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TITLE OF THESIS. THE LIFE HISTORY, POPULATION DYNAMICS AND PRODUCTION OF <u>LEPTODIAPTOMUS MINUTUS</u> LILLJ. (COPEPODA: CALANOIDA) IN BLUFF LAKE, NOVA SCOTIA

UNIVERSITY. DALHOUSIE UNIVERSITY

DEGREE FOR WHICH THESIS WAS PRESENTED. DOCTOR OF PHILOSOPHY

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THE LIFE HISTORY, POPULATION DYNAMICS AND PRODUCTION OF LEPTODIAPTOMUS MINUTUS LILLJ. (Copepoda: Calanoida) in Bluff Lake, Nova Scotia.

by

John M. Cooley

Submitted in partial fulfilment of
the requirements for the Degree of
Doctor of Philosophy at Dalhousie
University (Fall, 1973).

Approved by: [redacted]

[redacted]

DALHOUSIE UNIVERSITY

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Department or School Biology

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ABSTRACT

The life history, population dynamics, and production of Leptodiaptomus minutus (Calanoida: Copepoda) was investigated in a small oligotrophic lake (Bluff L.) near Halifax, Nova Scotia, from Oct. of 1970 to May 1972.

An overwintering population of adults began producing subitaneous eggs in February which hatched in March to provide a first generation of animals that developed slowly and began maturing in mid-August. A second generation of animals resulted from eggs laid by these "new adults". In addition there was a small recruitment of first naupliar instars which hatched in March from diapausing eggs formed by adults in the previous fall. These latter eggs spent the winter on the lake bottom.

For purposes of analysis, recruitment and development of all individuals were divided into 3 cohorts. A crude estimate of survivorship in each instar was obtained for each cohort using a new graphical method of analysis developed by Rigler and Cooley. Mortality was greatest from May through October and was most likely due in part to predation by Epischura nordenskioldi and Mesocyclops edax.

Production expressed as dry weight was estimated for each of the 3 cohorts using the survivorship estimates from Rigler and Cooley's method as well as 3 other methods referred to as Allen curve method, Soviet graphical method, and death rate method. In general there was good agreement in production estimates among the 4 methods.

Information was also collected on subitaneous and resting egg development, and first naupliar development as related to temperature for L. minutus and a larger less numerous congener also in Bluff L. Aglaodiaptomus spatulocrenatus.

ACKNOWLEDGEMENTS

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My dedicated and capable assistants, Harold Birnbaum, Stephanie Guildford, and Aileen Waller made it possible to complete the study in 1973. Without their expertise I would most likely still be counting copepods.

Other friends and colleagues provided field assistance at various times during the course of the investigation. Wayne Stobo, Ken Ross, John Railton, Pierre Brien, John Underwood, Jeremy Gay, and John Pringle. The last of the aforementioned deserves a special thanks for venturing onto 2" thick ice to help me get those critical April samples, and then pulling me out.

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INTRODUCTION

Ecological research is undertaken with the ultimate hope and view that if enough information was acquired on the dynamics of processes occurring in ecosystems, it would be possible to manipulate them confidence and predict the consequences of our actions. Some workers (Andrewartha 1961) see the problem reduced to an ability to predict the numbers and forms of organisms occurring in space and time. Lindeman (1942) in recognizing "the ecosystem is.....the more fundamental ecological unit" suggested that in dealing with organisms they first be grouped according to their mode of obtaining energy: primary producers, secondary producers, tertiary producers, etc., each group being "more or less discrete" and representing a trophic level. He pointed out that the energy content of any level is in a state of constant flux, continually receiving energy from the previous level and passing a portion on to the next trophic level. Since this trophic-dynamic approach to ecosystem analysis has had wide acceptance from European as well as North American workers it seems reasonable to assume that its progressive development will in the future depend directly on the ability to clarify processes of production. Thus the stated aim of the freshwater section of the recently completed five year International Biological Program (IBP) was "to study the basic factors of production and metabolism at all trophic levels in representative standing and running waters" (Anonymous 1967). However Rigler in a recent discussion of the adequacies and inadequacies of the IBP program (Rigler 1972a) pointed out that the predictive ability desired by ecologists and environmental planners will result from useful scientific theories which at present are in short supply. He also noted that theories derived from erroneous data are unlikely to provide the predictions needed.

If Rigler's statement is correct then the foundation of theoretical ecology will be laid by the accumulation of goal oriented data and not by the mere accumulation of facts which he points out is common in much of the present ecological literature. Andrewartha (1961) suggests three levels of complexity at which ecological studies should be focussed. The first level concerns the physiology and behaviour of the individual, the second populations, and the last communities. Although ecologists are working at all levels, it has become apparent that in the limnetic environment a lack of knowledge of the life cycle and ecology of most species is one barrier between us and the generalizations we seek. Limnologists, particularly in North America, have attempted to obtain ecological generalizations without knowing the role of individual species in the community or the natural history of these species. Recently McLaren (1969) concluded that "zooplankton production cannot be measured or explained without detailed quantitative studies of life histories."

In the present study I have attempted to obtain quantitative information on the life history, population dynamics, and production of a single freshwater calanoid copepod, _Leptodiaptomus minutus_, in a temperate lake. _Leptodiaptomus minutus_ is a logical choice for a quantitative study because it is very common in north temperate lakes, being a numerically important constituent of the great lakes (Davis 1961, Patalas 1969), and frequently a dominant inhabitant of smaller lakes in both Northern and Southern Ontario (Rigler and Langford 1967, Patalas 1971). Wilson (1959) lists its range as north to the Northwest Territories, Iceland, and Greenland, west to Wyoming, south to North Carolina, and east to the Atlantic coast of Canada and the U. S. A. Recently Davis (1972) stated that in Newfoundland lakes _L. minutus_ appeared to be the most important of the zooplankters.

Perhaps it is because of its wide range that a body of information already exists concerning its size, spatial and temporal distribution, vertical migrations, congeneric occurrences and breeding habits (Langford 1937, Rigler and Langford 1967, Sandercock 1967, Turvey 1968, Carter 1971, Patalas 1971, Schindler and Noven 1971, Cunningham 1972). These pre-existing data not only provide a foundation of information to plan and work from but also permit a more general explanation of the significance of results from an in-depth study.

Ultimately the trophic-dynamic analysis of a single species population requires information on abundance of animals over time. These data are then converted into units of biomass and perhaps energy using some conventional empirically derived conversion factor. Because the errors associated with this latter step are probably small compared with the problem of accurately estimating population sizes I will concentrate further discussion on this latter point. The term production will be used as defined by Ricker (1968) as an increase in biomass of individuals of a population occurring in a given period of time but not necessarily surviving to the end of that period. Under this definition the term production is viewed as having the same meaning as "net production" in the sense of previous authors who considered it necessary to distinguish between "net" and "gross" production, the latter including not only the growth increment but also metabolic energy lost because of respiration and egestion (Winberg 1971). Under recent IBP guidelines the terms "production" and "net production" are viewed as synonymous (Mann 1971).

Under this definition the concept of secondary production becomes conceptually simple and reduces to summing growth increments of all members of a given population for all populations (i.e. species) in a community over time. In practice however the task can be quite formidable because of the dynamic nature of zooplankton populations. Mortality and often reproduction are continuous but rarely do rates of change remain constant for extended periods of time. Freshwater temperate copepods such as Diaptomus spend less than a day in some of the early naupliar instars making it possible for a part of the population to enter and leave the zooplankton community before they have had a chance to be sampled. If for example the first stage of a zooplankter has a population size of X individuals on two consecutive sampling days the possibilities exist that A) there has been no recruitment to that instar during the sampling interval, B) the population has entirely replaced itself in the interval, or C) a situation between A and B has occurred. Production in the last 2 cases will be significantly higher than in the first but unless there is some information available on the amount of time spent in that instar it cannot be determined. Unfortunately obtaining instar development times is generally difficult and at the very least expensive and time consuming. Methods which can estimate animal numbers without tedious laboratory culturing will necessarily be useful to both population and production ecologists working in freshwater.

The genus Diaptomus contains 78 North American species but on the basis of morphological criteria can be further divided into a number of subgenera (Wilson 1959). Two subgenera contain the 2 species of Diaptomus found in Bluff Lake, Leptodiaptomus minutus and Aglaodiaptomus spatulocrenatus, which I will subsequently refer to as L. minutus and A. spatulocrenatus. As more data are accumulated on N. American species these subgenera as taxonomic units may become more meaningful in discussions of congeneric competition.

In development, diaptomids hatch from an egg and pass through 6 naupliar instars here designated with Arabic numbers and a capital N (i.e. N1 to N6) and 6 copepodite instars designated with Roman numerals and a capital C (i.e. CI to CVI). The last copepodite instar is more usually referred to as the adult instar, either male or female.

MATERIALS AND METHODS

1. Bluff Lake

Most of the information on L. minutus came from the population inhabiting Bluff Lake (W. 63^{o} 39', N. 44^{o} 33', Figure 1) which is located approximately 11 km. west of Halifax, Nova Scotia, and has been briefly described and studied on several past occasions (Hayes et al 1952, Gorham 1957, Ogden 1972). It is a kettle lake located in a drumlin field whose soils are derived from Wolfville till and support a mixed second growth hardwood-spruce woodland approximately 60 to 80 years old. The bottom of the lake contains large areas of mud and towards mid-summer large patches of waterlily (Nuphar sp.) are visible on the surface around most of the lakes perimeter.

In past years Bluff L. was used as a baseline indicator for disturbed lakes in the area because it was oligotrophic, very clear, and its watershed was undisturbed, but recently extensive forest clearance of a drumlin along the northeast edge has allowed large quantities of silt laden runoff to enter the lake. As a result transparency has decreased dramatically (Table 1). In 1949 and 1970 a Secchi disc was clearly visible on the bottom in the deepest spot (approximately 7m) but after a large storm (Hurricane Beth) on Aug. 15 and 16 in 1971 on subsequent days the disc disappeared at depths less than 2.2 m and water colour had a distinctive muddy appearance but dissolved oxygen concentrations in the thermocline and below were still only slightly less than the saturated epilimnetic waters. A brief summary of the chemical characteristics of Bluff L. is presented in Table 2 to show its oligotrophy, and volumes of various strata sampled for zooplankton are presented in Table 3.

FIGURE 1

A contour map of Bluff L. (after Hayes et al., 1952).

The five major sampling stations are marked with capital letters.

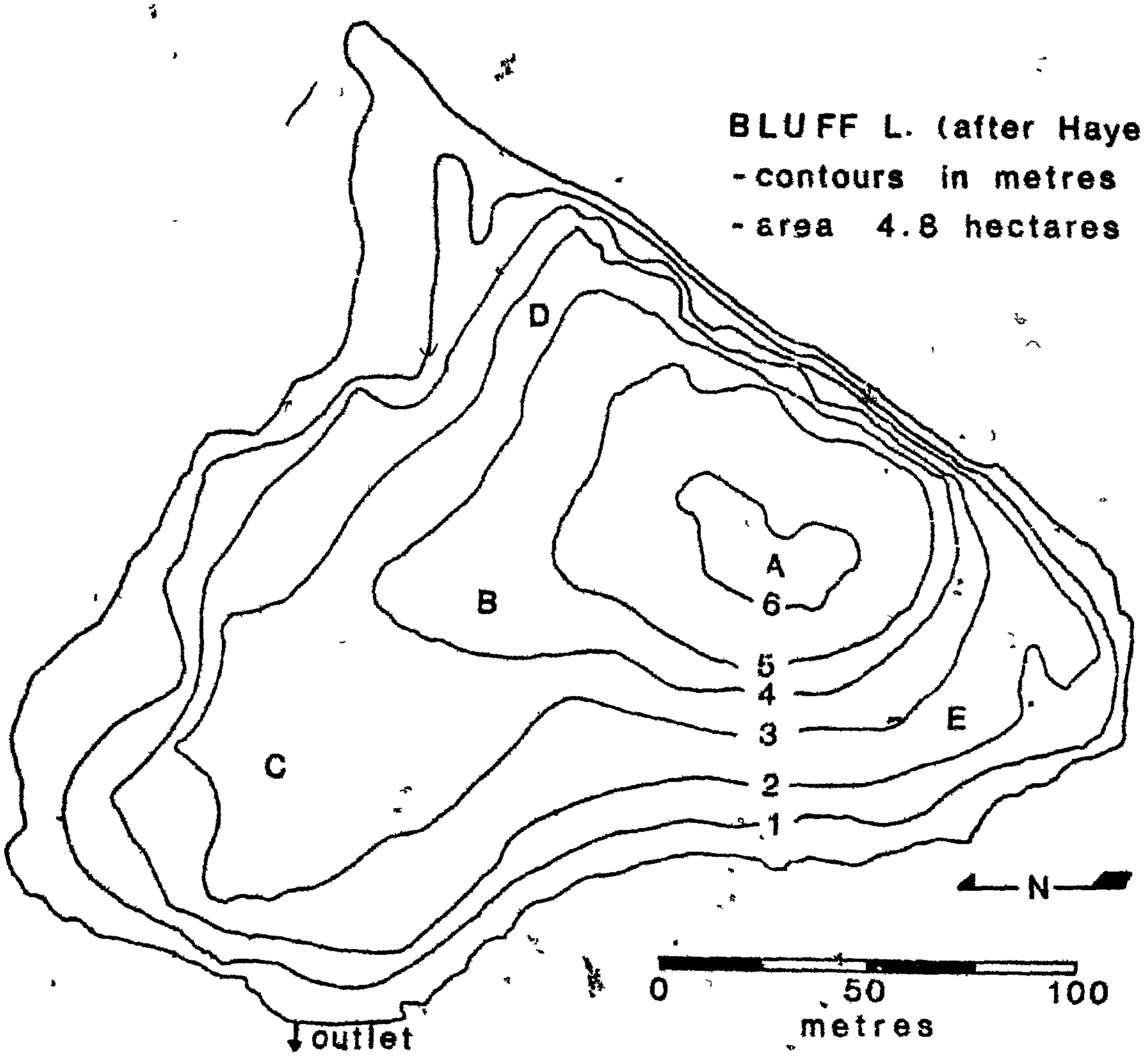

BLUFF L. (after Hayes et al, 1952)
-contours in metres
-area 4.8 hectares
A
B
C
D
E
6
5
4
3
2
1
N
0
50
100
metres
outlet

TABLE 1

Seasonal changes in the transparency of Bluff L. water as indicated by the depth of disappearance of a 25 cm. diameter Secchi disc. All readings were taken at the deepest spot in the lake and are expressed in metres.

Summer 1949*	Summer 1970	Aug. 1 1971	Aug. 17 1971	Aug. 21 1971	Aug. 25 1971	Sept. 3 1971
7 bottom	7 bottom	4.3	0.3	0.5	0.7	0.9

Sept. 8 1971	Sept. 16 1971	May 7 1972
1.2	1.3	2.0

On August 15 and 16, 1971, approximately 20 to 25 cm of rain fell on Bluff L. as Hurricane Beth passed over the Halifax-Dartmouth area.

*(from Hayes et al 1952)

TABLE 2

A summary of various chemical parameters of Bluff L. (after Gorham 195~~7,~~ and Ogden 1972).

	PARTS PER MILLION								
	Na	K	Ca	Mg	Cl	SO_4	Soluble PO_4	Cond.[1]	pH
Gorham, 1955 winter	4.9	.3	.9	.6	8.1	4.5	-	39	5.3
Ogden, 1971 summer	3.6	.3	.8	.6	8.0	4.5	.01	25	6.8

[1] conductivity expressed as micromhos/cm at 20°C

TABLE 3

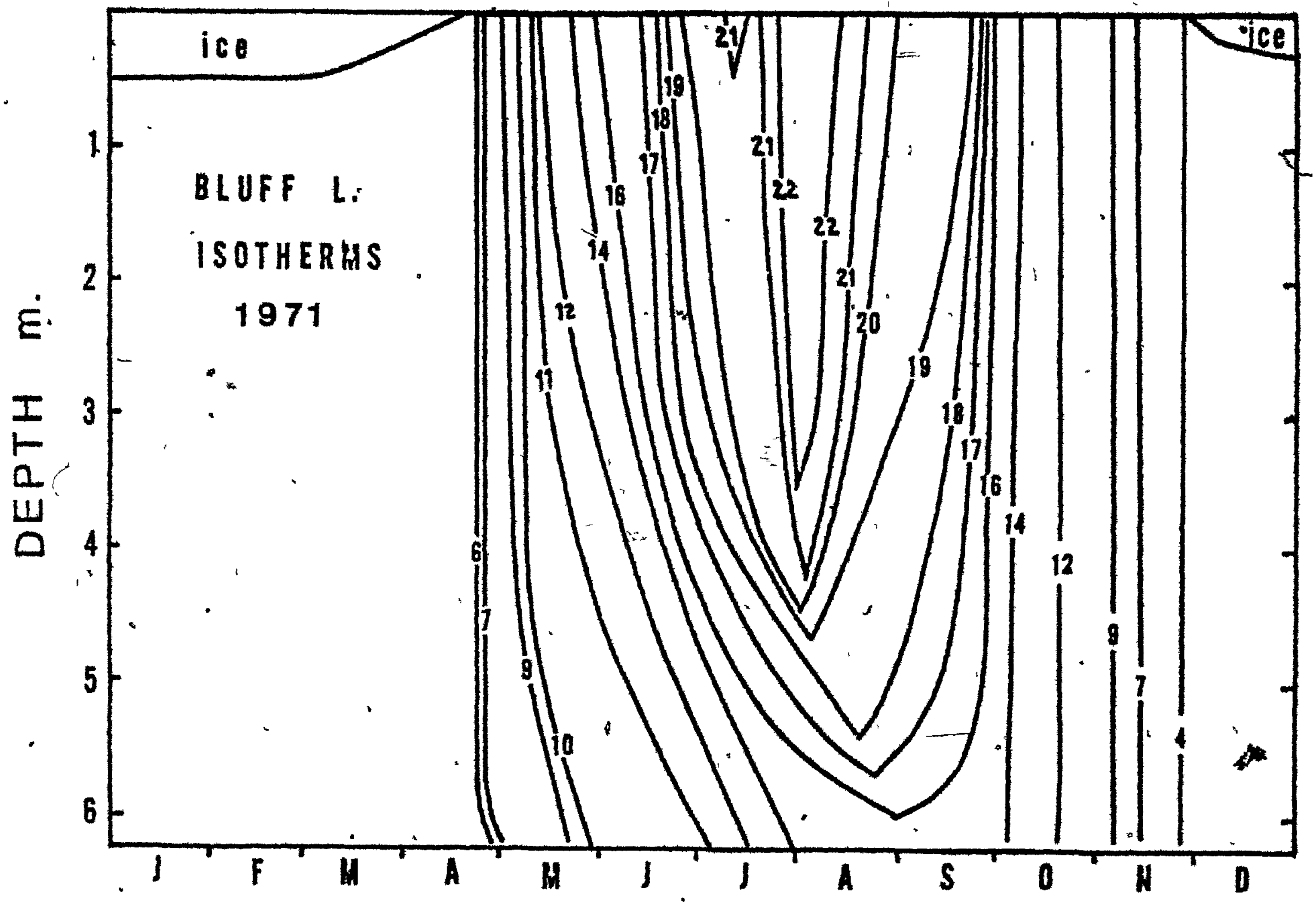
Volumes of various strata sampled in Bluff L. These figures are based on the area of the contours in Fig. 1.

Contour (m)	Area (hectares)	Volume (x10^7 litres)
Surface	4.84	
		2.28
0.5	4.39	
		2.06
1.0	3.94	
		1.86
1.5	3.59	
		1.69
2.0	3.23	
		1.47
2.5	2.73	
		1.23
3.0	2.23	
		0.97
3.5	1.71	
		0.71
4.0	1.19	
		0.52
4.5	0.91	
		0.38
5.0	0.64	
		0.25
5.5	0.38	
		0.11
6.0	0.11	
		0.04
6.5	0.06	
		0.01
7.0		
Total Volume		13.58

FIGURE 2

Isotherms (°C) for Bluff L. at the deepest point in 1971.

Approximately 75% of Bluff L. is above 4m and remains unstratified throughout the year. Due to equipment failures temperatures were not recorded beneath the ice.


BLUFF L.
ISOTHERMS
1971
ice
ice
DEPTH m.
1
2
3
4
5
6
J
F
M
A
M
J
J
A
S
O
N
D
6
7
9
10
11
12
14
16
17
18
19
21
21
22
22
21
20
19
18
17
16
14
12
9
7
4

2. Sampling of Bluff L.

Quantitative samples of the limnetic zooplankton in Bluff L. were taken from Oct. 17, 1970 to May 19, 1972 using a ½ metre high 32 litre transparent trap (Schindler 1969) with a 75 micron opening nylon mesh from a small boat anchored at various stations on the lake. Sampling throughout the late fall was approximately every 6 to 7 days, throughout winter prior to ice breakup once or twice a month, every 5 days in May, and throughout summer and early fall every 4 days. On most days samples were taken at 5 fixed stations (see Fig. 1) but occasionally fewer stations were sampled during the winter of 1970/71 and especially when the ice was thin. On all days the entire water column was sampled to within ½ metre of the bottom at each station and preserved in a 4% solution of formaldehyde. Temperatures were routinely recorded throughout the water column (Fig. 2) using either a YSI thermistor (Yellow Springs Instrument Co.) or a Whitney thermistor (Whitney Co.) in the deepest part of the lake. In all a total of over 2300 thirty-two litre Schindler trap samples were collected and analysed.

3. Counting of Preserved Samples

a. *Leptodiaptomus minutus*

In order to obtain estimates of the size of the *L. minutus* population preserved samples were analysed quantitatively in a small, homemade counting cell measuring 6 cm x 4 cm x 1 cm containing a bottom grid with a Wild M5 binocular dissecting microscope (Wild Co.). For most sampling days all 32 litre trap samples from a given stratum were combined, diluted to a known volume of either 50, 100, or 150 ml, thoroughly mixed and then subsampled with a 5 ml Hensen-Stempel pipette (Wildco Co.). This 5 ml aliquot was then emptied into the counting cell and thoroughly mixed before a portion was counted and recorded to instar. In general counting was continued until a minimum of 100 nauplilar instars had been recorded or if few nauplii were present until 100 copepodites excluding adults had been identified. For several sampling days each sample from each stratum was diluted, subsampled, and counted in a similar manner. On some days an entire 5 ml aliquot was staged for the adult instar when specific calculations depended on very accurate estimates of adult numbers. Final estimates of all zooplankters are expressed as numbers per square metre of lake surface area (Appendix 1).

b. Other Zooplankters in Bluff L.

Quantitative estimates of the abundance of other limnetic species were obtained from almost every other series of quantitative 32 litre trap samples. Less emphasis was directed toward these species because they were numerically minor constituents of the zooplankton as compared with L. minutus. On most days the entire sample from a given stratum was identified for the categories of species listed in Table 4. Often, although such a sample represented 160 litres of filtered lake water (i.e. a 32 litre trap sample from a given depth at each of 5 different stations) the numbers were still quite low.

4. Dry Weights

Estimates of the dry weight of various instars of L. minutus and A. spatulocrenatus were made at various times throughout 1971 and 1972. Live animals from Bluff L. plankton tows no older than 2 or 3 days were lightly anaesthetized using a saturated solution of chloretone and removed individually to previously tared aluminum boats, dried for 24 hours in an oven at 60°C, and weighed on the 1 mg scale of a Cahn G-1 electrobalance (Cahn Instrument Co.). The number of animals per boat was never less than

TABLE 4

Categories of zooplankton identified in addition to *L* *minutus* from quantitative Bluff L. samples.

SPECIES	CATEGORIES IDENTIFIED
Aglaodiaptomus spatulocrenatus	total adults, females with egg sacs
Epischura nordenskioldi	total adults
Mesocyclops edax	total copepodites (CI to Adult)
Daphnia pulex	all individuals
Bosmina longirostris	all individuals
Diaphanosoma brachyurum	all individuals
Holopedium gibberum	all individuals

In addition, other very minor constituents of the limnetic zooplankton that appeared infrequently in samples were:

Leptodora kindtii

Polyphemus pediculus

Tropocyclops prasinus

Chaoborus sp.

Very few rotifers were seen in preserved samples most likely due to the fact that a 75 μ mesh opening would let many of the smaller forms through during filtering.

50 for some of the larger *L. minutus* instars and usually much larger for the smaller instars.

5. Development of *L. minutus* and *A. spatulocrenatus*

Estimates of development time were obtained at 6 temperatures for the egg and first naupliar instar of both *L. minutus* and *A. spatulocrenatus*. A fresh plankton sample containing egg carrying females from Bluff L. was anaesthetized with a few drops of chloretone solution in a small petri dish. Those eggs judged to be in an early part of the cleavage cycle and therefore only a few hours old at most (Appendix 2) were removed from the female with a fine pin and immediately transferred using an Irwin loop (Sargent Welch Co.) to a glass vial containing a few ml of filtered Bluff L. water and placed in constant temperature (± 0.1 °C) water bath.

Because of a paucity of egg bearing females of *A. spatulocrenatus* even in concentrated plankton samples, it was often necessary to isolate adult females and adult males in small aquaria at room temperature and allow them to breed. The aquaria were checked often and any females which had formed egg sacs were removed and treated as above. The vials were checked regularly (i.e. approximately every 20 to 30 minutes) as hatching time approached and in most cases the time to 50% hatch was recorded. Often first nauplii hatching from incubated eggs were allowed to develop into the second instar. In these experiments subtraction of time of hatch from time of first ecdysis provided direct estimates of NI development time.

6. Diapause Experiments

a. The Onset of Diapause in *L. minutus* and *A. spatulocrenatus*

The onset of diapause in eggs of *L. minutus* and *A. spatulocrenatus* was examined by removing egg sacs from females collected from fresh live Bluff L. plankton tows and incubating them at 17 °C ± 1 °C. Records were kept of the number of egg sacs that did not hatch and/or were judged to be dead from groups of eggs collected from Aug. 30 through Oct. 17, 1971.

b. Diapause Development

A preliminary investigation was begun on the effect of temperature on the development of diapausing eggs of L. minutus and A. spatulocrenatus. Diapausing eggs were collected from fresh plankton samples and were incubated under various temperature regimes over varying periods of time from Sept. 1971 to June 1972. For experiments involving A. spatulocrenatus egg sacs, incubation occurred in a single vial containing approximately 25 to 30 ml of filtered Bluff L. water while for experiments involving L. minutus each egg sac was incubated in a separate small vial containing several ml of filtered lake water. The temperatures of incubation depending on the regime followed were as follows: 4 ± 0.5 °C, 8 ± 0.5 °C, and 13 ± 1 °C. Fluorescent lights from normal room lighting were used where the experiment called for development to occur in a lighted environment.

c. Dropping of Diapausing Eggs by L. minutus

In late October L. minutus carrying resting eggs were collected from fresh live plankton samples and isolated in 8 dram glass vials of filtered Bluff L. water at 13 ± 1 °C. The vials were checked daily and records were made of the time taken for each egg sac to be dropped.

d. Diapausing Eggs Caught in Sediment Traps in Bluff L.

In order to estimate the number of diapausing eggs that were being deposited by L. minutus in nature, pairs of 30 cm high cylindrical sediment traps (opening 78.5 cm^2) were anchored approximately ½ metre above the bottom at each of the 5 main sampling stations in Bluff L. A line was attached to a small float near the surface and to the middle of the inside bottom of the trap by means of an eyebolt. The trap was kept vertically in place by a 20 cm square floatation collar of 2.5 cm thick styrofoam sandwiched between 2 pieces of 1.5 cm thick plywood and by a 1/2 metre line joining a common building brick and the bottom of the trap. The traps were emptied by raising them vertically at a slow constant speed from a small boat. The contents of each trap were filtered through a 75 micron opening nylon filament sieve and preserved with a 4% solution of formaldehyde. In the laboratory each sediment sample was individually washed with a saturated solution of $MgSO_4$ into a 50 ml centrifuge tube and spun at low speed for 2 minutes. The resulting supernatant was sucked into a large mouth pipette and emptied onto a 75 micron opening nylon filament sieve. The material caught by the sieve was washed with a 4% solution of formaldehyde into a counting dish and examined under a compound dissecting microscope.

7. Sampling for Zooplankton in Other Lakes

From mid-June through early Sept. of 1971 a total of 38 lakes within a radius of 20 km of Halifax were sampled with a 75 micron opening nylon filament townet 25 cm in diameter to obtain qualitative estimates of the calanoid copepods present. The lakes visited together with information on morphometry are presented elsewhere (Table 10, page 43) Subjective decisions were made on the relative abundance of the four species of calanoids found locally (L. minutus, A. spatulocrenatus, Epischura nordenskioldi, and Epischura lacustris) to all other zooplankters present in the sample. These data were first presented by Cooley, and by Ogden in a report to the Metropolitan Area Planning Commission of the Halifax-Dartmouth area (Ogden, 1972) but have been recalculated for presentation here.

8. Calculation of Population Statistics Using the Graphical Method of Rigler and Cooley

Southwood (1963, page 279) has shown that "crude" estimates of the number of individuals passing through a given instar can be obtained by dividing the area (in units of animal-days) of the curve of instar abundance plotted against time by the length of time spent in that instar. This last statistic is usually derived from laboratory studies relating temperature and development time and applied to the environmental temperature experienced by the population. However for calanoid copepod instars exclusive of egg and first nauplius, development is not exclusively dependent on temperature and development times are also dependent on food availability and nutrition (Eichhorn 1957, Cooley 1970). For these later instars in particular it would be desirable to infer development times from some property or properties of the population. If samples in the field were frequent and representative enough one could use the interval between the appearance of the first individual of instar *n* and instar *n*+1 as an estimate of development time for instar n, but since some naupliar instars have an existence of less than a day and the required precision of sampling has never been achieved this method has been rejected. Instead a method was chosen which used all of the sampling days in both instar *n* and *n*+1 in order to estimate t_n (the development time of instar n).

The statistic needed for the calculation is called the "mean pulse time" (M_n) and is defined as the abscissa (in this case day number) of the center of gravity of that pulse. A pulse here is defined as the increase and decrease in numbers of an instar as animals pass through it and a cohort is defined as members of a population that are born within a specified period of time. As will be described later some subjectivity is used in naming pulses and cohorts and where generations overlap a pulse may be an arbitrarily chosen maximum in the curve of abundance with time.

The basis of this method is illustrated in Fig. 3 which shows a cohort of one animal passing through 2 instars. The difference between the mean pulse time of the 2 successive instars ($M_{n+1} - M_n$) is equal to half the time spent in both instars.

$$M_{n+1} - M_n = \tfrac{1}{2}(t_n + t_{n+1}) \qquad \text{Equation 1}$$

In this simplest of cases the pulse is symmetrical so that the mode, median and mean of the pulse are identical. It can be shown graphically that for individual cases of skewed pulses the same relation is true. In using this equation two assumptions are made neither of which is likely to be verified.

ASSUMPTION 1: mortality of each instar is uniform and symmetrically distributed about the mean pulse time

ASSUMPTION 2: development time of an instar remains constant throughout the pulse

Analysis of population data for the complete life history of a copepod cohort yields a series of equations listed below in which the number of unknowns is one more than the number of equations, preventing direct solutions.

$$M_{N2} - M_{N1} = \tfrac{1}{2}(t_{N1} + t_{N2})$$

$$M_{N3} - M_{N2} = \tfrac{1}{2}(t_{N2} + t_{N3})$$

....

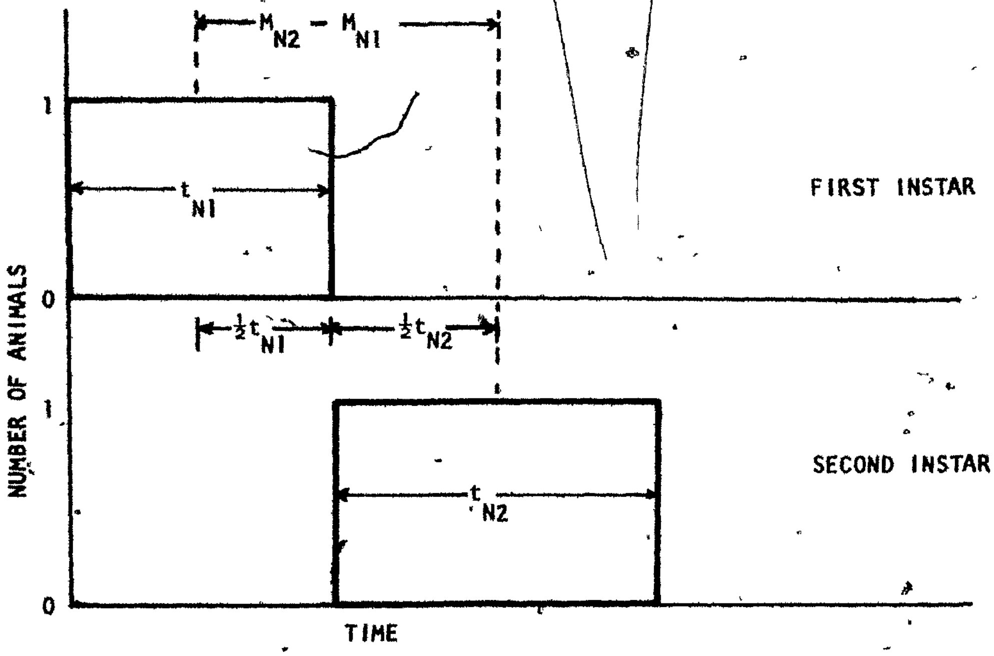
....

$$M_{CV} - M_{CIV} = \tfrac{1}{2}(t_{CIV} + t_{CV})$$

Depending on data available one can proceed to solve these equations in a number of ways. If the development time of any instar has been measured this value can be substituted into the appropriate equation and all other equations can then be solved. With calanoid copepods this development time

FIGURE 3

A diagrammatic representation of a pulse of 1 animal passing through the first two instars.



$$M_{N2} - M_{N1} = \tfrac{1}{2}(t_{N1} + t_{N2})$$

M = mean pulse time
t = development time

It can be shown graphically that this relation holds true for a skewed pulse of many animals.

should be for the first naupliar instar since it does not feed and its development time is a function of temperature. Lacking I development time an iterative approach can be used by guessing at I development time and then solving for all others. If the guess underestimates the duration of the instar then the calculated time generated for the following instar by solution of an equation will be an overestimate of its true duration and so on. Since the total number of animals passing through an instar is directly related with the area under the curve of numbers plotted against time (hereafter referred to as the area under the numbers curve) then the sign of errors in population estimates will be opposite to the duration estimates. If inspection of the results shows negative mortality to be excessive (a somewhat subjective decision) then a new time is chosen and this procedure is continued until negative mortality is minimized.

Although this method uses all of the data, sampling may still have been inadequate. On several occasions the calculated mean pulse time (M_n) of one instar came after the mean pulse time of the next instar (M_{n+1}). This could have been caused by heavy mortality of animals late in the cohort as they moulted into the next instar but in the absence of such information it is assumed that this is the result of inadequate sampling and that

ASSUMPTION 3: the duration of each instar is equal to or longer than the preceding instar.

Therefore the difference between successive mean pulse times should either be constant or increase. If a smooth curve is drawn through calculated differences in mean pulse times then values read from this curve can be used in subsequent calculations (i.e. these differences are the solutions to the left hand side of Equation 1). In practice it may be first necessary to smooth out a curve of M_n's plotted against instars (see Fig. 10). The areas under the numbers curves for each instar were determined by joining datum points with straight lines and using the trapezoidal method to calculate the area under the constructed polygon.

To calculate the day when the centre of gravity occurs (the mean pulse time, M_n) the products of number of animals x day number were summed at regular intervals of one day and divided by the summed number of animals as illustrated below:

$$M_n = \frac{\sum \text{number of animals x day number in the year}}{\sum \text{number of animals}}$$

The division of the area under the numbers curve by an average instar development time (t_n) will yield numbers of animals that:

a. will be an estimate of the total number of animals that entered the instar if there is no mortality or if mortality occurred at ecdysis

b. approximate the total size of the population reaching the median age of the instar ($\frac{1}{2}t_n$) if mortality is constant over the stage.

For simplicity and subsequent calculations I will assume that the situation in b is most closely approximated in nature and refer to these estimates as the number of animals passing through an instar.

RESULTS AND DISCUSSION

1. Cohorts of L. minutus in Bluff L.

Freshwater zooplankton in general and calanoid copepods in particular have a variety of life patterns which have been defined by Hutchinson (1967). An organism exhibiting a single generation in a year is said to be univoltine, and one having several generations is said to be multivoltine. Analysis of population statistics will necessarily be more complicated in the latter case if there are members from two or more generations coexisting at the same time.

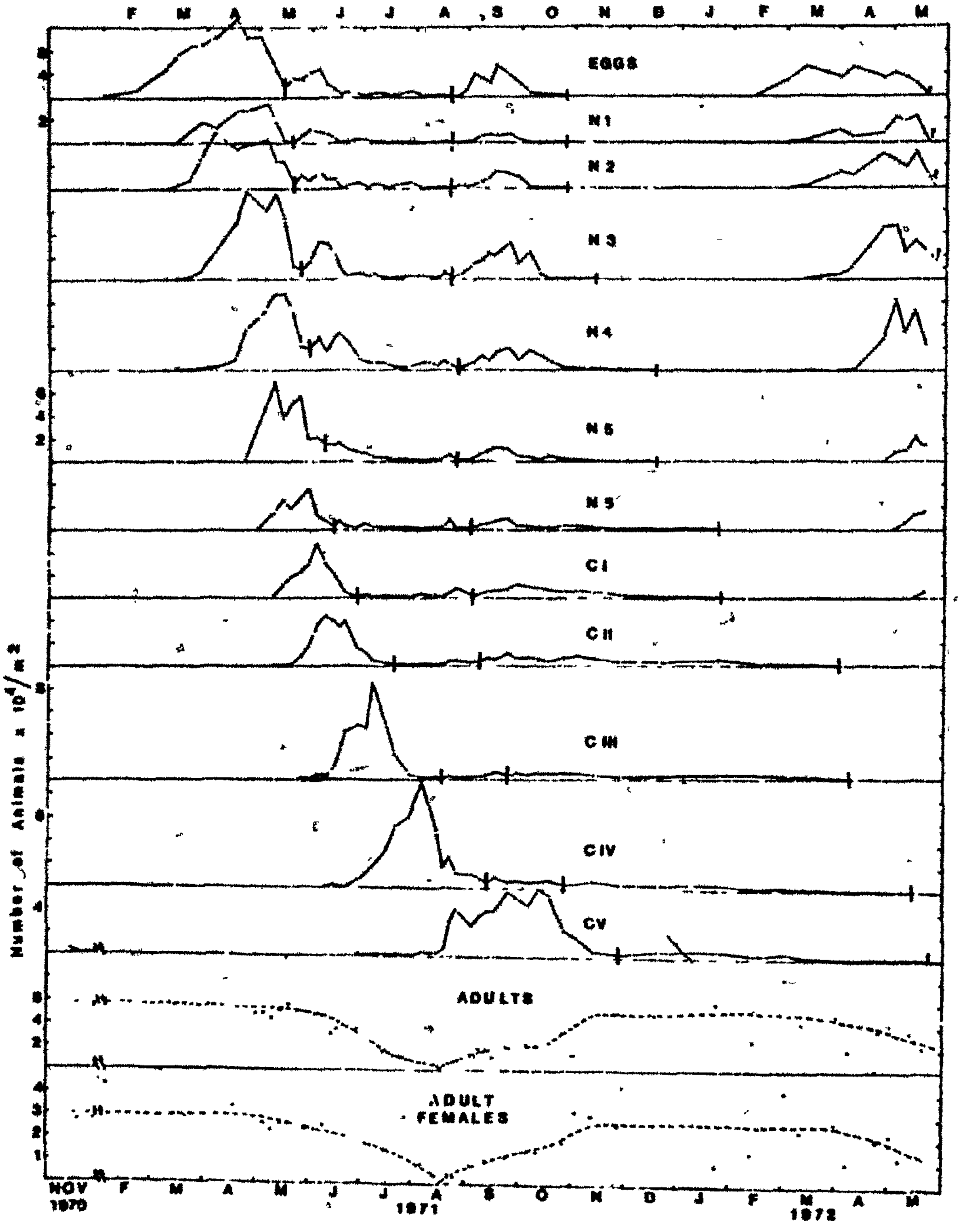
The L. minutus population in Bluff L. is multivoltine. First nauplier instars appear in early March (Fig. 4) and begin a slow process of development through five more nauplier instars and six copepodite instars (CI to CV plus adult). The adult instar is a breeding stage and first appears in August. Recruitment from prexisting overwintering adults in the form of nauplii hatching from subitaneous (non diapausing) eggs is continuous from Feb. until mid-October when all eggs produced become diapausing (often referred to as resting eggs) and with hatching of the last subitaneous eggs in early October nauplier instars begin to sequentially disappear completely from the lake (Fig. 4).

Inherent in any set of population data are variations resulting from sampling inadequacy. In some instances it is possible and desirable to correct deviations from trends before analyses are carried out. In 1970 and 1971 the overwintering adult population of L. minutus consisted almost entirely of adults with no effective recruitment from CV instars occurring (see Fig. 4). In this instance the population of adults can only remain the same or decrease and a best estimate of adult numbers over time can be made by using all the data and drawing a smooth curve through daily estimates of adult numbers (Fig. 4, bottom). The small

FIGURE 4

Population dynamics of L. minutus in Bluff L. from November 15, 1970 to May 19, 1972.

All numbers are expressed as x$10^4/m^2$ surface area. Subsequent calculations requiring estimates of either female or adult abundance were taken from smooth curves drawn by eye through data points. The curve of egg abundance (top row) was determined using the "smoothed" estimates of female abundance together with empirically derived estimates of eggs/sac and percent females with eggs. The vertical bars represent the end of one cohort and the beginning of the next.


F M A M J J A S O N D J F M A M
EGGS
N1
N2
N3
N4
N5
N5
CI
CII
CIII
CIV
CV
ADULTS
ADULT FEMALES
Number of Animals x 10^4/m^2
8
4
2
6
4
2
8
6
4
6
4
2
4
3
2
1
NOV 1970
F M A M J J A S O N D J F M A M
1971
1972

amount of scatter about this curve suggests sampling was adequate for purposes of indicating population trends. A similar smooth curve was drawn through estimates of total females and together with "corrected" values read from this curve and empirically derived estimates of viable eggs per female and percent females bearing eggs (Fig. 5) a curve of egg numbers versus time was constructed (top panel in Fig. 4). All subsequent calculations involving eggs and adults used these smoothed values read from the curves. Unless otherwise stated calculations involving all other instars used the original "unsmoothed" data.

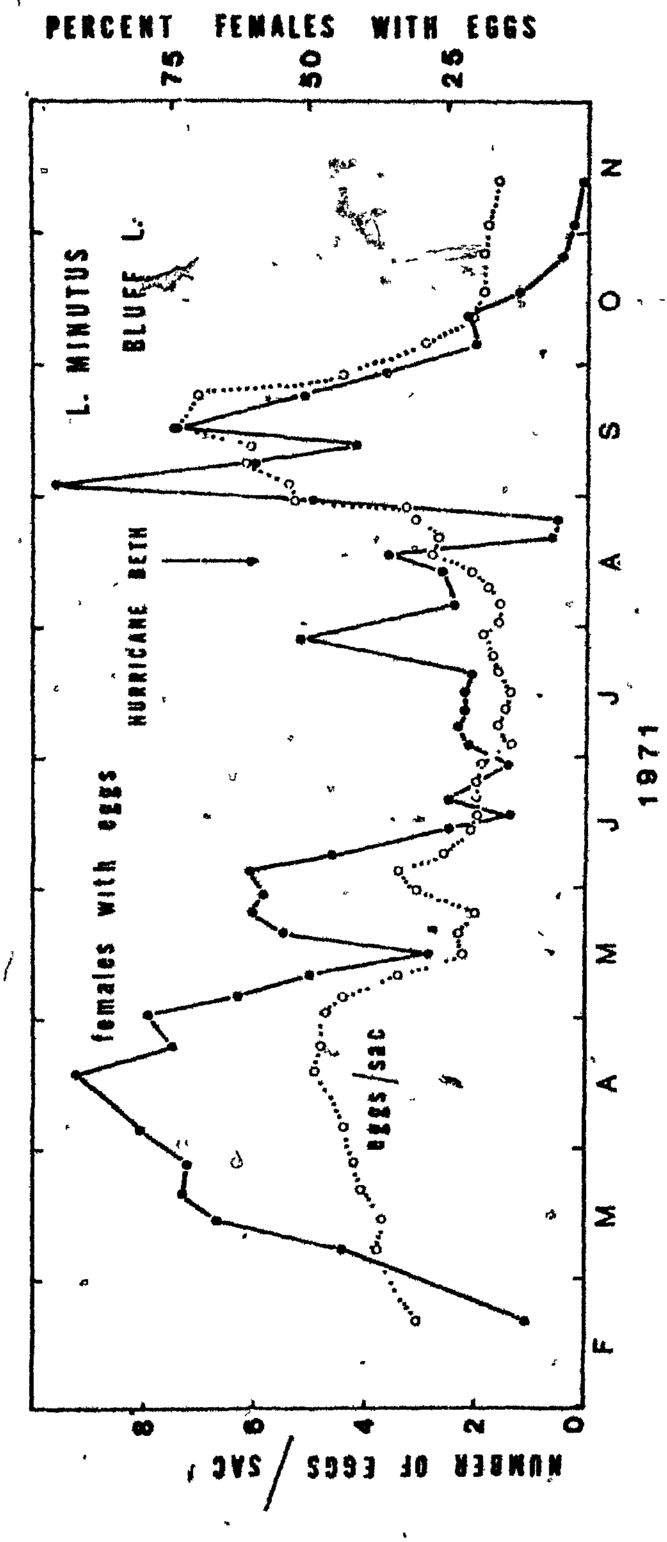
For purposes of analysis the corrected curve of egg abundance could arbitrarily be separated into a number of pulses. These pulses occur as a result of several processes and are common in copepods where recruitment is continuous over a large fraction of the year (Rigler and Cooley unpublished data, Comita 1972, Ravera 1954, Edmondson, Comita and Anderson 1962). When phytoplankton abundance is high, especially at spring and fall overturn, there is an increase in both the percentage of females carrying egg sacs and the number of eggs per sac creating the first pulse (Fig. 4 top panel, and Fig. 5). From mid-May through mid-June another distinct pulse (second pulse) is evident followed by a period of low reproductivity in the warmest part of the year (third pulse). A fourth pulse began in late August and continued until mid-November when egg production stopped.

The first pulse in particular was distinct for most instars since shifts in peak numbers for subsequent stages could be followed easily and was treated as a first cohort. The smaller second pulse was easily separable in the eggs and first few naupliar instars from an even smaller less obvious third pulse (see Fig. 4, top panel). However the later

FIGURE 5

Number of eggs/sac and percent females carrying eggs for *L. minutus* in Bluff L. from Feb. to November 1971.

On August 15 and 16 approximately 20 to 25 cm. of rain fell on the drainage area of Bluff L. as Hurricane Beth passed over the Halifax-Dartmouth area.


PERCENT FEMALES WITH EGGS
75
50
25
L. MINUTUS
BLUFF L.
HURRICANE BETH
females with eggs
eggs/sac
F
M
A
M
J
J
A
S
O
N
1971
8
6
4
2
0
NUMBER OF EGGS / SAC

copepodites in the second and third pulses were inseparable and for purposes of analysis the second and third pulses were treated collectively as a second cohort. The fourth recognizable pulse which continued into 1972 was distinct and was treated as a third cohort. In summary the population of L. minutus in Bluff L. in 1971 was divided for analysis arbitrarily into 3 cohorts. Although information on abundance in 1972 is available only up until May 19 the beginning of a first cohort comparable to the previous year is evident.

Before the field work was started it was decided that the sampling program would be intensive in order to obtain good data on population dynamics of the main zooplankter L. minutus since a previous similar study on another diaptomid (Rigler and Cooley, unpublished) had shown that infrequent sampling could lead to a condition where pulses could not be easily separated making analysis for instar mortalities difficult and open to many subjective decisions. However even with frequent sampling there were times when two pulses were not distinct. In particular the end of the first pulse for the N4 and N5 instars was not clear. There was also difficulty and some subjectivity used in separating the first and second pulses in the copepodite instars because apparent mortality early in the nauplIar instars eliminated any noticeable modes in later instars. This is most apparent after the CII instar where it becomes impossible from the data to separate the second pulse from the third. By the CV instar the second and third pulses of animals seem to have disappeared completely. For this reason analysis was carried out as described in the materials and methods for the cohorts as defined in Table 5. This will introduce an error which I assume to be insignificant.

The third cohort produced in 1971 developed through the winter and

TABLE 5

Beginning and ending dates for the 4 cohorts of L. *minutus* in Bluff L. in 1971 and 1972.

First Cohort 1971 (71/1) Eggs to CV
-begins Feb. 20, ends Nov. 27, 1971

Second Cohort 1971 (71/2) Eggs to CIV
-begins May 15, ends Oct. 26, 1971

Third Cohort 1971 (71/3) Eggs to CV
-begins Aug. 21, ends May 19, 1972

First Cohort 1972 (72/1) Eggs to N3
-begins Feb. 13, end of pulse of N3's assumed to occur on June 5, 1972.

into spring of 1972 but the sampling program for Bluff L. was ended on May 19 before all of the CV had either completed their development into adults or died. Since the numbers are small (Fig. 4) it was assumed that all CV animals alive on May 19 survived into adulthood. Again this will introduce a small insignificant error but simplify comparisons between cohorts.

The overwintering females began producing subitaneous eggs at about the same time in Feb. of 1972 as they did in the previous year but the first cohort of 1972 which is shown in Fig. 4 up to May 19 is obviously smaller in size than that of 1971 in both the eggs and early nauplIar instars. By May of 1972, as in 1971, a few CI of the first cohort were found in samples. It should also be noted that there was much more scatter about the smoothed curves of abundance of adults and adult females even though sampling was more intense during the winter of 1972.

In all subsequent discussion for simplicity unless otherwise stated all numbers of L. minutus instars refer to whole lake estimates and will be expressed in units of $10^2/m^2$, all areas under curves in units of $10^2/m^2$, and all production figures as grams dry weight/m^2. The first three cohorts produced in 1971 and the first cohort of 1972 will be referred to as 71/1, 71/2, 71/3, and 72/1 respectively. Subitaneous eggs will be referred to as simply "eggs" as opposed to diapausing or resting eggs.

2. Empirically Derived Development Times

Previous workers (Elster 1954, Eichhorn 1957, Cooley 1970) have shown that development rates of eggs and first nauplIar instars of freshwater calanoid copepods are temperature dependent. The results of laboratory experiments on these two stages for L. minutus and A. spatulocrenatus are illustrated in Fig. 6. The data for each stage of each species were fitted to Bělehrádek's temperature function

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

where D is development time, T is temperature, a, b, and α are constants, because it has been shown to adequately describe development rate and temperature when the relationship is monotonic and slightly curvilinear (McLaren 1965, 1966, McLaren, Corkett, and Zillioux 1969, McLaren and Cooley 1972, Corket 1972). The constant α was chosen to achieve the best least squares fit between the natural logs of D and $(T-\alpha)$. Although a simpler form of this power curve (without α) would describe the data as well, the extra step is included here because of the suggestion by McLaren (1963, 1965, 1966) that the 3 constants of Bělehrádek's function may have biological meaning at least within related groups such as copepods. Thus these fitted equations (Fig. 6) may be useful to future workers when more information on egg and first naupliar development rates become available.

Information derived from field sampling on the density of animals in each ½ metre stratum and water temperatures (Fig. 2) for each sampling day of a cohort were used in the following manner to estimate an average temperature experienced by a particular instar (egg or NI) in the lake. The mean daily temperature experienced by an instar was calculated by multiplying the temperature of each stratum by the density of animals, summing over all strata, and dividing by the total number of animals in the lake. These mean daily temperatures weighted (multiplied) by the population size of the instar were used to estimate a mean temperature over the entire cohort and were then converted into an average cohort development time for that instar by using the appropriate equation in Fig. 6.

FIGURE 6

Egg and NI development times plotted against temperature for L. minutus and A. spatulocrenatus.

Bělehrádek's temperature function was fitted to the data points to obtain an equation for each curve. The statistics of the fit for each curve are located in Appendix 3.

L. minutus

$$D_{egg} = 156046(T+8.0)^{-2.314} \qquad \text{Equation 2}$$

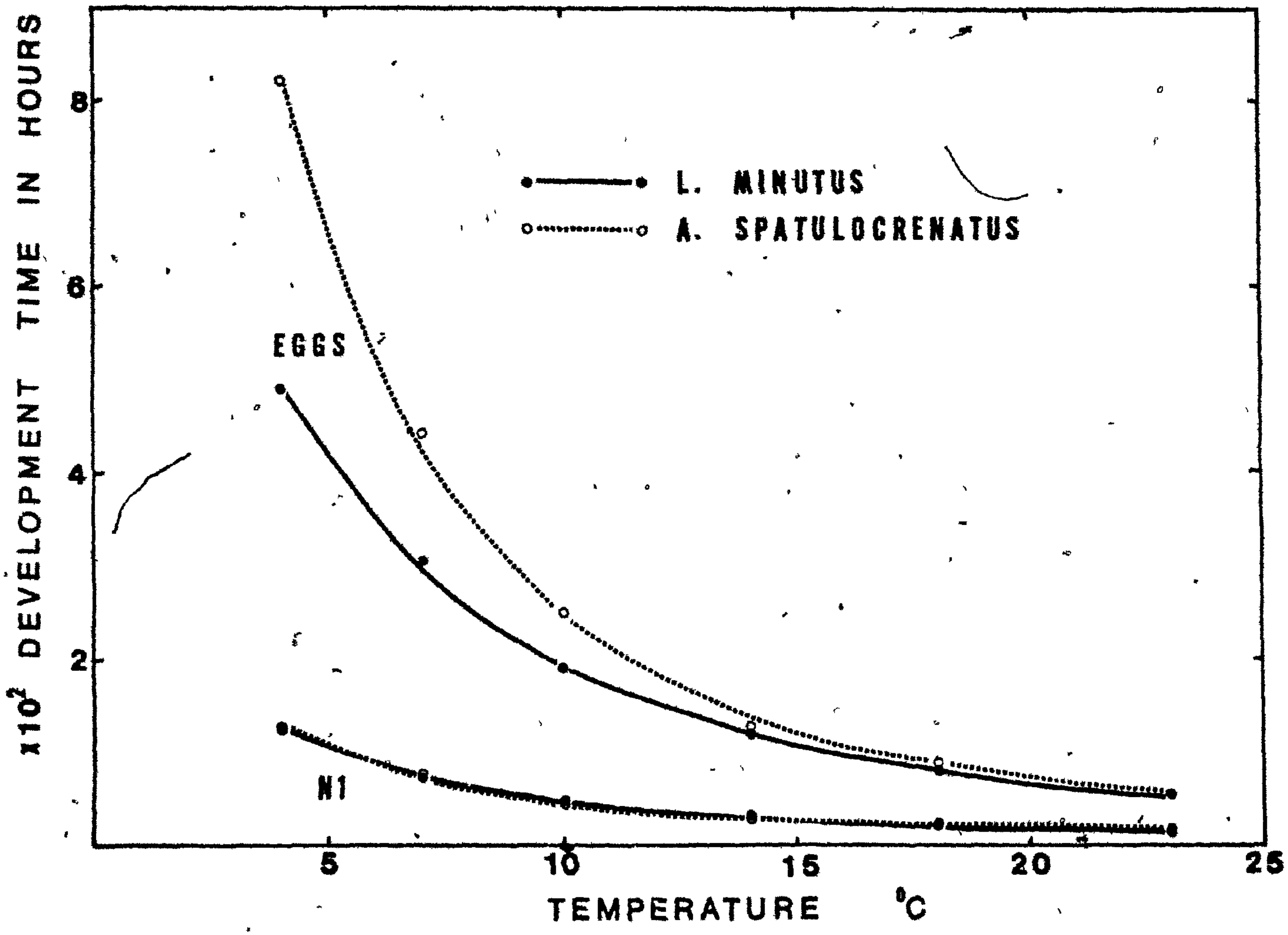
$$D_{NI} = 14065(T+6.0)^{-2.048} \qquad \text{Equation 3}$$

A. spatulocrenatus

$$D_{egg} = 160020(T+4.9)^{-2.402} \qquad \text{Equation 4}$$

$$D_{NI} = 27790(T+6.6)^{-2.282} \qquad \text{Equation 5}$$

D= development time in hours
T= temperature in degrees centrigrade


x10² DEVELOPMENT TIME IN HOURS
8
6
4
2
5
10
15
20
25
TEMPERATURE °C
L. MINUTUS
A. SPATULOCRENATUS
EGGS
N1

For this and subsequent calculations it was assumed that any diurnal vertical migration that might be occurring by egg carrying females and NI did not affect the daily estimates of mean temperature. This assumption is supported by the fact that on a given day almost the entire population was located in the top 3.5 metres of the lake (Table 6) which was also the unstratified epilimnion (Fig. 2). Also Cooley (1970) found that the vertical distribution of the first naupliar instars of Skistodiaptomus oregonensis had the same mean depth in the water column during the day and at night even though vertical migrations became larger with increasing age in the copepodites and adults.

3. Population Estimates of Eggs and NI

Estimates of the number of eggs and NI passing through each of the 3 cohorts of L. minutus produced in 1971 and the first cohort of 1972 were calculated in 2 slightly different ways (Table 7). The first estimate involved converting the mean cohort temperature for eggs and NI to mean development times using Equations 2 and 3 and dividing these times into the area under the numbers curve (Southwood 1963). The second method has been used by several workers for estimating birth rates of rotifers, cladocerans, and copepods (Edmondson and Winberg 1971). It assumes that on a given day the fraction of eggs hatching is 1/D where D is the duration of egg development in days determined from Eqn. 2, and thus 1/D × egg number will give the absolute number hatching in a day. If one takes an average of the number hatching on consecutive sampling days and multiplies this number by the interval between the 2 sampling days then an absolute estimate is obtained of the number of eggs hatching in the interval and summing over all intervals in a cohort gives an estimate of the total number of animals hatching. The same procedure was applied for NI moulting

TABLE 6

Seasonal changes in percentages of eggs and N1 of *L. minutus* found in the top 3.5 metres of water in Bluff L. when stratified.

Date 1971	% of Eggs in top 3.5 metres	% of N1 in top 3.5 metres
May 15	97	93
June 14	94	94
July 15	99	95
Aug. 13	100	95
Sept. 16	97	96
Oct. 17	98	None present

TABLE 7

Estimates of the number of animals passing through the egg and first naupliar instars assuming. A) an average development time over the entire cohort, and B) 1/D animals hatch or moult each day of the cohort. All answers are expressed as number of animals x$10^2/m^2$.

	First Cohort 1971		Second Cohort 1971		Third Cohort 1971		First Cohort 1972	
	eggs	NI	eggs	NI	eggs	NI	eggs	NI
A	4384	3933	2933	3177	3490	2813	2279	2633
B	4180	3733	3145	3488	3430	2818	2038	2375

into N2. A bias is introduced into these latter calculations if the age distribution of the eggs is not uniform. Table 7 illustrates that the estimates of eggs and N1 using these 2 methods are similar and for simplicity in subsequent calculations the results from the first method will be used.

4. Dry Weights of Instars of L. minutus and A. spatulocrenatus

Animal numbers were converted to production units using the dry weight values listed in the first column of Table 8. The values marked with an asterisk were derived from 1 to 3 weighings on a microbalance as described in the materials and methods. The dry weights for the N1 to N4 instars were approximated in the following manner. It was assumed that animals would have a lower mean dry weight as compared with eggs until at least the second or possibly third naupliar instar (Rigler and Cooley unpublished, because feeding does not begin until N2) and that a semilog plot of mean dry weight versus instar for the N2 to N6 instars would approximate a straight line. The dry weights of N5 and N6 from Table 8 were plotted semilogarithmically and the resulting straight line was extrapolated by eye to the second naupliar instar and N2, N3, and N4 dry weights were interpolated along the ordinate axis from this line. Similarly the ordinate at the mid-point of a line connecting egg and N2 dry weights gave an estimate of N1 dry weight.

Although these values were used for the 3 major cohorts analysed for instar mortalities, it is probable that a given instars dry weight can vary throughout the year depending on the nutritional state of the food being assimilated. The dry weights that were determined came from instars collected when their numbers were at peak levels in the first cohort of 1971. Similar experiments done on the 1972 population at the same time of year proved to be significantly higher in the CII and CIII instars

TABLE 8

Dry weight values of Leptodiaptomus minutus used in converting animal numbers to production estimates. Values marked with an asterisk were determined from laboratory weighings. The number of animals weighed for each determination is given in brackets.

INSTAR	MICROGRAMS DRY WEIGHT First Cohort 1971	 First Cohort 1972
Egg	.30	.30(300)*
N1	.25	
N2	.23	
N3	.26	
N4	.30	
N5	.35 (76)*	
N6	.40 (100)*	.42 (100)*
CI	[a].52 (100)*	.51 (92)*
CII	.71 (47)*	.95 (75)*
CIII	1.10 (51)*	1.63 (100)*
CIV	[b]2.86 (200)*	
CV	5.02 (100)*	
Adults	[c]5.33 (160)*	

[a] Average of 3 replicates from May 15, May 20, and May 26 of .52, .52, and .51 micrograms dry weight respectively.

[b] Average of 3 replicates from Aug. 1, and Aug. 5 twice, all equal to 2.86 micrograms dry weight.

[c] Average of males and females (see Table 9).

(approximately 32 and 48% respectively, Table 8). To illustrate the magnitudes of possible seasonal instar variances Table 9 lists dry weight values of adult males and females for both L. minutus and A. spatulocrenatus at various times in the year. These data indicate that from mid-November of 1971 to late July of 1972 adult males and females mostly from the same cohort underwent almost a 50% loss in dry weight. Similar large seasonal differences in dry weight were recorded for the larger A. spatulocrenatus. For both species the highest values occurred continually from late fall through the winter. However in 1972 A. spatulocrenatus had its highest average adult weight on May 24 at a time when the dry weight of L. minutus was decreasing to its lowest value of 2.9 micrograms.

These data show that using one set of dry weights for cohorts produced at different times in the year or in different years will introduce errors into production estimates if expressed as dry weight. However because I have only 1 set of dry weights from 71/1 they will be used in estimating production for the other cohorts even though the errors may run as high as 50%.

5. Zooplankters Other Than Diaptomids in Bluff L.

Figure 7 illustrates seasonal life histories for 7 species of zooplankton other than L. minutus in Bluff L. for the period from April 18, 1971 to March 30, 1972. Because these data were collected only to indicate when competitive interactions with L. minutus might be occurring, sampling was less frequent. The seasonal occurrence of each species as indicated in Fig. 7 will be briefly presented below.

a. Holopedium gibberum

The rather sudden appearance of this animal early in May together with its total absence during winter indicates that it spent the winter in the

TABLE 9

Seasonal changes in dry weight values of individual adult males and females of L. minutus and A. spatulocrenatus in Bluff L. The number of animals used in each determination is given in brackets. The dates progress sequentially from 1971 to 1972. All dry weight values are expressed in micrograms.

		May 17	Nov 14	Nov 16	Nov 29	Jan 24	Feb 15	Apr 10	May 24	Jul 13	Jul 28
L. minutus	males	3.0 (65)	5.2 (80)	5.2 (80)	4.7 (60)	4.6 (75)	4.2 (70)	3.2 (60)	3.1 (90)	2.8 (100)	2.7 (100)
	females	3.7 (60)	5.4 (80)	5.5 (80)	5.4 (50)	5.3 (70)	4.8 (70)	3.7 (60)	3.5 (80)	3.0 (100)	3.1 (100)
Average		3.4	5.3	5.3	5.1	5.0	4.5	3.5	3.3	2.9	2.9

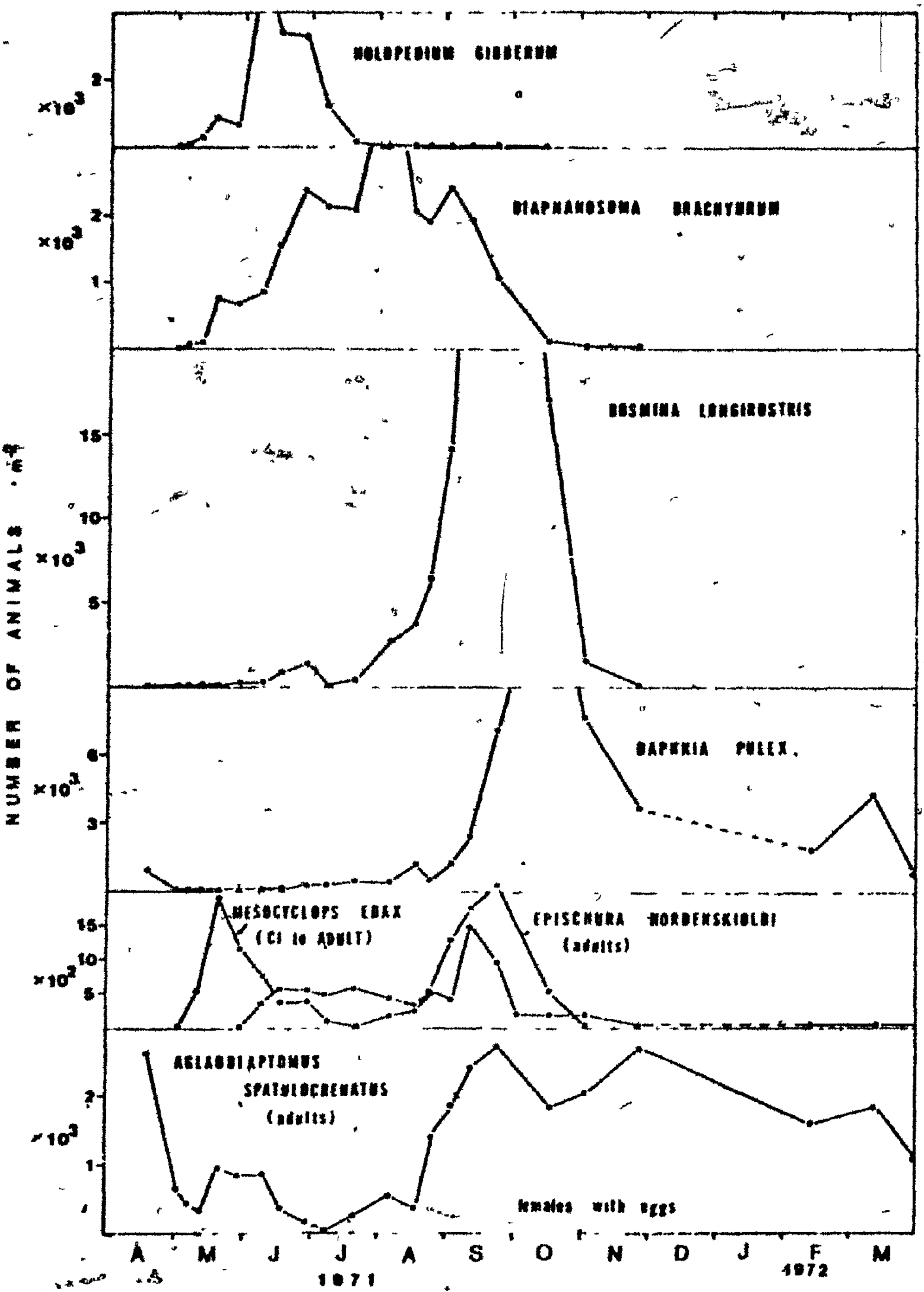
		May 18	Aug 9	Aug 15	Nov 25	Jan 24	Feb 17	Apr 10	May 24	Jul 13
A. spatulocrenatus	males	9.2 (16)	9.6 (10)	9.1 (30)	12.2 (25)	12.4 (32)	11.4 (31)	11.1 (26)	11.7 (41)	7.3 (29)
	females	15.2 (35)	11.0 (19)	12.9 (14)	18.8 (22)	15.9 (28)	15.4 (30)	15.5 (50)	20.4 (41)	9.5 (31)
Average		12.0	10.3	11.0	15.5	14.2	13.4	13.3	16.1	8.4

[redacted]

FIGURE 7

Population dynamics of zooplankters other than L. minutus common in preserved samples from Bluff L. from April 18, 1971 to March 31, 1972.

Diaphanosoma brachyurum had a peak population of 4438 /m^2 on Aug. 5, 1971. Daphnia pulex had a peak population of 14,827 /m^2 on Oct. 17, 1971. Bosmina longirostris had peak population levels of 38,290 and 44,458 /m^2 on Sept. 12 and Sept. 24, 1971 respectively and at this time was approximately 1/5th as abundant as L. minutus.


HOLOPEDIUM GIBBERUM
DIAPHANOSOMA BRACHYURUM
BOSMINA LONGIROSTRIS
DAPHNIA PULEX.
MESOCYCLOPS EDAX
(CI to ADULT)
EPISCHURA NORDENSKIOLDI
(adults)
AGLAODIAPTOMUS
SPATULOCRENATUS
(adults)
females with eggs
NUMBER OF ANIMALS · m⁻²
×10³
2
×10³
2
1
15
10
×10³
5
6
×10³
3
15
10
×10²
5
2
×10³
1
A M J J A S O N D J F M
1971
1972

form of resting eggs. The population (animals of all sizes) rose quickly in late May with peak numbers of approximately 5000 /m^2 occurring throughout June and then rapidly declined during the first 3 weeks of July. Small numbers were present from Aug. through Oct. and none were seen in November.

b. Diaphanosoma brachyurum

This species was commonly found near the surface in open water trap samples in summer and was not restricted to weedy margins of the lake as is normally the case (Hutchinson 1967). Hutchinson (1967) describes it as a common summer species and notes that some workers do not separate the 2 described species of Diaphanosoma (brachyurum and leuchtenbergianum) regarding the latter as just a planktonic form of the former. A summer peak was also observed in Bluff L. of approximately 4500 /m^2 in July and August. Its sudden appearance in May and disappearance in November suggest that it too spends the winter as resting eggs.

c. Daphnia pulex

This species is commonly found in both lakes and ponds all over the continent (Brooks 1959). In Bluff L. two population maxima occurred; one in mid-Oct. of approximately 12000 /m^2 and a smaller one in mid-March of 1972 of approximately 4500 /m^2, but it is present in small numbers at all times of the year. Because of the confusion regarding the taxonomy of the genus and because all specimens recorded could not be individually keyed it is possible that small numbers of another species of Daphnia were also present since multiple congeneric associations are not uncommon (Tappa 1965, Haney 1970).

d. Bosmina longirostris

This species was the only other zooplankter in Bluff L. that at any time approximated the abundance of *L. minutus*. A large increase in population size occurred during Sept. 1971 with maximums of 38000 /m^2 and 44000 /m^2 recorded on Sept. 12 and 24 respectively. In contrast, at the same time numbers of *L. minutus* (all instars excluding eggs) were of the order of 200,000 /m^2. The total absence of this animal in winter suggests it passes the winter as diapausing eggs.

e. *Epischura nordenskioldi*

Almost no information is availa[illegible] on the distribution and biology of this species although it is a reg[illegible] but uncommon inhabitant of lakes in the Halifax-Dartmouth area. This is to be expected since the genus *Epischura* is known to be predatory (Main 1962). The sudden appearance of naupliar instars in May when no adults are found indicates it overwinters as resting eggs. Development i[illegible]arently rapid during May with a few adults present by late May (Fig. 7). The large peak in adult numbers through Sept. may be derived from offspring of the second or perhaps third generation. The data are not adequate to be certain. Davis (1972) reports it as having 2 generations in Hogan's Lake in Newfoundland. By mid-Nov. in 1971 all instars were absent from the lake.

f. *Aglaodiaptomus spatulocrenatus*

Adults are present in varying numbers throughout the entire year (Fig. 7) but breeding is apparently restricted to May through August. Peak numbers of adults were observed from Sept. through Dec. apparently suffering little mortality but even during this latter period it is numerically a minor constituent of the zooplankton. As a congener of *L. minutus* in Bluff L. its size is important and the adults were observed to be approximately 50 to 65% longer and much heavier than adult *L. minutus* (Table 9). Even when adults were most abundant they were outnumbered by adult L. minutus by approximately 20 to 1.

6. L. minutus in Other Halifax-Dartmouth Area Lakes

Table 10 shows the occurrence of L. minutus and other calanoids in lakes in the Halifax-Dartmouth area. Only 1 of the 38 lakes listed (Russel Lake) did not contain adult calanoid copepods while L. minutus was present in the remaining and judged to be the numerical dominant in 22. It is also worth noting that L. minutus was found dominant in lakes large and small, oligotrophic and eutrophic, stratified and unstratified. Although 27 of 38 lakes contained an Epischura species, only First Lake contained both E. lacustris and E. nordenskioldi. This may indicate an inadequacy in the sampling method or a possible competitive interaction between congeneric species.

7. The Onset of Diapause in L. minutus and A. spatulocrenatus

Figure 8 illustrates when the shift to the production of diapausing eggs from subitaneous eggs occurred for the 2 diaptomids in Bluff L. in 1971. An egg was assumed to be in diapause if it did not hatch when expected by using Eqn. 2 and did not decompose and appeared healthy after several weeks at 13 °C. For L. minutus the data indicated that from 2 to 10% of all egg sacs found in Sept. were diapausing but, contrary to a suggestion of Cooley (1970), these were indistinguishable morphologically from the subitaneous variety. By Oct. 11 all eggs collected from live plankton samples were in diapause.

It was observed that A. spatulocrenatus also switched to the production of diapausing eggs, but because of small sample sizes the time cannot be documented as precisely. On Aug. 30 and Sept. 8 one of 4 and 6 of 8 egg sacs respectively were judged to be in diapause. By Sept. 12, thirteen of 14 egg sacs failed to hatch in the expected time interval (Fig. 8).

TABLE 10

Calanoid copepod associations in selected Halifax-Dartmouth area lakes. All samples were collected with a conical tow net (75 micron mesh) near the deepest spot in each lake in the summer of 1971.

Name of Lake	Area (hectares)	Mean Depth (m.)	Max. Depth (m.)	Stratif.	Secchi Depth (m.)	Trophic Status	Calanoid Copepods Found L.m.	A.s.	E.n.	E.l.
Albro	23.5	1.8	6.1	Yes	5.7		D		+	
Bell	9.7	3.1	8.5	No	2.2		D			
Bissèt	79.7	2.0	9.1	No	0.9		D		+	
Bluff	4.8	2.0	7.0	Yes	4.9		D	+	+	
Charles	158.6	9.1	28.3	Yes	6.1		D			+
Chocolate	8.9	3.9	13.4	Yes	3.6		D	+	+	
Colbart	22.3	5.6	12.2	Yes	2.3		D		+	
Cranberry	11.3	1.6	4.0	No	1.1	Eu	D		+	
First	80.9	5.8	22.9	Yes	0.2		D		+	C
Governor	41.7	4.7	14.3	Yes	1.1	Eu	+			
Henry	13.2	2.0	6.1	Yes	1.0	Eu	D		C	
Kearney	63.9	9.1	26.2	Yes	4.0	Ol	D		+	
Kidston	11.7	1.4	4.6	No	2.0		D		+	
Lemont	9.3	2.9	5.5	No	--	Ol	D		C	
Long	204.8	7.4	30.2	Yes	2.5	Ol	D		C	
Long Pond	16.2	-	5.6	Yes	1.0		D	+	+	
Loon	68.8	3.2	6.1	No	1.6		+			
Lovett	15.4	2.1	7.0	Yes	1.6	Eu	+	+	D	
Maynard	7.1	4.8	13.1	Yes	6.5		C	+		
Micmac	146.9	3.2	6.1	No	4.3		D		+	
Morris	148.1	2.8	7.6	No	1.7		+		+	
Oathill	4.2	3.0	8.5	Yes	5.5		C			
Otter	93.9	4.2	11.6	No	1.9	Ol	D			
Paper Mill	31.6	1.6	6.1	No	3.6		+		+	
Penhorn	4.5	9.1	2.9	Yes	--		+			

[redacted]

TABLE 10 (cont'd)

Name of Lake	Area (hectares)	Mean Depth (m.)	Max. Depth (m.)	Stratif.	Secchi Depth (m.)	Trophic Status	Calanoid Copepods Found L.m.	A.s.	E.n.	E.l.
Powder Mill	23.5	1.7	6.1	Yes	5.2		+		+	
Power Pond	7.3	2.6	10.7	Yes	--		+			
Rocky	186.6	2.2	11.0	Yes	5.8		+			+
Russel	33.6	3.1	7.9	No	1.2*	Eu				
Sandy	66.8	7.6	19.2	Yes	2.1		C		+	
Second	103.6	3.7	22.9	Yes	2.9*		D			
Spruce Hill	89.0	3.4	11.6	No	3.0*	01	D		+	
Third	91.9	24.4	8.5	Yes	4.0*	01	+			+
Three Mile	16.2	3.6	11.3	Yes	6.0		+			
Topsail	59.1	2.5	6.7	No	6.3	01	D		+	
Webber	37.2	5.1	16.8	Yes	1.0*	01	D			
Lake William	338.7	28.3	11.6	Yes	6.1		C			+
Williams	46.5	2.5	20.1	Yes	4.9*		D		+	

Explanation of Terms and Symbols Used in Table 10

-- data not available

Stratif. - Yes if lake had a well developed hypolimnion and/or metalimnion

Trophic Status - only those lakes which on the basis of water chemistry and/or algal blooms were obviously oligotrophic (01) or eutrophic (Eu) have been categorized

* Secchi disc readings taken within 3 weeks after hurricane of August 15 and 16; Most likely these figures are significantly lower than normal due to large amounts of runoff entering the lake from the drainage basin.

Presence of Calanoid Copepods

D - obviously the numerical dominant zooplankter of all species present in the sample
C - common in the sample(s)
+ - present in small numbers

L.m.=<u>Leptodiaptomus minutus</u>   A.s.=<u>Aglaodiaptomus spatulocrenatus</u>
E.n.=<u>Epischura nordenskioldi</u>   E.l.=<u>Epischura lacustris</u>

Even with the small numbers it seems clear that diapause egg production begins approximately 1 month sooner in the larger diaptomid.

8. The Dropping of Diapausing Egg Sacs by *L. minutus*

An attempt was made in the laboratory to estimate the average amount of time taken by female *L. minutus* to drop an egg sac containing diapausing eggs. Normally subitaneous eggs are carried by the female until hatching but neither diapausing nor subitaneous eggs can be produced until previous eggs either hatch or fall off. Some diapausing eggs took 4 to 7 days to be dropped but the average was 2.4 days (standard deviation= 1.4 days). If it is assumed that there is an even distribution of eggs of all ages, an estimate of the average amount of time an egg sac is carried before being dropped would be 2x the mean= 2x2.4 =4.8 days, rounded off to 5 days.

An estimate can be made of the total number of diapausing eggs deposited on the mud sediments if the area under the numbers curve of diapausing eggs is divided by the average length of time each egg sac is carried. This is likely to be an overestimate of the true number of diapausing eggs dropped since females in the laboratory were in an artificially small and unnatural environment and were observed to bang into the walls of the incubation vial which conceivably hastened the removal of the egg sac.

Since quantitative sampling of Bluff L. was begun on Oct. 17, 1970, almost a full week after the total switchover to diapausing eggs had occurred in 1971, a number of assumptions had to be made about the female population as it existed before this date. A few qualitative samples collected on Sept. 15 and Sept. 26, 1970 with a tow net were used to estimate the % of females carrying egg sacs and the number of eggs per sac. From Table 11 it can be seen that in both years the absolute number of females in the lake determined from quantitative samples is remarkably similar

TABLE II

A comparison of available parameters from Bluff L. samples needed to calculate the total number of diapausing eggs deposited on mud sediments by L. minutus in the fall of 1970 and 1971.

1970				1971			
Date	# of fem. x $10^2/m^2$	% of fem. carrying egg sacs	# of eggs per sac	Date	# of fem. x $10^2/m^2$	% of fem. carrying egg sacs	# of eggs per sac
Sep 15[1]	?[3]	90	1.7	Sep 16	74	74	7.4
Sep 26[1]	?[3]	36	1.4	Sep 24	58	51	6.0
Oct 17[2]	115	13	1.4	Oct 17	115	12	1.9
Nov 15	285	4	1.8	Nov 12	298	1	1.6
Nov 29	270	1	1.8	Nov 27	260	1	1.6

Final estimates of the number of diapausing eggs deposited on mud sediments:
1970 = 376 x$10^2/m^2$
1971 = 452 x$10^2/m^2$

[1] Estimates of the % of females carrying egg sacs and the number of eggs per sac were determined from qualitative samples taken with a tow net.

[2] Quantitative sampling of Bluff L. with a 32 litre Schindler trap began on this date.

[3] The size of the total adult female population in Bluff L. in 1970 on Sept. 15 and Sept. 24 respectively was assumed to be the same as it was in 1971 on Sept. 16 and Sept. 24 respectively.

$$\text{Total number of diapausing eggs in the population on any day} = (\#\text{ of Fem.}) \times \left(\begin{array}{c}\text{fraction of}\\ \text{fem. with}\\ \text{eggs}\end{array}\right) \times \left(\begin{array}{c}\text{fraction of}\\ \text{eggs in}\\ \text{diapause}\end{array}\right) \times (\#\text{ of eggs/sac})$$

Equation 6

The fraction of the eggs in the population that was in diapause on any date was determined from Fig. 8 and was assumed to be the same in both years.

but the % of females with eggs and the number of eggs/sac are considerably lower in 1970 during late Sept. and Oct. To make the necessary calculations it was assumed that a) the onset of diapause was the same in both years, b) the absolute number of females was the same, and c) the number of eggs/sac from Sept. through Nov. in 1970 was 1.8. The percentage of females carrying eggs at any time was read from a straight line plot of available information for the 5 qualitative and quantitative sampling dates in 1970. The final estimates of $376 \times 10^2/m^2$ for 1970 and $452 \times 10^2/m^2$ for 1971 suggest that the number of diapausing eggs deposited on the sediments was very similar in both years.

9. Eggs Caught in Sediment Traps (Fall 1971)

Sediment traps were set in Bluff L. in the fall of 1971 in order to obtain another independent estimate of the number of diapausing eggs that were dropped by L. minutus females. The results from this experiment were not entirely consistent with the estimates resulting from the analysis of diapausing egg abundance over time. Assuming that 1/5 of all diapausing eggs are dropped each day (the inverse of 5 days, the amount of time an egg sac is carried before being dropped) and solving Eqn. 6 in Table 11 with the necessary parameters from field data will produce an absolute estimate for the number of eggs dropped on a per m^2 basis on Oct. 17 and Oct. 26 of 780 and 304 respectively. Assuming a constant change in the production rate between the 2 days the expected 9 days accumulation of eggs would be

$$\frac{780 + 304}{2} \times 9 = 5328 \ /m^2.$$

The results from the analyses from the 10 sediment trap samples are given in Table 12. Two different kinds of eggs were found which had the same approximate size and appearance of L. minutus and A. spatulocrenatus eggs respectively. However it is possible that some of the smaller eggs

TABLE 12

The numbers of eggs found in each of 10 sediment traps from October 17 to Oct. 26 1971 in Bluff L. The "small eggs" were assumed to belong to _L. minutus_ and the "large eggs" to _A. spatulocrenatus_. Two traps were located at each of the 5 major sampling stations in Fig. 1.

Station	Max. Depth (m.)	Small eggs _L. minutus_	Large eggs _A. spatulocrenatus_
A1	7.0	15	
A2		13	
B1	4.5	20	
B2		22	1
C1	3.8	20	5
C2		14	3
D1	3.5	28	1
D2		12	3
E1	2.5	25	
E2		19	

for the small eggs:

mean number per trap = 18.8
variance per trap = 25.4
standard deviation = 5.0
standard error = 1.6

belonged to Epischura nordenskioldi since 1 inconclusive laboratory experiment showed that its eggs were slightly smaller but generally similar to those of L. minutus and Fig. 7 shows that its adults were present but rapidly decreasing in numbers in late Oct. No information is available on the number of eggs this species lays per clutch or how often this occurs. Almost all of the free eggs in the sediment traps were single even though they are most likely deposited in a sac by diaptomids. According to available information Epischura lay their eggs singly (Main 1962) but it is likely that the membrane around a diaptomid egg sac is destroyed as a result of the treatment encountered before being analysed under the microscope. The average number of eggs found per trap was 18.8 with a standard deviation of ± 5.0 eggs. Since most of the population is above 3 metres it is not unusual that the same number of eggs were found in the shallow water traps as compared with the deep water ones.

Assuming that all of the small eggs belonged to L. minutus and that an average of 18.8 eggs fell onto each 78.5 sq. cm of mud surface (the area of the opening of each trap was 78.5 cm^2) then the number accumulated over the 9 day interval between Oct. 17 and Oct. 26 would be 2395 $/m^2$, or slightly less than 1/2 of the expected 5328 $/m^2$ from the previous estimate. Also implicit in the former estimate is that the traps are 100% efficient in catching and retaining everything falling directly above the opening.

10. The Effect of Temperature on the Development of Diapausing Eggs

To determine how temperature affects the development of diapausing eggs of L. minutus and A. spatulocrenatus from Bluff L. the procedures listed in Table 13 were carried out.

TABLE 13

Experiments performed in the laboratory on diapausing eggs of L. minutus and A. spatulocrentus from Bluff L. in 1971.

Expt. #	Date eggs collected	Light conditions	Temperature treatment (degrees centrigrade)	No. of egg sacs	No. of eggs	% hatching
			L. minutus			
1	Oct 28	dark	transferred to 14 after 1 wk at 4	15	30	0
2	Oct 28	dark	transferred to 14 after 2 wk at 4	20	37	0
3	Oct 28	dark	transferred to 14 after 3 wk at 4	19	40	0
4	Nov 4	dark	transferred to 14 after 1 mo at 4	50	84	5
5	Oct 28	dark	transferred to 14 after 3 mo at 4	51	105	72
6	Oct 26	light	kept continuously at 4	28	48	94
7	Oct 29	dark	kept continuously at 4	94	190	93
8	Nov 4	dark	kept continuously at 8	96	153	52
9	Oct 29	dark	kept continuously at 14	20	38	0
			A. spatulocrenatus			
10	Sept 16	light	kept continuously at 4	15	72	47
11	Sept 16	light	transferred to 14 after 3 mo at 4	10	46	70
12	Sept 3	dark	kept continuously at 4	14	77	4
13	Oct 11	dark	kept continuously at 4	14	35	0
14	Sept 24	dark	kept continuously at 14	8	35	0
15	Sept 12	dark	kept continuously at 8	12	66	0

Equipment failure on May 1, 1972 forced termination of the experiments at $8^{\circ}C$.
All A. spatulocrenatus eggs from each experiment were incubated in a single vial, while each egg sac of L. minutus was incubated in a single vial.
All experiments were terminated on June 19, 1972. On this date:
Expt. 12 - some eggs still appeared to be alive
Expt. 13 - 33 of the 35 eggs appeared to be alive

a. L. minutus

The results in Table 13 and Figure 8 show that in general greater numbers of diapausing eggs hatch sooner at moderate temperatures of about 14 °C than at 4 and 8 °C. The results from Expts. 1 through 3 show that a minimum amount of time of approximately 1 month is needed before any diapausing eggs will hatch even if they are transferred to warmer temperatures sooner. Figure 8 suggests that eggs incubated under lighted conditions hatch sooner at 4 °C than eggs incubated in the dark. The results of Expt. 8 (incubation in the dark at 8 °C) show however that diapausing eggs do not absolutely require incubation at temperatures of 4 °C, approximating winter conditions under ice before they will hatch since after 6 months at 8 °C (Expt. 8) diapausing eggs began hatching. However none of the eggs incubated at 14 °C ever hatched unless they had a prior cold treatment at 4 °C.

b. A. spatulocrenatus

Scarcity of material allowed fewer experiments involving fewer eggs to be performed on this species but the results seem to be consistent with those of L. minutus. Apparently A. spatulocrenatus also requires that its diapausing eggs develop at a cold temperature before hatching will occur and diapause development in the light again seemed to be faster (Expts. 10, 12, and 13). Eggs could also be made to hatch sooner by completing development at a moderate temperature of 14 °C providing they had spent 3 months at 4 °C. Without this time at 4 °C no eggs hatched after almost 9 months at 14 °C. In contrast to the results on L. minutus, no eggs hatched at 8 °C.

FIGURE 8

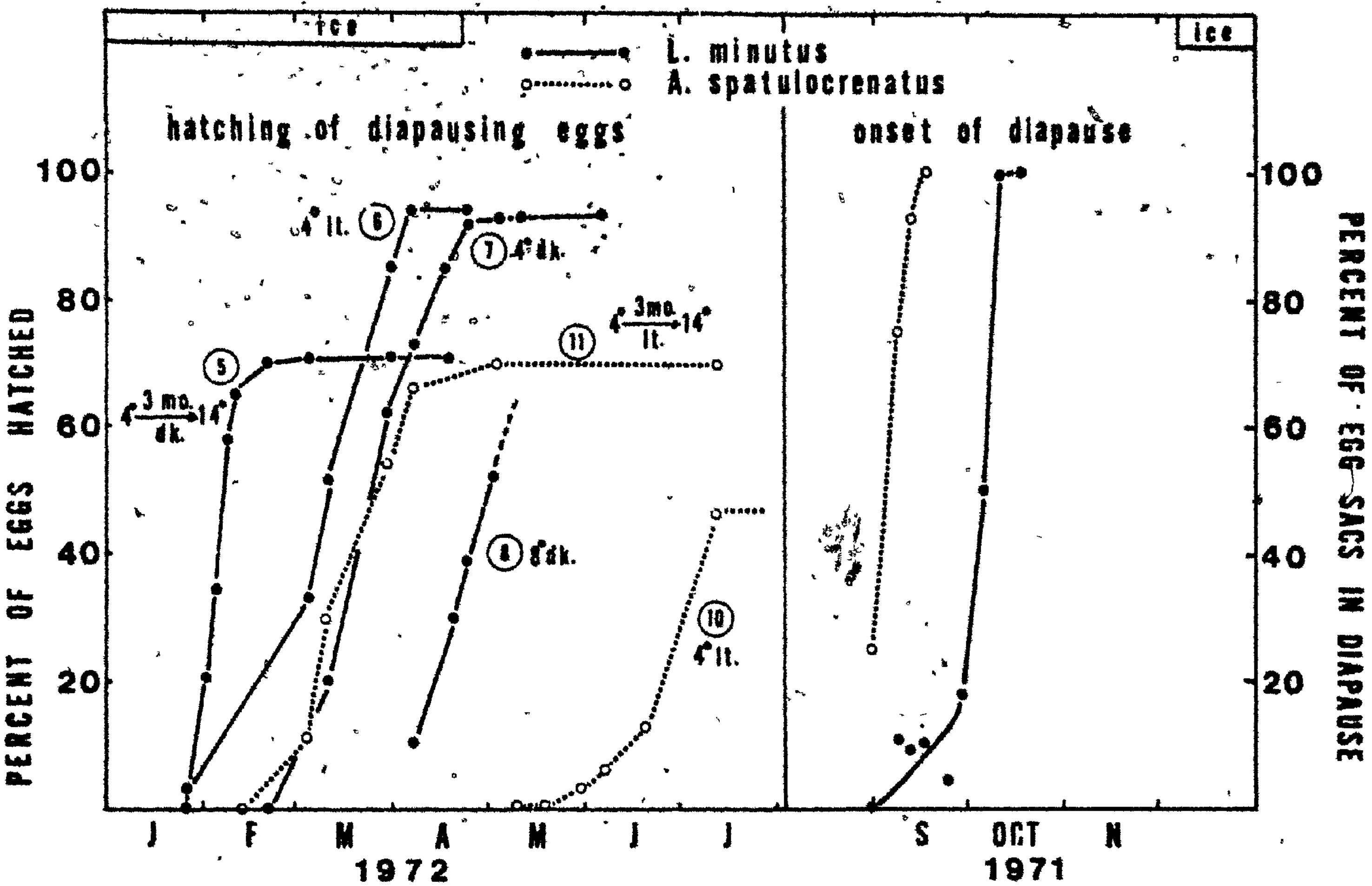
The results of experiments performed on diapausing eggs of L. minutus and A. spatulocrenatus and the time of onset of diapause.

All of the diapausing eggs used in these experiments were collected from Bluff L. between Oct. 28 and Nov. 4, 1971 for L. minutus, and Sept. 3 to Oct. 11, 1971 for A. spatulocrenatus and incubated under the varying temperature and light regimes listed in Table 13.

Symbols used in Figure 8

dk - eggs incubated in dark
lt - eggs incubated in light
mo - months

Numbers in circles refer to experiment numbers in Table 13.


ice
ice
L. minutus
A. spatulocrenatus
hatching of diapausing eggs
onset of diapause
PERCENT OF EGGS HATCHED
PERCENT OF EGG SACS IN DIAPAUSE
100
80
60
40
20
J
F
M
A
M
J
J
1972
S
OCT
N
1971
5
4° 3 mo. dk. 14°
6
4° lt.
7
4° dk.
8
8° dk.
10
4° lt.
11
4° 3mo. lt. 14°

II. Analyses of Population Data of L. minutus

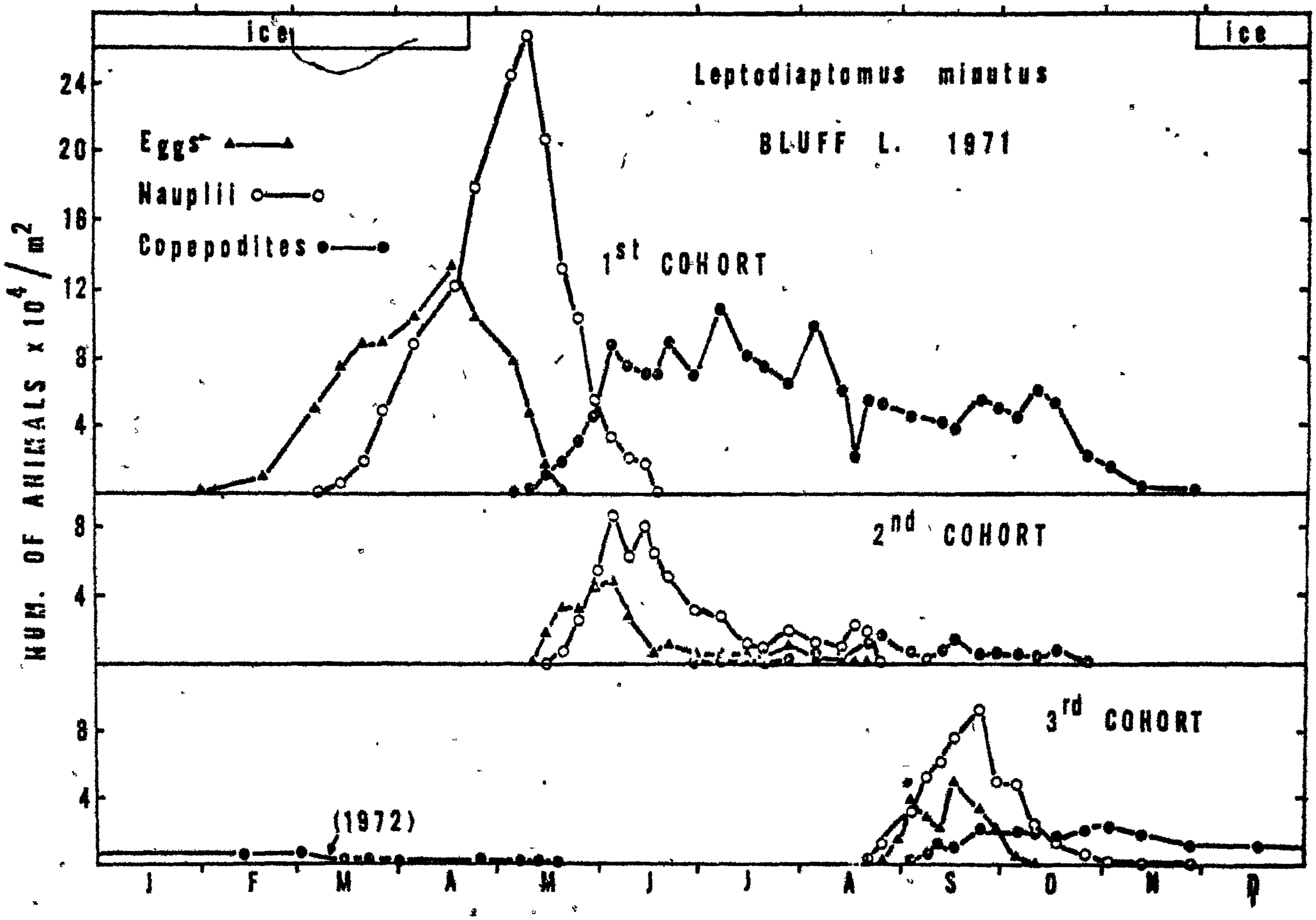
Because of the cost and time involved it is not unusual to find that analyses of data on copepods are done only on major life-history subdivisions such as egg, nauplii, copepodites, and adults. In such analyses the population in each of these 4 groups should rise to a maximum and then fall to 0 as mortality and/or moulting exceeds recruitment from the younger group. The data of Fig. 4 have been replotted in this manner and are presented in Fig. 9 to illustrate several obvious anomalies. With the disappearance of the last N6 instar in the first cohort on June 17 the total abundance curve for copepodites should only decrease. Even with the scatter among the points on the copepodite curve the trend seems to substantiate the prediction of an increase in numbers until late June or early July before falling. The copepodite estimatesfor Aug. 5 and 17 appear too high and too low respectively. With greater amounts of time spent in copepodite stages one would expect the curve to be positively skewed to the right and it is.

To a lesser extent a similar problem exists in the second cohort. After the last naupliar instar has moulted the CI to CIV curve drops as expected from Aug. 25 to Sept. 8 but then rises on Sept. 16 only to fall again. Most likely these anomalies are due to inadequate sampling of the lake because numbers were very low and many more trap samples would be needed before estimates could be quantitative enough to approximate the true situation better. The amount of scatter in the third cohort of copepodites appears to be even less.

In summary, although anomalies exist in the data they appear small and I will assume they will lead to insignificant errors in the final estimates of instar mortality and production. The results of the analyses using the

FIGURE 9

Change in abundance with time for eggs, nauplii, and copepodites of *L. minutus* in each of the 3 cohorts produced in Bluff L. in 1971.


ice
ice
Leptodiaptomus minutus
BLUFF L. 1971
Eggs
Nauplii
Copepodites
1st COHORT
2nd COHORT
3rd COHORT
(1972)
NUM. OF ANIMALS x 10^4 / m^2
24
20
16
12
8
4
8
4
8
4
J
F
M
A
M
J
J
A
S
O
N
D

graphical method of Rigler and Cooley are presented in Fig. 10. Parts of the data from Fig. 10 together with estimates of mean development time are summarized in Table 14. Each vertical panel in Fig. 10 represents an analysis of each of the 3 cohorts produced in 1971. In each of these panels the top figure is a smooth curve drawn through a plot of the mean pulse time (M_n) against instar. The differences in smoothed values of M_n read from the top curve are plotted in the figure below (M_{n+1} - M_n against instar). The third row contains estimates of instar survivors greater than 100 x$10^2/m^2$, including eggs, (but not diapausing eggs) which were determined independently of the graphical method for reasons given elsewhere.

a. First Cohort 1971 (71/1)

In 1971 the first cohort was the most important of the cohorts in terms of production and absolute number recruited. There was very little mortality from the eggs through the N3 instar and from N6 to the CIV instar. Most of the mortality could be accounted for in 3 instars, N4, N5, and CV. The eggs, CIV, and CV instars accounted for approximately 28, 34, and 20% respectively of the total production for this cohort.

b. Second Cohort 1971 (71/2)

Although egg numbers for the second cohort were approximately 2/3 of the first cohort, total production was only about 1/4 as large. This can be explained by the large mortality beginning with N2 and continuing through until CIV, the last instar included in this cohort. Of approximately 2900 eggs formed for this cohort only 60 to 90 or 3% made it as far as the CIV instar. This accounts for the fact that 88% of the total production of this cohort was in the eggs.

FIGURE 10

The results of analysis of each of the 3 cohorts of L. minutus produced in Bluff L. in 1971 using the graphical method of Rigler and Cooley.

The first row is a plot of mean pulse time of each instar (M_n) versus instar. The second row is a plot of the successive differences in mean pulse time against instar. The third row is a histogram plot of the number of animals reaching the mid-point of development of each instar. The fourth row is the production of each instar plotted individually and cumulatively on the day when the mean pulse time occurs for each instar.

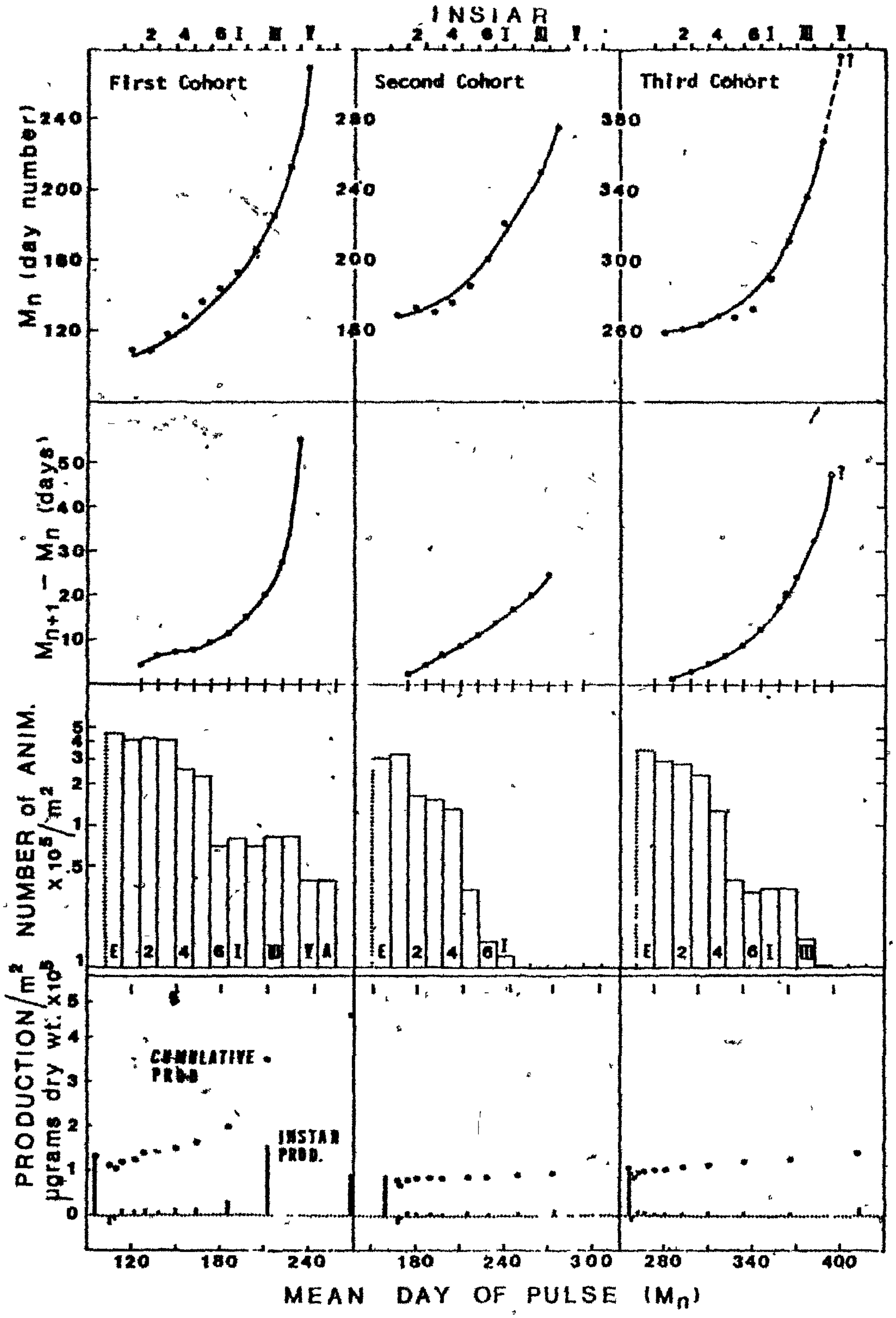

INSTAR
2 4 6 I III V
First Cohort
Second Cohort
Third Cohort
Mn (day number)
120 160 200 240
160 200 240 280
260 300 340 380
Mn+1 − Mn (days)
10 20 30 40 50
NUMBER of ANIM. x 10^5/m^2
1 .5 1 2 3 4
E 2 4 6 I III V A
E 2 4 6 I
E 2 4 6 I III
PRODUCTION/m^2 μgrams dry wt. x10^5
0 1 2 3 4 5
CUMULATIVE PROD
INSTAR PROD.
120 180 240 300 280 340 400
MEAN DAY OF PULSE (Mn)

Table 14

Data used in the graphical method of Rigler and Cooley to estimate instar mortality and production of L. minutus in Bluff L. in 1971.

Instar	Area	M_n (day number) Raw	Smooth	Estimated t_n (days)	# of Anim. ($x10^2/m^2$)	Instar Prod.	% of Total
First Cohort							
Egg	66637	-	-	15.2[a]	4384	1315	28
N1	12585	109.1	105.5	3.2[b]	3933	-197	- 4
N2	20270	108.4	109.6	5.0	4054	- 81	- 2
N3	26588	117.4	115.5	6.8	3910	117	3
N4	18848	128.3	122.6	7.4	2547	102	2
N5	17876	137.4	130.3	8.0	2235	112	2
N6	7447	143.4	139.5	10.4	716	36	1
CI	9734	153.2	150.7	12.0	811	97	2
CII	12421	165.4	165.4	17.4	714	136	3
CIII	20171	185.8	185.8	23.4	862	336	7
CIV	27037	213.1	213.1	31.2	867	1525	34
CV	32495	268.5	268.5	79.6	408	881	20
AD[c]	-	-	-	-	408	126	3
TOTAL COHORT PRODUCTION = 0.45 grams dry weight/m^2							
Second Cohort							
Egg	13490	-	-	4.6[a]	2933	880	88
N1	3495	168.4	169.2	1.1[b]	3177	-159	-16
N2	5056	173.0	171.3	3.1	1631	- 33	- 3
N3	7769	170.5	175.4	5.1	1523	46	5
N4	9257	176.0	181.6	7.1	1304	52	5
N5	3407	185.3	190.0	9.7	351	18	2
N6	1771	200.4	200.8	11.9	149	7	1
CI	1866	220.9	214.1	14.7	127	15	2
CII	1199	231.9	230.6	18.3	66	13	1
CIII	1234	250.4	250.4	21.3	58	23	2
CIV	2377	274.7	274.7	27.3	87	153	15
CV[d]	-	-	-	-	-	-	-
AD[c]	-	-	-	-	-	-	-
TOTAL COHORT PRODUCTION = 0.10 grams dry weight/m^2							
Third Cohort							
Egg	11167	-	-	3.2[a]	3490	1047	65
N1	2250	258.1	259.8	0.8[b]	2813	-141	- 9
N2	3825	260.0	260.9	1.4	2732	- 55	- 3
N3	8948	262.9	263.5	3.8	2355	71	4
N4	6106	268.7	267.7	4.6	1327	53	3
N5	3214	267.4	273.9	7.8	412	16	1
N6	2799	271.9	281.9	8.2	341	17	1
CI	5613	288.0	293.7	15.4	364	44	3
CII	7413	314.8	311.0	19.2	387	74	5
CIII	5132	339.0	335.0	28.8	178	69	4
CIV	4179	369.3	367.0	35.2	118	208	13
CV	4845[e]	-	414.0[f]	58.8?	82	177	11
AD[c]	-	-	-	-	82	25	2
TOTAL COHORT PRODUCTION = 0.16 grams dry weight/m^2							

Key to Symbols used in Table 14 and Explanation of Calculations

a = development times calculated using Equation 2 and in situ water temperatures
b = development times calculated using Equation 3 and in situ water temperatures
c = all adult estimates in each cohort assumed to be same as estimate of CV's
d = in second cohort it was assumed that no CIV's made it into the CV instar or adult instar
e = area under the numbers curve for CV up to May 19/72.
f = determined by extrapolation in Fig. 10

Sample calculation: Number of Animals Passing Through N1 and N2 instars in First Cohort

Number of animals passing through an instar in a cohort

$$= \frac{\text{area under the numbers curve}}{\text{mean cohort development time}} \qquad t_n = \text{mean cohort development time}$$

$$\text{For N1} = \frac{12585}{3.2} \frac{\text{anim-days}}{\text{days}} = 3933 \text{ animals}$$

Using Equation 1 $\quad M_{N2} - M_{N1} = 1/2(t_{N1} + t_{N2})$

Assuming that $t_{N1} = 3.2$ days (from in situ water temps. and Eqn 3)

therefore $109.6 - 105.5 = 1/2(3.2 + t_{N2})$

and $t_{N2} = 5.0$ days

Therefore for N2

the number of animals is $= \frac{20270}{5.0} = 4054$

(Note: all estimates in this example of areas and animals are $\times 10^2/m^2$)

Area = area under the numbers curves in animal-days ($\times 10^2/m^2$)
M_n = mean pulse time, given as day number in the year
Raw = M_n estimated from raw or "unsmoothed" data
Smoothed = M_n estimated from adjusted or "smoothed" data
t_n = estimated mean instar development time
Instar Prod. = expressed in micrograms dry wt. $\times 10^2/m^2$

c. Third Cohort 1971 (71/3)

Of approximately 3500 eggs in the last cohort of 1971 only about 70 or 2% made it to the CV instar. Mortality was greatest from N3 to N5 when nearly 2000 or 58% of the initial cohort died as survivors dropped from 2355 to 412. Although sampling was terminated in 1972 before all of the overwintering CV had moulted into the adult instar or died, for the calculations it was assumed that all CV (approximately 72) made it into the adult stage. As in the second cohort eggs accounted for most of the total production (approximately 65%).

d. First Cohort 1972 (72/1)

Only a portion of the population dynamics for this cohort are shown in Fig. 4 because sampling ended on May 19, 1972 just as CI were beginning to appear. Using Eqn. 2 and Eqn. 3 and in situ water temperatures estimates were made of the number of subitaneous eggs and NI produced respectively and have already been presented in Table 7. These results suggest that the first cohort of 1972 was only about ½ as large as the first cohort of 1971. The abundance curves for the other instars represented in samples from 72/1 are too incomplete to permit further analyses at this time.

e. Adults 1971-72

An estimate of the number of adults produced in a cohort cannot be obtained by solving Eqn. 1 as was done for the other instars since they do not pass out of this instar in the same way that juvenile animals do and therefore calcuation of a mean pulse time is superfluous. For the purpose of estimating production it was assumed that all CV animals became adults although the true figures are likely smaller. In early Aug. of 1971 the number of adults that had overwintered from the previous year dropped to 20 before rising because of recruitment from CV of 71/1. The estimate of CV in the first cohort of 1971 was 408 and the maximum number of adults from the smoothed curve of adult numbers was 500 (Appendix I). In terms of added production the difference between these two independent adult estimates is small since the dry weight increment for CV to Adult on the average for males and females is only 0.3 micrograms. Estimating adult numbers recruited from the second cohort of 1971 was not a problem since it was assumed for reasons given elsewhere that no animals made it past CIV. The estimate of CV and therefore adults for the third cohort was 82 and in terms of production by the adults represented only 2% of total cohort production. Even if none of the 82 CV reached adulthood the error involved is considered insignificant.

12. Other Estimates of Production of L. minutus in Bluff L.

For purposes of comparison, 3 other approaches were employed to estimate the production of L. minutus in each of the 3 defined cohorts produced in 1971. For convenience these methods will be referred to as a) Allen curve method, b) Soviet graphical method, and c) death rate method.

Because of the extra time and cost of obtaining data on all instars, it is not unusual to find that individuals of a population have been placed into age categories such as egg, nauplii and/or copepodites, and adults (i.e. not all individuals have been identified to a specific instar). This practice while considerably reducing labour will inevitably lead to a loss of information concerning the population dynamics of individual instars but it is possible that for purposes of estimating production by the population they may be adequate.

In the Soviet graphical and death rate methods I have made the necessary calculations by assuming that I only had data on eggs, total nauplii, total copepodites, and adults in each cohort. For the Allen curve method I have used the data on all instars as was done for the Rigler and Cooley graphical method. The question I wish to answer is are there significant differences in production estimates that use data on age categories as opposed to individual instars for a given cohort?

The data on abundance of all instars excluding eggs and adults have been replotted for each cohort in Fig. 11 and a smooth curve has been drawn through the points. In subsequent calculations where estimates of daily cohort abundance are needed they will be read from the curve. By doing this it is assumed that sampling errors will be reduced and that if a sampling error was present on a particular day it affected all instars proportionally. This last point is most likely not rigidly correct (Cooley 1970) but it is assumed that the error involved as a result of the correction will be minimal and will lead to a better overall estimate than if no correction for obvious anomalies was made at all.

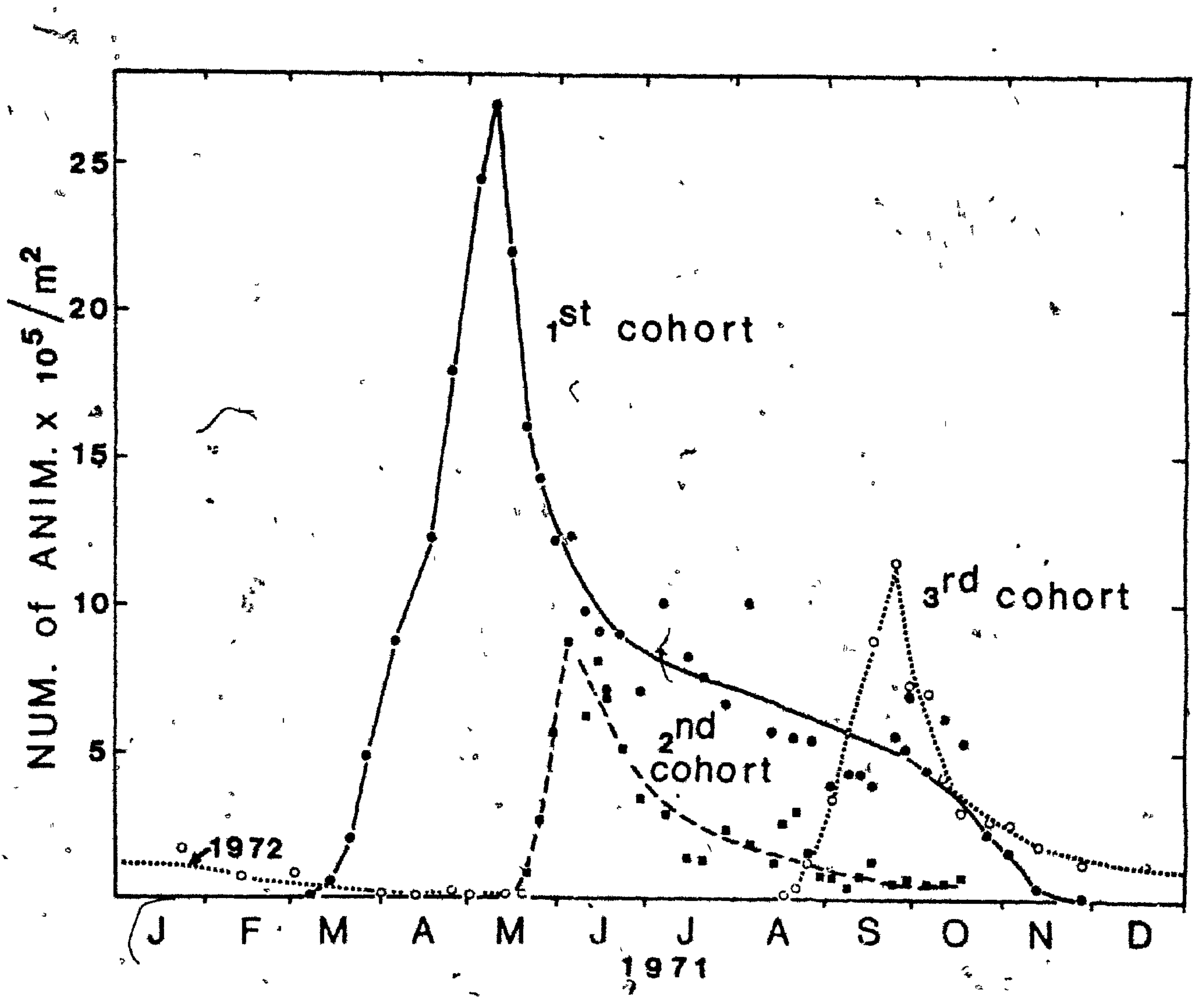
In each of these alternative methods it was also necessary to estimate the number of eggs and the number of animals reaching the last instar of the cohort (adults for 71/1 and 71/3, and CIV for 71/2). For eggs the simplest and most direct approach was to divide the area under the egg abundance curve by a mean development time as described previously, and thus in all 4 methods the absolute estimate of egg contribution will be the same for a particular cohort.

Estimating the number of adults in a cohort is more difficult since animals do not moult through this last instar and the amount of time they spend in it is determined by predators, food supply, and senility. An estimate of an average time spent in the adult instar is impossible even with information available on temperature and food supply. The adult

FIGURE 11

Changing abundance with time for the total number of animals in the NI to CV instars in each cohort.

Smooth curves have been drawn by eye through the data points after peak numbers have been attained and the cohort abundances have begun to decline. In subsequent calculations where cohort abundance estimates are needed they are interpolated from the curve.


NUM. of ANIM. x 10^5/m^2
25
20
15
10
5
1st cohort
2nd cohort
3rd cohort
1972
J
F
M
A
M
J
J
A
S
O
N
D
1971

population may even be made up of individuals derived from different cohorts in different years. For example in Fig. 4 the adults of Nov. 1970 can clearly be followed to mid-August of 1971 at which time new adults began to appear. In spite of these difficulties a minimum estimate of the number of adults contributed by each cohort can be derived by taking the observed adult population size near the time when the last CV disappears in the cohort. For example in 71/1 the last CV are found near the end of November when the maximum adult population of 500 was found (Appendix I). Assuming all overwintering adults from 1970 have died (the population was approximately 20 on Aug. 17, 1971) this population represents a minimum estimate of the number of adults recruited from 71/1. The estimate from the method of Rigler and Cooley was 408 (Table 14) which further suggests that 500 adults produced in 71/1 is not an unreasonable figure. However it should be noted that if mortality early in the life of an adult is large a severe underestimate will result from this approach.

The second cohort could not be traced with confidence past the CIV instar and for simplicity it was assumed that no instars reached CV although it is probable that a few did. The last CIII of 71/2 appeared on Sept. 24 when the size of the CIV population was approximately 50. On the previous sampling day of Sept. 16 the estimated number of CIV was 83 but the "smoothed" cohort total for all instars on this day from Fig. 11 was 60 as opposed to the unsmoothed estimate of 131. Assuming all instars were equally affected by this apparent sampling anomaly a corrected estimate of CIV abundance would be 60/131 x 83 = 46. Similarly corrected estimates of CIV abundances for Sept. 29 and Oct. 5 when recruitment from the lower instar had ended were both 50. Therefore it was assumed that at least 50 CIV were recruited in 71/2. The independent estimate from the method of Rigler and Cooley was 87.

In a similar fashion it was estimated that 44 CV were recruited in 71/3. On Jan. 23 the unsmoothed CV population was estimated to be 57, but the smoothed and unsmoothed cohort totals on this day were 100 and 161 respectively. Therefore the adjusted estimate of CV for Jan. 23 is 100/161 x 57 = 44. The estimate from Rigler and Cooley's method is 82. For purposes of comparison with their method it was also assumed that all of these 44 CV became adults.

These arbitrary assumptions will almost certainly lead to errors in final production estimates but because the number of animals involved is so small and because the weight increment from CV to adult is small compared with increments between other copepodite instars these errors will be unimportant to overall cohort production.

a. Allen Curve Estimates of Production

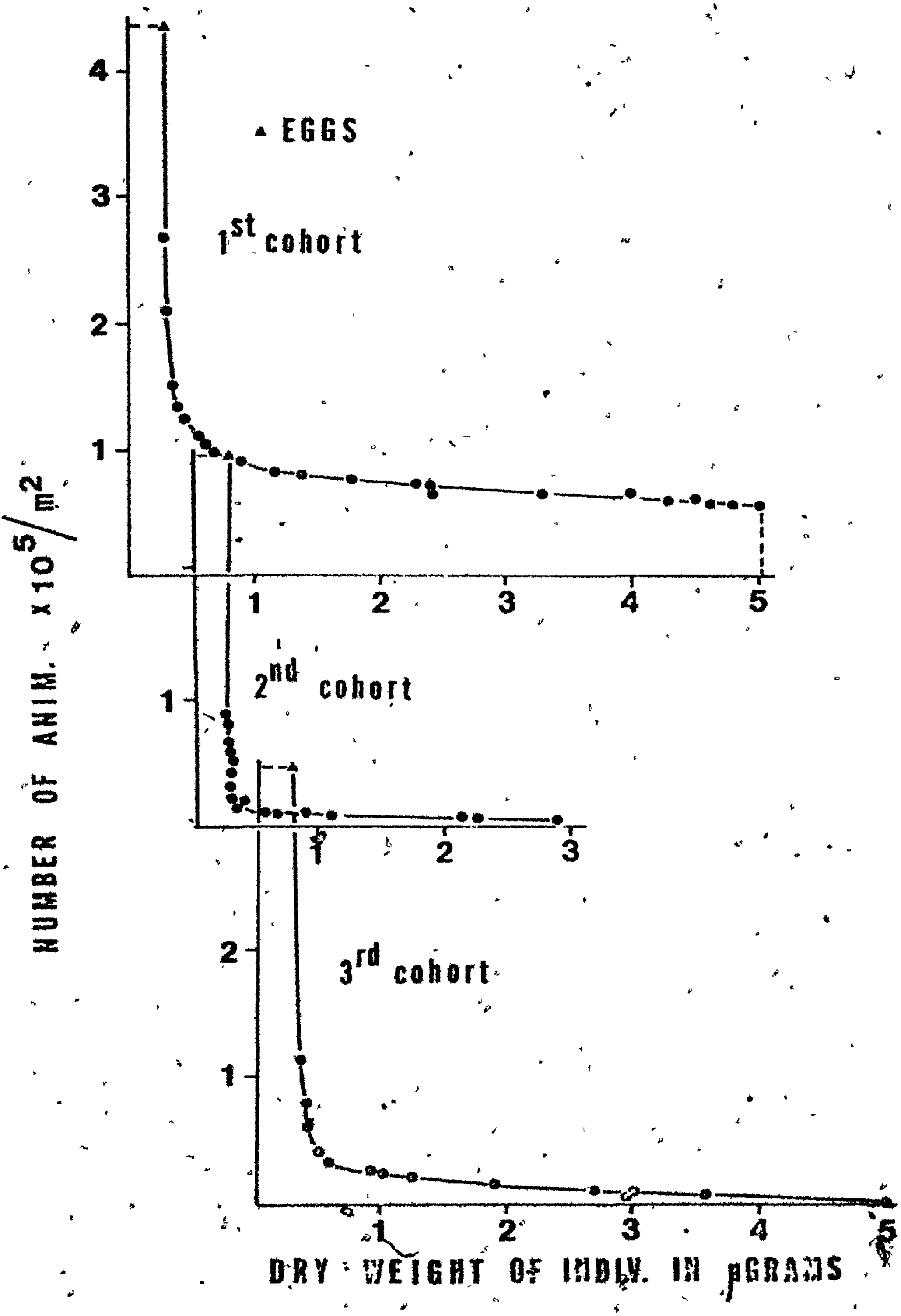
A curve which approximates the decline in numbers of a cohort against changing mean weight of an individual is often referred to as an Allen curve (Waters 1969) although Mann (1969) has recently pointed out that the concept can be traced as far back as Boysen Jensen in 1919.

In plotting the Allen curve a mean dry weight representing all individuals excluding eggs and adults on each sampling day of each cohort was determined by multiplying the dry weight of each instar from Table 8 by its abundance (Appendix 1). The top left point in each Allen curve is the number of eggs that were laid to form the cohort. Since an Allen curve follows the decline of a cohort the next lower point and all subsequent points in each curve were determined by the declining numbers read from the right hand side of the cohort peaks from Fig. 11. This type of an estimate does not directly make use of the information

FIGURE 12

Allen curves for estimating production by L. *minutus* in Bluff L. for each of the 3 cohorts produced in 1971.

The top left point in each curve is an estimate of the number of eggs produced in each cohort. All other estimates of animals numbers are excluding eggs and adults and were obtained by interpolation from Figure 11.


▲ EGGS
1st cohort
2nd cohort
3rd cohort
NUMBER OF ANIM. x10^5/m^2
DRY WEIGHT OF INDIV. IN μGRAMS
4
3
2
1
1
2
3
4
5
1
1
2
3
2
1
1
2
3
4
5

describing the initial rise of a cohort when hatching rate exceeds mortality.

Until N4 animals do not gain weight and it is possible for the mean dry weight of an individual to be less than that of eggs after peak numbers in a cohort (from Fig. 11) have been reached. This was the case in the second cohort and these losses are taken into account in the calculations.

Estimates of production as the area under Allen curves were determined planimetrically. The area under the 3 curves in Fig. 12 representing the 3 cohorts includes production by all instars, including eggs, but excluding adults. The contribution to total cohort production by nauplii and copepodites was calculated by subtracting the contribution of the eggs (maximum number of eggs x mean dry weight). For purposes of comparison the results are summarized in Table 16 (page 74) as production by 1) eggs, 2) nauplii and copepodites, and 3) adults. A discussion of the production estimates for each category will be deferred until similar calculations have been presented for the next 2 methods.

b. Soviet Graphical Method for Estimating Production

When data are available only for general age categories (eggs, nauplii, copepodites, adults) a graphical method developed by the Soviet workers Winberg, Pechen, and Shushkina (1965) can be used to estimate cohort production. This method is illustrated in Winberg (1971) and Edmondson and Winberg (1971) and for simplicity I will refer to it as the Soviet graphical method.

Four separate graphs for each cohort are used to estimate the production of immature instars excluding eggs. The top row is a plot of the decline in numbers over time based on 4 estimates of population size (Figure 13). Basically their approach is to estimate the number of eggs

FIGURE 13

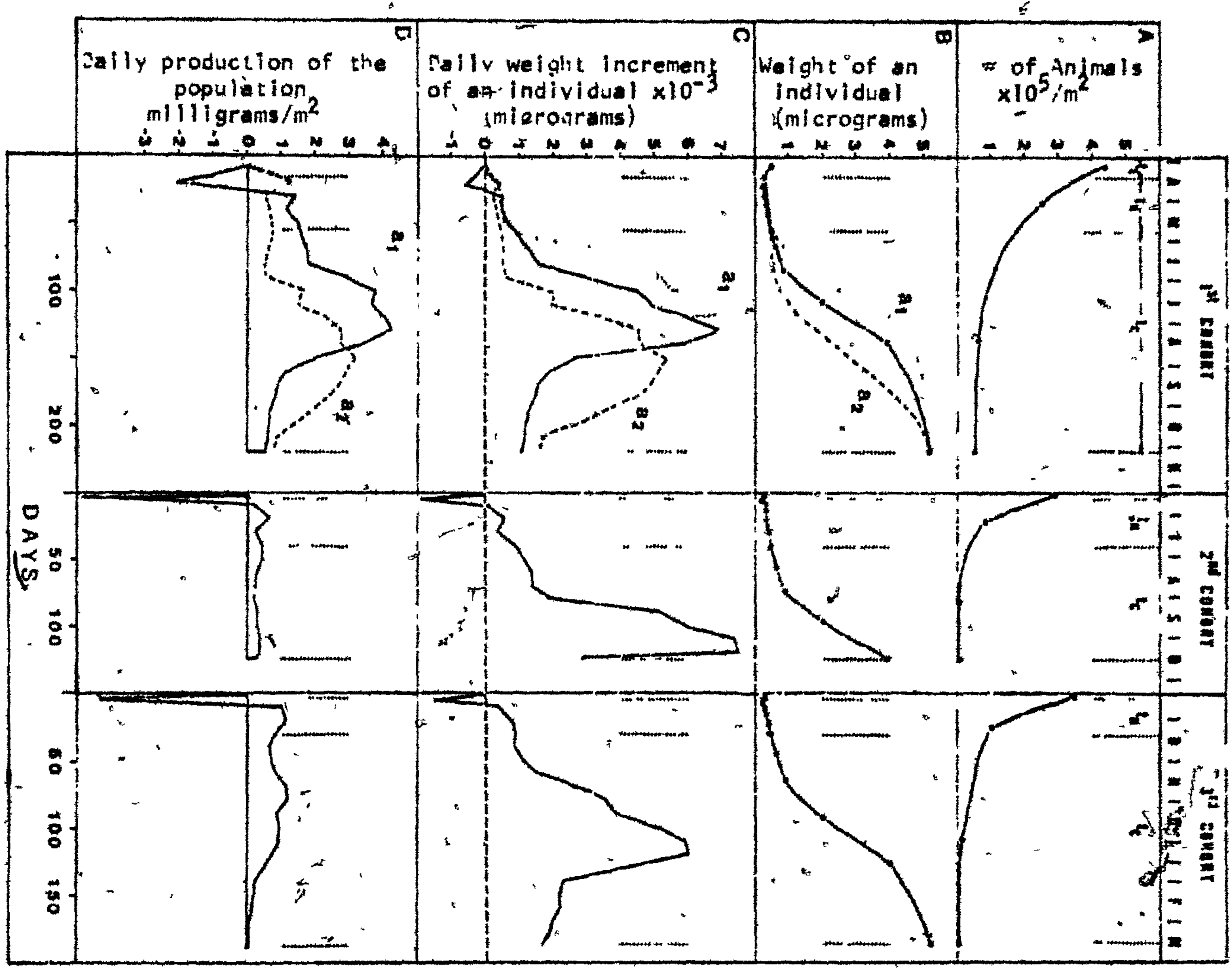
The Soviet graphical method of calculating copepod production for the 3 cohorts of L. minutus in Bluff L. (after Winberg, Pechen, and Shushkina 1965, and Pechen and Shushkina 1964, from Edmondson and Winberg 1971).

The alternate estimates of cohort production in 71/1 using a_1 and a_2 growth curves for the individual in row B are: 0.424 gm/m^2 and 0.310 gm/m^2 respectively, as compared with 0.348 gm/m^2 using the more empirically derived growth curve.

Symbols used in Figure 13

- t_E is the average egg development time over the cohort
- t_N is the average total naupliar development time over the cohort
- t_C is the average total copepodite development time over the cohort

t_E, t_N, and t_C were taken from Table 14


D
Daily production of the population milligrams/m^2
-3 -2 -1 0 1 2 3 4
C
Daily weight increment of an individual x10^{-3} (micrograms)
-1 0 1 2 3 4 5 6 7
B
Weight of an individual (micrograms)
1 2 3 4 5
A
# of Animals x10^5/m^2
1 2 3 4 5
a1
a2
DAYS
100
200
50
100
50
100
150
1st COHORT
2nd COHORT
3rd COHORT

(N_E), nauplii (N_N), and copepodites (N_C) produced by a cohort by dividing the total number of a given stage by its development time for each day of its life. Since I do not have the necessary laboratory derived information on instar development times to make these calculations I will use the estimates of total naupliar and total copepodite development times generated by the graphical method of Rigler and Cooley (Table 14) and my estimate of the average number of animals produced in each major group will be derived by dividing these times into the area under the appropriate abundance curve. The necessary information needed to construct the four curves for each cohort is summarized in Table 15.

For example in the first cohort of 1971 the average development times for eggs, nauplii, and copepodites are 15.2, 40.8, and 163.6 days respectively and are marked on the X axis as shown in the first column of the first row of Fig. 13. The average number of individuals for each major category is determined by dividing the development time into the area under the numbers curve (from Fig. 9) for that category. In the first cohort the area under the naupliar curve was 10,302 animal-days which when divided by the average naupliar development time of 40.8 days yields an average nauplii estimate of 2520 animals. This and similar estimates for copepodites are placed in the middle of the segment on the X axis which corresponds to the length of development for that age category. The last point in this first curve is the number of adults produced and is placed after all egg, naupliar and copepodite development is completed. A line joining the 4 points is assumed to approximate the decline in individuals of a cohort over time.

The second row in Fig. 13 traces the increase in mean dry weight of an individual as it ages. The information on <u>in situ</u> instar

TABLE 15

Various parameters needed to calculate production of *L. minutus* in each of the 3 cohorts produced in 1971 using the Soviet graphical method.

		First (71/1)	Second (71/2)	Third (71/3)
Average development times in days for each major age category (from Table 14)	Eggs	15.2	4.6	3.2
	Nauplii	40.8	38.0	26.6
	Copepodites	163.6	81.6	157.4
Areas under the numbers curves in animal-days for each of the major age categories (Fig. 9) ($\times 10^2/m^2$)	Eggs	66637	13490	11167
	Nauplii	10302	31944	27301
	Copepodites	102942	6153*	25610
Average number of animals produced in each major age category ($\times 10^2/m^2$)	Eggs	4384	2933	3490
	Nauplii	2520	840	1030
	Copepodites	625	75	164
	Adults	500	0*	44

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* In 71/2 it was assumed that only 50 CIV's were produced and that none of these animals made it past this instar

Dry weight of an egg at the mid-point of its development = 0.3 μgms.
Dry weight of a CI at the beginning of its development = $\frac{1}{2}(.40 + .52) = .46$ μgms.
Dry weight of an adult at the beginning of its development = $\frac{1}{2}(5.02 + 5.33)$ = 5.18 μgms.
For second cohort only, dry weight of a CIV at the end of its development = $\frac{1}{2}(2.86 + 5.02) = 3.99$ μgms.

development times from Table 14 was again used to draw the S shaped curve of the second row. However the Soviet method is supposed to be applicable to situations where information on development and dry weight is only avilable for 3 major life divisions and from these 3 points an S shaped curve is assumed to approximate true individual growth. Thus for the first cohort two altermate S shaped curves a_1 and a_2 were drawn by eye using only the weight of N1, C1, and Ad individuals at the beginning of their development period.

The third row in Fig. 18 contains graphs of the daily weight increment of an individual in the population over time. These points were obtained by interpolating the dry weight increment of an individual at regular 10 day intervals in the previous graph.

The last row of graphs is a plot of daily production by the cohort obtained by multiplying the interpolated number of animals in the population determined from the first row of figures by the daily individual dry weight increment of the third row of figures and plotting these numbers at the same 10 day intervals over time. The area under this curve is total production for the cohort.

The adult production is determined by taking estimates of the number of adults produced in a cohort and multiplying them by the weight increment from CV to adult. It should be pointed out that the dry weights of all instars of L. minutus in Table 8 more closely approximate the weight of an instar after $\frac{1}{2}$ of the development has been completed. Thus if the dry weights of CV and adults are 5.02 and 5.33 micrograms respectively then the weight of a CV just before it moults or conversely an adult as it enters this instar is $\frac{1}{2}(5.02 + 5.33) = 5.18$ micrograms. Therefore in this method the production increment of adults will be the surviving adults x (5.33 -

5.18) = 0.15 micrograms dry weight. Similarly the weight of an animal at the end of egg development will be $\frac{1}{2}$ the dry weight of an egg and an NI = $\frac{1}{2}(0.3 + 0.25)$ = 0.28 micrograms. This accounts for the negative daily dry weight increment per individual in the third row of figures as eggs pass into the first nauplIar instar, and the subsequent negative daily production early in the cohort as depicted in the last row of figures in Figure 13.

A summary of the contribution of each of these major groups to total production is given in Table 16. The estimates of production by NI to CV instars in the first cohort based on the 2 alternate assumed S shaped growth curves a_1 and a_2 are 0.424 and 0.310 gms dry wt./m^2 as compared with 0.348 gms dry wt./m^2 from the more empirically derived curve. This corresponds to differences of +22 and -11% respectively. In terms of total cohort production the differences are even smaller at +15 and -8% respectively since in all 3 cases the contribution by eggs and adults would be the same.

c. Death Rate Method for Estimating Production

Another estimate of cohort production was determined, based on an estimate of the finite death rate of the cohort (excluding eggs and adults). The total production by the cohort was taken as the sum of 1) the production of eggs (mean dry weight x number) 2) the dry weight increment from the previous instar of surviving adults (5.33 - 5.02 x number of adults produced by the cohort), and 3) the biomass lost due to mortality in the NI to CV instars. The last term is determined by calculating the biomass lost between 2 consecutive sampling days of interval t days and summing for all intervals over the cohort until all CV have either died or become adults. The production lost in each interval P_t is defined by

$$P_t = \left(\frac{w_o N_o + N_t w_t}{2}\right).t.D \qquad \text{Equation 7}$$

where w_o and w_t and N_o and N_t are the average weight of an individual and the size of the cohort on 2 consecutive sampling days respectively of interval t days, and D is the finite death rate for the cohort over the interval. In a simpler form Equation 7 becomes

$$P_t = \overline{B}.t.D \qquad \text{Equation 7'}$$

where $\overline{B}$ is the average cohort biomass over the interval.

The instantaneous death rate d of the cohort was determined from the equation

$$d = b - r \qquad \text{Equation 8}$$

where b is the instantaneous birth rate determined from

$$b = \frac{\ln(E/A) + 1}{D} \qquad \text{Equation 9}$$

and E is the total number of eggs in the population, A is the total number of adults, D is egg development time, and r is the instantaneous rate of increase of the cohort determined from two successive estimates of cohort size N_o and N_t from

$$r = \frac{\ln N_t - \ln N_o}{t} \qquad \text{Equation 10}$$

(see Appendix 4 for an explanation of Equation 9). Once d is known then the finite mortality rate of the cohort can be approximated by

$$D = 1 - e^{-d} \qquad \text{Equation 11}$$

where e is the base of natural logarithms.

In using these equations one assumes that over a sampling interval b and r remain constant (stable age distribution) but this is usually not the case because of the dynamic nature of various parameters controlling rates of increase and decrease. The magnitude of deviations in both b and r over the interval will determine the error in D which will directly affect the production estimate.

Theoretically r should never be greater than b but was at the beginning of each cohort. This is most likely due to inaccurate estimates of cohort size when the population is small and changing environmental conditions over the interval. Since r is determined from successive estimates of cohort size this error will be inherent in r estimates. On those few occasions when r was greater than calculated b it was assumed that d was zero. Most likely in these instances d was in fact small but since this anomaly occurred only when numbers were small the total production will also be small and the error in P_t will be minimal.

Estimates of production using the death rate method are summarized in Table 16.

13. Production in Bluff L. by *L. minutus* - the 4 methods

The estimates of production summarized in Table 16 show remarkable agreement for the 4 methods discussed above in all 3 cohorts with 1 exception. Assuming that the first 3 methods more closely approximate the true figures, because in all instances they are nearly the same, then the estimate for 71/3 using finite cohort death rates is twice as large and probably anomalous. The estimate for 71/1 using this last method is also slightly larger than the other 3 while for 71/2 it is approximately the same as the others. Possible explanations for these differences will be treated in the General Discussion after cohort survivorship curves have been presented to explain partially the discrepancy.

One reason for the close agreement in these methods is that production of eggs was calculated in the same way for all methods and contribute a significant proportion to total cohort production. In the 3 cohorts eggs

TABLE 16

A summary of production estimates using 4 different methods for the 3 cohorts of L. minutus produced in Bluff L. in 1971.

All production figures are expressed as gms. dry wt. /m^2. The production by eggs was calculated in the same manner for all 4 methods. It was assumed for reasons given elsewhere that no animals developed past CIV in 71/2.

		Method Used to Estimate Production			
		a	b	c	d
Cohort	Age Category	Rigler and Cooley	Allen Curve	Soviet	Finite Death Rate
First (71/1)	Eggs	.132	.132	.132	.132
	NI - CV	.306	.337	.348*	.415
	Adults	.013	.016	.007	.016
	TOTAL	.451	.485	.487	.563
Second (71/2)	Eggs	.088	.088	.088	.088
	NI - CIV	.014	.010	.017	.014
	TOTAL	.102	.098	.105	.102
Third (71/3)	Eggs	.105	.105	.105	.105
	NI - CV	.053	.057	.074	.262
	Adults	.003	.001	.001	.001
	TOTAL	.161	.163	.180	.368

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*Alternate estimates of production by NI-CV for 71/1 using the Soviet method and 2 different assumed growth curves (a_1 and a_2 in Fig. 13) for the individual are .449 and .563 gms. dry wt. / m^2 respectively

2 OF/DE 2

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accounted for approximately 29, 88, and 63% respectively of total cohort production. However there is still close agreement for estimates of total nauplii and copepodite production between the methods excluding the one exception noted above.

GENERAL DISCUSSION

The primary purpose of this study was to obtain information on the population dynamics and production of an important zooplankter *Leptodiaptomus minutus*. The population in Bluff L. was chosen because its overwhelming numerical dominance suggested that the situation would be a simple one for study. The small and shallow nature of Bluff L. made it easy to sample all strata while the lack of an inlet and only a trickling outlet prevented significant immigrations and emmigrations of any plankters, again simplifying the system. Since most of the lake is isothermal, it was relatively easy to obtain good estimates of mean temperatures experienced by various fractions of the population over extended periods of time. Although isolated, Bluff L. was still close enough to the laboratory to make it readily accessible at any time, and a continuing study on its chemical characteristics (Ogden unpublished) provided important accessory data. It was decided that to interpret the results from field sampling more fully information was needed on a variety of parameters that could only be determined from laboratory experiments. As a result information on egg and naupliar development as related to temperature, dry weights, and diapause development of *L. minutus* and a possible competitive congener, *A. spatulocrenatus*, have also been included.

I. The Life Cycle of *L. minutus* in North Temperate Lakes

Information on abundances of calanoid life stages or groups of life stages (egg, nauplii, copepodites, adults) are needed to elucidate fully the life cycle of copepods. Without such data sampling variability will make it difficult to say with certainty that small peaks and accompanying depressions represent true population phenomena (Cassie 1971). Although, to my knowledge, this is the first in depth study of the population dynamics of this species, the prexisting information on abundance of egg, nauplii, copepodite, and adult groups reveal that there is a consistency in the life cycle of L. minutus in the western and eastern limits of its range. An overwintering population, primarily adult, begins breeding intensely late in winter under ice or early in spring, and continues to do so until late in the fall. Throughout the summer, egg production is quite low but may increase again in the fall as was the case in Bluff L. in 1971. By including data on juvenile abundance Davis (1972) was able to argue convincingly that L. minutus in Hogan's Lake in Newfoundland had 2 distinct generations. In 2 consecutive years summer pulses of juveniles in July and mid-October gave rise to peak adult numbers in August and late fall respectively. He further clarified the life cycle by noting that throughout the winter naupliar instars were absent and suggested that egg carrying females were producing diapausing eggs. This description is consistent with the population in Bluff L. except that no eggs were present in the population from Nov. to Jan. Schindler and Noven (1971) report a basically similar life cycle for L. minutus in Lakes 122,132, and 229 of the Experimental Lakes Area in the Kenora region of Northern Ontario and in Clear Lake in Southern Ontario.

The data from these studies suggest that one can expect to find a large population of adult L. minutus in small north temperate lakes during the winter. However Rigler and Langford (1967) noted an absence in the winter in Silver L. in Southern Ontario of L. minutus adults which in the summer represented more than 80% of the total number of adult diaptomids of 3 congeneric species (Leptodiaptomus sicilis, Leptodiaptomus minutus, and Skistodiaptomus oregonensis). In the winter L. sicilis represented 100% of the adult population of diaptomids. In Leland Lake which contained 2 diaptomid species, L. minutus and L. sicilis, they found 99% of the adults were L. minutus in summer to only 1% for L. sicilis. The exact reverse was true for the winter population of adults. Clearly the situation in these last 2 lakes is more complicated but in view of the results from Bluff L. and the others mentioned it appears that there is competition in the winter for some resource and that L. sicilis has a significant effect in limiting population numbers of L. minutus. The fact that both of these species have been put in the same subgenus on the basis of morphology further suggests that they are closely related even though L. sicilis adults are approximately 50% longer. A study of the population dynamics of both species coexisting in a lake like Leland or Silver would be a logical extension of the results from this study.

It also appears as though A. spatulocrenatus does not significantly influence the population of L. minutus in Bluff L. since its numbers are always at least 20x smaller. Three mechanisms have been suggested whereby species such as L. minutus and A. spatulocrenatus reduce competition between themselves (Sandercock 1967): 1) size differences implying different sizes of food filtered, 2) vertical separation, and 3) seasonal separation. Like L. sicilis, A. spatulocrenatus is larger than L. minutus by about 50% (i.e. for adults) in length and at times as much as 5x heavier as indicated by dry weight (Table 9). Both species appear to suffer little mortality through winter but the faster developing larger species quickly approaches adult size in the warmer part of the year and thus prolonged competition of similar sized instars is probably minimal. There was no obvious vertical separation of adults which may be partially accounted for by the fact that most of the lake was unstratified and quite shallow. Rigler and Langford (1967) in examining congeneric occurrences of Diaptomus species in 100 small Southern Ontario headwater lakes noted that generally, coexisting species tended to congregate at different depths but vertical separation was not as complete as had been reported by some authors previously in a few isolated cases (Langford 1937, Worthington 1931). Although more data are needed it appears at most times of the year at least 2 of the mechanisms for reducing competition, seasonal and size differences, were in effect for L. minutus and A. spatulocrenatus in Bluff L. A similar conclusion was arrived at by Sandercock (1967) for 3 coexisting diaptomids inhabiting stratified Clarke L. in Ontario. Whatever the reasons, A. spatulocrenatus was never more than 5% as abundant as the dominant L. minutus in Bluff L. and was never more abundant in any of the other 5 lakes in the Halifax-Dartmouth area that contained both species.

2. The Importance of Diapausing Eggs and Their Development

Although both L. minutus and A. spatulocrenatus appear to survive the winter in Bluff L. with little mortality neither species breeds over the whole period and both produce resting eggs in early October and late August respectively, that are dropped to the sediments apparently in preparation for winter Diapause is an obvious and common mechanism to insure that the species will not be eliminated from the lake if for example it were to go anaerobic under ice. Depending on the species there may be several parameters (food shortage, density, temperature) which play a role in the induction of diapause (Stross 1969, Watson and Smallman 1971, Elgmork 1959, 1967) but photoperiod may be most important. Termination of a specific diapausing stage may also be controlled by different factors in different species. Brewer

(1964) found diapausing eggs of Aglaodiaptomus stagnalis, an inhabitant of seasonal ponds, had 2 periods of blocked development, one in summer and the other in winter. In this instance a reduction of dissolved oxygen was a necessary condition for terminating the diapause. Cooley (1971) found that diapausing eggs of Skistodiaptomus oregonensis incubated under winter temperatures of 4 °C would hatch at the same time in the laboratory as diapausing eggs that had spent the winter on the bottom of the lake. He also found that these resting eggs could be induced to hatch sooner if they were subjected to warmer temperatures only after a minimum amount of time at 4 °C. Elgmork (1959) working with diapausing copepodite stages of Cyclops strenuus strenuus found the diapause "may be terminated by internal physiological changes alone in a constant environment". Later (1967) he suggests that there is an internal clock that can wake the animals in the absence of environmental fluctuations. These statements accurately describe the diapause development of eggs of S. oregonensis and probably L. minutus and A. spatulocrenatus, all North temperate calanoid copepods. For the latter 2 species in this study it was observed (Fig. 8) that they hatched at the same time as the overwintering adults began to produce subitaneous eggs in the lake, in late Feb. and mid-May respectively, so that nauplii from the two kinds of eggs cannot be distinguished from preserved samples.

Other factors may also modify the diapause development of copepod eggs. For example, the results also suggest that exposure to light over the period of incubation may speed development rate (Expt. 8, Table 13) and Cooley (1971), from experiments on resting eggs of S. oregonensis, and Main (1962) working with diapausing eggs of Epischura lacustris, suggest that low concentrations of dissolved oxygen over the period of incubation may slow the development rate.

It is of interest that diapausing and subitaneous eggs of both L. minutus and A. spatulocrenatus were a reddish-brown colour and indistinguishable morphologically. Cooley (1971) in noting that the subitaneous eggs of S. oregonensis were green and the diapausing eggs were reddish-brown had suggested that the difference might be found in other calanoids and thus useful in recognizing the 2 types of eggs. It is clear now that this is not universally true.

In Bluff L. the production of diapausing eggs does not appear to be absolutely necessary for the continuation of the species. The maximum estimates of 380 and 450 ($x10^2/m^2$ of mud surface area) deposited in the fall of 1970 and 1971 respectively are small compared to the 4384 and 2280 ($x10^2/m^2$) subitaneous eggs laid by the overwintering adults. However it has been noted that the estimate of 5 days as the average time diapausing eggs are carried before being dropped is too low and an artifact of experimental design suggesting the number of diapausing eggs laid may be less. The results from the sediment traps also suggest that the contribution of diapausing eggs may be smaller by about one-half. Clearly more field and laboratory experiments are needed before accurate estimates of the number of diapausing eggs dropped to the sediments can be made.

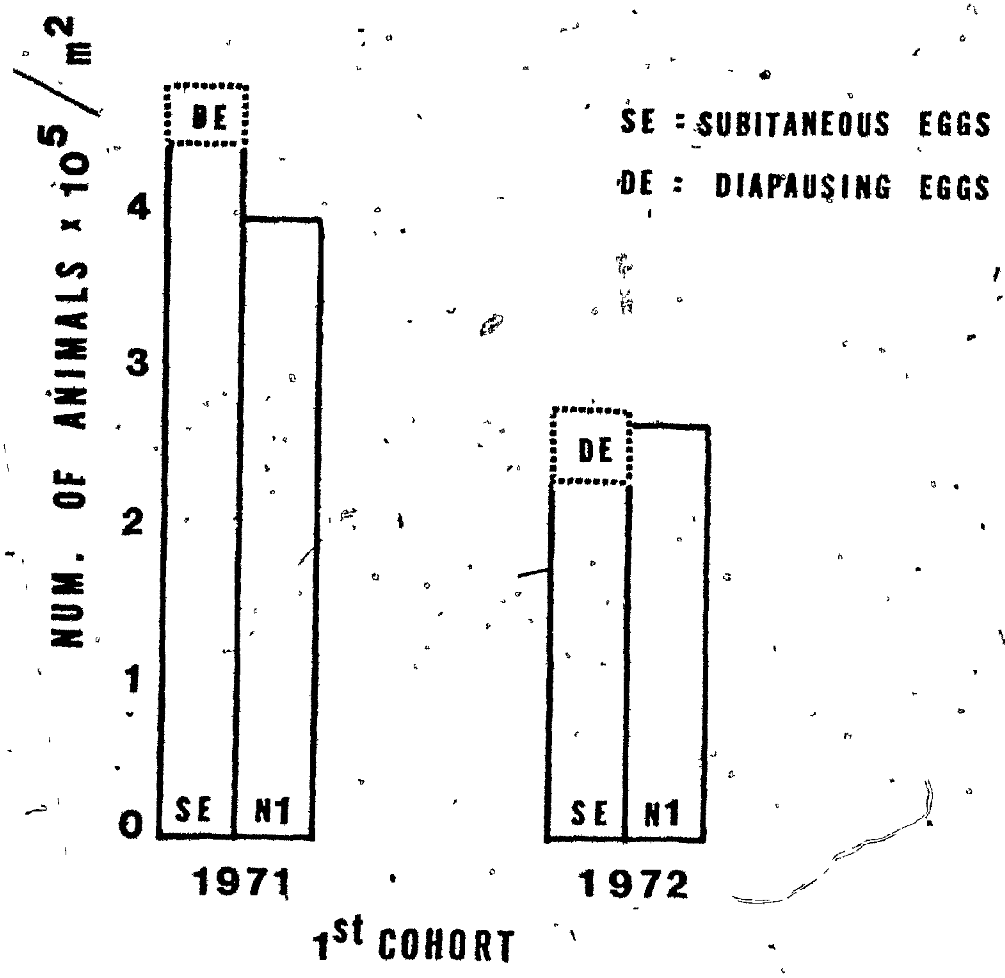
In any case if there is little mortality in the development of diapausing eggs as indicated by the laboratory experiments and there is little mortality in the first cohort of subitaneous eggs as indicated by analysis of field data then it is not surprising that the first cohort of N1 in 1972 (2633) was slightly larger than the number of subitaneous eggs formed (2279, see Fig. 14). The "extra" diapausing eggs on the

FIGURE 14

A diagram to show the relative number of diapausing and subitaneous eggs and the number of N1 in the first cohort of 1971 and 1972.

The numbers of diapausing eggs shown in the figure are based on an estimate of 5 days as the length of time a female carries an egg sac before it is dropped. Independent but inconclusive experiments involving sediment traps suggest that the number of diapausing eggs dropped may have been approximately ½ the numbers shown in the figure.

LEPTODIAPTOMUS MINUTUS · BLUFF L.



bottom of the lake could account for this difference but it should be noted that these 2 figures are at best only approximate. Also the mortality observed in the culturing of subitaneous eggs in the laboratory was close to zero, and predators that might selectively prey on animals the size of NI are almost nonexistent in March and April (Fig. 7).

While the evidence suggests that the production of resting eggs of L. minutus in Bluff L. are unnecessary for its continued existence there from year to year there is at least 1 documented case where they are essential. In Teapot L., Southern Ontario, S. oregonensis and all other zooplankters are annually eliminated from the limnetic zone in the winter due to anaerobosis under ice. In this extreme case the entire first generation of this species is recruited from mud sediments (Rigler and Cooley unpublished).

A full discussion of the importance of resting eggs for the continuation of A. spatulocrenatus in Bluff L. is impossible due to the lack of good quantitative data, however it appears that the situation may be the same as for L. minutus. Resting eggs are apparently produced late in August until early November, at which time all egg production stops (Figure 7). An overwintering population of adults begins forming subitaneous eggs in May which provide the basis of a new generation.

The situation for the other calanoid in Bluff L., Epischura nordenskioldi, is different. Apparently the entire first generation is derived from resting eggs since there are no adults in the lake from November through May. Further it was observed that plankton samples in May contained nauplii which were clearly neither L. minutus nor A. spatulocrenatus, nor typically cyclopoid in shape. These nauplii in fresh preserved plankton samples had a greyish tinge, noticeably different from the reddish diaptomid nauplii but morphologically similar to the diaptomids. They were first observed in May samples and by the first of June Epischura adults were present. Since there are no recorded instances of Epischura species diapausing in copepodite instars as is common in cyclopoids (Elgmork 1967), it is reasonable to assume these were Epischura nauplii and the entire development from NI to adults took approximately 1 month.

3. Subitaneous Egg Development

The integration of field and laboratory derived data has been encouraged (Hall 1971) for workers interested in defining and elucidating processes of production in freshwater zooplankton. As a result, information on egg development as a function of temperature has proliferated for many freshwater crustaceans. Schindler (1972) in a recent summary of the literature on this subject noted a "great similarity in the development times required by eggs of different species of freshwater crustacean zooplankton" and subsequently fitted a curve to data representing 11 different species including calanoids and cladocerans. McLaren (1965) and McLaren and Cooley (1972) have shown that Bělehrádek's temperature equation $D = a(T-\alpha)^b$, a power curve, when fitted to empirical data on egg development for marine copepods and for frogs respectively, adequately describes the process. They have shown that the constant α is related to temperature adaptation and a with egg diameter if b is assumed to be the same for all species of a related group. They suggest that it should be possible to predict egg development rates in related groups of species such as marine copepods and frogs, from a minimum of empirically derived data. It is this latter hypothesis that justifies the extra work involved in using an equation with 3 constants, a point apparently overlooked by Winberg (1971, page 51) who recommends simpler equations to describe egg development in copepods.

Table 17 is presented to show estimates of egg development at several temperatures over the natural range for the 2 diaptomids found in Bluff L. using Schindler's general equation and results from laboratory experiments. Schindler's equation does seem to describe adequately egg development for both species especially at temperatures above 10 °C but is clearly inadequate for *A. spatulocrenatus* at lower temperatures. In Bluff L. at least, this would not pose a problem since subitaneous eggs of this species were not present when water temperatures were this low. The large mortalities observed in eggs of *A. spatulocrenatus* incubated at 4 °C imply they are not adapted to survive these extremes. More information on other common north temperate zooplankters is needed before it can be said with certainty that the relation is adequate.

4. Estimating Naupliar and Copepodite Development Times

a. Rigler and Cooley's Graphical Method

Laboratory derived equations relating instar development and environmental temperatures are useful in estimating survivorship and production but there is a lack of information for life stages other than eggs. Freshwater copepods are notoriously difficult to culture successfully in a laboratory situation with excessive mortality often casting doubt on the reliability of applying the data to *in situ* conditions. Soviet workers apparently commonly estimate development rates at a variety of temperatures for instars other than eggs by employing a temperature correction factor based on an empirically derived curve (commonly called Krogh's curve) relating respiratory measurements of different species of animals (Winberg 1971). The basis of these cor-

TABLE 17

Egg development times for L. minutus and A. spatulocrenatus at several temperatures obtained from laboratory experiments (Appendix 3) and Schindler's general equation which is suppose to adequately describe 'egg development for a variety of north temperate zooplankters'(Schindler 1972).

Schindler's equation for all north temperate species (modified)

$$D = \frac{1}{.0426 + .0008T^2}$$

where D = egg development time in days

T = temperature in °C

Temperature °C	Egg Development Times in Days Schindler's Equation	L. minutus (derived from laboratory experiments)	A. spatulocrenatus
4	18.1	20.4	35.3
7	12.2	12.8	18.5
10	8.2	7.9	10.4
14	5.0	5.1	5.5
18	3.3	3.4	3.7
23	2.1	2.3	2.3

rection factors is that while absolute development times change depending on the animal the rate at which they change from temperature to temperature is constant for a given stage of a given animal. Thus if a development time is known at any 1 temperature the development time at any other temperature can be determined by multiplying the known time by a conversion factor. A table of the necessary conversion factors and the calculations involved can be found in Winberg (1971) and Edmondson and Winberg (1971).

It was the almost complete lack of information on development rates for freshwater calanoid copepod instars other than eggs and N1 at any temperature that led to the development of Rigler and Cooley's graphical method of estimating in situ development times. With these elusive parameters for each instar of a cohort it is possible to estimate the number of animals that pass through each instar and thus estimate mortality at each stage of an animals life. To fully interpret how an animal is adapted to and interacts with its environment it is necessary to understand how various factors affect its development and mortality.

Because some of the assumptions in theory or methodology are not rigidly correct the results are subject to error, but if gross they would necessarily be reflected in the data on survivorship. An excessive amount of negative mortality in the succeeding instars would be a criterion for rejection, but in none of the 3 cohorts is this seen to be a serious problem and small amounts of observed negative mortality are assumed to result from sampling errors and minor violations of the 3 stated assumptions.

It is unfortunate that the methodology of Rigler and Cooley's approach is open to a number of subjective and perhaps biased decisions which ultimately could affect the final results. In particular the drawing of smooth curves through plots of M_n against instar and $M_{n+1} - M_n$ against instar is in many cases a matter of some choice. However Rigler and Cooley (unpublished manuscript) found that while varying the shapes of possible curves may alter final instar numbers, especially in the younger naupliar instars, final production estimates are very similar. This results because implicit smoothing always occurs in the naupliar instars, because their life span is short compared with older stages but the number of sampling days determining their abundance curves is not proportionally greater. Therefore the estimate of a mean pulse time (M_n) from the field data for a naupliar instar is less accurate than for a copepodite instar. For example the estimated mean development time of NI in the second cohort of 1971 was 1.1 days (Table 14). A change of 0.1 days would result in a 0.1/1.1 x 100% = 9% change in estimates of the number of NI passing through this instar. A difference of 0.1 days in a later stage would have a decreasing effect on estimated numbers because development times would be greater in these older instars. By the CIII instar that had a calculated mean development time of 21.3 days the change would result in only a 0.1/21.3 x 100% = 0.5% difference and in terms of production would result in an insignificant change. Because of this weakness in the method and because mean development times are related to differences in consecutive mean pulse times (Equation 1) it seemed best to have independent estimates of the mean development time of the NI instar. This necessitated culturing the animals under varying temperatures in the laboratory and applying this information to <u>in situ</u> conditions. Another weakness in the method is that it does not provide a direct estimate of the number of eggs laid because of the violation of the assumption that development times are longer in successive instars. It has been shown in this study and in others (Elster 1954, Eichhorn 1957) that development times are longer in eggs as opposed to N1. This fact could also be deduced from the observation that the area under the numbers curve for eggs is always much larger than for the first few naupliar instars. A massive egg mortality could also explain this observation. For these reasons eggs were also cultured in the laboratory at various temperatures.

b. Cohort Survivorship

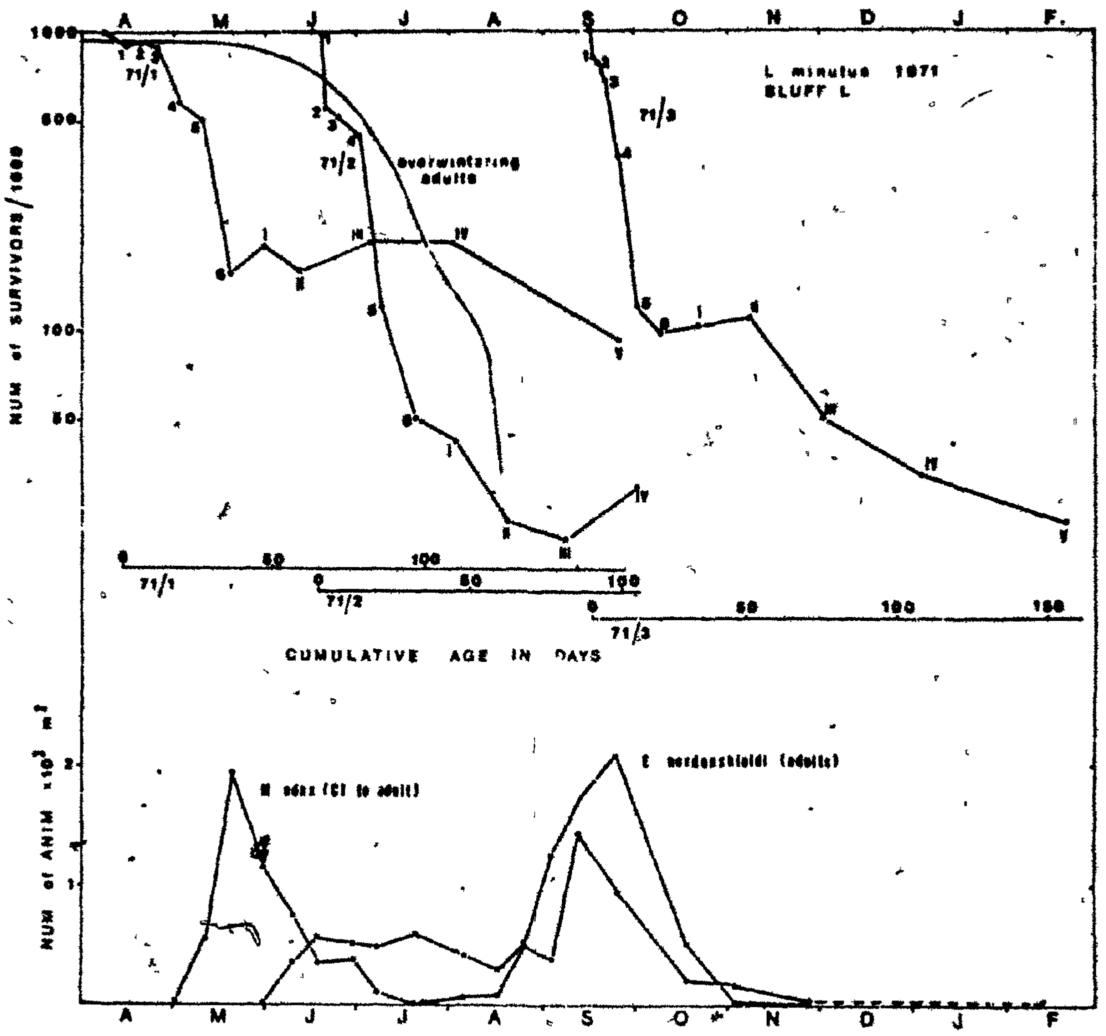
Assuming that this method does yield approximations of the number of animals that reach the median age in an instar or pass through that instar, a discussion of the factors contributing to instar mortality is warranted. The number of survivors of each instar in a given cohort have been replotted against cumulative age (i.e. Σt_n) in Figure 15. Also a survivorship curve for the overwintering adults of 1970 has been included and was calculated by assuming that their maximum numbers were 580 ($x10^2/m^2$) on Nov. 15, 1970. Survivorship has been expressed as the number of survivors/1000 born for each of the cohorts and in a semi-log plot such as this a straight line implies constant rates of mortality with respect to age. Besides predation, mortality can result from old age, disease, and perhaps nutritional deficiencies. Poor food conditions may prevent an animal from completing a moult or force it to spend longer times in instars. I have observed death at the moult with apparently healthy N1 and N2 in culturing vials in the laboratory but because this is a highly artificial and unnatural environment I cannot state with certainty that this happens regularly in nature.

In the absence of predators it would seem reasonable to expect eggs

FIGURE 15

Survivorship curves for the 3 cohorts of L. minutus produced in 1971, overwintering adults from 1970, and major zooplanktonic predators present during 1971.

Arabic numbers refer to naupliar instars and the Roman numerals refer to copepodite stages. The first point in each of the 3 cohort survivorship curves is an estimate of the number of eggs laid (excluding diapausing eggs) to form the cohort.


A M J J A S O N D J F.
1000
500
100
50
NUM of SURVIVORS/1000
L minutus 1971
BLUFF L
71/1
71/2
71/3
overwintering adults
1 2 3 4 5 6
I II III IV V
0 50 100
71/1
0 50 100
71/2
0 50 100 150
71/3
CUMULATIVE AGE IN DAYS
NUM of ANIM ×10³ m²
2
1
(CI to adult)
E nordenskioldi (adults)
A M J J A S O N D J F

and N1 to pass into the next instar with minimal mortality since these stages do not feed, their development rate being determined by temperature. Cooley (1970) found that development times could also be predicted above 10 °C for N2 of S. oregenensis from Teapot L. if phytoplankton was added to culturing vials in the laboratory. The amount of food necessary to insure predictable times was not determined, but may be minimal since stored food would most likely still exist from the egg stage. If this is true, then the success of N2 could vary depending on the availability and kind of foods that were present when the egg was formed by the female. There may also be a difference in food reserves for future naupliar development past N1 between diapausing and subitaneous eggs.

A low early naupliar mortality rate is evident in the data on survivorship in April of 71/1, when major zooplanktonic predators were absent (Fig. 15). Ignoring the presumably small contribution to the N1 from diapausing eggs, 89% of the eggs make it past the N3 instar and if all of the estimated 380 ($x10^2/m^2$) diapausing eggs laid also hatched the success is still as high as 82%.

The lack of data over the entire first cohort of 1972 prevents a similar calculation but rough estimates can be made if a number of assumptions about early instar development times are made. The calculated mean temperature experienced by eggs, N1, and N2 in both years is similar (for eggs, N1, and N2 in 71/1 the mean temperatures experienced are 5.7, 6.9, and 7.0 °C respectively, and in 72/1 are 6.0, 7.8, and 7.6 °C respectively). If it is assumed that the N2 of both years experienced similar food conditions (their requirements are assumed to be minimal anyway) then the estimated t_{N2} of 5.0 days from 71/1 (Table 14) can be used to estimate the number of N2 in 72/1 by dividing it into the area under the 1972 N2 numbers curve. Although only approximate this estimate 11,812/5.0 = 2362 N2 is very close to both the estimated number of eggs laid, 2730, (i.e. 2280 subitaneous eggs + 450 diapausing eggs) and surviving number of N1 produced, 2630 (from Table 7). A similar calculation can be made for the N3 in 72/1 if the decrease in their numbers is extrapolated to zero (at approximately June 5, 1972 in Fig. 4) and the area under the numbers curve is calculated. Using the t_{N3} from the previous year in 71/1 of 6.8 days yields an estimate 16385/6.8 = 2409 animals, suggesting an actual increase in N3 from N2 which although quantitatively impossible implies little actual mortality. Thus the data from the first cohort in both years suggest little mortality in the first 3 nauplIar instars.

Assuming that food does not play an important role in N2 development in nature it may also be possible to obtain independent estimates of t_{N2} for each of the 3 cohorts produced in 1971 and for the first cohort of 1972 independently of Rigler and Cooley's graphical method. Table 18 shows that any of the equations describing N1 development with respect to temperature for the 2 diaptomid species investigated here and S. oregonensis from Teapot Lake (Cooley 1970) could be used interchangeably to estimate development time of N1 if the mean temperature experienced by that instar over the cohort is known. If food was unimportant then it is possible that the same interchangeability could be true for the N2 of these 3 species and the equations relating N2 development and temperature available for S. oregonensis can be used to predict N2 development times for L. minutus in Bluff L. (Table 18). In 71/1 and 71/3 the estimated whole cohort mean development times for N2 based on water

TABLE 18

Estimates of *L. minutus* N1 and N2 *in situ* development times for the 3 cohorts of 1971 and the first cohort of 1972.

Cohort	Calc. mean temp. °C experienced	Estimated N1 development times in days in Bluff L. *Using eqns. for *S. oregon.* (Cooley, 1970)	Using t_{NI} for *L. minutus* (Equation 3)	Using t_{NI} for *A. spatulocr.* (Equation 5)
71/1	6.9	3.2	3.2	3.0
71/2	15.3	1.0	1.1	1.0
71/3	19.1	0.7	0.8	0.7
72/1	7.8	2.8	2.7	2.6

Cohort	Calc. mean temp. °C experienced	Estimated N2 development times in days in Bluff L. *Using eqns. for *S. oregon.* (Cooley, 1970)	Generated from graphical method of Rigler & Cooley (Table 14)
71/1	7.0	4.8	5.0
71/2	15.8	2.0	3.1
71/3	18.8	1.5	1.4
72/1	7.6	4.5	cohort incomplete

*Equations Describing Egg, N1, and N2 development of *Skistodiaptomus oregonensis* from Teapot L. (after Cooley, 1970)

t = development time in hours   T = temperature in °C

egg development time: $t = 47690(T+4.3)^{-2.08}$ Equation 12

total egg + N1 development time: $t = 98300(T+5.3)^{-2.21}$ Equation 13

total egg + N1 + N2 development time: $t = 119957(T+5.8)^{-2.15}$ Equation 14

To obtain N1 development time at any temperature T, solve Eqn 12 and Eqn 13 for T and subtract former from latter.

To obtain N2 development time at any temperature T, solve Eqn 13 and Eqn 14 for T and subtract former from latter.

temperature and laboratory derived development data for N2 of *S. oregonensis* are remarkably similar.

The dissimilarity of the estimates for t_{N2} in 71/2 (2.0 versus 3.1 days) might be attributed at least in part to food supply which circumstantial evidence suggests may have been low from mid-June to mid-August because both the number of eggs per sac and the number of females carrying eggs were near the lowest levels recorded at any time during the year (Fig. 5).

c. Instar Development Times Using Krogh's Curve

For each instar excluding adults of each cohort produced in 1971 the average development temperature experienced over the whole cohort together with "q" read from Krogh's curve (page 54, Winberg 1971) and the estimated development time generated by the graphical method of Rigler and Cooley are presented in Table 19. If the development time is known for any instar (t_k) at temperature T_k and a development time is desired for that same instar at another temperature T_u, then by interpolating the conversion factors q_k and q_u from Krogh's curve at temperatures T_k and T_u respectively, t_u can be derived from the following equation:

$$\frac{t_k}{t_u} = \frac{q_k}{q_u} \qquad \text{Equation 15}$$

The use of Equation 15 is explained in Table 19.

Much of the variation between the calculated and predicted t_n values of 71/2 and 71/3 based on t_n values of 71/1 and Krogh's curve can be explained if it is postulated that food abundance or quality varied significantly over the year causing changes in development rate for a given instar that could not be explained knowing only temperature. For example, if it is assumed food was abundant and acceptable in the

TABLE 19

The use of Krogh's curve to estimate _in situ_ development times for all instars (excluding adults) in 71/2 and 71/3 using the development times generated for 71/1 by the graphical method of Rigler and Cooley.

For each instar of 71/2 and 71/3 Equation 15 was solved for t_u using calculated mean instar temperatures experienced in the lake over the cohort and the generated development times for 71/1 from Rigler and Cooley's graphical method (Table 14). Thus the known temperatures (T_k) and known development times (t_k) for Equation 15 in all cases came from data of 71/1. The necessary conversion factors q_k amd q_u were read from Krogh's curve (page 54 Winberg, 1971) at each temperature.

Instar	First Cohort			Second Cohort				Third Cohort			
	T_k	q_k	t_k		q_u	t_u	R&C	T_u	q_u	t_u	R&C
Egg	5.7	4.75	15.2	15.1	1.55	5.0	4.6	18.9	1.10	3.5	3.2
N1	6.9	4.02	3.2	15.3	1.53	1.2	1.1	19.1	1.08	0.9	0.8
N2	7.0	3.98	5.0	15.8	1.37	1.7	3.1	18.8	1.11	1.4	1.4
N3	8.5	3.25	6.8	16.4	1.38	2.9	5.1	17.7	1.24	2.6	3.8
N4	10.8	2.44	7.4	17.0	1.31	4.0	7.1	16.8	1.34	4.1	4.6
N5	12.2	2.11	8.0	18.2	1.18	4.5	9.7	16 8	1.34	5.1	7.8
N6	12.9	1.95	10.4	19.0	1.09	5.8	11.9	16.8	1.34	7.1	8.2
CI	14.6	1.64	12.0	20.1	1.01	7.4	14.7	14.3	1.69	12.4	15.4
CII	16.4	1.38	17.4	19.6	1.04	13.1	18.3	13.1	1.91	24.1	19.2
CIII	19.0	1.09	23.4	19.2	1.07	23.0	21.3	10.6	2.49	53.5	28.8
CIV	21.0	0.92	31.2	15.8	1.37	46.5	27.3	6.3	4.36	147.9	35.2
CV	16.6	1.36	79.6	--	--	--	--	5.0	5.19	303.7	58.8?

Explanation of the Derivation of t_u using Krogh's Curve

For any instar·

t_k = "known" development time from 71/1 at temperature T_k from the graphical method of Rigler and Cooley (R&C).

t_u = "unknown" development time from either 71/2 or 71/3 that is to be calculated using Krogh's curve and t_k from above and compared with a similar estimate generated from the graphical method of R&C.

q_k = Krogh's conversion factor read from Krogh's curve at temperature T_k, the estimated mean temperature experienced by the instar as it developed in 71/1.

q_u = Krogh's conversion factor read from Krogh's curve at temperature T_u, the estimated mean temperature experienced by the instar as it developed in either 71/2 or 71/3.

Example of Calculation of t_u for the eggs of 71/2

$$\frac{t_k}{t_u} = \frac{q_k}{q_u} \qquad \text{Equation 15}$$

$$\frac{15.2}{t_u} = \frac{4.75}{1.55} \qquad \text{therefore } t_u = 5.0$$

spring (April and May) and fall (September and October) at times near overturn and that the reverse was true in summer (June, July, and August) then the variations in predicted Krogh development times follow a pattern. Animals developing in the summer have in all cases proportionally slower development times than their counterparts of spring and fall. For example both the CIII of 71/1 and 71/2 developed in summer, experienced mean temperatures over their cohort of approximately 19 °C and spent approximately 23 days in that instar (Table 19). The fall population of CIII from 71/3 experienced a much lower mean temperature, 10.6 °C, but was observed to have a mean development time of approximately 28 days. Based on Krogh's curve and the suspected slow rate of development by the 2 summer populations the CIII of the last cohort would have been expected to take nearly 54 days.

Even though these calculations are unlikely to be very precise they nevertheless do suggest that food quality in a lake can play a very large role in development rates of feeding copepod instars, perhaps even the second instar, and that trying to predict development rates at one time of the year based solely on water temperatures using Krogh's curve or any other temperature function can lead to serious errors. Rigler and Cooley's method tries to avoid this possibility by estimating t_n *in situ* from cohort abundance curves but clearly more laboratory work is needed on instar development times and their relationship to temperature and food so that their assumptions can be evaluated independently. Also there may be subtle variations in development rate masked by these 2 factors including density effects and seasonality.

Corkett and McLaren (1970) found that the values of b and α in Bělehrádek's equation derived from egg development could also be applied to describe larval development (hatching to CI) in 4 species of marine copepods providing food was abundant. If their suggestion is correct then it is only necessary to measure development rates of older stages at 1 temperature (in order to solve Bělehrádek's equation for a) to calculate rates at any other temperature. This hypothesis may be true for freshwater copepods and should be tested.

Rigler (1972b) has shown that the instars from N4 to adult of *Limnocalanus macrurus* from Char Lake showed a continuous shift of optimum sized particles filtered. Although there was substantial overlap smaller instars had a smaller preferred food size. Thus high fecundity values may not indicate ample food supplies for small nauplii since the latter are more restrictive in the size of food they filter.

5. Predation on *L. minutus*

While the rate of development is determined by food and temperature, predators are probably most important in determining the number of animals that survive in each instar. In Bluff L. these would include possibly Brook trout (*Salvelinus fontinalis*), *Leptodora kindtii*, *Polyphemus pediculus*, *Chaoborus* sp., *Mesocyclops edax*, and *Epischura nordenskioldi*. Since I have only limited information on the population dynamics of the last two (probably most important) in this list (Fig. 7) it is impossible to assess quantitatively the role of predators in Bluff L. in determining mortality and population levels of *L. minutus*. There are however some striking correspondences between high mortality in *L. minutus* cohorts and times when *Mesocyclops edax* copepodites and *Epischura* adults are abundant. For example the highest mortality rates occurred in 71/3 in Sept. at a time when both these predators were near their highest levels and when phytoplankton levels as evidenced by high fecundity levels were high. In 71/1 mortality was not high until the N4 instar at about the same time that Mesocyclops edax diapausing copepodites began emerging from the bottom. A striking feature of the survivorship curve for the first cohort is the change after the N6 instar, when mortality seems to have become very small up to the CV stage. This abrupt change in rate is to a lesser extent evident in the other 2 cohorts of 1971. There are several interpretations that could account for these changes. A strong size-selective predation may act on smaller instars. It is also possible that copepodites of L. minutus are more able than are nauplii to avoid their predators because their major swimming appendage, the first antenna, is more highly developed. An additional explanation might be that the figures generated by the method of Rigler and Cooley are in error and mortality rates do not change with the onset of the CI instar.

Assuming, however, that the results do approximate the true situation then it seems reasonable to postulate that the overwintering adults which begin to die off in early June and are almost completely gone by mid-August are not doing so because of predators. In the late part of July the survivorship curve for the first cohort of 1971 and the overwintering adults from 1970 cross, and the rates of mortality of these 2 different populations are very different even though the sizes of individuals are similar (CIII and CIV from 71/1, and adults from 1970). At this time and shortly after it is reasonable to assume that both populations were being influenced by the same food supplies and predators but only the adults are dying, probably therefore from old age. Similarly the survivorship curves for 71/2 and 71/1 cross in early July, with the N4 of 71/2 dying rapidly while the copepodites from 71/1 are sustaining their numbers.

From early Nov. of 1971 through Feb. of 1972 the CII through CV of 71/3 are dying at a fairly constant rate at a time when Epischura and Mesocyclops are virtually absent from the zooplankton. In this instance it is probable that death is in part due to food conditions in the lake.

Without supporting data concerning the abundances of other possible predators of L. minutus in Bluff L. and information on their preferred prey it is impossible to assess with certainty the effect other populations had on the cohorts of L. minutus. Whatever the causes it is obvious that only small percentages of eggs laid to form the 3 cohorts of 1971 were alive by the first copepodite stage (approximately 16, 5, and 10% respectively.

6. Production by L. minutus in Bluff L.

In calculating production using finite cohort death rates it was assumed that the average weight of an animal leaving the population due to mortality was the same as an average animal surviving at the same time. By using the data on the number of animals dying and surviving and their mean weight at each instar up to N6 from data of Rigler and Cooley's method (Table 14), it is possible to approximate for each cohort the average dry weight of a survivor over this period (.29, .29, and .37 gm respectively) and an animal dying (.32, .28, and .29 gm respectively). There is good agreement in average weight of animals lost and surviving in the first and second cohorts but not in the third which was also the case when production was compared by the finite death rate method and the other 3 methods. While once again these figures are unlikely to be very accurate they do provide a possible explanation for an observed discrepancy. The finite death rate method is not desirable for calculating production where a population is divided arbitrarily into cohorts and each cohort is followed independently. While there is no standard by which to judge, the close agreement of the other 3 methods suggests they more closely approximate the true situation.

The easiest method to apply for production estimates is the Allen curve but serious errors could arise with this approach if the maximum size of the cohort (number of eggs produced) cannot be approximated.

The graphical approach employed by Soviet workers is conceptually simple but not without some questionable techniques. They also make good use of egg development times to set the upper limit of the cohort but also require information on total development times of nauplii and copepodites obtained from laboratory studies. For reasons given elsewhere I am sceptical about the accuracy of such data especially when they are applied to dynamic situations such as lakes. They apparently minimize the laboratory rearing of instars by growing them at 1 temperature and then apply Krogh's curve to obtain development times at other temperatures. I believe serious errors can be introduced with this approach. Comita (1972) also noticed that the rate at which different cohorts developed at different times in the year could not be entirely explained by temperature differences.

Assuming an individual's growth curve is S shaped and then drawing it from only 3 points is also a questionable practice. The Soviets also recognize this deficiency (Winberg 1971) and correctly suggest more data are needed with a view that an empirically derived general equation describing the process would be useful.

In the application of the Soviet approach in this study both the declining numbers curve for the cohort and the S-shaped growth curve of the individual were derived in part from data obtained from Rigler and Cooley's method. This would partially account for the close agreement in final results between these two methods.

Rigler and Cooley's graphical method for cohort analysis is the most difficult of all methods to apply because the data must be good enough to define instar pulses or cohorts before any analysis can begin and is heavily dependent on the concept of a weighted mean (mean pulse time), which over extended periods of time will include a large variance. Final estimates of instar numbers indicate anything from the number of animals entering to leaving the instar, or reaching a median age depending where mortality has occurred. The calculations are made assuming mortality is constant over thepulse affecting animals of all ages within an instar. While such assumptions of constancy are common in all production methods they can conceivably lead to serious errors. Where data are applicable for this treatment I feel the final results justify the effort, but the need for more work with different types of zooplankton is obvious.

Though each of these methods has required information relating egg development time and temperature as a means of setting the upper limit of the cohort such data are useful in other ways. When egg development times are fitted to Bělehrádek's equation and compared with similar data on related species (other copepods) the fitted constants may have biological meaning (McLaren 1965, Corkett and McLaren 1970). The shape of the egg development cuves for _L. minutus_ and _A. spatulocrenatus_ are consistent with these ideas. _A. spatulocrenatus_ adults though present throughout the year only produced subitaneous eggs from mid-May to August when water temperatures were warmest while _L. minutus_ adults also present annually had its greatest period of reproduction of subitaneous eggs in spring and fall. At summer temperatures of approximately 16 to

23 °C the 2 curves separate until at 4 °C the "summer" species eggs (*A. spatulocrenatus*) take approximately 70% longer to develop. Also the resting eggs of *A. spatulocrenatus* did not hatch until May whereas those of *L. minutus* began ~~emerging in the~~ winter under ice.

The shape of the NI development curves which are also temperature dependent are also consistent with the idea that *A. spatulocrenatus* is a "summer" species and *L. minutus* more of a "spring and fall" species since at warmer temperatures *A. spatulocrenatus* NI actually develop faster.

SUMMARY AND CONCLUSIONS

1. A method is presented for estimating the number of animals passing through each instar of a copepod cohort and is demonstrated with 3 cohorts of *Leptodiaptomus minutus* (Calanoida: Copepoda) from Bluff L. Nova Scotia.

2. The 1970/71 overwintering population of mainly adult *L. minutus* produced subitaneous eggs in Feb. which provided the basis of a first cohort or first generation that developed slowly through spring and summer to provide a new population of adults that formed subitaneous eggs in Sept. for a second generation. Most of the second generation died before reaching adulthood so that the overwintering population in 1971/72 was mainly adults from the first generation.

3. In the fall, apparently in preparation for winter, *L. minutus* females switch from producing subitaneous to diapausing eggs. These eggs pass the winter on the bottom of the lake and hatch at approximately the same time in the next year (March) as subitaneous eggs formed in Feb. by the overwintering females.

4. A summer or second cohort of *L. minutus* had a proportionally slow rate ~~of~~ development which most likely resulted from food conditions in the lake at the time. Heavy mortality through naupliar instars in all cohorts of 1971 is probably due to predation by other zooplankters. In the absence of predators in the first cohorts of 1971 and 1972 little mortality was observed in eggs and the first 3 naupliar instars.

5. Four methods are presented to estimate production in each of the 3 cohorts of *L. minutus* in 1971: 1) Rigler and Cooley graphical, 2) Allen curve, 3) Soviet graphical, and 4) death rate. For all 3 cohorts the first 3 methods give very similar estimates but the last is judged

inadequate. A curve relating egg development and temperature derived in the laboratory is presented and used in each of the 4 methods to estimate egg numbers. A similar curve for NI is used in the first method for estimating the number of NI produced in each cohort.

6. Data on NI, subitaneous and diapausing egg development were also collected for the larger but less numerous congener of *L. minutus*, *A. spatulocrenatus*. The data indicate that the 2 are not in complete competition with each other.

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APPENDIX I

A table to show instar abundances for *L. minutus* in Bluff L. from Oct. 17, 1970 to May 19, 1972. These data are graphed in Fig. 4.

Key to Symbols Used

N - naupliar instar
C - copepodite instar
M - adult male
F - adult female
FE - adult female with an egg sac
E - egg sac

Cor Ad - refers to corrected adult totals obtained from a smooth curve (Fig. 4) drawn by eye through all adult estimates from each sampling day

On some days (dashes) quantitative samples were collected but were not analysed for all instars. In some cases portions of these samples were used to estimate the percentage of females carrying egg sacs and the number of eggs per sac.

1970

DATE	Day No	N1	N2	N3	N4	N5	N6	CI	CII	CIII	CIV	CV M	CV F	CV Tot	M	F	Fe	E	Tot E	Tot F	Tot Ad	Cor Ad
Oct 17								2	7	10	64	228	241	469	87	100	15	0	15	115	202	
Nov 15									1	3	3	15	22	37	281	276	9	1	10	285	566	580
Nov 22								1	2	3	8	5	5	10	258	263	1	1	2	264	522	580
Nov 29											3	3	7	10	270	267	3	0	3	270	540	580
1971																						
Jan 16	16																					580
Feb 1	32									1	9	3	3	6	450	435	0	0	0	435	885	580
20	51										10	3	0	3	407	539	26	35	61	574	981	580
Mar 7	66	3	1								22	21	19	40	300	494	159	59	218	494	793	560
14	73	19	35	4	2					1	7	2	0	2	248	185	112	86	198	297	545	560
21	80	100	75	17	2						8	8	2	10	204	164	120	87	207	284	488	560
27	87	168	255	66	1					1	7	7	4	11	309	211	122	119	241	333	642	560
Apr 5	95	131	490	237	23							9	2	11	290	171	132	110	242	303	593	550
18	108	289	349	504	87	2				1		6	3	9	292	187	152	158	310	339	631	540
24	114	291	384	774	342	9						1	2	3	221	145	124	95	219	269	490	540
May 1	121	-	-	-	-	-						-	-	-	255	119	111	71	182	230	485	540
5	125	343	424	607	520	481	70					2	1	3	234	188	73	91	164	261	495	540
10	130	178	240	764	657	690	142	27	1			1	1	2	217	183	46	69	115	229	446	540
15	135	35	233	537	646	371	257	110	3			6	1	7	252	243	19	57	76	262	514	530
20	140	31	41	111	531	506	181	188	18			2	3	5	302	221	38	103	141	259	561	530
25	145	69	116	80	206	569	270	226	78	7		2		3	246	225	52	116	168	277	523	520
30	150	129	82	156	191	206	358	291	171	9					262	193	47	95	142	240	502	500
June 4	155	101	156	334	283	216	133	467	376	43	2				236	207	35	112	147	242	478	490
9	160	88	93	312	136	155	71	294	431	32	3		1	1	219	211	40	76	116	251	470	470
14	165	40	96	210	285	147	29	210	387	118	15	2	3	5	132	154	26	27	53	180	312	440
17	168	18	23	105	311	163	75	126	353	221	6	0	0	0	171	183	8	19	27	191	362	430
21	172	24	35	40	256	132	32	61	398	425	10	0	1	1	212	169	12	34	56	181	393	390
25	176	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	360
29	180	44	53	55	74	79	17	18	153	474	63	4	4	8	178	171	15	12	27	186	364	320
Jul 3	184	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	290
7	188	31	55	50	68	41	26	20	50	856	186	10	1	11	75	133	37	2	39	170	245	250
11	192	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	210
15	196	6	21	14	44	29	7	19	32	467	330	20	7	27	25	121	26	7	33	147	172	180
20	201	12	42	24	23	7	6	9	11	223	529	0	0	0	30	83	18	3	21	101	131	130
24	205	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
28	209	31	63	41	28	19	23	17	11	48	608	3	1	4	18	44	27	10	37	71	89	90

DATE	DAY NO	N1	N2	N3	N4	N5	N6	CI	CII	CIII	CIV	CV M	CV F	CV Tot	M	F	FE	E	TOT E	TOT F	TOT Ad	COR Ad
1971																						
Aug 1	213	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	80
5	217	7	3	30	63	13	12	41	23	27	943	25	12	37	21	65	19	1	20	84	105	70
9	221	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60
13	225	6	19	21	28	11	10	17	11	36	505	20	7	27	12	37	6	5	11	43	55	50
17	229	20	26	73	71	22	21	8	12	10	177	29	32	61	7	9	2	2	4	11	18	20
21	233	5	12	19	34	52	97	46	41	30	262	149	151	300	24	33	1	1	2	34	58	50
25	237	17	37	31	16	6	16	85	43	23	124	218	200	418	32	39	1	1	2	40	72	70
30	242	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100
Sep 3	246	34	39	141	60	22	21	20	35	32	124	128	140	268	56	57	20	54	74	77	133	130
8	251	75	72	171	118	60	41	34	32	36	75	192	160	352	75	88	23	44	67	111	186	160
12	255	82	99	231	76	75	55	51	64	30	45	206	184	390	91	80	21	21	42	101	192	170
16	259	71	157	214	147	111	67	60	48	51	83	209	179	388	51	39	19	24	43	58	109	180
24	267	83	137	328	179	110	93	78	108	33	49	302	260	562	91	89	22	34	57	111	202	190
29	272	42	125	151	89	53	32	109	64	51	60	275	245	520	-	-	-	-	-	-	-	200
Oct 5	278	3	5	240	163	42	31	96	73	41	50	245	201	446	86	136	7	22	29	143	229	210
11	284	2	1	49	121	21	[illegible]	92	63	49	52	323	287	610	65	113	16	11	27	139	204	220
17	290	0	2	5	61	37	[illegible]	75	46	48	72	279	264	543	90	108	7	7	14	115	205	240
26	296		0	1	12	16	[illegible]	60	73	44	32	125	99	224	152	171	6	0	6	177	329	330
Nov 2	306			1	1	2	25	57	82	49	41	85	77	162	270	309	9	1	10	318	588	370
12	316			0	4	2	3	44	56	29	49	16	19	35	295	296	2	0	2	298	593	440
27	331				1	1	2	24	30	20	19	13	11	24	239	259	1	0	1	260	499	500
Dec 18	352				0	0	0	4	30	25	13	21	26	47	262	227	0	0	0	227	489	490
1972																						
Jan 23	388							0	33	35	41	29	28	57	292	304	0	0	0	304	596	490
Feb 13	409	0	0	0	0			1	8	17	20	16	12	28	128	142	1	4	5	143	271	490
Mar 1	426	3	3	1	1			0	2	16	24	22	20	42	410	381	35	92	127	416	826	490
11	436	16	18	6	1				4	6	12	6	4	10	208	188	52	65	127	240	428	490
31	456	102	143	54	1				0	0	1	0	1	1	224	209	66	45	111	275	499	490
Apr 7	463	55	106	96	5	0				3	4	4	2	6	90	70	30	28	58	100	190	470
25	481	77	288	446	277	4	0			0	8	9	6	15	170	137	69	55	124	206	376	390
May 1	487	210	243	463	616	78	7				4	1	4	5	199	154	78	58	136	232	431	350
7	493	181	178	[illegible]	335	89	55				2	2	2	4	105	89	37	42	79	126	231	320
13	499	224	313	[illegible]	523	214	133	10	0		6	4	2	6	179	140	53	60	113	193	372	280
19	505	59	137	246	229	140	155	50	2		0	4	3	7	102	84	29	17	46	113	215	240

APPENDIX 2

One set of data all production methods used in this thesis have in common is their need at some point in the calculations for information relating egg development and temperature. This common need suggested to me that very accurate estimates of this parameter could be very useful. One approach tried was to isolate males and females without eggs in 300 ml. aquaria, observe frequently, and then remove any females carrying the newly formed egg sacs to constant temperature baths. This approach proved tedious and also I found that very young eggs (i.e. less than 1 hour old at room temperature) were susceptible to damage because egg membranes had not hardened sufficiently to permit routine transfer from aquaria to a culturing vial. An alternative approach that did not, I believe, sacrifice any significant accuracy was based on a method described by Cooley (1970) and modified slightly for this study. I found with practice that <u>L. minutus</u> eggs in the cleavage cycle and therefore very young could be distinguished from all other eggs at older stages of development. Cooley (1970) also found this working with <u>S. oregonensis</u> eggs from Teapot L. and was able to approximate the time taken to pass through the early cleavage divisions at various temperatures. His results are presented below:

Temp.	Time taken to reach cleavage stage (hours)						
°C	1 cell	2 cell	4 cell	8 cell	16 cell	32 cell	64 cell
4	3.9	7.9	11.8	15.7	19.7	23.6	27.5
7	2.6	5.3	7.9	10.6	13.2	15.8	18.5
10	1.7	3.4	5.1	6.8	8.5	10.2	11.9
14	1.2	2.4	3.6	4.8	6.0	7.2	8.4
18	1.0	1.9	2.9	3.8	4.8	5.8	6.7
23	0.8	1.6	2.3	3.1	3.9	4.7	5.5

Since egg development times for *S. oregonensis* and *L. minutus* are similar I used the above table in calculating development times for *L. minutus*. Fresh live Bluff L. plankton samples were anaesthetized at room temperature with a few drops of saturated chloretone solution and any egg sac observed to be in a recognizable cleavage stage was removed from the female with a fine pin and isolated in a single culturing vial of filtered Bluff L. water at a specified temperature. If for example an egg sac was at the 8 cell stage and the incubation was at 14 °C then the total egg development time would be the time taken to hatch during incubation + 4.8 hours as a correction for the development that had already occurred at room temperature before incubation. One further method employed to reduce variance was to use development times only for those egg sacs that were observed in the hatching process.

Cleavage divisions could not be distinguished at dissecting microscope magnifications in the eggs of *A. spatulocrenatus* because they were too heavily pigmented. For this species the "tedious" procedure previously described was used and eggs were allowed 1 to 2 hours development at room temperature before being transferred to a culturing vial.

Obtaining accurate estimates of N1 development times for both species proved to be a little easier. In many cases eggs that had been observed in the hatching process were allowed to develop to the first moult. As ecdysis time approached a few drops of formalin were added to the culturing vial and the contents were then immediately examined in a small petri dish with a dissecting microscope. Only those vials that on fixation contained both N1 and N2 animals were used in estimating N1 development times. By observing freshly preserved nauplii it was possible to determine if the animals had been alive immediately prior to fixation.

APPENDIX 3

The results of fitting data on subitaneous egg and NI development to Bělehrádek's temperature function for L. minutus and A. spatulocrenatus.

Bělehrádek's temperature function $D = a(T-\alpha)^b$

where D = development time in hours
T = temperature in °C
a, b, and α are fitted constants

All temperatures listed below are ± 0.1°C. Sample size (n) refers to the number of egg sacs incubated.

Temp °C	n	Obs. dev. time ± 1 s.d. (hrs)	Est. dev. time (hrs)	Percent Difference
Subitaneous eggs of Leptodiaptomus minutus				
4	20	490.3 ± 15.1	496.6	-1.2
7	16	306.7 ± 10.2	296.3	3.5
10	4	190.7 ± 1.8	194.3	-1.9
14	5	121.8 ± 2.2	122.1	-0.2
18	9	82.1 ± 1.1	83.0	-1.0
23	9	55.8 ± 1.5	55.2	1.0

For best least squares fit: a = 156046 b = -2.314 α = -8.0
correlation coefficient = -.9997

Temp °C	n	Obs. dev. time ± 1 s.d. (hrs)	Est. dev. time (hrs)	Percent Difference
Subitaneous eggs of Aglaodiaptomus spatulocrenatus				
4	8	846.9 ± 22.0	839.0	0.9
7	9	443.4 ± 16.6	417.6	6.2
10	8	250.5 ± 3.8	243.3	3.0
14	9	131.7 ± 5.5	137.4	-4.1
18	1	88.5	86.7	2.1
23	2	55.2 ± 0.1	53.9	2.4

For best least squares fit: a = 160020 b = -2.402 α = -4.9
correlation coefficient = -.9995

APPENDIX 3 (cont'd)

Temp °C	n	Obs. dev. time ± 1 s.d. (hrs)	Est. dev. time (hrs)	Percent Difference
NI's of *Leptodiaptomus minutus*				
4	22	122.7 ± 9.5	125.9	-2.5
7	11	72.9 ± 3.0	73.6	-1.0
10	16	47.6 ± 2.2	48.1	-1.0
14	10	30.4 ± 0.9	30.5	-0.3
18	14	20.0 ± 1.3	17.8	12.3
23	4	14.4 ± 0.5	14.2	-1.4
For best least squares fit:		a = 14065 correlation coefficient = -,9997	b = -2,048	α = -6.0
NI's of *Aglaodiaptomus spatulocrenatus*				
4	3	126.5 ± 8.0	127.1	-0.5
7	10	78.5 ± 7.9	72.0	-9.0
10	4	45.0 ± 5.1	45.7	-1.5
14	8	26.6 ± 3.0	27.9	-4.5
18	2	19.5 ± 2.3	18.6	4.8
23	3	12.2	12.2	0
For best least squares fit:		a = 27790 correlation coefficient = -.9976	b = -2.282	α = -6.6

APPENDIX 4

Recently there has been a reconsideration of formulas defining rates of increase by planktonic species (Caswell 1972, Edmondson 1972). Caswell (1972) has suggested that the commonly cited formula relating the instantaneous and finite rates of increase

$$b = \ln(1 + B) \qquad \text{Equation 16}$$

where b is the instantaneous rate of increase and B is the finite per capita rate of increase is incorrect, pointing out that such a relationship depends on the overall instantaneous rate of increase r, and citing Leslie (1948) suggests the correct formula should be

$$b = \frac{rb}{(e^r - 1)} \qquad \text{Equation 17}$$

The finite per capita birth rate B is defined as

$$B = \frac{E/A}{D} \qquad \text{Equation 18}$$

where E is the total number of eggs in the population, A is the total number of adults, and D is the development time in days of the eggs.

However, more recently Paloheimo (unpublished manuscript) has shown that Caswell's or more appropriately Leslie's formula (Equation 17) is "exact under rather specific assumptions" and "fails to account for the fact that the egg ratio (E/A using my notation) per development time (D) is not an appropriate measure for the finite per capita birth rate". He furthers goes on to develop a "correct" formula relating B and b which is

$$b = \frac{\ln(E/A) + 1}{D} \qquad \text{Equation 9}$$

Paloheimo points out that B is readily calculated from Leslie's original formula, Equation 17 as

$$B = \frac{b/r}{(e^r - 1)}$$ Equation 19

once b is known and that B depends on the rate of growth r, while b can in fact be calculated without the knowledge of r. Further he shows that in a sense Edmondson's old often cited "incorrect" equation for b is more appropriate than Caswell's new equation but still "underestimates the true value of b (from Equation 9) when $D < 1$ and overestimates it when $D > 1$ and that the magnitude of the bias depends on both D and E/A when $D \neq 1$.

Since Paloheimo's equation relating b to egg ratios and egg development time will most likely be universally adopted I have used it exclusively in calculations requiring instantaneous birth rates.

APPENDIX 5

Although it was not an objective of the study, it seems worthwhile to compare estimates of annual production by L. minutus in Bluff L. with similar estimates for other herbivorous copepods. These values are summarized in Appendix Table 1. In many cases data were converted so that all production estimates could be expressed in kcal per square metre of surface area in one year. It was assumed that 1 gm dry wt of organic matter represented 10 gm of fresh or wet weight, was 44% carbon, and contained 5.6 kcal. Although these values are likely to be crude estimates of the true situation because of different techniques and assumptions used in calculation, they should nevertheless be adequate for the purpose of indicating simple "trends" between lake type and production.

Clearly no simple relationships are evident from the data presented. This is not unexpected because of the dynamic nature of the factors controlling secondary production. The total amount of secondary production will be determined in part by lower and higher trophic levels (primary production and predators) as well as by the kinds and abundance of other herbivores "competing" for similar food stuffs.

In eutrophic lakes a higher primary productivity will not necessarily be accompanied by a proportional increase in herbivores because nannoplankton (the preferred food size of herbivores) does not necessarily increase proportionally. In fact Pavoni (1963) found that the ratio of nanno : net phytoplankton decreased as lakes became more eutrophic. Haney (1970) from an *in situ* study of freshwater zooplankton grazing rates concluded that phytoplankton renewal rates in oligotrophic lakes are far in excess of zooplankton grazing rates

APPENDIX TABLE 1

Annual production estimates of herbivorous copepods.

Species	Body of Water, Type	N. Lat.	Max Depth m	Area (h)	Production kcal/m^2/yr	Author
Arctodiaptomus salinus	Aral Sea	45° 00'	68	62×10^6	2.6	Yablonskaya (1962)
Leptodiaptomus minutus	Bluff L., Oligotrophic	44° 30'	7	4.8	4.0	This Study
Mixodiaptomus laciniatus	Titisee, Mesotrophic	47° 54'	40	11	4.8	Eichhorn (1957)[1]
Pseudocalanus minutus	Ogac L., Oligotrophic	62° 52'	60	148	5.4	McLaren (1969)
Oithona similis	" "	" "	"	"	3.3	"
Skistodiaptomus oregonensis	Teapot L., Dystrophic	43° 45'	12	0.5	6.6(1965) 15.0(1966)	Rigler and Cooley (unpublished)
Eudiaptomus graciloides	Taltowisko, Mesotrophic	54°?	?[2]	?	9.5	Hillbricht-Ilkowska *et al* (1966)
" "	Mikolajskie, Eutrophic	"	?	?	11.8	
Eudiaptomus graciloides	Severson L., Eutrophic	46° 53'	5	11.2	13.9	Comita (1972)
Eudiaptomus gracilis	Elizabeth II Reservoir	53° 30'?	16	120	52	Kibby (1971)
Eudiaptomus graciloides	Lake Erken, mod-Eutrophic	59° 25'	20	2287	134	Nauwerck (1963)
Calanus finmarchicus	SW part, coastal area Barents Sea	68°?			36.4	Yablonskaya (1962)
Calanus finmarchicus	Coastal areas of E. part, Barents Sea	68°?			30.8	Yablonskaya (1962)

[1] calculated using the graphical method of Rigler and Cooley

[2] hypolimnion below 10m

[redacted]

suggesting grazing of algae in oligotrophic lakes may be of little importance. On the other hand he suggested that in eutrophic lakes very high grazing rates in mid-summer may control the abundance of nannoplankton. He concluded that secondary production in oligotrophic lakes is not limited by food supply.

Predators are most likely as important as food supply in determining production by herbivores. In this study for example high mortality rates in early instars are correlated with predator abundance. It is assumed that if predation had not occurred overall production would have been greater because of greater survivorship.

The range of values for annual production by freshwater herbivorous copepods would seem to be quite large (from 2.6 to 134 kcal/m^2/yr) but most ~~are~~ less than 15 kcal/m^2/yr. The estimates by Kibby and Nauwerck for Eudiaptomus gracilis and E. graciloides (52 and 134 kcal/m^2/yr) seem unusually high but because of the limited amount of data available it cannot be said that these are anomalous values. Clearly more work on these and additional species is needed.