

ΔW = change in weight from previous age group*

T = duration of development

* W for eggs is the entire egg weight.

The method is explained in Fig. 1.

c) Allen-curve

Another graphical method, where the numbers of survivors are plotted against the mean individual weight on each sampling day, until the last adults disappear. The area under the curve drawn through these points represents the production for that cohort (Fig. 2) in units of the axes. This method gives good approximation of production when the

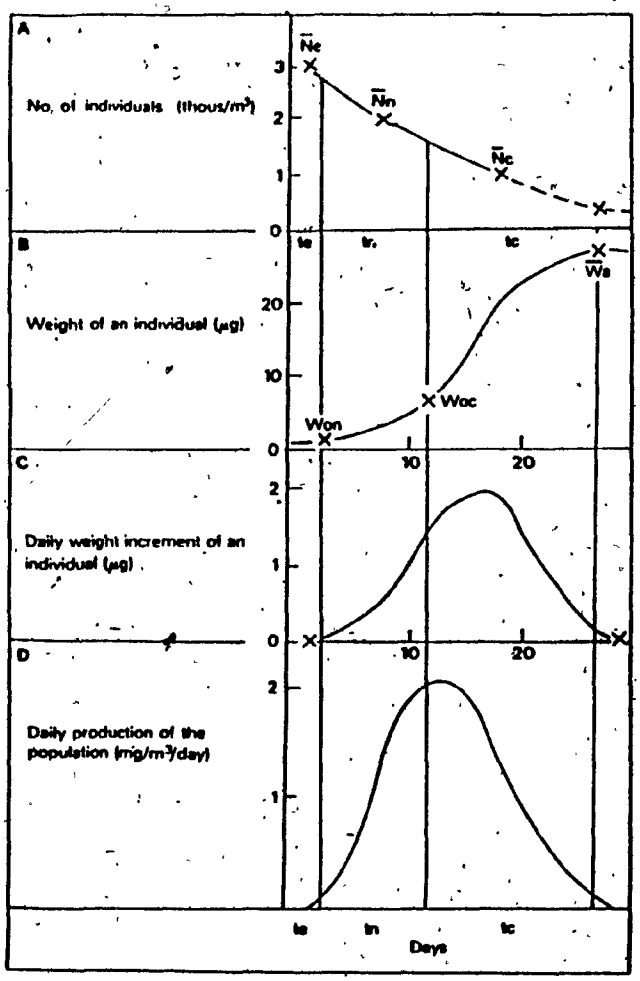
Figure 1. Graphical method

-A. The development times of the eggs (t_e), nauplii (t_n) and copepodids (t_c) are marked on the X-axis. The area under the curve of a given stage (A_n) is divided by the development time of that stage (t_n) to obtain the mean number of individuals (N_n) in that stage. This value is marked above the midpoint of the segment t_n on the X-axis. The 3 points are joined and to obtain the number of adults, the line is extrapolated to the end of segment t_c.

-B. The growth curve of an individual is constructed on the same X-axis as above. The initial weight of each successive state (W_{on}, W_{oc}) is marked on the Y-axis. This requires estimation of egg weight (as initial weight of nauplii) as well as N6 and CI since the mean of those two is the initial weight of copepodids. Finally, the average weight of the adult (W_a) is marked at the end of the curve. Assuming that the growth curve of an individual is sigmoid, the 3 points are joined.

-C. A daily weight increment curve is obtained by marking the increase in weight of an individual over the previous day for every day of its development. The information is drawn from curve B.

-D. Production is obtained by multiplying curve A by curve C. The area under the curve is total production and each point of the curve represents production for that day.



From Winberg, 1971.

Figure 2. Hypothetical Allen Curve. The black dots represent the estimated numbers per unit area and mean weight of an individual on 6 sampling dates. A, first sample; B, breeding population, C, number of young produced, calculated from fecundity data (from Mann, R.H., 1971).

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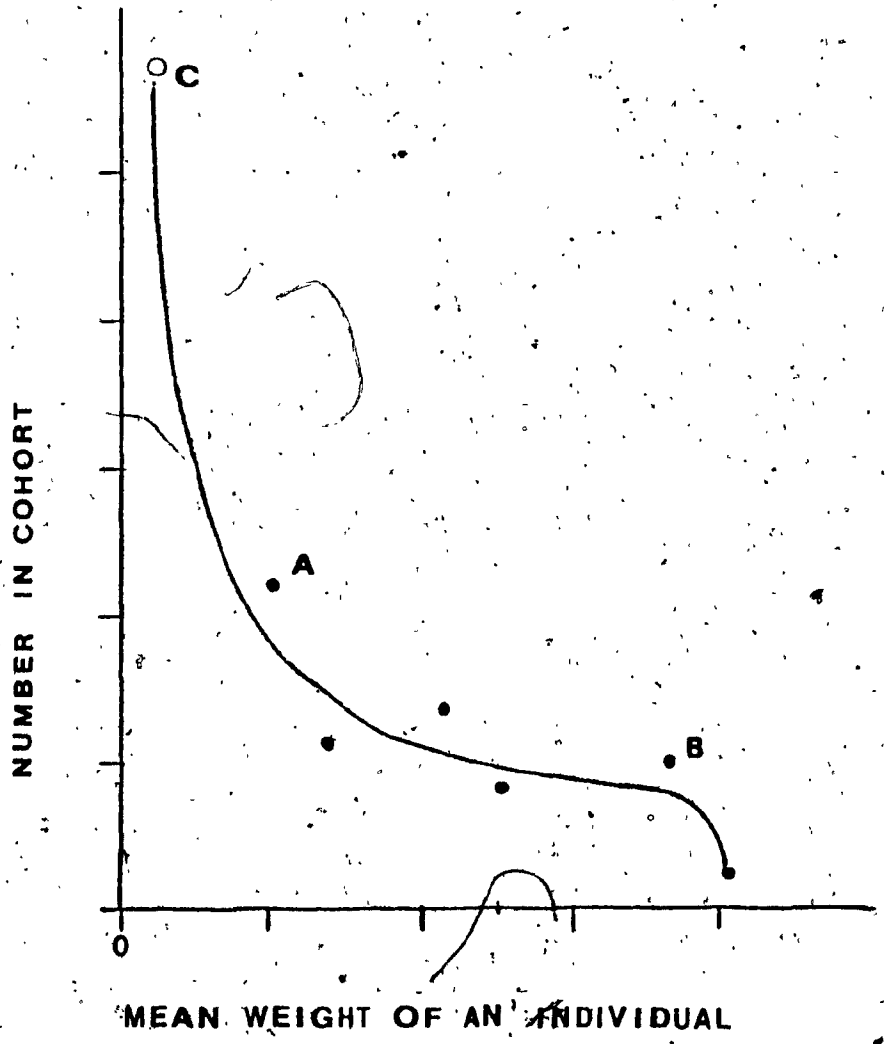


cohort is clearly delimited, i.e., a generation is synchronous and well identified (Cooley, 1973), but it has limited usefulness in populations with overlapping generations where age distribution is variable.

Indirect methods of estimating production

The tedious nature of obtaining production estimates directly has prompted the search for predictive methods, shortcuts, which consist usually of establishing a relationship between production values obtained directly and some other parameter that is easier to measure. When a constant function is found between the two values, it can be applied to the easily measured parameter in another location or time to obtain an estimate of production there.

Many predictive functions have been developed in the last few years which may not be specific to copepods but secondary producers in general. The production to biomass ratio (P/B) has attracted much attention (Waters, 1977; Makarewicz and Likens, 1979; Nauwerck et al., 1980), the assumption being that the P/B ratio is fairly similar for related species universally. This ratio can then be used to predict production of other species knowing their biomass. Many factors have been found to affect this ratio and these will be covered in more detail in the "General Discussion", together with a comparison of P/B values obtained in this study to values reported in the literature.

Correlations between primary and secondary production have also been investigated (Brylinsky, 1980, Blazka et al., 1980) and could be useful if significant, since primary production is much easier to estimate. Quantitative comparisons between primary and secondary productions will be presented in this study in the "General Discussion".

Instar durations

The number of animals in a given developmental stage cannot be estimated directly from the collected samples because the probability of an individual being caught is proportional to the time it spends in a particular stage (Southwood, 1966). This argument is best explained schematically and is presented in figure 3.

The importance of instar duration in elucidating population statistics of copepods has prompted many researchers to look for methods of estimating and predicting these durations. Comita (1972) used the difference in time between the first appearance of each stage, thus, the difference in days between the appearance of the first individual of instar N_i and the appearance of the N_{i+1} equals the duration of the instar N_i. The assumption inherent in this method is that the duration of the instar remained constant throughout its development. Since temperature has been shown to affect rate of development in crustaceans (Bottrell, 1975) and food has been postulated to play an important role as well (Weglenska, 1971; Rigler and Cooley, 1974) it is very likely that the error generated by this assumption would be considerable if food were a limiting factor -the earlier individuals would have a more abundant food source- or if the duration of the instar were long enough for important changes in temperature to occur.

Another method for estimating instar durations is to use the peaks (modes) of abundance between stages (Weglenska, 1971). Although this method provides an estimate of durations closer to the mean, it is not

Figure 3. Schematic representation of the development of 2 successive instars.

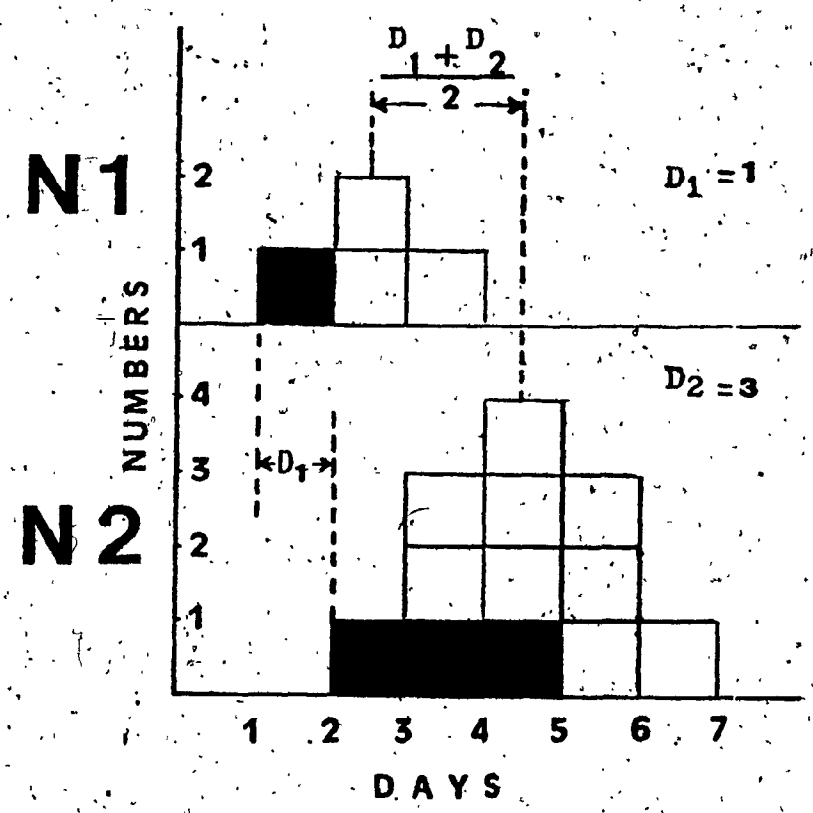
N1, N2 = First and second naupliar stages

D = instar duration in days

A = area of squares in animal x days

Consider a pulse of 4 animals that hatch in 3 successive days beginning on day 1. Assuming they are in a normal distribution (1:2:1) and that it takes them 1 day (D_1=1) to molt to the next instar (e.g. from N1 to N2), then the area (A) under the population curve of that instar will be 4 squares or 4 animal x days. If the same 4 animals take each 3 days (D_2=3) to molt from N2 to the next instar, each animal will be represented by 3 squares (blackened squares) and as the pulse of N2 proceeds, the 4 animals in the N2 pulse will be represented by 12 squares (A=12 animal x days). It can be seen that to estimate the number of animals, the area A must be divided by the instar duration D. Notice that the difference between the first appearance of the 2 instars is equal to D_1, but the difference between the means of the curves is equal to the mean of the 2 durations $(D_1+D_2)/2$. When the modes are compared (in this simplified example the means and modes are the same) their difference is also equal to $D_1+D_2/2$ unless they are skewed differently.

3



possible to deduce directly from the peaks the instar durations since the difference between 2 peaks is equal to half the times that an animal spent in each stage.

$$\text{Peak } n+1 - \text{Peak } n = \frac{t_n + t_{n+1}}{2}$$

where t_n and t_{n+1} are the durations of 2 successive instars.

In order to obtain the duration values, it is necessary to either guess one of them and solve the others by iteration until the least amount of negative mortality between stages is obtained, or experimentally determine the duration of one of the instars.

Rigler and Cooley (1974) presented a method which makes use of the entire pulse (members in an instar of the same generation) and not just limited numbers of animals in a pulse. The mean duration of each pulse is used, rather than the mode, to obtain an estimate of $(t_n+t_{n+1})/2$. Although probably closer to the true mean than the other methods, (there are still some unresolved assumptions) the sampling precision required for obtaining the mean durations renders the use of this method impractical in cohorts where pulses overlap since a good estimate of the beginning and the end of all pulses is required. Although an excellent method for obtaining detailed information on the population dynamics of a single species, it is prohibitively time-consuming when entire communities in which several closely related species coexist, are studied.

A method which predicts individual instar durations from the total generation time was developed by Ivanova (1973). It is based on mean instar durations derived from published values of laboratory grown animals. As this is one of the methods used in this study, a more detailed outline is presented in the "Materials and Methods" section.

The study site

Lake Memphremagog is a long (40Km) and narrow (mean width 2.4Km) glacial, mesotrophic lake located on the Quebec-Vermont border (45° 06'N, 72° 17'W) (Fig. 4). Approximately two thirds of the waters entering the lake are introduced by 3 rivers at the southern end where agricultural runoff and sewage effluent contribute over 80% of the phosphorus entering the lake. Because the bulk of hydrological and nutrient inputs are from the South and the outflow (Magog river) is in the northern end, a nutrient gradient has been established from South to North with corresponding gradients in primary (Ross and Kalff, 1975; Watson, 1979), benthic invertebrate (Dermott, 1974) and fish production (Nakashima and Leggett, 1975). General characteristics of Lake Memphremagog are listed in Table 1.

TABLE 1

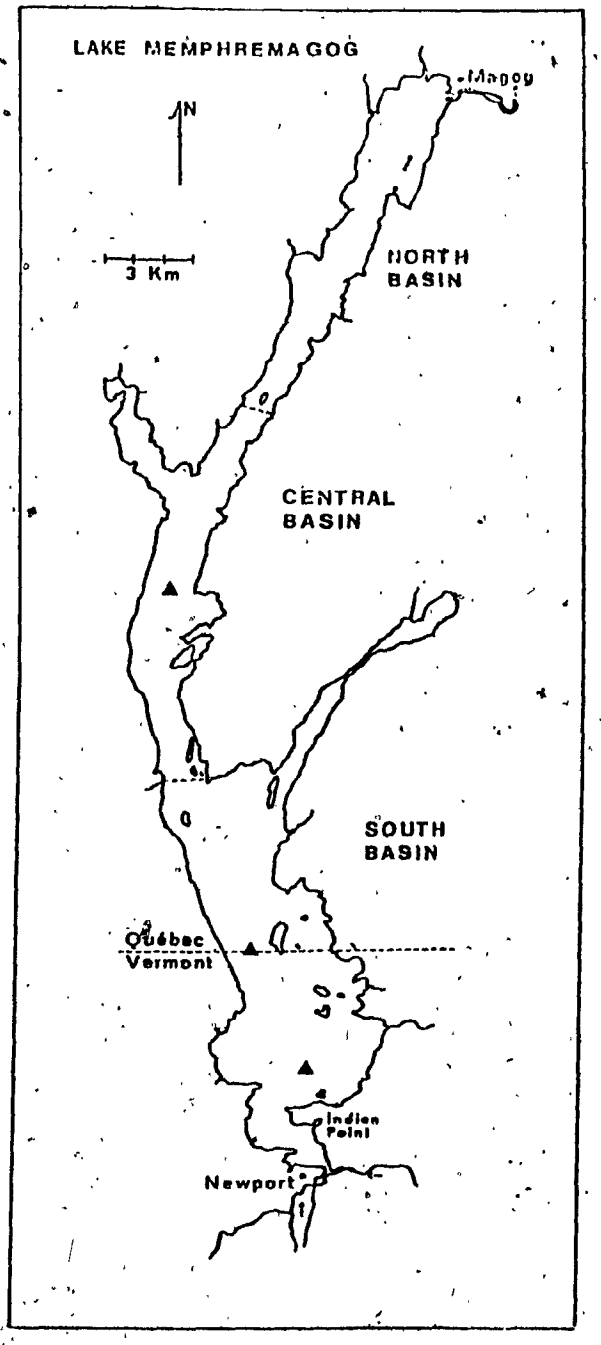
General characteristics of the south and central basins of Lake Memphremagog

BASIN	SOUTH	CENTRAL
Area (m^2)	4.4×10^7	2.2×10^7
Volume (m^3)	3.2×10^8	1.0×10^9
Mean depth (m)*	7.0	51.0
May-Sept., 1973 integrated as $gC.m^{-2}$ per $^{-1}(14C)$	145	123
Mean seasonal Chl *a* ($mg.m^{-3}$) 1976 **	10.0	5.0
Mean seasonal light penetration (Secchi) (m)	2.4	3.6

* from Ross and Kalff (1975)
** from S. Watson (1979)

Figure 4. Lake Memphremagog. The triangles show the 3 sampling stations.

4


LAKE MEMPHREMAGOG
Magog
N
3 Km
NORTH BASIN
CENTRAL BASIN
SOUTH BASIN
Québec
Vermont
Indian Point
Newport

MATERIALS AND METHODS

A) Sampling

Weekly samples were collected from two basins of the lake, from mid-May to mid-November 1976 during the ice-free period. The south basin, having a larger surface, was sampled in 2 locations: Indian point and at the Vermont-Canada border (Fig. 4). The central basin was sampled in one location.

A Clarke-Bumpus sampler, equipped with a 64um net was used to collect the samples in successive 5m layers. In the shallow south basin only the top 5m were sampled and on two occasions (June 8 and July 20) additional samples were taken below five meters with a 30 liter Schindler trap at 1m intervals to the bottom.

The central basin was sampled to a depth of 50m in 5m layers through the first 30m followed by two 10m layers. Analysis of the collected samples showed that the bottom 25m contained less than 5% of the total numbers of copepods (Appendix A) therefore only the first 25m of the water column were used for detailed analysis.

The Clarke-Bumpus sampler was towed from a boat moving at a speed approximating 100m/min, within the recommended 50 to 125m/min (Tonolli, 1971) and was lowered from the top of the layer as the boat moved. The messenger which triggered the shutting of the sampler was sent at the time appropriate for the trap door to shut as the sampler reached the bottom of the layer. Between 100 to 400 liters were filtered in each run.

The sampler was lowered from a boom extending away from the boat by approximately 1m to reduce the effect of the boat's wake. Initially a hand winch was used but it was replaced at mid-season with an electric winch. The wire was kept at an angle of 45° with the vertical and the desired depth was obtained by lowering the sampler with a length of wire determined by the formula;

$$D = L \cdot \cos 45^{\circ}$$

where D is the depth of the sampler and L is the length of the wire. However, since the cable does not remain straight in the water but curves upward as a reversed catenary (Tonolli, 1971) the actual depth the sampler reaches may be different than the desired depth. To obtain an estimate of the error involved a thermistor probe was attached to the sampler on a day when the water temperature formed a strong vertical gradient and was lowered to depths where this gradient was steepest. The temperature recorded by the thermistor attached to the sampler, at those depths, was compared to a vertical temperature profile obtained with the same thermistor probe while the boat was immobile. The sampler was found to be approximately 10% higher than the desired depth. Details are in Appendix B.

The times of sampling were kept as regular as conditions permitted: the south basin was sampled late in the morning and the central basin in the early afternoon of the same day.

A YSI thermistor (Yellow Springs Instruments Co.) was used to obtain temperature profiles of the entire water column in the south

basin and of the first 30m in the central basin. Temperatures at the 3 stations are presented in Appendix F.

Since zooplankton tend to aggregate along current lines (Langmuir circulation) which run parallel to the surface waves (Stommel, 1949 cited in Tonolli, 1971) the sampler was towed in a straight line perpendicular to the waves to compensate for possible patchiness.

Calibration of the sampler was performed in a fiberglass mould of a tractor inner tube. The mean number of liters per counter revolution for 3 runs was 4,2 with less than 5% error.

Replicate samples were collected on one occasion (August 3) to obtain an estimate of sampling error. Results are presented in Appendix C.

B) Analysis of Samples

Although samples were collected weekly, they were analyzed bimonthly except for the first two months where rapid growth warranted counting all samples. The filtrate from each sample was poured into a 64um sieve and washed into snap-cap jars filled with approximately 90ml of 2% neutralized formaldehyde. One ml subsamples were counted in a Sedgwick-Rafter cell, using a Zeiss compound microscope at 100 X magnification. More subsamples were counted if copepodid numbers were low (<40).

An ocular micrometer was used to measure all adults and a few individuals from all other instars. Measurements are accurate to the nearest 0.016mm. Species were identified using Wilson (1959) for calanoids and Yeatman (1959) for cyclopoids. Initially, all instars of

all copepod species were recorded separately, but the task of identifying nauplii belonging to closely related cyclopoid groups became overwhelmingly time consuming and this procedure was abandoned. Cyclopoid nauplii were recorded in 3 groups: early, middle and late stages, without species identification. All 6 stages of calanoid nauplii were, however, recorded individually.

C) Dry Weights

Dry weights of adults were estimated from published sources (Comita and Schindler, 1963; Hall et al., 1970; Dumont et al., 1975); copepodid and naupliar weights (except for N1, the first naupliar stage) were obtained by applying regression equations determined for individual species, or groups of species, from published sources (Dumont et al., 1975; Bottrell, 1975; Rosen, 1981). The dry weights of N1, W_{N1}, which do not usually fit regression lines (Cooley, 1973; Rigler and Cooley, 1974) were computed as follows:

Assuming that $d^3/W_E = k$ (a constant) (equation 1)

where d = diameter of an egg

W_E = dry weight of an egg of the same species

and $W_E/W_{N1} = k'$ (a constant) (equation 2)

where W_{N1} = dry weight of N1 of the same species

then $d^3/W_E \times W_E/W_{N1} = kk'$

and $d^3/W_{N1} = kk'$ (equation 3)

or $W_{N1} = d^3/kk'$ (equation 4)

From the ratio of the diameter of an egg over the weight of the first naupliar stage of a species a constant can be obtained which allows the calculation of W_{N1} of another species knowing the diameter "d" of its egg. The weight of N1 of Diaptomus minutus was obtained from Cooley (1973) and its egg diameter, which shows very little seasonal or local variation (see Appendix D), was measured from Lake Memphremagog samples as well as from other Quebec lakes (Maly, 1983). The constant between egg diameter (mm) and N1 weight (ug) for D. minutus thus obtained was 4.63×10^{-3}. It was used to compute the N1 weights of Lake Memphremagog species, since egg diameters were known. A similar calculation was made for the N2 cyclopoid nauplii since no size measurements were available.

A constant k" was obtained from

$W_E/W_{N2} = k"$ where W_{N2} = weight of D. minutus N2

therefore

$$d^3/W_{N2} = kk" \qquad \text{(equation 5)}$$

and $$W_{N2} = d^3/kk" \qquad \text{(equation 6)}$$

The constant kk" for N2 was 5.02×10^{-3}. See Appendix D for calculations.

D) Production

The "increment-summation" method was used in calculating production (Winberg et al., 1965). The weight increment of an individual in each of the developmental stages was multiplied by the number of individuals in that stage to obtain the production of that stage. The number of individuals in each stage was obtained by dividing the area under the

curve of abundance (e.g., see Fig. 5) of that stage by its duration. The area was estimated by drawing the curves on paper, cutting it, and comparing the weight of the area under the curve to the weight of a known surface from the same sheet of paper.

Total production of a cohort is the sum of the productions in all stages:

$$P = \frac{A_E \cdot W_E}{D_E} + \frac{A_1 \cdot \Delta W_1}{D_1} + \frac{A_2 \cdot \Delta W_2}{D_2} + \text{etc.}$$

where P = production (ug/m^2/period (187 days))

A = area under abundance curve (animal-days/m^2)

E = egg

W = dry weight (ug)

ΔW = change in weight from previous instar

D = instar duration (days)

numerals = developmental stages

Note: Since calculation of production begins with the egg stage, the entire egg weight is multiplied by the number of eggs.

E) Instar durations

Whenever possible, differences between the first occurrence of instars or differences between abundance peaks were used to estimate instar durations (see "Instar durations", p. 13). However, when overlap in generations or small population numbers prevented an estimation of durations from the populations curves, Ivanova's (1973) method was used.

Ivanova's method is based on the observation that copepods develop through a fixed number of stages (11 or 12). From a collection of

published values of laboratory grown animals, she observed that the proportion of each instar's duration remains a fairly constant fraction of the entire generation length (time of emergence from the egg to the last molt). The durations of individual stages from 9 different sets of observations, expressed as a percentage of the total generation time, were pooled and a mean duration obtained for each stage (Table 2). An estimate of the error was also provided. This empirical formula was based, however, on observations made in controlled laboratory conditions. Its limitations are that in situ conditions of temperature and food availability are known to vary and thus to affect growth rates (Rigler and Cooley, 1974; Bottrell, 1975).

In order to evaluate the magnitude of the error introduced by variations in temperature, a set of instar durations was calculated taking into account temperature fluctuations in the central basin. The procedure to correct for temperature and a set of production values estimated with temperature corrected instar durations are presented in the "Results and Discussion".

Table 2

Duration of individual stages of copepods*

Stage	Duration of Stage
	% of Total
Nauplii	
1	2.54 ± 0.24
2	4.07 ± 0.36
3	5.01 ± 0.36
4	6.94 ± 0.89
5	9.56 ± 0.94
6	8.25 ± 0.54
Copepodids	
I	10.50 ± 0.90
II	10.73 ± 0.54
III	12.34 ± 0.42
IV	14.16 ± 0.98
V	16.90 ± 1.78

* As a % of the duration of development from the time of emergence from the egg to the last molt. From Ivanova (1973).

RESULTS AND DISCUSSION

1. The Species

Of the eight copepod species found in Lake Memphremagog, only four occurred in the samples with frequencies that allowed elucidation of their life cycles. These were Cyclops bicuspidatus thomasi Forbes 1882, Cyclops vernalis Fischer 1853, Mesocyclops edax Forbes 1891 and Diaptomus sicilis Forbes 1882. The other 4 (Diaptomus minutus Lillejeborg 1889, Epischura lacustris Forbes 1882, Tropocyclops prasinus mexicanus Kiefer 1938 and Senecella calanoides Juday 1923) occurred sporadically and their numbers were too low to be sampled adequately. Six species occurred throughout the lake; E. lacustris was never found in the central basin and S. calanoides was not found in the south basin.

2. Life Cycles (Central Basin)

a) C. b. thomasi

This species was dominant in the lake. It occurred in large numbers in the spring and fall. A common North American limnetic cyclopoid (Wilson, 1959), it is the most abundant copepod in the St. Lawrence Great Lakes (Wells, 1960; Carter, 1969; Patalas, 1972) with the exception of western Lake Erie where C. vernalis dominates. Although basically a spring and winter species, summer peaks have been recorded (Wells, 1960; Carter, 1969). The interpretation of the life cycle of C.b. thomasi in Lake Memphremagog is difficult and inevitably involves some subjective treatment of the data. Its short and continuous

reproductive cycles prevent an accurate description of the cohort's development, and although 5 cohorts appeared to have developed in the central basin during the ice-free period (Fig. 5), the 3rd and 4th generations show considerable overlap and could well be continuous. When sampling started, ovigerous females were already present and a peak of egg production occurred in mid-May which indicates that either an entire generation had developed under ice or diapausing copepodids had emerged from C IV (Carter, 1974) and molted into C V and finally adults. The generation that followed formed the largest single copepod population for 1976. Large numbers of eggs were recorded in the May 18 samples and the early nauplii* (N1+N2) peaked in the May 25 samples (Fig. 6). The first copepodid stage reached its peak in early June and took approximately one month to develop into adults. The mean length of these adults ($\bar{X}$=0.93mm) was significantly smaller than the adults present in May and early June ($\bar{X}$=1.06mm, $p < 0.001$) indicating that this was probably the beginning of a new generation. Clutch size was also smaller (Mean (X) of 1st generation, G1 = 17.6; G2 = 44.6 , $p < 0.001$).

---

* Although the cyclopoid nauplii were not identified to species quantitatively, it was still possible to obtain some qualitative estimates concerning the presence, absence or dominance of the 3 main species. Nauplii were identified to species from laboratory cultures. It was observed that some characteristics of copepodid and adult stages of each species were represented in the nauplii: M. edax nauplii were rounder, wider than the others; C. vernalis nauplii had longer, stouter furcal setae and C.b. thomasi nauplii were slender and had short spines. N1 of C. vernalis and C.b. thomasi could not be distinguished from each other. Of the 4 main peaks of nauplii (Fig. 6) the first one was made up almost exclusively by C.b. thomasi with some C. vernalis nauplii; the 2nd, 3rd and 4th had all 3 species present but largely dominated by C.b. thomasi.

Figure 5. Seasonal abundance of Cyclops bicuspidatus thomasi in the central basin: copepodids and adults. Generations are delimited by dashed lines.

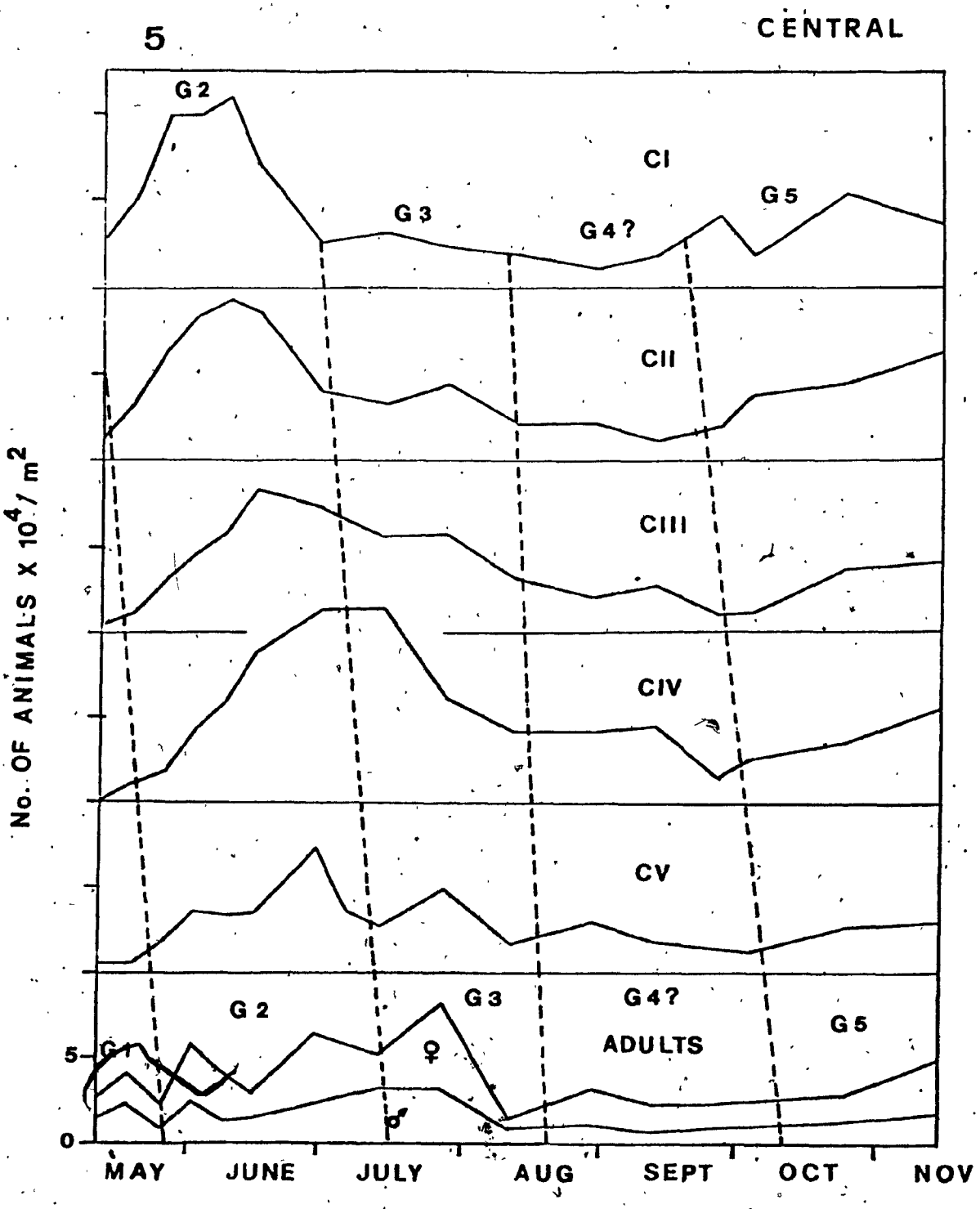
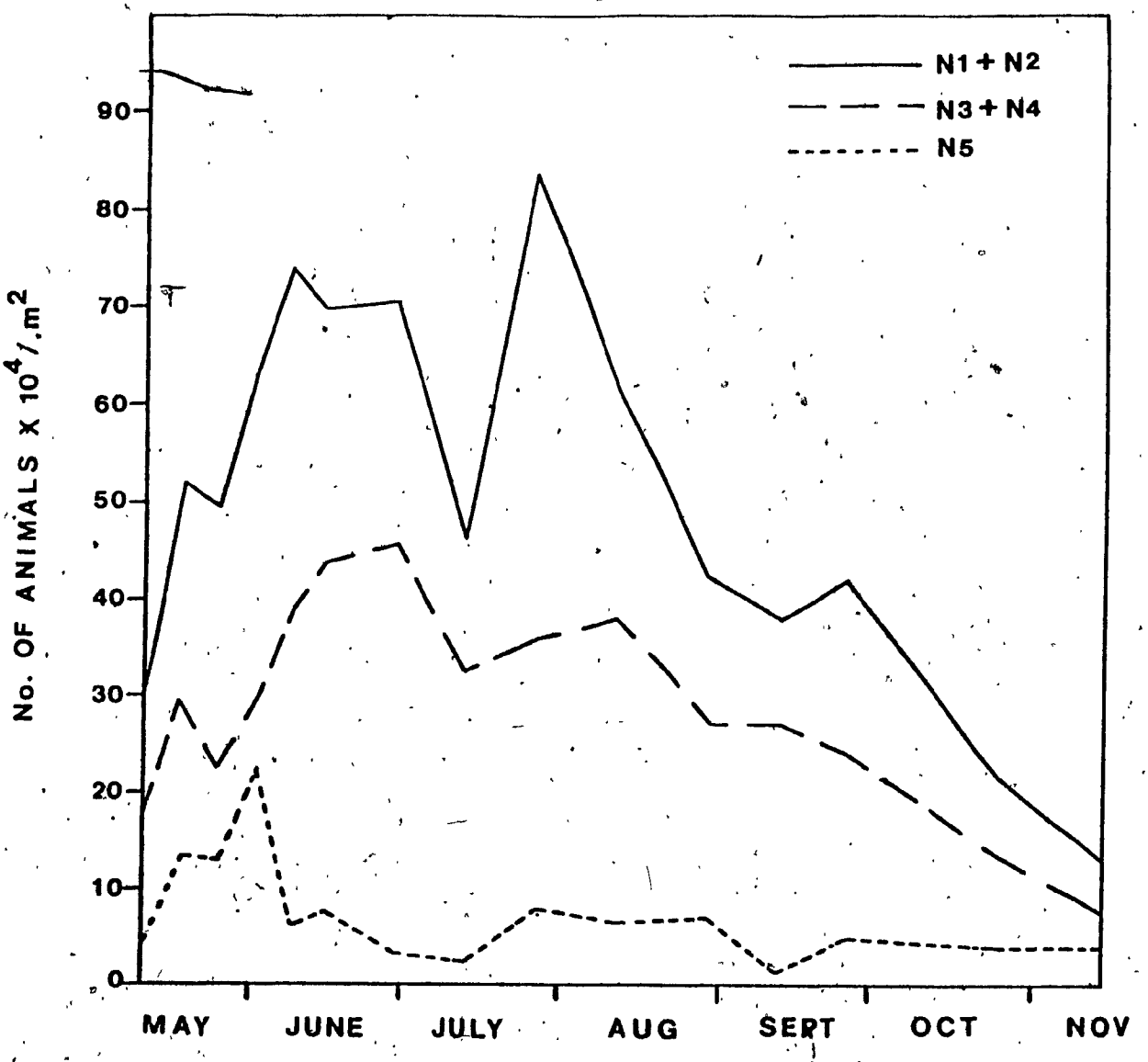

5
CENTRAL
G2
CI
G3
G4?
G5
CII
CIII
CIV
CV
No. OF ANIMALS X 10^4/ m^2
G2
G3
G4?
G5
ADULTS
♀
♂
5
0
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

Figure 6. Abundance curves of cyclopoid nauplii. Solid line is N1 + N2. Dashed line is N3 + N4. Dotted line is N5.

6 CENTRAL


N1 + N2
N3 + N4
N5
No. OF ANIMALS X 10^4/.m^2
0
10
20
30
40
50
60
70
80
90
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

The large number of ovigerous females in the June 29 samples and the high numbers of early nauplii at the end of June indicate the presence of a third summer generation. However, large mortality in the naupliar stages seems to have reduced this generation's amplitude considerably. The overlap in the copepodid stages between G2 and G3 makes it impossible to delineate the two generations but a pulse of females carrying egg sacs at the end of July suggest that the generation arrived at its completion and produced sufficient numbers of females to start a new generation (G4) as evidenced by large numbers of early nauplii of this species at the end of July and early August. This 4th generation also suffered heavy losses in its early stages but the survivors reached the adult stage and produced eggs by mid-September from which it can be deduced that G4 took 5 to 6 weeks to develop despite the warm temperature of that period. The last generation (G5) began in mid to late September and developed very slowly. This was undoubtedly a small population judging from the small number of late nauplii, but which formed sizeable instar curves because of increased duration of development times.

b) M. edax

Mainly a summer species this copepod is found throughout North America. Carter (1969) found it in great abundance in fish-free acid ponds near Georgian Bay. It forms a sizeable portion of the crustacean zooplankton of Lake Erie (Davis, 1962) but is scarce or absent from the rest of the 14 Great lakes examined by Patalas (1975). Variable in its number of generations, it usually emerges from diapause at C IV (Carter,

1974) in late Spring and reenters it in early Autumn.

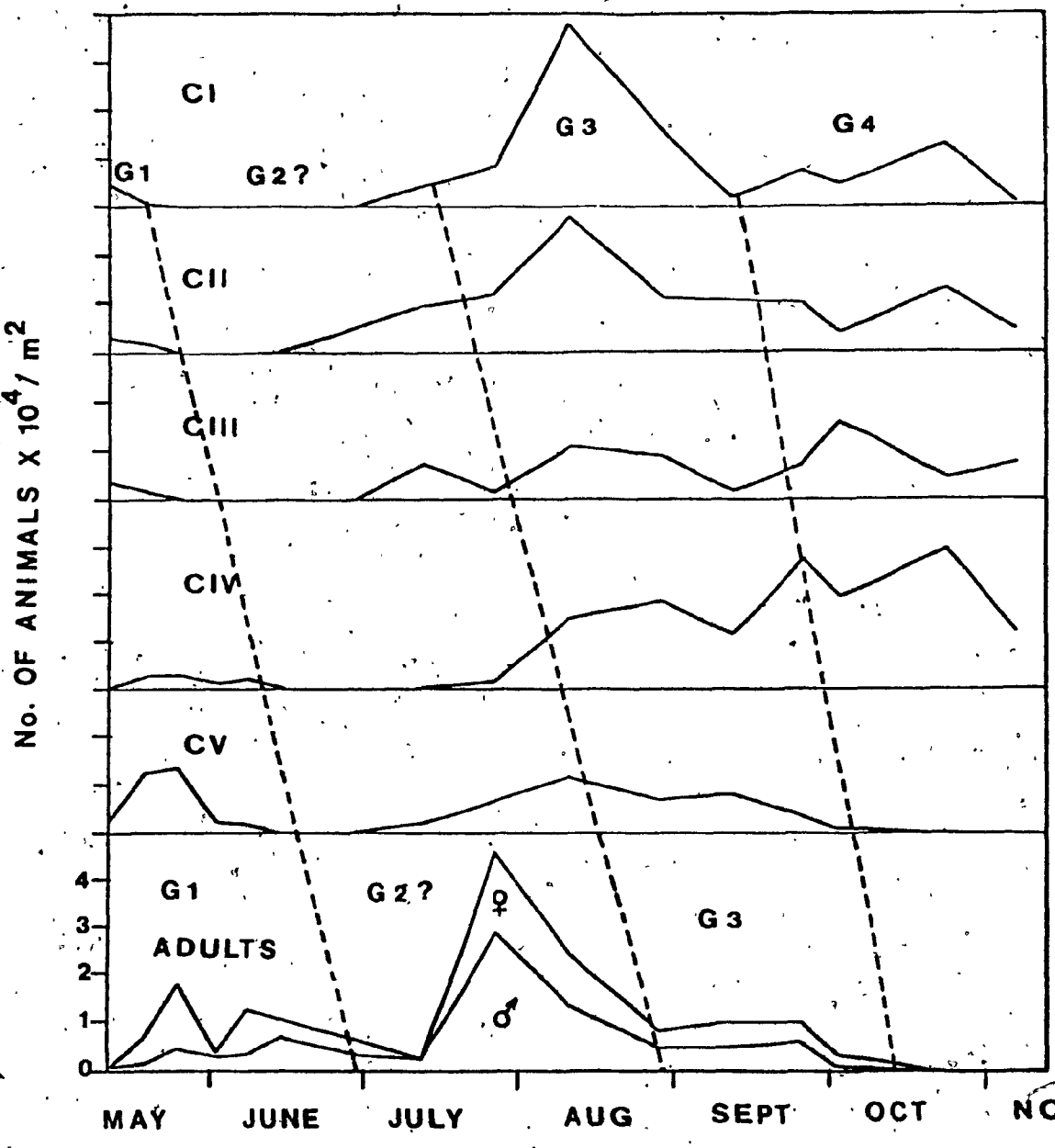
Although numbers were low in Lake Memphremagog and the sampling error quite considerable, it appears that the diapausing C IV copepodids developed into C V in late May and rapidly became adults (Fig. 7). Sample bottles from the latter half of May contained large numbers of females with eggs and the burst of nauplii in early June (Fig. 6) was made up to a considerable extent by M. edax nauplii. This second generation however failed to reach the copepodid stage. The predation pressure from the presence of adults of the 3 carnivorous species (C. b. thomasi, M. edax and C. vernalis) may be in part responsible for the failure of this generation.

The emergence of adults in mid-July is not explained by the population curves (Fig. 7). There were no sizeable numbers of juvenile stages preceding the adult population which suggests that this second group of adults matured and appeared in the epilimnion from C IV or C V copepodids which either emerged from their diapause in the sediments or entered the limnetic zone from the littoral zone.

The 3rd generation, the one produced by adults at the end of July and early August, formed the largest M. edax population of the year. Many M. edax nauplii were found in late July, and survival to copepodid stages was more successful than the previous generation. As C IV was reached, however, many individuals seemed to enter diapause, judging from the low numbers of C V and adults following it. The final generation was smaller and ended in C IV. No C V or adults were found in late October and November.

Figure 7. Seasonal abundance of the *Mesocyclops edax* population in central basin. Generations are delimited by dashed lines.

7 CENTRAL


CI
G1
G2?
G3
G4
CII
CIII
CIV
CV
No. OF ANIMALS X 10^4 / m^2
G1
ADULTS
G2?
♀
♂
G3
0
1
2
3
4
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

c) C. vernalis

Another common summer cyclopoid of North American waters C. vernalis is characterized by very short generation times. Ewers (1936 cited in Andrews, 1953) found it developing from egg to adult in 8 to 10 days in Western Lake Erie, with new clutches of 100 to 150 eggs produced every 3 days.

In the central basin, 4 short generations could be identified but the resolution required for delimiting the curves of abundance was not obtained with the sampling program and the generation lengths are estimated approximately (Fig. 8). C. vernalis never reached high peaks in numbers and was not dominant at any time.

The 4 generations were delimited as follows: G1, from end of May to mid-June; G2, from July 20 to August 5; G3 was not clear, adults appeared at the end of September; G4, from the end of October to C IV where they apparently entered diapause.

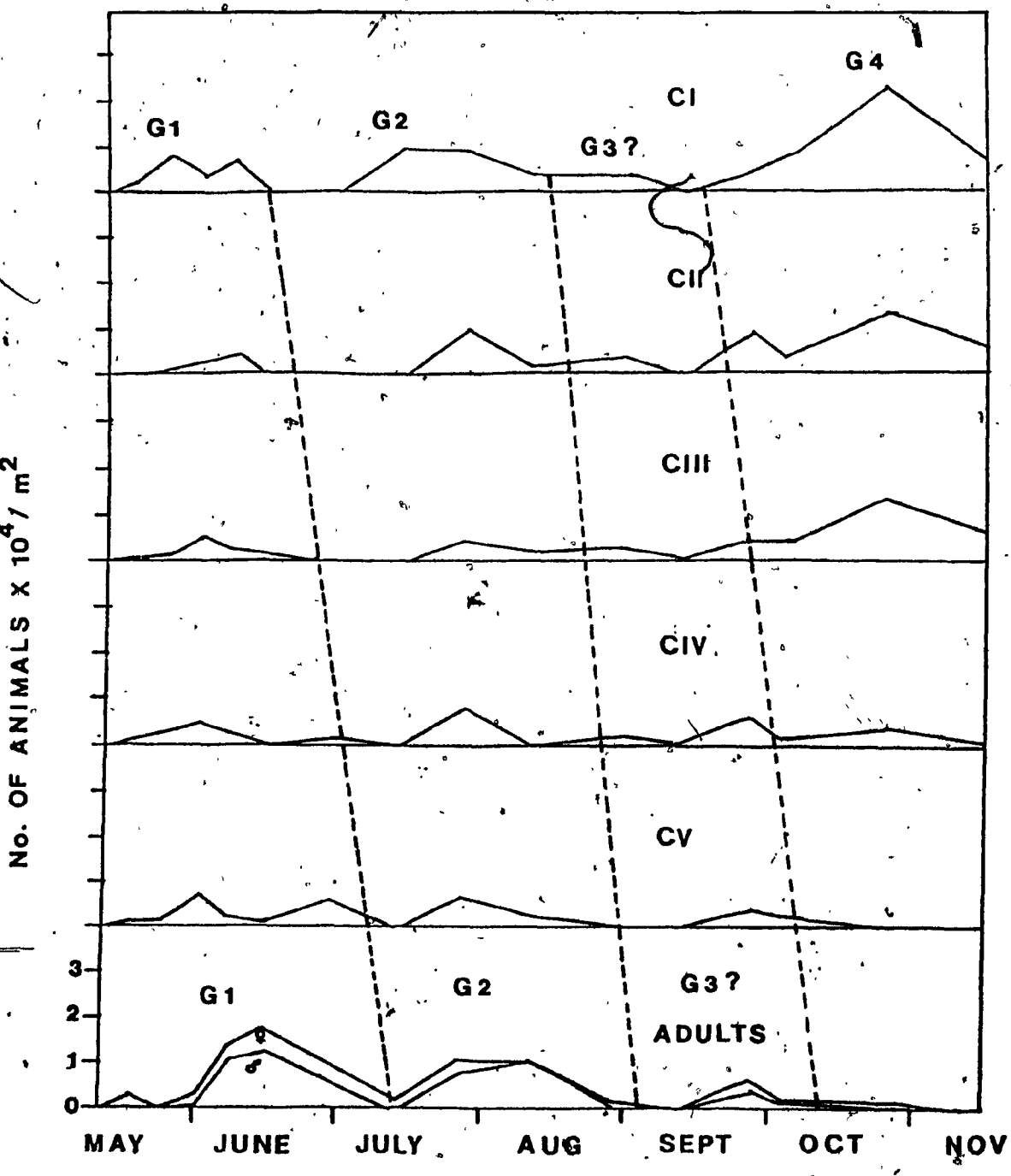
d) D. sicilis

Generally accepted as a cold water species, D. sicilis is common throughout Canada and the northern U.S.. Found in abundance in the more oligotrophic Great Lakes, it makes up over 81% of the crustacean plankton of Great Bear Lake 45% in Lake Superior. D. sicilis was the dominant zooplankton in Lake Lenore which has a salinity of 15 g/l and a pH near 10 (Anderson et al., 1955). Moore (1978) found it in all 18 arctic and subarctic lakes he surveyed where it was often dominant.

In the present study, the 1st D. sicilis generation was very small and resulted in adults that peaked at the end of June (Fig. 9). The

Figure 8. Seasonal abundance of the Cyclops vernalis population in the central basin. Generations are delimited by dashed lines.

8 CENTRAL


G1
G2
G3?
G4
CI
CII
CIII
CIV
CV
G1
G2
G3?
ADULTS
No. OF ANIMALS X 10^4/ m^2
0
1
2
3
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

main generation followed, taking 3 months to develop. Additional peaks in the early naupliar stages in mid and late summer could be D. minutus nauplii, which were very difficult to differentiate from D. sicilis, or D. sicilis which failed to develop into distinct cohorts. The presence of adults throughout the season supports this last possibility.

Summary

C.b. thomasi produced 4 or 5 cohorts from mid-May to mid-November. Mean generation times was 5 weeks. The first cohort was already present when sampling began, the second was the largest, the 3rd and 4th suffered high naupliar mortality and were difficult to distinguish at the copepodid level. The last cohort started in September and had not been completed by mid-November. Continuous reproduction causes overlap in generations and some subjective treatment of the data is inevitable.

M. edax emerged from diapause late May and went through 3 generations of which the first one failed or nearly failed to develop after N4, and the 3rd ended in diapause at the C IV stage.

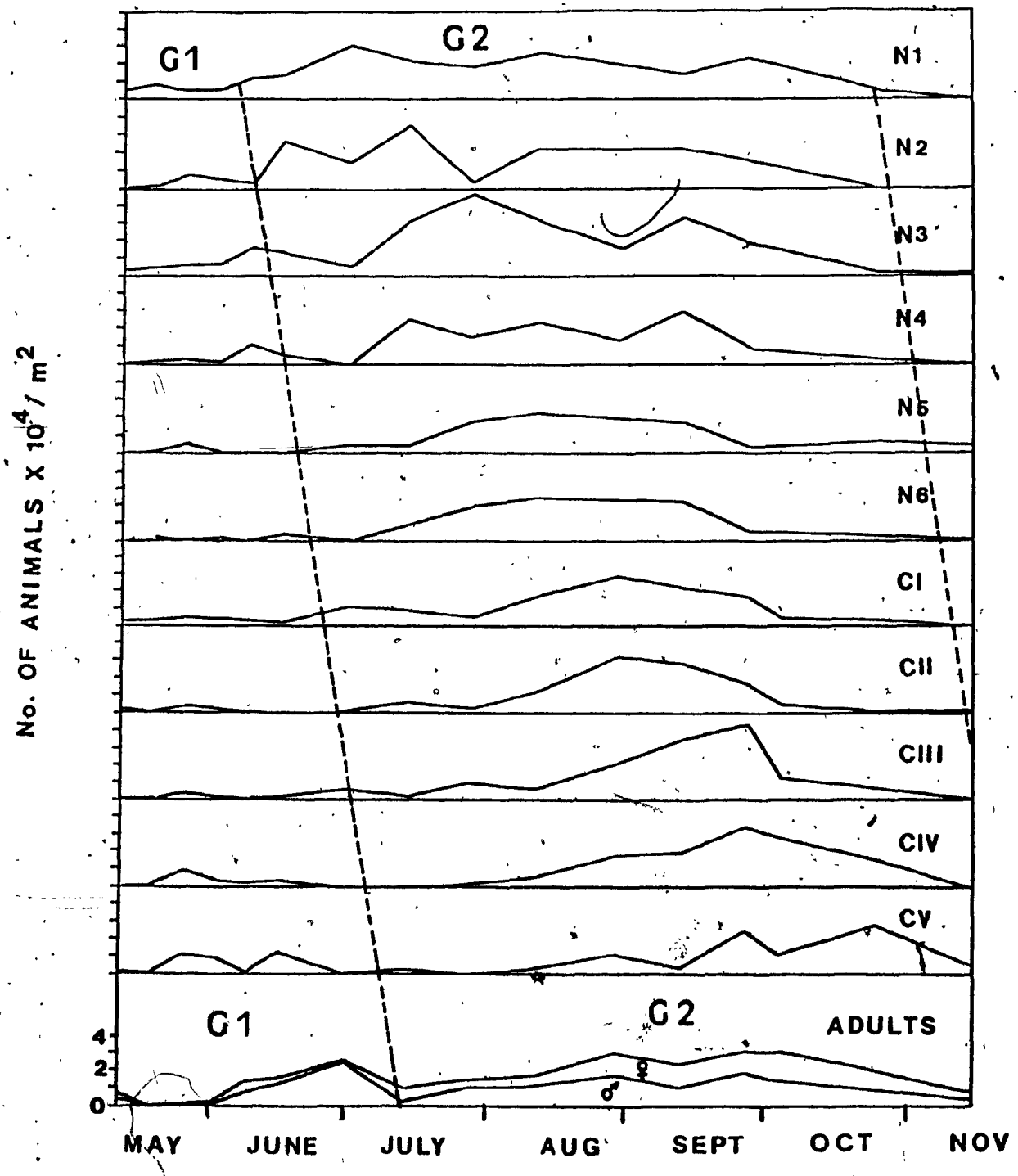
The fast growing C. vernalis produced 4 short generations and its numbers remained relatively low throughout the season. D. sicilis produced one generation which developed slowly over three months.

3. Dry Weights

As mentioned earlier, the cyclopoid nauplii were grouped in the 3 categories: early (N1 + N2), middle (N3 + N4) and late (N5). This was done mainly on the basis of body length but also from morphological characteristics such as the number and relative sizes of furcal setae (Ravera, 1953).

Figure 9. Seasonal abundance of the Diaptomus sicilis population in the central basin. Generations are delimited by dashed lines.

9 CENTRAL


G1
G2
N1
N2
N3
N4
N5
N6
CI
CII
CIII
CIV
CV
G1
G2
ADULTS
♀
♂
No. OF ANIMALS X 10^4 / m^2
4
2
0
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

The dry weights of the cyclopoid middle and late stage nauplii were calculated from a regression equation relating weight to length calculated for Cyclops scutifer nauplii by Bottrell et al. (1976):

$$\ln W = \ln a + b \ln L$$

where W = dry weight in ug

L = length in mm

ln a = 2.5442,

b = 2.3696

Since cyclopoid and calanoid nauplii are fairly similar in body shape, the same equation was used to calculate dry weights of all D. sicilis nauplii except N1.

There are two reasons for not using the regression equation to calculate the weights of the early cyclopoid nauplii (N1+N2) and calanoid N1:

1) Regression equations are calculated for a range of body lengths within which the equation predicts the weight with acceptable accuracy. Beyond the range of lengths for which an equation was formulated, the loss of predictive power could be considerable. The first 2 stages of the cyclopoid nauplii and N1 of D. sicilis fell beyond this range.

2) The first naupliar instar does not feed (Cooley, 1973) but it grows in length when molting to the second. The normal length-weight relationship is reversed in this case as the animal grows in length while losing weight. Regression equations do not take this into consideration and would predict a lower weight for N1 than N2.

To obtain the dry weights of the N1 instars, egg sizes (Table 3) were used in the equation:

$d^3/W_{N1} = kk' = 4.63 \times 10^{-3}$ (equation 3, p. 22)

To obtain the dry weight of the cyclopoid N2 instar, egg sizes were used in the equation:

$d^3/W_{N2} = kk'' = 5.02 \times 10^{-3}$ (equation 5, p. 23)

The naupliar dry weights are presented in Table 4.

Dry weights of C.b. thomasi, M. edax and C. vernalis copepodids and adults were obtained from the regression equation (7) calculated by Dumont et al. (1975) for cyclopoid copepodids and equation (8) for cyclopoid adults:

$W(ug) = 1.10 \times 10^{-5} L^{1.89}(um)$ (equation 7)

$W(ug) = 1.10 \times 10^{-7} L^{2.59}(um)$ (equation 8)

The dry weights of D. sicilis copepodids and adults were obtained from equation (9) for calanoids, also from Dumont et al (1975):

$W(ug) = 7.9 \times 10^{-7} L^{2.33}(um)$ (equation 9)

Copepodid and adult dry weights are presented in Table 5.

TABLE 3

Egg sizes of copepod species in Lake Memphremagog

SPECIES	MEAN EGG SIZE (mm)	n*
C. b. thomasi	0.086 ± 0.006	81
M. edax	0.109 ± 0.007	46
C. vernalis	0.080 ± 0.008	47
Pooled cyclopoid *	0.092 ± 0.013	174
D. sicilis	0.116 ± 0.007	127

* From 8 to 10 eggs were counted from egg sacs collected on May 25 and July 27 when females were largest ($\bar{X}$ = 1.10 mm ± 0.05) and smallest ($\bar{X}$ = 0.91 mm ± 0.05), respectively.

TABLE 4

Naupliar lengths, L (mm) and dry weights, W (ug) in Lake Memphremagog.

D. sicilis			CYCLOPOID SPECIES		
STAGE	L[a]	W[b]	STAGE	L [c]	W[d]
N1	0.14	0.34	N1	0.13	0.17
N2	0.17	0.23	N2		0.16
N3	0.20	0.28	N3+N4	0.19	0.25
N4	0.23	0.39	N5	0.26	0.52
N5	0.27	0.56			
N6	0.32	0.86			

a: means of 10 or more measurements

b: all except N1 determined from W = 2.5442 + 2.3696 X L (p. 38).

N1 determined from $d^3/W_{N1} = kk'$ (equation 3, p. 22)

c: means of size classes of 3 cyclopoid species determined from preliminary measurements of individual stages.

d: N1 determined from $d^3/W_{N1} = kk'$ (equation 3, p. 22);

N2 determined from $d^3/W_{N2} = kk''$ (equation 5, p. 23);

N3 + N4, N5 from W = 2.5442 + 2.3696 X L (p. 38).

TABLE 5.

Copepodid and adult lengths*, L (mm) and weights, W (ug)

SPECIES	*C. b. thomasi*		*M. edax*		*C. vernalis*		*D. sicilis*	
STAGE	L	W	L	W	L	W	L	W
CI	0.38	0.83	0.45	1.14	0.40	0.91	0.47	1.33
CII	0.47	1.23	0.56	1.72	0.49	1.34	0.60	2.35
CIII	0.56	1.72	0.65	2.28	0.60	1.96	0.73	3.71
CIV	0.67	2.41	0.76	3.06	0.69	2.55	0.87	5.58
CV	0.80	3.37	0.92	4.40	0.81	3.45	1.07	9.04
Male	0.85	4.25	0.87	4.52	0.77	3.29	1.19	11.60
Female	0.97	5.99	1.19	10.16	1.04	7.17	1.31	14.48
Mean adult	0.91	5.12	1.03	7.34	0.91	5.23	1.25	13.04

* Entire lengths (without spines) determined from approximately 10 individuals from each of Spring and Summer samples (20 for adults).

4. Production

Production of Cyclopoid nauplii and eggs

Production by cyclopoid nauplii and eggs is presented in Table 6. Because the nauplii of the 3 cyclopoid species were grouped, they had to be treated as one species for calculating production. The numerals 1, 2, 3 in the increment-summation equation from page 24:

$$P = \frac{A_E . W_E}{D_E} + \frac{A_1 . \Delta W_1}{D_1} + \frac{A_2 . \Delta W_2}{D_2} + \text{etc.}$$

refer to the early (N1 + N2), middle (N3 + N4) and late (N5) stages of the grouped cyclopoid nauplii.

The error introduced by these successive groupings has 2 sources: first, mortality between N1 and N2 and between N3 and N4 cannot be evaluated; second, the 3 species are assumed to be equally represented. The error in the 1st case is probably minimal since an underestimate of the first stage in the grouping will result in an overestimate of the second e.g. an underestimate of N1 will result in an overestimate of N2 since the total number of N1 + N2 are fixed. The second error cannot be evaluated, since the relative numbers in each species were not known.

The estimation of naupliar production was further simplified by treating the entire population of the 3 species as one cohort and estimating a mean duration for the entire season for each of the 3 stages. This simplification was justified because there were low numbers of nauplii at the beginning and at the end of the sampling season (Fig. 6, p. 30). If nauplii had been abundant when sampling started or ended, finite curves could not have been obtained and

TABLE 6

Production of cyclopoid eggs and naupliar stages (May-Nov.).

STAGE	Animal days (No.m^{-2}) x10^7	Instar. duration (days)	Animals (No.m^{-2}) x10^7	Weight (ug)	ΔW (ug)	Production (g.m^{-2}.per^{-1})
Egg			1.59	0.20	0.20[a]	3.2
N1	8.89	2.8	1.59	0.17	-0.03	-0.5
N2			1.59	0.16	-0.01	-0.2
N3 + N4	5.18	5.1	1.02	0.23	0.07	0.7
N5	1.13	4.1	0.28	0.50	0.27	0.8
Total						4.0 g.m^{-2}.per^{-1}

a: Since the egg is the first stage, its entire weight is produced.

Table 7

Development times* of cyclopoid nauplii in the central basin of Lake Memphremagog.

Stage	% of Total Generation	Grouped Stages	Stage Duration (days) in Lake Memphremagog
N1	2.54 ± 0.24	6.61	2.8 (b)
N2	4.07 ± 0.36		
N3	5.01 ± 0.36	11.95	5.1
N4	6.94 ± 0.89		
N5	9.56 ± 0.94	9.56	4.1
N6 (c)	8.25 ± 0.54	-	-
		28.12	12.0

* Derived from Ivanova's (1973) proportional breakdown method (see "Materials & Methods", p. 24).

a) Stages were grouped as early (N1+N2) middle (N3+N4) and late (N5) stages.

b) Example of calculation: duration of N1+N2 = $\frac{6.61 \times 12.0}{28.12}$ = 2.8 days

c) N6 was ignored, because cyclopoid nauplii in Lake Memphremagog have only 5 naupliar stages.

mortality estimates between groups would have remained unknown.

To estimate the mean duration of the 3 naupliar groups, an overall duration for all nauplii was obtained which was then subdivided among the early, middle and late nauplii according to Ivanova's (1973) percentage breakdown for each instar (Table 7).

The overall duration was estimated from the peaks of naupliar abundance as compared to the peaks of the CI abundances. For example, in Fig. 10A the difference between the first early naupliar peak and the C.b. thomasi CI peak is 13 days. Similarly, the 3rd early naupliar peak (July 27) was followed by a sharp M. edax CI peak on August 11 for a 15 day difference (Fig. 10B).

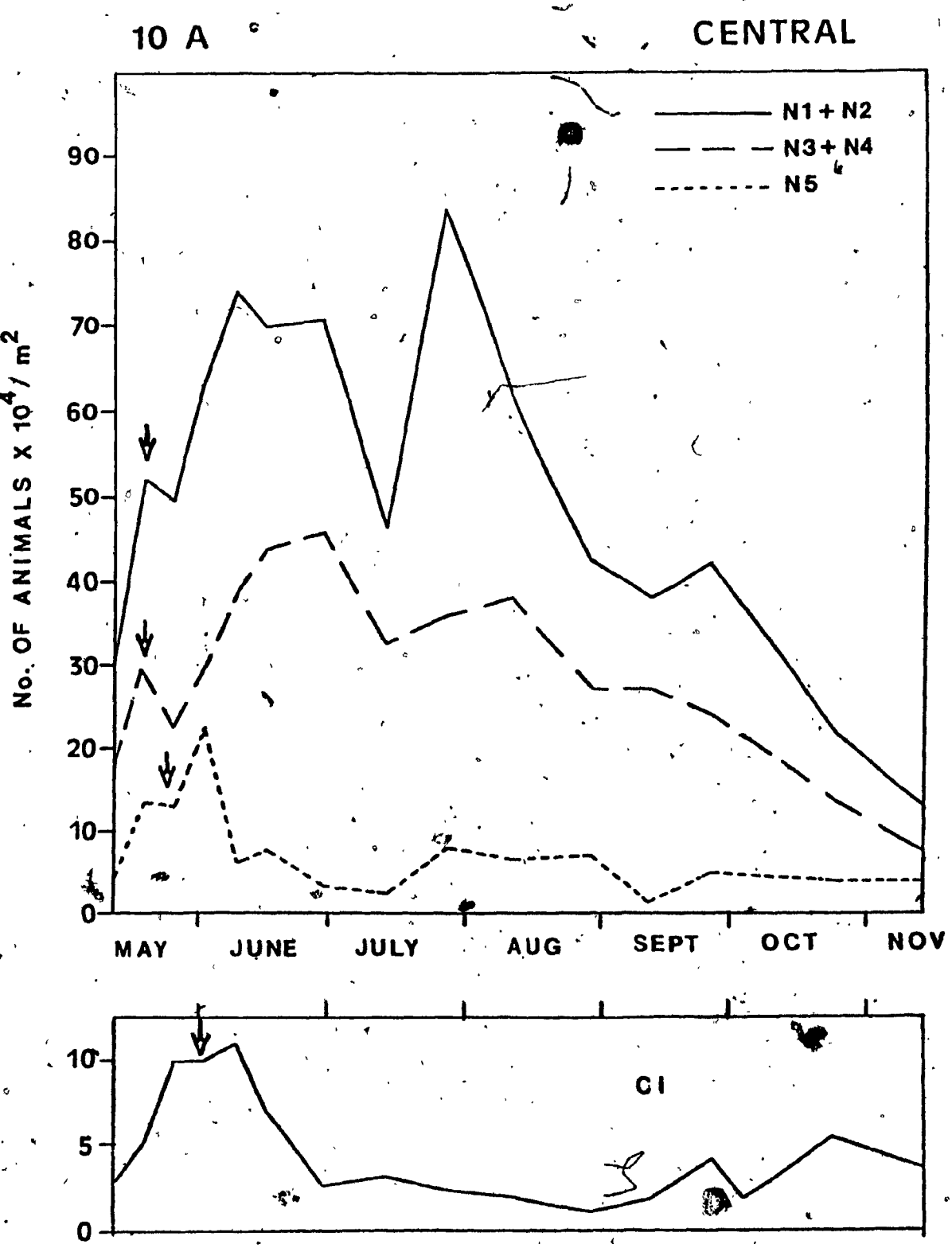
This last step probably introduces the single largest source of error in the calculation of cyclopoid naupliar production; sampling was not frequent enough to pinpoint the days on which peaks occurred and as shown earlier (see "Instar durations", p. 13) the differences between peaks do not provide exact duration values.

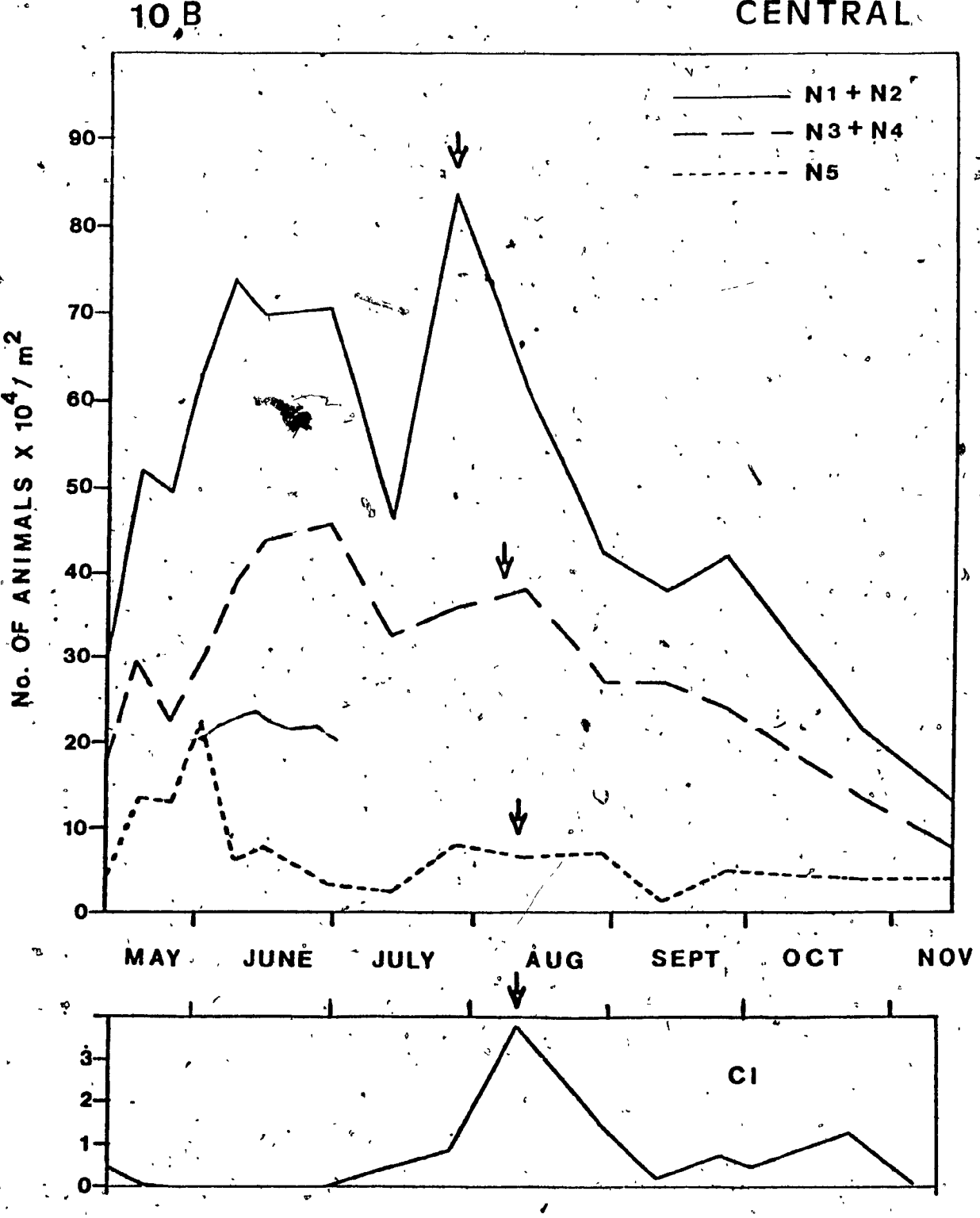
Published sources provided more duration estimates of the species involved. Comita (1972) found total naupliar durations (N1 to N5) for M. edax in Severson Lake of 14.5 and 10 days in 2 successive summer populations. In Marion Lake (McQueen, 1969) C.b. thomasi molted from N1 to N5 in 16 days. C. vernalis which grows faster (Andrews, 1953) probably lowers the mean duration in the present study, but its numbers were never high enough to be of significant importance.

Based on the above information, an arbitrary duration of 12 days was chosen as the mean duration of the entire seasonal naupliar

Figure 10. A. Comparison between the CI curve of C.b. thomasi and the first peaks of the grouped cyclopoid nauplii in central basin.

B. Comparison between the CI curve of M. edax and the 3rd peaks of the grouped nauplii in the central basin.


10 A
CENTRAL
N1 + N2
N3 + N4
N5
No. OF ANIMALS X 10⁴/ m²
0
10
20
30
40
50
60
70
80
90
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
CI
0
5
10


10 B
CENTRAL
N1 + N2
N3 + N4
N5
No. OF ANIMALS X 10^4 / m^2
90
80
70
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
CI
3
2
1
0

population. The breakdown by Ivanova's method (Table 7) yielded the following durations for the 3 stages:

Early nauplii (N1 + N2) = 2.8 days

Middle " (N3 + N4) = 5.1 days

Late " (N5) = 4.1 days

Since eggs were not counted, it was not possible to evaluate directly their contribution to production. To obtain an estimate of the minimum egg numbers it was assumed that there were as many eggs as N1, i.e. egg loss was ignored. The same assumption was implicit between N1 and N2 numbers since they had not been identified separately and the mortality between N1 and N2 was unknown. From the above assumption, it can be deduced that the numbers of egg, N1 and N2 were presumed equal.

The area under the curve of abundance of early nauplii (N1 + N2) was divided by 2.8 (the duration of N1 + N2) to obtain the total number of early nauplii. This total was then divided by 2 to get the numbers of N1 or N2:

$$\frac{\text{Area (animal x days) of N1 + N2}}{2.8 \times 2} = \text{N1 or N2}$$

The number obtained was, as was shown above also equal to egg numbers and therefore egg production could be calculated. Egg dry weights were calculated from the relation

$$d^3/W_E = k \qquad \text{(equation 1, p. 22)}$$

The production of cyclopoid eggs and nauplii could thus be calculated using the increment-summation equation. Results are presented in Table 6.

Estimation of egg numbers with an independent method

Since production of eggs was so large compared to that of the nauplii (Table 6) (80% of total) a means to verify its accuracy was sought.

In the calculation of egg production, egg numbers were assumed to be equal to N1 numbers. This assumption can only underestimate egg production because hatching success is unlikely to be 100% and could not contribute to the large discrepancy between egg and naupliar production.

A major possible source of error was the estimation of naupliar development times which directly affect the overall numbers. These durations were obtained through an arbitrary total (12 days), for combined naupliar stages, subsequently divided into Ivanova's (1973) percentages, themselves subject to considerable error.

An independant test was devised to estimate the duration of N1, which was 1.1 days according to the Ivanova method (Table 7).

To estimate the duration of N1, Bělehrádek's equation, as described by McLaren (1963) was used:

$$D = a(T - \alpha)^b$$

where D = development time

T = temperature

a, α, b = fitted constants

This equation has been used (McLaren, 1963; Cooley, 1973; Cooley and Minns, 1978) to predict the development time of copepod eggs by measuring these times at a few temperatures and interpolating to other temperatures.

Cooley and Minns (1978) determined the values of the constants a, α and b using the least squares method and provided the "best fit" to Bělehrádek's equation for a number of calanoid and cyclopoid species egg development times. They also measured constants for N1 durations, since the growth rate of this stage is solely dependant on temperature (Cooley, 1973). The constants they measured for N1 durations were, however for a selection of calanoid species only.

The 3 cyclopoid species; C.b. thomasi, M. edax and C. vernalis were among the species whose constants for egg development times were provided by Cooley and Minns (1978). Because they did not provide the constants for N1 of the same species of this study, the assumption was made that:

D_{N1}/D_E (calanoid) = D_{N1}/D_E (cyclopoid)

at a given temperature

The average daytime temperature at the Central basin, to which the N1 population was exposed, was calculated for the entire sampling season. This was done by obtaining a mean temperature for each 5m layer, for each sampling day, and multiplying it by the number of N1 + N2 nauplii at that depth. The values obtained (numbers x degrees) were summed and finally divided by the total number of N1 + N2 nauplii. The mean temperature was 12.4°C. The effect of vertical migration was not considered.

The development times of 5 calanoid species' eggs and N1's (all those whose constants for both egg and N1 were provided) were obtained at 12.4°C by using the logarithmic form of Bělehrádek's equation:

$\ln D = \ln a + b \ln (T-\alpha)$.

The ratio D_{N1}/D_E of each calanoid species was used to obtain the D_{N1} of each cyclopoid species, knowing its D_E. The range of values obtained was:

C.b. thomasi : 0.9 - 1.3 days

M. edax : 1.1 - 1.6 days

C. vernalis : 0.7 - 1.0 day

These duration estimates for N1 compare favorably with those obtained using Ivanova's method, especially since the mean duration of C.b. thomasi, the dominant species, was also 1.1 days (Calculations in Appendix E). The relatively close agreement between the egg development time estimated with the two independent methods provides some confidence to the calculated egg production.

Production of C.b. thomasi copepodids and adults

The estimation of the instar durations of this species was not feasible by the more accurate methods (first appearance of an instar; mean duration of an instar) described earlier (p.13), because of the continuous reproduction and resulting overlap in generations (Fig. 5, p. 29). Since the spring generation (G2) was by far the largest population produced, it was used to derive instar durations which were applied to the entire copepod population with the exception of the last generation (G5) which was not included in the calculation of production because it was still developing when sampling was terminated and its numbers could not be determined.

To determine durations of individual stages of copepodids CI to CV a total duration from CI to adults was obtained which was subsequently

divided by Ivanova's method (see "Materials & Methods", p. 24).

From the first occurence of CI, around April 28 (obtained by extrapolation) to the first adults of the cohort, an estimate of 27 days was obtained. The first adults probably molted from CV around May 25 since the samples collected on that day contained very few eggs but the samples from a week earlier and a week later contained large numbers of ovigerous females indicating that on May 25 the females from the previous generation were disappearing or were not producing new clutches and the females from the new generation had not yet started producing eggs.

The time between the CI peak and the adult peak was approximately 37 days. The two durations obtained from the difference between first appearances (27 days) and the difference between peaks (37 days) were combined and a mean duration of 32 days from CI to adult was used as the basis from which individual instar development times were derived.

To obtain production values for each of the instars, the area under the abundance curve of each stage (Fig. 5) could now be divided by the duration of the stage and multiplied by the weight gained by that stage during its development from the previous one. The total production of all copepodid instars (except adults) could be estimated using the general form of the increment-summation equation from page 24:

$$P = \frac{A_1 \Delta W_1}{D_1} + \frac{A_2 \Delta W_2}{D_2} + \text{etc.}$$

In the case of the adults, the weight increment is equal to half the difference in weight between the adult (CVI) and CV. This has been

TABLE 8

Production of C.b. thomasi copepodids and adults (May-Nov.).

A) Without Temperature Correction

STAGE	Animal days[a] (No.m^{-2})x10^6	Instar duration (days)	Animals (No.m^{-2})x10^6	Weight (ug)	ΔW (ug)	Production (g.m^{-2}.per.$^{-1}$)
CI	4.88	5.7	0.86	0.83	0.33	0.28
CII	5.09	5.9	0.86	1.23	0.40	0.34
CIII	5.83	6.5	0.90	1.72	0.49	0.44
CIV	8.30	6.9	1.20	2.41	0.69	0.83
CV	4.46	8.0	0.56	3.37	1.75	0.98
CVI (adult)			0.56[b]	5.12[c]	0.89[d]	0.50
TOTAL						3.37 g.m^{-2}.per^{-1}

B) With Temperature Correction

STAGE	Instar duration (days)	Animals (No.m^{-2})x10^6	Production (g.m^{-2})
CI	6.6	0.74	0.24
CII	5.7	0.89	0.36
CIII	6.4	0.91	0.44
CIV	6.9	1.20	0.83
CV	7.1	0.63	1.10
CVI		0.63(b)	0.56
TOTAL			3.53 g.m^{-2}.per^{-1}

a: represents the area under the curve of abundance.

b: adult numbers assumed equal to CV - see text for explanation (p. 55).

c. average of male and female dry weights.

d: $\Delta W/2$- see text for explanation (p. 53).

pointed out by Cooley (1973) who noted that the dry weight estimate for each instar approximates the weight of the instar after half of the development has been completed. Since the adult instar does not increase in weight after it enters that stage, the weight it apparently gains is in fact that gained by the CV individual during the second half of its development. The weight increment, therefore, from CV to CVI was ½ (5.12-3.37) or 0.89 ug. For the purpose of estimating CV production, it was assumed that all individuals in that instar reached the adult stage and therefore the numbers of adults are the same as that calculated for CV. This is necessary because the time a copepod spends in the adult stage is impossible to determine. Adults do not moult and their disappearance is due to disease, predation or natural death and since an estimate of their life span is not obtainable, their numbers cannot be estimated from population samples either. The results are summarized in Table 8A.

There should be no negative mortality as was found between CII and CIII as well as between CIII and CIV. The increase in numbers between CII and CIII is very small and could be due to sampling error. The apparent negative mortality between CIII and CIV, however, is quite large and could be caused by a fraction of the CIV population entering diapause. The process of entering the resting stage could be longer than that of molting to the next instar, or some of the diapausing individuals could still be in suspension and this longer stay in the CIV stage is not accounted for by Ivanova's method. The actual duration of the instar is therefore underestimated and the numbers in that instar overestimated.

Correction for temperature

Since Ivanova's method is based on growth at a constant temperature, some error could be introduced if instars develop at different temperatures. In order to provide an estimate of such an error, 2 sets of instar durations were computed: one without temperature correction and the other with a correction based on the temperature to which each instar was exposed during its growth (Table 8A & B). The method employed to obtain the mean temperature for each instar is the same as that described for N1 and N2 in the previous section.

The correction for temperature was done by assuming that egg and copepodid instar durations are affected in the same proportion by a change in temperature (Bottrell et al., 1976; McLaren, 1978). Bělehrádek's equation and the constants provided by Cooley and Minns (1978) to measure egg development rates were used to solve the equation:

$$D_{CI} \text{ (corrected)} = D_E(TI)/D_E(\bar{T}) \times D_{CI} \text{ (uncorrected)}$$

where TI = temperature at which CI developed

$\bar{T}$ = the mean temperature at which all copepodids developed

Production estimates using temperature corrected instar durations were very similar to the uncorrected ones ($3.53 g.m^{-2}$ and $3.37 g.m^{-2}$ respectively). For this reason, no temperature correction was applied to the instar durations of other species.

Production of M. edax copepodids and adults

The large mid-Summer cohort was used as the basis from which the entire copepodid development time was derived (Fig. 7, p. 33). It was observed that:

a) From the peak of the main CI pulse (August 11) to the approximate development of the adult instar there was a 4 to 5 weeks difference.

b) There was a 47 day interval from one period of abundance of ovigerous females to the next, (July 27-Sept 12) from which the naupliar duration of 13 days (28% of total by Ivanova's estimates) must be subtracted to arrive at a copepodid development time of 34 days.

A reasonable duration of 30 days was adopted as the development time of copepodids. This total was subdivided into individual instar durations by Ivanova's percentages (Table 2, p. 26) and production was estimated with the increment-summation method. Results are presented in Table 9.

Production of C. vernalis copepodids and adults

A mean duration of 15 days for development from CI - CV was derived from the abundance curves of this species (Fig. 8, p. 35). The low numbers recorded in the samples as well as the fast development rate of this species do not allow higher precision in the estimate of durations.

As before, the total duration time was divided into the instars with Ivanova's method.

Table 10 summarizes the results.

Production of D. sicilis

Since all instars of this species were recorded separately it was possible to follow its development from hatching to adults.

D. sicilis produced one main generation in the central basin (Fig.

TABLE 9

Production of M. edax copepodids and adults (May–Nov.).

STAGE	Animal days (No.m^{-2})x10^5	Instar. duration (days)	Animals (No.m^{-2})x10^5	Weight (ug)	ΔW (ug)	Production (g.m^{-2}.per.$^{-1}$)
CI	15.6	5.3	2.94	1.14	0.64	0.19
CII	16.0	5.5	2.91	1.72	0.58	0.19
CIII	9.1	6.1	1.49	2.28	0.56	0.08
CIV	19.2(a)	6.5	1.29	3.06	0.78	0.10
CV	8.1	7.5	1.08	4.40	1.34	0.14
CVI			1.08(b)	7.34	1.48(c)	0.16
TOTAL						0.84 g.m^{-2}.per.$^{-1}$

a: This value was not used in the calculation of the number of animals for CIV. As this stage enters diapause, its development time extends into the following season and using a duration derived from Ivanova's method becomes meaningless. To obtain a more realistic estimate of CIV the mean of CIII and CV was used.

b: number of adults assumed the same as CV – see text (p. 55).

c: $\frac{\Delta W}{2}$. See C.b. thomasi production (p. 53).

TABLE 10

Production of C. vernalis copepodids and adults (May-Nov.).

STAGE	Animal days $(No.m^{-2})x10^5$	Instar. duration (days)	Animals $(No.m^{-2})x10^5$	Weight (ug)	ΔW (ug)	Production $(g.m^{-2}.per.^{-1})$
CI	13.9	2.7	5.15	0.91	0.41	0.21
CII	9.1	2.8	3.25	1.34	0.43	0.14
CIII	7.8	3.0	2.60	1.96	0.62	0.16
CIV	5.0	3.2	1.56	2.55	0.59	0.09
CV	4.7	3.7	1.27	3.45	0.90	0.14
CVI			1.27(a)	5.23	0.84(b)	0.11
TOTAL						0.85 $g.m^{-2}.per.^{-1}$

a: assumed equal to CV - see text (p. 55).

b: $\frac{\Delta W}{2}$. See C.b. thomasi production for explanation (p. 53).

9, p. 37). The peak of N1 abundance was recorded at the end of June and the population took approximately 3 months to develop into adults. A total cohort development time of 90 days was distributed over the 12 instars with Ivanova's method. Egg numbers were assumed equal to N1 and egg weight obtained from the equation.

$d^3/W_E = k$ (equation 1, p. 22)

where d = diameter of a D. sicilis egg

W_E = dry weight of a D. sicilis egg

Total and individual instar productions are computed in Table 11.

Total copepod production:

Total copepod production for the ice-free period was 11.24g.m^{-2}. Of this total, 3.71 g (33%) was contributed by eggs. As mentioned earlier, egg numbers were assumed the same as N1 numbers which can only underestimate the true egg numbers since some mortality between egg and N1 probably occurred. Cooley (1973) found little mortality from egg to N1 in 3 D. minutus cohorts in Bluff Lake ($<10\%$), where egg production amounted to 45% of the total production of this species. The contribution of eggs to production by Boeckella dilatata, a calanoid copepod inhabiting Lake Hayes, New Zealand, was 31% (Burns, 1981) suggesting that eggs often make up important fractions of a copepod's production. Naupliar production was relatively low (6.7%) due in part to the weight loss after hatching.

The 3 cyclopoid species shared 81% of the basin's production, D. sicilis contributing the remainder, C. b. thomasi contributed 67% of the

TABLE 11

Production of D. sicilis (May-Nov.).

STAGE	Animal days (No.m^{-2})x10^5	Instar. duration (days)	Animals (No.m^{-2})x10^5	Weight (ug)	ΔW (ug)	Production (g.m^{-2}.per.$^{-1}$)
Egg			12.7(a)	0.40(b)	0.40	0.51
N1	29.3	2.3	12.7	0.34	-0.06	-0.07
N2	26.8	3.7	7.2	0.23	-0.11	-0.19
N3	33.9	4.5	7.5	0.28	0.05	0.04
N4	21.9	6.2	3.5	0.39	0.11	0.04
N5	18.0	8.6	2.1	0.56	0.17	0.04
N6	19.8	7.4	2.7	0.86	0.30	0.08
CI	20.1	9.5	2.1	1.33	0.47	0.10
CII	16.6	9.7	1.7	2.35	1.02	0.17
CIII	21.2	11.1	1.9	3.71	1.36	0.26
CIV	20.1	12.7	1.6	5.58	1.87	0.30
CV	17.6	15.2	1.2	9.04	3.46	0.42
CVI			1.2(c)	13.04	4.00(d)	0.48
TOTAL						2.18 g.m^{-2}.per.$^{-1}$

a: assumed equal to N1 numbers.

b: obtained from relationship $d^3/W_E = k$ (equation 1, p. 22).

c: assumed equal to CV. - see text (p. 55).

d: $\frac{\Delta W}{2}$. See C. b. thomasi production (p. 53).

total production by cyclopoid copepodids and adults and although its share of the cyclopoid eggs and nauplii is unknown, this species was probably more productive than all other copepod species together.

5. Biomass

Central basin

C.b. thomasi was the dominant zooplankter, with 47% of the biomass of copepodids. Table 12 lists the mean monthly and mean seasonal biomass distribution of all copepod species. The other cyclopoids, M. edax and C. vernalis made up 13% and 5% of the total copepodid biomass. As for D. sicilis, although its numbers were never very large, its large size contributed to this species making up 1/3 of the total biomass.

Since all three cyclopoids are known predators (Anderson, 1970; Carter 1974), a mechanism could exist, such as temporal or spatial segration whereby D. sicilis avoids predation.

To ascertain whether D. sicilis and the predators are indeed separated, paired correlations between D. sicilis and the copepodids and adults of each of the other 3 species were done for their seasonal distribution.

The two largest contributors to the basin biomass, C.b. thomasi and D. sicilis, were significantly negatively correlated ($r=-.84$; $p<.01$). A weaker negative correlation was obtained between M. edax and D. sicilis ($r=-.51$; $p<.10$). Other correlations between pairs of cyclopoid species were very low, and insignificant. Of course, a negative correlation between pairs of species does not necessarily

TABLE 12

Mean monthly and mean seasonal biomass ($mg.m^{-2}$) of 4 copepod species (May-Nov.) in the central basin.

Month	Cyclop nauplii	Cyclopoid copepodids & adults C.b.thomasi	M.edax	C.vernalis	calanoid nauplii	D. sicilis copepodids	Total biomass ($mg.m^{-2}$)
May	177	327	102	20	8	125	759
June	252	845	70	88	16	237	1508
July	210	850	235	71	47	249	1662
Aug.	191	444	295	54	55	570	1609
Sept.	138	327	105	47	44	860	1601
Oct.	86	407	138	70	9	683	1393
Nov.	38	665	60	27	9	178	977
Seasonal Mean	156	552	155	54	27	415	1360

indicate that they avoid each other. If the cyclopoid were depressing the calanoid population through predation, the result would be the same. It can be observed from figure 9 (p. 37) that the first D. sicilis generation, which coincided with the main C.b. thomasi generation (fig. 5, p. 29) was very small, possibly because of predation.

Spatial distribution was not examined because daytime distributions are not sufficiently indicative of the habitat limits of a species (McLaren, 1963) and vertical migration in the central basin was not assessed.

Biomass comparison between the central and south basins.

Although a complete comparison between the central and south basins was initially planned to provide a more representative picture of the lake, the comparison was restricted to the 0 to 5m layer of the two basins because of sampling problems.

The Clarke-Bumpus sampler requires that a weight be attached approximately 2m below it to keep the line taut and the sampler at the desired depth. Since the mean depth of the basin is 7m, the depth limit to which the sampler could be lowered was 5m. It was initially planned to complete the sampling with a 30 liter Schindler trap at 1m intervals below 5m, however, the 1st samples collected below the 0-5m layer (Table 13) showed a homogeneous distribution of copepods in the water column. It was decided then to discontinue the monitoring of the basin below 5m and assume the water column to be homogeneous.

Upon analysis, it became apparent that as the season advanced, many

TABLE 13

Comparison of C.b. thomasa numbers between samples collected in the top 5 m with the Clarke-Bumpus sampler and at 5.5 m, 6.5 m and 7.5 m collected with a 30 liter Schindler trap on June 8, 1976 in the south basin. Depth at sampling point was 8 m.

STAGE	0-5 m* (No./liter)	5-8 m** (No./liter)
N1+N2	108.8	121.5
N3+N4	34.7	31.6
N5	8.3	1.4
CI	13.0	11.4
CIIII	10.7	10.0
CIII	6.0	5.8
CIV	7.8	11.7
CV	3.2	4.9
Adults	12.0	10.3

A t-test for paired comparisons showed no significant difference between the 2 sets ($p < .05$)

* numbers multiplied by 5/3 to correct for inefficiency of towed nets (Schindler, 1969).

** corrected for lake volume at 1 m intervals.

instars, especially the late copepodids and adults, concentrated in the deeper strata. Figure 11 shows the population of C.b. thomasi copepodids and adults at the Indian Point station (farthest south), collected in the 0-5m layer. With the exception of CI and CII, the population suddenly disappeared at the end of June. Other species showed the same trend. The same phenomenon was observed at the Border station.

To verify whether this disappearance was caused by mortality or movement out of the sampled zone, 2 sources of data were examined:

a) The 0-5m stratum of the central basin was checked for a similarity in the population pattern between basins. Figures 12A and 12B show that the same phenomenon occurred in both basins. However, in the central the C.b. thomasi population was found in the deeper samples providing evidence that they had only migrated to lower depths and not been eliminated.

b) Other samples, taken for another purpose by S. Watson at 0m, 2m, 5m and 7.5m in the south basin were examined. These were 110ml. subsamples from 4 liter Van Dorn bottles which, although insufficient for a complete analysis, nevertheless indicated the presence of a substantial population during July, confirming the suspicion that the population was present in the water column but not in the top 5m.

For this reason, comparisons between the 2 basins are limited to the first 5m of each basin.

Even though the populations inhabiting the surface waters are not representative of the entire populations of the water column, the

Figure 11. Cyclops bicuspidatus thomasi at Indian Point (0 to 5m) showing the disappearance of most instars after June 29.

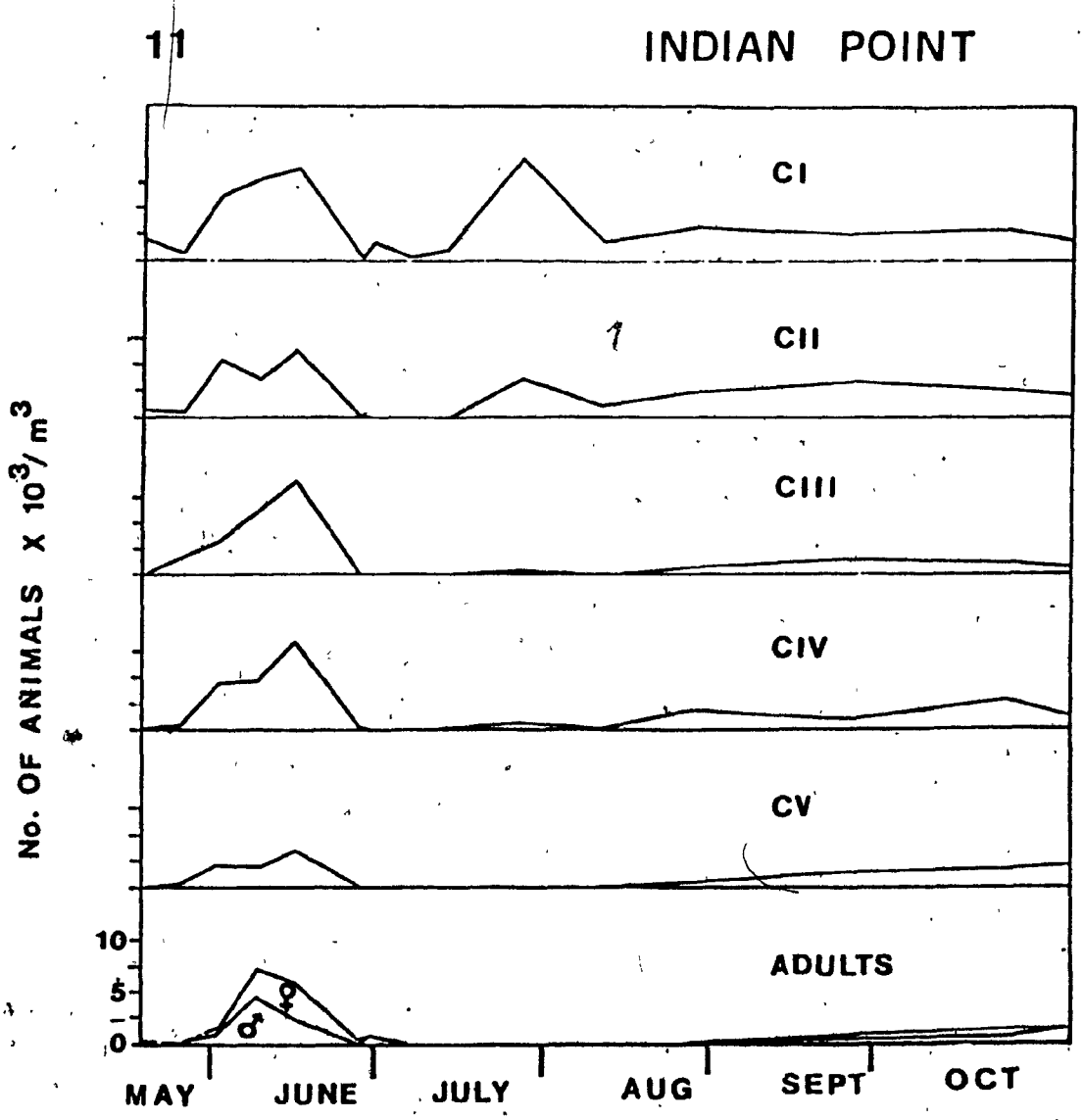
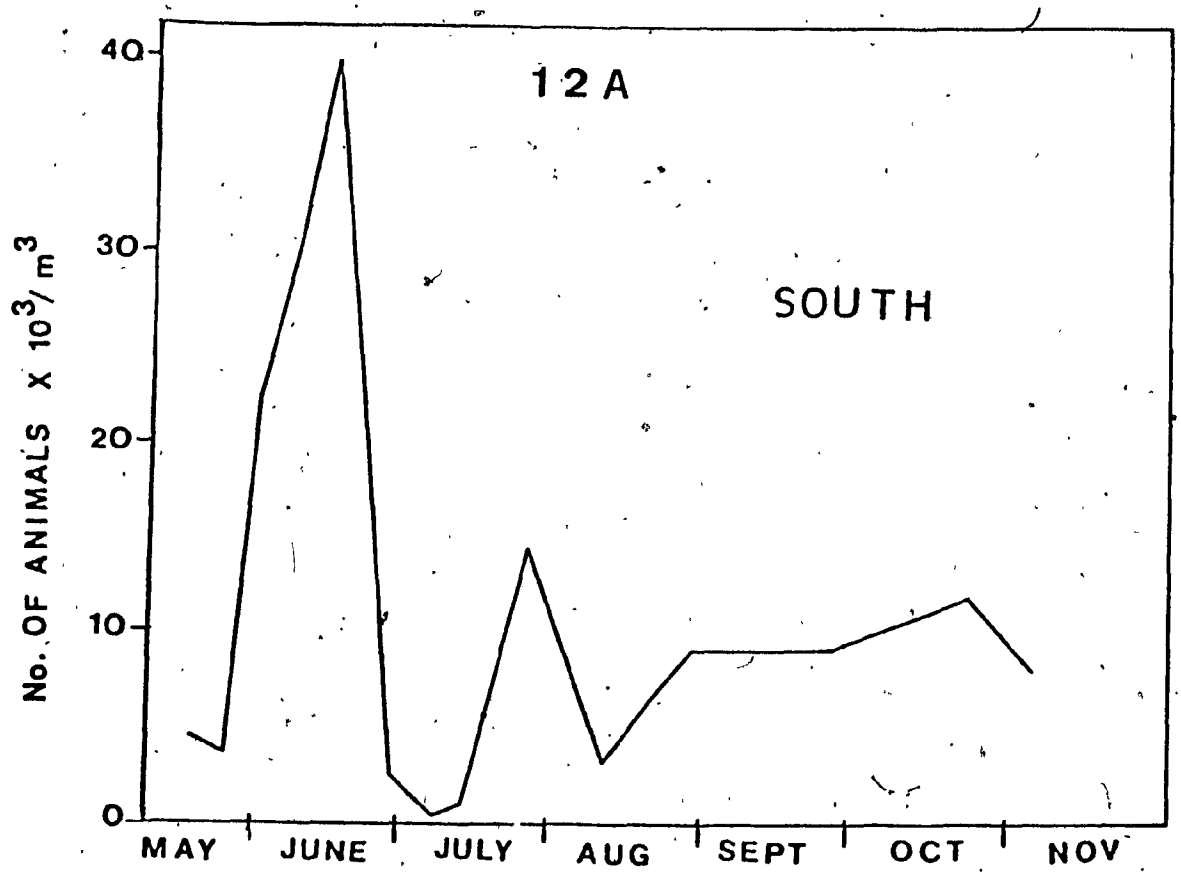
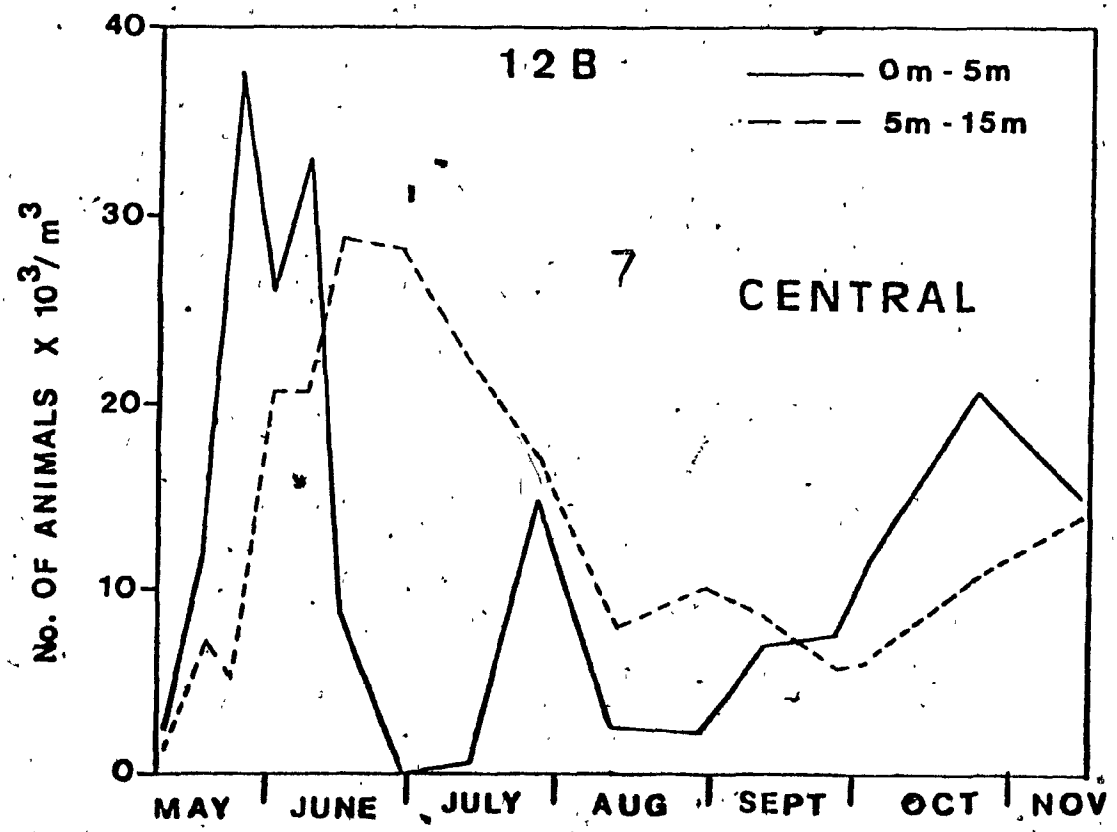

11
INDIAN POINT
CI
CII
CIII
CIV
CV
ADULTS
10
5
0
♂
♀
No. OF ANIMALS X $10^3/m^3$
MAY
JUNE
JULY
AUG
SEPT
OCT

Figure 12. A. C.b. thomasi copepodid and adult population (0-5m) in the south basin (Indian Point)

B. Solid line: C.b. thomasi copepodid and adult population (0-5m) in the central basin;

Dashed line: C.b. thomasi copepodid and adult population in the 5-15m layer of the central basin.


12 A
SOUTH
No. OF ANIMALS X $10^3/m^3$
40
30
20
10
0
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV


12 B
0m - 5m
5m - 15m
CENTRAL
No. OF ANIMALS X $10^3/m^3$
40
30
20
10
0
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV

comparisons between the top 5m layers is probably valid. If some species or particular instars avoid the surface waters during certain times of the year, this phenomenon is probably occurring in both basins and the proportion of the biomass remaining in the top layer should be roughly proportional to the entire biomass of the water column. The comparisons between the biomasses of the 0 to 5m layers, therefore, should give some indications about the total biomass in each basin.

Biomass comparison of the 0 to 5m strata: 3 stations

The data presented earlier on the central basin was given in units of organisms per surface area (e.g. biomass/m^2) in order to describe the entire contents of the water column, irrespective of depth. This is the usual procedure (Morgan, 1980) which allows comparisons between water bodies of different depths, without introducing large dilution factors due to relatively deep and unproductive hypolimnia.

The present section, however, can be presented in units of volume (m^3) because finite and equal depths from the two basins are compared.

Comparison of the 0 to 5m strata showed that despite the higher primary productivity and chlorophyll content (Table 1) of the south basin, the copepod biomass was not higher there. In fact, the 0 to 5m layer in the central basin contained a larger copepod biomass than either of the 2 stations in the south (Table 14).

A large portion of the difference was due to D. sicilis, which made up 1/3 of the biomass in the central basin but only 13% and 14% at Indian Point and Border, respectively (Table 15). M. edax was also more common in central than in the south since its biomass in central was

TABLE 14

Mean monthly and seasonal copepod biomass ($mg.m^{-3}$) in the 0m-5m stratum at 3 stations, (May-Nov.).

STATION / MONTH	INDIAN POINT	BORDER	CENTRAL
May[a]	19.3 (2)[c]	68.1 (2)	83.1 (2)
June	92.6 (4)	78.3 (5)	60.2 (4)
July	27.6 (4)	20.3 (4)	52.7 (2)
August	44.4 (2)	40.6 (2)	63.4 (2)
September	53.5 (2)	75.1 (2)	116.0 (2)
October	37.0 (1)	45.2 (1)	130.1 (2)
November[b]	25.8 (1)	52.7 (1)	48.5 (1)
Mean Seasonal	42.9 (16)	53.9 (17)	79.1 (15)

A Wilcoxon signed-ranks test for paired observations showed a significant difference ($p < 0.05$) between Central and Indian Point.

a: first sampling date May 18

b: last sampling date Nov 14

c: number of sampling days

TABLE 15

Biomass proportions (%) of copepod species[a] in each of 3 stations in the 0m-5m stratum (May-Nov.).

STATION / SPECIES	INDIAN POINT	BORDER	CENTRAL
C. b. thomasi	52	55	39
M. edax	15	15	22
C. vernalis	20	16	9
D. sicilis	13	14	31

a: copepodids and adults only.

slightly more than double that of the Border biomass and over 3 times that of Indian Point. A Wilcoxon signed-rank matched pairs test showed a significant difference for the above 2 species between central and Indian Point, but not between central and Border.

These results suggest 3 possibilities:

1) Food is not limiting the growth of copepods and other variables, such as depth, are more important;

2) High mortality in the south basin is keeping the standing stock low.

3) The results obtained do not represent the real population numbers in the south basin.

Of course, a combination of these possibilities could be operating.

If variables other than nutrient levels are limiting growth then temperature and depth could be important, especially for a species such as D. sicilis which is known to occur in relatively cold waters (Carter, 1969). A lower depth, such as in the central basin, by providing a cooler environment (see temperature data in Appendix F), could enhance the growth of this species. The larger population could then be proportionally represented in the higher strata. Moore (1978) in his study of 18 arctic and subarctic lakes found no correlation between phytoplankton density and D. sicilis numbers. He did not find any correlation with temperature or depth either, but these were already considered cold lakes and depth may contribute to growth of D. sicilis only inasmuch as it harbors colder waters.

The second possibility to consider is that if the biomass is lower in a particular environment, it does not necessarily mean that less biomass has been produced. If predation pressure from fish fry is higher in the south than in central, copepods may be lost as they are produced. The fact that there are more fish in the south basin (Nakashima and Leggett, 1975) provides some support to this possibility. Nakashima (1979) also found that copepods dominated the diet of juvenile perch in early Summer and Fall.

There are some indications that the south basin is more productive, at least for some species. In the Spring, the mean clutch size of C.b. thomasi ($\bar{X}$ = 52.9±15.2; n=20) was significantly higher ($p < .001$) in the south basin than in central ($\bar{X}$ = 34.6±8.9; n=26). The maximum spring biomass recorded for any day occurred at Indian Point where it was 134.4 $mg.m^{-3}$. The highest day in central and Border were 118.1 $mg.m^{-3}$ and 107.7 $mg.m^{-3}$ respecitvely.

Thirdly, the observed lower biomass in the south basin could be caused by the heterogeneous distribution of the copepods not only vertically but also in their aggregation in the littoral zone which is much more important in the shallow south than in the central basin. The lower biomass recorded could also be due to different seasonal growth patterns between the two basins. It was observed that the C.b. thomasi spring population reached its peak of numbers approximately two weeks later in the south than in central (figures 12A and 12B, p. 68). The disappearance of the populations from the 0 to 5m layer was, however, synchronous and consequently, the south basin population resided in the

0-5m layer for a shorter duration. It is possible that one complete generation had already developed in the south basin when sampling began although there were few ovigerous females in the first samples.

In conclusion, although the data comparing the two basins are incomplete, the higher biomass in the central basin suggests that depth could be playing an important role in determining standing stocks of copepod populations.

GENERAL DISCUSSION

The copepod community in the central basin of Lake Memphremagog has the typical composition of temperate lakes throughout the world. From the IBP survey of freshwater bodies (Nauwerck et al., 1980) it was observed that most temperate zone lakes contain one to three planktonic cyclopoids, at least one of them belonging to the cyclops group, frequently a Mesocyclops and one or more diaptomid species; usually one in Old World lakes and two in North American lakes. In Lake Memphremagog Diaptomus sicilis was the dominant diaptomid but D. minutus was also found. Cyclops bicuspidatus thomasi is the most frequent cyclopoid copepod in North America and is the dominant species in this lake.

In terms of total production values, the estimate of 11.24 g/m^2/productive season corresponds to the upper range of values reported elsewhere for copepods (Waters, 1977). Based on copepod production alone, the central basin would be rated fairly eutrophic. The proportion of copepod production to the remainder of the zooplankton production is, however, unknown and the number of studies reporting total copepod production are not numerous enough to allow such generalizations about lake trophy to be significant.

An important factor to consider is the depth of the basin, which has been found to be positively correlated with zooplankton biomass and production (Brandl, 1973 cited in Nauwerck et al., 1980; Brylinsky, 1980). The relatively large depth of this basin could introduce a

sizeable amount of variability which would reduce the predictive power of the lake's trophic state on copepod production.

Trophic relationships between primary producers and copepods will be considered later as a means to predicting copepod production instead of the direct method of collecting and counting specimens.

Sources of error using the direct method: Estimating production of copepods with the direct method, which involves identifying every stage of every species, is extremely difficult in large lakes where many similar multivoltine species coexist. Even if some temporal and spatial segregation occurs, the overlap is considerable in the samples. The earlier stages are almost indistinguishable from each other, especially in species such as C.b. thomasi, M. edax and C. vernalis whose overall shape and size are very similar and must be identified at high power (100-400x). At present, there are no keys for identifying nauplii (except Ewers, 1930, covering 13 species, none from Memphremagog) and complete production studies, covering all developmental stages to date have not been performed in water bodies containing 3 or more related copepod species. Some shortcuts are inevitable if data are to be obtained within reasonable time periods with reasonable cost/benefit ratios.

The major sources of error in this study are due to: 1- The sampler, 2- Subsampling, 3- Sample analysis, 4- Estimation of dry weights, 5- Estimation of instar development times.

1. Errors due to sampler: At present, the only means of estimating efficiency of a sampler is to compare it to a more efficient one but the

accuracy of the most efficient sampler cannot be evaluated, therefore, absolute estimates of error are not available. Volume samplers such as the Schindler-Patalas, collect the largest numbers (160% of towed nets) per volume (Schindler, 1969) but require more samples because they collect smaller samples and heterogeneous distribution of animals must be overcome. Towed nets if equipped with small mesh size will clog up and water will back out without being filtered and, on the other hand, if large mesh size is used, small nauplii will not be caught. Avoidance of towed nets by the larger and faster swimming instars is documented (Fleminger and Clutter, 1965) and could bias the samples.

In this study, a correction factor for the inefficiency of towed nets was not applied to the production estimates to keep them comparable to other studies where correction factors were not applied either.

2. Subsampling error: Samples can easily reach volumes of a few hundred liters, each liter containing a hundred or more individual copepods in all stages. Such large volumes are necessary to overcome patchy zooplankton distributions but counting entire samples would be impractical. Subsamples are taken, which add to the error, but reduce effort. The combined sampling and subsampling errors that can be quantified are in the range of 20% (from Appendix C).

3. Analysis of samples: Identification of the individual stages could be a source of error especially with naupliar and early copepodid stages. Keys are made for adult stages and species characteristic traits (spines, etc.) are sought in earlier stages for their identification. Since such characteristics are less pronounced in

younger instars, some confusion among species is possible. The error caused by the analysis of samples is probably very small since the overall number of animals in the sample does not change.

4. Biomass, dry weights: Seasonal size differences commonly occur within species (see Results section, p. 28) and each generation exposed to different temperature and nutrient conditions could and usually does develop to a different size.

Direct estimation of dry weights consists of the isolation and drying of a number of individuals from each stage such that representative mean weights are obtained. Preserved specimens, however, have significantly different dry weight than fresh specimens (Pace & Orcutt, 1981) and either a correction factor must be applied, involving some error, or fresh specimens have to be picked from the collected samples for immediate weighing, a time consuming task.

An alternative to weighing specimens is the use of regression equations based on length-weight relationships calculated for individual or closely related groups of species with similar body shape (e.g. Bottrell et al., 1976; Dumont et al., 1975, Rosen, 1981). Of course some error is associated with these predictive equations.

5. Instar development times: The error due to estimating instar development times is probably the most difficult to quantify. In this study, for each species, a total development time was estimated for each generation, a mean generation time was calculated which was subsequently divided into individual instar durations using Ivanova's (1973) proportional breakdown of total generation time.

Two sources of error are apparent here: the first is in the estimation of the total generation time; the second is in the use of an empirically derived subdivision of total generation time into individual stage durations.

In the first case, errors in the estimate of generation length will have a direct and opposite effect on the estimate of production, e.g. a 10% overestimate in generation length will underestimate production by 10%. In the second case, an overestimate in the duration of an instar will result in an underestimate of the instar following or preceeding it. The error in the second case is probably less important than in the estimation of total generation time unless there was a large difference in the weight gained during the two successive instars. This rarely occurs.

It would be very difficult to provide an estimate of the error involved in estimating generation lengths since they were obtained by using a combination of parameters, such as first appearance of instars, peaks of abundance of instar, relative abundance of egg bearing females and published values. A subjective estimate would place the upper limit of the error at 20%.

As for the error in assessing individual instar durations, the values published by Ivanova (1973) are provided with estimates of error in the 10% range but the application of values obtained from laboratory reared animals to predict duration in the natural habitat is subject to an unknown amount of variability.

The various sources of error listed above, when summed, will probably amount to an error margin between 50% and 100% of the estimated values. Assuming the error to be 100%, copepod production would then be between 50% and 200% of the estimates reported in this study.

Indirect methods of estimating production:

The two indirect methods of estimating production which have been selected for comparison with the values obtained in this study are 1) the estimation of production from production/biomass ratios (P/B) and 2) the prediction of secondary productivity from primary productivity. The reasons for selecting these methods were outlined earlier (p. 12).

1. The P/B ratio. The production to biomass ratio is very useful because it is an expression of specific production, independent of lake size or total amounts of production or biomass. It is a measure of the growth efficiency of different secondary producers and allows comparisons between different bodies of water. It can also be used to estimate production from biomass values alone if a constant relationship can be universally established for the P/B ratio.

It has been suggested (Waters, 1977) that P/B is constant for zooplankton populations of mixed ages and species as long as voltinism (the number of generations per year) is taken into account. Waters proposes a ratio of 4-6 per generation. According to the same author, P/B calculated on an annual basis (i.e. total production of the year over the mean biomass, $\bar{B}$) is approximately 20 for multivoltine (4-5 generation per year) zooplankton.

The constancy of the P/B ratio has been questioned by many authors (Banse and Mosher, 1979; Nauwerck et al., 1980; Downing, 1984) who have noted that many variables other than voltinism affect the P/B ratio. Downing (1984) suggests that the effect of voltinism is not the cause but a consequence of the productive rate; fast growth rates resulting in many generations per year. Based on the IBP survey of 33 lakes, Nauwerck et al. (1980) have found a curvilinear relationship between P and B. P/B was lower in cold oligotrophic and very warm eutrophic lakes than in moderately warm lakes. They explain this lower productive efficiency in the cold lakes by a slowing down of metabolism and by food limitation in the very warm eutrophic lakes.

Another factor affecting the P/B ratio is the ability of individual species to adapt to environmental conditions by developing physiological characteristics which affect productive rate such as short generation spans. An example of such an adaptation is found in Cyclops vernalis which has the shortest recorded generations among copepods in temperate areas (Andrews, 1953; Carter, 1969).

Trophic efficiency differences among secondary producers are also reported; herbivores are thought to be generally more productive than carnivores (Waters, 1977). Cladocerans usually have higher P/B ratio than copepods, a trend which is more pronounced with increasing lake trophy (Nauwerck et al., 1980), from cold oligotrophic to warm eutrophic lakes.

Many attempts have been made to rank P/B according to parameters

which could predict the largest possible amount of variability among P/B ratios of different groups of organisms. Banse and Mosher (1980) have reviewed some of them (life span, maximal life span, maximal biomass) and present a regression equation based on mean adult body mass as a scaling factor for P/B:

$$P/B = aM^b \qquad \text{(equation 10)}$$

where M is body mass at maturity expressed in Kcal and a and b are fitted constants.

Using published P/B data for invertebrates ranging in size from clams to copepods, a size range of 10^5 fold, Banse & Mosher (1980) arrived at an allometric equation describing the change in P/B ratio (a 100-fold range) with adult mass. They found that 90% of the animals with habitat temperatures ranging from 5°C to 20°C had P/B ratios between 50% and 200% of the predicted values.

In order to verify whether scaling by body mass could accurately predict P/B values of the 4 dominant copepod species in Lake Memphremagog, their mean adult masses (from table 5) were converted to Kcal (1g dry wt = 5.5 Kcal: Pederson et al., 1976) and the values for the constants a and b provided by Banse and Mosher (1980, table 2, equation 3) replaced in equation 10 to arrive at a value for P/B for each species. Since the egg and naupliar stages of the 3 cyclopoid species had been grouped together and consequently no estimates of total production of individual species were available, the cyclopoid egg and naupliar production was divided into the 3 species in the same proportion as the copepodids and adults.

The results in table 16 show that 3 out of 4 species in Lake Memphremagog fell below the "confidence interval" of 50% to 200%.

The 31 species of invertebrates used by Banse and Mosher to arrive at their equation contained 6 copepod species of which 3 only were within the confidence limits. The other 3 were all lower in their productivity than predicted by the model. This suggests that this method predicts copepod P/B less accurately than for other invertebrates. It should also be mentioned that the P/B values obtained in the present study were not annual figures but for the vegetative period (ice-free period). If taken on an annual basis, they would be even lower because some copepods species maintain a sizeable standing stock throughout the year although growth becomes negligible. Data provided by Banse and Mosher on P/B of vegetative periods confirm this:

The low accuracy in predicting P/B ratio of copepods by scaling with adult body mass could be due to two reasons: the first is that copepods reproduce sexually and therefore only half of the population is producing offspring. When compared to, say, cladocerans which reproduce mostly parthenogenetically, the copepods will be less productive. Secondly, 3 out of the 4 copepod species in Lake Memphremagog are carnivorous and productivity was shown to decrease with trophic level (Waters, 1977; Jonasson, 1978). The authors of this method suggest that their model be used not to replace direct methods but rather as a tool that allows "recognition of rule and exception". They also suggest that their relation be used to estimate production of the less important species in an ecosystem while the more dominant ones be estimated with more accurate approaches.

TABLE 16

Calculated and predicted $\bar{P}/\bar{B}$ ratios for copepod species in the central basin of Lake Memphremagog. $\bar{P}/\bar{B}$ ratios predicted from: $\log (\bar{P}/\bar{B}) = -0.19 + (-0.37) \log M$ (Banse and Mosher, 1980; equation 3, table 2).

Species	$\bar{P}$ ($g.m^{-2}.period^{-1}$)	$\bar{B}$ ($g.m^{-2}$)	$\bar{P}/\bar{B}$ (calculated)	M $(Kcal) \times 10^{-5}$	$\bar{P}/\bar{B}$ (predicted)
C.b. thomasi	6.05	0.675	9.0	2.8	28.3
C. vernalis	1.5	0.070	21.4	2.9	28.1
M. edax	1.5	0.175	8.6	4.0	24.9
D. sicilis	2.18	0.440	5.0	7.2	20.4

2. Estimating secondary production from primary production.

Highly significant correlations have been reported (Brylinsky, 1980) between primary and secondary production. When the zooplankton is subdivided into herbivores and carnivores, the relationship maintains its significance with both subgroups (at the 99% level). Multivariate analysis has shown (Brylinsky, 1980) that up to 50% of the variability in zooplankton production is explained by primary production and the amount of variation accounted for is the same for herbivores and carnivores.

Although the relationship between the available food (primary production) and the secondary producers is positive, it has also been suggested that the response of secondary producers to increases in primary production is curvilinear because the efficiency of utilizing the food source may vary with different lake trophic levels (Pederson et al., 1976; Parsons, 1980). More eutrophic lakes will usually support larger proportions of blue-green algae which are less readily utilized by filter-feeding zooplankton than green algae (Hilbricht-Ilkowska, 1972 cited in Pederson et al., 1976).

In Lake Memphremagog, primary production estimates are available (Ross and Kalff, 1975) but total secondary production is not known, therefore, it is not as yet possible to verify directly whether secondary production is accurately predicted from primary production values. Carnivorous zooplankton production, however, is equally well predicted by phytoplankton production (Brylinsky, 1980). The 3 cyclopoid species in the central basin are all known predators

(Anderson, 1970; Carter, 1974; Nauwerck et al., 1980) and the only other known predator in the collected samples was Leptodora kindtii, a cladoceran that was only occasionally found in the samples and probably did not contribute significantly to total production. The 3 cyclopoid species were, therefore, assumed to represent the carnivorous fraction of the zooplankton. The nauplii were not included in the carnivorous zooplankton production (CZP) because they are assumed to be particle and suspension feeders (Nauwerck et al., 1980). The fraction of production attributed to eggs was, however, included since their biomass is derived from animal tissue eaten by the females. CZP was calculated as 8.26g/m^2/period or 45.4 Kcal/m^2/period.

The primary production and CZP data from 22 lakes included in the IBP survey (Brylinsky, 1980 for primary production; Nauwerck et al., 1980 for CZP) were used to derive the regression equation:

$$CZP = -0.55 + 0.0138 \text{ primary production} \qquad \text{(equation 11)}$$

(expressed as Kcal/m^2/yr)

The correlation coefficient ($r=0.73$) is significant ($p<0.01$) and the coefficient of determination ($r^2=0.53$) suggests that about half the variation is accounted for (Fig. 13).

To ascertain whether primary production in Lake Memphremagog could be used to predict CZP, the phytoplankton production estimate of 123gC/m^2/period (May-Sept 1973) from Ross and Kalff (1975) for the central basin was converted into energy units (1gC=13.8 Kcal) and equation 11 solved. The CZP predicted by this relation was 22.9 Kcal/m^2/period which represents 50% of the calculated CZP of 45.4 Kcal/m^2/period.

Fig. 13. Relationship of carnivorous zooplankton production to primary production in 22 lakes surveyed for IBP. Data obtained from Brylinsky (1980) for primary production and from Nauwerck et al. (1980) for zooplankton production.

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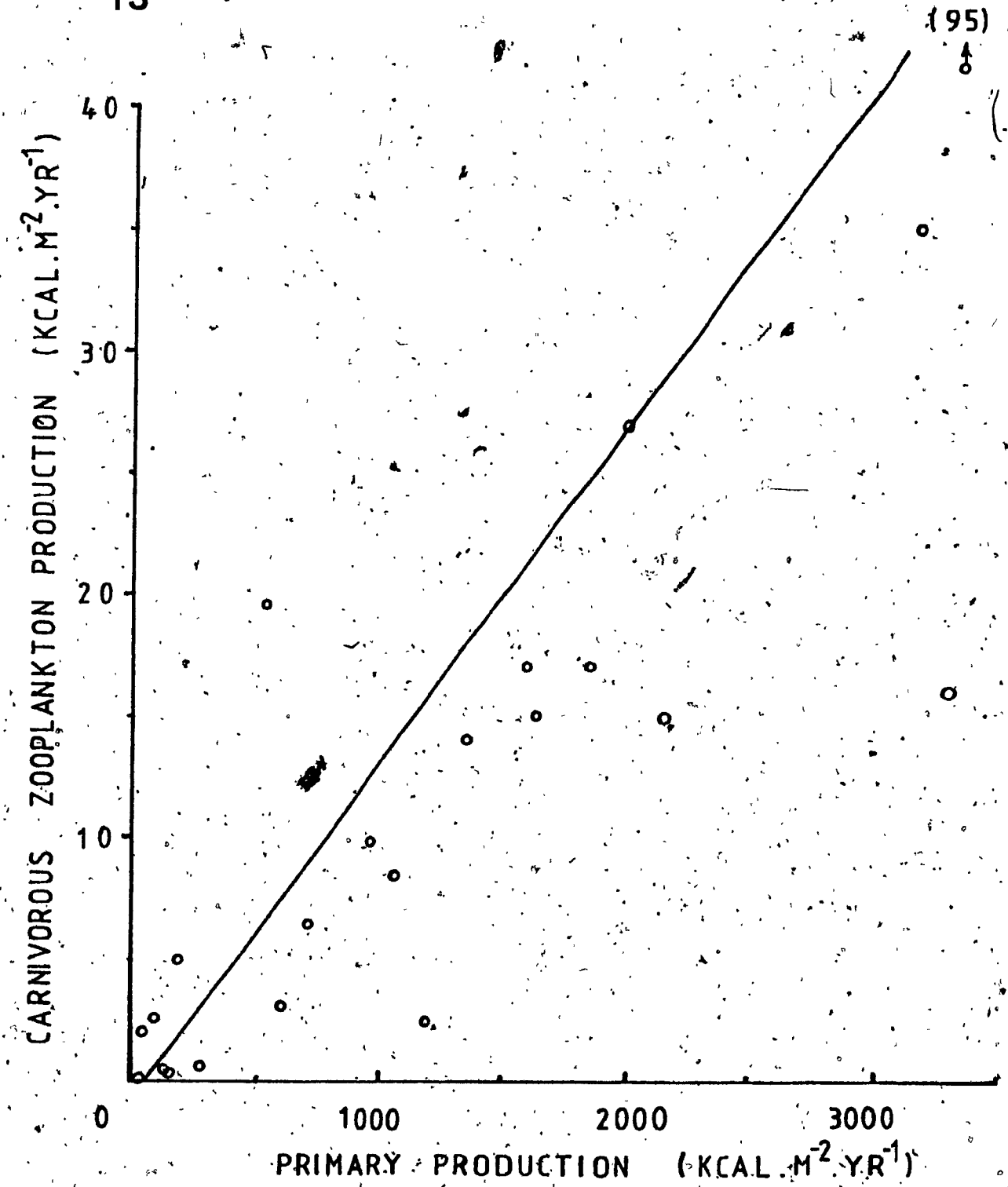
(95)
40
30
20
10
0
1000
2000
3000
CARNIVOROUS ZOOPLANKTON PRODUCTION (KCAL.M^{-2}.YR^{-1})
PRIMARY PRODUCTION (KCAL.M^{-2}.YR^{-1})

This method has the advantage that it requires no gathering of zooplankton samples and could be used for rough approximations where primary production data are already available. It is interesting to note that the slope of the regression line (0.0138) indicates a 1.4% transfer of energy between primary production and CZP, confirming the usually accepted 10% transfer rate between trophic levels.

The results predicted by the two methods do not indicate a trend. The P/B ratio overestimated production (although it could be argued that it underestimated biomass instead) and the second method predicted less than half the calculated production. If the magnitude of the error associated with the calculated production is taken as 100%, a slight overlap with the predicted values would result.

Although the number and accuracy of the data points, in this study, do not allow much further comparisons between methods, they do suggest that predictive methods could be used advantageously. Considering the amount of effort required for gathering copepod population numbers and life histories, the "short-cut" approaches, when refined, could probably yield sufficiently accurate production estimates for many ecological purposes.

CONCLUSIONS

Both direct and indirect methods have their usefulness in estimating production and the choice of method should be dictated by the use that will be made of the data. The direct method requires considerable resources in manpower, if all sources of error are to be accurately measured and the magnitude of the error kept low. This is much more difficult to accomplish in large lakes where many similar species coexist. At present, the vast majority of copepod production studies involve untested assumptions, such as using laboratory derived instar durations on field populations, or short-cuts, such as lumping all naupliar or copepodid stages in one group. Most studies do not provide confidence limits to their production values.

The indirect methods are probably accurate enough for resource management purposes or preliminary studies. The usefulness of such methods could be greatly enhanced, however, if the production estimates used to develop them were more reliable. Brylinsky (1980) has pointed out that it was not worth, at this point, refining predictive methods such as the relationship between primary and secondary productions. Improving such relationships is not worthwhile because the variability due to the experimental techniques used to measure the productions is comparable to that of the relationship.

In short, accurate production estimates are needed in order for the predictive methods to be more reliable.

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APPENDICES

APPENDIX A

Estimation of the copepod population below 25 m in the central basin.

DEPTH m	June 29 No/L*	Sept 12 No/L*	Oct 24 No/L*
0-5	3.2	61.7	126.0
5-10	78.5	43.7	89.6
10-15	133.5	74.7	37.9
15-20	46.5	13.2	18.8
20-25	20.3	6.8	3.5
25-30	12.8	5.2	4.6
30-40	3.9	4.9	3.9
40-50	0.8	2.7	4.6
% below 25 m	6.3	6	4.5

* corrected for lake volume at different depths

APPENDIX B

Estimate of error in lowering of Clarke-Bumpus sampler using the temperature profile of the water column.

DEPTH (m)	T(°C)(a)
6	14.5
7	14.0
8	13.9
9	13.5 ◁
10	▶ 13.0
11	12.5
12	11.0
13	8.0
14	7.0 ◁
15	▶ 6.5
16	6.0
17	5.5

▶ = expected depth(b)

▷ = observed depth(c)

a: temperature profile from 6 m to 18 m in the Central basin on June 18, 1977. Temperature recorded in every meter.

b: expected depth caltulated by lowering the sampler with a length of wire $L = \frac{D}{\cos 45^{o}}$ where D= expected depth.

c: actual depth of sampler obtained by attachment of thermistor probe to sampler. Each arrow represents mean of 2 measurements.

APPENDIX C

Error estimate in sampling and subsampling.

DEPTH	SAMPLE	MEAN(a) ± S.D.	OVERALL S.D.
0-5 m	1	14.2 ± 3.3	
	2	17.6 ± 2.0	
	3	12.6 ± 1.4	± 2.9
	4	15.8 ± 2.3	
5-10 m	1	11.8 ± 1.3	
	2	12.9 ± 1.6	
	3	13.8 ± 0.7	± 3.7
	4	12.4 ± 1.9	
10-15 m	1	32.6 ± 1.1	
	2	25.6 ± 3.2	
	3	27.9 ± 2.7	± 3.7
	4	25.8 ± 2.6	
15-20 m	1	10.2 ± 2.1	
	2	16.4 ± 1.7	
	3	12.3 ± 2.5	± 3.5
	4	17.3 ± 1.6	

a: Mean of 4 subsamples.

A one way ANOVA was done on the 16 samples (4 replicates each) after normalizing the depths. No significant difference was found between the variance due to samples and that due to subsamples.

APPENDIX D

CALCULATIONS

Calculations to obtain the constants k, k' and k" used in equations 1-6 (pp. 22-23).

The relationships that yield the constants k, k' and k" are:

$$d^3/W_E = k$$

$$W_E/W_{N1} = k'$$

$$W_E/W_{N2} = k''$$

The measurements needed to obtain the constants are:

1) d: egg diameter (mm) of Diaptomus minutus

2) W_E: egg dry weight (ug) of Diaptomus minutus

3) W_{N1}: dry weight (ug) of N1 of Diaptomus minutus

4) W_{N2}: dry weight (ug) of N2 of Diaptomus minutus

1. Source and measurements of "d" of Diaptomus minutus

LAKE	SEASON	MEAN EGG DIAMETER "d"(mm)	n	
Memphremagog		.112 ± .006	24	
Knowlton*	Spring	.106 ± .003	22	
	Summer	.107 ± .004	17	
Grand Bouleaux*	Spring	.101 ± .005	25	
	Summer	.104 ± .003	20	
Brome*	Spring	.102 ± .005	12	
	Summer	.105 ± .004	12	
Overall mean diameter "d"		.105 ± .004	132	*Maly (1983)

APPENDIX D (continued)

2. W_E = 0.30 ug (Cooley, 1973)

3. W_{N1} = 0.25 ug (Cooley, 1973)

4. W_{N2} = 0.23 ug (Cooley, 1973)

The constants can now be calculated:

$k = (0.105)^3/0.30 = 3.86 \times 10^{-3}$

$k'_f = 0.30/0.25 = 1.20$

$k'' = 0.30/0.23 = 1.30$

$kk' = (3.86 \times 10^{-3}) \times 1.20 = 4.63 \times 10^{-3}$

$kk'' = (3.86 \times 10^{-3}) \times 1.30 = 5.02 \times 10^{-3}$

APPENDIX E

Calculation of cyclopoid N1 development times at a given temperature (12.4°C), using the relationship:

D_{N1}/D_E (cyclopoid) = D_{N1}/D_E (calanoid) (p. 51)

when development times (D) of calanoid N1, calanoid eggs and cyclopoid eggs are known from Belehrádek's equation:

D (hours) = $a\ (T-\alpha)^b$

Constants a, α and b for all species listed below obtained from Cooley and Minns (1978).

a) Egg development times (hours) of calanoid species at T=12.4°C.

SPECIES	a	α	b	D_E (hours)
Diaptomus denticornis	48064	-3.13	-2.06	169
D. laciniatus	6872	-2.17	-1.46	130
D. minutus	349637	-9.61	-2.51	149
D. spatulocrenatus	314446	-5.73	-2.59	173
D. oregonensis	53223	-4.48	-2.11	137

APPENDIX E (continued)

b) N1 development times (hours) of calanoid species at T=12.4°C.

SPECIES	a	α	b	D_{N1} (hours)	D_{N1}/D_E
D. denticornis	2523	-1.08	-1.62	37	0.22
D. laciniatus	2313	-3.60	-1.65	24	0.18
D. minutus	23792	-7.08	-2.19	36	0.24
D. spatulocrenatus	204552	-9.39	-2.83	33	0.19
D. oregonensis	2300251	-14.63	-3.34	38	0.28
Mean ± S.D.					0.22±0.04

c) Egg development times of cyclopoid species at T=12.4°C

SPECIES	a	α	b	D_E (hours)	D_E (days)
C.b. thomasi	18932	-4.79	-1.77	123	5.1
M. edax	556	+8.07	-0.91	147	6.1
C. vernalis	3622	-0.31	-1.45	91	3.8

d) N1 development times of cyclopoid species at T=12.4°C.

C. b. thomasi D = (0.22±0.4)x5.1 = 0.9 - 1.3 days

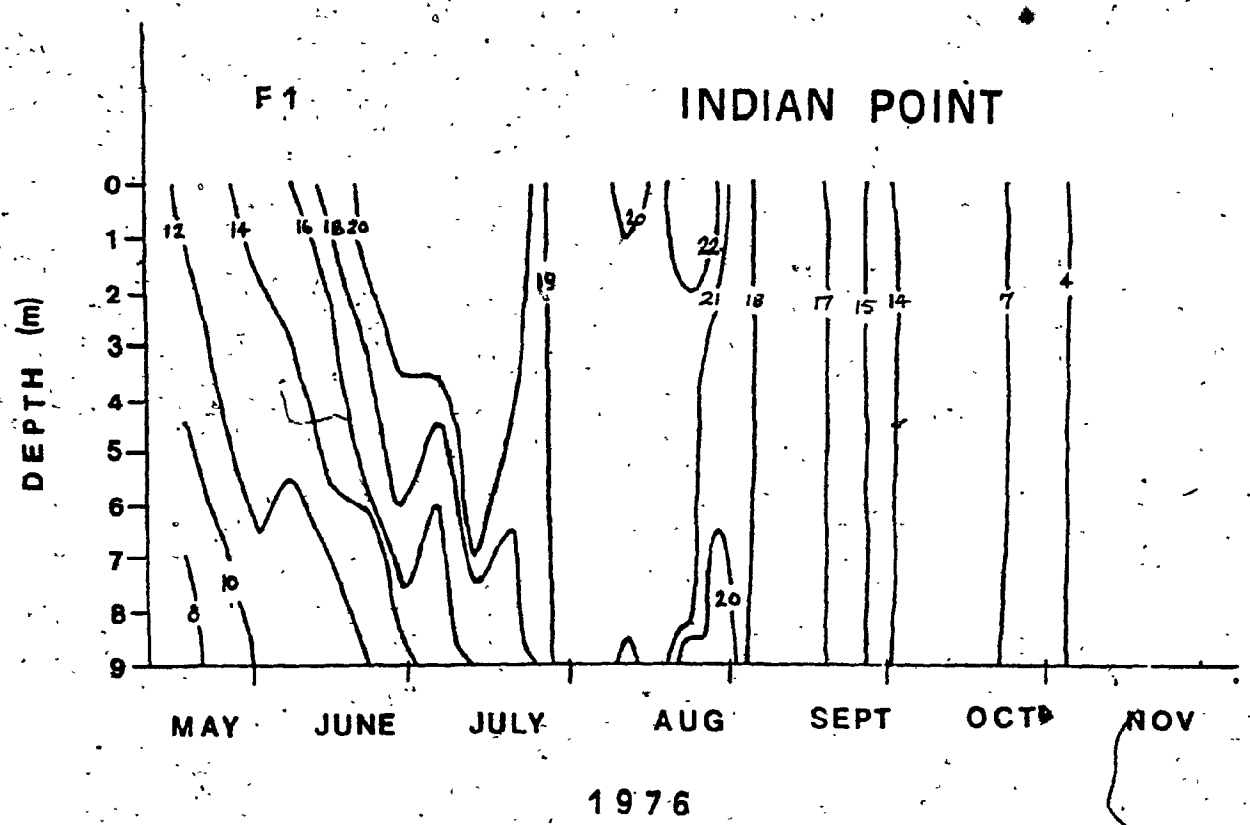
M. edax D = (0.22±0.4)x6.1 = 1.1 - 1.6 "

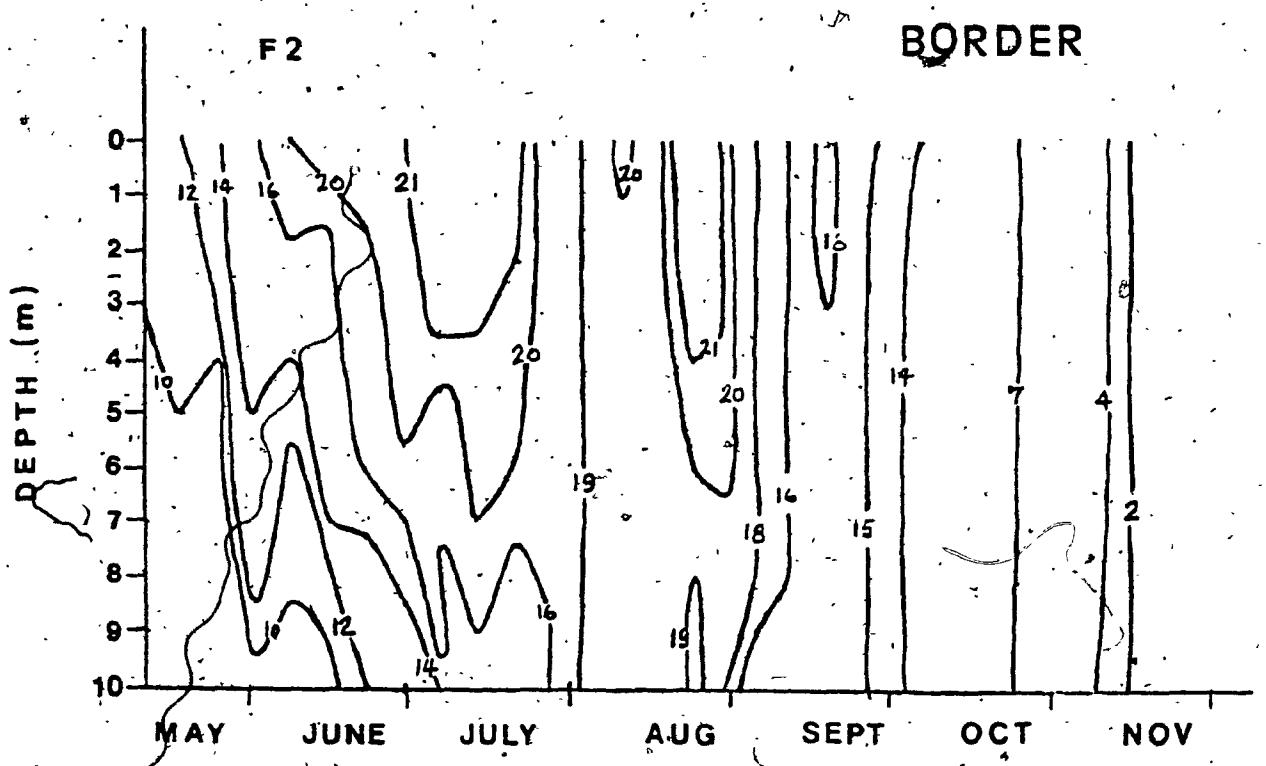
C. vernalis D = (0.22±0.4)x3.8 = 0.7 - 1.0 "

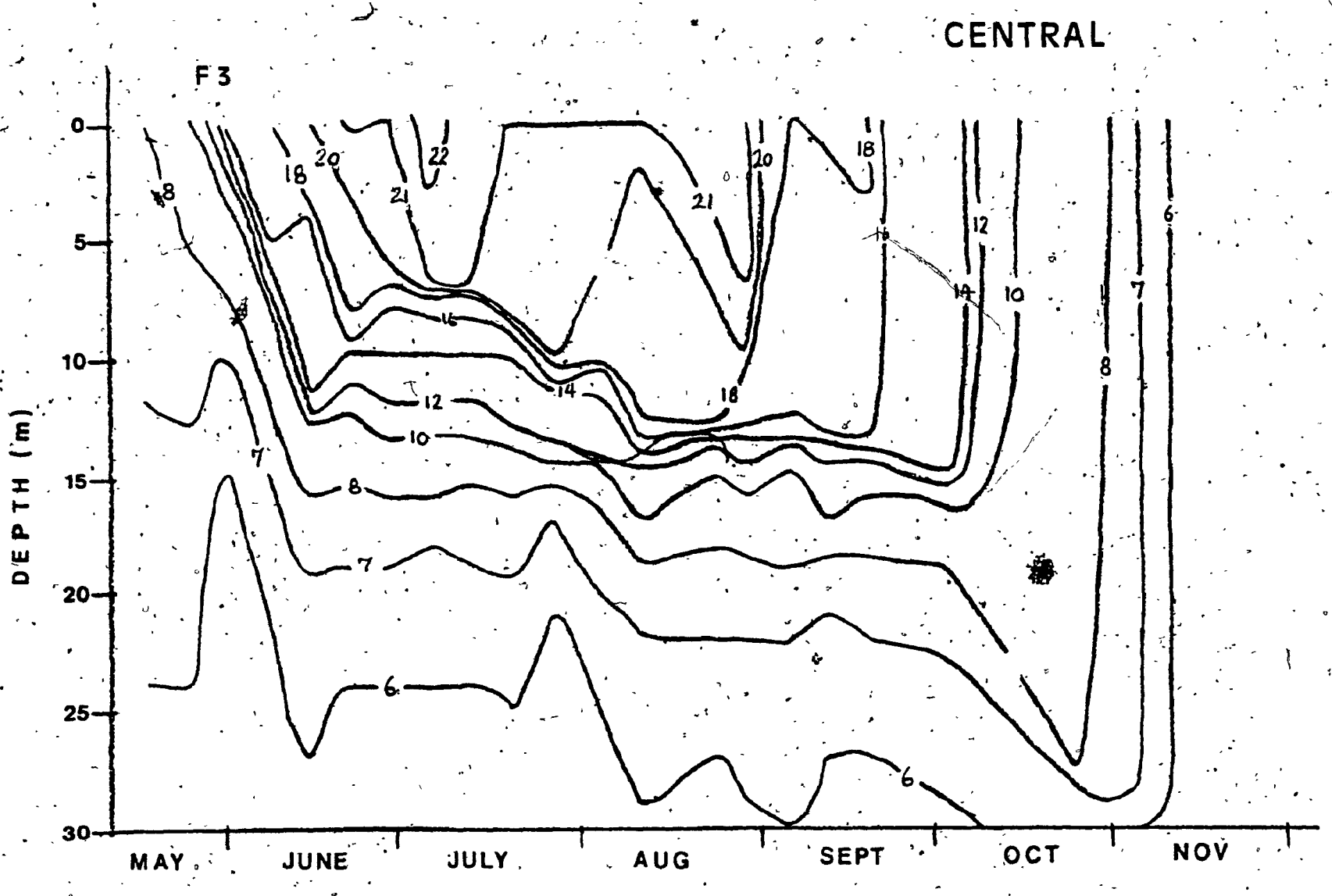
Mean cyclopoid N1 development time = 0.9 - 1.3 days.

APPENDIX F

Isotherms of 3 stations in Lake Memphremagog from May 18 to Nov. 14, 1976.


F1
INDIAN POINT
DEPTH (m)
0
1
2
3
4
5
6
7
8
9
12
14
16
18
20
19
30
22
21
18
17
15
14
7
4
10
8
20
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
1976


F2
BORDER
DEPTH (m)
0
1
2
3
4
5
6
7
8
9
10
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV


CENTRAL
F3
DEPTH (m)
0
5
10
15
20
25
30
MAY
JUNE
JULY
AUG
SEPT
OCT
NOV
1976
8
18
20
22
21
16
14
12
10
7
6