THE UNIVERSITY OF MANITOBA

LIFE HISTORY, BEHAVIOUR, POPULATION DYNAMICS

AND PRODUCTIVITY OF <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u> (FORBES)
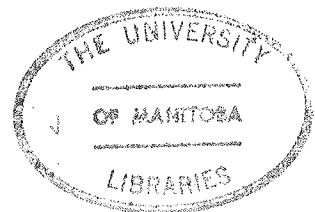
IN WEST BLUE LAKE, MANITOBA

by

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LIFE HISTORY, BEHAVIOUR, POPULATION DYNAMICS
AND PRODUCTIVITY OF DIACYCLOPS BICUSPIDATUS THOMASI (FORBES)
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A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ABSTRACT

The life history, behaviour, population dynamics and
productivity of Diacyclops bicuspidatus thomasi in West Blue
Lake was investigated over a two-year period. Analysis re-
vealed that the population was multivoltine, consisting of
three cohorts developing annually with reproduction occur-
ring in the spring, summer and winter. Highest fecundity
occurred in the spring and was significantly higher in 1974
than in 1972. Copepodid stage 4 of cohort 1 exhibited dia-
pause, entering the profundal sediments in late spring and
emerging in the autumn, coinciding with the development of
the same stage from cohort 3 in the water column. Diacyclops
b. thomasi showed no strong evidence of diel vertical migration,
but each life history stage was generally located at a certain
depth which varied seasonally. Population strategies of dia-
pause and stage depth selection are discussed.

Population structure and abundance trends did not vary
significantly among sampling stations. Population estimates
were highest in the spring, followed by summer and winter
periods, and were approximately two-fold higher in 1974 than
in 1972. Population estimates based on a single deep station
were not representative of the lake. Instantaneous mortality
estimates were also highest in the spring and/or summer, and
lowest in the winter.

Length-weight relationships were described for D. b.
thomasi in both carbon and nitrogen units. Relative and

instantaneous growth rates varied for each stage or groups
of stages both within and between cohorts. Productivity,
over the May to August period, estimated with both the in-
crement summation and instantaneous growth methods, averaged
approximately .21 g C m^{-2} in 1972 and .33 g C m^{-2} in 1974.
Productivity estimates in calories were 1.15 kcal m^{-2} in
1972 and 2.42 kcal m^{-2} in 1974. Productivity based on a
single deep station over-estimated productivity for the lake.
Naupliar stages 1-5 contributed less than 10% of total pro-
ductivity in both years. Copepodid stages 2, 4 and 5 made up
approximately 70 and 61% of the total productivity during
1972 and 1974, respectively.

ACKNOWLEDGEMENTS

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INTRODUCTION

Diacyclops bicuspidatus thomasi (FORBES) is a major cyclo-
poid species in temperate North American lakes (Pennak 1957).
Although this species is found in virtually every pond and
lake in most temperate regions, there have been only limited
studies on its life history (McQueen 1969, Carter 1974, Selgeby
1975, Armitage and Tash 1967, Moore 1980, Peacock 1982). Unfor-
tunately, this information on copepod life history is essential
for limnologists to understand the role of copepods as secondary
producers in aquatic systems. In addition, there has been only
limited detailed work on the behaviour, population dynamics and
productivity of D. b. thomasi in any lake system. The objective
of this thesis is to describe the life history, behaviour, popu-
lation dynamics and productivity of D. b. thomasi in West Blue
Lake, Manitoba. The information obtained in this thesis is not
only applicable to D. b. thomasi in other lakes, but is also
useful in describing the ecology and role of other copepod species
in aquatic systems.

Typical of other temperate copepod species, the popu-
lation of D.b. thomasi is multivoltine, with several co-
horts developing annually. Multivoltine populations tend
to be complex because of a large degree of stage overlapping
(Allan and Goulden 1980, Paquette and Pinel-Alloul 1982).
Consequently, a detailed analysis of the population requires
identification and enumeration of all or most life history

stages. This can be a formidable task especially when 12
life history stages are involved and also since the identifi-
cation of some of the naupliar stages is still of taxonomic
concern (Lewis et al. 1972). In addition, frequent sampling
is essential so that the development of life history stages
is not missed.

As part of the life history information on D. b. thomasi,
data were obtained on diapause and diel vertical migration of
this species in West Blue Lake. The majority of work on cope-
pod diapause has been conducted in Europe, and has been de-
tailed for a number of cyclopoid species (Elgmork 1980).
Zooplankton species entering diapause may have a competitive
advantage over other species which remain in the water column.
Although diapause of D. b. thomasi in lake systems has been
known for some time (Birge and Juday 1908), the importance
and occurrence of this behaviour as part of a population
strategy has not been fully demonstrated. Almost no infor-
mation on vertical migration of D. b. thomasi is available
in the literature (Hutchinson 1967). This is unfortunate
since diel migration of this species may result in stages
or groups of stages migrating through or selecting preferred
temperatures and/or food concentrations which can signifi-
cantly affect productivity estimations. Several hypotheses
have been put forth suggesting that migration may have
advantages in terms of metabolic efficiency and female
fecundity (McLaren 1974, Enright 1977), and may also act
as a mechanism to avoid predation from visually oriented

planktivores (Zaret and Suffern 1976, Wright et al. 1980,
Stick and Lampert 1981). Too few detailed field studies have
been conducted on stage migration or depth selection by
limnetic copepod species to understand the strategy involved
in vertical migration (Hutchinson 1967, Ringelberg 1980,
Orcutt and Porter 1983). In West Blue Lake, a detailed
analysis of stage distribution of D. b. thomasi was conducted
prior to and following the onset of thermal stratification.
The life history strategy of vertical migration or depth
selection of D. b. thomasi is discussed in the text.

Information on zooplankton population structure,
fecundity, growth, and even numerical abundance has often been
derived from a single deep station which is assumed represen-
tative of the lake (Kajak and Hillbricht-Ilkowska 1972, Ward
and Robinson 1974, Paquette and Pinel-Alloul 1982). However,
this assumption may be erroneous, especially in large lake systems,
where large variability in zooplankton populations occurs (Patalas
1969, Patalas and Patalas 1978). In West Blue Lake, the popu-
lation structure and numerical abundance of D. b. thomasi were
compared among several sampling stations in the lake. Population
estimates were determined for the mean depth of the lake.

Several estimates of zooplankton mortality are avail-
able in the literature, most involving primarily the roti-
fer and cladoceran groups (Edmondson 1977, Keen and Nassar
1981). The procedure most frequently used for estimating
mortality is the egg-ratio approach (Edmondson 1977), a

method which is inappropriate for zooplankton groups with complex life histories such as the copepods (Taylor and Slatkin 1981). Few mortality estimates of copepod species have been determined with more reasonable approaches (e.g. Comita 1972, Confer and Cooley 1977). In West Blue Lake, total mortality was estimated for each cohort of D. b. thomasi.

A number of studies are available in the literature describing growth of limnetic populations from field samples (Cooley 1973, Rigler and Cooley 1974, Borgmann et al. 1979, Paquette and Pinel-Alloul 1982). Field derived estimates usually require well defined cohorts which involve laborious identification and enumeration, and frequent sampling. For this reason, many investigators estimate growth in the laboratory to simulate conditions of field growth (Winberg 1971, McLaren and Corkett 1981, Landry 1983). However, problems arise as to which temperature(s) and food concentration(s) to use in the laboratory, since the species may exhibit diel vertical migration in the field (Bell and Ward 1970). In West Blue Lake, growth was estimated from field samples for each cohort of D. b. thomasi. In addition to relative growth, instantaneous growth was determined using a procedure developed for fish (Chapman 1968, Ricker 1975), which has since been applied to invertebrate populations (Waters 1977, Rigler and Downing, in press).

Although many estimates of copepod productivity are available in the literature, only a few studies have been conducted in North America (Comita 1972, Cooley 1973,

Schindler 1972, Rigler and Cooley 1974, Swift and Hammer 1979, Borgmann et al. 1979, Tremblay and Roff 1983). Many researchers have determined development times in the laboratory rather than from field data (Winberg 1971 and others). However, as indicated above, it may be difficult to extrapolate these laboratory results to the field. In addition, several researchers have calculated productivity for multivoltine populations based solely on one growth curve generally laboratory derived (Kajak and Hillbricht-Ilkowska 1972). The magnitude of error for a single growth curve is not known. Others, because of limited data collections, have estimated productivity based on the production to biomass (P/B) ratios calculated from adult body mass using an empirical relationship. This approach has been severely criticized by McLaren and Corbett (1984).

In West Blue Lake, productivity of D. b. thomasi was estimated for each cohort using two popular methods: the increment summation method (Winberg 1971, Waters 1977) and the instantaneous growth method (Chapman 1968, Ricker 1975). These approaches are discussed in detail by Downing and Rigler (in press). Generally, the increment summation method is described as a discrete linear model whereas the instantaneous growth method involves an exponential approach (Gillespie and Benke 1979). If sampling intervals are small relative to changes in mortality and growth, then both increment summation and instantaneous growth should yield similar estimates of productivity. Productivity estimates of D. b. thomasi were ex-

pressed in both carbon and calories, and the advantage and disadvantages of both measurements considered. In addition, productivity estimated from one growth curve was compared to estimates for all cohorts in an attempt to assess error associated with estimates based solely on one growth curve.

Most researchers investigating copepod productivity have either neglected or combined naupliar stages (Winberg 1971, Kajak and Hillbricht-Ilkowska 1972, Swift and Hammer 1979). Unfortunately, the importance of individual stages to total productivity has not been resolved, and the magnitude of error associated with neglecting or combining stages is not fully known (Rigler and Cooley 1974, George 1976). On theoretical grounds, one would not expect production to be highest in the early life history stages. A detailed life history analysis is required for a better understanding of productivity and the contribution of individual stages to production. In West Blue Lake, productivity of D. b. thomasi was estimated for most life history stages in each cohort, and the importance of naupliar production is discussed in the text.

This study was conducted in West Blue Lake in west central Manitoba during the period 1972 to 1975.

LITERATURE REVIEW

1. Taxonomy and Distribution

The genus Cyclops, first described by O.F. Muller 1075, belongs to the subfamily Cyclopinae, one of the three subfamilies of the family Cyclopoidea. The Cyclops genus is mainly confined to temperate North America, Asia, and Europe (Hutchinson 1967). Yeatman (1959) records 29 species of the genus Cyclops in North America.

Cyclops bicuspidatus was first identified by Claus in 1857, and can bé divided into two sub-species in North America: C. b. lubbocki Brady 1868, and C. b. thomasi Forbes 1882. There are two morphological differences between these subspecies (Edmondson 1959). One difference is the number of segments comprising the first antennae. Cyclops bicuspidatus thomasi has 17 segments whereas C. b. lubbocki has only 14. Another major difference is that the outer terminal spine of the endopod of leg 4 is twice as long as the inner terminal spine for C. b. thomasi, and only 1.5 times as long as the inner spine for C. b. lubbocki.

The subspecies present in West Blue Lake is C. b. thomasi which is the common lacustrine form in North America (Hutchinson 1967).

Recently, several investigators have used the genus Diacyclops instead of Cyclops to describe Cyclops bicuspidatus thomasi (e.g. Carter et al. 1980). For consistency with current literature, the genus Diacyclops is used throughout the text.

Diacyclops bicuspidatus thomasi is the dominant cyclopoid copepod in temperate North American lakes. Pennak (1944, 1957) described it as one of the dominant cyclopoid species in the mid-western United States. Dodds (1919) found it in Colorado lakes at elevations ranging from 1250 to 3700 m.

In Canada, it is widely distributed. It is a dominant component in the plankton from Lake Okanagan in British Columbia (Patalas and Salki 1973) to small lakes in New Brunswick (Patalas pers. comm.). It has been found in every major temperate lake (Patalas 1975, Watson 1974), except those perhaps in the maritime provinces (Carter et al. 1980). Its exclusion from the maritime provinces may be related to either competition or the simple fact that it has not yet dispersed there (Carter et al. 1980). Its northern distribution is somewhat restricted. Patalas (1975), and Patalas and Patalas (1978) noted D. b. thomasi in Great Slave Lake but not Great Bear Lake. Archibald (1977) reported it in only one of the 36 lakes he investigated in the Yukon territory. Moore (1980), however, had observed this species in Yellowknife Bay in the subarctic. Similarly, Sutherland (1982) reported it in the Tuktoyaktuk Harbour in the Northwest Territories. D. b. thomasi is also present in high alpine lakes in Alberta (Anderson 1972).

Diacyclops bicuspidatus thomasi has been found to be a major component of the Great Lakes plankton (Patalas 1972, Patalas 1975, Leach 1973, Watson and Carpenter 1973, Watson 1974, Selgeby 1975, and Hawkins and Evans 1976). Watson and Carpenter (1973) reported adult concentrations exceeding

200,000 ind. m^{-3} in the central and western basins of Lake
Erie during June and July. In Lake St. Clair, Leach (1973)
also found that maximum numbers occurred in July (40,000 ind.
m^{-3}). Early spring and fall periods showed lower abundances.
Patalas (1969) found levels as high as 1000 ind. cm^{-2} in
August around Toronto Harbour in Lake Ontario. Similarly,
high summer densities have been observed by Davis (1954,
1962), and Rolan et al. (1973) in the Cleveland Harbour area
of Lake Erie. Patalas (1969) reported variable horizontal
distribution of D. b. thomasi in Lake Ontario from June to
October. During August, spatial distribution ranged from
100 to 400 ind. cm^{-2}. Temporal variation of D. b. thomasi
in Lakes Erie and Ontario have also been reported by Watson
and Carpenter (1973).

2.   Life History

Most investigations of the population structure of D. b.
thomasi has been restricted to counting adult stages only or
combining stages (Patalas 1969, Leach 1973, Watson and Carpenter
1973, Peacock 1982). There are few detailed studies of the
population structure of D. b. thomasi in temperate lakes.
Detailed population investigations require the identification
and enumeration of all or most life history stages. For
D. b. thomasi, there are six naupliar stages and six copepo-
did stages, the last being the adult (Ewers 1930). Infor-
mation on life history stages is required for the identifi-
cation of cohorts. A cohort refers to all those animals
developing from eggs within the same reproductive period.

A cohort can give rise to one or more generations. McQueen (1969) found a univoltine population in Marion Lake, B.C., a temperate lake. Duration from egg to copepodid stage 4 was estimated to be 45 days, with egg production occurring in late May. Similarly, Moore (1980) observed only a univoltine population of this species in a subarctic lake. In Leavenworth County State Lake, Kansas, Armitage and Tash (1967) observed two or three cohorts annually of this species. The duration of each cohort was approximately 35 days. Similarly, Hawkins and Evans (1976) reported three cohorts of D. b. thomasi in Lake Michigan. Selgeby (1975) reported two generations (cohorts) of this species in Lake Superior. Durations were not reported in either study. Peacock's (1982) data on D. b. thomasi in Placid Lake, B.C. suggests two cohorts developing during the May to September period. Estimated duration of the spring cohort was approximately 67 days. Generally, most temperate lake copepod species have multivoltine populations, the number of cohorts ranging from two to five depending on the trophic level of the lake (Rigler and Cooley 1974, Comita 1972, Carter 1974, George 1976, Allan and Goulden 1980, Paquette and Pinel-Alloul 1982). In subtropical and tropical lakes, extreme multivoltism may occur with as many as ten cohorts occurring annually (Burgis 1971, 1974, Allanson and Hart 1975). In contrast, subarctic or arctic copepod populations are generally univoltine (Roff and Carter 1972, Moore 1980). Semivoltine (2 year life history) calanoid populations (e.g. Senecella calanoides) have also been observed in some temperate lakes (Carter et al 1984).

Results from laboratory and field research on copepods have indicated that life history duration is a function of several environmental factors (Allan and Goulden 1980, Vijverberg 1980). Temperature has generally been considered the most important factor affecting duration for most copepods (McLaren 1963,

Winberg 1971), including D. b. thomasi (Moore 1980). For example, life
cycle duration of C. strenuus ranged from 30 days at $22^{\circ}C$ to 120 days at $5^{\circ}C$
(Elbourn 1966). Vijverberg (1980) summarizes the duration and growth of
five copepod species as related to temperature. Some researchers have
accurately predicted durations in the field based solely on laboratory der-
ived temperature curves (McLaren 1978, McLaren and Corkett 1981). Still,
others have pointed out the importance of food quantity and quality as factors
affecting copepod development (Vijverberg 1980). Development of several cope-
pod species took approximately 56 days when food concentration was 0.2 - 1.0
gm^{-3} (Sushkina 1964). Food quality may also affect duration of life cycle.
Fed on an algal food source (Scenedesmus), Acanthocyclops viridis took 61.8
days to complete its life cycle (Smyly 1970). When the food source was
replaced by nauplii and cladocerans, the duration was reduced to 31.4 and
48.2 days, respectively. In another study, the developmental times of three
copepod species was related to water temperature and food availability
(Paquette and Pinel-Alloul 1982).

Diapause is an important phase in the life history of
fresh-water copepods. As early as 1908, Birge and Juday (1908)
reported the arrest of the fourth copepodid stage of D. b. thomasi
in Wisconsin Lakes. During the summer, this stage left the pelagic
zone and entered the profundal sediments. Subsequently, Moore
(1939) and Cole (1953) have described this phenomenon for D. b.
thomasi in Michigan and Minnesota lakes, respectively. Peacock
(1982) also observed D. b. thomasi to overwinter in Placid Lake,
B.C. In contrast, however, diapause was not reported for D. b. thomasi in
Yellowknife Bay, a subarctic lake (Moore 1980), or in Lake Superior
(Selgeby 1975). Other species of cyclopoids have also been
shown to diapause. A complete arrest of development in the

fourth or fifth copepodid stage has been described for

C. vernalis (Coker 1933). C. Leukarti (Fryer and Smyly (1954),

C. strenuus (Elgmork 1959), Diacyclops navus (Watson and Smallman

1971), C. vicinus (George 1976) and Tropocyclops prasinus (Paquette

and Pinel-Alloul 1982). Diapause has also been reported for cope-

podid stages II and III for several cyclopoid species (Elgmork

1980). Diapause in cyclopoids has been noted to be similar to

diapause in insects (Southwood 1968, Watson and Smallman 1971).

Seasonal patterns of induction and termination of diapause

varies with species. In Leavenworth County State Lake, Kansas,

Armitage and Tash (1967) suggested that D. b. thomasi went into

diapause in the sediment in late spring and remained there until

winter. George (1976) noted that C. vicinis left the open water

in mid-summer and remained in diapause until the following spring.

A similar pattern has been described for D. b. thomasi in Marion

Lake, B.C. (McQueen 1969). In Lake Cromwell, Quebec, Paquette

and Pinel-Alloul (1982) noted Tropocyclops prasinus to enter dia-

pause in the fall. In southern Norway, Elgmork (1980) observed

C. strenuus to enter diapause in summer, winter and fall

periods. In each case, diapause terminated in the spring.

The adaptive significance of diapause may involve an

escape from an unfavourable environment or an important

timing in the species' life cycle (Elgmork 1980). Under

extreme conditions, such as low oxygen or high temperatures

in a pond environment, the diapause stage may be the only

means of survival. In limnetic systems, diapause may give

the species an ecological advantage over other members in

the planktonic zone. Food availability, predators, and

competition are all selective forces for cyclopoid diapause (Nilssen 1980). Although several environmental factors have been suggested as cues for inducing and terminating diapause, day length and temperature are considered the major variables (Watson and Smallman 1971, George 1976).

3. Behaviour - Vertical Migration

Vertical migration can be defined as "daily changes in the vertical movement of animals in a column of water" (Hutchinson 1967). Although zooplankton migration has been known since 1877, there have been surprisingly few detailed studies on diel vertical migration of freshwater copepod species (Hutchinson 1967, Kerfoot 1980). In North America, studies on cyclopoids have generally been restricted to adult stages, with little information presented on life history stage migration. Furthermore, almost no research has been conducted on cyclopoid migration throughout an entire season (Langford 1938). There appears to be only one migration investigation of D. b. thomasi, in which Pennak (1944) observed that adults generally showed little evidence of migration in four Colorado lakes. Most research on cyclopoid migrations has been conducted in Europe, and generally concerned C. scutifer, C. strenuus and C. tatricus (Siebeck 1960, Hutchinson 1967).

Few studies have dealt with the migration of nauplii. Data on nauplii migration of D. b. thomasi are not available, but for C. strenuus, Southern and Gardiner (1926) observed that nauplii concentrated at the surface at night and were

randomly distributed during the day. A slight reverse migration of nauplii of C. strenuus was observed in Lake Lucerne (Worthington 1931). In Lake Nipissing, Langford (1938) found no evidence of migration of Cyclops spp. Generally, most European studies have suggested that naupliar stages migrate to a lesser extent than older stages.

Detailed freshwater seasonal migration studies of zooplankton are few. Epischura lacustris showed different migration patterns during each month in Lake Nipissing (Langford 1938). No migration pattern was found in June whereas in July there was a slight reverse migration as thermal stratification was established. During July and August marked reverse migration was evident. Different migration patterns of Daphnia pulicaria have been observed in West Blue Lake (Bell and Ward 1970). During May animals showed a somewhat uniform distribution throughout the water column with little evidence of any migration. However, in August and September, a marked nocturnal migration pattern was evident. Similarly, Weider (1984) reported differences in the migration patterns of Daphnia pulex in a small pond in Illinois. He attributed these differences to distinct genotypes of the cladoceran, and that the migration pattern was dependent on its genetic composition. George and Fernando (1970) also found that different rotifer species can undergo nocturnal migration in one season and reverse migration in another.

Several theories on the adaptive significance of vertical migration have been proposed and all involve some life history population strategy. Populations undergoing diel vertical migration may have advantages in terms of metabolic efficiency (McLaren 1974, Enright 1977), and increased fecundity (McLaren 1963, 1974). It may be an

evolutionary response to more efficient feeding at higher water temperatures, and more efficient growth at low temperatures which leads to large size and hence to increased fecundity. In a thermally stratified lake, zooplankton migrate upward to feed in the warm epilimnion and downwards to assimilate food in the cooler hypolimnion. In this sense, Kerfoot (1970) maintains that zooplankton migrate as part of a "food exploitation strategy". McLaren (1963, 1974) postulates that migrants in a thermally stratified lake have a distinct advantage over non-migrants. Recently, Orcutt and Porter (1983) tested the theory of a thermal demographic advantage using life-table studies of Daphnia parvula cohorts fed on an algal food diet. They found no apparent 'thermal' advantage to vertical migration at either high or low food levels, but observed maximum fitness for animals residing in the warm, surface waters at all times.

Others have argued that vertical migration has evolved as a mechanism to avoid predation from visually orienting planktivores (Zaret and Suffern 1976, Stavn 1975, Wright et al. 1980, Stick and Lampert 1981). The larger, more mature stages seek deep water as a refuge from predators. Disadvantages of slowed growth at these temperatures is offset by the relative freedom from predators. Migration may be advantageous for juvenile stages of copepods or small zooplankton species (e.g. bosminids), since these groups may not be heavily preyed upon by fish (or other predators) under any condition (Wright et al. 1980).

As indicated above, Weider 1974 reported a genetic component to vertical migration in the Daphnia pulex populations he studied. The presence of different genotypes in the migratory behaviour may have an influence on the sensitivity of a population to perturbations and changing selection pressures.

4. Population Dynamics

Copepod fecundity (number eggs/female) varies seasonally. Few studies on fecundity of D. b. thomasi have been conducted (Armitage and Tash 1967, Selgeby 1975, Moore 1980, Peacock 1982). In Leavenworth County Lake, Armitage and Tash (1967) reported that mean egg number of D. b. thomasi ranged

from approximately 24 in May to 43 in April. In a subarctic lake, clutch size was significantly lower, ranging from 7 in September to 13 in July (Moore 1980). Peacock (1982) reported a clutch size ranging from 21-26 eggs/♀ in experimental closure tests conducted in two B.C. lakes. Clutch sizes in other species, such as C. strenuus, have been known to vary seasonally (Elgmork 1959). Generally, maximum egg numbers have been reported in early spring or late autumn for most cyclopoid species (Ravera 1955, George 1976, Elgmork 1959, Elbourn 1966, Paquette and Pinel-Alloul 1982). An inverse relationship between egg number and egg diameter has been noted for several copepod species (Czeczuga 1960, Cooney and Gehrs 1980). These variations in egg number and diameter have recently been suggested as an adaptive strategy in the copepods life history (Nilssen 1980). Few, large nauplii generally have a competitive advantage over many, small ones.

Data on the relationships between female size or temperature against fecundity are not available for D. b. thomasi, but in C. strenuus, egg number was negatively correlated with temperature and positively correlated with animal size (Elbourn 1966).

Several researchers have considered temperature as the prime factor controlling fecundity (Elgmork 1959, McLaren 1963). Still, other factors such as changing daylength, food quantity and quality have also been suggested as important variables. In a subarctic lake, Moore (1980) reported that changing daylength and the availability of food were the major variables affecting fecundity for D. b. thomasi.

Weglenska (1971) found direct relationships between fecundity and food concentration for several crustaceans. She also noted that time intervals between broods were shortened when animals were placed in dense food concentrations. Smyly (1970) reported variable fecundity of A. viridis when fed different food types. With an algal food source, A. viridis averaged 18.5 eggs per brood compared to 82.6 eggs per brood when fed a cladoceran diet. With Artemia salina as a food source, A. viridis averaged over 100 eggs per brood. Peacock (1982) also observed that fecundity of Diacyclops bicuspidatus thomasi increased with an increase in fertilization (nutrient input) to experimental enclosures.

No estimates of birth or growth rates are available for Diacyclops bicuspidatus thomasi in the literature. For mortality, Selgeby (1975) did report that mortality appeared higher for the summer breeding generation than the one present during and after overwintering. Peacock (1982) observed highest mortality in naupliar stages in Placid Lake, B.C. which was related to predation (including cannibalism). Most detailed studies on the population dynamics of zooplankton concern the cladoceran and rotifer groups. The most widely used technique for studying the dynamics of natural populations (Hall 1964, Keen 1973, Burgis 1971) is the egg ratio method (Edmondson 1960, Keen and Nassar 1981, DeMott 1980, Rigler and Downing, in press). The egg-ratio method is used to estimate instantaneous rates of birth and death. Initially, population change is described by the exponential growth equation:

$$N_t = N_o e^{rt} \text{ or } r = \frac{\ln N_t - \ln N_o}{t}$$

where N_o and N_t represent population size initially and t units of time later, respectively, and r is the instantaneous rate of population change. The instantaneous birth rate, b, is

calculated from the egg-ratio as follows (Edmondson 1960):

$$* \quad b = \ln(B+1) \quad \text{where } B = \frac{E}{D}$$

B is the finite birth rate, E is the number of eggs per female in the sample, and D is the developmental time of the eggs. An estimate of the instantaneous death rate, d, is obtained from the difference of the estimates of the instantaneous rates of birth (b) and population change (r): i.e. d = b-r

The use of birth rate data to compute instantaneous mortality rates (or other kinds of mortality rates) for copepod species may be erroneous because it assumes that all eggs develop at the same time, with 100% hatching success. Sampling intervals must all be short relative to the duration (life span) of the animal (Hillbricht-Ilkowska and Patalas 1967). In addition, the calculation of r is independent of the prevailing age structure (Birch 1948). A stable age distribution is assumed; that is birth and death rates do not vary in response to crowding, predation and other environmental factors.

Few investigators have considered other approaches in estimating mortality or the number of survivors in a natural population. Survivorship curves have been determined for both Mesocyclops edax and Diaptomus siciloides by developing a series of regression equations relating the

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* This equation has been modified by several investigators (Paloheimo 1974, Keen and Nassar 1981).

natural logarithm of abundance to each life history stage,
the slope being the instantaneous mortality rate (Comita
1972). Cooley (1973), and Confer and Cooley (1977) also
calculated survivorship curves for Leptodiaptomus minutus
using catch curve statistics originally developed by Ricker
(1968, 1975) for fish populations. For each cohort the
natural logarithm of abundance for each stage was plotted
against the (accumulated) age (duration) of the population.
The slope of each regression was the instantaneous mortality
rate.

5. Productivity

Productivity (net) of a specific population can be defined as the
sum of growth increments of the population during a given time period.
Others have defined it simply as the biomass accumulated by that population
per unit time (Rigler and Downing, in press). The units employed are
similar to that used for standing crop (i.e. units of quantity, spatial unit),
with the addition of a time unit. Consequently, since a rate is implied,
the term "productivity" is probably more precise than the term "production".

No estimates of Diacyclops bicuspidatus thomasi pro-
ductivity are available in the literature. The two basic
methods of determining productivity are the energetic and
biometric approaches. In the energetic approach, Schindler
(1968) used a modification of Sorokin's (1968) C^{14} method to
estimate assimilation (incorporation, Bell and Ward 1970)
rates of Daphnia. Respiration was measured by a micro-
Winkler titration method, with growth (G) estimated as the

difference between assimilation (A) and respiration (R) i.e. A-R = G. Growth is the estimate of the productivity of an individual. Productivity of a cohort can be calculated by multiplying growth increments by the number of individuals in that cohort. For more recent applications of this approach see Klekowski et al. (1972), and Sorokin (1972).

Several inherent problems are associated with the energetic approach, and it has been questioned as a method for estimating productivity (Ward and Robinson 1974). It is difficult to construct natural field experiments. Major problems relate to the complexity and the variability of the food source. Seasonal changes in the composition of bacterioplankton, phytoplankton, zooplankton (nauplii, rotifers), and detritus may all affect assimilation rates. Although assimilation of organic carbon is mainly controlled by temperature (Bell and Ward 1970, Schindler 1968), the question of which temperature to use becomes complex when several life history stages may perform variable diel vertical migrations through different temperature regimes (see section on vertical migration).

The recycling of the isotope occurring during the feeding experiment can be a major source of error (Conover 1961, Conover and Francis 1973). Freshly assimilated radiotracer may be channelled into different compartments of respiration and excretion, leading to significant errors in determining assimilation. During a 6 h feeding experiment

with Daphnia pulex, approximately 40% of the assimilated material was lost as respiration (Lampert 1975). Significant losses (40%) have also been reported for Mesocyclops edax after 24 h assimilation experiments (Brandl and Fernando 1975). There has also been concern about possible containment or "bottle" effects from enclosing zooplankton and water in small containers (Roman and Rublee 1980). The magnitude of this error is unknown.

Various biometric procedures are commonly used to estimate productivity of copepod populations. All procedures require life history data, population abundance, mortality and/or growth rates, and/or fecundity (Rigler and Downing, in press). Some methods require distinct separation of cohorts (instantaneous growth rate method) whereas others can be applied to overlapping populations (e.g. increment summation method). One approach, referred to as the removal summation method (Petrovich et al. 1961), estimates productivity by calculating total cohort mortality. If accurate assessments of instar losses can be made from successive field collections, and assigned a mean weight value (as loss or elimination), then productivity would be equivalent to the summation of total losses over the entire life span of the organism (Waters 1977). Biomass estimates (elimination) for each instar at each sampling date can be calculated from the difference between the theoretical and the actual biomass as follows:

$$Be = Bp \times T/D$$

where Bp is the actual biomass of the preceding instar in
the preceding sampling period

Be is the eliminated biomass

D is the stage duration (days) and T is the sampling
period (days).

For more recent applications of this method see Smyly (1973),
and George (1976). Leblond and Parsons (1977) have simpli-
fied this method in calculating productivity of a cohort by
modifying it in an exponential form.

Productivity has also been determined from calculating
turnover times (the time taken for the population to replace
itself), and is calculated by dividing daily biomass by the
turnover time. Turnover time (T) is the reciprocal of
finite birth rate (B) as follows:

$$T = \frac{1}{B} \quad \text{where} \quad B = \frac{E}{D}$$

(see page 18 for clarification of B, E, and D)

Several unrealistic assumptions are made applying this
approach to crustacean populations. A population with a stable
age structure is assumed (Winberg 1971a). The finite birth
model assumes no egg mortality and requires that most of the
growth occurs in the embryonic stage. This may be true for groups
such as the rotifers (Edmondson 1977, Romanovsky and Polishchuk
1982) but, in crustaceans, major growth increments occur in the
juvenile stage (Hillbricht-Ilkowska and Patalas 1967). In
addition, turnover time of numbers is not the same as turn-

over time of biomass (Winberg et al. 1972), especially since
weight (biomass) of an individual varies with the cube of
its length. An adult stage of Macrocyclops albidus can be
several hundred times heavier than an early naupliar stage
(Klekowski and Shushkina 1966). Still, the approach is
widely used in estimating crustacean productivity (Stross
et al. 1961, Wright 1965, Stepanova 1971, Burgis 1971, 1974).

Another method, referred to as the increment summa-
tion method, estimates productivity as a summation of all
growth increments through the life span of a cohort. This
method was initially developed by Pechen and Shushkina
(1964), and Winberg et al. (1965), and is commonly referred
to as the "Pechen-Shushkina" or the "Russian" method. In
general, Gillespie and Benke (1979) has indicated that this
method appears to be the simplest approach in calculating
productivity as compared to the removal summation, instan-
taneous growth, and the Allen curve methods. In the increment
summation method, a series of samples are taken at regular
intervals throughout the cohort life. From one sample to
the next, growth increments are calculated for each life
history stage or series of stages (from laboratory or field),
and are next multiplied by the abundance of that (those
stage(s) to obtain an estimate of productivity. The formula
follows:

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

where P is the productivity in weight units/day of the

cohort.

Ne, Nn, Nc refer to the number of eggs, nauplii and

copepodid stages.

ΔWe, ΔWn, ΔWc is the weight increment (initial minus

final) during the particular stage.

Te, Tn, Tc is the time of development (duration) of

the particular stage.

One major advantage of this method is that cohorts
do not need to be defined, and this method can be applied
to any continuously reproducing population (Edmondson and
Winberg 1972). Winberg (1971a) describes a graphical method
by which increment summation can be used to estimate pro-
ductivity. Mean individual weights, specific daily growth
increments, and numbers in the cohort population are plotted
to derive productivity.

Several investigators have compared estimates of
productivity using the increment summation method with other
approaches. Smyly (1973), and Winberg et al. (1965) noted
that the removal summation method invariably gave higher
estimates of productivity than the Russian method (increment
summation). They attributed this discrepancy to the use of
mean estimates of biomass in the removal summation method,
instead of initial and final weights of individual instars
in the increment summation method. Allanson and Hart (1975)
compared the increment summation method with the turnover
time method for the population of Pseudodiaptomus hessei in

Lake Sibaya, South Africa. On average, turnover time esti-
mates of productivity were four times as large as the incre-
ment summation estimates, and were attributed to an over-
estimate of growth based on birth rate statistics.

Although it appears a more accurate measurement of
estimating productivity, there are still several potential
problems associated with the increment summation method.
Developmental time (T_e, T_n, T_c), a major component of the
formula, is difficult to determine for natural populations.
Most European workers have either used the "Krogh curve"
(Winberg 1971a, Winberg et al. 1972) or have used laboratory
derived development times (Pechen and Shushkina 1964, Winberg
et al. 1965, Winberg 1971a, Kajak et al. 1972, Allanson and
Hart 1975, and others). The basic assumption, in both
methods, is that temperature is the major variable control-
ling the time of development. Although this has been demon-
strated to be true by some investigators (McLaren and
Corkett 1981), there is still some questions as to which
temperature(s) to use.

The diel vertical migration patterns of some zoo-
plankton migrating through variable temperature regimes
makes the situation complex (Hutchinson 1967, Bell and Ward
1970). Secondly, other factors such as food have been
considered important in determining stage development.
Smyly (1970) has shown for Acanthocyclops viridis, that
development can be decreased by 59% when nauplii are used
as a food source instead of unicellular algae at a constant

temperature of 17°C. Similarly, Shushkina (1964) found developmental times of cyclopoids will vary greatly as a function of food concentration. Weglénska (1971) determined productivity for six crustaceans based on developmental times derived from laboratory experiments with temperature alone, and temperature and food combined. During the August period, productivity estimates were 34% higher with measures derived from temperature alone.

Recently, several investigators have questioned the reliability of laboratory-derived developmental times and have calculated stage development times from field data. Comita (1972) provided the first quantitative approach to obtain developmental values from population data for two copepods in Lake Severson. The abundance of each instar within a cohort was plotted against time. Duration of each instar was assumed to be proportional to the length of the time-abundance curve for that instar, that is, the period between the appearance of an individual in any sample and its disappearance. Although this is a valid method to estimate stage duration, Comita (1972) failed to calculate duration in precise mathematical terms, and has been strongly criticized by Rigler and Cooley (1974). Still, their method is being used to estimate stage duration (Peacock 1982). Rigler and Cooley (1974), and Smyly (1973) estimated stage duration as the difference between mean (midpoint) pulses of successive stages (i.e. pulse of an instar to that of the previous one). In this approach at least two stages are considered in the analysis for each calculation. Smyly (1973) estimated the

midpoint of each stage from a plot of instar abundance versus time. Similarly, Rigler and Cooley (1974) described mean pulses for each stage from a series of equations relating abundance against time for several instars. Their approach, which assumes that duration of each instar is greater than that of the previous stage, however, can be unrealistic. For multivoltine populations which reproduce in the winter, duration of naupliar stages developing in the winter months may indeed exceed that of later stages developing in early spring.

Another biometric approach used to estimate productivity is the instantaneous growth rate method. This method was originally developed for fish populations (Ricker 1968, Chapman 1968) and this method or modifications of it are now being used to estimate secondary productivity (Gillespie and Benke 1979, Rigler and Downing, in press). In its simplest form, productivity is the product of instantaneous rate of growth (G) and mean standing crop ($\bar{B}$).

$$i.e. \ P = G\bar{B}$$

where P = productivity for a given period of time in weight/
spatial unit/time period

G = instantaneous growth rate for the time period

$\bar{B}$ = mean standing crop during the time period, in
weight/spatial units.

In this method, one assumes that weight or growth of an individual (or instar) increases exponentially rather than linearly, as in the increment summation method. Thus, the time period for sampling must be short to validate this assumption. One advantage of the instantaneous growth rate

method is that developmental times are not required in the
calculation. However, it does require that cohorts must be
defined which may be difficult to determine in some multivoltine
populations. Applications of this method for fish populations
are given by Kelso and Ward (1972), and Schweigert et al. (1977),
and for secondary producers are given by Rigler and Downing (in
press). Allen (1951) has represented the instantaneous growth
formula graphically, which is commonly referred to as the "Allen
curve". Mathematically, Allen curves and the instantaneous
growth equation are similar (Gillespie and Benke 1979). Allen
curves also require identification of cohorts before they can
be applied to a multivoltine population. Lysack (1976) compared
the productivity of a univoltine population of Chaoborus flavicans
in West Blue Lake using both Allen curve and increment summation
methods. Net productivity determined by both methods were similar:
Allen curve: 1982 mg dry weight $m^{-2}y^{-1}$, and increment summation:
2074 mg dry weight $m^{-2}y^{-1}$. Allen curves have been widely used
to calculate benthos productivity (Edmondson and Winberg 1972,
Waters 1977).

Gillespie and Benke (1979) has numerically compared the increment
summation and the instantaneous growth methods for estimating productivity.
If growth and mortality of a population are exponential, and sampling intervals
are large, then use of the instantaneous growth method yields a somewhat
better estimation of productivity than the increment summation method. Rigler
and Downing (in press) have also indicated that if the population density is
increasing (decreasing) at an exponential rate, then the logarithmic mean
(instantaneous growth) would be a more accurate estimate of the average popu-
lation than the arithmetic (increment summation) mean. However, if the
sampling intervals are small relative to growth and mortality, the discre-
pancy between both methods would be minimal.

Other methods are available for estimating copepod pro-
ductivity. Borgmann et al. (1979) developed a method of esti-
mating copepod productivity based on the size fractionation of
the population   using a series of filtered screens. More
recently, Romanovsky and Polishchuk (1982) developed a production
equation using an instantaneous growth component for both somatic
(body weight growth) and germinated (reproductive) production.

Many of these methods require an extensive data set with
abundance estimates and weight determination for a variety of
instar or larval forms. Some researchers, with limited data sets,
have estimated productivity based on more simplified methods,
such as the production to biomass ($\frac{P}{B}$) ratio (Tremblay and Roff
1983). In this method, it is assumed that the annual production/
biomass ratios for copepods are negatively related to adult body
mass by:

$$\log \frac{P}{B} = -0.16 - 0.34 \ (\log M)$$

where M is adult body mass in kilocalories. This equation is
from Banse and Mosher (1980) and is based on the data sets of
32 invertebrate species. This approach has been strongly criti-
cized by McLaren and Corbett (1984) as a method for estimating
productivity because of a lack of a true dependence of development
rate and specific growth to body size in copepods. Banse (1974)
also suggests that applications for relating production to bio-
mass are most suitable for estimating productivity for planning
field research or for developing the theory of food web relations.

Few copepod productivity estimates exist in North America.
The only annual productivity estimate of a cyclopoid species that

I have found is Comita's (1972) study of Mesocyclops edax in
Severson Lake, Minnesota. M. edax productivity amounted to
1813.5 cal. $m^{-3}y^{-1}$.

Other cyclopoid productivity estimates are available in
the European literature. Patalas (1970) estimated productivity
of Mesocyclops spp., which ranged from 1.5 g $m^{-2}y^{-1}$ in heated
Lake Lichenskie to 0.86 g $m^{-2}y^{-1}$ in unheated Lake Mikorzynskie.
George (1976) found annual productivity of C. vicinus amounted
to 2.71 mg m^{-3} (4.29 g m^{-2}) in 1970 and 2.10 g m^{-3} (4.8 g m^{-2})
in 1971 in Eglwys Nynydd, Wales. In the English lake district,
Smyly's (1973) annual productivity estimates for C. strenuus
abyssorum ranged from 155 mg wet weight m^{-3} for Rydal Lake to
600 mg wet weight m^{-3} for Esthwaite Water. Alimov et al. (1972)
calculated annual productivity of C. scutifer in Lakes Krivoe
and Krugloe. During the ice free season, productivity was 1.8
kcal m^{-2} in Lake Krivoe and 0.19 kcal m^{-2} in Lake Krugloe.
Winberg et al. (1972) calculated productivity of Cyclops sp.
in three different types of lakes. Annual productivity was highest
in the slightly eutrophic Lake Batorin (25.2 kcal m^{-2}), followed
by the highly eutrophic Lake Myastro (11.2 kcal m^{-2}). The meso-
trophic Lake Naroch produced 4.8 kcal m^{-2} of Cyclops sp. annually.

MATERIALS AND METHODS

1. Study Area

West Blue Lake is located in Duck Mountain Provincial Park in central Manitoba (Figure 1). The lake is long, narrow, and steep-sided with an area of 160 ha. The maximum length is 4.8 km; the maximum depth 31 m; and the mean depth 11.3 m. Diacyclops bicuspidatus thomasi is the dominant copepod species in the lake. A detailed description of the lake including species lists is given by Ward and Robinson (1974).

2. Sampling

Sampling of Diacyclops bicuspidatus thomasi was done at stations 2, 3, 4, and 5 throughout the study (Figure 1). Station 2 is 30 m, station 3 is 20 m, station 4 is approximately 7 m, and station 5 is 17 m. The stations selected were assumed to be representative of the lake and were based on earlier and other ongoing research with other zooplankton species (Ward and Robinson 1974). Collections were made at the following depths:

STATION	DEPTH SAMPLED (m)
2	0, 1, 3, 5, 7, 12, 17, 20, 25, 30
3	0, 1, 3, 5, 7, 12, 17, 20
4	0, 1, 3, 5, 7 (8)
5	0, 1, 3, 5, 7, 12, 17

Figure 1. Sampling locations of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> in West Blue Lake.

STATION 5

STATION 4

STATION 3

STATION 2

LAKE WINNIPEG

DUCK MOUNTAIN
PROV. PARK

BLUE
LAKES

SASKATCHEWAN

RIDING
MOUNTAIN
NATIONAL PARK

LAKE MANITOBA

MANITOBA
ONTARIO

WINNIPEG

0   100
KILOMETER

CANADA
USA

N

N

1 KILOMETER
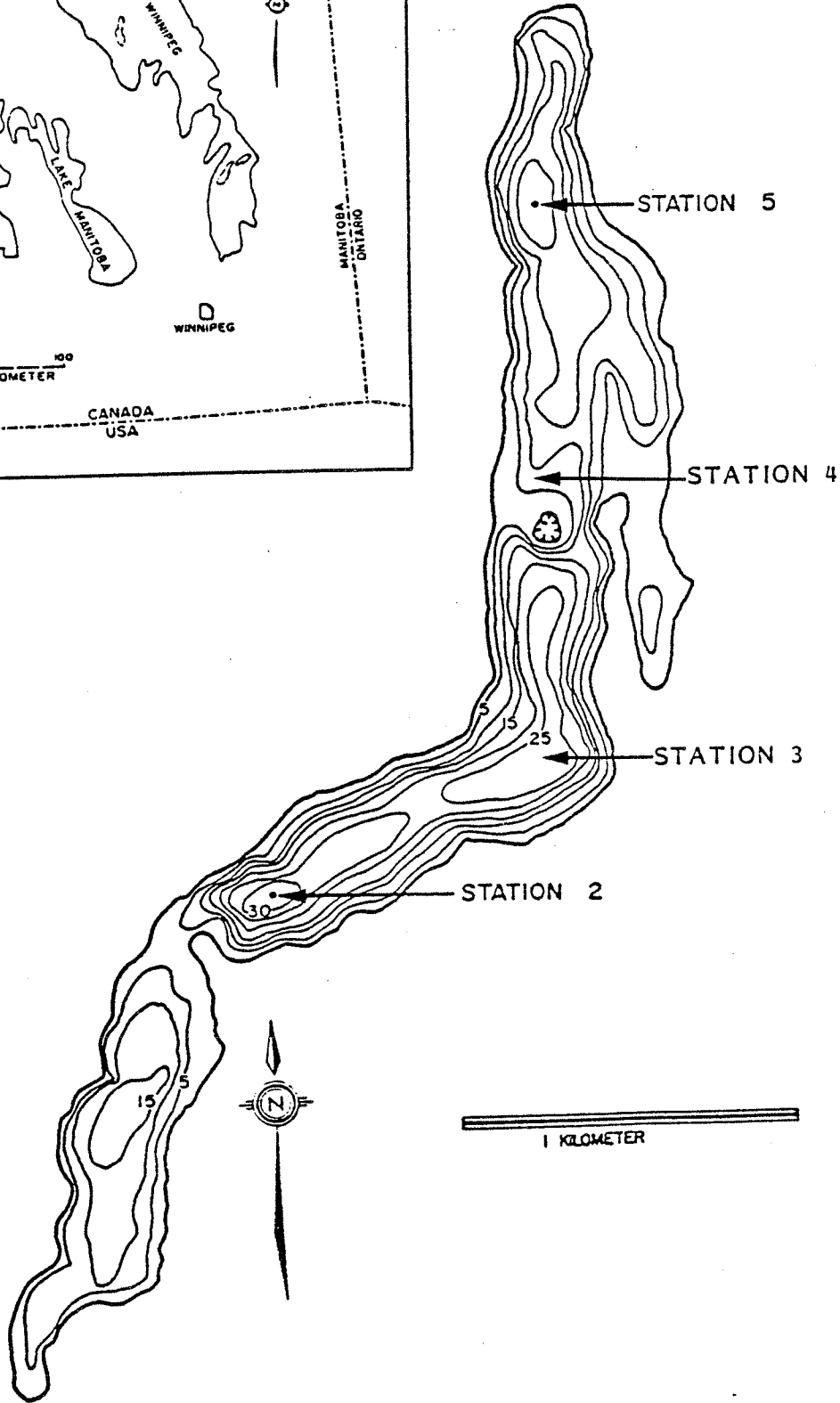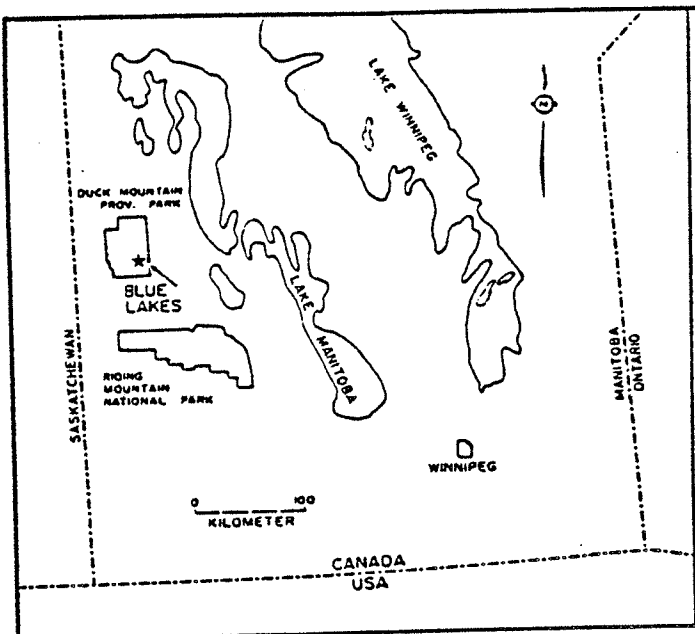
During the spring and summer of 1972 and 1973, collections were made approximately weekly at station 2 and bi-weekly at all other stations. During 1974, collections were made more frequently at station 2, approximately every 3 days. All other stations were sampled bi-weekly. Winter samples for all three years were conducted approximately monthly and were carried out at station 5 only.

Samples collected during 1972 and 1974 were obtained with a 29 L Schindler-Patalas trap (Schindler 1969), fitted with a 73μ nitex mesh. During 1973, the mesh size was 243μ which resulted in an underestimate of smaller life history stages, particularly the nauplii (Table 1).

Table 1.   Comparison of the ratio of total copepodids to total nauplii during 1972, 1973 and 1974.

| MONTH | RATIO | | |
	1972	1973	1974
May	1.5	7.0	1.6
June	1.4	3.7	1.3
July	1.3	8.4	0.8
August	0.5	4.4	0.6
Overall mean	1.2	5.9	1.1

During both 1972 and 1974, the ratio of total copepodids to total nauplii was similar over the May to August period, with an overall mean ratio of 1.2 in 1972 and 1.1 in 1974. In contrast, however, this ratio was considerably higher in

1973 since even naupliar stage 6 would be able to pass through the 243 μ mesh.Consequently, data collected from 1973 were used only for qualitative purposes.

All samples collected in the trap were rinsed from the net into pre-marked 35 mm square bottles, and were preserved with formalin (5%). Generally, the entire sample was placed in a counting cell and mounted on a Zeiss inverted microscope. The sample was allowed to settle at least 60 minutes prior to counting (under 100X magnification). On a few dates sampled in May, the sample was subsampled because of the large number of organisms and particulate matter present.

All life history stages of D. b. thomasi were identified and counted. Copepodid stage identification followed the outlines provided by Edmondson (1959) and Patalas (pers. comm.). Nauplii were grown in cultures to confirm earlier work conducted by Ewers in 1930. Fecund females were collected from West Blue Lake in December and brought to the laboratory. Eggs were removed from the females and placed individually in 50 mL beakers each containing filtered lake water. Cultures were maintained on Ankistrodesmus sp. and a protozoan mixture, and were held in a controlled environmental chamber at 12°C with a 14 h light - 10 h dark cycle. The procedure for culturing was similar to that described by Lewis et al. (1972). Every two days, each beaker was inspected, and detailed diagrams were made of the naupliar stage(s) present. Diacyclops b. thomasi was noted to have six naupliar

stages which were accurately described by Ewers (1930).

Benthic samples were taken approximately weekly at
stations 2 and 5 during 1974 and monthly at station 5 during
1975. Samples were also taken once in 1974 and 1975 at
stations 3 and 4. Collections were made to investigate whether
D. b. thomasi entered diapause at a late copepodid stage as
has been previously reported for the species (Birge and Juday
1908). Samples were collected with a multiple corer
(Hamilton et al. 1971), and observations were made for D. b.
thomasi in both the water suspended directly above the sedi-
ment as well as in the sediment sample. The water sample
was filtered through a 73 μ nitex screen, washed into 35 mm
pre-labelled bottles and preserved in 5% formalin. Samples
were later counted with the Zeiss inverted microscope and
copepod abundance was expressed as the number of individuals
per liter. The sediment samples were washed through a series
of large nitex screens (>1 mm) to remove small stones and
large detrital material. The samples were next screened and
washed onto a 73μ nitex mesh, and the contents were rinsed
into labelled bottles and preserved. Presence or absence of
any life history stage of D. b. thomasi was noted. The in-
tention was to sample for presence and absence rather than
quantitative estimates of numbers in the sediment.

Four diel vertical migration collections were made
during 1974: May 28, June 11, July 19 and August 16.
Samples were collected at station 2 which was assumed to be
representative of the lake. Collections were made with a

Schindler-Patalas trap at depths of 0, 1, 3, 5, 7, 12, 17, 20, 25 and 30 m. With the exception of May 28, collections started at 10:00 h and continued at 2 h intervals for 24 h on each sampling date. May 28 collections were made at 4 h intervals. Each sample was labelled, preserved in formalin, and all life history stages of D. b. thomasi were counted under the Zeiss inverted microscope. Temperature, oxygen, and particulate carbon depth profiles accompanied each vertical migration collection. Measurements were taken throughout the water column at similar depths as the plankton samples and followed procedures described earlier in Ward and Robinson (1974).

3. Calculations of Abundance, Mean Lake Estimates and Depth-Weighted Peaks

Abundance of Diacyclops bicuspidatus thomasi was expressed as the number of individuals per square metre. The number of individuals per litre was estimated (from the trap), and was multiplied by 10^3 to obtain the number of individuals per cubic metre. This was done for each sampling depth and integrated for the entire water column. The resultant was the number of individuals per square metre. Population estimates were determined for the mean depth of the lake by developing regression equations relating abundance and station depth. The calculated correlation coefficient indicated the amount of horizontal variation in the sampling. Population estimates were interpolated for the

mean depth of the lake (11.3 m). Confidence limits (95%) accompanied each population estimate. Mean lake population estimates were determined over the entire sampling period (long term regressions). Calculated mean lake population estimates were used in productivity calculations. It should be noted that this procedure is merely a method for obtaining an estimate of mean abundance and should not be considered to have great theoretical importance. This method will yield a significant correlation between station depth and numbers (i.e. self-correlation) when vertical migration approaches uniformity.

Depth-weighted peaks ($\overline{D}$) were calculated for various life history stages of each vertical migration period. For each migration period (e.g. May 0800), the number of animals in each stage (m^3) was estimated for each sampling depth (0, 1, 3, 5, 7, 12, 17, 20, 25, 30 m). These were next interpolated for each depth throughout the entire water column. Depth-weighted peaks next were calculated as follows:

$$\overline{D} = \frac{\sum (A \times d)}{\sum A}$$

where $\overline{D}$ = depth-weighted peaks in m which refers to the depth at which the median level of the population occurs.

A = # of animals m^3 at each depth (for all depths in the water column)

d = depth in m (all depths in the water column)

Depth-weighted peaks of all instars are given in Appendix G.

4. Cohort separation

A cohort is defined as those animals developing from eggs to adults in the same reproductive period. It can give rise to one or more separate generations. Cohorts were defined subjectively from field collections at stations 2 (spring, summer) and 5 (fall, winter). Inspection of any given field sample indicated the presence of at least one dominant naupliar and one dominant copepopid stage (generally late). This suggested the presence of at least two cohorts in the population. Based on the abundance peaks of these dominant stages over successive sampling periods, it was possible to follow the life history development from early naupliar to late copepodid stages for each cohort. Using this approach, it was assumed that all individuals of a given stage had similar development. It was also assumed that field collections from stations 2 and 5 were representative from the lake. Information on the percentages of gravid females in the population was also used to separate cohorts. It was assumed that the highest percentage of gravid females in a sample would represent the beginning of a cohort. Although imperfect, there is no better way than a subjective evaluation of the data in defining cohorts.

5. Mortality Estimates

Mortality of Diacyclops bicuspidatus thomasi was estimated using Ricker's catch-curve method. Instantaneous mortality was calculated from abundance data for each cohort.

These were determined by linear regression procedure, relating
the natural logarithm of abundance to time of sampling. The
resultant negative regression coefficient was the instantaneous
mortality rate z.

6. Length Measurements

Egg size was determined for adult copepods collected
from cohort 2 (May) in 1972, and from cohorts 1 (December,
January), 2 (May) and 3 (August) in 1974. Egg sacs were
removed with fine forceps from adults, and egg diameter was
measured with an Olympus ocular micrometer. This micrometer
was calibrated to $\pm 1.0 \mu$ (at 100X magnification) by the use
of a stage micrometer. To minimize variability, more than
100 eggs were selected from several copepods for each cohort.
In addition to egg measurement, estimates were made on
female fecundity within each cohort.

Lengths were also determined for all other life his-
tory stages of Diacyclops bicuspidatus thomasi using the
ocular micrometer at lower binocular powers (4X, 10X magni-
fication). Estimated accuracies for 4X and 10X magnifications
were approximately $\pm 10 \mu$ and $\pm 100 \mu$ respectively. More
than 20 individuals were measured for each life history
stage. Both metasomal and total lengths were determined for
the copepodid stages.

7. Determination of Carbon, Nitrogen and Calorific Content

Carbon and nitrogen contents were determined for several life history stages of Diacyclops bicuspidatus thomasi. These determinations were only made on stages developing within cohort 2 (spring-summer). During the spring and summer, plankton samples were inspected frequently to assess which stage or groups of stages were abundant at those times. After the initial inspection, each plankton sample was screened into several size classes by passing it through a series of nitex screens: 1050μ, 500μ, 243μ, and 110μ. Nauplii and copepodid stages were retained primarily on the 110μ, 153μ, and 243μ screens, and were later rinsed and filtered onto a Gelman 45 mm 0.45μ filter. Daphnia pulicaris (adults) and Chaoborus flavicans (larva) were removed from the sample onto both the 1050μ and the 500μ screens. Moist filters were next placed under a binocular scope (40X), where abundant stages of D. b. thomasi were identified, and removed with 'micro' pins. Approximately 70-100 individuals from each stage were placed into carbon free aluminum boats, dried at 105°C, and combusted in a Perkin-Elmer Elemental Analyzer Atomic Model 240 for carbon and nitrogen contents. Egg sacs, dissected from adult D. b. thomasi, were retained on the 243μ screen and were analyzed similarly.

Calorific content of D. b. thomasi was determined approximately monthly during 1974. Samples were collected by towing plankton nets vertically through the water column, and animals collected were screened in the same way as for

carbon and nitrogen analysis. <u>Daphnia</u> <u>pulicaria</u> and <u>C</u>.
<u>flavicans</u> were removed on the larger sized screens. Copepods
collected on the 110μ, 153μ and 243μ screens were com-
bined, and rinsed into petri dishes containing 10 mL of
filtered lake water. The sample was next inspected under a
binocular scope (40X) and copepodid species present other
than <u>D</u>. <u>b</u>. <u>thomasi</u> were removed by pipette. A subsample
was then taken (n = 100 individuals), and both the percent
composition and stage make-up of <u>D</u>. <u>b</u>. <u>thomasi</u> were assessed.
If <u>D</u>. <u>b</u>. <u>thomasi</u> composed less than 95% of the total number
of animals, the screening and sorting procedure was repeated.
Samples were then filtered onto a Gelman .45μ filter, dried
at 105°C for 24 h, and weighed on a Cahn electronic micro-
balance. Calorific content of each sample was determined
with a Phillipson micro-bomb calorimeter (Gentry Instruments).
Actual procedures were similar to that described by Phillipson
(1964) and Schindler <u>et</u> <u>al</u>. (1971). Pellet size ranged from
approximately 2 to 11 mg dry weight.

8. Growth Rate Estimates

Both relative and instantaneous growth rates were
estimated for <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u>. Relative
growth rates were estimated for each cohort and were based on
weight increments between successive instar stages (Winberg
1971a). Carbon and nitrogen content of the various life
history stages of <u>D</u>. <u>b</u>. <u>thomasi</u> were first determined from
two regression equations: one expressing the relationship
of nitrogen content to length and the other the relationship

of carbon to length. Weight increments in terms of both carbon and nitrogen were determined by the differences between adjacent instar weights (for example for carbon, $\Delta Wc = W2c - W1c$). For each cohort, the weight increment of each stage was regressed against time of development or duration of each stage. The slope of the regression equation (g) was an indication of the growth rate of that particular cohort.

Instantaneous growth rates (G) were also calculated for Diacyclops bicuspidatus thomasi following the procedure outlined by Chapman (1968) and Ricker (1975) for fish. Estimates were determined for each cohort according to the formula:

$$G = \frac{\ln C2 - \ln C1}{t}$$

where C2, C1 = weight (carbon, nitrogen) of individual

cohorts at time t

9. Developmental Times

Stage developmental times were determined for each cohort from field samples collected at stations 2 and 5 during both 1972 and 1974. Cohort development for spring and summer periods were derived from the station 2 data whereas cohort development in the fall and winter were calculated from data collected at station 5. Stage development or duration was defined as the difference in time between the mean abundance peaks of two adjacent instars where N is abundance, t is time, and D is instar duration as follows:
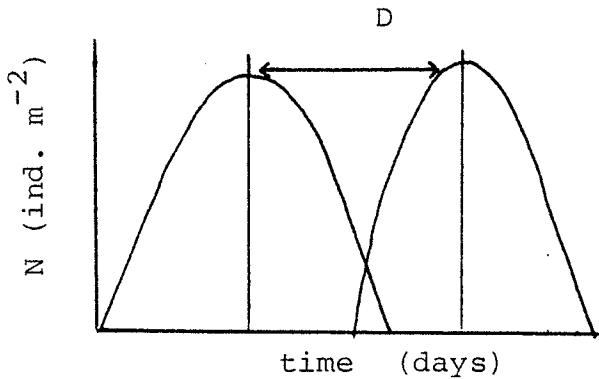
The number of individuals of each stage within a cohort was plotted against time. The total area under the abundance-time curve for each stage was first determined with a planimeter. The midpoint (mean) was next calculated for each successive stage, the difference (in days) between each stage was an estimate of development. This approach was similar to that used by Smyly (1973) for _Cyclops strenuus._ Three assumptions are made using this procedure for estimating stage development.

1. All individuals of a stage have the same development time. This assumption can be violated if animals show strong diel vertical migration. For example, all individuals of a stage may not perform diel vertical migration through the thermocline to the same extent as other individuals. This assumption is discussed in more detail on page 58 of the Vertical Distribution section.

2. Mortality is constant for all individuals throughout the development of each stage. If stage specific mortality occurs, the calculated midpoint for estimating stage

development may be in error. This assumption is difficult to test since quantitative mortality and recruitment rates are needed for each stage.

3. Stage developmental times determined from stations 2 (spring, summer) and 5 (fall, winter) are representative of the entire lake. This assumption will be supported in pages 89-90 of the Population Dynamics section.

10. Calculation of Biomass

Biomass expressed as either carbon or nitrogen was determined as follows. Length-weight (as organic carbon, nitrogen) relationships were calculated for both metasomal and total length measurements of Diacyclops bicuspidatus thomasi. Using the appropriate equation, the weight value of a particular stage was calculated from the mean length. Multiplying the mean weight of an individual stage by the abundance of that stage during a given period yielded a biomass estimate for that period. Stage biomasses were summed giving total biomass.

11. Productivity

Productivity of Diacyclops bicuspidatus thomasi was estimated using two biometric approaches, the increment summation (Russian) method and the instantaneous growth method. (Ricker-Chapman).

The Russian method of calculating productivity, or increment summation method, was initially put forth by

Pechen and Shushkina (1964) and later Winberg (1971a), and describes productivity as a summation of all growth increments in the population. The basic components of the method are growth increments ($\frac{\Delta W}{D}$) and numerical abundance (N), and is described as follows:

$$P = \frac{Ne\Delta We}{De} + \frac{Nn\Delta Wn}{Dn} + \frac{Nc\Delta Wc}{Dc}$$

where

P = productivity in weight units (e.g. μg C)

Ne, Nn, Nc = number of eggs, nauplii and copepodids

ΔWe, ΔWn, ΔWc = weight increments of an individual of a particular stage

De, Dn, Dc = time of development or duration of each stage

From a series of sample collections, the growth increment of a stage or series of stages was calculated as the increase in mean individual weight over that time period. This was next multiplied by numerical abundance of that stage or stages for that period to obtain an estimate of productivity for that period. Annual productivity is the summation of productivity for each cohort. Although productivity estimates using this approach may include members of more than one cohort (Winberg 1971a), productivity of D. b. thomasi in West Blue Lake was estimated for each cohort. Consequently, separate growth curves ($\frac{\Delta W}{D}$) were determined for each cohort which involved a subjective

separation of cohorts. Winberg (1971a) also describes a graphical method to obtain cohort productivity by plotting mean individual weights, daily growth increments and abundance.

The instantaneous growth method of productivity was initially developed for use in fish production (Ricker 1946, Chapman 1968) but also has been considered for the estimation of invertebrate productivity (Waters 1977). Allen (1951) has extended the formula to a graphical representation commonly referred to as the "Allen curve". In its simplest form, the instantaneous growth method is the product of the instantaneous rate of growth and mean biomass:

$$P = G\overline{B}$$

where

> P = productivity for a given period of time in weight units
>
> G = instantaneous growth rate for the time period
>
> $\overline{B}$ = mean standing stock or biomass during the time period in weight units

For application to an invertebrate population, the cohorts must be identifiable (Waters 1977). For this reason, the method does involve a subjective separation of the cohort. However, this problem of subjectivity is inherent in analyzing all multivoltine populations, and has been noted by several investigators (Rigler and Cooley 1974, Comita 1972, Swift and Hammer 1979, Carter 1974 and others).

For $\underline{D}$. $\underline{b}$. $\underline{thomasi}$ in West Blue Lake, Chapman productivity was determined as follows:

Based on the population structure of $\underline{D}$. $\underline{b}$. $\underline{thomasi}$ cohorts were first defined. For each cohort, biomass (C) was determined for each time period by multiplying stage abundance (N) by the stage biomass (measured in carbon). This biomass was next divided by the total number of individuals (all stages) found during that period, resulting in a mean carbon content of individuals in that cohort (for example week 1).

$$\text{i.e.} \quad C = \sum_{S=1}^{12} \frac{(Cs.Ns)}{\sum Ns}$$

where

S = life history stage 1 to 12

N = numerical abundance

C = standing crop or biomass in carbon units

The mean carbon content of individuals (μg ind^{-1}) multiplied by the number of individuals in that cohort will yield a biomass estimate for that cohort.

This procedure was repeated for the next sampling period (week 2). Instantaneous growth rate was next calculated by taking the natural logarithm of the mean carbon value of individuals in week one (C1), substracting it from the natural logarithm of the mean carbon value in the same cohort in week two (C2), and dividing by the sampling period t (1 week or 7 days).

This procedure was repeated for each sampling period. Mean biomass was next calculated between the sampling periods by summing the biomasses of weeks one and two, and dividing by two. This was repeated for each sampling date and resulted in a series of mean biomasses ($\bar{B}$). Productivity

SAMPLE CALCULATION OF CHAPMAN PRODUCTION

Date	Numerical abundance (no.ind.m^{-2})	Biomass of total population (mgCm^{-2})	$\overline{B}$ (mgCm^{-2})	Biomass of average ind. (μgCm^{-2})	lnB	G (daily)	Productivity (mgCm^{-2}day^{-1})
May 25	663 745	533.724		0.801	-0.221		
			518.239			0.048	24.875
28	541 718	502.756		0.928	-0.075		
			549.899			0.089	49.000
31	492 226	597.043		1.212	0.192		

(P, weekly) is the product of the instantaneous growth rate
(G) and the mean biomass. Productivity (i.e. $P = G \cdot \bar{B}$) was
determined for each cohort, with cohort totals yielding
annual productivity.

Mean lake productivity (both Chapman and Russian
approaches) were determined based on predicted population
estimates for the mean depth of the lake (section 3), and
on growth rate data supplied from stations 2 (spring, summer)
and 5 (fall, winter) over a comparable time period. In
these estimates, growth from stations 2 and 5 were assumed
to be representative of the lake, supported in pages
of the Population Dynamics section.

A comparison was made in productivity (mg C m^{-2} day^{-1})
(Russian method calculated) between estimates derived from
the growth of only one cohort and the natural population. It
was reasoned that if estimates were similar it may be possible
to predict productivity for multivoltine populations over the
spring-summer season (May to August) based on only one
growth curve. Cohort 2 was selected for the one cohort esti-
mates since development occurred during the spring and summer
period.

12. Data analysis

Data collected from stations 2 (spring, summer and
5 (fall, winter) were used for life history analysis, cohort
timing, abundance trends, mortality and growth. Comparison
of productivity derived from one cohort compared to that of

the natural population (applied growth) was also made using these data. Stage contribution to total productivity and an analysis of vertical migration data were also made from station 2 collections. Data collection from all four stations (2, 3, 4 and 5) were used to estimate mean lake abundance, mean lake biomass and productivity, and population turnover rates. A comparison of productivity between Chapman and Russian methods was made using both stations 2 and 5, and mean lake (4 station) data.

RESULTS

1. Life History and Vertical Distribution

Life history

The Diacyclops bicuspidatus thomasi population in
West Blue Lake is multivoltine and consists of three cohorts
(Figure 2). Cohort separation was based on the percentage
of gravid females in the population (Table 2) as well as
the occurrences and abundances of early naupliar stages
Figure 2). High percentages of gravid females in 1972 and
1974 generally occurred in three major pulses which were
closely followed by large numbers of early nauplii. It is
noteworthy that the percentage of gravid females in 1974
was consistently higher than in 1972 (at least double) for
each cohort.

Times of occurrence and duration of each cohort is
given in Table 3. Cohort duration in 1973 was not estimated
because the sampling method did not quantitatively sample
all life history stages (Table 1).

Cohort 1 which began approximately the 20th of
February in 1972 (eggs present), and January 28 in 1974,
had developmental times of approximately 108 and 136 days,
respectively (Table 3). Although cohort 1 duration could
not be accurately defined in 1973, it also began sometime in
January (presence of eggs, and early naupliar stages).
During mid-June of each year, there was a sharp decline in
numbers of copepodid stage 4 (Figure 2). The abundance of

Figure 2. Population structure of <u>Diacyclops</u> <u>bicuspidatus</u>
<u>thomasi</u> in West Blue Lake 1972, 1973, 1974.
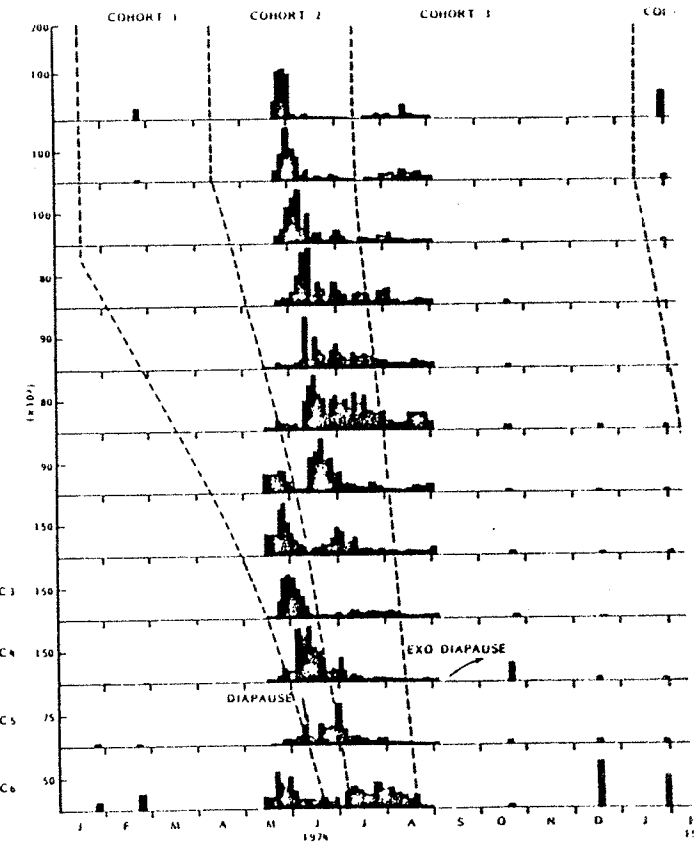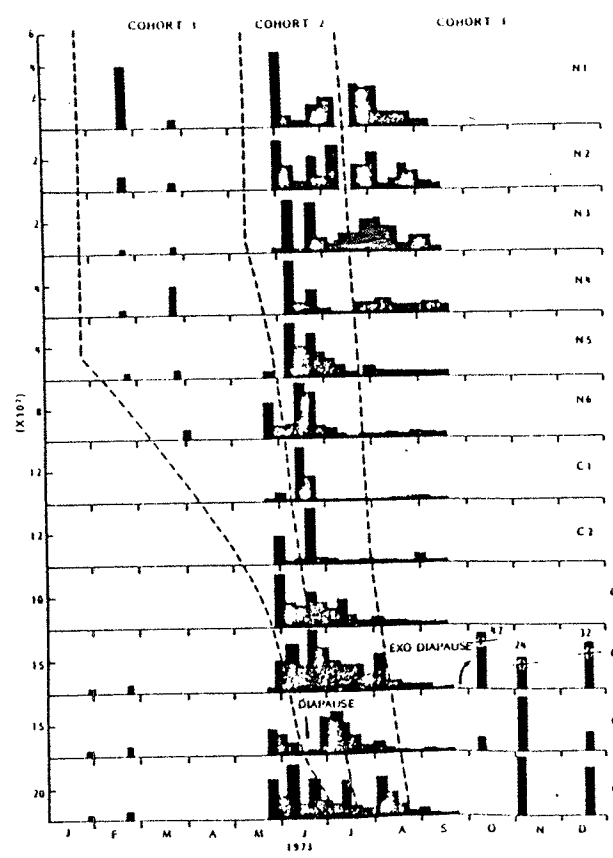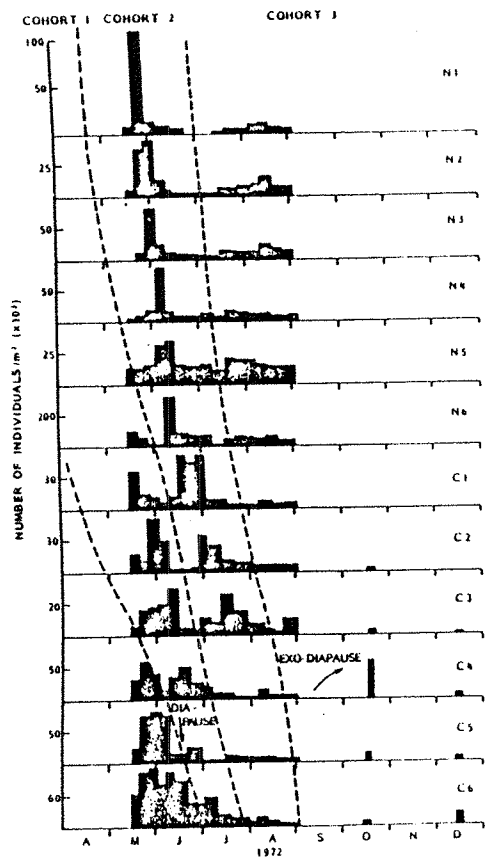
Table 2. Percentage of gravid females, and adult female abundance in 1972 and 1974 (station 2, 5 data).

	1972				1974		
Date	% Females gravid	Cohort number	Numerical abundance (# females m^{-2})	Date	% Females gravid	Cohort number	Numerical abundance (# females m^{-2})
May 17/72	13.5	C2	53927	May 16/74	20.5	C2	21483
24	20.2		90958	22	45.2		61961
30	6.7		97027	25	42.7		40617
June 6	1.0		73167	28	39.4		35342
13	0		47513	31	37.5		56651
20	0		47479	June 2	27.6		32963
27	0		31204	4	25.0		16343
July 3	2.5	C3	27825	7	8.1		17033
11	1.6		15757	9	22.2		16550
18	7.2		19585	12	4.0		13309
25	5.4		13913	15	0		16964
August 1	8.5		10827	18	7.1		10413
8	25.3		12033	21	0		6689
15	0		7448	23	8.1		11123
29	0		7534	25	0		8500
October 14	0		1517	28	5.0		4870
December 14	0		6275	July 2	0		4276
January 27/73	0		1896	4	5.0	C3	16861
February 20	eggs present	C1	2793	7	8.6		17102
March 24	eggs present		6137	14	1.9		15033
				19	42.4		9034
				23	31.9		19792
				26	20.1		30480
				29	27.1		15793

Table 2. Continued.

Date	% Females gravid	Cohort number	Numerical abundance (# females m^{-2})
		1974	
August 2	39.4		9103
6	20.4		5776
9	0		21192
16	0		10621
23	36.9		19103
September 2	0		1793
October 19	0		414
December 16	0		38997
January 20/75	12.7	C1	34963
February 19	9.5		25343
April 3	0		

Table 3. Times of occurrence and duration of cohorts of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> during 1972 and 1974.

Year	Cohort 1		Cohort 2		Cohort 3	
	Occurrence	Development (days)	Occurrence	Development (days)	Occurrence	Development (days)
1972	Winter-spring	108	Spring-summer	63	Summer-winter	138
	February-June		May-July		July-December	
1974	Winter-spring	136	Spring-summer	62	Summer-winter	110
	January-June		May-July		July-December	

this stage remained low throughout the summer until October when there was a sudden increase in numbers. These abundance increases during 1972 and 1974 were approximately 24 and 11.6 times respectively, greater than numbers recorded at the previous sampling date. These data indicate that copepodid stage 4 was leaving the water column, entering the profundal sediments in mid-June, and returning to the water column in October. Additional evidence of diapause was available from the multiple corer data (Figure 3). The corer samples indicated that copepodid stage 4 was present in the sediment from late June to October during both 1974 and 1975. Prior to diapause, there were large concentrations of this stage in the water column (floc) directly above the mud. Copepodid stage 4 numbers were estimated as high as 864 ind. L^{-1}. Diapause was observed at only stations 3 (20m), 4 (7-8m), and 5 (17m).

Cohort 2 began approximately May 7 in 1972, sometime in May in 1973 and May 16 in 1974 and ended in late July for each year (Figure 2). Developmental times of this cohort were estimated at approximately 63 days in 1972 and 62 days in 1974 (Table 3). This cohort was particularly definable. On May 23, 1974, approximately 1×10^5 eggs m^{-2} were estimated.

Cohort 3 started approximately July 3 in 1972, sometime in July in 1973 and July 4 in 1974 and extended throughout the winter period. The development of copepodid stage 4 within this cohort coincided with the emergence of the copepodid stage 4 from cohort 1 coming out of diapause (Figure 2). Duration of cohort 3 was approximately 138 days

in 1972 and 110 days in 1974 (Table 3). Cohort 3 was less distinct or defined than either cohorts 1 and 2 because of the high degree of stage overlapping. Adults reproduced in January in both 1972 and 1973, and in mid-February in 1974.

Comparisons were made on the fecundity of Diacyclops b. thomasi between cohorts in 1974, and for cohort 2 in 1972 and 1974. Mean adult female size varied significantly among cohorts in 1974 (ANOVA $F_{2,78} = 5.1$, $p < 0.05$) with largest individuals recorded in the winter. Differences were also noted in the mean clutch sizes (no eggs/♀) for each cohort (Table 4). In 1974, cohort 2 (spring) had statistically the highest mean clutch size followed by cohorts 3 (summer) and 1(winter, $F_{2,59} = 139$, $p < 0.01$). Clutch size also varied for cohort 2 females between 1972 and 1974 (Table 4). Results of an analysis of variance indicated that cohort 2 females in 1974 had, on average, 12.3 more eggs than females belonging to the same cohort in 1972. In addition to higher clutch size, there was a higher percent composition of gravid females in the population in 1974 than in 1972 (Table 2).

Egg size (diameter) also varied considerably among cohorts in 1974 (Table 4). The largest eggs were found in the winter (cohort 1), and the smallest in the spring (cohort 2). All three cohorts were compared with respect to mean egg size using an analysis of variance procedure. Results of the ANOVA and follow up multiple range test indicated that cohort 1 had the largest eggs, followed by cohorts 3 and 2 ($F_{2,30} = 478$, $p < 0.01$).

Figure 3. Presence or absence of <u>Diacyclops</u> <u>bicuspidatus</u>

<u>thomasi</u> in the sediments (copepodid stage 4).
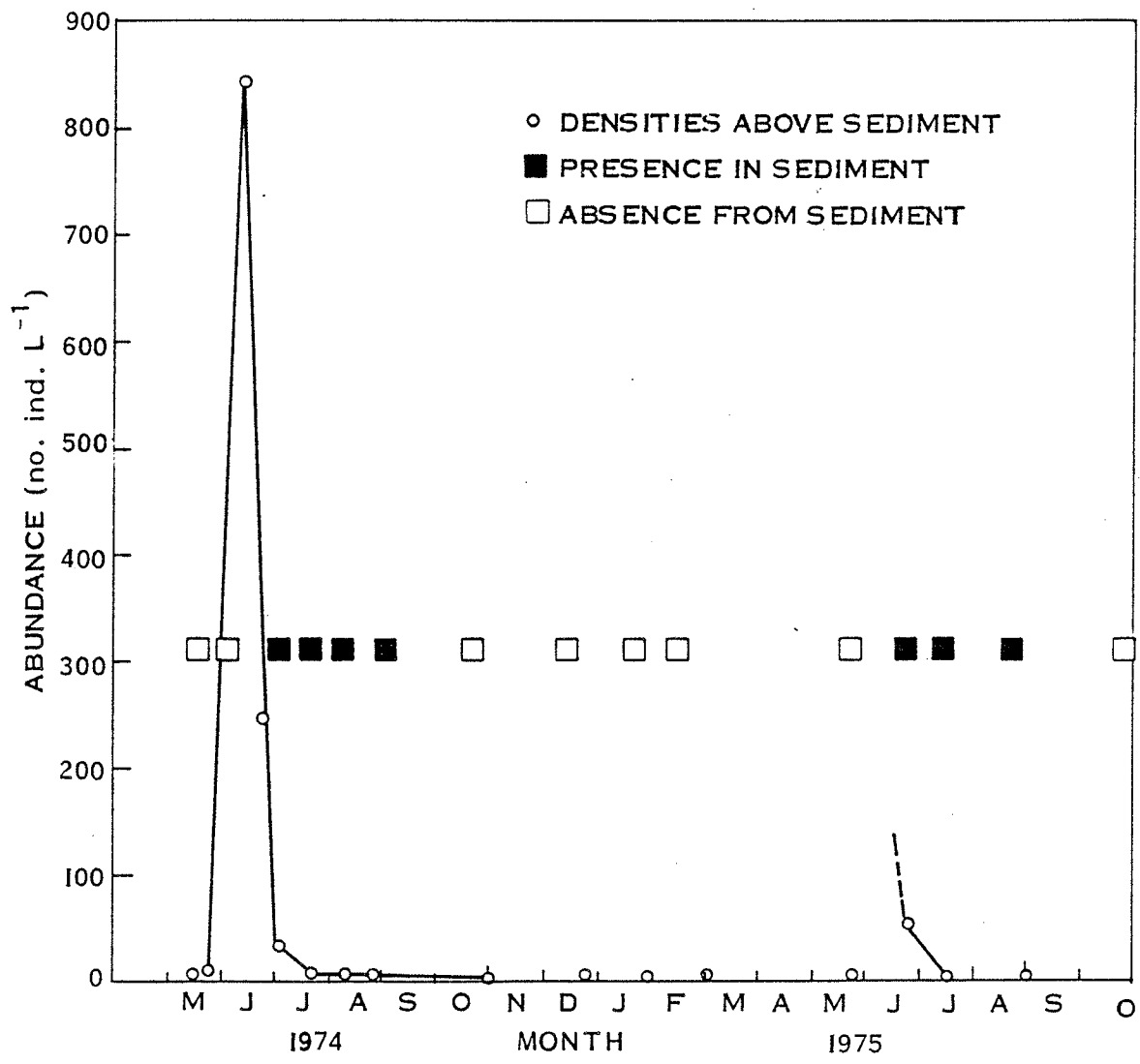
Egg size also varied from cohort 2 between 1972 and 1974 (Table 4). Results of an analysis of variance indicated that cohort 2 females in 1974 had smaller sized eggs than the same cohort in 1972 ($F_{1,22} = 112$, $p < 0.01$).

An inspection of the 1972 and 1974 egg data showed an inverse relationship between clutch size and egg diameter (Table 4). Mean clutch volumes derived from these data varied only slightly among cohorts. During 1974, clutch volume ranged from 0.97 mm^3 x 10^{-2} for cohort 1 to 1.31 mm^3 x 10^{-2} for cohort 2. The clutch volume of cohort 2 in 1974 was slightly higher than for the same cohort in 1972.

Data were also collected on the calorific content of selected life history stages at various times of the year (Table 5). Calorific content of _Diacyclops_ _b_. _thomasi_ varied considerably, with highest values recorded during the winter and early spring and lowest values found during the summer. Estimates ranged from approximately 4639 cal g^{-1} in the late June to approximately 8200 cal g^{-1} in April. This variable seasonal calorific content was unrelated to differences associated with different life history stages. For example, in August, when nauplii constituted approximately 65% of the total numbers, the calorific content was only 4846 cal g^{-1}. However, in February and April, a similar composition of naupliar stages yielded a calorific content over 6000 cal g^{-1}. In December, when nauplii constituted less than 1% of the total numbers, the calorific content was still 6041 cal g^{-1}.

Table 4. Fecundity, gravid female size, egg diameter and mean clutch volumes for spring, summer and winter cohorts in 1974 and the spring cohort in 1972*.

Cohort	Female size (μ)	# eggs/female	Egg diameter (μ)	Mean clutch volume $(mm^3 \times 10^{-2})$
1 1974 (winter)	1315 ± 52.8	26.21 ± 1.43	89.10 ± 0.58	0.97
2 (spring)	1292 ± 52.8	52.00 ± 3.11	78.37 ± 0.37	1.31
3 (summer)	1240 ± 38.8	33.32 ± 1.70	83.67 ± 0.36	1.02
2 1972 (spring)	- - - -	39.70 ± 2.30	81.71 ± 0.36	1.13

* Values shown are means accompanied by 95% confidence intervals.

Table 5. Mean calorific content of Diacyclops bicuspidatus
thomasi recorded during 1974-5.

Date	Stages present	Percent composition	Mean calorific content $(cal.g^{-1})$	Confidence intervals (95%)
May 22	N1-N6	29.8	6177	744.5
	C1-C6	70.2		
June 7	N1-N6	54.6	5571	340.2
	C1-C6	45.4		
June 25	N1-N6	43.4	4639	155.9
	C1-C6	56.6		
July 14	N1-N6	59.2	4670	158.8
	C1-C6	40.8		
August 9	N1-N6	64.8	4846	344.0
	C1-C6	35.2		
Oct. 19	N1-N6	22.8	5542	- - - - -
	C4	55.6		
	C5-C6	10.2		
	N1-N6	0.6		
Dec. 16	C1-C4	8.5	6041	542.2
	C5-C6	90.9		
Feb. 19	N1-N6	75.3	7016	224.3
	C1-C6	24.7		
April 3	N1-N6	86.7	8200	- - - - -
	C5-C6	13.3		

The high calorific contents in late fall and winter also cannot be totally attributed to egg production. Eggs were only present in high abundances during May, August and February. High calorific levels were probably related to the presence of fat globules which were observed in the body cavities during the fall and winter periods. These globules had a reddish color in both nauplii and copepodid stages.

Vertical distribution

Vertical distribution patterns from May to August of dominant stages of _Diacyclops_ _bicuspidatus_ _thomasi_ are described. A listing of the depths selected by all stages of _D. b. thomasi_ is given in Appendix G.

(i) May 28-29

On May 28-29, there was no significant indication of stage migration over the 24 h sampling period (Figure 4). The lake water temperatures were almost isothermal on these dates, ranging from approximately 4 to 6°C (Figure 5). Particulate carbon distribution in the water column was generally highest in the upper 12 m with a peak of approximately 660 mg C L^{-1} occurring at 7 m (Figure 6). Values less than 375 mg C L^{-1} were noted below 17 m. Naupliar stages were distributed fairly uniformly throughout the water column with most individuals found in the upper 10 m of water (Figure 4). Copepodid stage 6 distribution over the 24 h period

Figure 4. Vertical distribution of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> on May 28-29, 1974. (N refers to the number of individuals per m^2).

N   ⊢⊣ 20%

22696   21003   17796   28484   34412   29792   19109

N1

41034   107040   36828   38277   50871   65033   41590

N3

4968   7107   5106   6555   7038   6279   5313

N6

42547   35795   51647   69650   39237   55383   62892

C2

18420   16964   18215   22075   12834   19113   19109

C4

67378   54900   88898   115796   41235   62334   40221

C6º

Depth (m)

0   10   20

1000   1400   1800   2200   0200   0600   1000

Time of Day

149796-RD
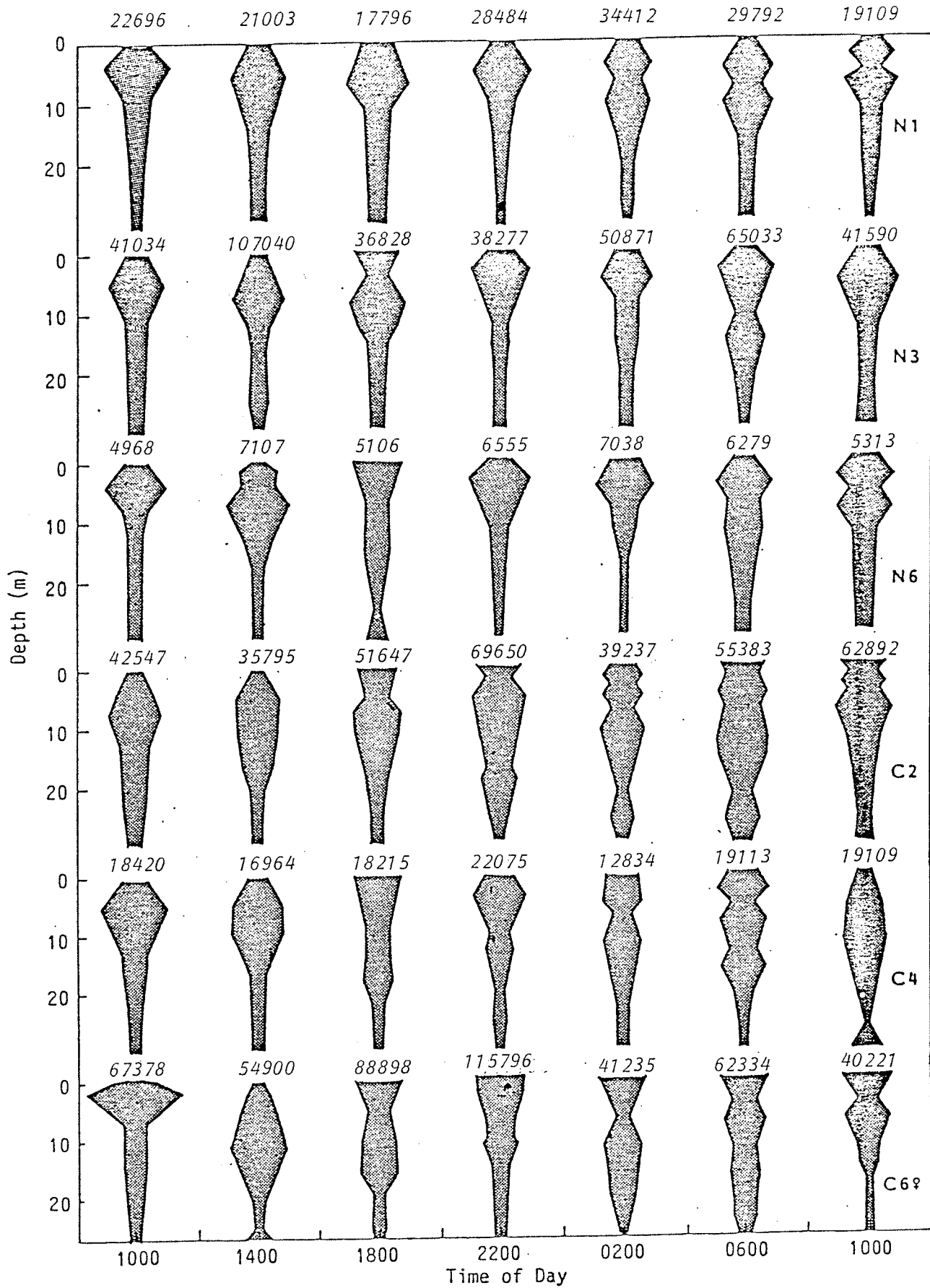
Figure 5. Temperature profiles in West Blue Lake
           during 1974.
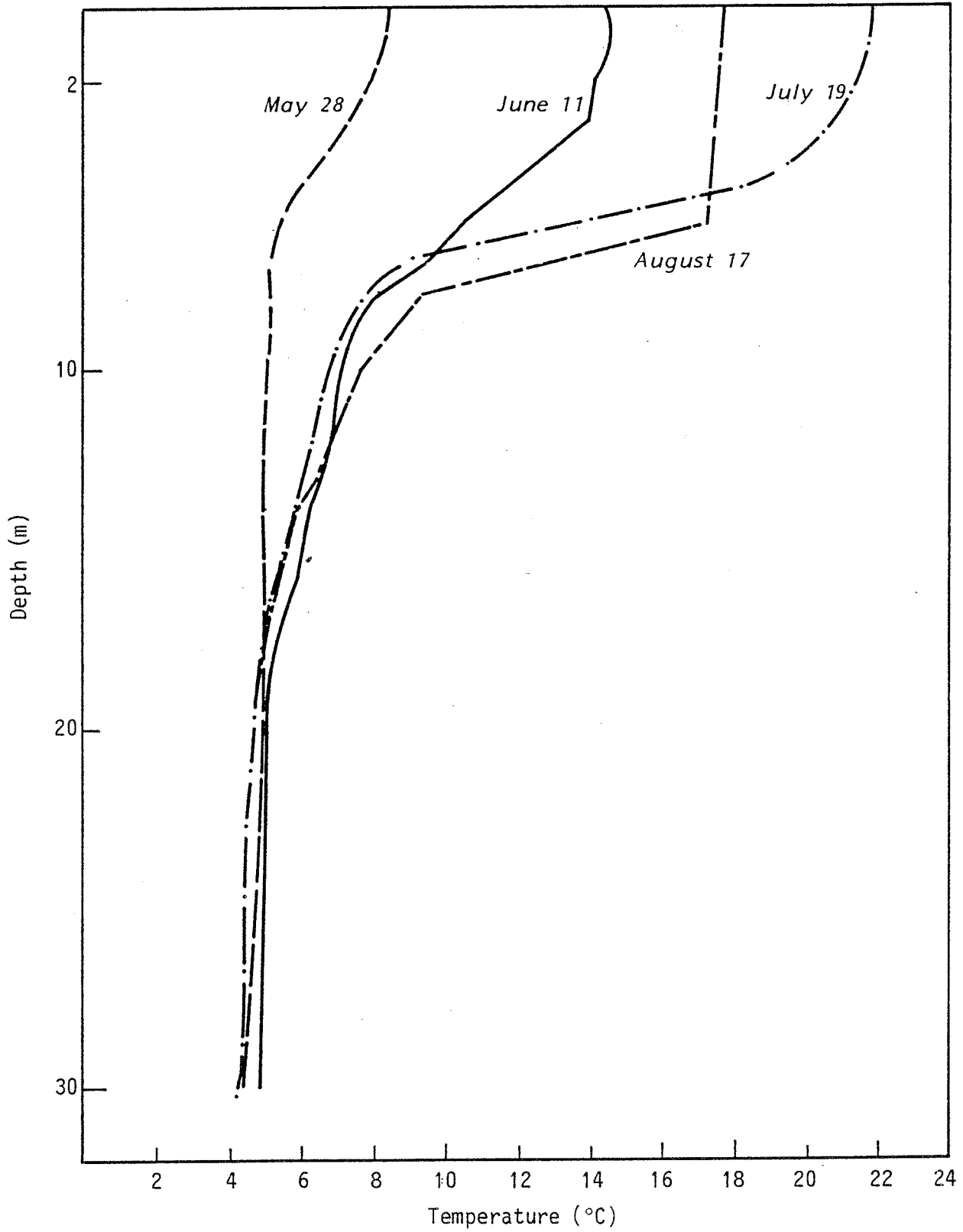
Figure 6. Particulate carbon profiles in West Blue

Lake during 1974.
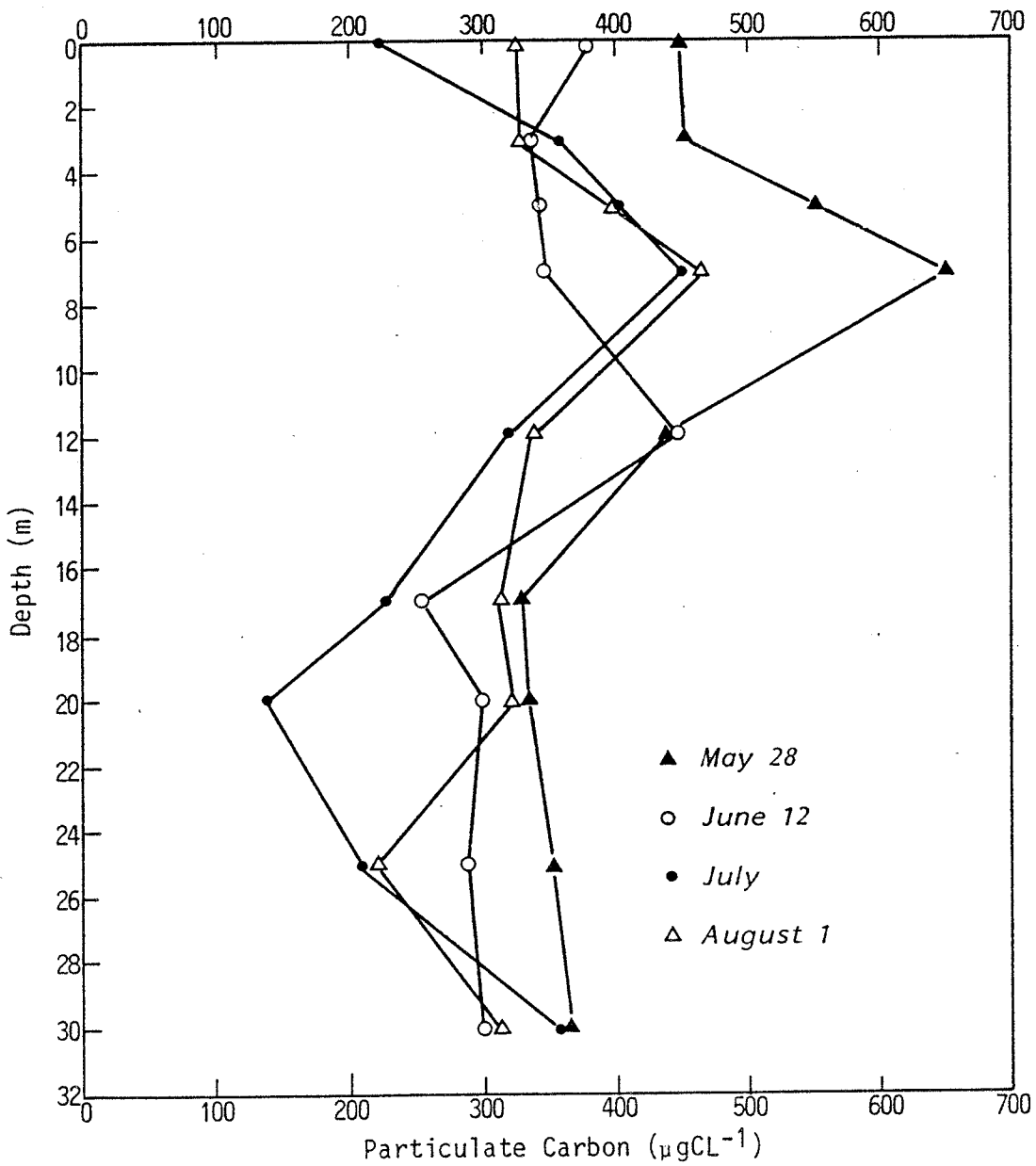
Figure 7. Vertical distribution of Diacyclops bicuspidatus

thomasi on June 11-12, 1974. (N refers to the

number of individuals per m^2).

N   ⊢━⊣ 20%

149797-RD
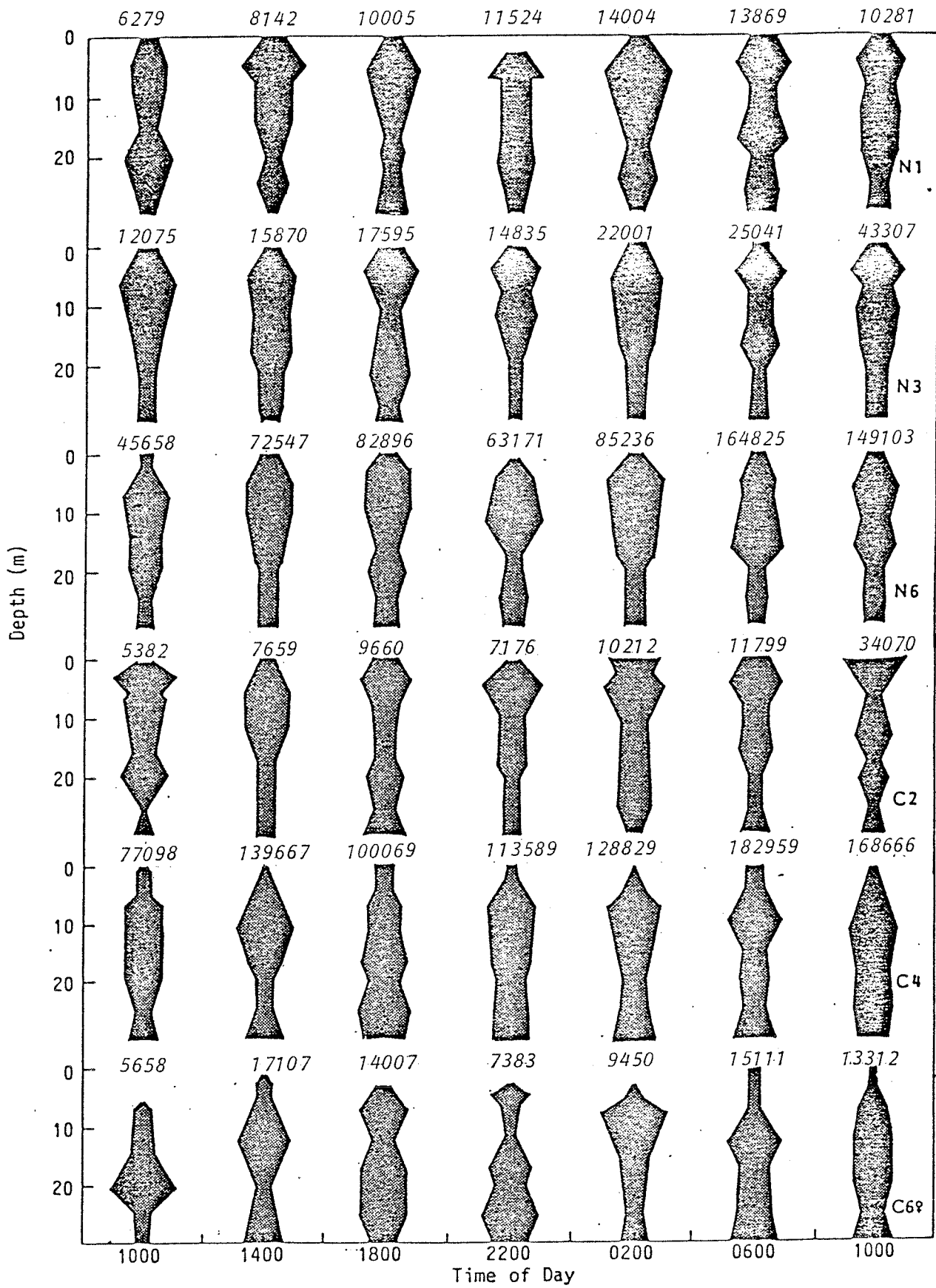
varied more than the other copepodid stages, and showed a slight indication of a reversed migration pattern. Other copepodid stages showed no consistent pattern but were generally positioned in the upper 15 to 20 m of the water column.

(ii) June 11-12

On June 11-12, the lake was beginning to stratify with a thermocline occurring at approximately 3 meters (Figure 5). Particulate carbon levels were lower than those recorded in May, and ranged from approximately 250 mg C L^{-1} at 17 m to 400 mg C L^{-1} at 12 m (Figure 6). Similar to the May sampling period, copepodid stage 6 was the only copepodid stage exhibiting some form of a migration pattern (Figure 7). The distributions of naupliar stages were more uniform in the water column than during late May (Figures 4, 7). Similar vertical distribution patterns were noted for copepodid stage 2 for both months. In contrast, however, noticeable differences were observed in the distributions of copepodid stages 4 and 6. On June 11-12, there were obvious reductions in the numbers of these stages present in the upper three meters of the water column where they were quite abundant in May. This observation was also noted for copepodid stages 3 and 5 (Appendix G). Several nauplii and copepodid stages were more abundant in June than in May at the 30 m depth where oxygen levels were less than 4 mg L^{-1} (Figures 7, 8).

Figure 8.   Oxygen profiles in West Blue Lake
             during 1974.
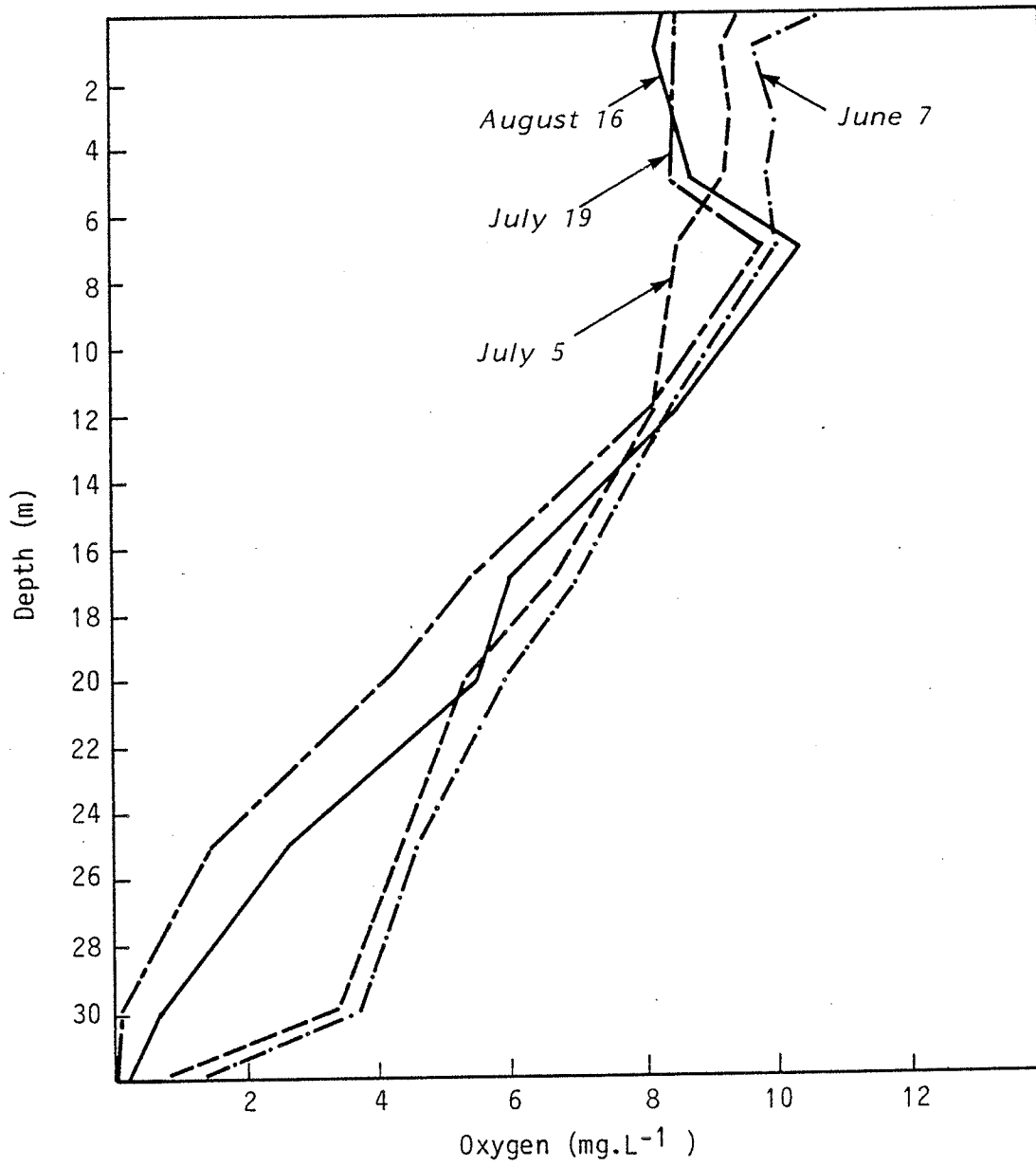
Figure 9. Vertical distribution of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> on July 19-20, 1974. (N refers to the number of individuals per m^2).

N   ⊢—⊣ 20%

5175   2036   3795   2001   1242   3554   5589

N1

3312   9521   2381   6521   11454   11040   4244

N3-4

114968   103623   94002   92864   112551   82139   99204

N6

20543   41179   18732   17423   24350   27735   16698

C2-3

16215   23768   18455   16388   25875   18424   21592

C4-5

19274   41003   41892   30964   51312   35135   46548

C6?

Depth (m)

0 10 20

1000   1400   1800   2200   0200   0600   1000

Time of Day

149798-RD
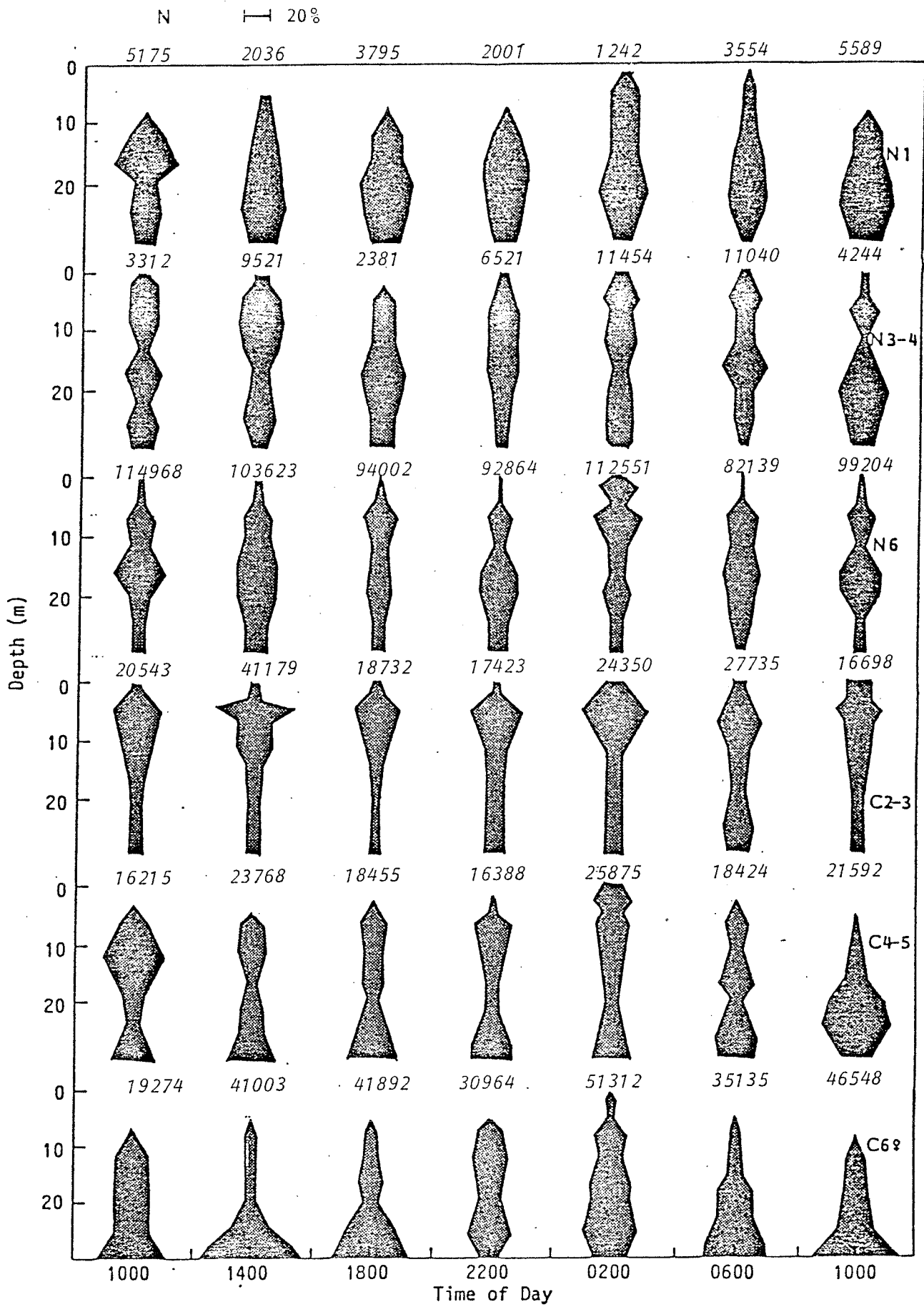
(iii)   July 19-20

On July 19-20, the thermocline was firmly established at a depth of approximately 5.0 m (Figure 5).   Temperatures ranged from approximately $4.3^\circ C$ at 30 m to $21.9^\circ C$ at the surface.   Highest particulate carbon levels (450 mg C L^{-1}) were recorded just below the thermoclinc (7 m, Figure 6). Similar to patterns recorded in May and June, most stages showed little evidence of migration throughout the water column (Figure 9).   The only noticeable exception was at 0200 at the surface where numbers of all stages were generally higher than at any other time of the 24 h cycle. This suggests that some sort of migration may be occurring in the upper few metres of the water column.

Overall in July, significantly fewer nauplii were reported in the upper five metres of water compared to numbers recorded in June and particularly, May.   This was especially evident for naupliar stage 1 which was rarely observed above the thermocline.   Similarly, copepodid stages 4, 5 and 6 were generally absent near the surface.   Notice- able exceptions were copepodid stages 2 and 3 which were generally observed in the upper 10 m of the water column. All copepodid stages, especially C6, were collected at 30 m where oxygen levels were less than 1 mg L^{-1} (Figure 8).

(iv)   August 16-17

On August 16-17, the established thermocline had begun to sink and occurred at approximately the 7-9 m depths (Figure 5).   Highest particulate carbon estimates occurred near the thermocline (465 mg C L^{-1}, Figure 6) with lowest values found at 25 m.   Similar to the July pattern, the dominant naupliar stages, especially naupliar stage 1, were generally absent or found in low abundances above the thermocline (Figure 10).   Moreover, late copepodid stages (especially copepodid stage 6) were almost entirely absent in waters above the thermocline.   Similar to patterns found in the earlier months (May-July), copepodid stage 2 was generally distributed in the upper 10-15 m of the water column.   Copepodid stage 6 was still recorded in large numbers near the lake bottom where oxygen levels were minimal (Figure 8).

(v)   Summary May-August

The median depth below which 50% of the population was located in the water column (i.e. depth-weighted mean), was calculated for each stage over the monitoring period (Figure 11).   Copepodid stage 6 was the only stage showing signs of a migration pattern (July, Figure 9).   For each sampling date, the depth-weighted mean of each life history stage varied with the development of the metalimnion (Figure 11).   In May, before the thermocline was established, most stages were

Figure 10. Vertical distribution of <u>Diacyclops</u> <u>bicuspidatus</u>
<u>thomasi</u> on August 16-17, 1974.   (N refers to the
number of individuals per m^2).

N   ⊢—⊣ 20%

18004   25788   17143   16862   12179   14141   14973   N1

14096   20691   19143   21344   15077   17211   14244   N3

47654   65892   66381   65066   48828   62485   66271   N6

3761   4727   4416   6590   4761   4623   5106   C2

11662   9315   8935   14352   8453   10764   6762   C4-5

10621   22277   24690   33866   25172   38447   26549   C6♀

Depth (m)

1000   1400   1800   2200   0200   0600   1000

Time of Day

149799-RD
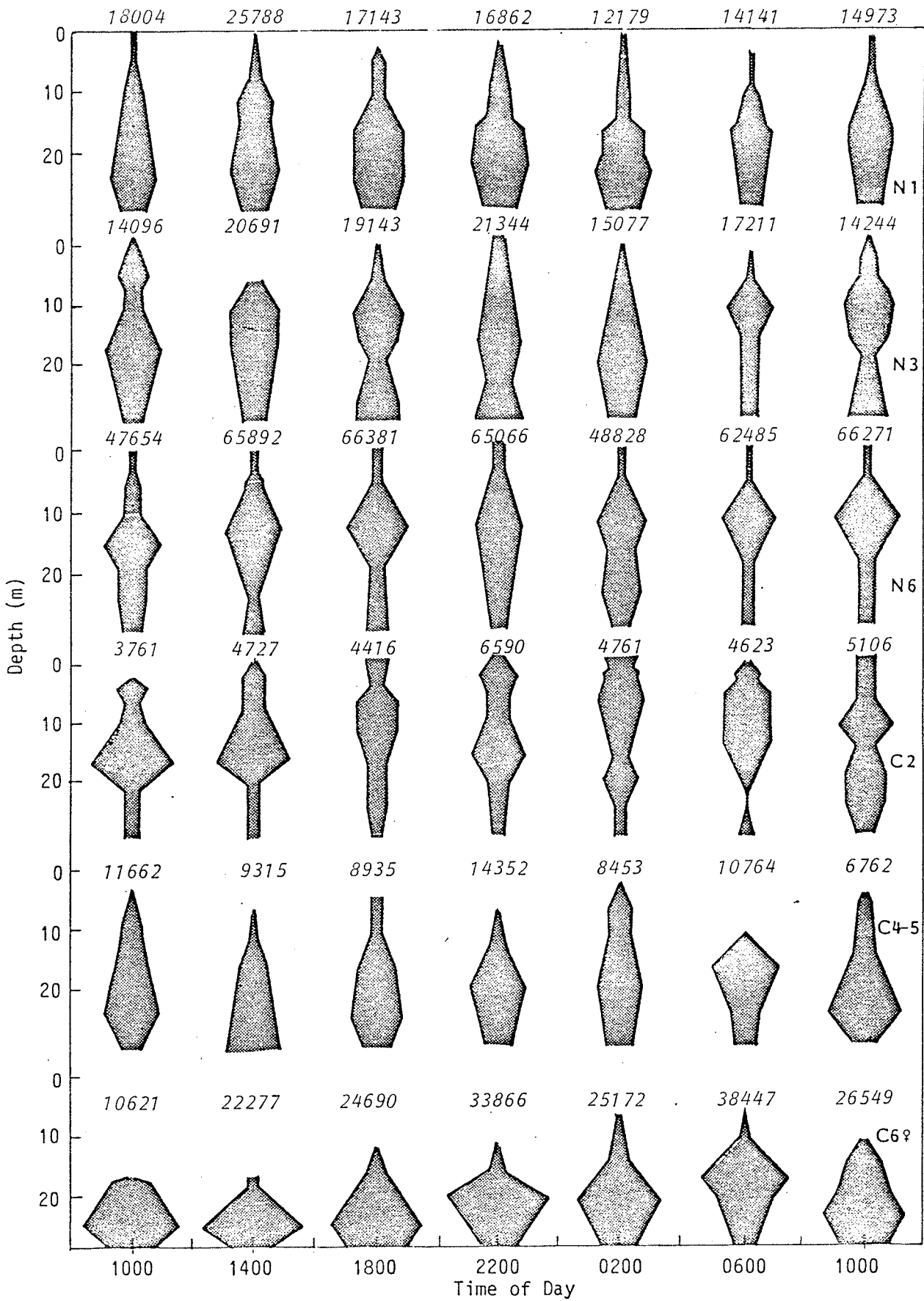
Figure 11. Average median depth of life history stages of

Diacyclops bicuspidatus thomasi over a 24 hour

period on four occasions, between May 28 and

August 17, 1974.

TEMPERATURE (°C)

E = EGG (Attached to ♀)
N = NAUPLII
C = COPEPODID
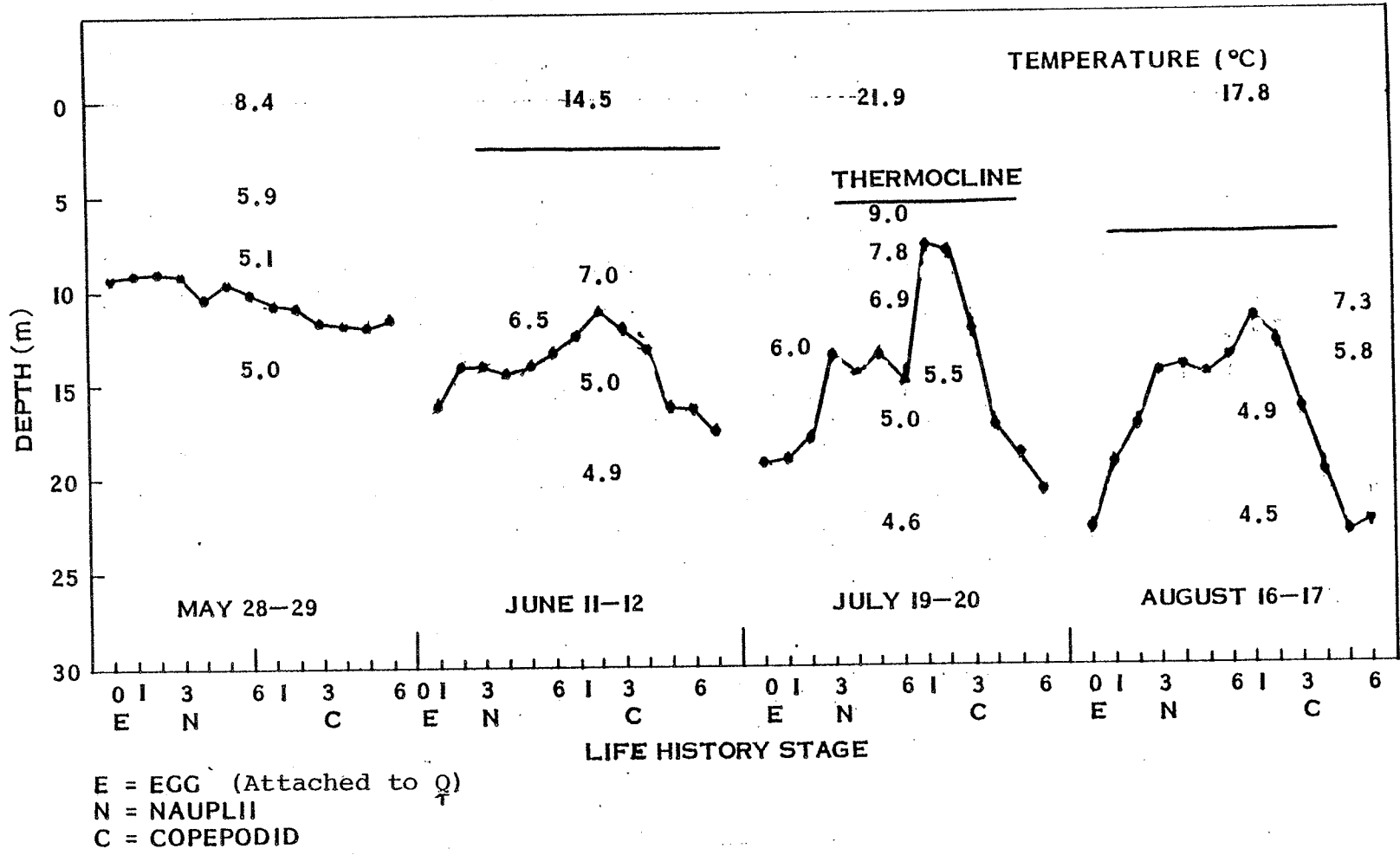
recorded at approximately the same mean depth over the entire 24 h period. However, as the thermocline gradually developed, there was a tendency for successive naupliar stages beginning with N1 to be found higher in the water column especially during July and August. In contrast, successive copepodid stages, beginning with C2, selected the deeper depths where water temperature was progressively cooler. On average, the median depths below which 50% of the population were located occurred below the thermocline (exception copepodid stage C1). In August, when the thermocline began to sink, these mean depths tended to be even lower than in the corresponding July period.

Analysis of variance (one-way) was used to compare the depth weighted means of each stage among the four sampling periods (Table 6). The distribution of each stage varied significantly between the May to August period (significant F-tests). The multiple range tests indicated that, generally, most stages were recorded higher in the water column in May than in any other month. The only exceptions were copepodid stages 1 - 3 which selected their highest position in the water column in July. Overall, most stages preferred the deeper depths during the months of July and August. As indicated earlier, these preferences appeared to be related to the development and positioning of the thermocline.

Table 6. Analysis of variance statistics and multiple range test (S.N.K.) comparing the mean depths of life history stage over the May to August sampling period.

Stage	d.f.	F-test	Multiple Range Test (lowest → highest depth)			
N1	3,41	38.7*	M [1] 9.5 [2]	J 14.2	Jy 19.1	A 19.2
N2	3,37	15.7*	M 9.1	J 13.8	A 17.4	Jy 18.9
N3	3,35	14.6*	M 9.2	Jy 13.3	J 14.4	A 14.5
N4	3,41	6.8*	M 10.7	A 14.1	J 14.2	Jy 14.7
N5	3,41	19.4*	M 9.5	J 13.6	Jy 13.7	A 14.6
N6	3,42	15..6*	M 10.4	J 12.6	A 13.9	Jy 15.4
C1	3,41	12.6*	Jy 7.4	M 10.8	J 11.2	A 11.7
C2	3,41	20.4*	Jy 7.9	M 10.9	J 12.2	A 12.8
C3	3,41	8.6*	M 11.7	Jy 11.7	J 12.7	A 16.3
C4	3,41	15.8*	M 12.0	J 16.4	Jy 17.2	A 20.1
C5	3,41	27.3*	M 12.1	J 16.2	Jy 18.9	A 23.0
C6	3,41	26.8*	M 10.6	J 7.5	Jy 20.6	A 22.2

* $p < 0.05$

[1] Month

[2] Depth (m)

2. Population dynamics

Sampling variability

Sampling variability was estimated from the four 24 h vertical migration collections taken at station 2 in May (n = 7), June (n = 13), July (n = 13) and August (n = 13). Each sample set was analyzed as a replicate to determine sampling error (Table 7). With the exception of the June sampling period, sampling variability was less than 20% over the other collection periods. On the June date, sampling variability was approximately 39%.

Table 7. Sampling variability estimated from the vertical migration collections, May 28-29 to August 16-17

Date	Number of Replicates	Mean abundance (No. Ind./m²)	S.D.(x)	Per Cent Variability
May 28-29	7	878,937	127,077	14.4
June 11-12	13	495,846	192,532	38.8
July 19-20	13	233,184	29,317	12.6
August 16-17	13	207,708	31,890	15.3

Mean lake estimates

Population estimates, extrapolated from short term regression equations relating abundance and station depth, were calculated for the mean depth of the lake (11.3 m) for both 1972 and 1974 (Table 8). This procedure is merely a method for obtaining an estimate of mean abundance and should not be considered to have great theoretical importance. Correlation coefficients ranged from .90 to .99 for both years. Estimated monthly mean population estimates (adjusted means from regression) were higher in 1974 than in 1972, especially in May and June (Table 8). The largest populations were recorded in May for both years (1.41 x 10^5 ind.m^{-2} in 1972, 2.1 x 10^5 ind.m^{-2} in 1974) whereas lowest estimates occurred in late summer (1972 - 3.8 x 10^4 ind.m^{-2} August 8-15, and 1974 - 3.8 x 10^4 ind.m^{-2} July 28-29). Confidence limits (95%) associated with each mean were high, particularly in 1974. Levels ranged from 13.4 to 48.5% of the mean for the 1972 estimates, and from 39.7% to over 100% for the 1974 estimates.

The seasonal mean population (May-August) in both years was expressed as a relationship relating abundance to station depth (Figure 12). Based on these equations, the predicted 1974 mean lake (11.3 m) population (127 307 ind.m^{-2}) was approximately 2.2 times larger than the 1972 mean lake population (57 236 ind.m^{-2}).

Table 8. Mean lake abundance estimates during 1972 and 1974.

| | 1972 | | | 1974 | |
Date	Predicted Abundance (no.ind.m^{-2})	C.I. (95%)	Date	Predicted Abundance (no.ind.m^{-2})	C.I. (95%)
May 17-30	141202	16723	May 22	206177	98173
June 13-27	105797	47186	June 4	140345	163748
July 3-11	67389	9051	June 11-25	132705	101547
July 18-25	41889	20327	July 2-16	67865	87059
August 8-15	37758	7869	July 28-29	37709	44844
August 22-29	60397	14502	August 9-16	44631	71006
			August 20-29	45300	17730

One station estimate

A comparison of abundance of <u>Diacyclops</u> <u>bicuspidatus</u>
<u>thomasi</u> between 1972 and 1974 was also expressed for station
2 data (Figure 13), which was assumed to be representative
of the lake. Throughout the spring and summer periods (May-
September), total numbers of <u>D</u>. <u>b</u>. <u>thomasi</u> at station 2 in
1974 were approximately double those in 1972. Estimates
of the seasonal mean population (May-August) based on the
regression equation relating abundance to station depth
suggested similar differences in abundance between the two
years (Figure 12). Maximum abundances (irrespective of
cohort) were recorded in late May in 1974 (1.0×10^6 ind.m^{-2}),
and in early June in 1972 (0.5×10^6 ind.m^{-2}, Figure 13).
Lowest abundances occurred in August for both years (.77 x
10^5 ind.m^{-2} in 1972, and 1.59×10^5 ind.m^{-2} in 1974). The
nauplii and copepodid stages revealed similar patterns, and
estimates in 1972 were approximately half those in 1974
(Figure 13). Throughout the sampling period, nauplii com-
prised over 40% of the total numbers during both 1972 and
1974.

Abundance estimates in 1974 based on the mean depth
of the lake and for station 2 were compared (Figure 14).
Generally, both estimates showed similar trends over the
sampling period, with maximum numbers recorded in May
decreasing to the lowest values in August. Abundance esti-
mates of station 2 were approximately four times greater
than mean lake estimates for the same time period. A

Figure 12. Seasonal average abundance estimates for stations

of different depths.

ABUNDANCE (no. ind. m^{-2}) X 10^{4}

DEPTH (M)

1974 y = 18164 X–77946
r = 0.90

1972 y = 6901 X — 20745
r = 0.98
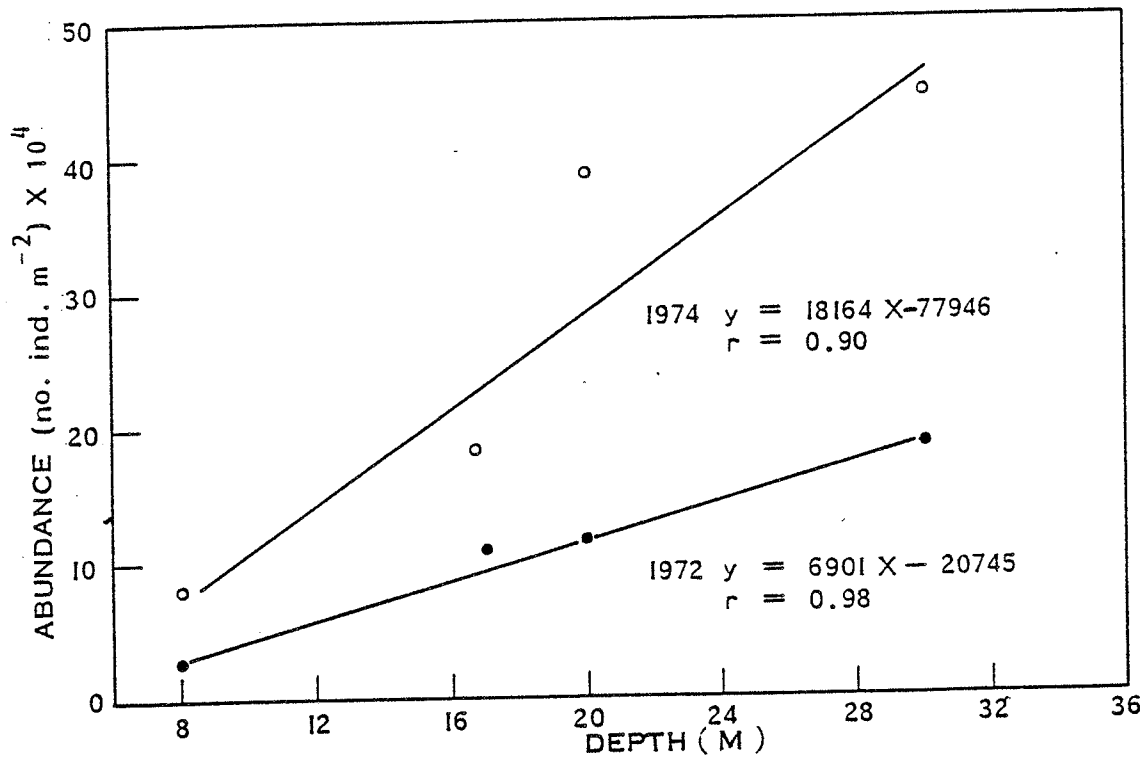
Figure 13.   Densities of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u>

recorded at station 2 in 1972 and 1974.

A. Total abundance comparison between 1972

and 1974.

B. Nauplii abundance comparison between

1972 and 1974.

C. Copepod abundance comparison between

1972 and 1974.

A. TOTAL

B. NAUPLII

ABUNDANCE (NO. IND. M^{-2}) × 10^3

C. COPEPODIDS

- 1972 n = 15
- 1974 n = 29

MAY   JUNE   JULY   AUGUST
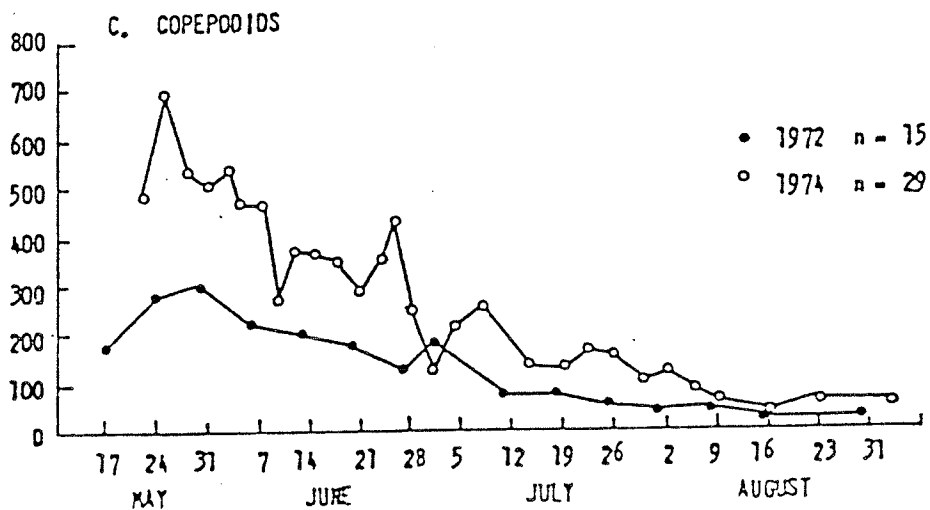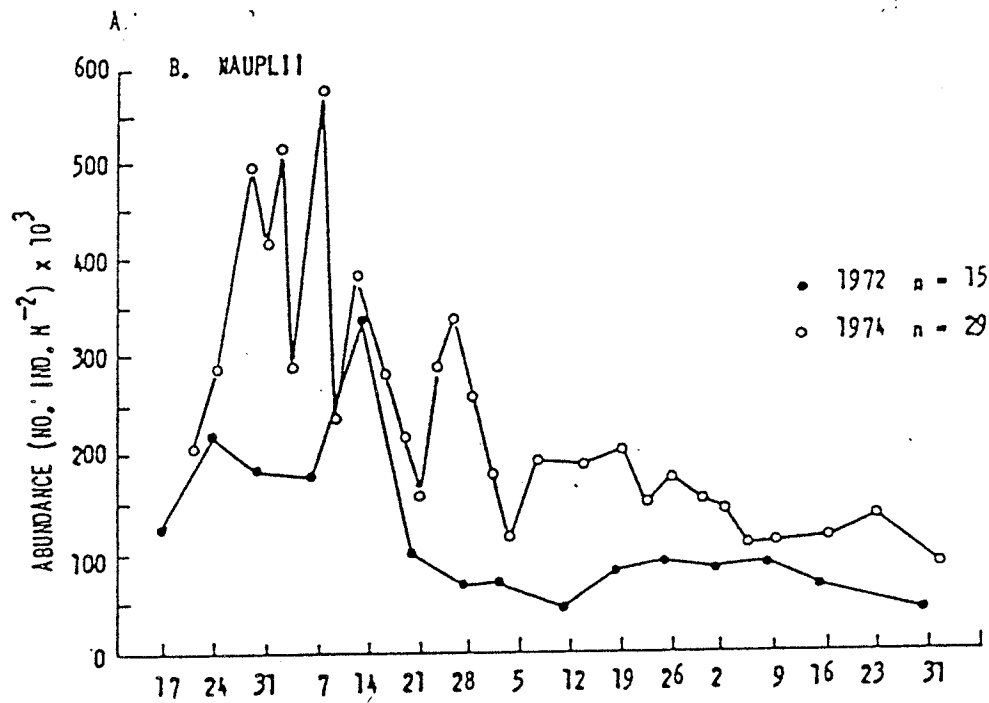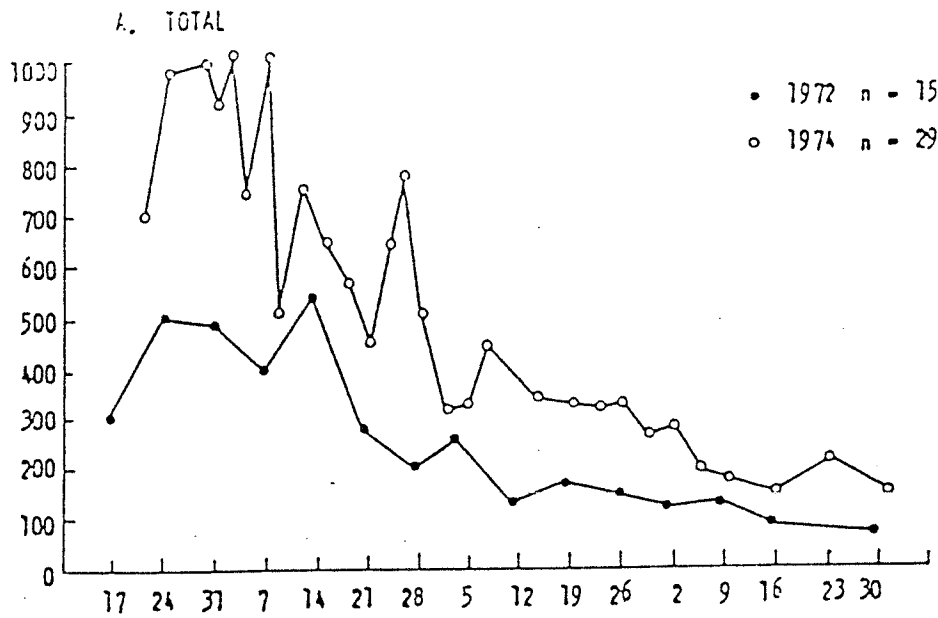
three fold difference would be expected solely on depth

differences (i.e. station 2 - 30 m, mean lake - 11.3 m),

if the vertical distribution was uniform from the surface

to the bottom. However, the vertical distribution data

does not show this trend (Figure 11).

Cohort abundances

Abundance trends of Diacyclops bicuspidatus thomasi

at four stations during 1974 were similar, showing noticeable

abundance peaks in May, June and August (Figure 15). These

data suggest that these peaks represent the presence of

different cohorts. Similar trends occurred in 1972 data

(Appendix C). A detailed analysis of cohort abundances during

1972 and 1974 based on station 2 (spring, summer) and 5 (Fall,

winter) data is shown in Figure 16. Although cohort abun-

dances have been higher at station 2 than at other stations,

it was suspected that timing and occurrences of cohorts at

station 2 would be representative of the total population.

Cohort 2 was the dominant cohort developing during the

spring and summer periods, and made up approximately 45 and

52% of the total numbers during 1972 and 1974, respectively

(Figure 16). Cohort 1 was the next most abundant one, and

constituted approximately 35% in 1972 and 32% in 1974 of

total numbers. Cohort 3 was the smallest cohort, which

during the ice-free season made up less than 15% of the

total numbers during both years.

Figure 14. Comparison of seasonal abundance estimates

between station 2 and the mean for the lake

derived from the depth-abundance regression

during 1974.
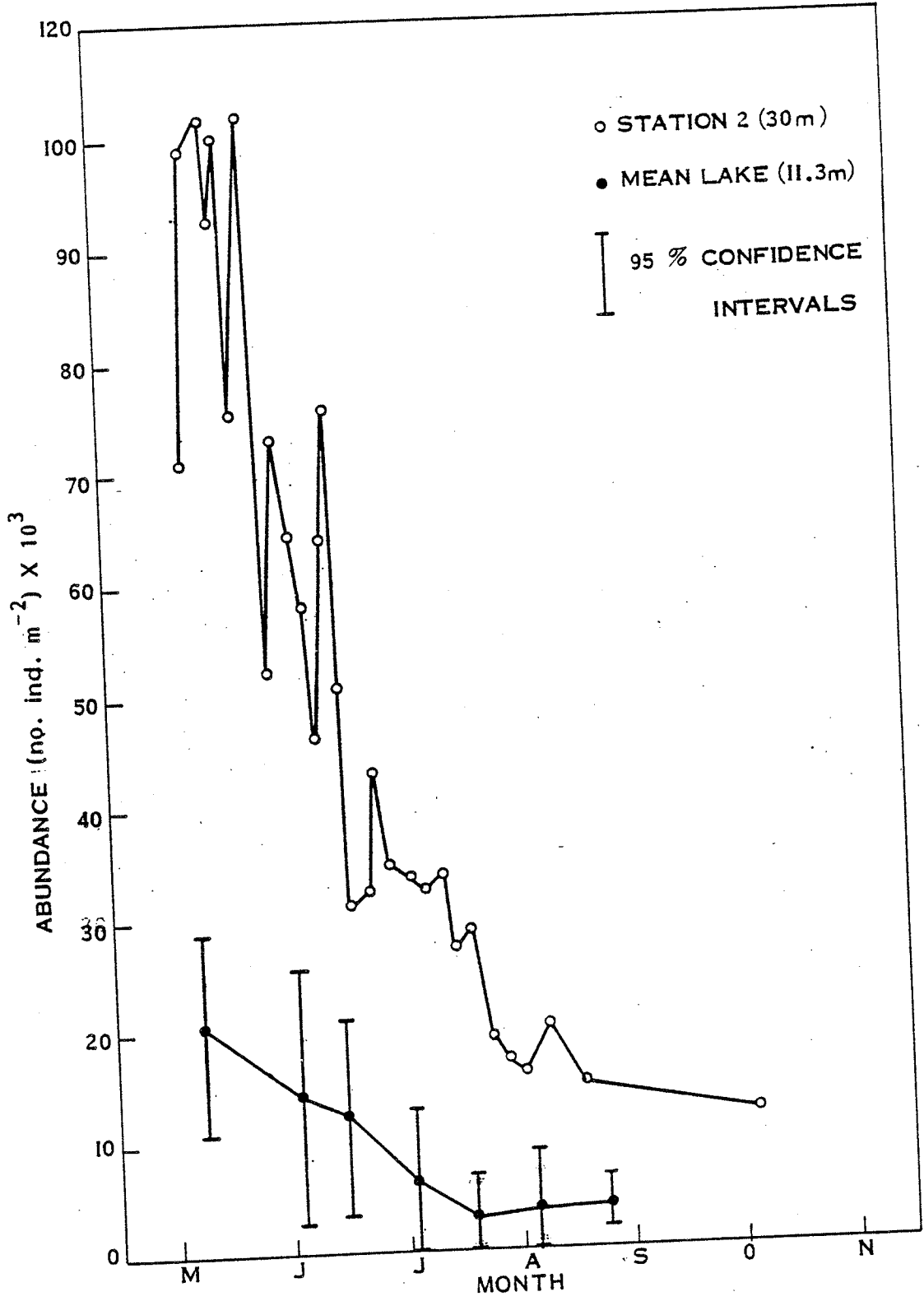
Figure 15.   Abundance trends of <u>Diacyclops</u> <u>bicuspidatus</u>

<u>thomasi</u> at stations 2, 3, 4 and 5 during 1974.
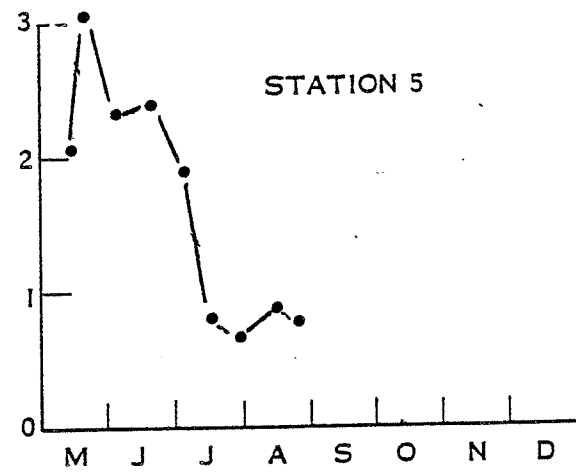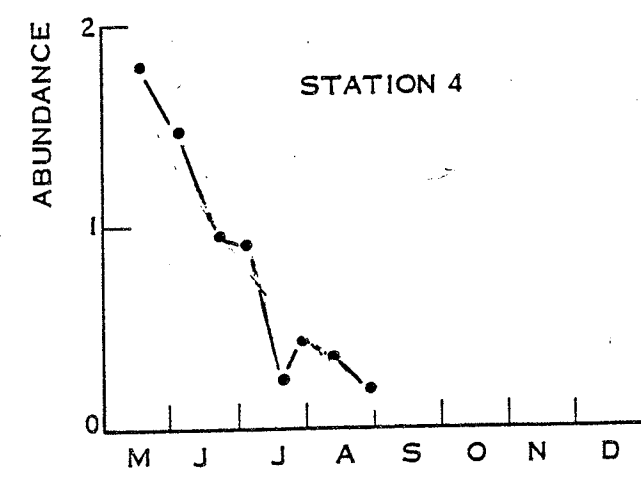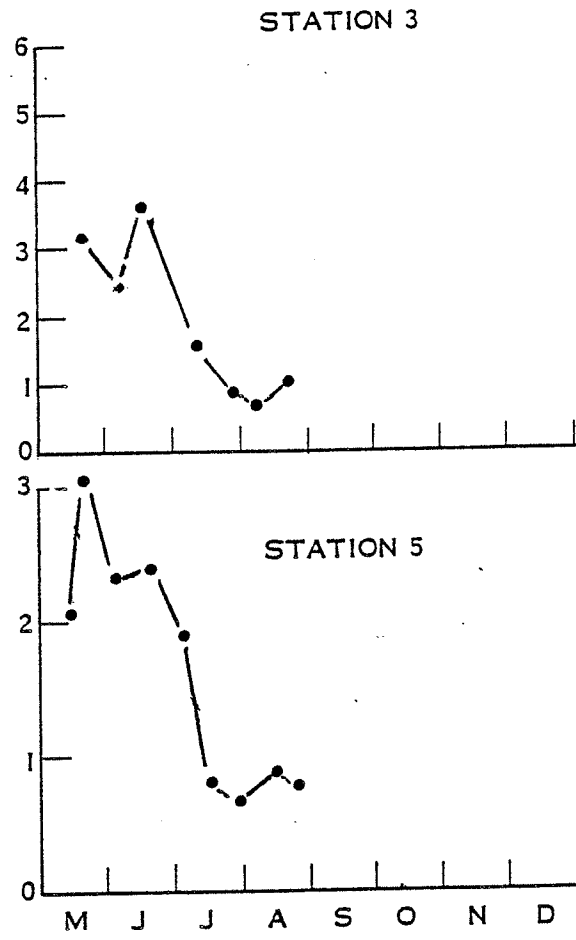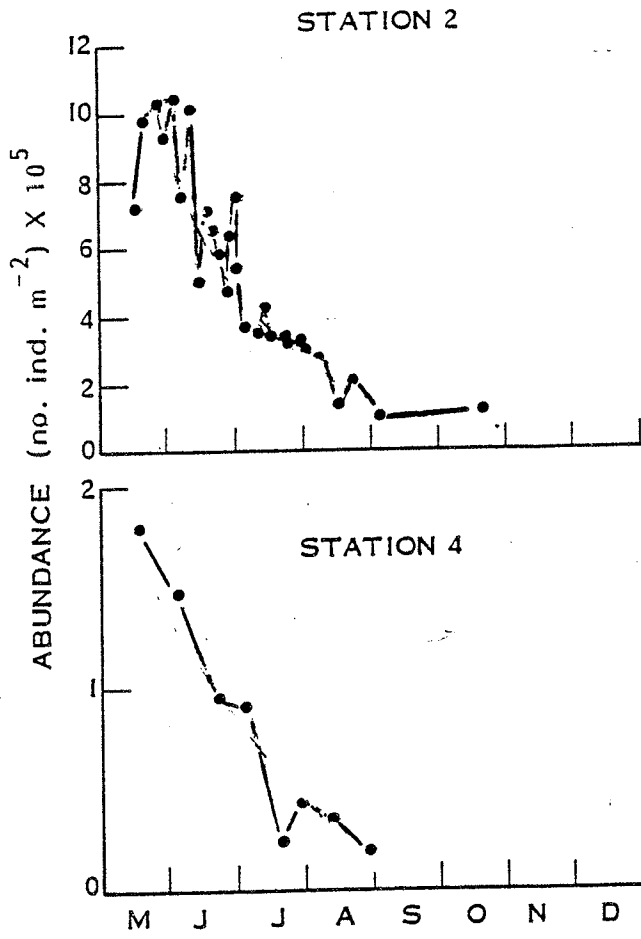
Figure 16.   Cohort abundance comparisons of <u>Diacyclops</u>

<u>bicuspidatus</u>ᵗ<u>thomasi</u> between 1972 and 1974.
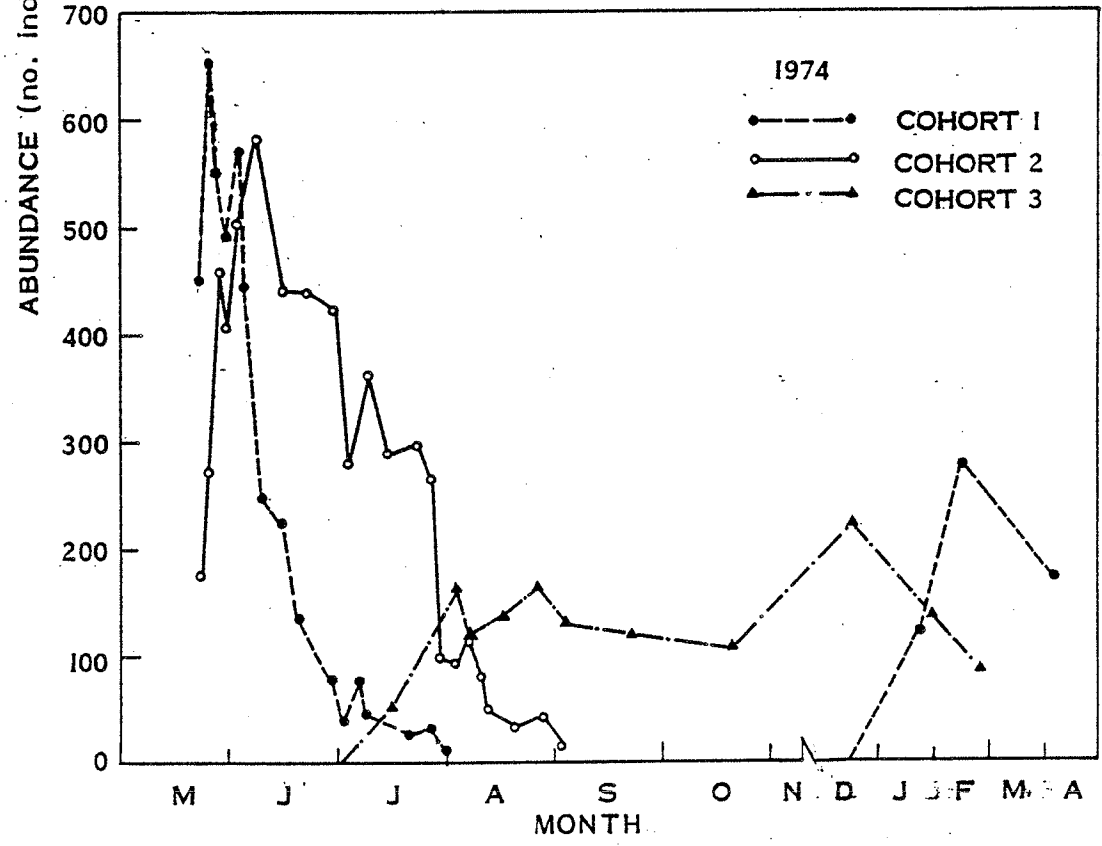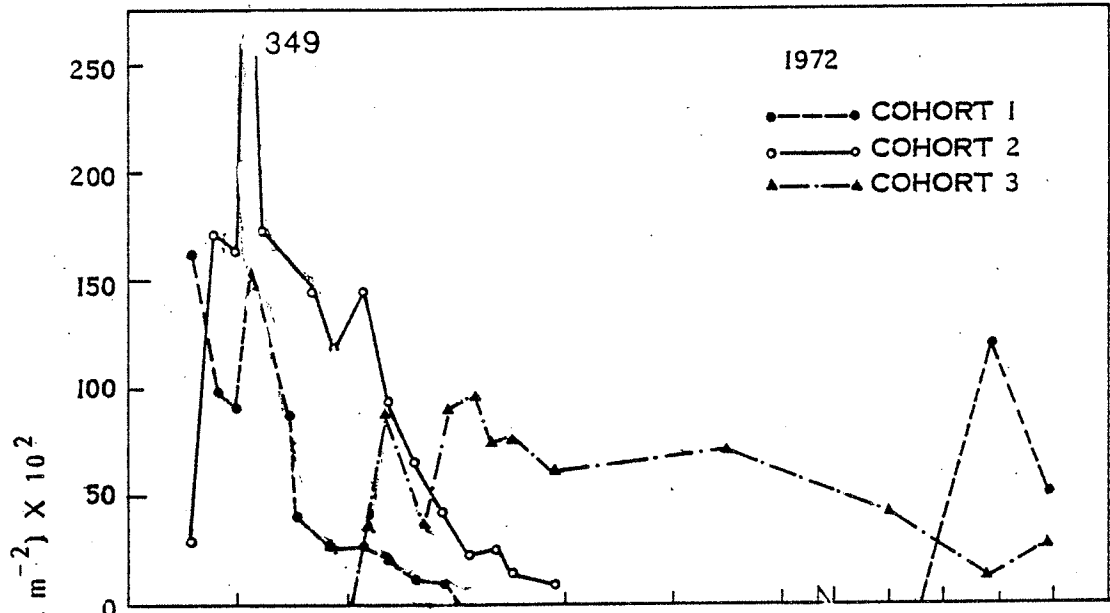
Occurrence and frequency of stages

The 1974 data are discussed before the 1972 data since it is based on a more intensive sampling program. With the exception of station 3 in August, dominant life history stages were similar in percent occurrence for all stations at each sampling date in 1974 (Table 9). For example, in May, copedid stage 2 was the dominant stage comprising 36.2 (st. 2), 36.7 (st. 3), 24.9 (st. 4) and 38.7 (st. 5) percent of the total numbers at all stations. Similarly, nauplius stage 1 was the dominant naupliar stage among the stations, making up approximately 10.4% at station 2, 20.6% at station 3, 23.1% at station 4, and 14.4% at station 5.

On June 4, nauplius stage 4 and copepodid stage 4 were the dominant stages at each station. In mid-June, all stations were dominated by naupliar stage 5 or 6, and copepodid stage 1. In early July, nauplius stage 6 was dominant comprising 25.6, 30.3, 20.6 and 31.6% of the total numbers at stations 2, 3, 4 and 5 respectively. Similarly, copepodid stage 2 was the major copepodid stage among the stations, making up 16.0% at station 2, 18.3% at station 3, 25.4% at station 4, and 11.3% at station 5.

In August 1974, naupliar stages comprised over 68% of the total numbers at all stations. However, differences were noted in copepodid distribution among stations especially at station 4. Copepodid stages 5 and 6 constituted only a small percentage of total numbers at station 4

Table 9. Percentage contribution of life history stages to total numbers for stations 2, 3, 4 and 5 during 1974.

1974	Station	N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5	C6
May 22	2	10.4	6.6	3.8	2.6	3.0	3.4	7.4	36.2	11.8	3.5	1.9	9.5
	3	20.6	10.5	3.4	1.1	0.9	1.8	8.9	36.7	5.2	2.3	2.4	6.0
	4	23.1	12.2	5.1	2.7	2.1	2.1	9.0	24.9	8.1	3.7	2.3	4.7
	5	14.4	6.4	3.0	1.8	1.2	1.4	11.0	38.7	7.3	3.6	1.7	9.5
June 4	2	1.4	2.4	7.7	19.5	4.0	1.8	2.3	4.5	15.0	35.3	3.8	2.2
	3	2.2	3.3	5.2	14.7	2.6	1.7	2.0	3.3	11.0	37.2	9.3	7.1
	4	2.4	3.9	8.9	26.8	6.2	4.0	2.0	2.4	9.6	25.0	5.4	3.3
	5	1.5	2.2	4.1	15.5	3.8	1.9	2.2	3.7	7.7	43.5	8,4	5.3
June 18	2	1.0	1.9	5.1	5.6	8.0	16.4	29.1	7.9	3.2	9.9	8.3	3.5
25	3	1.7	3.2	4.8	6.9	10.7	7.3	23.9	14.4	2.2	14.1	7.3	3.3
18	4	2.1	3.4	3.4	5.2	6.5	14.7	33.3	6.2	4.2	12.8	4.4	3.6
18	5	0.9	1.6	2.7	4.1	9.0	36.5	19.9	4.5	2.1	7.5	6.8	4.3
July 2	2	1.7	3.6	7.1	8.7	11.4	25.6	8.4	16.0	4.4	5.7	3.7	3.5
3	3	0	0.1	2.4	5.6	11.7	30.3	4.8	18.3	4.6	5.6	4.1	12.0
2	4	2.6	2.5	4.1	5.5	8.4	20.6	14.7	25.4	5.6	2.7	3.0	4.5
2	5	1.5	2.9	4.5	7.5	12.3	31.6	6.9	11.3	4.5	4.5	3.8	8.6
August 9	2	17.3	12.7	10.5	7.0	6.9	10.3	2.3	3.4	5.6	5.0	4.9	14.0
6	3	15.2	10.6	4.7	7.2	11.9	22.3	4.7	3.5	5.2	4.3	3.2	7.1
13	4	6.9	6.7	9.4	18.5	12.4	26.8	4.5	3.1	3.0	6.2	0.1	1.6
13	5	10.0	11.4	8.7	16.2	10.4	12.3	1.3	0.1	2.7	7.3	1.2	17.6

With the span "Life history stage" over columns N1–C6.

Table 10. Percentage contribution of life history stages to total numbers for stations 2, 3, 4 and 5 during 1972.

1972	Station	Life history stage											
		N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5	C6
May 17	2	5.2	0.6	0	0.9	4.0	30.5	11.3	5.4	1.8	11.5	8.3	20.1
	5	7.1	1.9	1.3	2.6	7.0	25.1	8.1	1.7	2.1	10.9	7.4	24.7
May 30	2	2.9	9.0	17.6	3.8	2.9	2.3	3.2	11.4	3.3	5.0	16.1	22.2
	4	2.9	8.3	19.9	2.8	1.8	1.8	3.2	17.7	3.0	6.5	10.3	21.7
June 20	3	0	1.0	1.7	3.6	7.5	28.1	14.2	2.4	1.3	18.8	2.0	19.4
27	2	0	1.2	3.2	4.7	6.3	21.1	18.9	4.0	1.9	13.1	2.6	22.9
	4	0	1.8	2.5	4.0	8.6	34.1	28.9	5.6	2.4	9.6	0.3	2.1
	5												
July 18	3	5.2	3.1	5.6	7.4	15.3	27.5	2.7	3.7	9.9	3.9	3.9	11.6
25	2	3.5	3.7	6.3	9.4	12.8	25.0	3.6	5.0	10.4	2.9	4.8	12.6
	4	3.6	3.5	4.4	6.4	14.6	33.1	4.5	4.5	13.0	3.4	3.4	5.4
	5	3.0	2.0	2.6	4.4	10.9	27.0	4.7	3.0	13.6	4.1	5.2	19.3
August 22	4	2.3	2.9	4.5	7.0	13.9	30.0	4.8	7.3	24.1	2.4	0.6	0.5
	5	2.6	3.1	5.3	9.9	14.9	38.8	4.9	6.3	7.9	1.9	1.2	2.8
29	2	2.0	2.7	4.6	7.3	13.0	27.1	7.5	8.2	12.3	2.6	1.7	10.7
	3	1.7	2.9	4.7	6.9	10.9	38.1	6.7	7.9	13.0	3.4	0.6	3.1

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(C5 - 0.1%, C6 - 1.6%) but made significantly greater contributions at the other stations. Copepodid stage 6 was also noted to be low in abundance at station 4 relative to the other stations.

Similar life history stage contributions were also found among stations from May to August in 1972 (Table 10). On May 17, naupliar stages 1 and 6 were the dominant naupliar stages at stations 2 and 5. Naupliar stage 3 made up approximately 18 and 20% of the total numbers at stations 2 and 4 respectively on May 30. In late July (18-25), naupliar stage 6 was the dominant stage, comprising 25.0, 27.5, 33.1 and 27.0% of the total numbers at stations 2, 3, 4 and 5 respectively. Copepodid stages 3 and 6 were the dominant copepodid stages recorded at each station in late July. Similar to the 1974 data, differences were noted among stations in late copepodid stage distribution during late August.

Generally, these stage frequency data suggest that development of life history stages was similar among stations, and that stations 2 and 5 may be representative of the lake.

3. Mortality Estimates

Instantaneous mortality

Instantaneous mortality estimates were calculated from cohort abundances during 1972 and 1974 (Figure 17). These were determined by relating, using linear regression

Figure 17. Instantaneous rate of decline of numbers of

Diacyclops bicuspidatus thomasi in cohorts 1,

2 and 3 during 1972 and 1974.
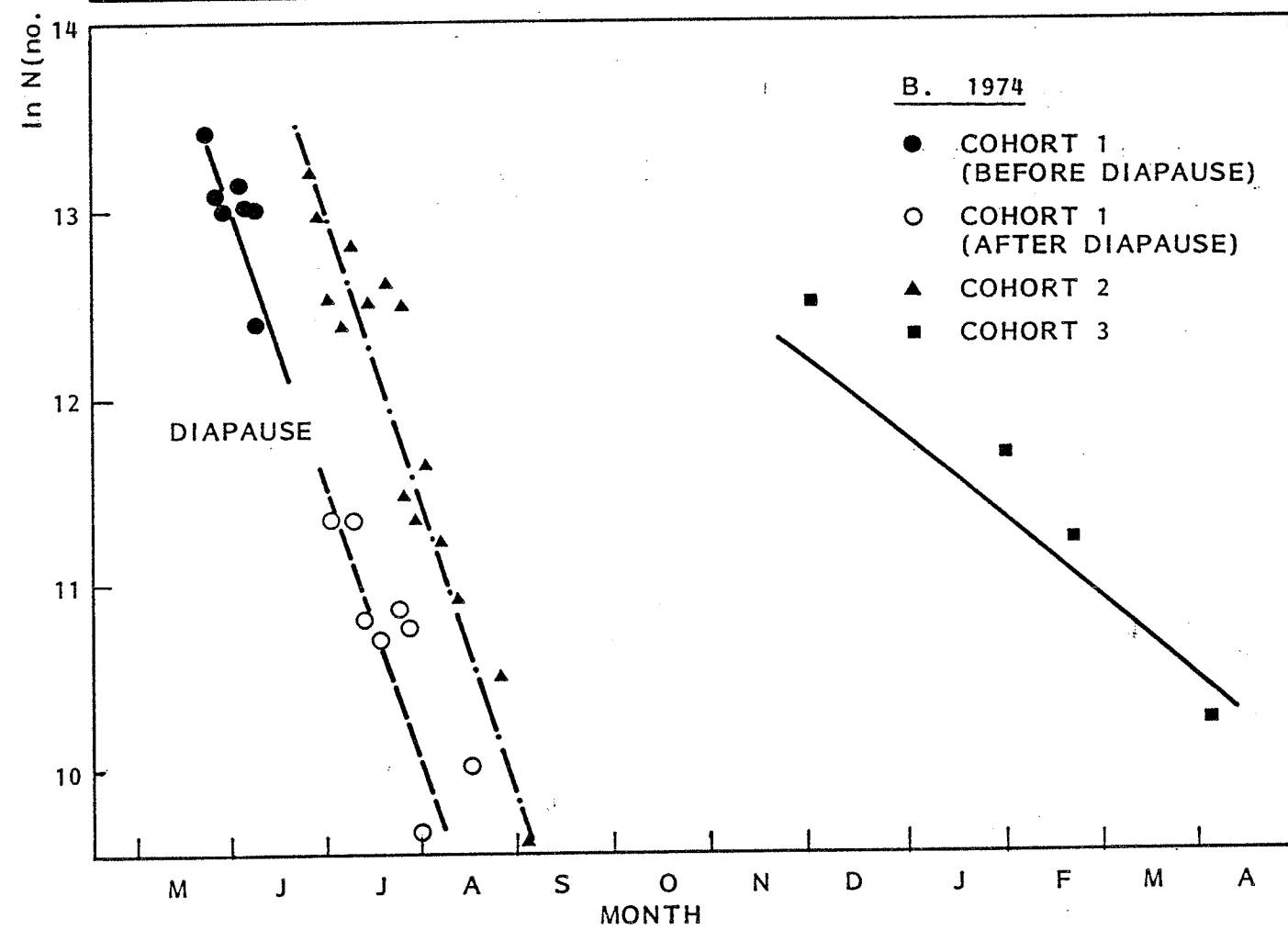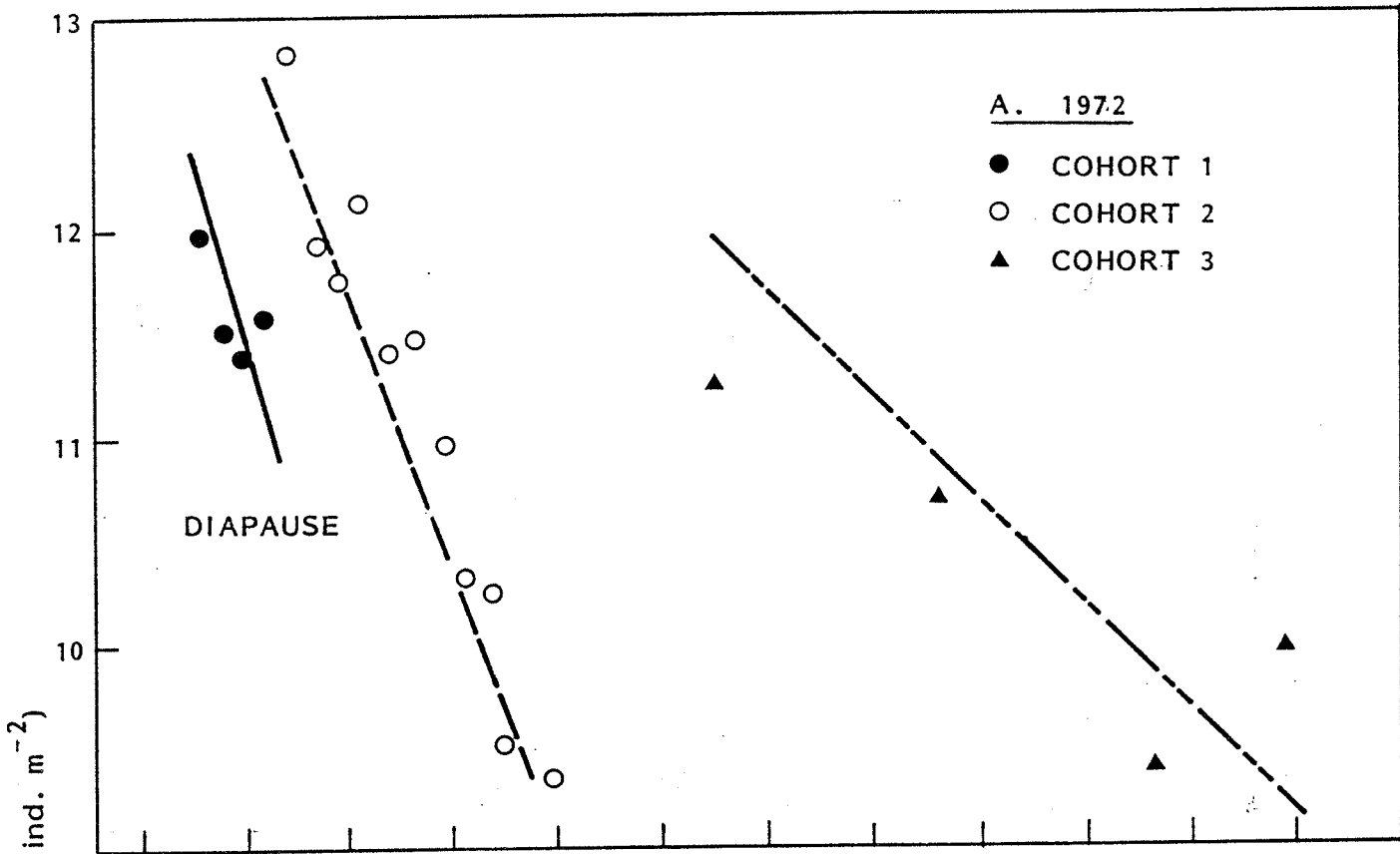
procedures, the natural logarithm of abundance estimates
to time of sampling. Mortality was estimated for each
cohort for both years. Estimates were also determined prior
to diapause in cohort 1 and following the exo-diapause
period in cohort 3.

Generally, <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> mortality
was highest for the spring cohort (1) whereas lowest morta-
lity occurred for the winter segment of cohort 3 (Table 11,
Figure 17). Instantaneous mortality rates (Z) ranged from
.050 (1972) and .056 (1974) in cohort 1 to .015 (1972) and
.016 (1974) in cohort 3. Analysis of covariance (Ho:Bi=o)
was used to compare mortality rates in cohort 1 before and
after diapause in 1974. No statistically significant diff-
erence was noted suggesting that significant additional
copepodid mortality did not occur during this period.
Mortality probably proceeded at the same ratio since 'before'
and 'after' slopes were similar. Mortality rates were also
similar between cohorts 1 and 2 in both years.

Table 11.   Instantaneous mortality rates (z) and regression
             equations calculated for each cohort of
             <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> in 1972 and 1974
             (descending limb).

Cohort		z	Equation	Correlation coefficients
1972	C1	.050	ln N=12.241-.050T	-.79 *
	C2	.040	ln N=12.375-.040T	-.92
	C3 (winter)	.015	ln N=11.784-.015T	-.88
1974	C1 (before diapause)	.053	ln N=13.469-.053T	-.91
	C1 (after diapause)	.056	ln N=11.488-.056T	-.80
	C2	.054	ln N=13.332-.054T	-.98
	C3 (winter)	.016	ln N=12.040-.016T	-.95

       p = .10 probability statement associated with r.

4.   Growth

Growth (length) factor

       The ratio of length of one instar to that of the

previous instar, or growth factor, varied among stages when

both metasomal and total length were measured (Figure 18).

Highest growth factors were obtained for the early copepo-

did stages (C1, C2) for the metasomal measurements, whereas

nauplius stage 6 showed the highest growth factor for

measurements based on total length. Small growth incre-

ments of less than 1.3 were noted for all other stages

based on the total length measurement data.

Figure 18.   The ratio of the mean length of each instar

to the mean length of the previous one (growth

ratio) for all life history stages of Diacyclops

bicuspidatus thomasi.
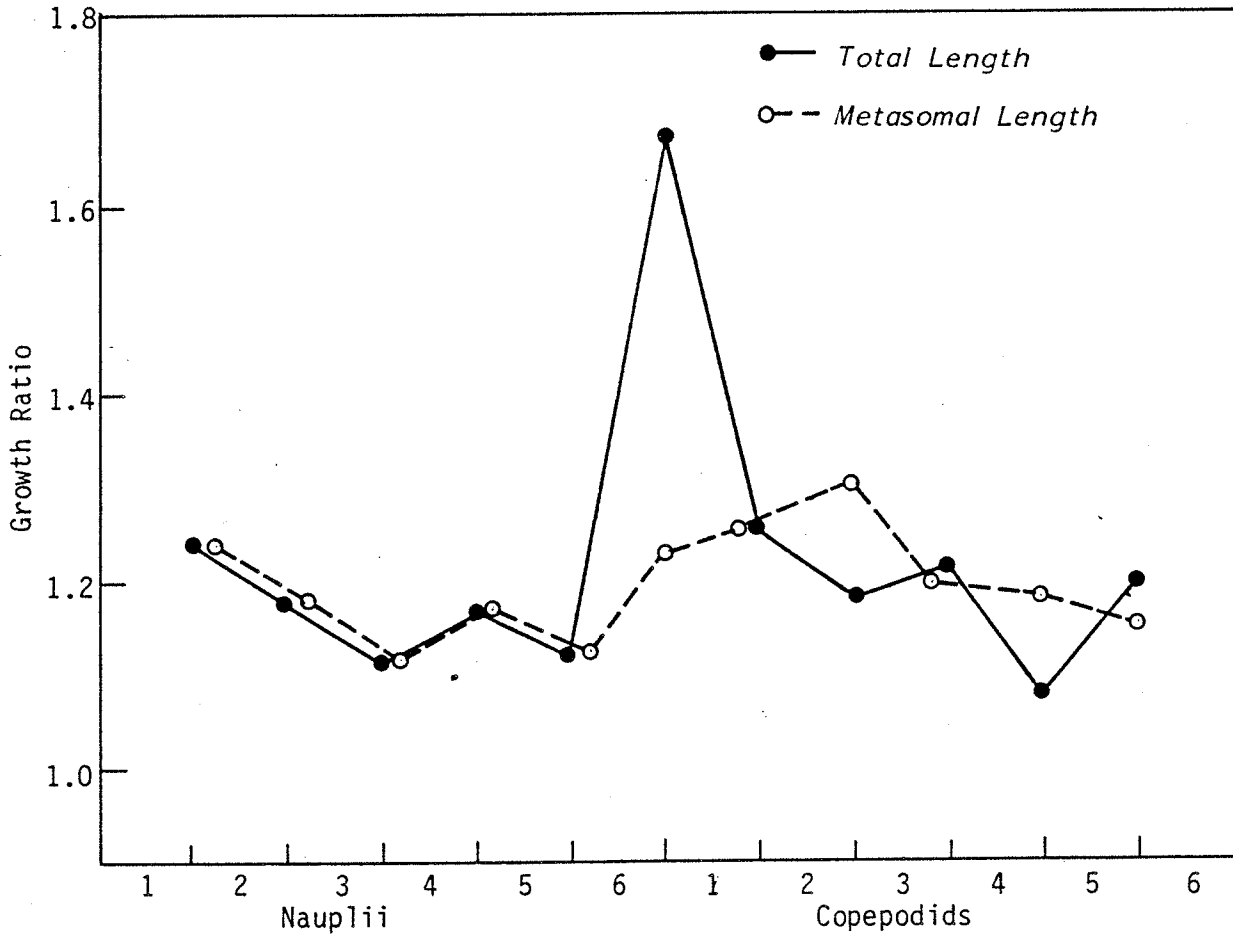
Length-weight relationships

Length-weight curves were calculated for Diacyclops
bicuspidatus thomasi (Table 12). Data were transformed logar-
ithmically to obtain a functional linear relationship in the
form:

$$\log_e W = \log_e A + B$$

where W = weight in carbon or nitrogen units

A = length (metasomal length, total length)

B = slope

The slopes of the total length-weight regressions expressed
in carbon and nitrogen units were 1.66 and 1.88, respec-
tively. The metasomal length-weight relationships showed
slightly higher slopes: 2.1 for carbon and 2.4 for nitrogen.

Developmental times

Developmental times were calculated for each stage
or combined stages by determining the time in days between
peaks of successive stages (Table 13). This technique was
only attempted when peaks were well defined for particular
stages. In cases where peaks of stages were poorly defined,
development was determined for several stages combined.

During both 1972 and 1974, cohort 2 had the shortest
development of all cohorts, taking approximately 63 days in
1972 and 62 days in 1974 (Table 13). Nauplii and copepo-
dids developed quickly during the spring and summer periods.
Cohort 3 had the longest development in 1972 (138 days),

Table 12. Length-weight relationships for _Diacyclops bicuspidatus thomasi_

Measurement (mm)	Carbon (μg)				Nitrogen (μg)			
	Intercept (a)	Slope (b)	r	d.f.	Intercept (a)	Slope (b)	r	d.f.
Total length	.516	1.66	.99*	6	.750	1.88	.98*	5
Metasomal length	1.524	2.10	.98*	6	.397	2.40	.99*	5

* $p < 0.05$

Table 13. Developmental times calculated for _Diacyclops bicuspidatus thomasi_ during 1972 and 1974.

Stage	1972 Developmental time (days)			1974 Developmental time (days)		
	Cohort 1	Cohort 2	Cohort 3	Cohort 1	Cohort 2	Cohort 3
N1	} 35.0	4.5	} 13.6	} 28.5	1.6	} 10.6
N2		2.6			2.3	
N3		5.0		31.0	5.0	
N4	} 25.0	3.0		} 34.5	5.4	
N5		5.8			3.1	
N6	} 14.2	12.0	} 65.0	5.0	5.5	} 56.9
C1		10.0		3.3	7.3	
C2	6.0	10.4		4.5	12.6	
C3	14.4	3.6		8.4	} 16.9	
C4	6.9		9.0	17.0		32.0
C5	6.9	2.8	50.3	3.6	2.6	11.0
C6	-	-	-	-	-	-
Total	108.4	63.3	137.9	135.8	62.3	110.5

whereas cohort 1 took the longest to develop in 1974 (136 days). Slow cohort development in cohorts 1 and 3 was attributed to a slow rate of nauplii and copepodid growth during the winter period.

Growth rates

Growth increments $(\frac{\Delta W}{D})$ were calculated for cohorts 1 and 2 using both length-carbon and stage developmental data. This was done using linear regression procedure, by developing a regression of the carbon increment of a particular stage on development times of that stage. Calculated regression equations for cohorts 1 and 2 in 1972 and 1974 as follows:

```
1972   Cohort 1   lnD = ln 2.949 C - 13.464 r =.94 6 d.f.
       Cohort 2   lnD = ln 1.290 C -  5.550 r =.90 9 d.f.

1974   Cohort 1   lnD = ln 2.098 C - 10.517 r =.80 8 d.f.
       Cohort 2   lnD = ln 0.986 C -  4.306 r =.89 9 d.f.
```

where D = development time, C = weight in carbon.

In both years, cohort 1 had a higher exponent growth equation than cohort 2, suggesting that it developed at a faster rate. Generally, the growth exponents of both cohorts 1 and 2 were slightly higher in 1972 than in 1974; but this was not shown statistically because of the few degrees of freedom. Because of few data points, growth equations were not derived for cohort 3 in either 1972 or 1974.

In addition to describing growth for the entire cohort, growth was also estimated for both naupliar and cope-

podid components within cohorts 1, 2 and 3 (Table 14, Figure 19).

Generally, growth of both nauplii and copepodid stages were slightly higher in 1972 than in 1974. Naupliar absolute growth proceeded more slowly than copepodid growth for each cohort, developing at rates of .006 and .004 g C day $^{-1}$ in 1972, and .001 and .005 g day $^{-1}$ in 1974. Copepodid growth during the spring in cohort 1 was rapid in each year, proceeding at a rate of approximately .045 g C day $^{-1}$ in 1972 and .043 g C day $^{-1}$ in 1974. Similar to cohort 1, cohort 2 copepodid growth was also developing in late spring and early summer at a rate of .088 g C day $^{-1}$ in 1972 and .047 g C day $^{-1}$ in 1974. Because of few data points, it was difficult to estimate growth rates for cohort 3 nauplii of both years. Cohort 3 copepodids grew considerably slower than those of either cohorts 1 or 2. A slower growth rate was primarily related to development in the fall and winter periods where water temperatures were considerably lower. Cohort 3 growth in 1974 was slightly higher than estimated in 1972.

Instantaneous growth rates

Instantaneous growth rates were calculated for each cohort during 1972 and 1974 (Figure 20). In both years highest growth occurred during spring and summer periods and lowest during the autumn and the winter. Growth in cohort 2 (spring-summer) was the fastest in both years, averaging approximately .050 g C m $^{-2}$ day $^{-1}$ and .048 g C

Table 14. Intercept, slope, and correlation coefficient (r) of regression
equations relating weight (in carbon) and development (in days)
of naupliar and copepodid stages of Diacyclops bicuspidatus thomasi

Year		Intercept	Slope (ΔC) (μg C/day)	d.f.	r	value prob.
1972	1A nauplii*	-.175	.006	2	.86	p<.05
	1B copepodids	-3.698	.045	4	.99	p<.05
	2A nauplii	.036	.004	5	.98	p<.05
	2B copepodids	-.735	.088	3	.86	p<.05
	3 copepodids	.327	.013	2	.96	p<.05
1974	1A nauplii	.024	.001	3	.96	p<.05
	1B copepodids	.238	.043	4	.97	p<.05
	2A nauplii	.039	.005	5	.99	p<.05
	2B copepodids	-.164	.047	3	.94	p<.05
	3 copepodids	-.001	.018	2	.93	p<.05

* includes estimate of copepodid stage 1 data point.

Figure 19.   Growth rates of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u>
in 1972 and 1974.

A.   Naupliar growth

B.   Copepodid growth
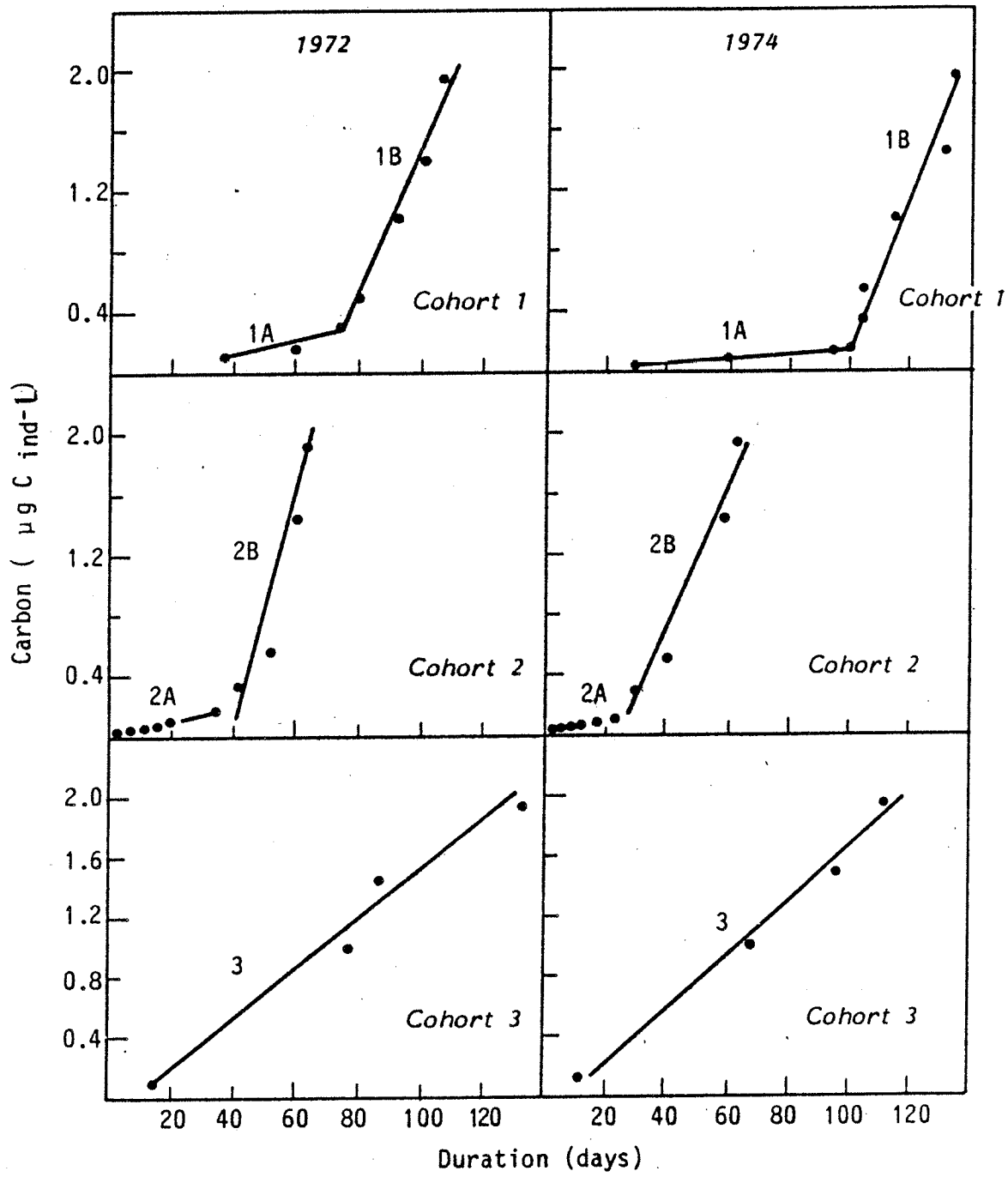
Figure 20. Instantaneous growth rates of Diacyclops

bicuspidatus thomasi in 1972 and 1974.
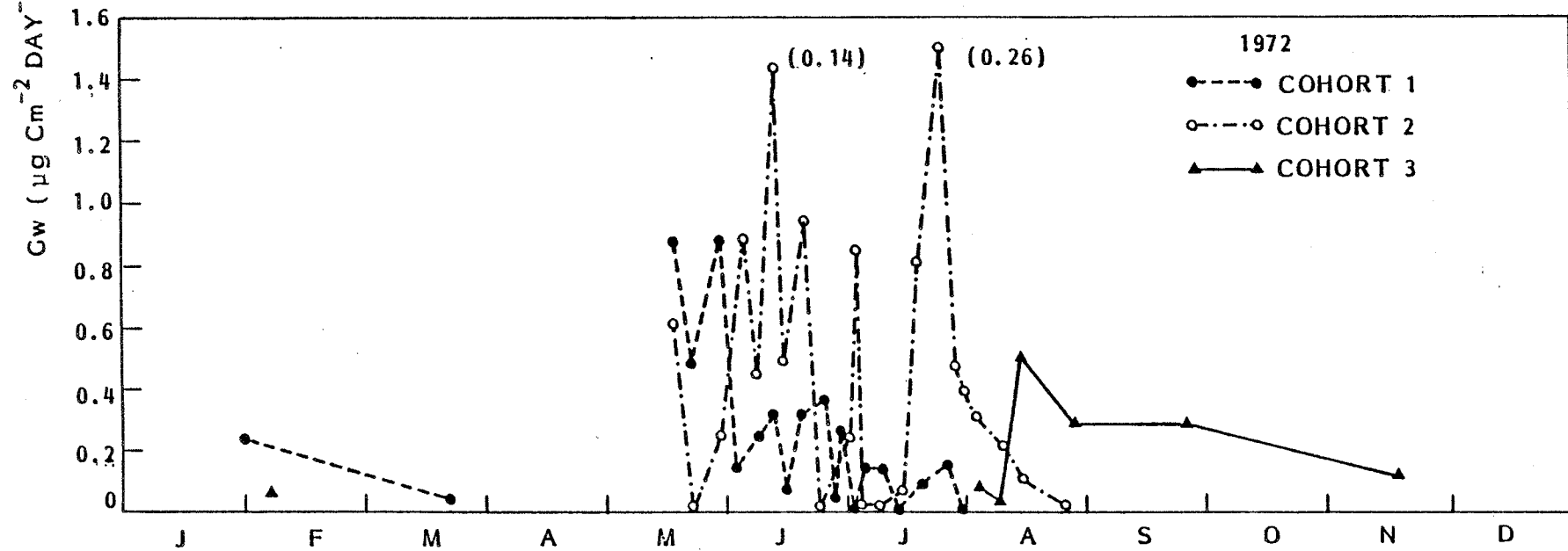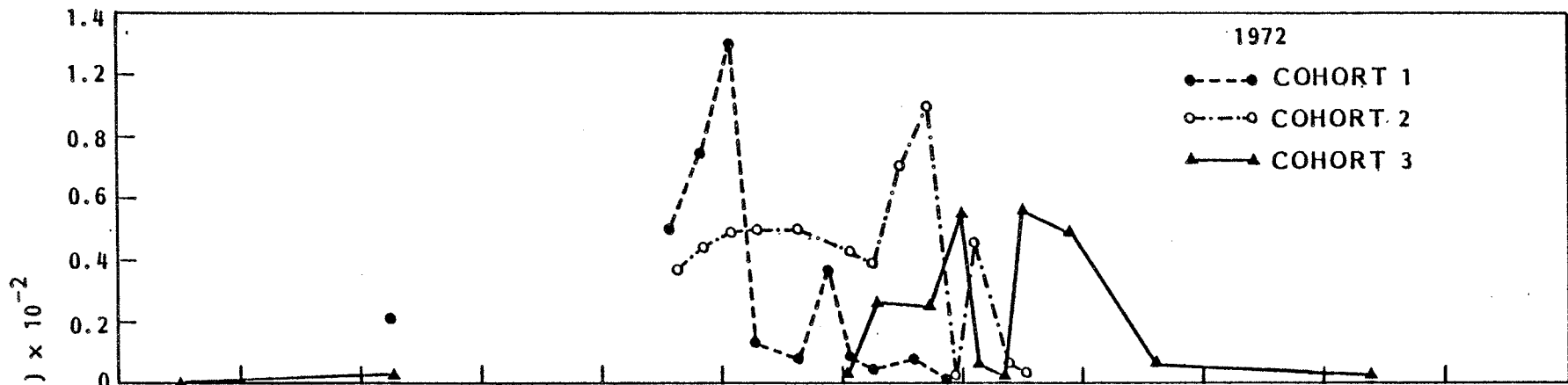
$m^{-2}day^{-1}$ in 1972 and 1974, respectively. Cohort 3 (summer-autumn-winter) growth was the slowest, averaging approximately .019 g C $m^{-2}day^{-1}$ in 1972 and .024 g C $m^{-2}day^{-1}$ in 1974. Growth in cohort 1 (winter-spring) averaged approximately .032 g C $m^{-2}day^{-1}$ in 1972 and .026 g C $m^{-2}day^{-1}$ in 1974. Similar to that found in the relative growth rate data (Table 14), growth in 1972 was slightly higher (average) than in 1974 (Figure 20). Generally, growth rate patterns for each cohort in both years were similar to cohort abundance estimates described earlier (Figure 16).

5. Productivity and Biomass

Data from a single station (station 2 spring, summer; station 5 autumn, winter) were used to compare Chapman and ussian methods of estimating productivity. One station data were also used to compare productivity estimates based on a single growth curve to that of the natural population. The contribution of life history stage to total productivity was also determined from single station data.

Data collected for all four stations (stations 2, 3, 4 and 5) were used to estimate mean lake productivity (both Chapman and Russian) and biomass, and population turnover rates.

One station estimates

(i) Comparison between Russian and Ricker-Chapman estimates.

Productivity, estimated using both Russian and Ricker-Chapman methods on station 2 (spring, summer) and 5 (autumn, winter) data, showed similar monthly trends in 1972 and 1974 (Table 15). In both years, highest productivity occurred in late May or early June, whereas lowest estimates occurred during the winter period. Annual productivity (g C m^{-2}) varied by approximately 30% between both methods in 1972 (Russian 1.34 g C m^{-2}; Ricker-Chapman .91 g C m^{-2}) and less than 10% in 1974 (Russian 3.32 g C m^{-2}; Ricker-Chapman 3.61 g C m^{-2}). Productivity in 1974 was approximately 2.7 times using the Russian method and 3.6 times using the Ricker-Chapman method, higher than estimates in 1972.

(ii) Comparison of productivity based on growth from one cohort (cohort 2) and the natural population (applied growth, cohorts 1, 2 and/or 3).

A comparison was made in productivity (mg C m^{-2}day^{-1}, Russian method calculated) between estimates derived from the growth of only one cohort (cohort 2) and the natural population (cohorts 1, 2 and/or 3, Table 16.). Results indicated, that using cohort 2 over-estimated productivity (May to August) by approximately 29% in 1972 (cohort 2 - 1.03 g C m^{-2}, cohorts 1, 2, 3 - .73 g C m^{-2}), and under-estimated productivity by approximately 12% in 1974 (cohort

Table 15. Estimates of stations 2 and 5 productivity estimates using the Russian and Ricker-Chapman methods during 1972 and 1974.

Month	1972		1974	
	Russian ($mg\ C\ m^{-2}day^{-1}$)	Ricker-Chapman ($mg\ C\ m^{-2}day^{-1}$)	Russian ($mg\ C\ m^{-2}day^{-1}$)	Ricker-Chapman ($mg\ C\ m^{-2}day^{-1}$)
May	9.81	5.03	39.68	37.73
June	6.56	6.71	19.36	10.40
July	5.32	3.93	10.52	11.69
August	2.21	1.02	3.68	3.59
October	3.06	2.65	2.35	2.33
December	0.35	0.51	1.65	4.95
February	1.20	0.00	0.95	1.96
March-April	0.90	0.015	0.98	0.05
Mean monthly ($mg\ C\ m^{-2}day^{-1}$)	3.67	2.46	9.90	9.09
Annual ($g\ C\ m^{-2}y^{-1}$)	1.34	0.91	3.61	3.32

Table 16. Comparison of productivity estimates based on growth from cohort 2 and the natural population (applied growth) during 1972 and 1974.

	Month	Productivity (natural population) mg C m^{-2}day^{-1}	Productivity 1 (cohort 2) growth curve mg C m^{-2}day^{-1}	Difference mg C m^{-2}day^{-1}
1972	May	9.81	12.89	-3.08
	June	6.56	11.96	-5.40
	July	5.32	5.84	-0.52
	August	2.21	2.78	-0.57
1974	May	39.68	24.77	14.91
	June	19.36	23.85	-4.49
	July	10.52	11.54	-1.02
	August	3.86	4.45	-0.59

2 - 1.99 g C m^{-2}, cohorts 1, 2, 3 - 2.26 g C m^{-2}). Major
differences between estimates in both years occurred in May
and June. During these months, cohort 1 contributed more
than cohort 2 to total productivity (1974). These data in-
dicate that one cohort developing during the spring-summer
period varies less than 30% in estimating productivity (May-
August) even though the population may be multivoltine.
These results may not be significant when one considers that
the confidence intervals on the population estimates can
exceed this value (Table 9). If the autumn and winter
periods are included it is expected that these differences
would become greater.

(iii) Stage productivity

Stage contribution to total productivity, determined
by the Russian method, in 1972 and 1974 varied with each
cohort and between years (Table 17). In cohort 1 during
both years, naupliar stages (N1-N5) made up less than 3% of
total production. In 1972, the dominant stages in this
cohort were copepodid stages 4 and 5. In contrast, in 1974
copepodid stages 2 and 4 contributed the most to total pro-
ductivity. In total, these stages contributed approximately
73 and 61% to total cohort 1 productivity in 1972 and 1974,
respectively. Cohort 1 made over 60% of annual productivity
in both years. In cohort 2, nauplius 6 made up a high per-
centage of total production, approximately 24.1% in 1972
and 31.3% in 1974. The other naupliar stages (N1-N5) con-

tributed less than 18% to total production during both years. In 1972 and 1974 cohort 2 comprised approximately 28% and 33% of total annual productivity, respectively. In cohort 3 in 1972, copepodid stage 4 made up 33.9 of total production. In 1974 in cohort 3, copepodid stage 5 contributed the most to total productivity (24.6). Total naupliar production (N1-N5) made up approximately 22.6 and 35.1% of total productivity during 1972 and 1974, respectively. However, cohort 3 made up less than 9% of annual productivity in both years (Table 17).

Mean lake estimates

(i) Mean lake productivity and biomass

Mean lake productivity estimates (mg C $m^{-2}day^{-1}$) were calculated from the depth-abundance regression using the mean depth of the lake to obtain an estimate of productivity applicable to the whole lake. Mean lake productivity (11.3 m) was calculated using both increment summation (Russian) and instantaneous growth rates (Ricker-Chapman) for the May to August period (Figure 21). During both 1972 and 1974, highest productivity estimated with both methods occurred during June and July in 1972, and May and June in 1974. Lowest productivity was estimated in late August in both years using both methods. Productivity estimated over the May to August period in 1972 was .23 g C m^{-2} (1.15 kcal m^{-2}) and .18 g C m^{-2} using Russian and Ricker-Chapman methods, respectively. In 1974, productivity estimates were .43 g m^{-2} (2.42 kcal m^{-2}) using the Russian method

Figure 21. Seasonal distribution of productivity and
biomass for the mean depth of West Blue Lake.
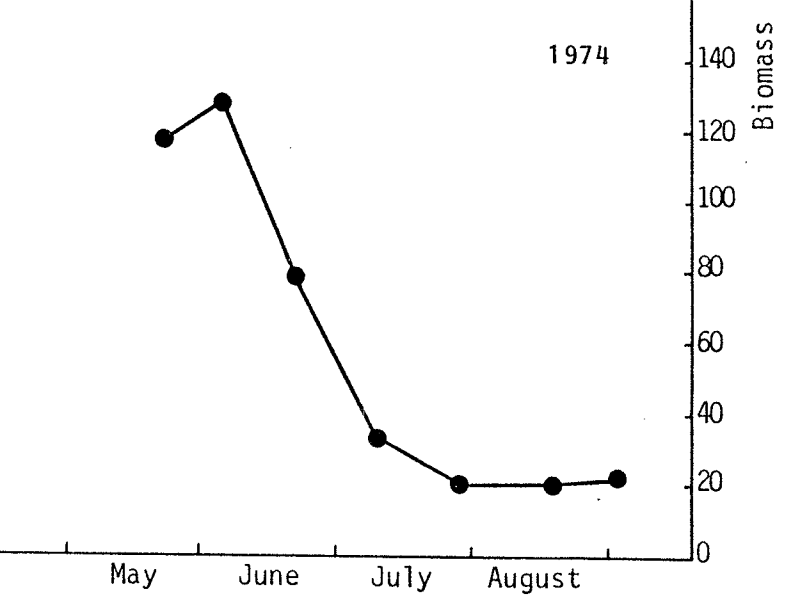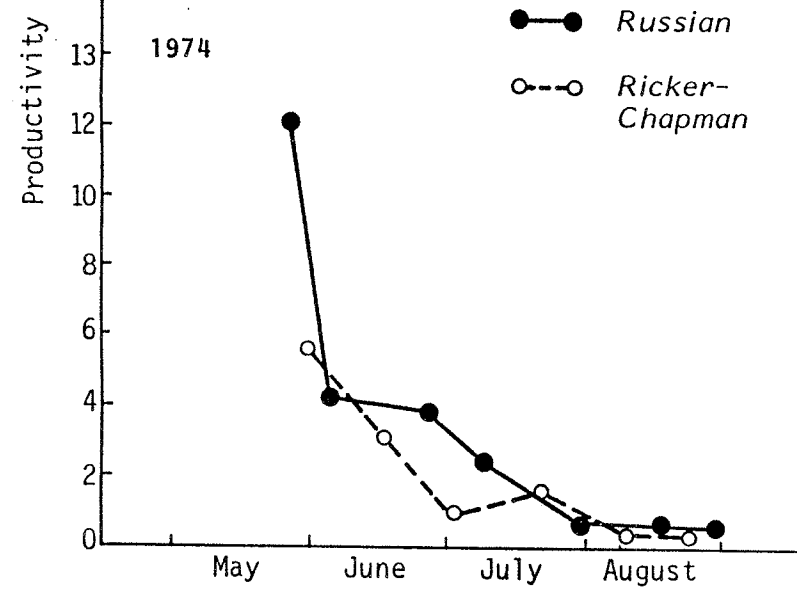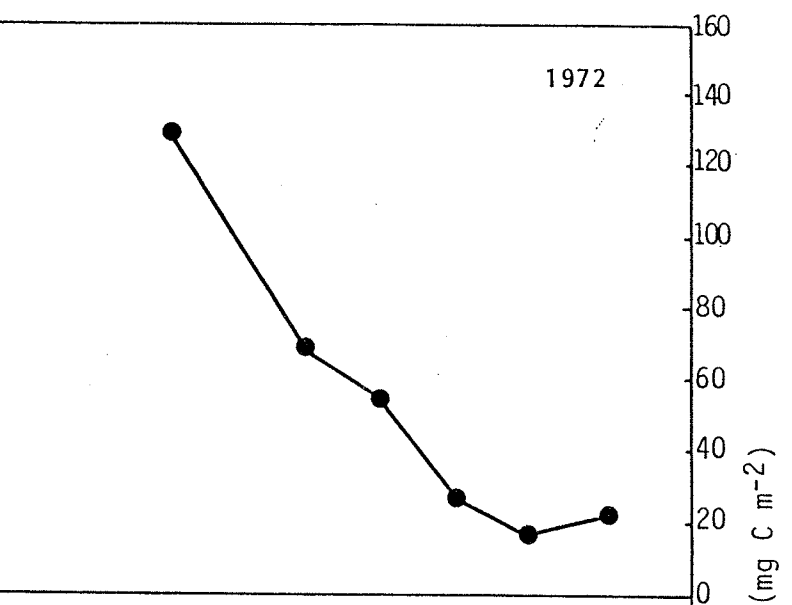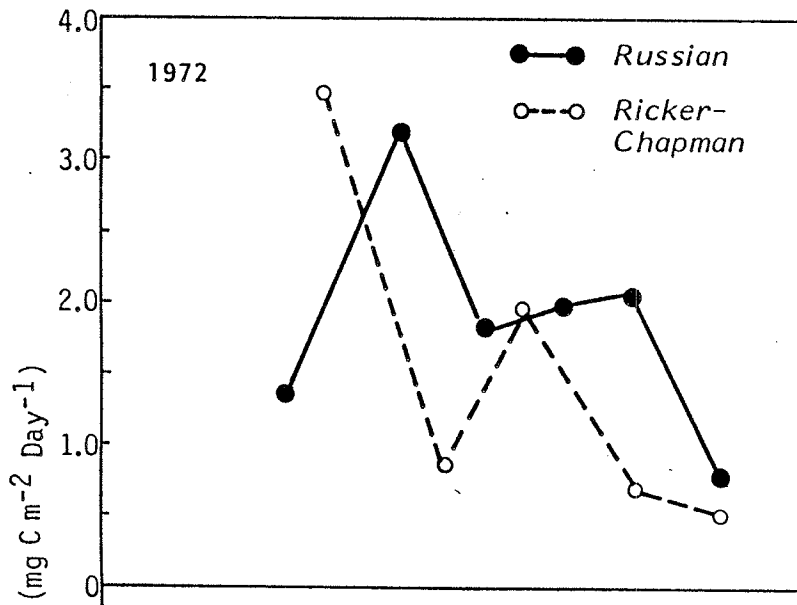
and .23 g C m^{-2} using the instantaneous growth method. Productivity in 1974 was approximately 1.9 times using the Russian method, and 1.3 times using the Ricker-Chapman method, higher than estimates in 1972.

Biomass, estimated for the mean depth of the lake, was based on mean population data (Table 8). Highest mean lake estimates occurred in May and June (1972 - 135.9 mg C m^{-2}, 1974 - 128.3 mg C m^{-2}) and were lowest in August (1972 - 19.4 mg C m^{-2}; 1974 - 21.6 mg C m^{-2}). Biomass estimated over the May to August period was 6.98 g C m^{-2} in 1972 and 7.53 g C m^{-2} in 1974.

(ii) Population turnover rates

Daily turnover rates or $\frac{P}{B}$ ratios calculated using Russian and Ricker-Chapman productivity estimates averaged .033 and .026 in 1972 and .057 and .031 in 1974, respectively. These ratios correspond to a turnover time ($\frac{B}{P}$) of approximately 30 and 38 days in 1972, and 18 and 32 days in 1974 using Russian and Ricker-Chapman productivity estimates, respectively.

DISCUSSION

Life History

Life histories of most copepods may be characterized as univoltine or multivoltine, the latter consisting of two or more generations. In West Blue Lake, Diacyclops bicuspidatus thomasi is multivoltine with three cohorts annually in 1972, 1973 and 1974. Similarly, Armitage and Tash (1967), and Hawkins and Evans (1979) reported three cohorts of this species in a temperate lake. In colder Lake Superior, Selgeby's (1975) data suggests only two cohorts. Similarly, Peacock's (1982) data suggests at least two cohorts developing in Placid Lake, B.C. McQueen (1969) noted only a univoltine population of D. b. thomasi in Marion Lake, B.C. However, Marion Lake is a temperate lake with an extremely high flushing rate (Hall and Hyatt 1974), which makes it difficult for continuously reproducing populations to occur. Moore (1980) also reported a univoltine population of D. b. thomasi in Yellowknife Bay, a subarctic lake. Generally, most temperate limnetic copepods have multivoltine populations (Allan and Goulden 1980), the number of cohorts ranging from two to six depending on the trophic state of the lake (Elgmork 1959, Comita 1972, Cooley 1973, Rigler and Cooley 1974, George 1976, McLaren 1978, Paquette and Pinel-Alloul 1982, and others). Still, univoltine populations of slow growing individuals have been reported for some species (e.g. Carter 1969, Swift and Hammer 1979) in temperate lakes which were either low in productivity or highly saline. A semivoltine population (2 year life history) has also been observed for some calanoid species in temperate lakes (Carter et al 1984).

Cohort separation of D. b. thomasi in West Blue Lake is somewhat subjective. This was especially evident when defining the cohorts where continuous overlapping of stages

occurred. This problem is inherent for all multivoltine populations, and multivoltine populations cannot be analyzed without some subjective treatment of data (Comita 1972, Swift and Hammer 1979, Rigler and Cooley 1974, Carter 1974, Paquette and Pinet-Alloul 1982, Rigler and Downing, in press). Subjectivity is especially severe in sub-tropical and tropical populations where extreme multivoltism leads to a complete over-lapping of generations (Allanson and Hart 1975, Burgis 1974).

As noted for other multivoltine species (Allan and Goulden 1980, Paquette and Pinel-Alloul 1982), D. b. thomasi in West Blue Lake generally overwinters as late copepodid or adult stages. Unfortunately, many investigators (Alimov et al. 1972, Andronikova et al. 1972, Winberg et al. 1972, Peacock 1982 and others) studying the life cycle of copepods neglect this period resulting in a loss of valuable information concerning the species. In West Blue Lake, winter reproduction occurs, which combined with the spring reproduction cohort, make up the familiar "spring bloom" which is characteristic of many copepodid species (Hutchinson 1967, Allan and Goulden 1980).

Diapause of D. b. thomasi in West Blue Lake is an important part of the life cycle. The fourth copepodid stage of cohort 1 enters diapause in the spring and remains in the profundal sediments until the fall. It is assumed that this emergence coincides with the development of copepodid stage 4 of cohort 3 in the planktonic zone. Copepodid stage 4 from cohort 1 could not be distinguished from the same stage in cohort 3. The contribution of this stage from the sediment to the lake population is not known. The intent of sampling

the sediment was to look for presence and absence. No growth
is assumed for copepodid stage 4 during the period of diapause.
Diapause in D. b. thomasi has been reported by other investigators
(Birge and Juday 1908, Moore 1939, Cole 1953, McQueen 1969, Armitage and Tash
1967, Peacock 1982). Still, other investigators who have studied
D. b. thomasi have not reported diapause as part of its life
cycle (Selgeby 1975, Moore 1980). In these latter studies, it is
probable that this species does not diapause because of the low
summer temperatures encountered. The arrestment of the fourth
and/or fifth copepodid stage species has also been observed for
other cyclopoid species (Fryer and Smyly 1954, Elgmork 1959,
Watson and Smallman 1971, George 1976, Elgmork 1980, Paquette
and Pinel-Alloul 1982). Although diapause is most frequently
observed in copepodid stages 4 and 5, it also has been noted to
occur in other instars (Elgmork 1980).

Generally, many investigators have shown that cyclo-
poids enter diapause as a response to unfavourable environ-
mental conditions, e.g. low temperatures, lack of oxygen or
simply ponds drying up (Elgmork 1959, Allan and Goulden 1980).
Watson and Smallman (1971) indicate that diapause is an
"individual physiological response" which occurs after an
animal encounters unpleasant environmental conditions.
Furthermore, Elgmork (1980) states that diapause leads to a
prolongation of the life cycle giving the species some repro-
ductive advantage compared to animals inhabiting the planktonic
zone. By terminating diapause in the fall, D. b. thomasi in
West Blue Lake may take advantage of the phenological niche

during that period before other members of the zooplankton community appear in sufficient numbers as competitors. It is noteworthy that termination of diapause is synchronized with the development of copepodid stage 4 in the planktonic zone. This stage develops into adults in the winter and commences reproduction initiating the winter cohort. Nilssen (1980) suggests that individuals reviving from diapause also have more energy available for later reproduction compared to the cohort remaining in the plankton. This was not verified in this study since calorific determinations were not done on animals collected from the sediments. In addition, Elgmork (1980) suggests that an increase in fecundity and survival may occur resulting from a "chilling effect" from diapause. McLaren (1963, 1974) has indicated for several copepods that survival varies inversely with temperature, with increased survival at the lower temperatures. An increased survival of D. b. thomasi in West Blue Lake may also occur, since individuals may have a refuge from fish predators by remaining in the sediment.

Several environmental factors are probably involved for inducing and terminating diapause of D. b. thomasi in West Blue Lake. Both daylength and temperature are generally considered key environmental cues for inducing and terminating diapause (Watson and Smallman 1971, George 1976). In addition, other factors such as oxygen concentration may be important for diapause to occur. Most of the evidence of D. b. thomasi exhibiting diapause in West Blue Lake comes from station 5 which is 17 m in depth. Diapause was also observed at stations 3 (20 m) and 4 (7-8 m). Although animals were present above the sediment, they were not observed to diapause at station 2 (30 m) where oxygen levels were below 1 mg/L during

the summer months. It is possible that copepodid stage 4 individuals

moved laterally to sediments where oxygen levels were more favourable for

diapause. Similarly, Lysack (1976) observed that Chaoborus flavicans did

not become benthic at this station.

Reproduction of Diacyclops bicuspidatus thomasi in West Blue Lake

occurs in each season except autumn with highest fecundity (no. eggs/♀) in

the spring. Similarly, Selgeby (1975), Armitage and Tash (1967) reported

highest clutch size of D. b. thomasi in the spring. Generally, most multi-

voltine copepod populations have highest fecundity in the spring (Ravera

1955, Elgmork 1959, George 1976, Allan and Goulden 1980, Paquette and Pinel-

Alloul 1982 and others), which seems to be highly dependent on food (phyto-

plankton levels) (Smyly 1973, Vijverberg 1980). Similarly, Peacock (1982) re-

ported a higher clutch size for D. b. thomasi in experimental enclosures with

increased fertilization. In West Blue Lake during 1972 and 1974, food levels

as measured by particulate carbon levels were generally higher in the spring

(Ward and Robinson 1974, present study). An increased abundance of rotifers

which are fed up by D. b. thomasi was also noticed in the spring. Moore (1980)

reported that fecundity of D. b. thomasi in a subarctic lake was related to

daylength.

An inverse relationship was found between egg diameter and female

fecundity for D. b. thomasi in West Blue Lake. Although only 26.3 eggs ind^{-1}

were produced in the winter of 1974, they contained almost as much mass as

the spring clutch of 52.0 eggs ind^{-1} (Table 4). Similarly, Czeczuga (1960),

and Cooney and Gehrs (1980) noted this relationship for several cyclopoid

and calanoid species. Hutchinson (1967), and more recently Nilssen (1980),

suggested that this variation in egg number and diameter may be an adaptive

advantage in life history strategy. Fewer larger nauplii (N1) hatching from

eggs in the winter period may require less food, and could maintain a higher survivorship than many, smaller ones (N1). In addition, these large nauplii may also develop and thus mature more rapidly than smaller nauplii (Cooney and Gehrs 1980). The large clutch size in the spring gives the population of D. b. thomasi in West Blue Lake the advantage of introducing additional members to feed on the abundant food levels during that period. This would tend to make the population more competitive.

Calorific content of D. b. thomasi in West Blue Lake varied seasonally with highest values recorded during the winter period (Table 5). Similarly, Schindler et al. (1971) reported highest calorific estimates of this species in the winter months in northeastern Ontario lakes. In West Blue Lake, Snow (1972) noted that calorific content of Daphnia pulicaria may exceed 10,000 cal/g in late winter. However, this value is probably over-estimated since it would indicate that D. pulicaria is composed primarily of lipids (Winberg 1971a). High winter calorific contents of crustacean zooplankton have been attributed to an accumulation of long chain polyunsaturated fatty acids in phospholipids (Farkas 1970). This winter in-crease in fat content usually precedes the production of eggs (Schindler et al. 1971, Snow 1972). In West Blue Lake, high winter calorific content of Diacyclops bicuspidatus thomasi was noted prior to and during the reproductive period. Energy available could be channelled into egg production. However, this was not observed prior to reproduction in the summer period. Other factors such as animal size may be a factor. Adult female size was significantly larger in winter than in summer. It is possible that large numbers of copepodid 4 that

merged from diapause may have contributed additionally to a total higher calorific content.

Calorific content of life history stages of D. b. thomasi can seriously affect productivity estimates. As noted above, calorific content does vary significantly seasonally for D. b. thomasi, ranging from approximately 46 39 cal/g June 25 to approximately 8200 cal/g on April 3. Productivity estimates expressed in calories would be expected to differ between these sampling dates even though productivity when based on a gram weight basis may show similar results. It is noteworthy that many investigators expressing productivity in calorific terms have erroneously converted gram weight estimates to calories using simple conversion statistics (e.g. 1 gm dry wt. zooplankton = 6000 cal, Alimov et al. 1972, Andronikova et al. 1972).

Vertical Distribution

Diacyclops bicuspidatus thomasi showed no strong diel migration patterns in West Blue Lake. Only copepodid stages 5 and 6 (adult) showed slight nocturnal migration in June and July. However, this migration was of small amplitude where temperature ranges were small. Pennak (1944) also reported that D. b. thomasi did not migrate to a large extent in Colorado lakes.

In West Blue Lake, the positioning of the stage or the depths selected by individual stages is probably an important population strategy. Seasonal temperature conditions appear to regulate to some extent the mean depth selected

by each stage. During almost isothermal conditions in May, most life history stages were found at similar depths, with nauplii situated slightly higher in the water column than copepodid stages. As thermal stratification in the lake was established, marked (mean) stage depth preference occurred with the older copepodid stages selecting the deeper depths. Eggs hatched in the deep, cool hypolimnion and developing naupliar stages preferred the warmer, shallower depths. Although stage selection or preference has been suggested or observed for several marine copepod species (Marshall and Orr 1972, McLaren 1969), few researchers have noted this phenomenon for freshwater cyclopoids (Langford 1938). In this study it is assumed that all individuals of the population of D. b. thomasi have the same genetic composition and that differences in stage selection are not related to differences in genotypes (Weider 1984).

The absence of strong diel vertical migration, and the depth preferences selected by individual life history stages, especially the later copepodid stages, obviously influences its productivity. With the exception of a few stages (e.g. C1, C3), there is no evidence suggesting that stages migrate toward the warmer, upper waters where the increase in food and temperature would probably result in increased growth. At these shallower depths, one would also expect increased mortality due to predation. However, the situation in West Blue Lake is generally different. During periods of thermal stratification older copepodid stages select the deeper, cooler depths where large size and increased fecundity can be achieved since both variables are inversely

related to temperature (McLaren 1974, Vijverberg 1980). At these depths, predation pressure is also probably low. In West Blue Lake, young-of-the-year perch, which feed on adult copepods, are generally not recorded below 15 m (Henderson 1976). Chaoborus are also in low abundance during this period (Lysack 1976). In the hypolimnion, egg survival is probably high (McLaren 1974), and recently hatched naupliar stages gradually seek out the warmer, shallower depths. Depth preferences may thus have advantages in terms of metabolic efficiency (McLaren 1974, Enright 1977) and increased fecundity (McLaren 1974), and may also act as a mechanism to avoid predation from visually orienting planktivores (Zaret and Suffern 1976, Stavn 1975, Wright et al. 1980, Stich and Lampert 1981). All these factors influence productivity.

In West Blue Lake, copepodid stages 1 - 3 were always recorded in high abundance near the thermocline (especially in July) in contrast to most other stages. Food, expressed as particulate carbon was also generally higher near the thermocline. Consequently, these stages may have an advantage over other stages of increased growth resulting from higher temperatures and food concentrations. At the shallower depths, these early copepodid stages (C1-3) may be at a disadvantage because of increased susceptibility to predation during these periods. Still, in West Blue Lake, young-of-the-year larval fish rarely ingest these stages (Henderson 1976). In addition, adult predatory stages of D. b. thomasi and other predaceous zooplankters such as Chaoborus flavicans were rarely observed in the upper water strata during these periods. Wright et al. (1980) have noticed that generally

small instar stages or small zooplankters such as Bosmina escape predation
in surface waters because of their small size.

Vertical distributions of copepodid stage 5 and adult stages are
also probably regulated to some extent by levels of oxygen. During July and
August, these stages rarely were observed or spent only short time periods
near the bottom (30m) where oxygen levels were less than 1 mg/L. Similarly,
Meyers (1980) noted that low oxygen levels elicited an up-water swimming
movement for several cladoceran species. Absence of diapause at this station
was also probably related to low oxygen levels.

Although the adaptive strategy of D. b. thomasi in West Blue Lake
may be somewhat similar to that proposed by McLaren (1963, 1974) concerning
zooplankton migration, there are major differences. In contrast to McLaren's
theory, D. b. thomasi in West Blue Lake does not exhibit strong diel verti-
cal migration. McLaren also proposed that adult females migrated to the
surface to deposit eggs. In West Blue Lake, eggs hatch and begin to develop
in the hypolimnion, and early naupliar stages begin to move to the warmer,
upper waters. This may have evolved as a mechanism to avoid predation.

Different selective pressures may also have been involved to account
for the depth preferences for selected life history stages.
Although Daphnia parvula was observed to migrate during strati-
fied conditions in a Georgian lake, this migration was not
found to provide a thermal demographic advantage to the population
(Orcutt and Porter 1983).

Depth selection of other dominant zooplankton species
in West Blue Lake may not occur. Other dominant zooplankton
species present, such as Daphnia pulicaria, exhibit diel
vertical migration (Bell and Ward 1970). However, it is
still not known whether these migrations vary with stage or
size class. Henderson (1976) has shown that during daylight

hours, large $\underline{D}$. $\underline{pulicaria}$ prefer the deep hypolimnetic waters whereas smaller individuals select the warmer, upper layers.

Population Dynamics

Size frequency distribution or population structure of $\underline{Diacyclops}$ $\underline{bicuspidatus}$ $\underline{thomasi}$ varied only slightly among stations throughout the sampling period in both 1972 and 1974, suggesting that life history stages develop at similar rates throughout the lake. Differences were noted, however, in the contributions of late copepodid stages especially at station 4 (8 m) during July and August. The vertical distribution data indicated that these stages (C4, C5, C6) rarely occurred above 10 m in the water column during these periods resulting in their low abundances at this shallow location.

Results from both the size frequency analysis and abundance decline data indicates that a deep station such as station 2 may be representative of the lake. These findings are significant, especially since estimates of stage development, growth, and population characteristics were made on animals collected at station 2 which was assumed to provide data representative of the whole lake. It is quite time consuming and costly to analyze populations from more than one site; therefore many investigators assume that a single deep station near the middle of the lake is representative of the system (Schindler 1971, Carter 1974, Ward and Robinson 1974, Paquette and Pinel-Alloul 1982). In small lake systems such as West Blue Lake, this assumption may be reasonable. However, in large lake systems where signi-

ficant variations in temperature and trophic conditions exist, information on population characteristics must be obtained from several locations (Patalas 1969, Patalas and Patalas 1978).

To obtain reliable abundance estimates (especially on a unit area basis), zooplankton samples must be collected from several sites even on small lake types such as West Blue Lake. Large spatial variability in zooplankton abundance exists, and occurs in most lake systems irrespective of size, trophic conditions or species present (Tonolli 1949, Bradshaw 1967, Patalas 1969). In West Blue Lake, although collections of D. b. thomasi at station 2 may accurately describe the population characteristics of D. b. thomasi in the whole lake, they are not representative of the mean lake population size. Linear relationships were found between abundance (per unit area) and station depth. Based on these regression equations, station 2 (30 m) abundance estimates were noted to be four fold higher than mean lake (11.3) estimates during both 1972 and 1974. A three fold difference would be expected solely on depth if the vertical distribution of stages was uniform throughout the water column. However, the vertical distribution was not uniform since the mean weighted peaks of most stages were generally located below the mean depth of the lake ($\bar{x}$ = 11.3 m, Figure 11). Other researchers have also observed relationships between abundance and station depth (Patalas and Patalas 1978, Ward 1981).

Highest mean population estimates of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> recorded in May are somewhat higher than those reported for this species in the literature (Table 18). The sampling program was more intensive for West Blue Lake than most other lakes (exception, Patalas's (1969) estimates on Lake Ontario). Leach (1973), studying Lake St. Clair, neglected to count naupliar stages, probably resulting in a gross underestimate of total population size. In West Blue Lake calculated confidence limits for mean lake population estimates of <u>D</u>. <u>b</u>. <u>thomasi</u> were quite high. Since sampling precision and variability in abundance estimates are rarely stated in the literature, it is difficult to compare these results. However, since most zooplankton populations show a contagious distribution (Tonolli 1949, Patalas 1969, Patalas and Patalas 1978, Watson 1974), high variability among population estimates is probably usual.

Both mean lake population estimates and station 2 abundance estimates during 1974 were approximately twice as high as comparable values recorded in 1972. Abundance differences between years are probably related to the differences in fecundity and the percentage of gravid females observed between years. During 1974 (spring), female <u>D</u>. <u>b</u>. <u>thomasi</u> averaged 12.3 more eggs than females in 1972. Assuming 1×10^3 gravid famales m^{-2}, the 1974 population would recruit 1.2×10^4 more nauplii m^{-2} than the 1972 population. The percent gravid females recorded in each cohort was also at lease twice as high in 1974 as in 1972.

Table 18. Abundance of _Diacyclops bicuspidatus thomasi_ reported in the literature.

Lake	General productivity		Abundance		Source
			no. ind. m^{-2}	no. ind. m^{-3}	
West Blue Lake	oligo-mesotrophic	1972 1974	1.4×10^5 2.1×10^5	1.8×10^4 3.5×10^4	present study
Placid Lake, B.C.	oligo-mesotrophic		---	1.0×10^4 (estimated)	Peacock (1982)
State County Lake, Ka.	mesotrophic		---	1.6×10^4	Armitage and Tash (1967)
Lake St. Clair	mesotrophic		---	4.0×10^{4}*	Leach (1973)
Lake Ontario (Toronto harbour)	eutrophic		1.0×10^5	---	Patalas (1969)

* naupliar stages were excluded in the abundance estimate.

An increase in fecundity has been shown to be related
to both temperature (Elbourn 1966, McLaren 1963, Vijverberg 1980,
McLaren and Corkett 1981), food (Smyly 1970, Winberg 1971, Allan
and Goulden 1980, Moore 1980), and daylength (Moore 1980). In
West Blue Lake, temperatures were similar during both years.
Since food preferences of D. b. thomasi are not well known,
it is difficult to relate fecundity to food sources. However,
particulate carbon estimates and rotifer abundances were noted
to be high in the spring of 1974. Daylength was generally
similar between both years.

During 1972 and 1974, total population instantaneous
mortality rates of D. b. thomasi were highest in the spring,
and lowest in the winter. Similarly, Comita (1972) reported
highest mortality in the spring for Mesocyclops edax in
Severson Lake, Minnesota. In Lake Superior, Selgeby (1975)
observed a lower rate of mortality during and after over-
wintering than in the summer breeding generation. During the
spring of 1972 and 1974 in West Blue Lake, approximately 5% of
the total population of cohort 1 died each day. Copepodid stages
comprised the majority of this cohort during the sampling period.
High spring mortality rates of D. b. thomasi may be partly attri-
buted to predation. In West Blue Lake, Henderson (1976), ob-
served that young-of-the-year Perca flavescens fed readily on the
late copepodid stages of copepods during a short period in the
spring. Lysack (1976) also reported that the fourth instar of
Chaoborus flavicans ingested copepodids during this period. The
preference of chaoborids for D. b. thomasi has been well es-
tablished (Peacock 1982). Predation by adult D. b. thomasi

on its own copepodid stages is also probable. The carnivorous behaviour of D. b. thomasi has been noted by Anderson (1972), McQueen (1970) and Peacock (1982).

Mortality rates of Diacyclops bicuspidatus thomasi may be independent of fish or invertebrate predation, and simply a function of population growth. Spring and summer cohorts would be expected to rise and fall at a faster rate than winter cohorts irrespective of predation because of more optimum temperatures and food supplies. For this reason, time or season can be important in defining mortality rates. There are numerous examples in the literature where zooplankton populations rise and fall in the absence of predators. For example, in Black Pond in Ontario, Kwik and Carter (1975) observed rapid spring growth and decline of Daphnia in the absence of fish. In West Blue Lake, although predation of D. b. thomasi does occur, it may not account for the population decline for each cohort. Cohorts which had the highest recruitment rate also had the highest mortality or decline.

It is difficult to compare these estimated mortality rates of D. b. thomasi with literature values. Many investigators have derived or calculated zooplankton mortality (Edmondson 1960) based on exponential models involving the birth rate of the species (Hall 1964, Keen 1973, Keen and Nassar 1981, and others). These models assume that all eggs develop at the same time and generally assume 100% hatching success. For estimates to be reliable, sampling intervals should be short relative to the duration of the animal's lifespan (Hillbricht-Ilkowska and Patalas 1967). However, in

practice, a short sampling frequency is difficult to achieve especially if egg development is only two days. In addition, the calculation 'r' (intrinsic rate of increase) is independent of the prevailing age structure. A stable age distribution is assumed (Deevey 1947) with birth and death rates not varying in response to the population increase (crowding). Since estimates are essentially derived from birth rate data, the egg-ratio method is more reliable for species where a large portion of their development is in the egg or embryonic stage. Edmondson (1960, 1977) developed this method for rotifers, a species with a simple life history with most of the growth occurring in the embryonic stage. However, for cladocerans and especially copepods which have more complex development, birth rate estimates are much less sensitive to deviations in the development of juvenile and adult stages. The egg-birth ratio should not be used for these groups.

Calculated mortality rates of <u>Diacyclops bicuspidatus thomasi</u> in West Blue Lake also have limitations. The slope, or z (instantaneous mortality rate, Figure 17, Table 11), for each regression equation is a mean estimate over the defined sampling period tested. However, actual mortality may be quite variable, fluctuating greatly within the sampling period. In addition, these mortality rate estimates are totally dependent on accurate sampling and cohort separation. However, as observed for naupliar stages, an under-estimate of actual abundances can occur resulting in a biased mortality rate estimate.

Growth and Productivity

The study of growth processes involves changes in body length or weight. Calculated growth factors (G.F.) or the ratio of the length of one instar to that of the previous ones were similar for Diacyclops bicuspidatus thomasi as has been reported for other species (Table 19). For each species, the growth factor was generally below 1.40. For Diacyclops bicuspidatus and Eudiaptomus vulgaris, highest growth factors occurred for nauplius stage 6 followed by copepodid stage 1. Although measurements for both Diaptomus siciloides and D. oregonensis involved only metasomal lengths, results also indicated that highest growth also occurred for copepodid stage 1. In copepods, the development of nauplius stage 6 to copepodid stage 1 is a major transition where significant growth occurs.

Length-weight exponents ranged from 1.5 for Lepto-diaptomus (Cooley 1973) to 2.98 for various copepod species (Pearre 1980, Table 20). Estimates for D. b. thomasi in West Blue Lake varied from 1.7 to 1.9 in carbon units, and from 2.1 to 2.4 in nitrogen units. These estimates are similar to values reported by Vijverberg and Frank (1976) for several cyclopoid species (Table 20). According to Winberg (1971), when geometric proportions of the copepod body are not altered, then the length-weight exponent of most aquatic animals should approximate 3.0. However, for copepods, this cubic relationship may not hold, because, in the transition from nauplius stage 6 to copepodid stage 1, a long urosome develops. This

Table 19. Growth (length) factor (G.F.) or ratio of length of instar
n to instar n-1 for several species of copepods.

| Stage | Author | | | |
	Gurney 1933	Comita and Tommerdahl 1960	Comita and McNelt 1976	Present study
	Eudiaptomus vulgaris	Diaptomus siciloides	Diaptomus oregonensis	Diacyclops bicuspidatus thomasi
N1	1.17	1.16	1.13	1.24
N2	1.09	1.24	1.20	1.17
N3	1.25	1.16	1.36	1.11
N4	1.15	1.14	1.09	1.16
N5	1.15	1.17	1.23	1.12
N6	1.40	*1.04	*1.03	1.69
C1	1.33	*1.33	*1.28	1.25
C2	1.29	*1.22	*1.18	1.18
C3	1.29	*1.19	*1.17	1.21
C4	1.25	*1.19	*1.18	1.09
C5	1.19	*1.13	*1.19	1.20

* metasomal lengths.

urosome may comprise as much as 40% of the total length of copepods as in the case of D. b. thomasi. Length-weight exponents calculated for D. b. thomasi were higher based on metasomal length measurements than on total length for both carbon and nitrogen units. It is noteworthy that cyclopoids have a larger metasomal/urosomal width ratio than calanoids (Pearre 1980) which suggests that their length-weight exponent should be somewhat lower than one derived for calanoids.

Accurate length-weight exponents are important because they are used in calculations of biomass and productivity; however, values range widely in the literature. Cooley's (1973) data on Leptodiaptomus showed approximately only a 25x increase in weight from egg to adult. In contrast, Klekowski and Shushkina (1966), and Pearre (1980) report over a 400x increase from egg to adult, sixteen times higher than the value reported by Cooley (1973). The length-weight relationships derived for D. b. thomasi in West Blue Lake predicted over a 110x increase in weight for both organic carbon and nitrogen weight indices from egg to adult.

Development time refers to the time for a stage to proceed or develop to the next stage (Winberg 1971). It is a major component of several biometric approaches used to calculate zooplankton productivity (Edmondson and Winberg 1972).

For D. b. thomasi in West Blue Lake, stage development was determined as the difference (days) between the midpoint (mean pulse) of two or more successive instars. This technique, similar to that used by Smyly (1973) for C. strenuus, involves

Table 20. Length-weight exponents of several copepod species.

Species	Length-Weight Exponent	Weight Expression	Author
Mesocyclops	2.73	wet weight	Klekowski and Shushkina 1966
Leptodiaptomus	1.5 (calculated)	dry weight	Cooley 1973
Cyclops spp	1.6-2.0	carbon	Vijverberg and Frank 1976
Copepods	2.98	wet weight (in formalin)	Pearre 1980
Themocyclops, Mesocyclops	2.49	dry weight (in formalin)	Burgis 1974
Diacyclops bicuspidatus thomasi			
total length	1.7	carbon	Present study
metasomal	1.9	carbon	" "
total length	2.1	nitrogen	" "
metasomal	2.4	nitrogen	" "

some subjective treatment of the data when identifying peaks

of abundances of particular stages. Several assumptions were

required to calculate development using this method. Mort-

ality rate was assumed to be constant throughout the duration

of each instar, and all individuals of each stage were assumed

to have the same development time. Both assumptions are

difficult to verify but are required for all field data based

methods. Because development times were calculated from

station 2 data, it was assumed that data from this station

was representative of the lake. Evidence to support this

assumption has been provided (Tables 9 and 10).

Since there has been only limited work on the life

history of D. b. thomasi in other lake systems it is difficult

to compare these developmental times. However, the development

of the spring-summer cohort (2) in West Blue Lake (approximately

62 days) was similar to that reported by Peacock (1982, 67.5

days) for a multivoltine population developing in temperate

Placid Lake.

Development times vary considerably among instars for

D. b. thomasi in West Blue Lake which is consistent with that

found for other copepod species (Rigler and Cooley 1974, Paquette

and Pinel-Alloul 1982). There was no evidence of isochronality

(Landry 1983) which is not unexpected given the life history of

D. b. thomasi in West Blue Lake (e.g. cohorts developing in

the fall-winter versus the spring-summer periods).

Development times of some stages of $\underline{D}$. $\underline{b}$. $\underline{thomasi}$ in West Blue Lake were difficult to estimate. For example, because of the long sampling intervals during the winter, maximum abundance peaks of several instars were missed resulting in determination of a development time for several stages. A necessary assumption is that all stages in the combination have equal development times which, of course, may not be true. Grouping or combining of stages also occurred for cohort 3 during the summer period when significant overlapping of stages appeared to occur. Fortunately, because cohort 3 comprised less than 15% of the total numbers during both 1972 and 1974, the magnitude of the error resulting from combinations was probably small. A subjective treatment of data is required by analyses of all multivoltine populations with continuous reproduction (Rigler and Cooley 1974, Comita 1972, Allan and Goulden 1980, Paquette and Pinel-Alloul 1982, Rigler and Downing, in press).

Other approaches are available for calculating stage developmental times from field data. Comita (1972) calculated that stage duration for Leptodiaptomus siciloides and Mesocyclops edax in Severson Lake, was proportional to the area under the time frequency curve for each instar. Although this approach has been criticized (Rigler and Cooley 1974), it is still being used (Peacock 1982). Rigler and Cooley (1974) proposed a simple mathematical approach to the calculation of stage durations, based on mean pulse differences between successive instars. Their method is less subjective than Smyly's (1973), but requires an additional assumption which may be difficult to

satisfy in some cases. The model assumes that the development time of any stage is always greater than that of the previous one. However, for a cohort developing during both winter and spring periods, this assumption may not be valid. Consider cohort 1 of D. b. thomasi in West Blue Lake in 1974. With reproduction occurring during the winter, early naupliar growth was slow, resulting in long developmental times in excess of 10 days. In the spring, as temperature and food availability increased, the development of late naupliar and copepodid stages proceeded quickly (less than 10 days). As a result, successive instars had shorter development times than preceding instars.

Most investigators have determined stage development times from laboratory experiments or by using the temperature dependent Krogh curve (Winberg et al. 1965, Pechen and Shushkina 1964, Patalas 1970, Winberg 1971a, Allanson and Hart 1975, George 1976, McLaren and Corkett 1981). Many researchers, especially the Russian workers, have concluded that development of most copepods may be mainly temperature dependent, and less affected by food levels. Supporting evidence, indicating that copepod development is primarily a function of temperature has been provided by McLaren and Corkett (1981) from their study of Eurytemora herdmani. Field-derived development times of E. herdmani were similar to those predicted from temperature-derived curves derived in the laboratory. Still, other researchers have pointed out the importance of food quality and quantity as factors affecting copepod development (Smyly 1970, Shushkina 1964, Weglenska 1971, Allan and Goulden 1980, Vijverberg 1980, Paquette and Pinel-Alloul 1982). The relative importance of temperature and/or food quality and quantity in zooplankton growth is still not resolved, and may vary with species, trophic state of

lake, and geography (tropical, temperate). Even if temperature solely con-
trolled development, a serious question arises as to which temperature(s)
to use in the laboratory. Different life history stages may be displaced
horizontally in variable epilimnetic temperatures (Patalas 1969, Patalas
and Patalas 1978, Watson 1976), or may exhibit diel vertical migrations
through wide temperature regimes (Bell and Ward 1970, Orcutt and Porter 1983).
The situation may be further complicated because life history stages may
select different depths or temperatures, and these depths may vary
seasonally. Depth preference by different life history stages
was noted for D. b. thomasi in West Blue Lake. Conse-
quently, unless comprehensive field studies are conducted
on the species in question, it may be difficult to select
either an experimental temperature or food level for labo-
ratory experiments designed to determine developmental times.
For these reasons, field derived developmental times have a
distinct advantage over laboratory ones. Field derived
estimates, although somewhat subjective, are far easier to
determine than laboratory ones because less background infor-
mation concerning the ecology of the organism is required.
In addition, most laboratory derived development times des-
cribe population growth as a function of only one factor such
as temperature (Winberg 1971a). However, in a natural situation,
several variables are probably involved. As noted for D. b.
thomasi in West Blue Lake, cohort development and growth varied
considerably among cohorts in both years.

Few investigators have determined growth curves for
multivoltine populations (Cooley 1973, Rigler and Cooley 1974,
Comita 1972, Paquette and Pinel-Alloul 1982). Two different growth rates

were determined for D. b. thomasi in West Blue Lake, which varied between cohorts for each year. Generally spring and summer cohorts displayed the fastest growth whereas winter cohorts showed the slowest growth. These differences in growth are probably a function of temperature, and/or food quality and quantity.

As indicated above, the importance of temperature on instar development has been well documented. In C^{14} tracer feeding experiments conducted with D. b. thomasi, temperature alone accounted for approximately 68% of the variability in incorporation rates (excluding excretion and respiration losses, Appendix A). Food quantity expressed as particulate carbon, accounted for less than 6% of the variability. However, the importance of food quality affecting copepod growth is not clear.

Annual productivity estimates based on the natural population (applied growth) curves varied between 12 and 29% higher (or lower) than one growth curve estimate during the May to August period in 1972 and 1974. These differences would even be greater if comparisons included estimates during the winter months. As indicated above, several researchers have calculated copepod productivity during the ice-free season based on only one growth curve even though some populations were multivoltine (Alimov et al. 1972, Winberg et al. 1972).

Productivity was estimated using the increment summation (Russian) and instantaneous growth (Ricker-Chapman) methods. The former method involves a discrete linear model whereas the latter method involves a continuous exponential model. If growth and mortality of copepod populations is exponential and the cohort is well defined, then the use of the instantaneous (exponential) growth method yields a somewhat better estimate of production (Gillespie and Benke 1979, Allen 1980). Similarly, Rigler and Downing (in press) have indicated that when the population is decreasing (increasing) at an exponential rate, the logarithmic mean would be a more reliable estimate of the population than the arithmetic mean.

Productivity estimates with both methods were similar for the 1974 data (within 10%), but differed significantly when the 1972 data were used (ᴧ30%). This is expected given the quality of data collected in 1974. Sampling frequency was considerably shorter in 1974 than in 1972. In 1974 samples were collected at approximately 3 days intervals during the spring and summer periods. Sampling frequency in 1972 was at least weekly. Since sampling intervals are quite short in 1974, the differences in production using discrete linear growth and exponential growth models would be minimal even though the population may be growing exponentially. Gillespie and Benke (1979) has shown this to be true mathematically. Likewise, if intervals between samples are relatively large, for example, in the 1972 data, differences in production using both methods would be expected to be more significant. Similarly, Romanovsky and Polishchuk (1982) noted that production errors or differences will increase when comparing different production methods with an increase in time interval between sample collections. Another reason for differences in estimates between the two production methods may be related to cohort separation. The instantaneous growth method requires well defined cohorts whereas the increment summation method is independent of cohort separation. In 1974, since sampling frequency was relatively short, cohort separation and hence stage developmental time could be more accurately determined than in 1972 (reduced sampling effort). One would expect the increment summation method to give a more realistic

estimate of productivity in the 1972 data than the instantaneous
growth method since the cohorts may not be well defined.
Cohort separation is perhaps the most difficult task involved
when analyzing zooplankton productivity data because it in-
volves some subjective treatment of data.

Annual mean lake productivity (per area unit i.e. m^2)
was approximately two and three times lower than station 2
(and 5) estimates in 1972 and 1974, respectively, suggesting
that one station estimates may not be representative of the
lake.   The horizontal and vertical displacement of plankton
in lake systems is well known (Hutchinson 1967, Patalas 1969,
Patalas and Patalas 1978, Tonolli 1949).   Several investi-
gators such as Smyly (1973), and Petrova et al. (1965) have
based their estimates on single deep stations which may be
biased if they use them to represent the whole lake (on an
area basis).

Annual mean lake productivity of D. b. thomasi was
approximately 1.5 times higher in 1974 than in 1972.   Other
investigators have also reported increased production for
multi-year studies but no reasons are given for these in-
creases (Smyly 1973, Rigler and Cooley 1974, George 1976).
In West Blue Lake, this increase in productivity was directly
related to numerical abundance increases between the two
years.   Mean lake population estimates in 1974 were approxi-
mately 1.8 times higher in 1972.   Similarly, Daphnia puli-
caria abundance in 1974 in West Blue Lake was almost double
that of 1972 (Ward 1981).   Growth of D. b. thomasi in West
Blue Lake did not increase appreciably to account for the pro-

ductivity difference in estimates between the two years.
The large population in 1974 was attributed to a significantly
higher female fecundity, and percentage of gravid females
present compared to estimates in 1972. For example, cohort
2 females in 1974 had, on average, 12.3 more eggs than females
belonging to the same cohort in 1972 (Table 4). The percen-
tage of gravid females in this cohort in 1974 was also at
least double that observed in 1972 (Table 2).

Productivity of D. b. thomasi was expressed in both
calories or energy units, as well as in carbon. Although
calories have been recommended as the most useful unit in
productivity studies (Winberg 1971b, Waters 1977), it is a
difficult unit to assess because of the amount of material
required for analysis. Calorific content of copepods does
vary with species and season (Snow 1972), and simple expres-
sions converting dry weight of an animal to calories should
not be used. In West Blue Lake, calorific content of D. b.
thomasi varied considerably between summer and winter estimates.

Several estimates of copepod productivity are avail-
able in the literature for various trophic conditions of
lakes (Table 21). Productivity estimates of D. b. thomasi
were expressed in both carbon and calories, and as a quan-
tity per volume (m^3) and area (m^2) for comparison with pub-
lished literature estimates. Generally, productivity of D. b.
thomasi was within the range estimated for other copepod
populations found in lakes of similar trophic status. For

1972 and 1974, productivity over the May to August period was approximately .23 and .43 g C m^{-2} (1.15 kcal m^{-2}, 2.42 kcal m^{-2}; .23 kcal m^{-3}, .34 kcal m^{-3}). West Blue Lake may be classified as being oligo-mesotrophic (Ward and Robinson 1974). These estimates are within the range for several diaptomid species determined by Cooley (1973), Rigler and Cooley (1974), and Swift and Hammer (1979). Still Cooley's (1973) estimate for Diaptomus minutus in Bluff Lake may be under-estimated because his length-weight curve developed for the species may be in error. Difference in weight between egg and adult D. minutus was only by a factor of 25. Productivity estimates, expressed in calories, for Diacyclops bicuspidatus thomasi were also similar to those reported in oligotrophic Russian lakes (Alimov et al. 1972, Andronikova et al. 1972). Many of these estimates for oligotrophic lake species are probably over-estimated because they were based on simple conversions from dry weight to calories (e.g. 1 gm dry wt. zooplankton = 6000 cal., Alimov et al. 1972, Andronikova et al. 1972). Data presented in this thesis indicate that calorific content does vary seasonally and may vary almost two-fold over the year. Schindler's (1972) estimate for Diaptomus minutus in two oligotrophic lakes was slightly higher than that calculated for Diacyclops bicuspidatus thomasi in West Blue Lake. However, productivity of Diaptomus minutus may be a slight over-estimate since calculations appear to have been determined using a single growth curve. Productivity estimates for the Diacyclops bicuspidatus thomasi West Blue Lake population (May to August)

Table 21. Productivity estimates for several copepod species of lakes of different trophic levels.

General productivity	Lake	Species	Annual $(g\ C\ m^{-2}y^{-1})$ $(g\ m^{-2}y^{-1})$	Productivity $(kcal\ m^{-2}y^{-1})$	$(kcal\ m^{-3}y^{-1})$	Source
oligotrophic	Red Lake,* U.S.S.R.	Mesocyclops leukarti	--	1.90	--	Andronikova et al. 1972
	Lake Krivoe,* U.S.S.R.	Cyclops scutifer	--	0.20	--	Alimov et al. 1972
	Lake Krugloe,* U.S.S.R.	Cyclops scutifer	--	1.80	--	Alimov et al. 1972
	Red Lake,* U.S.S.R.	Mesocyclops oithonoides	--	2.80	--	Andronikova et al. 1972
	Waldsea Lake,	Diaptomus minutus	0.60	--	--	Swift and Hammer 1979
	Clear Lake, Ont.	Diaptomus minutus	--	--	0.76	Schindler 1972
	Lake 229 Ont.	Diaptomus minutus	--	--	0.91	Schindler 1972
oligo- mesotrophic	Bluff Lake, N.S.	Leptodiaptomus minutus	0.60	--	--	Cooley 1973
	Teapot Lake,** Ont.	Diaptomus oregonensis	1.17 (1967) 0.52 (1968)	-- --	-- --	Rigler and Cooley 1974

 * ice-free season (May to October) estimate.
** April to December estimate.

Table 21. Continued.

General productivity	Lake	Species	Annual (g C m^{-2}y^{-1}) (g m^{-2}y^{-1})		Productivity (kcal m^{-2}y^{-1})	(kcal m^{-3}y^{-1})	Source
oligo-mesotrophic	West Blue Lake, Man.	Diacyclops bicuspidatus thomasi	Russian Ricker-Chapman	.23*** .18	1.15 --	.23 1972 --	Present study
			Russian Ricker-Chapman	.43 .23	`2.42 --	.34 1974 --	
mesotrophic	Lake Naroch,* U.S.S.R.	Cyclops sp.		--	4.8	--	Winberg et al. 1972
eutrophic	Esthwaite, U.K.	Cyclops strenuus		.70	--	--	Smyly 1973
	Rydal Water, U.K.	Cyclops strenuus		.15	--	--	Smyly 1973
	Lake Myastro* U.S.S.R.	Cyclops sp.		--	11.2	--	Winberg et al. 1972
	Lake Batorin*	Cyclops sp.		--	25.2	--	Winberg et al. 1972
	Eglwys Nynydd, U.K.	Cyclops vicinus		4.2 (1970) 4.8 (1971)	-- --	-- --	George 1976
	Severson Lake, U.S.A.	Mesocyclops edax		--	36.8	1.83	Comita 1972

*** May to August estimate.

derived from one growth curve (cohort 2) differed from productivity estimated for the natural population (cohorts 1, 2, 3) by approximately 12 and 29% in 1972 and 1974, respectively. Productivity estimates available for other species in eutrophic lakes were significantly higher than those for D. b. thomasi in West Blue Lake (Smyly 1973, Winberg et al. 1972, George 1976, Comita 1972, Table 26).

Several investigators working on copepod productivity have grouped or completely neglected the naupliar stages (Winberg et al. 1972, Alimov et al. 1972, Swift and Hammer 1979). The magnitude of this error is not known because only a few studies have attempted to estimate the contribution of various life history stages to total productivity. Exceptions are the studies of Cooley (1973), Rigler and Cooley (1974), and George (1976). Generally, their results indicated that copepodid stages contributed the most to total productivity. Cooley (1973) also reported the importance of eggs to total productivity. In Bluff Lake, Nova Scotia, egg production of Diaptomus minutus accounted for 24 and 88% of the total productivity in cohorts 1 and 2 respectively.

Similar to other studies, highest productivity occurred for the copepodid stages of Diacyclops bicuspidatus thomasi. However, it is noteworthy that different stages contributed the most to total productivity in each year. In 1972 copepodid stages 2 and 5 were the most productive stages, whereas in 1975 stages 2, 4, and 5 contributed the most to total productivity. With the exception of naupliar stage 6, naupliar contribution was less than 10% of total productivity for

cohorts 1 and 2 in both 1972 and 1974. Naupliar contribution

was higher for cohort 3 in both years; however this cohort made

up less than 9% of the annual productivity in 1972 and 1974.

These data suggest that productivity estimates neglecting or com-

bining naupliar stages may not be seriously in error. These

results are encouraging in that not all naupliar stages need

to be identified or counted thereby reducing the work load.

One of the most widely used indices of productivity

is the $\frac{P}{B}$ coefficient or ratio of productivity to biomass (Winberg

et al. 1972, Alimov et al. 1972, Waters 1977, Banse and Mosher

1980). This ratio has been used as an indication on how fast

the population is growing (Winberg 1971). The inverse of the $\frac{P}{B}$

ratio or turnover time is defined as the time required for the

population to replace itself. In West Blue Lake, daily $\frac{P}{B}$ ratios

of D. b. thomasi averaged .033 in 1972 and .057 in 1974 (incre-

ment summation estimates). These estimates are within the

ranges found elsewhere for copepod species in lakes of various

trophic types (Table 22). A similar $\frac{P}{B}$ ratio was recorded for

species in oligotrophic systems whereas slightly higher $\frac{P}{B}$ ratio

were noted for copepods in lakes with a higher trophic state. In

the literature $\frac{P}{B}$ ratios have often been misused. For example,

Ivanova (1974) compared various lake types by plotting P

(productivity) against biomass, and related the exponent k (i.e.

$P = aB^k$) to each lake type. However, since biomass and produc-

tivity are not independent variables, the regression analysis

should not have been attempted since it violated a key statistical

Table 22. A summary of $\frac{P}{B}$ ratios (May to August period) of cyclopoids in lakes of different trophic status.

Lake	Trophic state		$\frac{P}{B}$ ratio	Species	Author
Krivoe	oligotrophic		.040	Cyclops scutifer	Alimov et al. 1972
West Blue* Lake	oligo- mesotrophic	1972 1974	.033 .057	Diacyclops bi- cuspidatus thomasi	Present study
Russian lake	mesotrophic		.063	Mesocyclops leukarti	Petrova et al. 1965
Eglwys Nymydd U.K.	eutrophic		.06 (calculated)	Cyclops vicinus	George 1976 Banse and Mosher (1980)
Lichenskie	eutrophic		.140	Mesocyclops leukarti	Patalas 1970

* Russian productivity estimate.

assumption (Steele and Torrie 1960). Further, other researchers have attempted to estimate copepod productivity based on production to biomass ($\frac{P}{B}$) ratios calculated from adult body mass using an empirical relationship (Tremblay and Roff 1983). However, their approach has been strongly criticized by McLaren and Corbett (1984) since there is a lack of dependence of developmental rate and growth rate ($\frac{P}{B}$ ratios) on body size in copepods which was the main assumption of Tremblay and Roff's (1983) production model.

In summary, this thesis presents information on the life history, behaviour, population dynamics and productivity of D. b. thomasi in West Blue Lake. It provides a detailed investigation of an important cyclopoid species, and contributes to our general knowledge of zooplankton ecology. Data indicated that diapause and vertical migration (or absence of it) of D. b. thomasi are important aspects of its population strategy which can affect productivity. Mortality was estimated for the various cohorts of D. b. thomasi. Productivity was determined using two different biometric approaches (increment summation, instantaneous growth), and the advantages and disadvantages of each method were discussed. Errors associated with single station estimates (on a unit area basis), and estimates based on a single growth curve were also noted. Productivity results also indicated that combining or neglecting naupliar stages will not seriously affect total productivity estimates.

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APPENDIX A

FEEDING EXPERIMENTS (INCORPORATION RATES)

Introduction

The rate at which an animal consumes food is of basic importance since it affects the nutritive income of the consumer and sets a level for its productivity. Several researchers have attempted to calculate zooplankton productivity based on assimilation rates (Schindler 1968, Sorokin 1968). However, problems do arise as to what food source(s) to offer, and under what environmental conditions.

Generally, the feeding behaviour of most cyclopoids has not been well documented. Cyclopoids have been reported to be both herbivores and carnivores in nature, feeding on large algal forms, rotifers, and even on its own nauplii (Fryer 1957, Anderson 1970, McQueen 1969).

Most estimates of cyclopoid assimilation (incorporation) have been unrealistic (Schindler 1971, Sorokin 1968), since they have involved primarily unispecies cultures, and unnatural food sources and concentrations. Although "in situ" studies of the assimilation rates of cyclopoids are not available, Bell and Ward (1970) attempted to determine incorporation rates of Daphnia pulicaria under natural conditions. The objective of this study is to determine reliable estimates of incorporation for Diacyclops bicuspidatus involving "in situ" studies.

Materials and Methods

In situ feeding experiments

Experiments were conducted from June 19 to August 10.

Since a thermocline was present in West Blue Lake during that period, "in situ" experiments were conducted over a wide temperature range (8.0-21.5°C).

The food sources made available to Diacyclops bicuspidatus ranged in size from 25 μ to 153 μ. This included food items such as large phytoplankton, protozoans, nauplii, rotifers, and early copepodid stages. Items less than 25 μ were not considered since several investigators have shown that cyclopoids have low assimilation rates of bacteria and nannoplankton (Sorokin 1968, McQueen 1969).

Approximately 80 L of lake water were sampled with a Schindler-Patalas trap fitted with a 25 μ screen, and all organisms collected were concentrated into a 1 L container. Contents were then screened into a 1050 μ, 500 μ, 243 μ, and 153 μ mesh to remove Daphnia and adult copepods. The filtrate was next examined under a binocular scope (4X), and any adult copepods were again removed.

Approximately 30 μCi of ^{14}C in the form of $NaH^{14}CO_3$ was added to the food suspension, and contents were held under constant aeration and light conditions (200 lux at 23°C for 48 h). Prior to experiments four 10 mL aliquots of the food source were filtered through a .45 μ Millipore HA millipore filter. The specific activity of the food source on the filter, placed in a dioxane fluor (Bray 1960), was determined by liquid scintillation counting (Bell and Ward 1970). In addition, four 10 mL aliquots of the food source were also measured for organic carbon content (Perkin

Elmer Elemental Analyzer Model 205).

At the beginning of the feeding experiment approximately 30 animals, rinsed in lake water, were placed in four experimental containers (10 L capacity) filled with pre-filtered lake water (Figure 1). The labelled food was diluted to pre-concentrated levels, and next placed in three control and four experimental containers. All containers were sealed and were suspended at the desired depth where originally obtained. The feeding period lasted four hours.

At the end of the feeding period, animals were filtered onto a 153 μ screen, rinsed with filtered lake water, and placed into a non-labelled food source for 2.0 hours to remove labelled food from their guts (Sorokin 1968, Schindler 1968). Approximately 100 mL from each experimental and control container were filtered, placed in dioxane fluor and counted for specific activities.

After feeding on the non-labelled food source, each experimental group of animals were screened onto a 153 μ mesh, rinsed with filtered lake water, numerically counted, and placed in scintillation vials containing 0.5 mL of NCS. The digestion procedure and determination of sample specific radioactivity have been previously described (Bell and Ward 1970).

Figure A1. In situ experimental procedure for ^{14}C

feeding experiments.
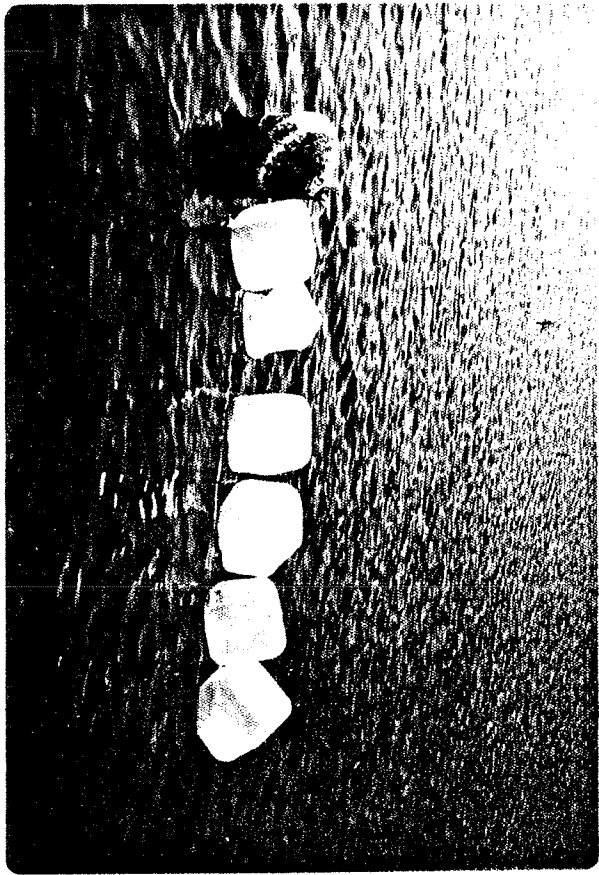
Results

Incorporation rates of Diacyclops bicuspidatus feeding on natural food items (25 μ-153 μ) are given in Table Al. Values ranged from .0011 μg C ind^{-1} h^{-1} to .0063 μg C ind^{-1} h^{-1} depending on temperature and food concentration (carbon content). Incorporation rates varied directly with temperature with a coefficient of determination (r^2) of .68 which indicated that approximately 68% of the variability in incorporation could be attributed to the regression of incorporation on temperature (Table A2). The addition of food concentration as a variable increased the correlation coefficient only slightly, an additional 5% of the variability explained.

Discussion

Although several researchers have determined incorporation rates for several cyclopoid species, most estimates were derived under artificial experimental conditions. A comparison of "in situ" incorporation rates of D. bicuspidatus with those of other cyclopoid species are listed below.

Species	Temperature (°C)	Food type	Incorporation (μg C ind^{-1} h^{-1})	Author
Diacyclops bicuspidatus	15	443 (natural 25-153 μ)	.002	Present study
Acanthocyclops viridis	15	Scendesmus	.0008	Sorokin 1968
Cyclops strenuus	15	Elakothrix (23 μ)	.00026	Schindler 1971
		Coelastrum (23 μ)	.00017	Schindler 1971

Table A1. Incorporation rates of <u>Diacyclops</u> <u>bicuspidatus</u> <u>thomasi</u> (food range 25 -153).

Date	Temperature (°C) X_1	Specific Act. Food (dpm L^{-1})		Carbon Content Food (µg C L^{-1}) X_2		Animal Activity (dpm ind^{-1})		Feeding Duration (h)	Incorporation (µg C $ind^{-1}h^{-1}$)
6/19/75	14.5	15178	1459.3	369.0	63.5	0.436	0.110	4.0	0.0026
	14.5	16664	1569.5	369.0		0.434	0.015	4.0	0.0024
	14.5	18550	2558.6	369.0		0.668	0.078	4.0	0.0033
7/7/75	21.5	10543	915.1	241.1	23.1	0.721	0.024	4.0	0.0041
7/17/75	20.0	8736	938.0	423.9	56.0	0.523	0.054	4.0	0.0063
7/24/75	8.0	34909	881.0	367.6	26.4	0.421	0.02	4.0	0.0011
8/2/75	12.5	44661	18421.1	546.5	54.1	0.936	0.078	4.0	0.0028
7/19/75	9.5	9960	823.4	387.9	49.2	0.259	0.031	4.0	0.0025
8/10/75	15.5	49957	550.7	517.1	49.9	0.985	0.098	4.0	0.0025
7/26/75	19.5	16334	1147.5	259.8	7.0	0.886	0.085	4.0	0.0035

Table A2. Statistical significance of the incorporation
          equation (linear model).

Source Variation	Degrees of Freedom	Sum of Squares	Mean Squares
Regression	1	1.237	1.237
Error	8	0.566	0.071
Total	9	1.803	
F-Test (H_o: B_1 0)	17.5*		
r^2	0.68		

* significant at 1% level.

$$\ln Y = .084T - .712$$

where   Y = incorporation in µg C ind^{-1} h^{-1}

         T = temperature in °C

Table A3. Statistical significance of the incorporation
equation (multiple regression model).

Source Variation	Degrees of Freedom	Sum of Squares	Mean Squares
Regression	2	1.326	0.663
Error	7	0.478	0.068
Total	9	1.804	
F-Test (H_o: B_1=B_2=0)	9.7*		
r^2	0.735		

* significant at 1% level.

$$lnY = .0941T + .011F - 7.706$$

where   Y = incorporation in μg C ind^{-1} h^{-1}

T = temperature in °C

F = food concentration in carbon μg C L^{-1}

At the same temperature, incorporation rates of D
bicuspidatus were approximately an order of magnitude higher
than other estimates. This is probably related to the size
range of natural food offered to D. bicuspidatus which in-
cludes algae, protozoans, nauplii and rotifers. Most cyclo-
poid species have been known to ingest all these food types
(Fryer 1957, Anderson 1970, McQueen 1969).

Temperature was the major variable affecting incor-
poration rates, concentration of food contributing little
as an influencing variable. This agrees with the results
of most feeding studies (Bell and Ward 1970, Edmondson and
Winberg 1972, Winberg 1971). The variable food quality, not
considered in this study, may also be a major factor affec-
ting feeding (Smyly 1970).

Estimates of incorporation of D bicuspidatus are
probably underestimated due to probable excretion and res-
piration losses. Fernando and Brandl (1975) estimated as
much as a 40% excretion loss for Daphnia magna over a 48 h
feeding period. Similarly, Lambert (1975) found major
metabolic pool losses studying assimilation rates of
Daphnia.

Because of the problems associated with metabolic
pools encountered in the experimental design (Appendix B),
an estimate of productivity based on calculated incorpora-
tion rates was not derived.

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APPENDIX B

METABOLIC POOL EXPERIMENTS

Introduction

The use of radio-tracers in estimating zooplankton
assimilation or incorporation rates for productivity esti-
mates has been questioned (Ward and Robinson 1974). In
addition to problems associated with realistic food sources
and environmental conditions, serious questions still arise
concerning metabolic pool pathways of the radionuclide
tracer used (Conover 1961, Lambert 1975, Brandl and
Fernando 1975). Significant losses due to key pools of
respiration and excretion could result in an underestimated
incorporation rate. These losses may occur both "during"
and "after" feeding experiments. The objective of this
study is to determine whether incorporation rates have to
be corrected for respiration and excretion losses 'after
and before feeding' at various holding times.

Materials and Methods

1. 'After feeding' experiments

Ten μCi of NaH^{14}CO$_3$ was added to a screened (25 μ-
153 μ), concentrated sample of lake phytoplankton and zoo-
plankton. This food source included algae, rotifers and
copepodid nauplii. The food suspension was incubated for
a 2-day period under constant light conditions at 18°C.

At the beginning of the experiment groups of Diacyclops
bicuspidatus were collected, screened on a 243 μ Nitex mesh,
rinsed and washed into a feeding basket suspended in a
beaker containing filtered lake water. (The feeding basket

had a 243 µ screen bottom to ensure no contamination from the labelled food source.) The labelled food source was then added and the animals were allowed to feed for 4 hours.

After the feeding period, the feeding baskets (which retained the animals) were rinsed twice in filtered lake water (filtered through a 0.45 µ membrane filter) and resuspended in holding beakers containing filtered lake water for various holding times (0, 5, 10, 20, 30, 45, 60, 90, 120 and 240 minutes).

At predetermined intervals animals were removed, rinsed and placed in scintillation vials each containing .5 mL NCS (Bell and Ward 1970). The specific radioactivity of these animals was determined by liquid scintillation counting procedure (Ward et al. 1970). Aquasol (Amersham Nuclear) was the scintillation cocktail. For each holding period, the ^{14}C egested, respired, and excreted was determined. The holding medium was filtered through a .45 µ Millipore HA membrane filter. Filters containing egested material were rinsed several times with filtered lake water, placed in vials containing Aquasol and counted. Both the organic and inorganic ^{14}C contents of the filtrate were determined using an acidification and shaking technique. Two mL of 2NHCl was added to each flask to drive off $^{14}CO_2$ which was measured directly using phenethylamine as a CO_2 trap (Figure B1). Each flask was shaken slightly on a rotator for 11 hours to ensure maximum efficiency of the phenethylamine. Preliminary recovery experiments involving

Figure B1. Apparatus for determining ^{14}C egestion,

respiration and excretion.

Filter
Sample
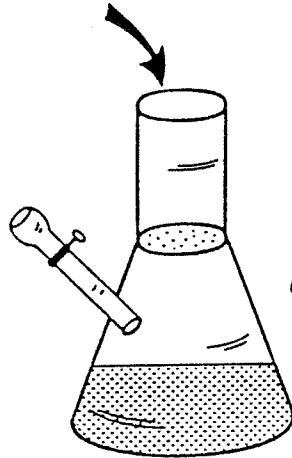
Fecal Pellets

0.45u Membrane
Filter

A. Egestion

ACIDIFICATION AND SHAKING

Rubber Stopper

2N Hc1

Phenethylamine
(trap)

Organic ^{14}C

Inorganic ^{14}C

Add Hc1

Flask Shaken
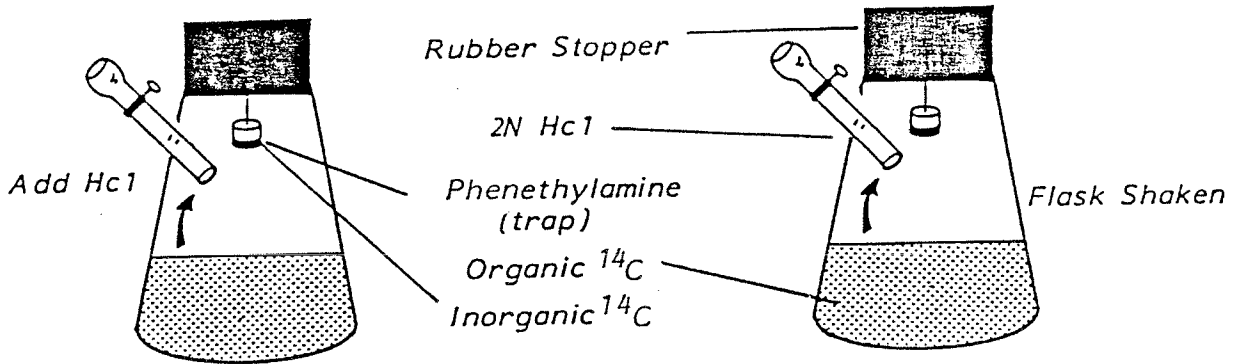
B. Respiration and Excretion

innoculating ^{14}C in bicarbonate form to a pre-filtered medium indicated that over 95% of the ^{14}C was trapped by phenethylamine over an 11 h period (Table B1).

2. 'Before feeding' experiments

Labelling of the food source followed the same procedure outlined in the 'after feeding' experiments. After labelling, the food source was again screened through a 25 μ-153 μ Nitex mesh and rinsed several times with filtered lake water. This prevented contamination of the dissolved ^{14}C in the experimental containers. Aliquots of the labelled food source was then washed into 8-150 mL beakers containing filtered lake water; 4 serving as controls* (food source only) and 4 serving as experimentals (food source + animals).

Approximately 24 hours prior to the experiment, experimental groups of Diacyclops bicuspidatus were collected from West Blue Lake, screened on a 243 μ Nitex mesh, and placed in beakers held at the experimental temperature (18 C) and light conditions. At the beginning of the experiment, groups of approximately 70 animals were placed in the experimental beakers.

Prior to the beginning of the experiment, the initial

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* Since algae (in the food source) are continually photo-synthesizing and respiring ^{14}C, there are actually not controls in current laboratory terms. However, for convenience in this report, they are designated as such.

radioactivity of both the control food source and experimental food source was determined by filtering three 10 mL aliquots through .45 μ Millipore HA membrane filters. Filters were placed in scintillation vials containing 10 mL Aquasol fluor, and later counted. The radioactivity of both control and experimental beakers (after animals had been removed) after the feeding period was determined by the same procedure.

Feeding experiments were run at 18 C for both 2 and 4 hours. After the feeding period, animals in the experimental beakers were removed, rinsed and placed in scintillation vials containing .5 mL NCS and later counted (Ward et al. 1970). Determinations of respiration (inorganic ^{14}C) and excretion (organic ^{14}C) were done using the acidification and shaking technique (described in 'after feeding' procedure) with one modification. Before the addition of acid, three 3 mL aliquots were taken from the filtrate. This was a measure of total inorganic and organic ^{14}C.

Results and Discussion

1. 'After feeding' experiments

Animal activity which, for each replicate, was generally below 10 dpm animal^{-1}, decreased significantly after 10 minutes of holding time as egestion occurred (Tables B2 and B3). In experiments 2 and 3, combined ^{14}C activity of both excretion and respiration far exceeded that of animal activity (Tables B3, B4). Similarly, in experiment 1,

Table B1. Recovery experiment using phenethylamine as CO_2 trap.

Time (hr)	$^{14}CO_2$ dpm	% of Activity Standard	^{14}C Filtrate dpm	S.E.	% of Activity Standard	Activity Standard dpm
1.0	48107	37.5	164.8	5.1	<1	175025 ± 12875
2.0	110685	63.2	105.8	1.2	<1	
3.0	122986	70.3	66.1	0.8	<1	
5.0	138361	79.1	81.2	1.4	<1	
7.0	158129	90.3	25.9	0.7	<1	
10.0	170294	97.3	42.4	0.5	<1	
12.0	(i)170294	97.3	77.6	2.5	<1	
	(ii)170294					
	(iii)170294					

Table B2.   Calculated amounts of ^{14}C lost by excretion 'after feeding'.

Replicate #1

No. of Animals	Holding Times in unlabelled medium (min.)	Animal Activity dpm animal^{-1}	Excretion dpm animal^{-1}	Percentage of animal activity
36	0	13.53		
31	5	10.49	2.76	26.3
32	10	8.57	1.68	19.6
28	15	9.20	2.55	27.7
32	20	7.79	2.34	30.0
26	30	8.10	4.32	53.3
31	45	6.77	2.19	32.3
34	60	5.14	4.83	94.0
36	90	5.77	2.55	44.2
37	120	6.07	2.43	40.0
39	240	5.63	2.49	44.2
28	480	5.85	4.86	83.1

79.38

Table B3. Calculated amounts of ^{14}C lost by respiration, excretion 'after feeding'. Replicate #2.

No. of animals	Holding Times in unlabelled medium (min.)	Animal Activity $\frac{dpm}{animal^{-1}}$	Egestion $\frac{dpm}{animal^{-1}}$	Animal Activity and egestion dpm animal^{-1}	Respiration $\frac{dpm}{animal^{-1}}$	Excretion $\frac{dpm}{animal^{-1}}$	% ^{14}C loss by respiration and excretion
25	0	26.12					
31	5	3.09	2.60	5.68	25.88	128.7	>200
32	10	2.12	0.83	2.95	12.08	1.86	>200
43	20	2.13	0.49	2.62	6.70	0.78	>200
30	30	2.19	0.94	3.13	8.37	1.71	>200
44	45	1.78	0.78	2.56	6.82	0.96	>200
27	60	2.16	1.63	3.79	7.23	1.86	
27	90	1.83	1.52	3.35	20.37	4.62	>200
33	120	2.20	1.63	3.83	8.72	1.47	>200
36	240	1.00	1.61	2.61	12.35	2.70	>200

Table B4. Calculated amounts of ^{14}C lost by respiration, excretion 'after feeding'. Replicate #3.

No. of animals	Holding Times in unlabelled medium (min.)	Animal Activity dpm animal^{-1}	Egestion dpm animal^{-1}	Animal Activity and egestion dpm animal^{-1}	Respiration dpm animal^{-1}	Excretion dpm animal^{-1}	% ^{14}C loss by respiration and excretion
10	0	3.17					
83	10	2.50	3.73	6.23	26.43	3.48	200
58	20	2.25	0.73	2.98	1.36	3.51	163
100	30	2.26	0.48	2.94	0.98	2.28	118
108	45	2.08	0.57	2.65	0.89	2.34	121
89	60	1.59	0.27	1.86	0.77	2.79	191
91	90	1.96	0.70	2.66	1.74	3.15	184
106	120	1.67	0.50	2.17	1.30	2.19	161
86	240	1.24	0.95	2.19	0.81	2.28	141

Table B5. Calculated percentages of ^{14}C lost by respiration and excretion 'during feeding'.

Feeding Period (NR)	Food Source ("control")				Animal Activity (dpm animal^{-1})		Food Source + Cyclops				Measured org. and inorg. ^{14}C (dpm mL^{-1})	% Total ^{14}C Acc. For	Corr. Factor for Algal Growth ("controls")	Corrected		% loss of Animal Activity	
	Resp. (dpm mL^{-1}) $\bar{x}$	S.D. ($\bar{x}$)	Excre. (dpm mL^{-1})	S.D. ($\bar{x}$)	$\bar{x}$	S.D. ($\bar{x}$)	Resp. (dpm mL^{-1}) $\bar{x}$	S.D. ($\bar{x}$)	Excre. (dpm mL^{-1}) $\bar{x}$	S.D. ($\bar{x}$)				Resp. (dpm animals^{-1})	Excre. (dpm animal^{-1})	Resp.	Excre.
2.0	66.145	0.706	2.423	1.13	0.488 (73)	0.196	62.240	0.522	2.053	0.741	75.99	90.2	0 no sig. diff.	---	---	0%	0%
4.0	162.4	2.21	4.928	0.233	0.670 (61.5)	0.07	165.0	4.83	5.99	0.441	74.24	87.5	16.9% decline	---	0.004	0%	1%
											228.6	73.3					
											216.6	78.9					

excretion accounted for high losses relative to animal acti-
vity over the holding times.

The extremely high activities recorded as both
excretion and respiration are difficult to explain. Con-
siderable research is still required to understand the
various pathways of radio tracers in living systems.

2. 'Before feeding' experiments

In contrast to results found 'after feeding' (Tables
B2, B3, B4), the contributions of both respiration and ex-
cretion as a percentage of animal activity was insignificant
(Table B5), suggesting that these metabolic pools may not
be of major concern during the feeding period of the experi-
ment. An independent measurement of total inorganic and
organic carbon accounted for approximately 75% in the 2.0 h
test and 76% in the 4 h test of the respired and excreted
activities. These results verify to some extent that the
proportion of excretion to respiration was reasonably
accurate.

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APPENDIX C

NUMERICAL ABUNDANCE AT STATIONS 2, 3, 4 AND 5

DURING 1972

Appendix C. Numerical abundance at stations 2, 3, 4 and 5 during 1972.
Table C1. Numerical abundance at station 2 during 1972.

						STAGE ABUNDANCE (no. ind.m^{-2})									
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
May 17	16146	1932	0	2794	12382	93787	129041	34690	16627	5658[1]	35380	25590	53626 8176	180047	307088
24	105514	34830	8625	6831	12556	56143	224499	16422	11661	15111[1]	68070	73031	90961 6003	281259	505758
30	14352	44205	86557	18837	14421	11454	189826	15870	56205	16006[1]	24690	79028	97031 12144	300974	490800
Jun 6	9452	10073	23625	80103	33339	15964	172356	8072	30553	20446[1]	11177	73179	72140 10764	224329	396685
13	4899	6382	8797	18207	36302	268265	342852	15553	3795	28864[1]	30103	15796	71657 36476	202244	545096
20	0	1413	6226	9910	13898	69863	101110	44528	3741	6761[1]	50132	9867	47478 23687	186194	287304
27	0	2397	6467	9522	12678	42846	73910	38394	8073	3880[2]	26588	5386	31200 15106	128627	202537
Jul 3	0	1345	6692	12932	15623	38342	94934	62240	33680	10042[2]	23275	5589	27828 24861	187515	262449
11	138	1449	6037	8728	11247	18554	46153	12314	26761	6244	9521	4553	15766 8314	83473	129626
18	6796	4829	8797	14283	20281	31208	86194	7451	10349	23481	5727	7831	19586 9901	84326	170520
25	5398	5621	9570	14350	19421	38031	92391	5451	9555	15899	4377	7279	13920 5187	59668	152059

Appendix C. Numerical abundance at stations 2, 3, 4 and 5 during 1972.
Table C1. Numerical abundance at station 2 during 1972.

	STAGE ABUNDANCE (no. ind.m^{-2})														
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
Aug 1	7361	7847	8311	10522	20616	32911	87568	4724	4722	9778	4327	5451	10830 1307	41139	1287C
8	11290	10847	10483	11569	16346	29975	90480	7051	4138	5568	7929	5133	12035 3170	45024	1355C
15	3346	3706	6351	7675	14832	32494	68404	4740	3415	2979	2928	1583	7450 1206	24301	927C
29	1531	2134	3602	5655	10101	21046	44069	5808	6378	9569	2044	1356	7537 789	33481	7755
Oct 14	0	0	0	0	0	0	0	0	1000	6555	49240	14966	1449 552	73762	737(

						STAGE ABUNDANCE (no. ind.m^{-2})									
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
Jun 20	0	1827	3657	7501	15472	58826	87583	29826	4949	2795	39395	4209	32827 7797	121798	209381
Jul 3	0	1759	2691	6831	11246	34997	57524	38686	15690	4033	15103	2585	10000 6038	92135	149659
18	4311	2587	4603	6141	12570	22686	52898	2222	3017	8166	3222	3225	6275 3310	29437	82335
Aug 15	1414	2138	4165	7174	9503	30358	54752	7588	4353	4453	2598	759	7269 1449	28469	83221
29	808	1396	2237	3289	5241	18239	31210	3223	3773	6237	1653	308	1360 138	16692	47902

Appendix C. Numerical abundance at stations 2, 3, 4 and 5 during 1972.
Table C3. Numerical abundance at station 4 during 1972.

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
							STAGE ABUNDANCE (no. ind.m^{-2})								
May 30	2967	8480	20276	2829	1863	1863	38278	3312	18070	3036	6690	10481	19656 2484	63729	102007
Jun 13	725	1173	1311	2519	5243	19208	30179	1173	862	2346	3345	690	2827 655	8416	38595
27	0	725	1000	1621	3449	13723	20518	11653	2279	966	3862	103	655 207	19724	40242
Jul 11	0	862	1000	1276	2173	7929	13240	3554	8550	828	2173	725	2173 828	18831	32071
25	566	551	704	1016	2325	5258	10420	723	723	2068	533	533	656 207	5443	15863
Aug 8	1912	1811	1828	2069	2532	4397	14549	1000	758	947	1534	242	413 104	4998	19547
22	447	552	861	1345	2672	8674	11551	913	1395	4629	464	119	103 0	7623	19174

STAGE ABUNDANCE (no. ind.m^{-2})

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ / C6-♀	Total Copepodids	Total
May 17	14826	4002	2691	5382	14691	52552	94144	17031	3657	4485	22753	15449	43244 / 8349	114968	209112
Jun 13	5244	6072	8073	10485	17927	53314	101115	7314	4071	15313	21962	5727	38484 / 17449	110320	211435
27	0	1380	4830	8142	16759	58618	89729	51998	7452	3174	17380	5175	34208 / 5175	124562	214291
Jul 3	0	931	2449	4899	8483	23548	40310	39930	7728	4312	10966	3036	17860 / 10342	94174	134484
25	2966	2001	2553	4381	10692	26548	49141	4588	2967	13418	4036	5140	13413 / 5586	49148	98289
Aug 8	5831	6417	6935	7832	10450	24654	62119	4554	2346	1552	2967	1138	10170 / 2346	25073	87192
22	1656	1965	3362	6260	9433	24496	49172	3105	4000	5002	1189	794	1587 / 207	15884	63056
Dec 16	0	0	0	0	0	0	0	0	0	517	2519	4623	6003 / 8795	22457	22457
Feb 20	36791	7452	2519	1207	3243	12417	63629	241	0	0	1173	1774	2726 / 0	5934	69563
Mar 24	1069	1586	3830	11241	2345	4899	24970	724	0	0	1483	3312	6003 / 0	11522	36492

APPENDIX D

NUMERICAL ABUNDANCE AT STATIONS 2, 3, 4 AND 5

DURING 1974

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
May 22	73939	46690	26810	18567	20964	24347	211317	52298	256024	83433	24564	13175	5080 61950	496524	707841
25	101252	91508	51030	18690	15247	16036	293963	54823	275998	226138	73652	18949	5172 40615	695347	989110
28	107193	190827	136620	20555	15314	23660	494149	34688	154479	231034	60754	20650	2098 35344	539847	1033996
31	93244	109783	148026	41340	10764	15046	418197	19868	118000	208552	84064	23376	5037 56655	515552	933749
Jun 2	25723	84758	164412	812759	29040	25835	512527	13731	57034	142278	270552	28103	2760 32969	542427	1054954
4	10350	17887	58418	147796	30356	13798	278605	17319	34208	114000	267236	29035	414 16353	478565	757170
7	19036	34277	100685	172272	164829	76588	567687	14973	28416	68897	292345	47461	2898 17043	472033	1039720
9	11834	9074	18242	27245	38140	132071	236606	20268	12696	28552	172034	23423	4140 16560	277673	514279
12	10281	14145	43307	61378	93865	149103	372079	115930	34070	27870	168691	19590	6348 13312	385811	757890
15	12765	14559	44686	45999	55515	110070	283594	124622	36413	16076	114693	52828	11178 16974	372784	656378
18	5934	10799	29728	32249	46557	94899	220166	164905	45833	18345	57311	47935	8177 12070	357576	577742
21	1173	6762	24559	31452	35797	57793	157536	100481	52897	16005	74139	42687	5568 6693	298560	456096
23	6503	15821	49940	63191	62188	90759	288402	111828	76076	27826	64119	55386	3006 11131	359354	647756

STAGE ABUNDANCE (no. ind.m^{-2})

Appendix C. Numerical abundance at stations 2, 3, 4, and 5 during 1974.
Table C1. Numerical abundance at station 2 during 1974.

| | | | | | | | | | | | | | C6-♂ | Total | |
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♀	Copepodids	Total
Jun 25	14938	21125	38438	77750	81125	106000	339376	55000	125750	23250	122374	101375	5875 / 8500	442124	781500
28	18125	19875	35313	49438	60750	77313	260814	61315	92875	20188	20315	39250	16875 / 4875	255691	516505
Jul 2	5379	11414	22690	27793	36207	81345	184828	26759	50866	14000	18138	11862	6966 / 4276	132967	317795
4	104	1415	7935	13145	26970	65619	115188	28344	53549	29660	39728	27798	18418 / 16867	214364	329552
7	0	0	6072	22801	51621	118685	199179	28933	70415	44594	34826	26688	21446 / 17107	244009	443188
14	7349	7970	21898	35039	45410	79173	196839	18212	27792	23481	17038	17004	16831 / 15034	135392	332231
19	2622	3450	17587	33552	47348	101036	205595	11106	27558	29485	17316	11730	22064 / 9039	128298	333893
23	5969	2105	18967	30386	41482	56686	155595	29090	22656	34347	20692	23932	18073 / 19795	168585	324180
26	17799	17455	24588	32901	36484	48098	177325	15177	24728	33381	18443	20210	16280 / 30479	158698	336023
29	13076	17452	20662	21045	32207	51726	156168	10496	19278	37141	12417	5589	6969 / 15794	107684	263852
Aug 2	19454	18354	34552	40206	16077	21179	149822	8798	13488	39589	18561	9108	11243 / 26553	127340	277162
6	5796	5900	16039	44207	19971	16353	108266	4347	4175	21284	13697	7176	5796 / 26967	83442	191708
9	30451	22338	18504	12368	12248	18216	114125	4002	6072	9798	8763	8691	3450 / 21171	61947	176072

STAGE ABUNDANCE (no. ind.m^{-2})

Table D3. Numerical abundance at station 4 during 1974.

						STAGE ABUNDANCE (no. ind.m^{-2})									
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
May 22	43036	22760	9448	5037	3864	3864	88009	16828	46484	15172	6899	4347	1035 7656	98421	186430
Jun 4	3519	5864	13171	39863	9174	6003	77594	2967	3588	14206	37173	8001	207 4761	70903	148497
18	1932	3105	3105	4761	5933	13312	32148	30207	5658	3795	11654	4002	759 2484	58559	90707
Jul 2	2314	2252	3657	4907	7439	18096	38665	12971	22376	5002	2407	2625	1250 2689	49320	87985
16	965	861	1345	1601	2777	6671	14220	5070	2880	2103	724	414	68 482	11741	25961
30	2001	2223	2604	3104	4121	7483	21536	3259	2948	5657	2484	1139	671 1172	17330	38866
Aug 13	2413	2324	3274	6434	4293	9294	28032	1552	1069	1033	2173	310	34 517	6686	34720
29	792	861	1963	2739	3514	7000	16869	861	567	1222	463	291	0 379	3783	20652

(Continued)

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
Aug 16	18004	15594	14076	10937	13904	47650	120165	7349	3761	4071	5210	6452	1794 10621	39258	159423
23	17725	21106	14490	19587	18556	46825	138289	16937	8625	5037	10592	3657	2484 19105	66437	204726
Sept 1	12558	10592	11937	13386	14835	28898	92206	22999	15353	7556	6417	2588	1794 0	56707	148913
Oct 19	0	0	2864	6210	9591	11903	30568	3622	4520	7004	74451	12246	1035 414	103292	133860

STAGE ABUNDANCE (no. ind.m^{-2})

Appendix D. Numerical abundance at stations 2, 3, 4, and 5 during 1974.
Table D3. Numerical abundance at station 4 during 1974.

								STAGE ABUNDANCE (no. ind.m^{-2})							
Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
May 22	43036	22760	9448	5037	3864	3864	88009	16828	46484	15172	6899	4347	1035 7656	98421	186430
Jun 4	3519	5864	13171	39863	9174	6003	77594	2967	3588	14206	37173	8001	207 4761	70903	148497
18	1932	3105	3105	4761	5933	13312	32148	30207	5658	3795	11654	4002	759 2484	58559	90707
Jul 2	2314	2252	3657	4907	7439	18096	38665	12971	22376	5002	2407	2625	1250 2689	49320	87985
16	965	861	1345	1601	2777	6671	14220	5070	2880	2103	724	414	68 482	11741	25961
30	2001	2223	2604	3104	4121	7483	21536	3259	2948	5657	2484	1139	671 1172	17330	38866
Aug 13	2413	2324	3274	6434	4293	9294	28032	1552	1069	1033	2173	310	34 517	6686	34720
29	792	861	1963	2739	3514	7000	16869	861	567	1222	463	291	0 379	3783	20652

Appendix D. Numerical abundance at stations 2, 3, 4, and 5 during 1974.
Table D4. Numerical abundance at station 5 during 1974, 1975.

STAGE ABUNDANCE (no. ind.m^{-2})

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
May 16	0	0	0	0	2553	12417	14970	56967	95379	7093	3864	6935	3485 21205	194908	209878
Jun 4	3519	5244	9453	35928	8763	4485	67392	5244	8556	18001	100965	19633	0 12351	164750	232142
22	44275	19654	9108	5589	3657	4298	86561	33793	118829	22346	11040	5382	3726 25656	220772	307333
Ju 18	2243	3726	6521	9759	21382	86967	130598	47133	10764	5141	17863	16311	2933 7452	107597	238195
Jul 2	2938	5438	8688	14188	23313	59963	114528	13063	21500	8563	8500	7250	9625 6625	75126	189654
16	690	1139	3968	6245	8832	21036	41910	5865	3174	6555	4037	3347	6797 5003	34778	76688
Jul 29	3588	2312	3519	5417	8487	23035	46358	3864	2622	5451	2864	656	1035 4275	20767	67125
Aug 13	8177	9281	7107	13243	8556	10040	56504	1070	690	2174	5966	1001	4482 9689	25072	81576
23	7349	6314	6314	9137	8315	22375	62535	8177	2519	1070	1725	207	0 966	14664	77199
Dec 16	0	0	0	0	0	621[3]	621	380[3]	1208[3]	863[3]	7176[3]	19587[3]	45239 37549	112002	112623

Appendix D. Numerical abundance at stations 2, 3, 4 and 5 during 1974.
Table D4.   Numerical abundance at station 5 during 1974, 1975.

STAGE ABUNDANCE (no. ind.m^{-2})

Date	N1	N2	N3	N4	N5	N6	Total Nauplii	C1	C2	C3	C4	C5	C6-♂ C6-♀	Total Copepodids	Total
Jan 28	48312	2967	863	138	138	8177	60595	1070	242	587	5037	9348	8073 33933	58290	118885
Feb 19	17523	31308	64001	7105	3312	6243	129492	2139	966	0	4244	8658	2243 24311	42561	172053
Apr 3	836	2734	7698	47368	15298	5103	79037	483	0	0	0	2964	5901 2600	12148	91185

APPENDIX E

FECUNDITY AND EGG SIZE OF <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u>

DURING 1972 AND 1974

Table E1. 1972 Cohort 2 (May 24 - June 6).

Fecundity (no. eggs/female)	Egg size (μ)			
33	82.35	81.93	80.04	80.04
27	80.88	80.46	79.83	82.56
42	83.61	83.19	82.35	79.41
46	83.19	81.17	82.98	80.46
41	80.25	82.35	77.94	80.46
34	85.08	83.19	81.09	82.98
46	81.09	81.09	77.94	80.67
37	85.92	80.46	84.24	78.15
45	82.98	83.82	81.72	80.67
36	81.72	81.51	79.83	78.57
41	81.51	80.67	78.15	79.62
44	84.87	82.35	79.41	79.62
45	83.61	81.30	80.67	80.04
34	83.19	85.08	79.41	
47	83.61	83.40	81.55	
44	85.92	81.51	83.40	
36	80.88	82.98	82.14	
36	85.08	83.82	85.29	
33	84.24	80.67	81.30	
37	83.61	82.56	84.66	
	81.09	79.83	82.97	
	80.25	80.46	81.09	
	82.19	79.41	81.09	
	82.56	80.88	83.40	
	84.24	80.67	80.67	
	83.40	79.62	79.41	
	84.24	80.04	81.51	
	83.61	81.51	82.35	
	81.09	82.98	80.46	
	80.67	80.25	85.29	
	79.62	82.35	84.03	
	80.45	79.41	82.14	

Table E2. 1974 Cohort 1 (January - February).

Fecundity (no. eggs/female)	Egg size (µ)		
26	89.70	94.75	82.98
25	89.70	92.65	83.19
29	87.18	85.71	82.35
24	92.86	91.39	87.18
24	89.07	88.02	91.60
20	89.07	89.29	90.34
22	90.55	86.55	93.49
24	92.65	86.13	90.55
28	93.91	88.65	89.92
25	91.81	86.76	91.60
30	89.28	94.75	87.81
29	91.39	89.29	85.92
31	86.13	93.38	87.18
25	85.92	90.13	89.08
24	85.08	90.55	89.50
27	88.23	92.86	88.49
30	82.98	90.55	85.71
26	88.23	94.75	86.13
29	91.39	89.29	86.34
	89.07	90.02	86.98
	85.71	89.92	84.21
	86.55	95.80	85.50
	84.03	92.44	89.50
	88.65	90.97	89.08
	84.50	92.49	90.75
	91.39	90.76	86.55
	89.50	94.33	88.65
	90.34	89.29	87.81
	89.29	85.08	85.92
	88.02	86.55	85.08
	87.18	86.76	86.55
	91.55	87.18	88.02
	94.96	91.39	86.97
	91.60	88.23	83.40
	91.81	83.61	

Table E3.   1974 Cohort 2 (May 31 - June 6).

Fecundity (no. eggs/female)	Egg size (μ)			
50	79.20	75.84	77.52	78.36
47	77.94	75.63	75.63	80.88
47	77.31	76.26	76.05	81.30
66	79.83	80.46	74.58	80.88
48	75.63	80.04	80.88	77.52
64	77.94	77.10	78.99	79.83
47	78.36	79.20	79.83	78.78
53	76.47	80.46	79.83	81.53
47	76.89	79.83	77.73	80.88
49	78.36	80.67	77.52	79.83
52	79.24	80.46	78.36	80.88
52	79.41	82.35	80.25	80.46
58	38.57	81.09	76.89	80.88
46	80.25	79.83	75.84	78.78
71	78.15	79.83	75.42	81.53
55	81.93	76.47	76.47	
51	80.88	78.78	76.47	
46	80.67	80.04	77.81	
45	79.41	79.41	75.21	
47	76.05	80.67	76.89	
54	80.04	76.89	76.26	
49	76.89	76.05	74.58	
	80.25	76.10	76.89	
	77.94	75.21	76.68	
	76.81	77.94	74.16	
	78.99	78.15	75.63	
	82.98	79.62	75.84	
	80.46	77.10	76.26	
	76.89	78.15	80.25	
	76.26	80.46	79.41	
	77.52	77.94	81.93	
	76.05	76.26	80.67	
	75.00	73.95	79.62	
	75.21	75.84	78.57	

Table E4. 1974 Cohort 3 (August).

Fecundity (no. eggs/female)	Egg size (μ)			
	84.03	86.13	83.61	84.87
39	86.55	86.67	84.03	82.35
32	85.71	83.40	85.29	82.56
33	83.40	84.24	82.56	80.67
34	84.87	84.45	82.98	83.61
40	85.08	85.08	81.93	83.40
36	81.51	87.18	84.45	80.88
28	80.46	83.40	85.92	85.08
29	80.88	84.24	83.82	84.03
28	79.20	82.56	83.82	85.92
32	80.04	87.60	85.92	85.71
30	80.88	87.60	96.13	83.19
31	84.66	86.34	81.30	81.09
30	81.72	83.40	83.82	
39	83.82	83.19	82.77	
40	81.30	81.09	84.87	
34	84.66	85.08	83.61	
30	81.30	80.88	84.24	
40	83.61	82.56	82.14	
30	85.92	87.18	82.77	
38	80.04	84.87	85.71	
34	82.14	85.50	86.13	
	84.66	81.93	80.88	
	85.29	82.35	81.97	
	84.92	83.82	82.98	
	84.24	85.92	81.09	
	81.50	81.09	85.71	
	85.50	87.18	85.50	
	84.45	86.34	81.93	
	85.29	83.40	80.88	
	87.60	84.03	83.40	
	83.40	80.46	81.72	
	85.92	82.56	85.71	
	81.09	80.46	85.29	
	83.19	82.56	83.40	

APPENDIX F

MEAN LENGTHS, CARBON AND NITROGEN CONTENTS

OF <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u>

Table F1. Mean lengths of _Diacyclops bicuspidatus_

Stage	Length $\bar{\chi}$ (μ)	S.D. $(\bar{\chi})$	S.E. $(\bar{\chi})$
N1	110.849	4.127	1.103
N2	137.927	6.356	1.640
N3	161.890	5.060	1.600
N4	178.853	5.560	
N5	206.779	6.770	
N6	232.988	9.118	2.279

	Total	Metasomal (μ)	Total	Metasomal (μ)	Total	Metasomal (μ)
C1	394.406	287.508	13.579	12.04	3.036	2.693
C2	491.483	358.220	14.950	18.010	3.343	4.028
C3	758.217	467.326	25.900	18.370	5.790	4.108
C4	910.098	560.490	38.065	21.890		5.020
C5	1096.489	668.950	57.056	46.860		9.990
C6	1081.292	647.818	45.411	32.255		7.212
C6	1315.693	761.050	64.72	57.420	12.455	11.050

Table F2. Mean carbon and nitrogen values of Diacyclops bicuspidatus

Stage	Carbon (μg C ind^{-1})			Nitrogen (μg N ind^{-1})		
	$\overline{\chi}$	S.D. $(\overline{\chi})$	S.E. $(\overline{\chi})$	$\overline{\chi}$	S.D. $(\overline{\chi})$	S.E. $(\overline{\chi})$
egg	0.0267	0.0676	0.0034	0.0040	0.0012	0.00056
N6	0.1203	0.0510	0.0290	0.0301	0.0178	0.0103
C2	0.5791	0.0876	0.0438	0.1248	0.0263	0.0132
C3	0.8560	0.0070	0.0840	0.2321		
C4	1.5974	0.7733	0.3458	0.3422	0.1420	0.0635
C5	2.2390	0.2172	0.1086	0.7690	0.0687	0.0396
C6	2.5680	0.1050	0.3240	-	-	-

APPENDIX G

DEPTH WEIGHTED MEANS OF <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u>

DURING THE VERTICAL MIGRATION PERIODS

Appendix G. Depth weighted means of <u>Cyclops bicuspidatus</u> during the vertical migration periods.

Table G1. May 28-29

| | NAUPLIAR STAGES | | | | | | | | | | | |
| | N1 | | N2 | | N3 | | N4 | | N5 | | N6 | |
Hour	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)
10:00	9.3	5.1	10.0	5.0	9.4	5.1	12.4	5.0	10.0	5.0	12.0	5.0
14:00	9.1	5.1	10.6	5.0	10.9	5.0	12.5	5.0	11.7	5.0	11.1	5.0
18:00	7.5	5.1	9.1	5.1	9.2	5.1	8.8	5.1	7.7	5.1	11.5	5.0
22:00	8.4	5.1	7.4	5.1	6.6	5.1	7.5	5.1	9.5	5.0	7.7	5.1
02:00	11.9	5.0	---	---	10.7	5.0	10.8	5.0	9.4	5.1	9.1	5.1
06:00	10.9	5.0	10.0	5.0	10.9	5.0	11.4	5.0	9.0	5.1	10.6	5.0
10:00	9.7	5.0	7.7	5.1	7.0	5.1	11.7	5.0	9.3	5.1	10.8	5.0
$\bar{x}$	9.5	5.1	9.1	5.0	9.2	5.1	10.7	5.0	9.5	5.1	10.4	5.0
S.E.(x)	0.560	0.02	0.54	0.02	0.68	0.02	0.71	0.02	0.45	0.02	0.56	0.02

Appendix G. Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G1. May 28-29

| | COPEPODID STAGES | | | | | | | | | | | | | | | | | | | | |
| | C1 | | | C2 | | | C3 | | | C4 | | | C5 | | | C6 ♀ | | | Egg | |
Hour	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm⁻³)	Depth (m)	Temp. (°C)
10:00	12.2	5.0	432.54	10.8	5.0	488.61	13.5	5.0	404.09	15.3	5.0	364.68	13.5	5.0	404.09	10.0	5.0	523.07	11.6	5.0
14:00	12.9	5.0	417.22	11.4	5.0	462.77	11.7	5.0	449.84	9.8	5.0	531.69	11.3	5.0	467.08	11.7	5.0	449.84	11.0	5.0
18:00	8.3	5.1	596.30	9.8	5.0	531.69	9.6	5.0	540.30	11.7	5.0	449.84	12.5	5.0	425.97	9.5	5.0	544.61	7.1	5.1
22:00	9.6	5.0	540.30	10.2	5.0	514.46	10.7	5.0	492.92	11.0	5.0	480.00	10.1	5.0	518.76	10.6	5.0	497.23	7.3	5.1
02:00	10.7	5.0	492.92	11.5	5.0	458.46	13.8	5.0	397.52	13.1	5.0	412.84	13.4	5.0	406.27	11.7	5.0	449.84	8.0	5.1
06:00	12.0	5.0	436.92	12.0	5.0	436.92	13.0	5.0	415.03	12.5	5.0	425.97	11.8	5.0	445.54	11.8	5.0	445.54	15.3	5.0
10:00	9.8	5.0	531.69	10.4	5.0	505.84	10.6	5.0	497.23	10.6	5.0	497.23	12.4	5.0	428.16	9.1	5.1	561.84	6.3	5.5
$\bar{x}$	10.8	5.0	492.55	10.9	5.0	485.54	11.8	5.0	456.70	12.0	5.0	451.75	12.14	5.0	442.27	10.6	5.0	496.00	9.5	5.1
S.E.(x)	0.63	0.01	25.33	0.30	0	12.91	0.61	0	20.70	0.69	0	21.28	0.45	0	15.19	0.43	0.01	18.41	1.23	0.07

Appendix G. Depth weighted means of <u>Cyclops bicuspidatus</u> during the vertical migration periods.

Table G2. June 11-12

| | NAUPLIAR STAGES | | | | | | | | | | | |
| Hour | N1 | | N2 | | N3 | | N4 | | N5 | | N6 | |
	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)
10:00	13.3	6.4	12.7	6.6	12.1	6.8	11.2	7.0	12.7	6.6	10.1	7.0
12:00	14.2	6.2	13.6	6.3	14.7	6.0	14.5	6.1	13.5	6.4	14.1	6.2
14:00	11.5	6.9	11.5	6.9	12.8	6.6	12.8	6.6	12.0	6.9	11.3	7.0
16:00	16.6	5.7	15.6	5.9	15.3	6.0	14.7	6.0	14.8	6.0	14.4	6.2
18:00	16.8	5.6	17.5	5.3	18.1	5.2	17.1	5.5	15.0	6.0	12.8	6.6
20:00	13.6	6.3	14.4	6.2	15.2	6.0	15.8	5.9	14.8	6.0	13.1	6.4
22:00	16.1	5.9	15.3	6.0	15.4	6.0	15.0	6.0	14.4	6.2	13.3	6.4
24:00	17.7	5.3	15.7	5.9	17.7	5.3	16.0	5.9	15.2	6.0	13.8	6.3
02:00	10.2	7.0	9.7	7.1	10.2	7.0	11.1	7.0	11.2	7.0	9.3	7.3
04:00	11.2	7.0	11.7	6.9	11.4	7.0	12.3	6.7	12.2	6.7	11.7	6.9
06:00	14.6	6.0	14.2	6.2	15.3	6.0	14.9	6.0	14.6	6.0	13.5	6.4
08:00	14.9	6.0	15.3	6.0	15.4	6.0	15.3	6.0	14.7	6.0	14.7	6.0
10:00	13.8	6.3	12.0	6.8	13.3	6.4	13.5	6.4	12.1	6.8	11.4	7.0
$\bar{x}$	14.2	6.2	13.8	6.3	14.4	6.2	14.7	6.2	13.6	6.3	12.6	6.6
S.E.(x)	0.63	0.15	0.60	0.14	0.64	0.16	0.52	0.13	0.39	0.11	0.47	0.11

Appendix G. Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G2.   June 11 - 12

Hour	C1 Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	C2 Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	C3 Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	C4 Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	C5 Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	C6 ♀ Depth (m)	Temp. (°C)	Part. (mgCm⁻³)	Egg Depth (m)	Temp. (°C)
									COPEPODID STAGES											
10:00	10.9	7.0	422.25	13.5	6.4	387.08	14.1	6.2	364.50	15.0	6.0	330.64	14.8	6.0	338.16	19.9	5.0	293.80	20	5.0
12:00	12.7	6.6	417.19	14.7	6.0	341.93	14.8	6.0	338.16	18.0	5.2	268.42	18.0	5.2	268.42	18.5	5.2	274.94	---	---
14:00	11.2	7.0	428.05	10.1	7.0	406.77	11.3	7.0	429.98	13.1	6.4	402.14	13.7	6.3	379.55	14.0	6.2	368.26	12.6	6.6
16:00	10.4	7.0	412.58	10.2	7.0	408.71	11.8	6.9	439.65	19.5	5.1	287.98	20.1	5.0	294.34	18.4	5.2	273.64	20.4	5.0
18:00	10.9	7.0	422.25	14.0	6.2	368.24	17.8	5.3	265.81	20.9	5.0	293.08	18.1	5.2	269.72	18.6	5.1	276.24	19.3	5.1
20:00	13.4	6.4	390.84	15.8	5.9	300.54	12.2	6.7	436.00	15.4	6.0	315.59	13.4	6.4	390.84	20.7	5.0	293.39	14.0	6.2
22:00	12.5	6.6	424.71	11.0	7.0	424.18	14.9	6.0	334.40	16.0	5.9	293.01	21.6	5.0	291.97	22.3	5.0	290.86	17.0	5.5
24:00	14.4	6.2	353.21	17.0	5.5	255.38	12.5	6.6	424.71	15.3	6.0	319.35	14.8	6.0	338.16	15.7	5.9	304.30	23.0	5.0
02:00	8.4	7.8	373.89	11.0	7.0	424.18	10.6	7.0	416.44	15.7	5.9	304.30	13.1	6.4	390.84	11.6	5.9	435.78	12.2	6.7
04:00	10.0	7.0	404.84	10.2	7.0	408.71	10.0	7.0	404.84	14.8	6.0	338.16	13.6	6.3	383.32	18.0	5.2	268.42	18.0	5.2
06:00	10.8	7.0	420.31	12.1	6.8	439.76	12.6	6.6	420.95	17.1	5.5	226.68	18.2	5.2	271.03	19.1	5.1	282.76	17.0	5.5
08:00	11.1	7.0	426.11	9.6	7.2	397.10	13.3	6.4	394.61	17.6	5.3	263.20	18.5	5.2	274.94	18.0	5.2	268.42	15.5	6.0
10:00	8.5	7.7	345.82	9.0	7.4	385.49	9.1	7.4	387.42	14.8	6.0	338.16	12.6	6.6	420.95	13.4	6.4	390.84	7.3	9.0
x̄	11.2	6.9	403.23	12.17	6.6	380.62	12.69	6.5	389.04	16.40	5.7	306.21	16.2	5.7	331.71	17.55	5.4	309.31	16.36	5.9
S.E.(x)	0.48	0.12	7.89	0.71	0.16	14.68	0.65	0.15	14.13	0.59	0.12	12.00	0.83	0.17	15.55	0.85	0.14	14.90	1.25	0.33

Appendix G.   Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G3.   July 19-20

| | NAUPLIAR STAGES | | | | | | | | | | | |
| | N1 | | N2 | | N3 | | N4 | | N5 | | N6 | |
Hour	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)
10:00	15.9	5.3	15.7	5.4	15.3	5.4	13.5	5.9	13.5	5.9	15.5	5.4
12:00	24.0	4.5	25.5	4.4	----	---	16.0	5.3	16.3	5.2	15.5	5.4
14:00	20.2	4.7	17.8	4.9	11.0	6.6	10.3	6.7	13.7	5.9	15.9	5.3
16:00	22.1	4.6	22.5	4.6	----	---	15.8	5.3	13.2	6.0	16.7	5.1
18:00	20.4	4.7	22.5	4.6	----	---	17.4	5.0	14.1	5.8	15.4	5.4
20:00	18.0	4.9	----	---	----	---	13.2	6.0	14.3	5.7	16.0	5.3
22:00	18.7	4.8	16.5	5.1	14.5	5.7	14.9	5.5	16.4	5.2	17.2	5.0
24:00	16.5	5.1	15.9	5.3	11.0	6.6	13.5	5.9	13.4	5.9	13.8	5.8
02:00	13.5	5.9	10.0	6.9	13.3	5.9	12.3	6.2	12.1	6.3	10.4	6.8
04:00	19.2	4.8	----	----	----	----	15.4	5.4	10.8	6.7	16.6	5.1
06:00	18.1	4.9	15.5	5.4	14.9	5.5	15.0	5.5	14.1	5.8	15.8	5.3
08:00	22.4	4.6	----	----	----	----	19.6	4.7	12.9	6.0	15.6	5.4
x̄	19.08	4.9	18.0	5.2	13.33	5.9	14.74	5.6	13.73	5.9	15.37	5.4
S.E.(x)	0.86	0.11	1.58	0.25	0.79	0.22	0.70	0.15	0.45	0.12	0.51	0.14

Appendix G. Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G3. July 19-20

					NAUPLIAR STAGES						
	N1		N2		N3		N4		N5		N6	
Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)
15.9	5.3	15.7	5.4	15.3	5.4	13.5	5.9	13.5	5.9	15.5	5.4
24.0	4.5	25.5	4.4	----	---	16.0	5.3	16.3	5.2	15.5	5.4
20.2	4.7	17.8	4.9	11.0	6.6	10.3	6.7	13.7	5.9	15.9	5.3
22.1	4.6	22.5	4.6	----	---	15.8	5.3	13.2	6.0	16.7	5.1
20.4	4.7	22.5	4.6	----	---	17.4	5.0	14.1	5.8	15.4	5.4
18.0	4.9	----	---	----	---	13.2	6.0	14.3	5.7	16.0	5.3
18.7	4.8	16.5	5.1	14.5	5.7	14.9	5.5	16.4	5.2	17.2	5.0
16.5	5.1	15.9	5.3	11.0	6.6	13.5	5.9	13.4	5.9	13.8	5.8
13.5	5.9	10.0	6.9	13.3	5.9	12.3	6.2	12.1	6.3	10.4	6.8
19.2	4.8	----	----	----	----	15.4	5.4	10.8	6.7	16.6	5.1
18.1	4.9	15.5	5.4	14.9	5.5	15.0	5.5	14.1	5.8	15.8	5.3
22.4	4.6	----	----	----	----	19.6	4.7	12.9	6.0	15.6	5.4
19.08	4.9	18.0	5.2	13.33	5.9	14.74	5.6	13.73	5.9	15.37	5.4
0.86	0.11	1.58	0.25	0.79	0.22	0.70	0.15	0.45	0.12	0.51	0.14

Appendix G. Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G3. July 19 - 20

	COPEPODID STAGES																				
Hour	C1			C2			C3			C4			C5			C6 ♀			Egg	
	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{C}$ (mgCm^{-3})	Depth (m)	Temp. (°C)
10:00	6.9	9.4	448.59	7.2	8.8	445.60	8.3	7.6	416.42	13.3	5.9	295.06	17.8	4.9	204.66	19.9	4.7	141.03	17.2	5.0
12:00	8.0	7.8	424.38	7.9	7.9	427.03	12.3	6.2	312.94	22.3	4.6	171.30	16.4	5.2	239.63	23.4	4.5	187.23	22.9	4.5
14:00	10.2	6.8	366.04	6.5	11.0	439.36	12.9	6.0	302.21	14.6	5.6	271.81	18.9	4.7	171.33	26.5	4.4	255.28	22.3	4.6
16:00	6.1	13.0	430.13	7.9	7.9	427.03	10.9	6.6	347.47	18.5	4.9	183.45	21.6	4.6	161.17	24.9	4.4	208.95	23.3	4.5
18:00	5.9	13.5	425.51	8.3	7.6	416.42	11.8	6.4	323.60	18.1	4.9	195.57	21.5	4.6	159.72	23.8	4.4	193.02	20.2	4.7
20:00	5.6	15.6	418.59	8.3	7.6	416.42	13.8	5.8	286.12	16.8	5.1	232.48	21.2	4.6	155.38	19.7	4.7	147.09	18.4	4.9
22:00	9.4	7.1	387.25	9.6	7.0	381.95	12.1	6.3	316.51	14.4	5.7	275.39	14.7	5.6	270.02	15.2	5.5	261.08	13.7	5.9
24:00	11.5	6.5	331.56	9.2	7.1	392.56	12.5	6.2	309.36	16.2	5.2	243.20	13.1	6.0	298.63	14.3	5.7	277.18	14.4	5.7
02:00	5.7	14.6	420.90	6.4	11.4	437.05	6.8	9.8	446.28	12.5	6.2	309.36	15.1	5.5	262.87	17.6	4.9	210.72	18.2	4.9
04:00	7.5	8.4	437.64	7.6	8.3	435.00	11.2	6.5	339.52	22.6	4.5	175.65	24.2	4.5	198.82	16.6	5.1	236.05	----	----
06:00	8.1	7.7	421.73	10.0	6.9	371.34	13.3	5.9	295.06	14.6	5.6	271.81	19.5	4.7	153.15	21.7	4.6	162.62	21.6	4.6
08:00	3.8	20.5	377.06	6.0	13.0	427.82	14.3	5.7	277.18	22.6	4.5	175.65	23.3	4.5	185.78	24.2	4.4	198.82	20.7	4.6
$\bar{x}$	7.4	10.9	407.45	7.91	8.7	418.3	11.7	6.6	331.05	17.2	5.2	233.39	18.9	4.9	205.10	20.6	4.8	206.59	19.3	4.9
S.E.($\bar{x}$)	0.63	1.28	9.94	0.37	0.59	6.88	0.63	0.33	14.83	1.05	0.16	14.78	1.03	0.14	14.62	1.17	0.13	12.79	0.99	0.14

Appendix G. Depth weighted means of <u>Cyclops bicuspidatus</u> during the vertical migration periods.

Table G4. August 16-17

| | NAUPLIAR STAGES | | | | | | | | | | | |
| | N1 | | N2 | | N3 | | N4 | | N5 | | N6 | |
Hour	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)	Depth (m)	Temp. (°C)
10:00	17.6	4.8	15.7	5.2	17.0	4.9	17.9	4.8	17.7	4.8	18.0	4.8
12:00	21.6	4.5	21.0	4.6	13.7	5.9	12.6	6.5	17.6	4.8	14.0	5.8
14:00	18.7	4.7	17.2	4.9	14.7	5.4	14.4	5.6	12.9	6.3	13.4	6.1
16:00	19.3	4.7	17.2	4.9	16.0	5.1	13.4	6.1	14.7	5.4	14.9	5.3
18:00	18.4	4.8	17.0	4.9	13.9	5.8	12.8	6.4	13.4	6.1	12.7	6.4
20:00	18.6	4.7	15.5	5.2	13.8	5.9	12.2	6.7	12.3	6.6	12.2	6.7
22:00	20.4	4.6	14.4	5.6	15.1	5.3	14.4	5.6	13.7	5.9	13.9	5.8
24:00	21.3	4.6	20.4	4.6	15.4	5.2	15.2	5.3	16.3	5.0	16.3	5.0
02:00	21.9	4.5	20.3	4.6	15.1	5.3	15.3	5.2	15.7	5.2	13.5	6.0
04:00	19.0	4.7	18.8	4.7	15.0	5.3	15.3	5.2	16.0	5.1	13.8	5.9
06:00	17.3	4.9	16.6	5.0	13.3	6.1	12.6	6.5	13.0	6.3	12.4	6.6
08:00	18.4	4.8	17.7	4.8	13.2	6.2	14.2	5.7	14.1	5.7	13.6	6.0
10:00	17.1	4.9	14.9	5.3	12.9	6.3	12.9	6.3	12.5	6.5	11.9	6.8
x̄	19.2	4.7	17.4	4.9	14.5	5.6	14.1	5.8	14.6	5.6	13.9	5.9
S.E.(x)	0.45	0.04	0.59	0.08	0.33	0.13	0.44	0.17	0.52	0.18	0.47	0.17

Appendix G. Depth weighted means of _Cyclops bicuspidatus_ during the vertical migration periods.

Table G4. August 16 - 17

| | COPEPODID STAGES | | | | | | | | | | | | | | | | | | | |
| Hour | C1 | | | C2 | | | C3 | | | C4 | | | C5 | | | C6 ♀ | | | Egg | |
	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)	Part. $\bar{\varsigma}$ (mgCm^{-3})	Depth (m)	Temp. (°C)
10:00	15.8	51.	319.85	14.8	5.4	324.81	9.8	7.8	394.49	19.0	4.7	320.70	22.8	4.5	265.30	23.4	4.5	252.70	20.7	4.6
12:00	11.2	7.2	358.99	12.7	6.4	335.23	12.0	6.8	338.70	19.6	4.6	322.74	21.7	4.5	288.40	21.8	4.5	286.30	21.6	4.5
14:00	12.7	6.4	335.23	14.0	5.8	328.78	15.1	5.3	323.32	23.1	4.5	182.89	24.3	4.4	233.80	24.5	4.4	229.60	24.5	4.4
16:00	14.2	5.7	327.79	13.5	6.0	331.26	18.4	4.8	318.66	22.2	4.5	169.86	26.5	4.4	246.97	27.3	4.4	261.83	26.7	4.4
18:00	11.3	7.1	356.45	13.1	6.2	333.24	17.2	4.9	314.58	22.1	4.5	168.41	24.4	4.4	231.70	24.1	4.4	238.0	23.7	4.4
20:00	11.4	7.1	353.92	13.4	6.1	331.76	16.8	4.9	314.89	20.3	4.6	317.80	22.8	4.5	265.30	21.6	4.5	290.50	22.8	4.5
22:00	7.9	9.8	442.68	13.2	6.2	332.75	16.5	5.0	316.38	21.5	4.5	292.60	22.0	4.5	282.10	21.2	4.6	298.90	21.6	4.5
24:00	10.0	7.7	389.42	11.9	6.8	341.24	13.6	6.0	330.76	18.7	4.7	319.68	24.3	4.4	233.80	21.7	4.5	288.40	23.3	4.5
02:00	10.6	7.5	374.20	10.5	7.5	376.74	14.1	5.7	328.28	18.0	4.8	317.30	19.9	4.6	323.76	21.2	4.6	298.90	21.0	4.6
04:00	12.0	6.8	338.70	13.0	6.3	333.74	17.8	4.8	316.62	19.7	4.6	323.08	24.2	4.4	235.90	20.1	4.6	322.00	20.8	4.6
06:00	11.7	6.9	345.31	10.4	7.5	379.28	19.1	4.7	321.04	19.3	4.7	321.72	18.8	4.7	320.02	18.0	4.8	317.30	18.8	4.7
08:00	12.2	6.7	337.71	13.6	6.0	330.76	21.7	4.5	288.40	21.5	4.6	292.60	23.2	4.5	256.90	21.7	4.5	288.40	21.9	4.5
10:00	11.0	7.3	364.06	12.5	6.5	336.22	19.3	4.7	321.72	16.5	5.0	316.38	23.7	4.4	246.40	22.5	4.5	271.60	22.5	4.5
$\bar{x}$	11.7	7.0	357.33	12.8	6.4	339.68	16.3	5.4	325.22	20.1	4.6	281.98	23.0	4.5	263.87	22.2	4.5	280.34	22.3	4.5
S.E.(x)	0.53	0.30	8.21	0.35	0.17	4.48	0.91	0.27	6.12	0.52	0.04	17.4	0.56	0.03	8.1	0.63	0.03	7.85	0.55	0.02

APPENDIX H

TEMPERATURE AND PARTICULATE CARBON LEVELS DURING

THE VERTICAL MIGRATION SERIES

Table H1. Temperature and particulate carbon levels
during the May 28-29 and June 11-12 vertical
migration series.

Depth (m)	May 28-29		June 11-12	
	Temp. (°C)	Particulate Carbon (μg C L^{-1})	Temp. (°C)	Particulate Carbon (μg C L^{-1})
0	8.4	444.40	14.5	376.70
1	8.3	448.50	14.5	362.49
2	7.9	452.60	14.2	348.28
3	7.5	456.70	14.0	334.07
4	6.7	505.60	13.0	337.25
5	5.9	554.50	11.6	340.44
6	5.5	603.40	10.5	343.62
7	5.1	652.30	9.5	346.81
8	5.1	609.22	8.0	366.15
9	5.1	566.15	7.4	385.49
10	5.0	523.07	7.0	404.84
11	5.0	480.00	7.0	424.18
12	5.0	436.92	6.8	443.52
13	5.0	415.03	6.5	405.90
14	5.0	393.14	6.2	368.26
15	5.0	371.25	6.0	330.64
16	5.0	349.36	5.9	293.01
17	5.0	327.47	5.5	255.38
18	5.0	329.96	5.2	268.42
19	4.9	322.46	5.1	281.46
20	4.9	334.95	5.0	294.50
21	4.9	338.91	5.0	292.92
22	4.9	342.86	5.0	291.34
23	4.8	346.82	5.0	289.75
24	4.8	350.77	5.0	288.17
25	4.8	354.73	5.0	286.59
26	4.7	357.37	4.9	289.23
27	4.6	360.00	4.9	291.87
28	4.6	362.64	4.9	295.50
29	4.5	365.27	4.9	297.14
30	4.4	367.91	4.9	299.78

Table H2. Temperature and particulate carbon levels
during the July 19-20 and August 16-17 vertical
migration series.

Depth (m)	July 19-20		August 16-17	
	Temp. (°C)	Particulate Carbon (μg C L^{-1})	Temp. (°C)	Particulate Carbon (μg C L^{-1})
0	21.9	223.50	17.8	325.60
1	21.8	268.53	17.7	328.33
2	21.5	313.57	17.6	331.07
3	20.9	358.60	17.5	333.80
4	20.4	381.67	17.4	366.72
5	18.3	404.75	17.3	399.65
6	13.0	427.82	17.2	432.57
7	9.0	450.90	13.1	465.50
8	7.8	424.38	9.4	440.14
9	7.2	377.86	8.6	414.78
10	6.9	371.34	7.7	389.42
11	6.6	344.82	7.3	364.66
12	6.3	318.30	6.8	338.70
13	6.0	300.42	6.3	333.74
14	5.8	282.54	5.8	328.78
15	5.5	264.66	5.3	323.82
16	5.3	246.78	5.1	318.86
17	5.0	228.90	4.9	313.90
18	4.9	198.60	4.8	317.30
19	4.8	168.30	4.7	320.70
20	4.7	138.00	4.6	303.10
22	4.6	166.96	4.5	282.10
23	4.5	181.44	4.5	161.10
24	4.5	195.92	4.4	240.10
25	4.4	210.40	4.4	219.10
26	4.4	240.32	4.4	237.68
27	4.4	270.24	4.4	256.26
28	4.3	300.16	4.35	274.84
29	4.3	330.08	4.3	293.42
30	4.3	360.00	4.3	312.00

APPENDIX I

ABUNDANCE RATES OF DECLINE FOR <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u>

IN WEST BLUE LAKE DURING 1974

Table Il. Abundance rates of decline for <u>Diacyclops</u> <u>bicuspidatus</u> in West Blue Lake
during 1974.

Station	Numerical Abundance ($\ln$ no. ind. m^{-2})	Time (days)	Station	Numerical Abundance ($\ln$ no. ind. m^{-2})	Time (days)
2	13.4699	1 May 22	3	12.6985	1 May 22
	13.8046	4		12.4208	14
	13.8489	7		12.8656	21
	13.7470	10		12.1060	35
	13.8690	12		11.9998	49
	13.5373	14		11.3866	68
	13.8545	17		11.1674	77
	13.1505	19		11.8044	91
	13.5383	22			
	13.3945	25	4	12.1358	1 May 22
	13.2669	28		11.9083	14
	13.0305	31		11.4154	28
	13.3813	33		11.3849	42
	13.5690	35		10.1643	56
	13.1548	38		10.5679	70
	13.6692	42		10.4551	84
	12.7055	44		9.9356	100
	13.0017	47			
	12.7136	54	5	12.6357	1 May 22
	12.7186	59		12.3551	14
	12.6890	63		12.3808	28
	12.7249	66		12.1530	42
	12.4831	69		11.2475	56
	12.5324	73		11.1143	69
	12.1637	77		11.3093	84
	12.0786	80		11.2541	94
	11.9793	87			
	12.2294	94			
	11.9111	105			

APPENDIX J

MORTALITY ESTIMATES OF <u>DIACYCLOPS</u> <u>BICUSPIDATUS</u> <u>THOMASI</u>

IN WEST BLUE LAKE

Table J1. Instantaneous mortality rates (descending
           limb).

1972 <u>Cohort 1</u>   May 17   Day ($\bar{x}$)   ln Abundance N (y)

1	11.9637

$y = 12.241-.050x$

8	11.5063
14	11.4490
21	11.5405

$r = -.79$

$F = 10.3, p =. 10$

<u>Cohort 2</u>   June 13

1	12.7894
8	11.9016
15	11.7301

$y = 12.376-.040x$

22	12.1051
30	11.4105
37	11.4651

$r = .96$

$F = 82.7, p<.05$

44	10.9498
51	10.2807
58	10.2494
65	9.4855
77	9.3696

<u>Cohort 3</u>   Oct. 14

1	11.2086
62	10.6764
130	9.3040

$y = 11.784-.015x$

163	9.9441

$r = -.88$

$F = 32.8, p<.05$

1974 <u>Cohort 1</u>   May 25

1	13.4056
3	13.1666
6	13.0827

$y = 13.469-.053x$

8	13.1946
10	13.0603
13	13.0488

$r = -.91$

$F = 36.4, p<.05$

15	12.4334
18	12.4405

                          June 15   21   12.3456
                                   diapause

                          June 4   1   11.3260
                                     3   11.3224

$y = 11.488-.056x$

10	10.7969
15	10.6651

$r = -.80$

$F = 8.1, p<.05$

19	10.8164
22	10.7528
25	9.3397

Table J1. Continued.

1974	Cohort 2	June 24	Day ($\overline{x}$)	ln Abundance N (y)
			1	13.2055
			4	12.9835
			7	12.5302
	y = 13.332-.054x		9	12.4155
	r = -.95		12	12.7953
	F = 132, p<.05		19	12.5414
			24	12.5722
			28	12.4962
			31	11.4800
			34	11.3598
			37	11.6244
			41	11.2242
			44	10.8565
			51	10.0890
			58	10.4868
			67	9.2872
	Cohort 3	Dec. 16	1	12.3870
	(winter)		44	11.8596
			66	11.3381
	y = 12.04-0.016x		109	10.1195
	r = -.83			
	F = 7.2, p<.05			
	Cohort 3	May 22	1	11.2923
	(spring)		4	10.9198
	y = 11.458-.113x		7	10.7907
	r = -.90		10	10.6581
	F = 13.0, p<.05		12	9.7906

APPENDIX K

CHAPMAN PRODUCTIVITY - 1972 (STATIONS 2,5)

Table K1. Chapman method of productivity - Cohort 1.

Date	No. ind. (m^{-2})	Biomass (mg C m^{-2})	$\overline{B}$	Gw	Productivity (mg C m^{-2}day^{-1})
May 17-30	27732	101.96			
			53.219	.058	3.087
June 13-27	51481	96.242			
			69.195	.004	0.302
July 3-11	20938	42.148			

Table K2. Chapman method of productivity - Cohort 2.

Date	No. ind. (m^{-2})	Biomass (mg C m^{-2})	$\overline{B}$	Gw	Productivity (mg C m^{-2}day^{-1})
May 17-30	47006	2.718			
			6.963	.047	0.327
June 13-27	54316	11.208			
			13.333	.028	0.373
July 3-11	46451	15.387			
			21.561	.096	2.070
July 18-25	21606	27.736			
			20.735	.021	0.435
August 8-25	6857	13.734			
			16.412	.003	0.052
August 22-29	9132	19.100			

Table K3. Chapman method of productivity - Cohort 3.

Date	No. ind. (m^{-2})	Biomass $(mg\ C\ m^{-2})$	$\overline{B}$	Gw	Productivity $(mg\ C\ m^{-2}day^{-1})$
July 18-25	20199	2.334			
			4.078	.024	0.100
August 8-15	30901	5.822			
			11.129	.038	0.424
August 22-29	51265	16.436			

APPENDIX L

CHAPMAN PRODUCTIVITY - 1974 (STATIONS 2,5)

Table L1. Chapman method of productivity - Cohort 1.

Date	No. ind. (m^{-2})	Biomass $(mg\ C\ m^{-2})$	$\bar{B}$	Gw	Productivity $(mg\ C\ m^{-2}day^{-1})$
May 22	131417	81.857	98.531	.060	5.920
June 4	87098	115.206	84.210	.019	1.600
June 18 (11-25)	30933	53.216	39.226	.01	0.392
July 9 (2-16)	12657	25.236			

Table L2. Chapman method of productivity - Cohort 2.

Date	No. ind. (m^{-2})	Biomass $(mg\ C\ m^{-2})$	$\bar{B}$	Gw	Productivity $(mg\ C\ m^{-2}day^{-1})$
May 22	51400	3.332	4.387	.040	0.175
June 4	43247	5.443	16.472	.070	1.144
June 18 (11-25)	101772	27.502	24.959	.020	0.500
July 9 (2-16)	55208	22.416	19.760	.058	1.154
July 28-29	13888	17.104	17.688	.024	0.425
August 13 (9-16)	10104	18.272	17.064	.01	0.171
August 25 (20-29)	7932	15.857			

Table L3. Chapman method of productivity - Cohort 3.

Date	No. ind. (m^{-3})	Biomass $(mg\ C\ m^{-2})$	$\bar{B}$	Gw	Productivity $(mg\ C\ m^{-2}day^{-1})$
July 28	23821	2.964			
			4.121	.013	.053
August 13 (9-16)	34526	5.278			
			6.013	.014	.084
August 25 (20-29)	37368	6.749			

APPENDIX M

PRODUCTIVITY ESTIMATED WITH THE RUSSIAN METHOD

AND BIOMASS DURING 1972 AND 1974 (STATIONS 2,5)

Table M1. Daily productivity and biomass in 1972
          (stations 2,5).

Date	Production $(mg\ C\ m^{-2}\ day^{-1})$	Biomass $(mg\ C\ m^{-2})$
May 17	7.584	262.790
24	8.689	538.145
30	13.382	536.912
June 6	5.382	427.813
13	9.399	418.868
20	6.790	300.425
27	4.701	191.410
July 3	6.927	226.221
11	4.175	110.563
18	5.734	137.325
25	4.446	97.253
Aug. 1	2.963	72.554
8	2.935	79.485
15	1.552	44.210
29	1.404	48.097
Oct. 14	3.064	112.225
Dec. 14*	0.182	44.798
Feb. 20*	0.624	27.116
Mar. 24*	0.465	27.260

* station 5 estimates.

Table M2. Daily productivity and biomass in 1974 (stations 2,5).

Date		Production		Biomass	
		mg C m^{-2} day^{-1}	mg N m^{-2} day^{-1}	mg C m^{-2}	mg N m^{-2}
May	16*	15.833	4.506	161.101	43.032
	22	41.783	12.129	490.492	131.610
	25	53.073	15.356	686.489	181.845
	28	38.153	10.978	603.242	159.821
	31	31.760	9.230	649.284	175.659
June	2	27.773	7.996	757.785	204.930
	4	20.556	6.218	570.319	154.592
	7	26.086	7.736	715.673	193.229
	9	15.819	4.730	417.826	113.766
	12	20.612	5.829	460.562	122.033
	15	20.003	5.809	446.526	120.233
	18	16.921	4.869	352.823	93.367
	21	14.112	4.183	317.101	85.290
	23	10.239	2.976	218.460	58.061
	25	26.178	7.818	554.784	150.902
	28	14.634	4.185	271.044	71.020
July	2	15.975	4.140	245.979	68.596
	4	11.391	3.348	275.741	75.208
	7	14.700	4.203	309.592	83.208
	14	8.960	2.522	198.947	52.657
	19	9.315	2.584	189.520	50.549
	23	9.680	2.837	240.713	65.849
	26	8.350	2.464	250.385	69.223
	29	5.803	1.684	154.556	41.586
Aug.	2	5.509	1.591	202.662	56.036
	6	4.089	1.184	153.700	43.115
	9	3.476	0.948	116.831	32.748
	16	2.852	0.790	73.197	19.799
	23	3.360	1.086	107.845	29.430
Sep.	2	2.827	0.602	48.116	12.759
Oct.	19	2.352	0.716	148.563	40.801
Dec.	16*	0.775	0.254	235.820	68.874
Jan.	28*	0.571	0.172	135.295	39.528
Feb.	19*	0.918	0.257	102.698	29.240
Apr.	3*	0.462	0.111	32.639	10.129