

RESPONSES OF TWO COEXISTING CYCLOPOID COPEPODS TO EXPERIMENTAL
MANIPULATIONS OF FOOD AND PREDATORS

by

ADRIENNE PEACOCK

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Department of Zoology

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date Feb. 16/81

ABSTRACT

Factors causing the population limitation of two species of cyclopoid copepods, Tropocyclops prasinus and Cyclops bicuspidatus thomasi, and the subsequent impact of these species on the zooplankton community, were investigated in two montane lakes of the University of British Columbia Research Forest. In Placid Lake, C.b.thomasi was abundant and T.prasinus was rare, while in Gwendoline Lake, T.prasinus was the more abundant species. Field and laboratory experiments were conducted to assess the importance of such factors as food, physical-chemical lake characteristics, and predation upon the population dynamics of these species.

The feeding appendages of adult T.prasinus and C.b.thomasi were compared and found to be structurally alike, although adult diets were quite dissimilar. T.prasinus was omnivorous in the later instars, eating algae, protozoans and probably dead macrozooplankters while C.b.thomasi was markedly carnivorous in copepodid and adult instars. Seasonal abundance peaks revealed a temporal separation of the naupliar instars of these species in both lakes studied. Consequently, competition between T.prasinus and C.b.thomasi was unlikely. Large scale enclosure experiments in Placid Lake, where C.b.thomasi was abundant, showed that lake densities of C.b.thomasi could limit the abundance of T.prasinus. Survivorship curves and laboratory feeding experiments indicated that the low abundances of T.prasinus was caused by two important factors: high T.prasinus naupliar mortality even in the absence of C.b.thomasi, and C.b.thomasi predation on

these T.prasinus instars.

When C.b.thomasi was transplanted to enclosures in Gwendoline Lake, where T.prasinus was the more abundant cyclopoid copepod, C.b.thomasi was able to grow and reproduce within the crustacean plankton community and became as abundant as in its home lake. Naupliar instars were the most mortality-prone stages in both lakes. Fertilization of a Gwendoline Lake enclosure increased the survivorship of C.b.thomasi about 22% over that observed in the unfertilized treatment. However, addition of the midge fly larvae common to Gwendoline Lake (C.trivittatus and C.americanus) to the enclosure plankton community resulted in a decrease in the standing crop of C.b.thomasi to a point at which samples became difficult to obtain. With Chaoborus in the enclosure, fertilization did not enhance the abundance of C.b.thomasi but rather, improved the survivorship of Chaoborus first and second instar larvae, and resulted in an acceleration of the C.b.thomasi nauplii decline.

The impact of C.b.thomasi on other zooplankton was also examined. C.b.thomasi appeared to dampen the fluctuations in total zooplankton biomass in enclosures without a Chaoborus population. However, in the fertilized treatment without Chaoborus, C.b.thomasi was unable to track prey demographic responses and caused no major compositional changes in the crustacean community at either high or low nutrient levels. Temporal - spatial overlap and predator and prey developmental responses were critical factors determining prey sensitivity to predation by C.b.thomasi.

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GENERAL INTRODUCTION

Explanations for the distribution and abundance of species have played a central role in the development of ecological thought from the early formulations of Darwin and Wallace. Wallace (1903) stated that it was the resemblances rather than the diversities that he observed in the distant continents and islands that were the most difficult to explain. Freshwater systems were particularly puzzling to the early ecologists because lakes, or at least lakes and their drainage basins, seemed like islands, separated from each other by barriers of land. In The Origin of Species, Darwin recalled his surprise in finding that "not only have many freshwater species, belonging to different classes, an enormous (geographic) range, but allied species prevail in a remarkable manner throughout the world".

Yet in spite of the evidence that many freshwater organisms were remarkably cosmopolitan, lake to lake differences were often great. In 1887 S.A. Forbes described the freshwater lake as a microcosm wherein each species was functionally interconnected with the whole species assemblage, and a change in one species' abundance influenced all others in the community. The microcosm analogy was probably stimulated by observations on the patchy interlake distribution of species.

Although Darwin confined his remarks to more visually obvious freshwater organisms, the widespread occurrence of many

genera in the order Copepoda led Sewell (1956) to use this group as evidence for the continental drift theory. Freshwater Copepoda are both geographically widespread and locally discontinuous (Gurney, 1931; Rylov, 1963; Pennak, 1957). Yet prodigious dispersal capabilities are on record. Beal (1881) described a "shower of Cyclops quadricornis" in Iowa. After a rain he noted that the ground had a blood-like appearance and, on examination, half a teaspoon contained about 500 Cyclops. Beal's report was undoubtedly an unusual mode of dispersal. Nevertheless, copepod species are remarkably ubiquitous in freshwater systems even though interlake differences are often great, particularly in the abundances of species. Pennak (1957), in a study of 57 lakes in Colorado, observed that the most abundant copepod species at any one time accounted for about 80% of all copepod individuals present. He concluded that this result was 'typical' of limnetic zooplankton communities. If copepods possess such extreme powers of dispersal, why are there so few abundant species within a given community?

The recognition that species interactions may be of major importance in structuring freshwater zooplankton communities is a relatively recent development (Hrbacek, 1962; Brooks and Dodson, 1965). The return to Forbe's perspective has encouraged investigation by experimentation probably because animals are easier to manipulate than their natural environments. With the use of 'controlled disturbances', some investigators have been able to provide mechanistic interpretations of the distribution and abundance patterns of

some zooplankton species (e.g. Hurlburt et al., 1972; Northcote et al., 1978; Neill, 1978; Lynch, 1979). However, explanations for the distribution and abundance of cyclopoid copepods are still vague, primarily because the role of these microcrustaceans within the plankton community has remained somewhat obscure. Nevertheless, the potential importance of cyclopoid copepods in structuring lacustrine communities has been generally recognized (Gurney, 1931; Rylov, 1963). Many different roles within the plankton community have been ascribed to these tiny crustaceans. Rylov (1963) points out their importance as intermediate hosts for many parasitic Cestodes and Nematodes which parasitize vertebrates, including humans. Various planktivorous fish are reported to feed on cyclopoids although Fryer (1957b) suggests that an abundant cyclopoid population may actually limit fish production because the adult cyclopoids attack newly hatched fry. It is known that many species of cyclopoid copepods are demonstrably carnivorous in the late copepodid instars (Fryer, 1957a,b; McQueen, 1969; Anderson, 1970a; Kerfoot, 1978; Brandl and Fernando, 1974,75,78). However, it is still a matter of debate whether cyclopoids have any significant effect even on other zooplankton (Hall et al., 1976; Lane, 1979; Lynch, 1979).

The influence of cyclopoid copepods on the distribution and abundance of other cyclopoid species is also unclear. Hutchinson (1957) describes several studies which suggest that temporal segregation of planktonic cyclopoid species by the intercalation of a diapause in their life history is critical in permitting two or more cyclopoid species to co-occur.

Smyly (1978) suggests that Cyclops abyssorum Sars and Mesocyclops leuckarti (Claus), co-occur rarely in the English Lake District (although both species are widely distributed) because different temperature optima result in the herbivorous instars of the slower growing species being eaten by the copepodid instars of the faster growing species. However, unraveling the various factors which produce observed abundance patterns is often difficult and the ability of cyclopoid species to co-exist may be mechanistically complex. Pennak (1957) points out that at any one time only one species in each "functional or 'food niche'" is the rule - that is, one cyclopoid copepod species per community. Pennak adds that if two species of limnetic cyclopoids are found together they are almost invariably of different genera and he assumes that this pattern reflects different 'food niches'.

Recent experimental studies (Brandl and Fernando, 1978; Lane, 1979; Lynch, 1979), potentially providing more definitive evidence, have left the role of cyclopoid copepods still somewhat ambiguous because they either use unrealistic densities of predator and prey, inappropriate temporal or spatial scales, potentially stressed animals or extrapolate the effects of the cyclopoid copepods from other studies suffering from these experimental problems. In this study I combined small scale laboratory experiments and morphological studies with large scale in situ perturbations and demographic observations of lake populations to mechanistically explain the relative abundances of two co-existing cyclopoid copepods, Tropocyclops prasinus (Fischer) 1860 and Cyclops bicuspidatus

thomasi (Forbes) 1882 (= Diacyclops thomasi (Kiefer, 1978)). Intensive sampling revealed that, where the one species was abundant, the other was scarce.

To explain the mechanisms underlying this pattern I focused my study on two nearby oligotrophic lakes where the relative abundances of the two species appeared to be reversed. I then examined 1) the morphological features of the feeding apparatus in C.b.thomasi and T.prasinus 2) the respective feeding habits of the two species 3) the population dynamics of both species in the two lakes and in 'disturbed' enclosures and 4) the way in which competition, predation and lake nutrient levels interact in the field to affect abundances of C.b.thomasi , T.prasinus and the zooplankton community.

The work is presented in four sections. Section one examines the feeding structures of T.prasinus and C.b.thomasi . Section two describes experimental manipulations of one zooplankton community, undertaken to investigate the C.b.thomasi - T.prasinus interaction. Section three discusses the C.b.thomasi transplant experiments. I transferred C.b.thomasi from Placid Lake to nearby Gwendoline Lake and altered both the density of Chaoborus (a predaceous midge larva) and the nutrient environment. Section four describes the effect on the Gwendoline Lake zooplankton community of varying both invertebrate predator populations and nutrient levels.

I. A MORPHOLOGICAL STUDY OF TROPOCYCLOPS PRASINUS FISCHER AND
CYCLOPS BICUSPIDATUS THOMASI FORBES

INTRODUCTION

In most animals there is a close relationship between the structure of the mouthparts and the diet (Hassall, 1977). Within the spectrum of apparently available food, it is often possible to identify the precise segment that the animal can use by studying the tools with which the animal eats. Gwyne and Bell (1968) were able to explain the relationships between large vertebrate herbivores in a grazing succession by examining simple differences in dentition. Unlike many vertebrates, invertebrate gut contents are often difficult to study and mouthpart morphology may provide the first insight into the nature of the diet (Room, 1975). Isley (1944) showed that a variety of grasshopper species could be identified as granivore, herbivore or carnivore by examining their mandibles. Anraku and Omori (1963) surveyed several species of marine copepods and showed that there is a close relationship between the structure of the mouthparts and the type of food taken. Itoh (1970) also examined marine copepods and he was able to differentiate herbivores, omnivores and carnivores on the basis of an "Edge index" derived from measurements of the cutting edges of the mandible. Zaret (1978) suggests that the feeding morphology of lacustrine animals is determined primarily by competition. However, in freshwater cyclopoid copepods the correlation between mouthpart morphology and food specificity doesn't seem obvious (Fryer, 1957a). Illustrations of individual appendages of various cyclopoid copepod species (Sars, 1918; Gurney, 1931) are remarkable for their similarity. In spite of this, Fryer (1957a,b) was able to identify

distinctly different diets (herbivorous versus carnivorous as adults) even within a closely related group of cyclopoid copepods. Lewis (1979) states that adult Thermocyclops hyalinus are unequivocally herbivorous and that "mouthpart morphologies confirm this conclusion", although he does not provide illustrations. Fryer (1957a) assembled individual appendages to illustrate how they function in vivo and suggested that the feeding mechanism is similar across diets. Although there has been some interest in the type of food taken (Smyly, 1970; Brandl and Fernando 1974, 75, 78) and food-seeking behaviour (e.g. Strickler and Bal, 1973; Kerfoot, 1978) there has been little advance in our knowledge of species-specific differences in the feeding tools since Fryer's classic paper, and many common species have never been described in detail.

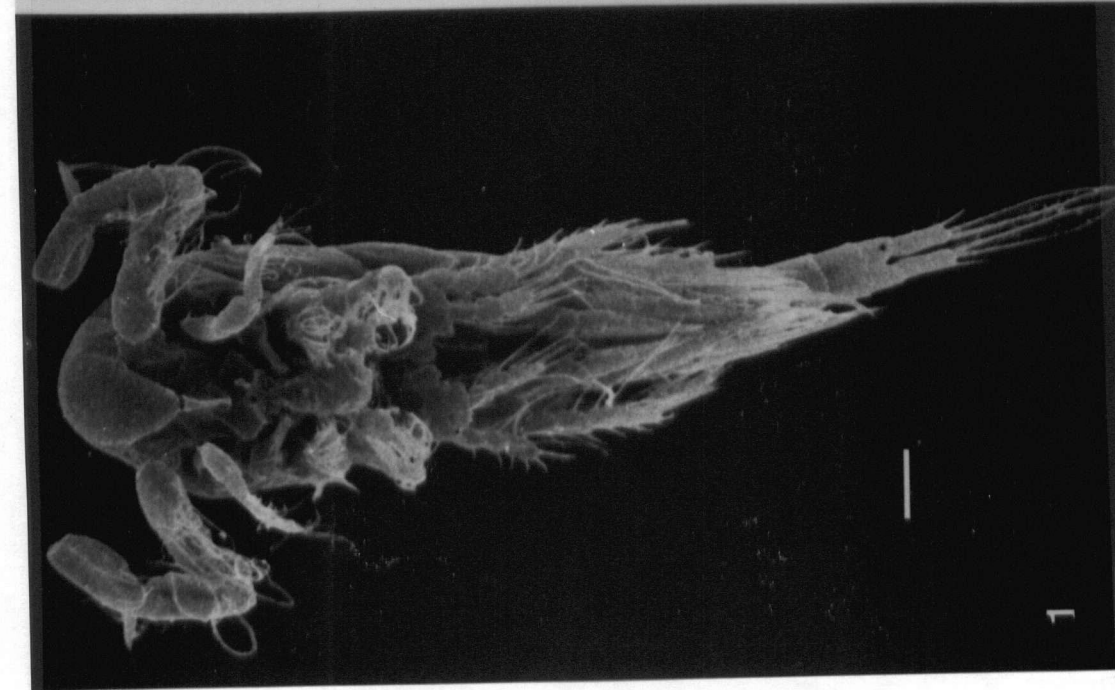
Cyclopoid copepods are among the most cosmopolitan of animals. They are found in a wide variety of freshwater habitats, from caves, wells and small puddles to the open waters of large lakes. Only a few species are typically limnetic, most being benthic-littoral creatures. Like other copepods, the cyclopoid copepod begins life as a nauplius; subsequent larval stages are classified as copepodid instars. There are normally six naupliar and six copepodid instars in free-living copepods (Elgmork and Langeland, 1970). The molt from nauplius VI to copepodid I results in a distinct change of form, from a typical soft-bodied nauplius to an unmistakable 'copepodan' form (with an elongate, chitinous segmented body). Reproduction in all the Copepoda is always bisexual. In male

cyclopoid copepods, unlike calanoid copepods, both antennae are geniculate (fig.1). These antennae are used for grasping the female during copulation, when the sperm is transferred to the female in a chitinous package called the spermatophore. The females store the sperm in the spermatheca, into which the oviducts open on the genital segment, and the eggs are fertilized as they are laid. One mating provides enough sperm to last the entire life of the female (Hutchinson, 1957). Lewis et al. (1971) observe that as many as 9 pairs of egg sacs can be laid per adult female. The eggs are carried laterally in two egg sacs (Fig.2). All the free-living adult Cyclopoida are raptorial, whether they are herbivores or carnivores (Hutchinson, 1967). The feeding appendages appear stout and spiny, appropriate for a grasping, but not a filtering, mode of food acquisition. Fryer (1957b) suggests that, in general, large species tend to be carnivorous as adults while the smaller species remain herbivores throughout their life history. As the feeding apparatus is grossly similar among many species examined (Sars, 1918; Gurney, 1931; Fryer, 1957a; Rylov, 1963) small differences in structure and/or size must be crucial in permitting the handling of the different types of food items, plant or animal.

This chapter presents details of mouthpart structure in two unrelated but exceptionally common limnetic cyclopoid copepods, Tropocyclops prasinus (Fischer) 1860 and Cyclops bicuspidatus thomasi (Forbes) 1882. Although C.b.thomasi and T.prasinus coexist in the oligotrophic montane lakes of the University of British Columbia Research Forest, where one

Figure 1. Adult male T.prasinus with geniculate antennae.
Scale - 50 um

Figure 2. Adult female T.prasinus with egg sacs. Scale -
50 um



species is abundant, the other is scarce, and the feeding apparatus may be important in explaining the observed distribution and abundance pattern in these lakes. As small differences in oral appendages can be translated into large differences in functional morphology, the mouthparts of both species are compared. Under a light microscope (LM) the general mouthpart morphology appears very similar between the two species. Both species are quite small and detail, which may be critical to the animal, is difficult to see under a LM. Therefore a detailed study was undertaken using a scanning electron microscope (SEM). This study represented a first step in understanding the relationships of these animals with each other and with their environment.

MATERIALS AND METHODS

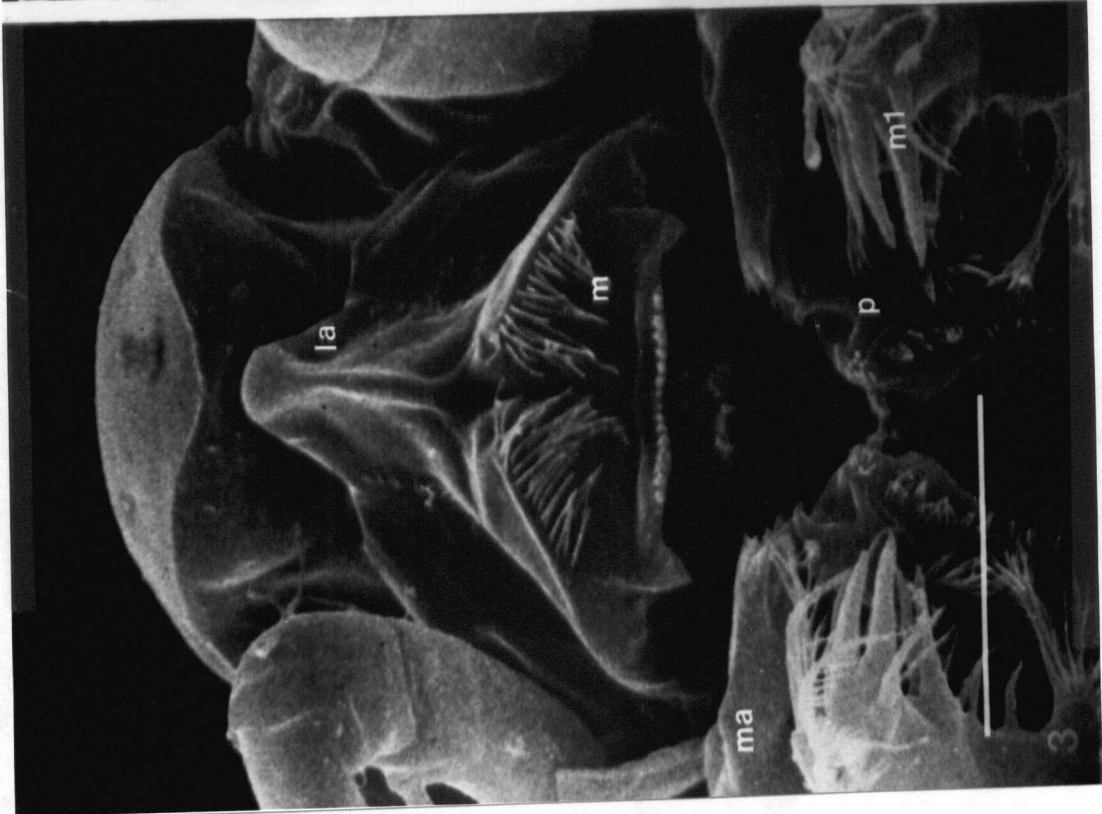
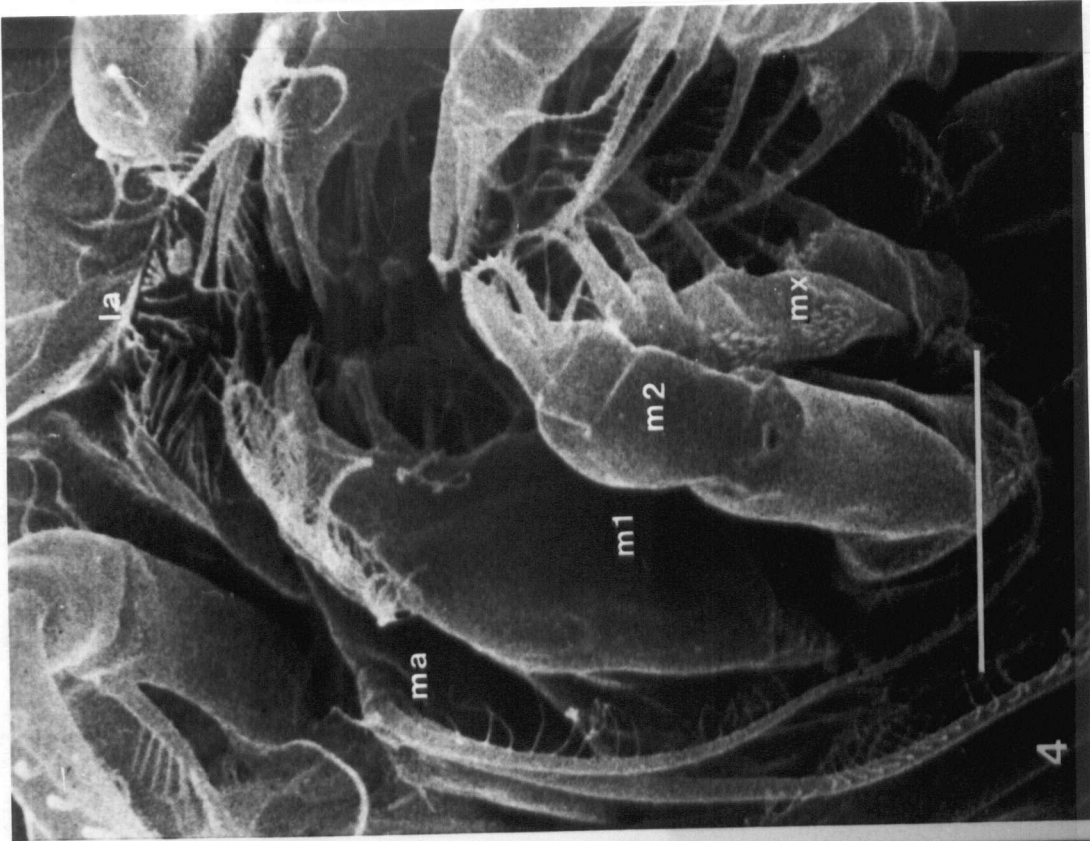
The mouthparts of T.prasinus and C.b.thomasi were prepared for structural studies under the LM by mounting the animals on separate slides in red polyvinyl lactophenol and removing the cephalothorax intact. Individual mouthparts were then removed using electrolytically sharpened tungsten needles and were drawn with the aid of a camera lucida. In addition, copepodids IV to adult of T.prasinus and C.b.thomasi were prepared for scanning electron microscopy. Over 50 different adult animals of both species were examined and the animals showed little variation, at least in the mouthpart structure. Best results were obtained with animals taken directly from the lake, anaesthetized with carbonated water, and then dehydrated with a series of ethanol solutions of increasing concentration, from 10% to 100%. The animals were critical-point dried, coated with gold/palladium and mounted for examination.

STRUCTURE OF THE MOUTHPARTS

In both T.prasinus and C.b.thomasi the oral cavity is bordered anteriorly by the labrum, laterally by the mandibles and posteriorly by paragnathae (Fig.3;p). From behind and lateral to the paired paragnathae arise three paired feeding appendages: the first maxillae or maxillules, the second maxillae and the maxillipeds. The second maxillae overlap the first while the maxillipeds are slightly below and inside the second maxillae (Fig.4;m2,ml,mx).

Figure 3. Oral region of adult female T.prasinus . Letters represent: la - labrum, m - 'mustache' or labral setae, ma - mandibles, p - paragnathae, ml - first maxillae. Scale - 50 um

Figure 4. Feeding appendages of adult female T.prasinus . Letters are defined as indicated above and in addition: m2 - second maxilla, mx - maxilliped. Scale - 50 um



MOUTH REGION

Labrum

The anterior of the labrum has a prominent beaklike structure. The 'beak' becomes a medial groove posteriorly which separates the two sides of a triangular flattened plate. Each side bears a row of regularly spaced stout hairs, bilaterally split to look like a sparse brush mustache (Fig.3;m). When the prey item is large enough, these hairs make contact with the food being ingested (Fig.5;pr). The hairs arise from the lower edge of the flattened, medially cleft plate which almost folds under to form a ridge of small teeth on the free margin, culminating in a single large coarse 'tooth' at either edge (Fig.3). The small teeth are situated medially, directly over the oral cavity, and they appear to be smaller and finer in the centre, becoming larger and somewhat splayed out toward the lateral edge (Fig.6;la). All the teeth point toward the mouth cavity.

Several ducts open on the internal (oral) face of the labrum. Although their function is unknown, Fryer (1957a), suggests that these are the openings of the salivary ducts leading from labral glands. Near these ducts are bilaterally symmetrical patches of short stout spiny setae, all of which point toward the oral cavity. This area is remarkably similar between the two species, T.prasinus and C.b.thomasi (Fig.7;lao), as is the entire labral region. The only

Figure 5. Adult male T.prasinus ingesting prey. Letters represent: la - labrum, pr - prey. Scale - 50 um

Figure 6. Oral cavity of adult female C.b.thomasi and T.prasinus.
C.b.thomasi. a. Oral cavity of an adult female
T.prasinus. b. The same area in an adult female
T.prasinus. Letters represent: p - paragnathae, ma - mandibles, ml - first maxillae, m2 - second maxillae, mx - maxillipeds. Scale - 50 um

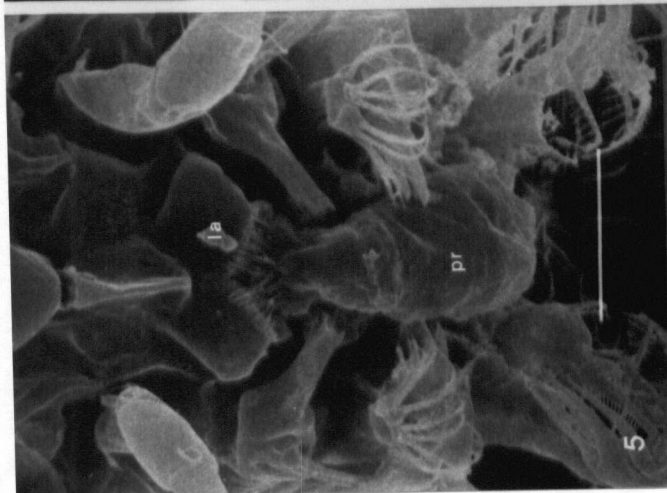
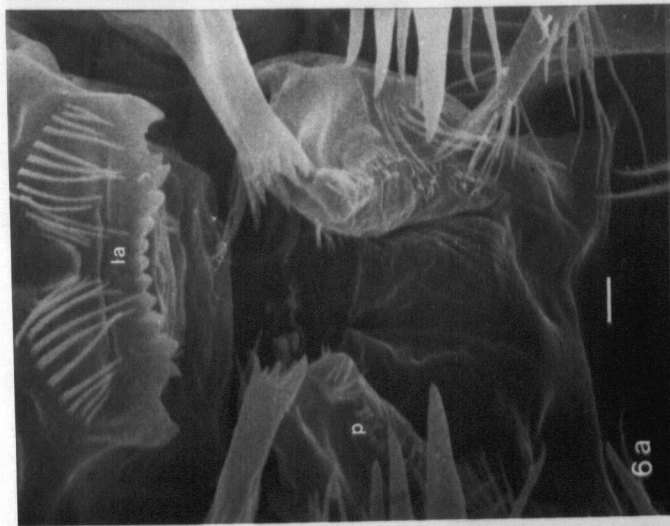
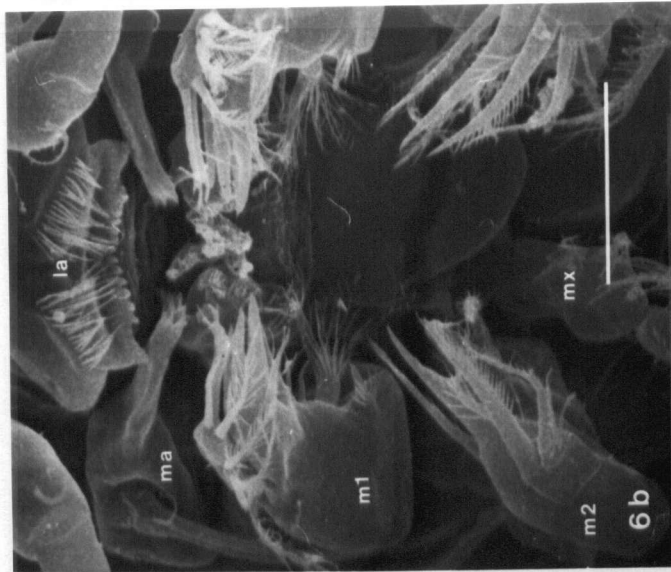
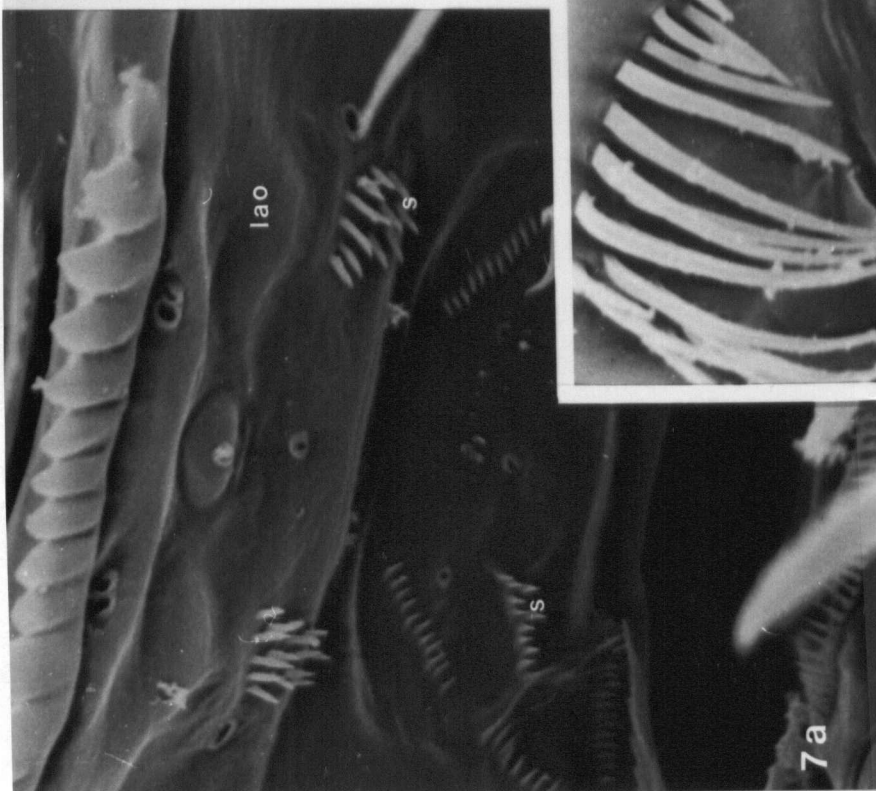
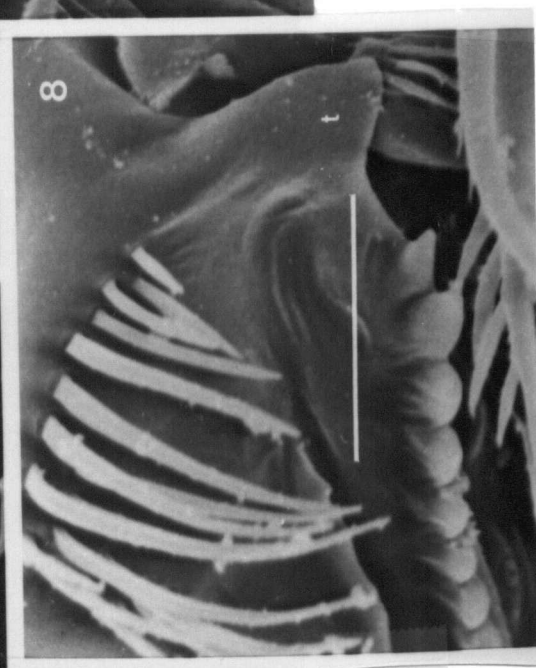
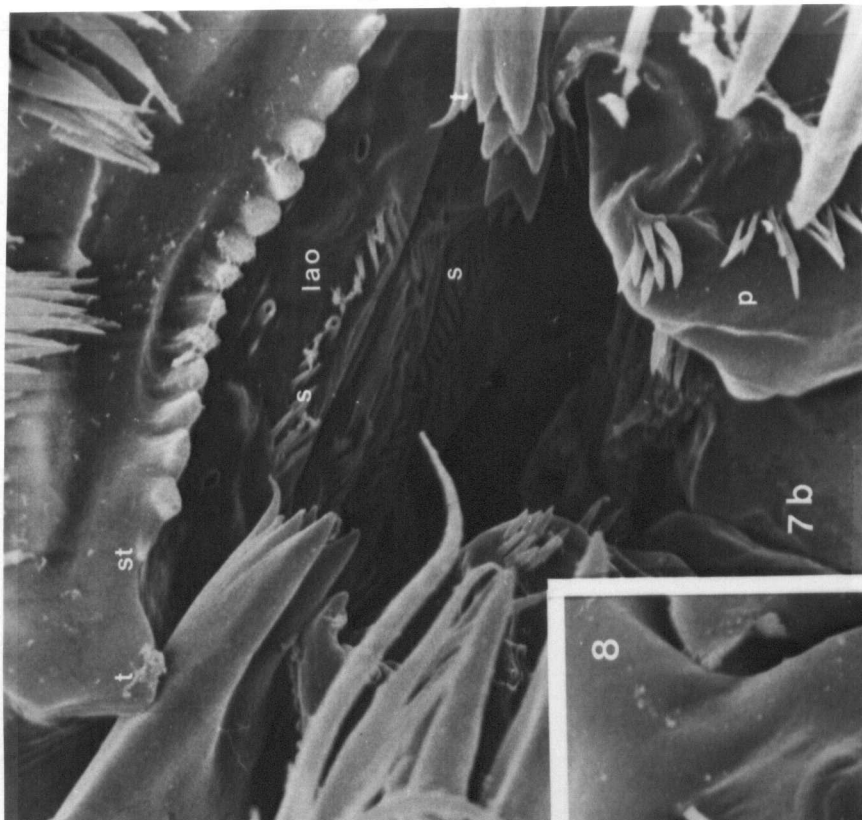


Figure 7. Oral face of labrum a. Oral face of the labrum of an adult C.b.thomasi female. b. The same area in an adult female T.prasinus showing similar features. Letters represent: lao - oral face of labrum, s - setae on oral face of labrum, t - tooth-like structures, st - small 'tooth' observed between the large and small labral teeth on T.prasinus.

Figure 8. Large labral tooth of adult female C.b.thomasi.
Scale - 50 um



differences are in the location and number of the stout spiniform setae on the inner face of the labrum (T.prasinus has more) and the existence of a small extra tooth between the large coarse tooth and the smaller medial teeth in T.prasinus. This small tooth is not present in C.b.thomasi (fig.7;t,st and 8;t).

Mandibles

The mandibles are situated laterally relative to the oral cavity, below the second antennae and above the first maxillae (Fig.6;ma). Each mandible consists of a stout shaft or gnathobase whose proximal end articulates with the cephalothorax sternite and whose distal extremity is drawn out into a horizontally flattened arm terminating in a 'toothed' masticatory edge. Fryer (1957a) accurately described the twisting of the mandibular gnathobase along this distal blade such that the toothed edge lies along the line of the oesophagus and not across it (Fig. 6,9;d). The cuspid edge of this blade appear bifid and, at points, trifid in the lateral view (Fig.6,7;t). In C.b.thomasi the 'tooth' proximal to the oral cavity is elongate, almost twice the length of the other points. This 'tooth' is similar in girth to the others but differs in structure in that the edges are cut into short spurs or serrations which point toward the distal end (Fig.6,10;just above and to the left of d). Unlike Macrocyclus albidus (Jurine) (Fryer,1957a), this projection is not more slender or delicate in structure than the other teeth on the distal edge of the mandible although, as suggested by

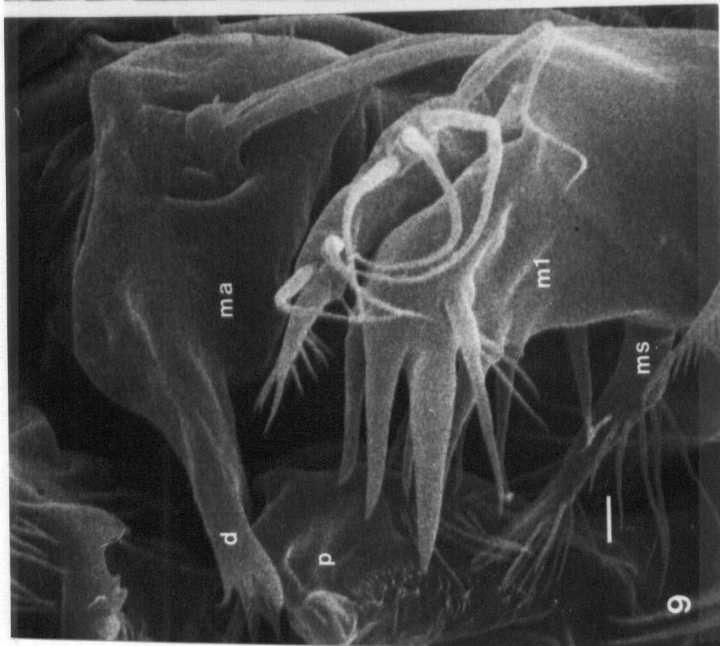
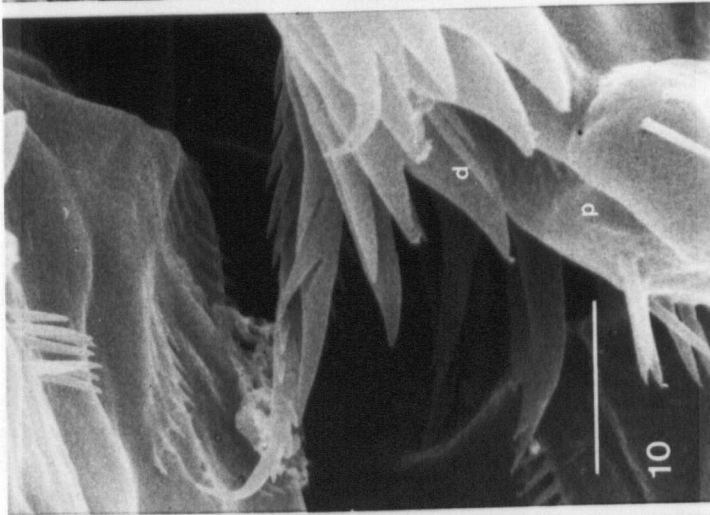
Fryer (1957a), it probably does serve a sensory function. It projects into the oral cavity and is not apparent in T.prasinus, although in this species the tooth closest to the oral cavity appears slightly longer than the rest of the 'teeth' and may also have a sensory function. There is also a small, finger-like projection, which seems peculiar to T.prasinus, arising from the buccal chitin just anterior to the paragnathae (Fig.11;f). This projection has serrate edges rather like those on the 'sensory' cusp of C.b.thomasi but is attached to the sternite rather than arising from the mandibular blade. Its function is probably sensory because it doesn't seem stout enough for grasping or crushing.

On the ventral surface of the mandibular gnathobase, toward the lateral edge, is a much-reduced palp connected to the basal plate by a moveable joint (Fig.6,12; to the left of 'ma' in both). This palp bears three posteriorly directed setae. Two of these setae are extremely long. In T.prasinus they reach back beyond the posterior edge of the cephalothorax (Fig.4), while in C.b.thomasi they appear to be somewhat shorter (Fig.13). The third seta is quite short in both species. In T.prasinus the seta lying ventrally appears plumose, bearing two rows of regularly spaced fine hairs or setules, from the tip to almost the palpal origin. The dorsally situated seta appears hairless from the palp to mid-length where it shows the same plumose pattern of fine hairs to the distal extremity. Fryer (1957a) reports using the movement of these setae, reflecting as they do the movements of the arm of the mandibles, to interpret the mode of action of

Figure 9. Mandibles of adult female C.b.thomasi showing 'teeth' on the distal end, paragnathae and first maxilla. Letters represent: ma - mandible, d - distal end of mandible, ml - first maxilla, ms - main sensory seta of first maxilla, p - paragnatha. Scale - 5 um

Figure 10. Elongate directly above and to the left of 'd', just below the labrum, this 'tooth' resembles a stout setae more than it does the rest of the 'teeth' on the distal end of the mandible. This structure was obvious on C.b.thomasi only. Scale - 5 um

Figure 11. Buccal cavity of adult female T.prasinus showing the finger-like projection from the buccal cavity. Letters represent: f- finger-like projection arising from the buccal chitin. Scale - 5 um



these miniscule appendages in live M.albidus. Their location and fine structure suggests a sensory function.

Paragnathae

The paired paragnathae lie behind the distal arms of the mandibles (Fig.14). They form a pair of stout chitinous projections that arise from the cephalothorax sternite and are distinct from the appendages. Joined medially, each arm is slightly subdivided into two lobes at the point most distal from the body. The medial lobe on each side is covered with a strip of short, coarse setae both anteriorly and posteriorly. If one peers toward the oral cavity from the posterior side of the paragnathae, the dorsally located setae project their stiff tips, almost like serrations, into the medial cleft through which food must pass to reach the oral cavity (Fig.14). The cleft itself is smooth and hairless. In M.albidus Fryer (1957a) has described these paragnathae as "small serrated chitinous knobs, attached to the lateral extremities of a chitinous bar". According to Hartog (1888), this post-oral-bar can contract forming a V. This causes the edges of the paragnathae to come together "like minute pincers" (Fryer, 1957a). There are no serrated edges in either T.prasinus or C.b.thomasi although the spiniform setae that protrude medially may have the same effect, holding the prey when the paragnathae contract. Animals observed with food in their grasp confirm the pincer-like function of the paragnathae (Fig.5).

GRASPING APPENDAGES

The First Maxillae

The first maxillae are very stout grasping appendages which articulate with the sternite just below the gnathobase of the mandibles (Fig.4,6,13). Each consists of a broad flattened base which curves over medially and narrows at its distal extremity to form three stiff heavily chitinized claws. On the ventral side of these apparently fixed claws lies a stout seta which appears to have a moveable base (Fig.9,16,17;ms). On the inner, medial face of the gnathobase are several short, spiniform setae. All these setae point toward the mouth. One of the most interesting of these setae is what Fryer (1957a) calls the "main sensory seta" of the inner face of the first maxilla. Unlike the others, this seta appears to have a fleshy stalk and is on a moveable base. It resembles a 'bottle-brush' in appearance as it has several whorls of setules, one set originating near the base and the other around the tip (Fig.9,15,16,17). The basal setules are longer than those at the distal extremity and all the setules appear quite stiff and spiny.

On the outer anterior side of the first maxilla lies a palp with two lobules, each of which bear moderately long setae - the posterior bearing four and the anterior one three. These arch over the distal extremity of the first maxilla, the anterior splaying over the mouth region and the posterior

Figure 12. Lateral view of the feeding structures of adult female C.b.thomasi showing how the mandibular palp is connected to the basal plate by a moveable joint. The palp bears 3 setae, 2 long and one short. Letters represent: ma - mandible (palp just to left of 'ma'), m1 - first maxilla, m2 - second maxilla, mx - maxilliped
Scale - 50 um

Figure 13. Feeding appendages of adult female C.b.thomasi .
Scale - 50 um

Figure 14. View of paired paragnathae in adult female T.prasinus viewed from the position of the first maxillae. Scale - 5 um

Figure 17. Main sensory seta on adult female T.prasinus showing the long sturdy setae and widely spaced setules on the maxilliped. Scale - 50 um

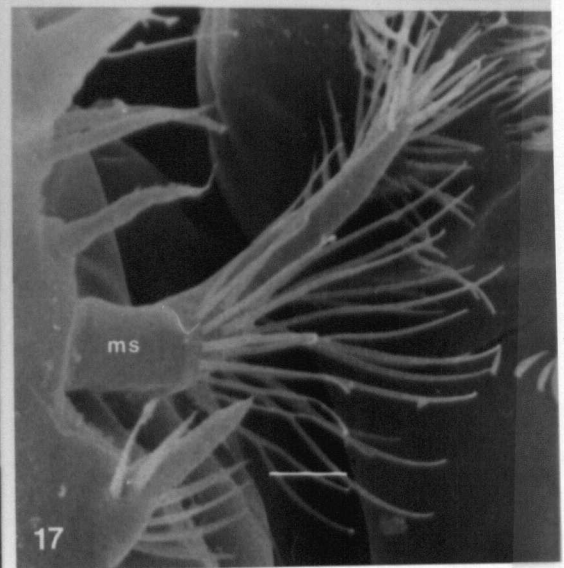
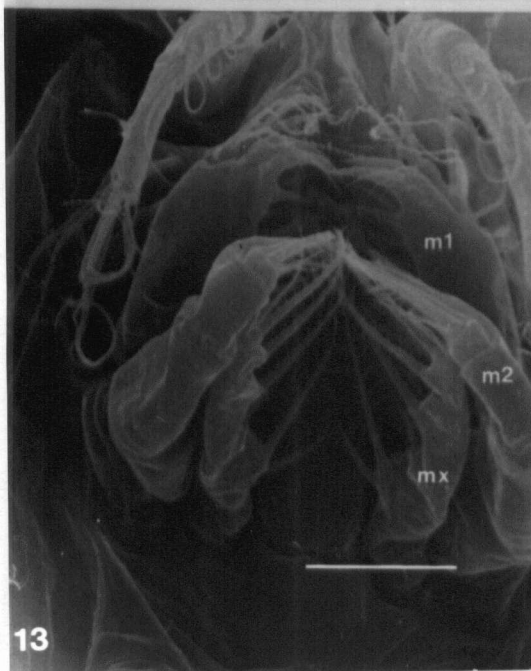
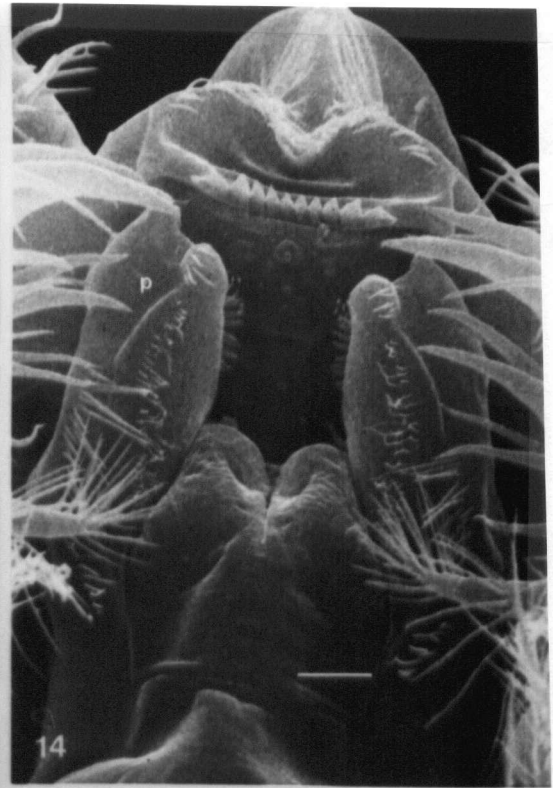
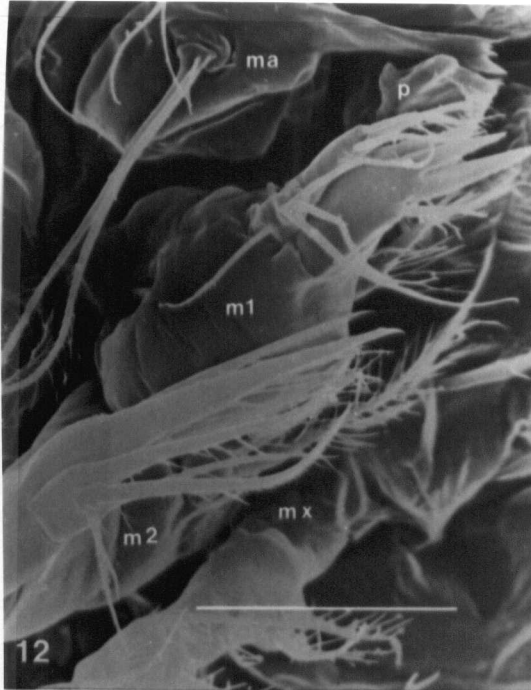
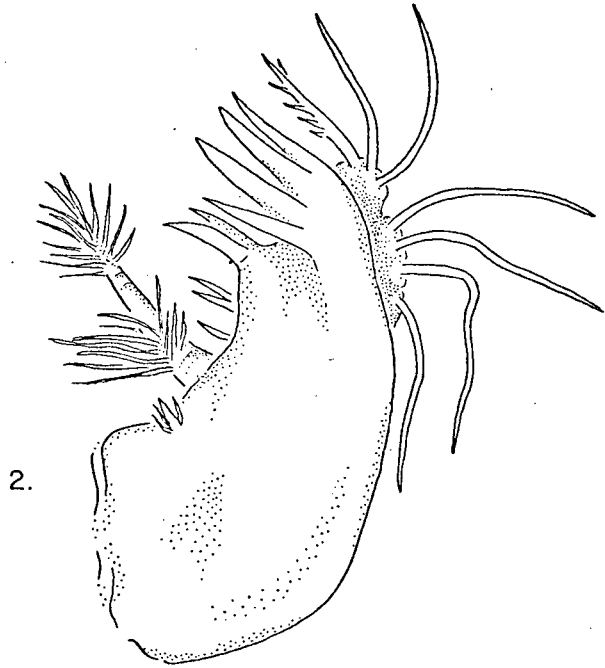
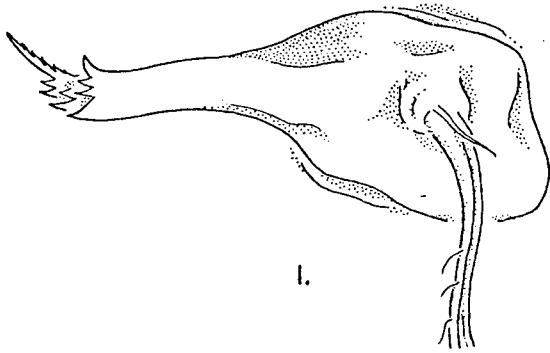


Figure 15. Mouthparts of adult female C.b.thomasi as drawn under a light microscope using a camera lucida attachment. Arabic numbers represent: 1 - mandible 2 - first maxilla 3 - second maxilla 4 - maxilliped.



0.1mm

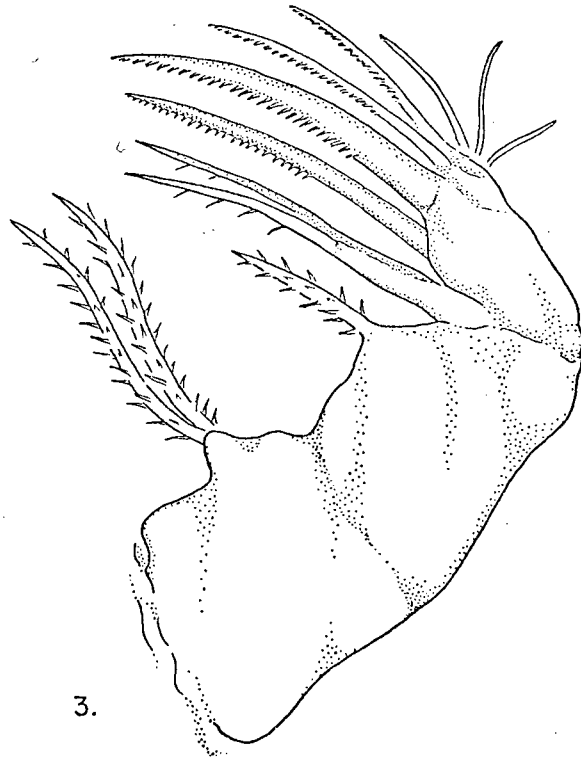
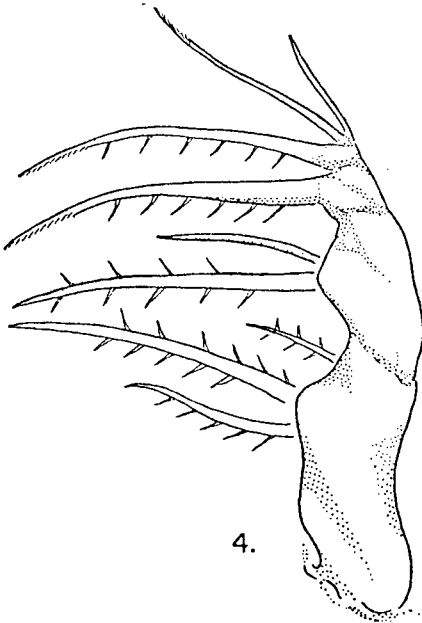
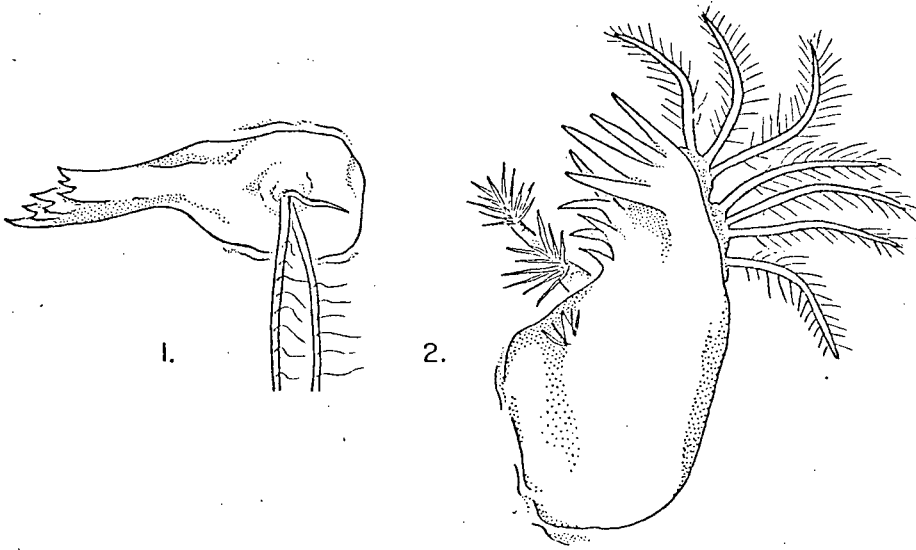
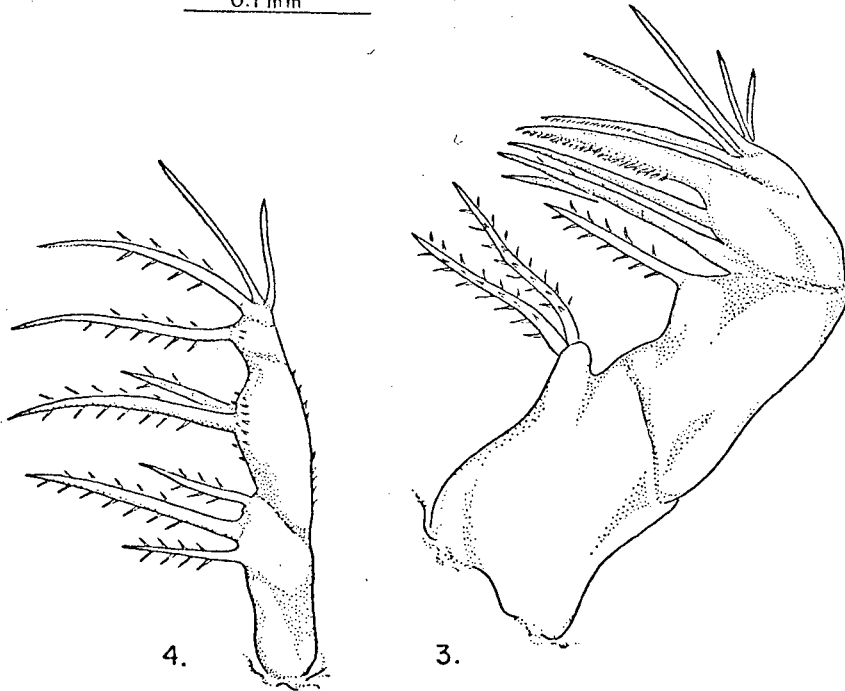


Figure 16. Mouthparts of adult female T.prasinus drawn as described above. Mouthpart numbers are the same as Fig. 15.



0.1 mm



lobule setae reaching over the ventral side of the posterior lobule. Their position was variable in some pictures suggesting considerable independent movement. Rylov (1963) suggests that these lobulate outgrowths of the palp are rudiments of the exo-and endopodite observed in calanoid copepods.

There are differences between the palpal setae in C.b.thomasi and T.prasinus. All the setae on the former are long and hairless except for the most distal seta on the anterior lobule, which has short serrate setae. By contrast, T.prasinus has fine setules on all the palpal setae.

The Second Maxillae

The second maxillae are stout jointed appendages which articulate basally with the sternite of the cephalothorax just below and slightly lateral to the first maxillae. Unlike the latter, there are several well-defined segments of which the first two (called the protopodite) are significantly larger than the others (Fig.16,17). The segments distal to the protopodite form the endopodite (Rylov,1963). The anterior joint of the endopodite terminates distally on the inner margin in one large claw-like projection with serrate edges along its distal extremity. On the anterior joint there is also a sturdy seta with spiniform setules and a slender simple seta at its base. The posterior joint is less robust and has two plumed setae. The most distal joint of the endopodite bears five setae, two of which are large with serrate tips (Fig.6,12). According to Fryer (1957a) the most important

sensory setae are the two pappose setae situated on the inner face of the basal segment. Some photographs (not shown here) show that these setae are clearly capable of movement independent of the entire appendage.

The second maxillae move laterally, like the first maxillae, but the former limbs appear to have more antero-postero movement than the first maxillae. The second maxillae hangs below the cephalothorax in some SEM photographs while in others they reach anteriorly as far as the mouth, with the tips of the distal extremity twisted up and converging.

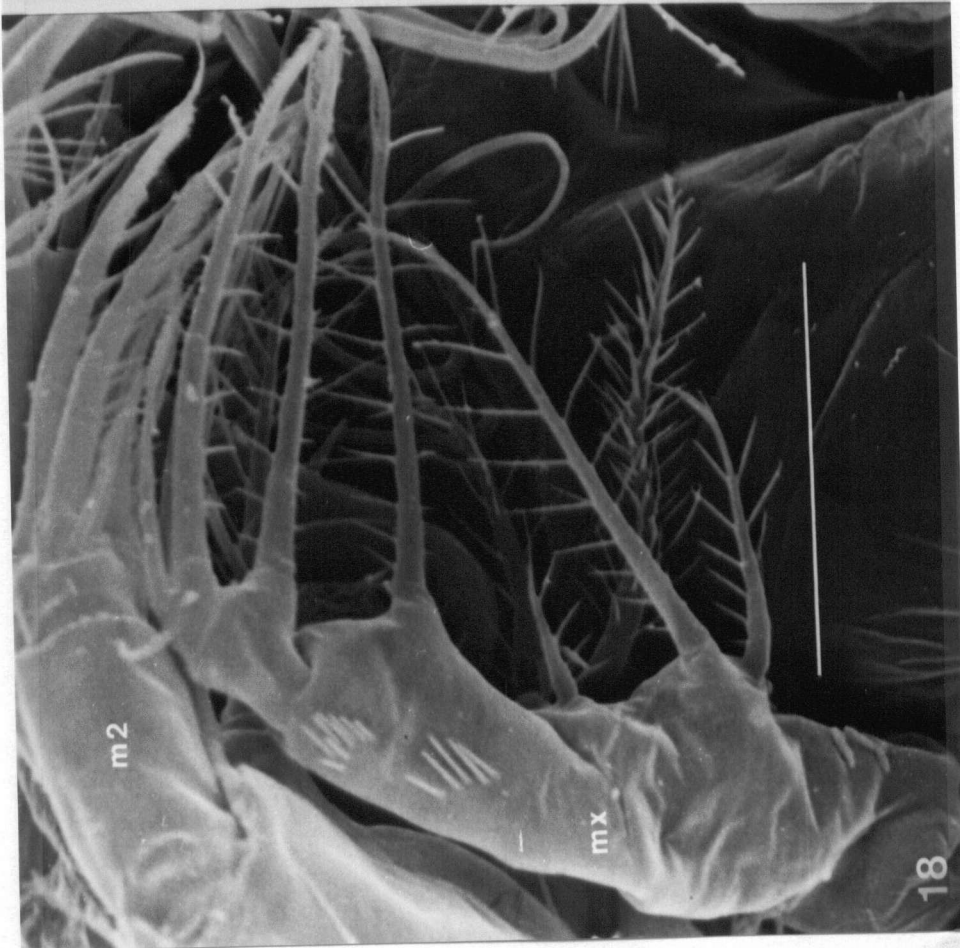
The only difference between the second maxillae in T.prasinus and C.b.thomasi is the presence of some short spiniform setae on the posterior basal segment of T.prasinus. This area is quite smooth, without setae, in C.b.thomasi.

The Maxillipeds

These appendages articulate with the chitinous sternite just below and medial to the second maxillae. Although somewhat similar in structure to the latter, the maxillipeds are more slightly built and more attenuated than the second maxillae (Fig.15,16). The setae are long and sturdy with widely spaced (about 4 μ m), spiny setules (Fig.4,13,18;mx). The basal segment has three setae, all of which are capable of independent movement. The setae on the distal segments are similar in structure to those on the first except that they terminate in serrate setae. The most distal seta is different, more attenuated - almost delicate - and smooth until the terminal serrations (Fig.4,18).

Figure 18. Maxilliped of adult male C.b.thomasi showing the long sturdy setae and widely spaced setules on the maxilliped. Scale - 50 um

Figure 19. The position of the feeding apparatus of an adult female T.prasinus showing the sweeping action of this appendages when handling clumps of food. Scale - 50 um



Movement of these appendages is probably quite similar to the second maxillae. Like the latter, they have a complex system of internal muscles, obvious under the LM, which permits individual segments some independent movement.

The maxillipeds are identical in structure between the two species except that T.prasinus has many more clusters of short spiniform setae, - on the ventral posterior face of the first two basal segments and on the dorsal face of the basal segment (Fig.4). On C.b.thomasi there are only two sparse patches of these setae - on the ventral face of the second segment (Fig.18).

FUNCTIONAL INTERRELATIONSHIP OF THE MOUTHPARTS

As described by Fryer (1957a), the first maxillae are the primary grasping appendages. The second maxillae and maxillipeds play their part in helping to steady the prey, holding or cradling it prior to pushing it forward. Some of the SEM pictures caught T.prasinus in the act of eating a food item and they illustrate the functional flexibility of the feeding appendages. As the animals are momentarily relaxed prior to fixation with ethanol, some of the pressure applied in the living situation is relaxed but the positions are generally maintained. Fig.5 shows a small food item being eaten by a male T.prasinus. The first maxillae clasp the prey on each side while the paragnathae provide a 'vise' ventrally (Fig.5). This immobilization allows the mandibular cusps to tear away at a fixed target from each side. Both the muscle action described by Hartog (1888) and the short spiny setules appear to be used in providing this 'vise' effect. The labral 'mustache' contacts the prey as the prey is forced down against the labral teeth and presumably provides sensory information about the position of the prey prior to contact with the short setae on the inner face of the labrum. These latter setae are stiff and spiny in appearance (all point toward the oral cavity) and may function as 'teeth' or holding devices to prevent the prey from slipping back away from the oral cavity. It is also possible that they function as sensory instruments. The two large outer labral teeth appear (Fig.5) to act as stabilizers. The prey is pushed between these two coarse chitinous projections. The paragnathae may permit more

centering of the prey while the mandibles 'punch' the food into the desirable size for the labral teeth and oral cavity. The cusps on the mandibles are clearly capable of tearing pieces from large food masses although Fryer (1975a) suggests that they are not used to any marked extent for masticating food. Evidence to support this view is provided by the fact that the ingestion of the coracidia of cestodes of the genus Triaenophorus by Cyclops bicuspidatus does not damage the parasite larvae (Miller, 1952). If the mandibles simply 'punch' the food into the appropriate shape for ingestion, small food items or the food mass in the centre of a large food item could be ingested intact. It is impossible to observe whether the labral teeth are simply holding tools or actually play some role in tearing larger prey items. Structurally they appear capable of the latter function as they seem to be hinged to the rest of the labrum (Fig.6). As a result of narcotization the second maxillae and maxillipeds have become displaced, although their cradling action can still be seen (Fig.5). The palpal setae of the first maxillae are also displaced from that in life where they usually splay out over the prey. Although the second maxillae and maxillipeds are clearly unsuitable filtering apparatus, they may be useful in sweeping large clumps of food material toward the mouth region, where the first maxillae can grasp it. This type of action is suggested by Fig.19. The serrate tips observed on the setae of the second maxillae and maxillipeds are probably important in sensing or 'tasting' the quality of the food before it is pushed forward to the mandibles. Sheldon and Laverack (1970)

showed that the serrate setae in the mouthparts of the European lobster Homarus gammarus (L.) are sensitive to chemical stimuli. This function might explain why only the tips are serrate. It would seem unlikely that chemosensitive setae would also be used for holding prey because the possibility of damage to their sensory surfaces would be increased.

As a generalization, T.prasinus has more setae and setules than C.b.thomasi. The plumose setae on the mandibular palp of T.prasinus may provide a finer-grained sensory input than the simple setae of C.b.thomasi. The patches of short spiniform setae on the two pairs of posterior feeding appendages of T.prasinus are probably also sensory instruments. If T.prasinus is a functional omnivore preferring smaller food items, this species may need to be more discriminating than C.b.thomasi to select between food and non-food particles in the environment. Gross movement of the food item will not provide the sensory cue for T.prasinus, that it apparently does for C.b.thomasi (Kerfoot, 1978), if copepodid and adult instars feed on non-motile algae.

DISCUSSION

The structure of T.prasinus and C.b.thomasi mouthparts are remarkably similar at the level of detail possible with the LM, although adult female T.prasinus appendages are approximately 15% smaller than C.b.thomasi. In the University of British Columbia Research Forest Lakes, T.prasinus adults appear in the plankton in early August, at a time when the major proportion of the C.b.thomasi population is in copepodid instars IV and V. Mouthpart structure between the two species is so similar (even in size in these stages) that one might predict, from a study of the feeding appendages alone, that intense competition is the reason for their inability to thrive together. However, under SEM some differences in mouthpart structure are apparent.

In general, T.prasinus has more sensory equipment (more setae and setules) than C.b.thomasi. The most striking differences are the longer, more plumose setae of the mandibular palp and the plumose setae (rather than simple setae as in C.b.thomasi) of the palp of the first maxilla. The more filamentous setae may reflect a greater sensitivity to the food environment than is possible for C.b.thomasi, permitting finer discrimination between edible and inedible particles. Alternatively, the finer construction of the adult T.prasinus feeding apparatus may have no functional importance. Thus the practical structure may be identical, although slightly smaller in size. As C.b.thomasi is a vigorous carnivore (McQueen, 1969; Anderson, 1970a; Brandl and Fernando, 1975, 1978), the remarkable similarity between C.b.thomasi and T.prasinus in adult mouthpart structure may indicate that T.prasinus is also

an active carnivore in the later instars. If this is true, T.prasinus may experience intense competition for scarce food resources, such that adult females may have difficulty sequestering sufficient food energy for egg production. The relative rarity of T.prasinus in Placid Lake may therefore be the result of a competitive interaction with C.b.thomasi. The latter species may have an advantage in that it appears in the spring and therefore reproduces before there is competition from T.prasinus for food. In any case, it is obvious from this study that adult mouthpart structures are too similar between C.b.thomasi and T.prasinus to provide clear evidence of dietary differences.

II. EXPERIMENTAL STUDIES ON THE FACTORS LIMITING TROPOCYCLOPS
PRASINUS IN AN OLIGOTROPHIC LAKE

INTRODUCTION

The resolution of the interactions that determine an organism's distribution and abundance is a basic problem in ecology. Dissecting the causative connections while maintaining some semblance of reality can be very difficult. The limnetic crustacean community in temperate aquatic ecosystems offers several advantages in examining distribution/abundance questions because many species are ubiquitous and yet each community is relatively simple in structure. Patalas (1971) noted that it is characteristic of these communities "that only a few species are generally abundant, the rest remaining scarce". Explanations for this phenomenon are numerous, but can be summarized by two basically different conceptual models which are exemplified by the following research: those studies that emphasize the role of 'habitat' in limiting an organism's success and those that focus on the importance of predation. The importance of some 'habitat' limitation in structuring the observed species association is emphasized by many investigators, although the relevant feature may be physical (Patalas, 1971), chemical (Sprules, 1975), spatial (Sandercock, 1967; Watson and Smallman, 1971), or some limitation in the quantity or quality of available food (Patalas, 1972; Sprules, 1972). However, others argue that predator-prey interactions are of major importance in structuring plankton communities (Brooks and Dodson, 1965; Hall et al., 1970; Dodson, 1974; Hall et al., 1976; Lane, 1978; Zaret, 1978). Several studies have suggested that even invertebrate predators have the potential

to act as significant mortality agents limiting the success of other limnetic macrocrustaceans (McQueen, 1969; Dodson, 1972; Fedorenko, 1973; Confer and Cooley, 1977; Boers and Carter, 1978; Lane, 1979). Among the invertebrate predators, cyclopoid copepods appear to have the ability to influence the abundance of other zooplankters and they may even dampen their own population numbers through intraspecific predation (McQueen, 1969; Lane, 1979). However, within any one lake there are rarely more than one or two numerically dominant cyclopoid copepod species although these species may be widespread across many different communities (Pennak, 1957; Patalas, 1971). Using classical descriptive techniques, it has proven quite difficult to conclusively demonstrate whether some 'habitat' limitation is all-important to these copepods or whether predators play the key role.

Tropocyclops prasinus (Fischer)1860 and Cyclops bicuspidatus thomasi (Forbes)1882 (Yeatman, 1959) are two very common species of cyclopoid copepods. T.prasinus is considered a warm water form (Guerney, 1931; Rylov, 1963; Yeatman, 1959), although T.p.mexicanus is common in deep water bodies (Patalas, 1971). C.b.thomasi is a species described by Patalas (1971) as common in large, deep lakes in the Experimental Lakes Area in northwestern Ontario and rarely found in small, shallow lakes. However, it is common in shallow lakes elsewhere (Patalas, 1964). Carl (1940) describes C.b.thomasi as occurring in ponds or lakes regardless of size or alkalinity and T.prasinus as "widely distributed". Anderson (1974) describes C.b.thomasi as common in cold low

salinity lakes although Whittaker and Fairbanks (1958) report C.b.thomasi in lakes of high salinities and Williams (1977) collected C.b.thomasi from Chesapeake Bay, a marine environment. There does not seem to be any easy identification of cyclopoid species with lake 'type', and it seems probable that species interactions are important in creating some of the observed distribution and abundance patterns.

This study was carried out to explore two questions relating to the distribution and abundance of cyclopoid copepods: are cyclopoid copepod interactions important in determining the dominant cyclopoid copepod species within a given community? and what part does 'habitat' limitation versus predator-prey interactions play in restricting the number of coexisting cyclopoid copepod species? This study experimentally examines the factors which determine the relative abundance of T.prasinus and C.b.thomasi in a small oligotrophic lake in coastal British Columbia.

Study Area

The montane lakes of the University of British Columbia Research Forest are particularly suitable systems in which to study cyclopoid copepod interactions because year to year differences are remarkably small in spite of a dynamic seasonal pattern (Walters, unpub. data). In addition, four of these lakes have been sampled regularly over the last six years so the seasonal patterns are known (Northcote and Clarotto, 1975; Neill, 1978; Northcote et al., 1978). Although cyclopoid copepods are present in all four lakes, only two species are abundant, T. prasinus and C. b. thomasi. Table 1 summarizes some of the physical, chemical and biological characteristics of two of these lakes, one where T. prasinus is relatively abundant (Gwendoline Lake) and the other (Placid Lake) where T. prasinus is quite rare. Despite some physical-chemical differences, both lakes contain the same assemblage of crustacean zooplankton (with the single exception of a calanoid copepod). The main differences in the crustacean communities are in the relative abundances of species. There are also different species of midge fly larvae, Chaoborus, between the two lakes and Placid Lake contains trout (Salmo clarki clarki) whereas Gwendoline Lake does not.

T. prasinus reaches higher densities in the deeper and cooler Gwendoline Lake (to a summer peak of 0.5 animals per litre compared to 0.1 per litre in Placid Lake) although the food base in Placid does not seem to differ significantly from that in Gwendoline Lake. Algal biomass (varying between 0.04 and 0.08 mg per litre ash-free dry weight) and particulate

Table 1

Some physical, chemical and biological characteristics of Placid and Gwendoline Lake.*

CHARACTERISTICS	Placid	Gwendoline
Elevation, m.	510	522
Drainage area, ha.	44	81
Surface area, ha.	1.6	13.0
Maximum depth, m.	7	27
Colour, Pt units	20-25	15
Transparency (Secchi depth, m.)	4-6	5-7
pH	6.6	6.6
Total Carbon (mg l-1)	5.0	3.0
Total Phosphorus (mg l-1)	0.006	0.003
Total Organic Nitrogen (mg l-1)	0.17	0.05
Total Dissolved Solids (mg l-1)	17-23	18

CRUSTACEAN ZOOPLANKTON SPECIES +

<u>Diaptomus kerai</u>	A	A
<u>Diaptomus oregonensis</u>	A	---
<u>Diaptomus lentonus</u>	---	A
<u>Daphnia rosea</u>	A	A
<u>Holopedium gibberum</u>	A	A
<u>Diaphanosoma brachyurum</u>	A	A
<u>Rosmina longirostris</u>	R	A
<u>Ceriodaphnia quadrangula</u>	R	R
<u>Polypheusus pediculus</u>	A	A
<u>Cyclops bicuspidatus thomasi</u>	A	R
<u>Tropocyclops prasinus</u>	R	A

* adapted from Neill (1978)

+ Key to symbols: A = abundant R = rare --- =absent

organic matter concentrations (particles passing through a 73 um mesh net) are low in both lakes (from 0.3 to 1.4 mg per ash-free dry weight). Bacterial populations also appear to be low ($<10^5$ cells per ml).

Placid Lake seems more suitable habitat than Gwendoline Lake for T.prasinus, being shallow and generally the warmer of the two lakes - that is, more pondlike. I chose Placid Lake for study because C.b.thomasi is much more abundant than T.prasinus in this lake in spite of the fact that Placid Lake seems physically more suited to T.prasinus.

MATERIALS AND METHODS

Laboratory Experiments

1. Diet of T.prasinus

Food limitation is often cited as one of the factors limiting the success of zooplankton populations (Gliwicz, 1969; Hall et al., 1970; LeBrasseur and Kennedy, 1972). Several studies have shown that C.b.thomasi is predaceous in the later instars (McQueen, 1969; Anderson, 1970). However, the trophic status of T.prasinus is unknown. Fryer (1957b) suggests that smaller cyclopoid copepod species tend to be herbivorous, even as adults. If T.prasinus is herbivorous in the copepodid and adult instars, this species may be competing with calanoid copepod and cladoceran grazers for scarce food resources. Alternatively, if the later instars are predaceous on other macrozooplankters, T.prasinus may suffer from resource and/or interference competition with late instar C.b.thomasi. In order to understand the role of T.prasinus in the Placid Lake food environment, the ability of this species to ingest and assimilate algae was first tested.

To accomplish this, four species of algae commonly found in the Research Forest lakes (Dickman, 1968; Stein, 1975) were fed to naupliar, copepodid and adult T.prasinus. Pure cultures were obtained from the laboratory of Dr.J.Stein,

Dept. of Botany, U.B.C. and the Indiana University Culture Collection of Algae. I cultured the algae on modified Chu's medium (Fogg, 1966) and illuminated the cultures by fluorescent light at $20 \pm 2^\circ\text{C}$. Algae for use as radioactive food were saturation labeled by adding 20 μCi of $\text{NaH}^{14}\text{CO}_3$ in 1 ml. of sterile distilled water to 50 ml. of log growth phase culture 2 days before use. Actively growing algal cells at a known concentration (determined by haemocytometer counts) were suspended in lake water which had been filtered through a glass fibre filter. Eight 300 ml bottles lined with a 73 μm mesh bag fitted with a draw-string were filled with the algal-water mixture and 30-70 animals were placed in each bottle. The bottles were mounted on a slowly rotating wheel at 0.25 rpm. Freshly collected zooplankton were preconditioned for 4 hours prior to the test by incubating the animals with the food type and at the temperature to be used in the experiment. After the acclimation period the non-radioactive algal suspension was siphoned away and the bottles were refilled with a radioactive diet of the same concentration and temperature. Loss of animals, particularly when nauplii were used, was prevented by siphoning outside the mesh bag. The animals were incubated for 8-10 hours, and then washed free of the labelled food with filtered lake water and exposed for 1 hour to non-labelled food in the same manner. After this period the animals were removed from the bottles in the mesh bag, sorted by instar group and species, anaesthetized in carbonated water, killed in hot water and transferred to glass scintillation vials, each containing 0.2 ml of Protosol tissue solubilizer. Each vial

was tightly capped and placed in an oven at 40°C overnight. Upon cooling, 10 ml of toluene scintillation solution (4 g PPO¹, 0.2 g POPOP² in 1 litre toluene) were added.

I checked possible background counts caused by inadequate washing, etc. by carrying a group of freshly killed animals through the experimental steps. This background was always negligible.

All experiments were conducted at an algal cell concentration of about 20×10^3 cells per ml. Whenever different T. prasinus instars had been fed together, equal numbers of each stage were included. Food radioactivity was determined by counting several 2 ml aliquots of the food suspension filtered on to 0.45 HA Millipore membranes and dissolving these in 10 ml Bray's liquid scintillator (Bray, 1960). Samples of identical non-radioactive diet were concentrated for weighing by filtering 100 ml on to a preashed tared glass fibre filter. I dried these samples overnight at $60 \pm 2^\circ\text{C}$, weighed them on a Cahn electrobalance, ashed the samples at 600°C for 3 hours and reweighed to determine ash-free dry weight. Detection and measurement of radioactivity was done by liquid scintillation spectrometry using a Searle Isocap 300 liquid scintillation counter. Counts were converted to disintegrations per minute (DPM) using an external standard to determine the efficiency of counting (Sorokin,

¹PPO = 2,5-diphenyloxazole

²POPOP = 1,4-bis-[2-(5-phenyloxazolyl)]-benzene

1966; Wolfe and Schelske, 1967). I determined dry weights for all groups of animals used in the experiments by sorting freshly collected zooplankton by instar and species and transferring them to preashed and tared glass fibre filters. After drying at 60°C for 2 days, at least three replicates of 40 or more animals were weighed on a Cahn electrobalance.

I observed T.prasinus eating protozoans in culture vessels, suggesting that T.prasinus is an omnivore. To test the acceptability of a plant versus an animal diet I fed copepodid I on a uni-algal (not bacteria-free) and a uni-protozoan diet. Copepodids were reared individually at 20±1°C in 20 ml of lake water cleared through a 0.45 µm HA Millipore filter. I added Chlorella vulgaris at 20 X 10⁶ cells/ml to 40 vials and Paramecium sp. at approx. 5 X 10² animals/ml to an additional 40 vials. According to Brandl (1973), both food densities were in excess of daily needs (visual checks ensured that abundant food was always present before the next food addition). The food densities therefore represent 'optimal' conditions on these diets. The water was changed, food added and instar analyzed under a dissecting scope at 25X magnification, every other day. Male and female adults from this experiment were put together in pairs, the number of females developing eggs noted and the egg-sacs dissected and eggs counted.

2. Feeding rates: C.b.thomasi on T.prasinus

As C.b.thomasi (IV, V and adult) are the most common stages in the lake when T.prasinus appears in the plankton, these instars were used as predators in experiments to determine predation rates of C.b.thomasi on T.prasinus. The design included single and multispecies prey experiments to assess the importance of alternative prey in altering predator impact. To check the effect of container size on predation rates, six copepodid V C.b.thomasi were placed in 1, 1.5 and 2 litre beakers with T.prasinus nauplii at a density of 50 animals per litre and placed in an environmental chamber for 24 hours at $20 \pm 1^\circ\text{C}$. There was no difference in predation rate between the 3 beaker sizes, and 1 litre vessels were used for all subsequent predation trials. Six predators and a known concentration of prey were added to each beaker. I obtained T.prasinus nauplii by hatching the eggs from wild ovigerous females in the laboratory. All other prey were obtained directly from the lake. The experiments were carried out in semidarkness (beakers covered with foil), and placed in a constant temperature chamber at $20 \pm 1^\circ\text{C}$ for 24 hours. At the end of this period all animals were sieved through a 54 μm plankton mesh and rinsed into a petri dish for counting at 25X magnification under a dissecting microscope. Five replicate controls containing 20 T.prasinus but no C.b.thomasi were used to assess natural mortality (there was none) and counting variation (less than 2%). Alternative prey species were provided to evaluate C.b.thomasi impact on T.prasinus nauplii when presented with a choice. These species included (in

descending order of abundance) immature Diaphanasoma brachyurum (<1.0mm), immature Daphnia rosea (<1.0mm), calanoid nauplii, and C.b.thomasi copepodids I-III. Fifteen alternative prey per litre were provided at a T.prasinus prey density of 1 nauplius/litre and 5 nauplii/litre, 30 alternatives per litre at 10 T.prasinus nauplii/litre and 45 alternatives at 30 T.prasinus nauplii/litre. Densities of alternative prey in the 5 T.prasinus nauplii/litre experimental beakers were the mean densities encountered at 1.5 m depth in Placid Lake in August, 1976. Prey eaten were not replaced during the 24 hour period.

Field Experiments

The importance of predation versus food limitation on the success of T.prasinus was experimentally examined under field conditions. The effect of vertebrate predators was not studied because Shepherd (1970) found that cyclopoids were rarely present in the gut contents of the only fish in the lake, cutthroat trout. It also seemed improbable that fish would selectively eliminate the smaller of the two cyclopoid species. Salamander predation (Taricha granulosa, Ambystoma gracile) is considered unlikely as such animals are only planktivorous for a short period in the midsummer (Giguere, 1973) and do not coincide with the cyclopoid cycles of seasonal abundance. Among invertebrate predators, only Chaoborus larvae and C.b.thomasi were sufficiently abundant in the plankton to have an important impact. Fedorenko (1973), extrapolating from single species laboratory experiments,

argued that Chaoborus trivittatus larvae could account for as much as 30% of the calanoid copepod mortality in a nearby lake in the Research Forest. However, Neill (1978) found no detectable net impact on any members of the zooplankton community when Chaoborus flavicans densities were increased by 3X that of the lake in large in situ enclosures sampled from July through September, 1975. However, adult numbers of C.b.thomasi declined faster in the Chaoborus bags than in those treatments without Chaoborus (Neill, pers.comm.). Experiments repeated in the spring of 1976 again showed no net impact on the prey zooplankton abundance at Placid Lake densities of the predator (Neill, pers.comm.). McQueen (1969), in a study on nearby Marion Lake, concluded that 25-35% of the C.b.thomasi population perished through cannibalism. As C.b.thomasi is abundant in Placid Lake, possible interactions between the two cyclopoid copepod species were evaluated through manipulations of the zooplankton community.

The manipulations were carried out in large in situ experimental enclosures from late June until November, 1976. The enclosures were similar in design to those used by Neill (1978). They were made of clear 4 mil polyethylene plastic bags, 1.5 m wide and as deep as the deepest part of the lake (6 m) but not in contact with the sediments because they were sealed at the bottom. These tubes were suspended from a wooden and polystyrene frame floating on the surface. The enclosures held approximately 10^4 litres of water and were first filled by pumping lake water through a 54 μ m mesh plankton net. This removed all the crustaceans yet permitted

passage of grazable seston. Natural lake densities of Placid Lake crustaceans were then added to the enclosures from pooled zooplankton samples obtained from depth-stratified horizontal tows with a Clark-Bumpus sampler. There were no fish or Chaoborus larvae in any enclosures. Three experimental conditions were produced: (1) T.prasinus plus all Placid Lake zooplankton, including C.b.thomasi (2) T.prasinus plus Placid Lake zooplankton, excluding C.b.thomasi (3) T.prasinus alone. All zooplankton were collected in Placid Lake and added at Placid Lake densities with the exception of T.prasinus. This species was added at 1.5X the low density found in Placid Lake to permit adequate sampling.

Plankton sampling

Zooplankton sampling was done every 5-7 days in these enclosures and in the lake with an electric pump, capable of pumping 25 litres per minute. Each sample was collected by filtering through a 54 um plankton net. Possible selectivity by this sampling gear was checked by adding nonovigerous representatives of the community to be sampled, Diaptomus sp., C.b.thomasi, and Daphnia rosea, to four 180 litre aquaria in known concentrations and resampling after 5 hours. A Chi-square analysis to test for replicability of the pump samples showed that all three species were obtained randomly (Table 2). This sampling method was thus considered suitable for

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Table 2

Comparison of 4 replicate samples of representative zooplankton in 180 l. aquaria using the electric pump (mean with S.E.).

	mean added (S.E.)	mean recovered (S.E.)	χ^2	p
<u>Diaptomus</u> <u>sp.</u>	1.3 (0.01)	1.2 (0.02)	5.62	>0.05
<u>D. rosea</u>	1.2 (0.005)	1.1 (0.02)	4.0	>0.05
<u>C. b. thomasi</u>	0.6 (0.002)	0.5 (0.01)	3.3	>0.05

estimating the abundance of the Placid Lake crustacean community. Copepods are noted for an effective escape response (Drenner et al., 1978). Therefore I field-tested the replicability of the pump samples for the copepods in Placid Lake by taking four tows in close succession at the same depth on May 7, 1976. I counted all D.oregonensis, D.kenai and C.b.thomasi collected. A Chi-square analysis showed that these copepods were obtained with equal efficiency (Table 3). This result confirmed the aquaria tests with representative crustacean populations and showed that the copepod species found in Placid Lake could be sampled with replicable results with the electric pump.

In the enclosures, 3 samples of 50 litres each were taken representing 3 depths: surface, mid-depth and bottom. In the lake, 100 litre samples were taken at one metre intervals from surface to bottom (5.5m), along a transect at the deepest part of the lake (Fig.20, Transect A). Three additional transects (Fig.20, B, C, D) were sampled, all of which were in different parts of the littoral zone. The same sampling gear used in the enclosures was used in the lake.

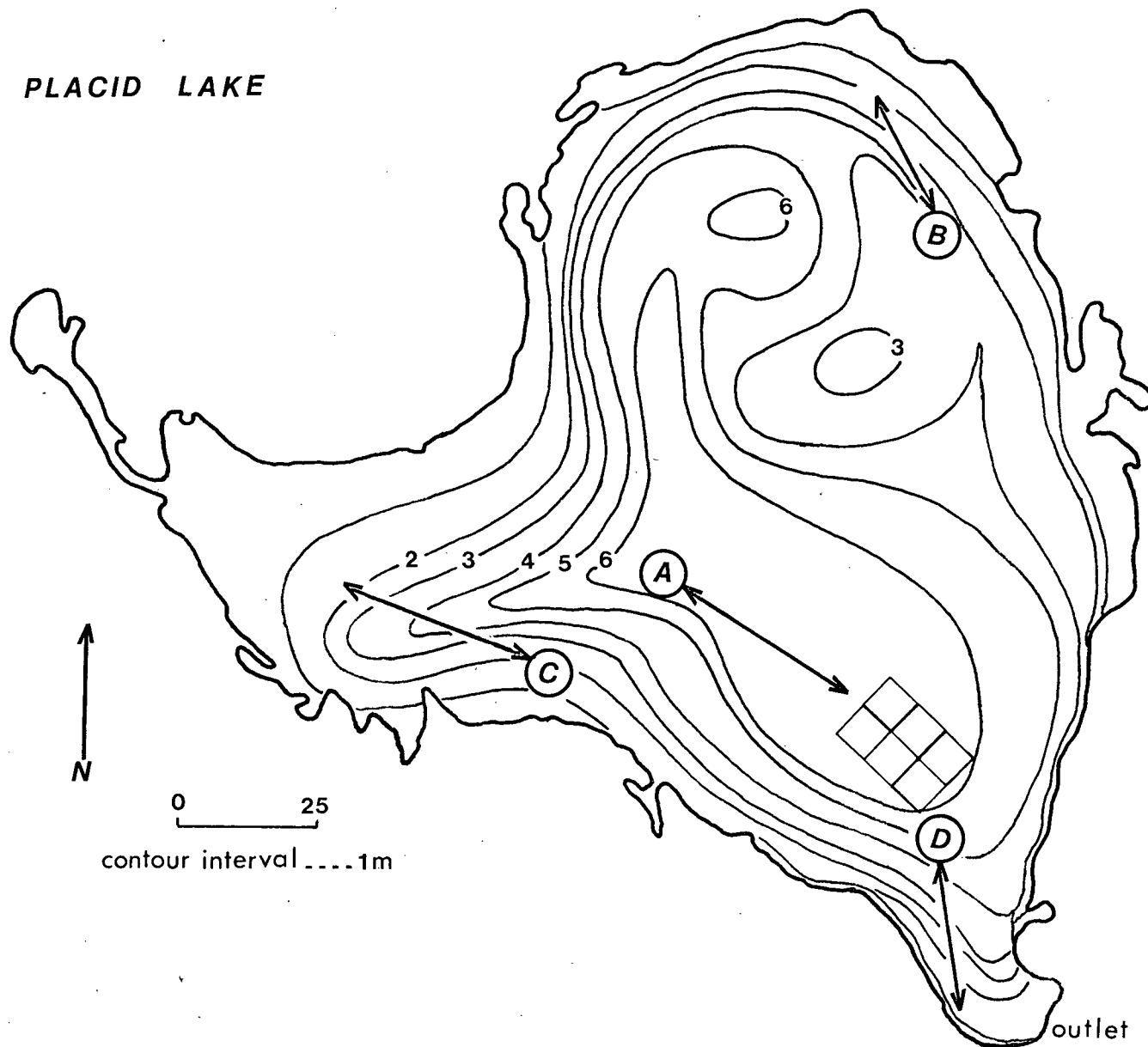
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Table 3

Comparison of 4 transects taken at 2.5 m. along transect A in Placid Lake.
values are given in numbers per 100 litres.

Tow No.	<u>D.oregonensis</u>	<u>D.kenai</u>	<u>C.b.thomasi</u>
1	273	73	238
2	276	90	242
3	267	70	246
4	248	58	240
χ^2	2.45	7.16	0.35
p	>0.05	0.05	>0.05

Figure 20. Contour map of Placid Lake in the U.B.C. Research Forest. Sampling transects are indicated by A, B, C and D. B, C and D represent different parts of the littoral zone. Squares indicate the location of the experimental enclosures.

PLACID LAKE



Plankton counting

Samples from the enclosures were examined in toto under 25X magnification for species' abundance, reproductive condition and instar distribution (Yeatman, 1959; Torke, 1974). Lake samples were always counted in their entirety for T.prasinus, or whenever numbers were below 100 animals, for all other species; otherwise, samples were diluted to 900 ml and two or three replicates of approximately 150 ml were taken for examination, using the subsampler described in Northcote and Clarotto (1975). Counts from these subsamples were averaged and adjusted to 100 l of lake volume sampled. The total numbers of rotifers, cladocerans by species, diaptomid nauplii, and diaptomid copepodids by species were recorded, as well as any mites, Chaoborus larvae, and chironomid larvae. C.b.thomasi and T.prasinus populations enumerated as nauplii I, II, III, IV, V and copepodid I, II, III, IV, V, adults, adult females, adult females with eggs and eggs. The number of eggs per clutch was also recorded for the cladoceran and copepod species. The same methods were used to collect and analyse samples during a 24 hour sampling regime to provide data on the vertical migration patterns of the zooplankton in the enclosures and in the lake.

Temperature, Oxygen and Grazeable Seston

Temperature and oxygen profiles in Placid Lake were monitored from surface to the 5.5 depth stratum at 1 m intervals using a Yellow Springs Instruments temperature/oxygen meter from May to November. Biweekly water samples were collected from all depths, pooled and 'fixed' with Lugol's Solution (Vollenweider, 1969) for laboratory examination of particulate organic matter concentrations. In the laboratory, all particles less than 73 μm were collected on a glass fibre filter, dried overnight at $60 \pm 2^\circ\text{C}$, and weighed on a Cahn electrobalance, ashed at 600°C for 3 hours and reweighed to permit calculation of the ash-free dry weight. Similarly, water samples were collected biweekly for examination of algal size and type. 100 ml of lake water was fixed with Lugol's Solution and filtered onto a 0.45 μm Millipore filter. All the filters were cleared in Cedar Wood oil for 10 days, mounted on glass slides and counted with a phase contrast microscope at 500X magnification. Cells were counted by size class and type to a minimum of 200 cells per field or 10 ocular fields. Size classes were enumerated as <2, 3-6, 7-10, 11-14, 14-20, >20 micrometres and cell type was identified as diatom, solitary, colonial or filamentous. Species were identified where possible according to Prescott (1970). The fields to be counted were randomly selected before counting began. Initial counting across the diameter of several cleared filters showed that the cells were randomly distributed across the surface (determined by a Poisson distribution and χ^2) and therefore this sampling method was appropriate.

RESULTS

FEEDING EXPERIMENTS

Diet of T.prasinus

To evaluate the status of T.prasinus in the trophic structure of Placid Lake, feeding experiments were conducted in the laboratory. If T.prasinus is herbivorous through all instars, the abundance and temporal spacing of the other grazers in the system could be critical in determining the success of T.prasinus. Alternatively, if animal food sources are required, T.prasinus might limit its own population through cannibalism, or compete with C.b.thomasi for food. A measure of this species' ability to assimilate algae was obtained by feeding the most palatable (Brandl, 1973) of the algae commonly found in the Research Forest (Dickman, 1968; Stein, 1975). Sorokin's (1968) "index of assimilation", the assimilated fraction of the carbon consumed (Appendix A), was calculated to compare the relative effectiveness of feeding among different instars and to permit comparison with known herbivores. Carbon content was assumed to be 50% of the ash-free dry weight of the animal (Vollenweider, 1969). Mean weights used in calculating assimilation are shown in Table 4. This method of estimating assimilation is a relative measure, undoubtedly a

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Table 4 Mean length and dry weight of D.rosea and T.prasinus
from Placid Lake, 1976.

	Length (mm)	Dry Weight (ug)
<u>D.rosea</u>	1.32	14.20
<u>T.prasinus</u>		
adult	0.70	2.57
copepodid	0.45	1.14
nauplii	0.10	0.17

low estimate of assimilation as it must assume that there is no loss of absorbed carbon through respiration or excretion. However, it is adequate for the purpose of comparison. The results of these experiments are shown in Table 5. T.prasinus seemed to utilize all algal types less efficiently than the cladoceran, Daphnia rosea. However, values for the assimilation of Ochromonas and Chlorella are comparable to those of a predaceous cyclopoid on a cladoceran prey (Sorokin, 1968). This result suggests that at least some algal types are efficiently assimilated by T.prasinus nauplii. Assimilation efficiency decreases by the adult instar.

T.prasinus adults in culture vessels were observed feeding on protozoans on the surface and cannibalism was not observed. When T.prasinus appeared in the plankton in late July particulate organic matter in the lake was very low, as was the standing crop of phytoplankton. Consequently, food limitation seemed a likely hazard for a population that first appeared in the plankton during this period. However, if a plant or animal diet was equally acceptable an opportunistic species might be able to circumvent this difficulty. It is also possible that T.prasinus might prefer microzooplankters and only supplement its diet with algae. To assess the acceptability of an algal diet versus an animal food source, copepodids were reared on a uni-algal (but not bacteria-free) and a uni-protozoan diet from copepodid I to adult. Survivorship, proportion of ovigerous females, and number of eggs per female were unaffected by the type of diet provided (Table 6). This result suggests that T.prasinus is probably

Table 5 Index of assimilation estimated for T.prasinus and D.rosea on different food species at 15+2 C. n=8

FOOD	CONSUMERS	Ca/C (SE)
<u>Chlorella</u>	<u>T.prasinus</u> adult	19.2 (2.3)
	C4-5	32.7 (1.4)
	C1-3	21.8 (1.2)
	N3-6	35.2 (0.8)
	<u>D.rosea</u> adult	39.6 (3.2)
<u>Ochromonas</u>	<u>T.prasinus</u> adult	20.5 (2.1)
	C4-5	25.3 (1.9)
	C1-3	26.7 (1.4)
	N3-6	29.6 (1.1)
	<u>D.rosea</u> adult	35.1 (2.0)
<u>Chlamydomonas</u>	<u>T.prasinus</u> adult	13.1 (1.2)
	C4-5	14.6 (0.9)
	C1-3	18.3 (1.2)
	N3-6	20.4 (0.7)
<u>Scenedesmus</u>	<u>T.prasinus</u> adult	2.1 (0.2)
	C4-5	1.0 (0.1)
	C1-3	0.2 (0.1)
	<u>D.rosea</u> adult	19.6 (1.2)

Table 6 Survivorship from copepodid I to adult T. prasinus, subsequent egg development and number of eggs per female (SE) on a plant versus animal diet. n=5

	% Survival	% Egg Development	No.Eggs/Female
Protozoa	92	81	16 (0.9)
Algae	83	79	15 (1.1)

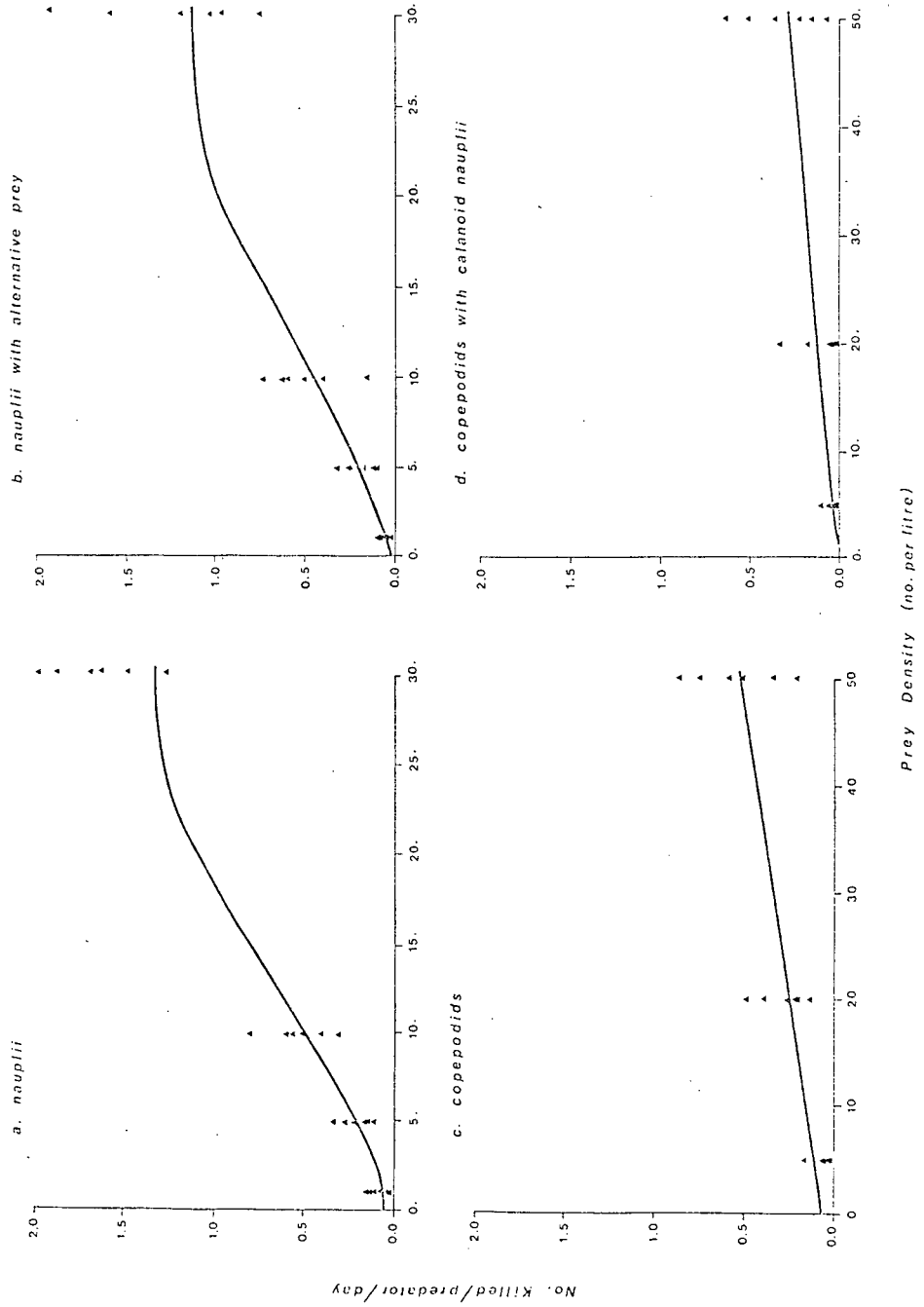
opportunistic in the wild, taking plant or animal food as available. However, as algae do not appear to be assimilated as efficiently by T.prasinus as by the herbivorous cladoceran tested, T.prasinus may be at a disadvantage when both microzooplankters and algal food resources are low. T.prasinus was also observed apparently eating dead zooplankters in culture vessels.

Effects Of C.b.thomasi Predation in Laboratory Experiments

T.prasinus nauplii and copepodids were fed alone and with alternative prey to C.b.thomasi copepodids IV, V and adults. In experiments with T.prasinus nauplii I-VI as prey (Fig.21a), predation rate reached a maximum of 1.9 prey per predator per litre per day at the highest prey density of 30 prey per litre. This predation rate was higher than the rate obtained by McQueen (1969) at about 190 C.b.thomasi nauplii per litre, the lowest C.b.thomasi naupliar prey concentration he tested. Anderson, (1970a) found a mean prey consumption per predator per day of 6.3 for Cyclops vernalis but only 0.19 for C.b.thomasi. The mean predator-to-prey size ratio in Anderson's study was 0.85/1 whereas the ratio of C.b.thomasi predator to T.prasinus prey in this study was about 2.6/1. This size ratio was comparable to that of C.vernalis in Anderson's study. However, both Anderson and McQueen used unnaturally high prey densities. Jamieson (1977) used more realistic prey densities and found that copepodid IV instars of Mesocyclops leukarti killed about 1.5 calanoid nauplii per litre per predator per day at a prey concentration of 30 prey

Figure 21. Predation rates for C.b.thomasi copepodids IV, V and adults on T.prasinus nauplii and copepodids with and without alternative prey as a function of density. Six replicates at each prey density are shown. Equations for the fitted regressions lines are given, PR represents the predation rate and x represents the prey density.

- | | | |
|----|---------------------|------------|
| A. | $PR = 0.07x^{0.87}$ | $r^2=0.85$ |
| B. | $PR = 0.05x^{0.93}$ | $r^2=0.88$ |
| C. | $PR = 0.01x + 0.08$ | $r^2=0.66$ |
| D. | $PR = 0.01x + 0.02$ | $r^2=0.50$ |



per litre.

When alternative prey were added (Fig.21b), the predation rate was essentially unchanged at the lowest prey concentration (mean of 0.05 prey per predator per day). Even at the highest prey concentration of 30 nauplii per litre with alternative prey the predation rates between those experiments with alternative prey and those without alternatives were not significantly different ($X^2=0.64$, $df=5$). McQueen (1969) also found that C.b.thomasi fed at similar rates on selected prey species when tested in mixed and single prey assemblages. However 1 T.prasinus nauplii/litre was slightly higher than density estimates for T.prasinus nauplii in the lake. The equation $y = 0.05x^{0.93}$ gave the best fit to the data ($r^2 = 0.88$), where x =prey density. Thus the estimated lake prey density was used to extrapolate the predation rate for each date on which predation could occur (August 11 to October 18).

The predation rate on T.prasinus copepodids I-IV with a smaller and probably more attractive alternative prey, Diaptomus nauplii, (Fig.21d) was 0.04 at 5 prey per litre, lower than the predation rate on T.prasinus copepodids I-IV alone (Fig.21c). When alternative prey were present, assuming a straight line relationship ($r^2=0.43$, $y=-0.02+0.01x$), the predation rate of the C.b.thomasi predators on T.prasinus copepodids dropped to zero by 2 prey per litre. As this concentration of T.prasinus prey was higher than that observed in the lake (maximum T.prasinus copepodid densities were 0.4 per litre), predation on these stages was probably not important. The T.prasinus population was sufficiently reduced

by the copepodid instars that few predators were encountered. Jamieson (1977) showed that switching did not occur when adult female Mesocyclops were fed large and small Ceriodaphnia. Mesocyclops killed its prey as a simple function of the relative abundance of the prey in the environment. It seemed probable that the very low predation rates of C.b.thomasi on T.prasinus copepodids, even at 5 prey per litre, was a reflection of apparent scarcity. The tendency for T.prasinus copepodids to concentrate near the surface, observed in laboratory aquaria, might have reduced encounter rates. The extent to which this behaviour occurs in nature is unknown but it appeared that the brunt of C.b.thomasi predation probably fell on the naupliar stages of T.prasinus .

FIELD EXPERIMENTS

Seasonal Abundance of C.b.thomasi and T.prasinus

C.b.thomasi

C.b.thomasi was the dominant cyclopoid copepod in Placid Lake. After ice broke up, the first individuals caught were stage IV and V (Fig.22). By mid-May these copepodids had moulted to the adult stage and produced eggs by the end of May. Eggs hatched in early June. By the end of June nauplii had moulted to copepodids and by the middle of July more than half the population had reached copepodid IV stage. The majority of the population was usually represented by only two or three instars (Fig.23). This uniformity of instar on any given sampling day has been noted in many natural cyclopoid copepod populations, and has been attributed to cannibalism (Smyly, 1961; McQueen, 1969; Anderson, 1970b). A small pulse of eggs was produced in early September but most of the population remained in the copepodid IV and V stages until they disappeared from the plankton in early November.

Figure 22. Changes in the standing crop of C.b.thomasi in Placid Lake in 1976.

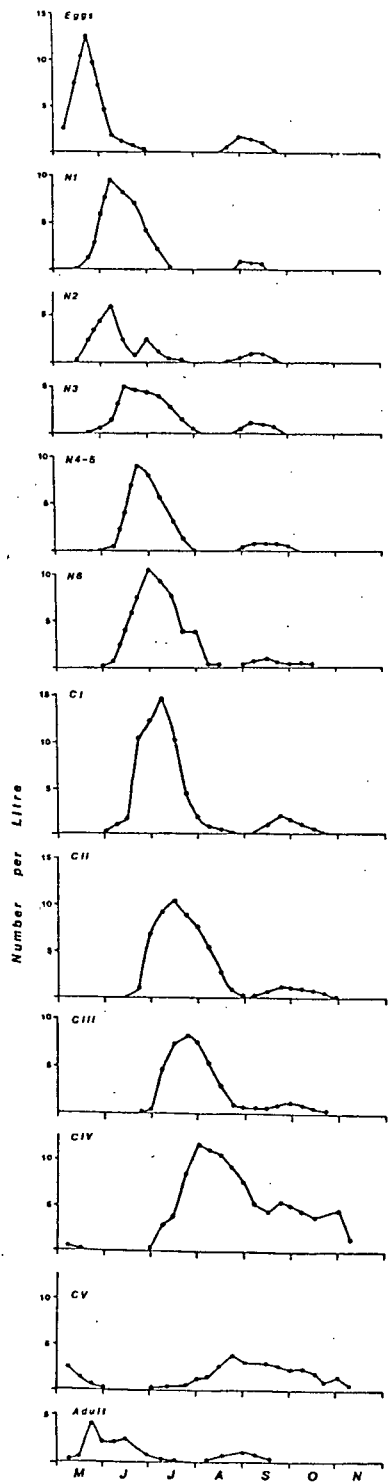
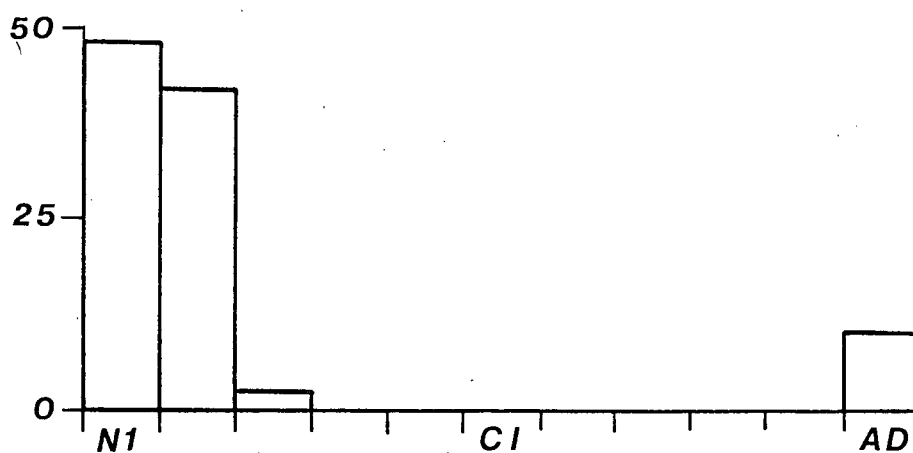
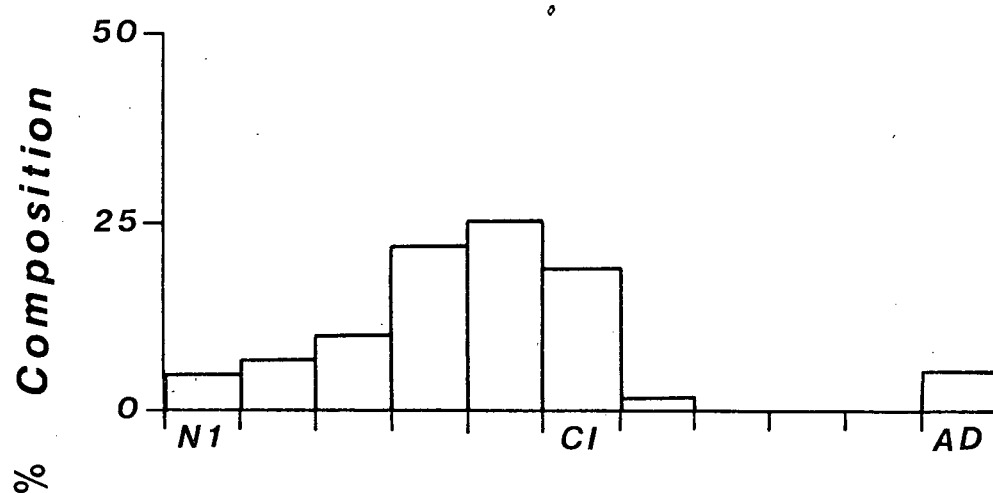


Figure 23. % Composition of C.b.thomasi instars in Placid Lake in 1976. Letters indicate: N1 - naupius 1, CI - copepodid I, AD - adult.

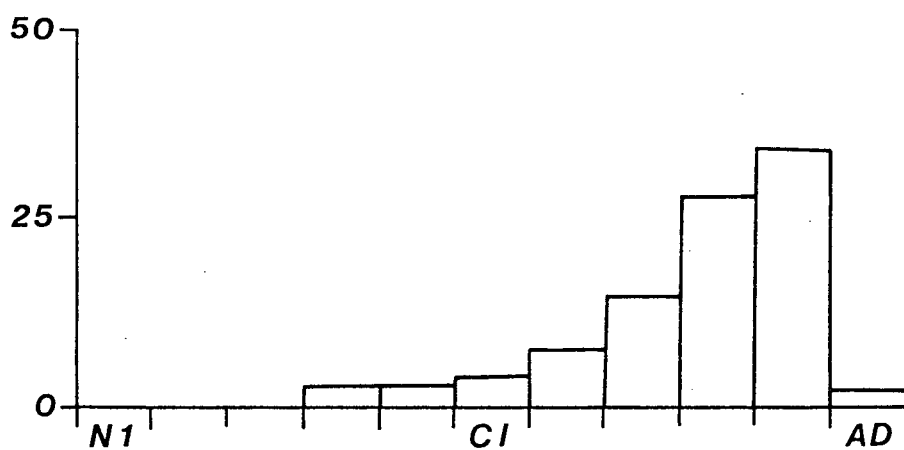
May 31



June 20



July 22



T.prasinus

This species occurred in low numbers in Placid Lake. The main pulse began in the plankton in mid-July, apparently emerging as copepodids II - adult (Fig.24). Because numbers were always low, the nauplii and copepodids of T.prasinus were collectively described. By early August egg sacs were observed. Nauplii were blue-green in colour and when first caught, could be distinguished from those of C.b.thomasi. The number of T.prasinus in the plankton increased through August-September, but by the beginning of November a rapid decline in the numbers collected was evident. By late October-early November several instars were present, suggesting that the population overwinters in a variety of stages, although principally in copepod IV, V and adult. In Gwendoline Lake, where T.prasinus was more numerous, a similar pattern was observed. The uniformity of instar on each sampling date noted in C.b.thomasi was not observed in this population.

T.prasinus does not appear to undergo any marked diel migration, unlike C.b.thomasi (Fig.25). This sampling also shows that differences between the lake and enclosures were minimal. The two cyclopoid copepod populations appear to maintain basically the same patterns of movement in the enclosures as in the lake.

Figure 24. Changes in the standing crop of T.prasinus in Placid Lake in 1976.

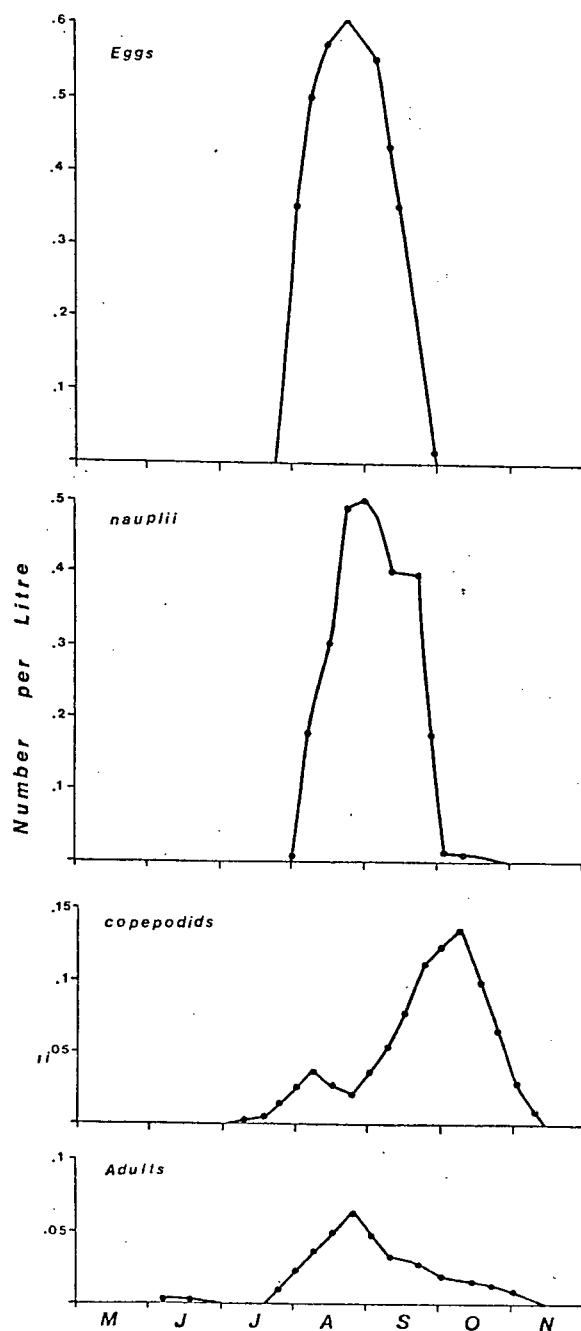
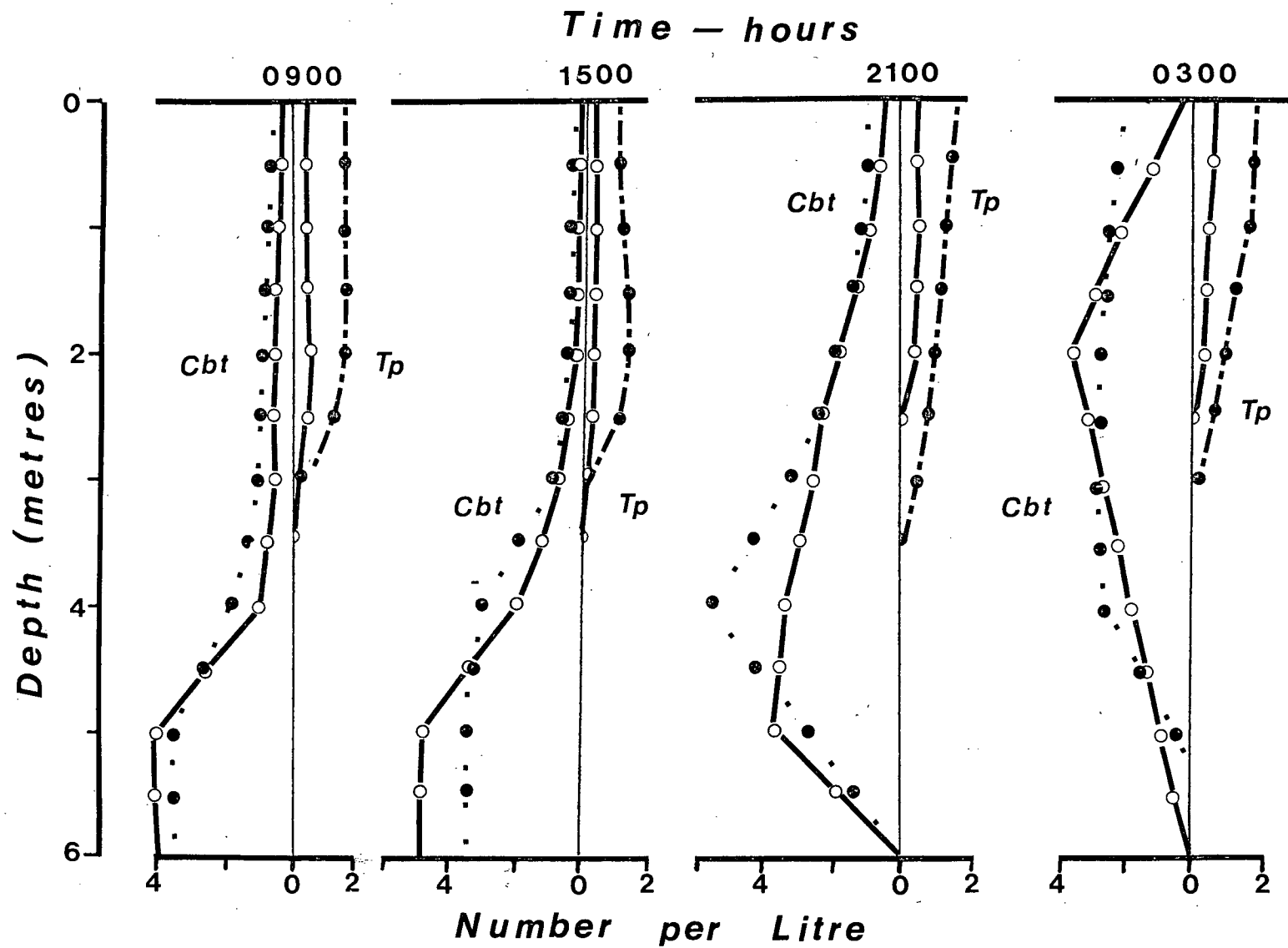


Figure 25. Diel vertical migration of C.b.thomasi (on the left indicated as Cbt) and T.prasinus (on the right indicated as Tp) as represented by abundance on Aug. 25, 1976. Solid circles represent Placid Lake and open circles represent the mean of two replicate enclosures. Density per litre as shown.



Effects of Enclosure

Many complex interactions are possible in the varying environment of the lake which are difficult to mimic in short-term laboratory experiments. Therefore it was important to examine the factors limiting the success of T.prasinus under field conditions. Tests were conducted by introducing T.prasinus at Placid Lake densities into large in situ experimental enclosures in Placid Lake. The community was manipulated in these enclosures to produce different conditions of predation and competition for the scarce food resources.

Figure 26 shows time series data for oxygen and particulate organic matter. Oxygen values were identical at the surface. Small differences in oxygen levels between the lake and enclosures occurred at the deepest depth measured. However, this should not have affected T.prasinus, a species which was never collected deeper than 3.5 m. There were no differences in temperature profiles between lake and enclosures (Fig.27). Particulate organic matter included all detritus and phytoplankton less than 73 μm in diameter. In an oligotrophic system such as Placid Lake, small changes in the particulate organic matter could represent significant changes in the food base. However, differences between the lake and enclosures were generally small, as were differences between enclosures.

The numerically important zooplankton species are shown in Fig.28. Variation between replicate enclosures was small, particularly within the Cyclops present and Cyclops absent treatments. Other organisms I occasionally sampled in low

Figure 26. Variation in oxygen and particulate organic matter (POM) shown for Placid Lake and the experimental enclosures. Circles on the POM data represent the mean of 2 replicate enclosures and vertical bars represent the 95% confidence interval. Squares represent oxygen at 4.5 m.; solid symbols represent the enclosures and open symbols represent the lake.

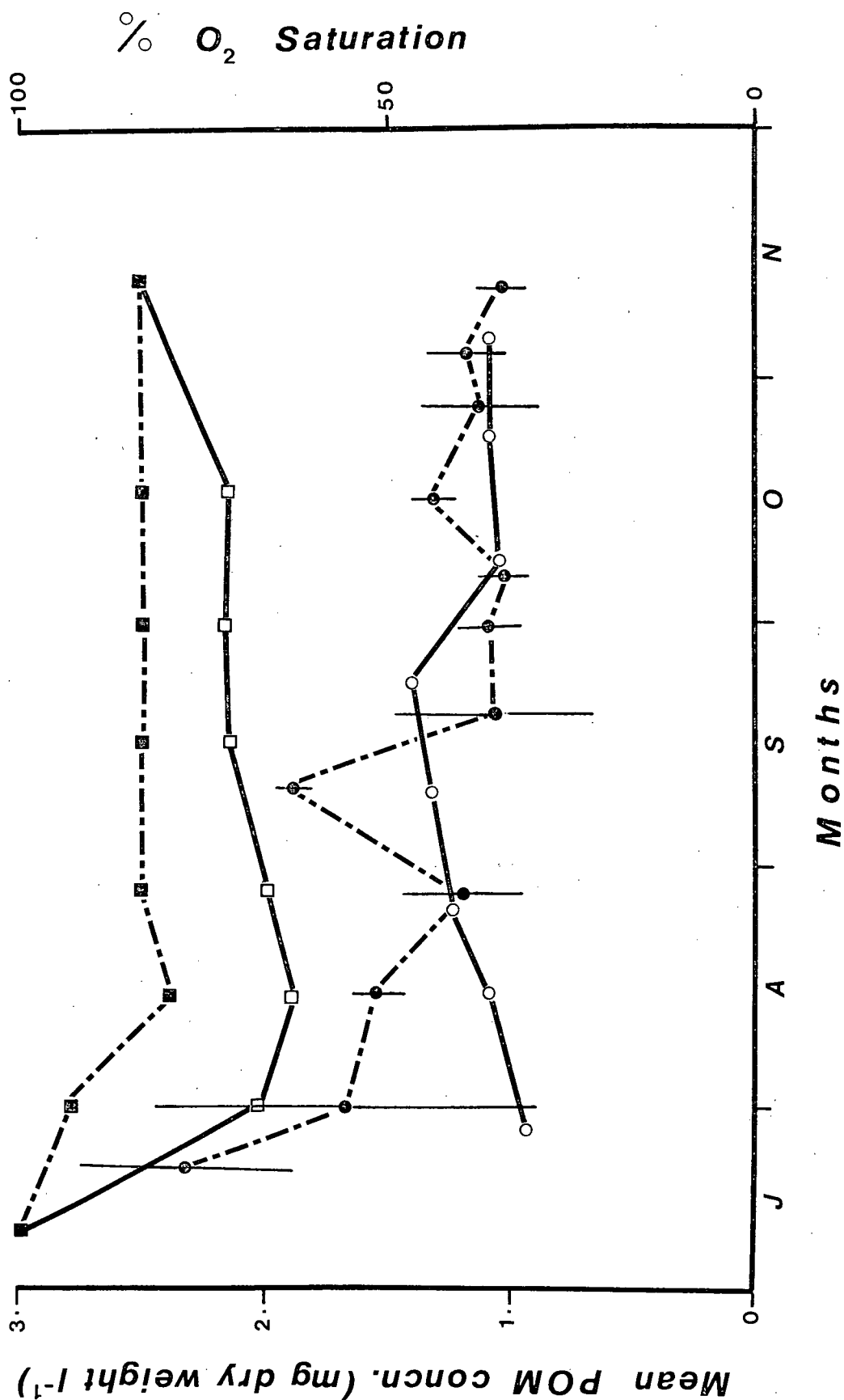


Figure 27. Changes in temperature at 0.5 m. and 4.5 m. for Placid Lake in 1976. Circles represent 0.5 m. and triangles represent 4.5 m. Open symbols represent the lake and solid symbols represent the enclosure data.

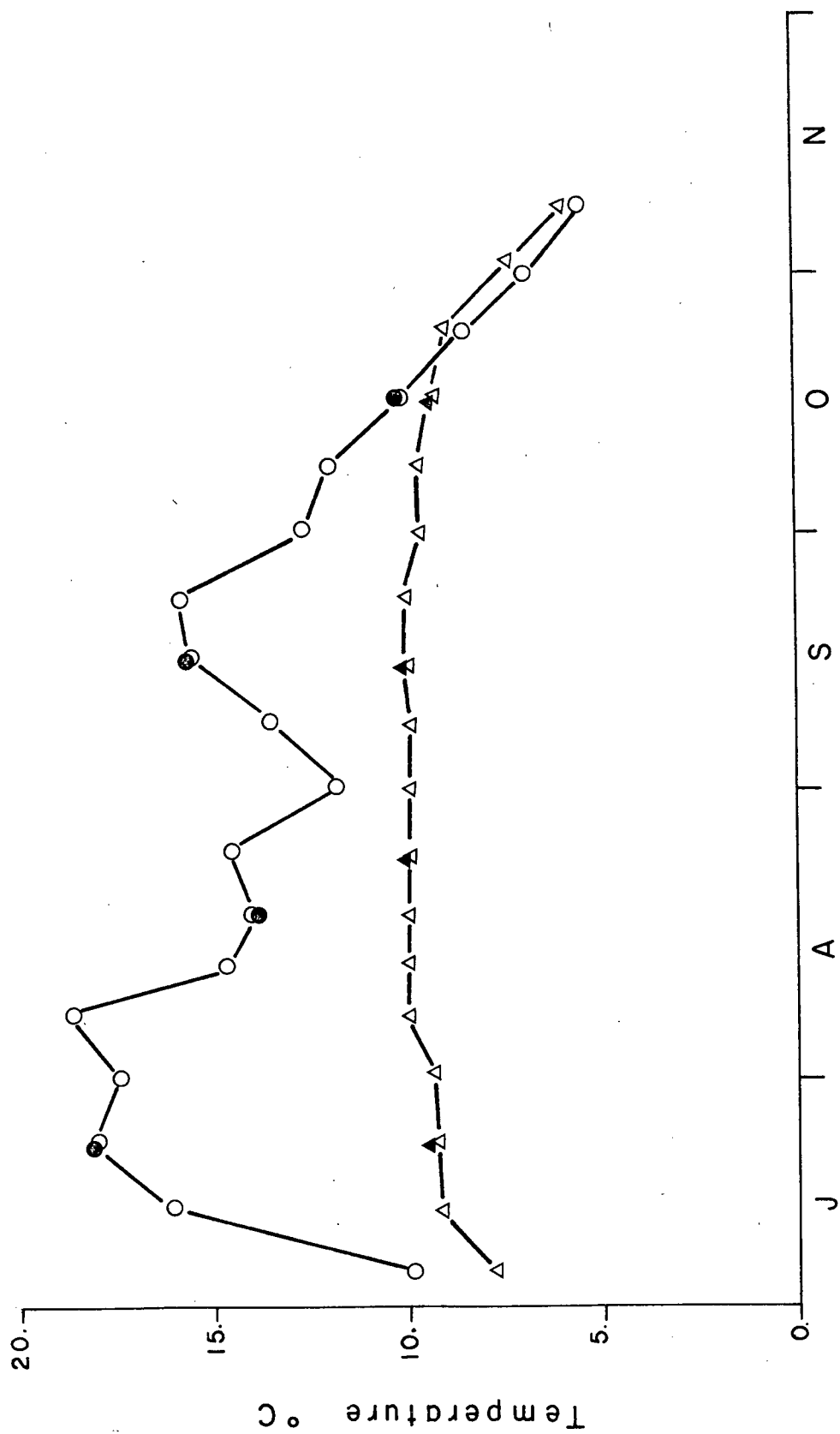
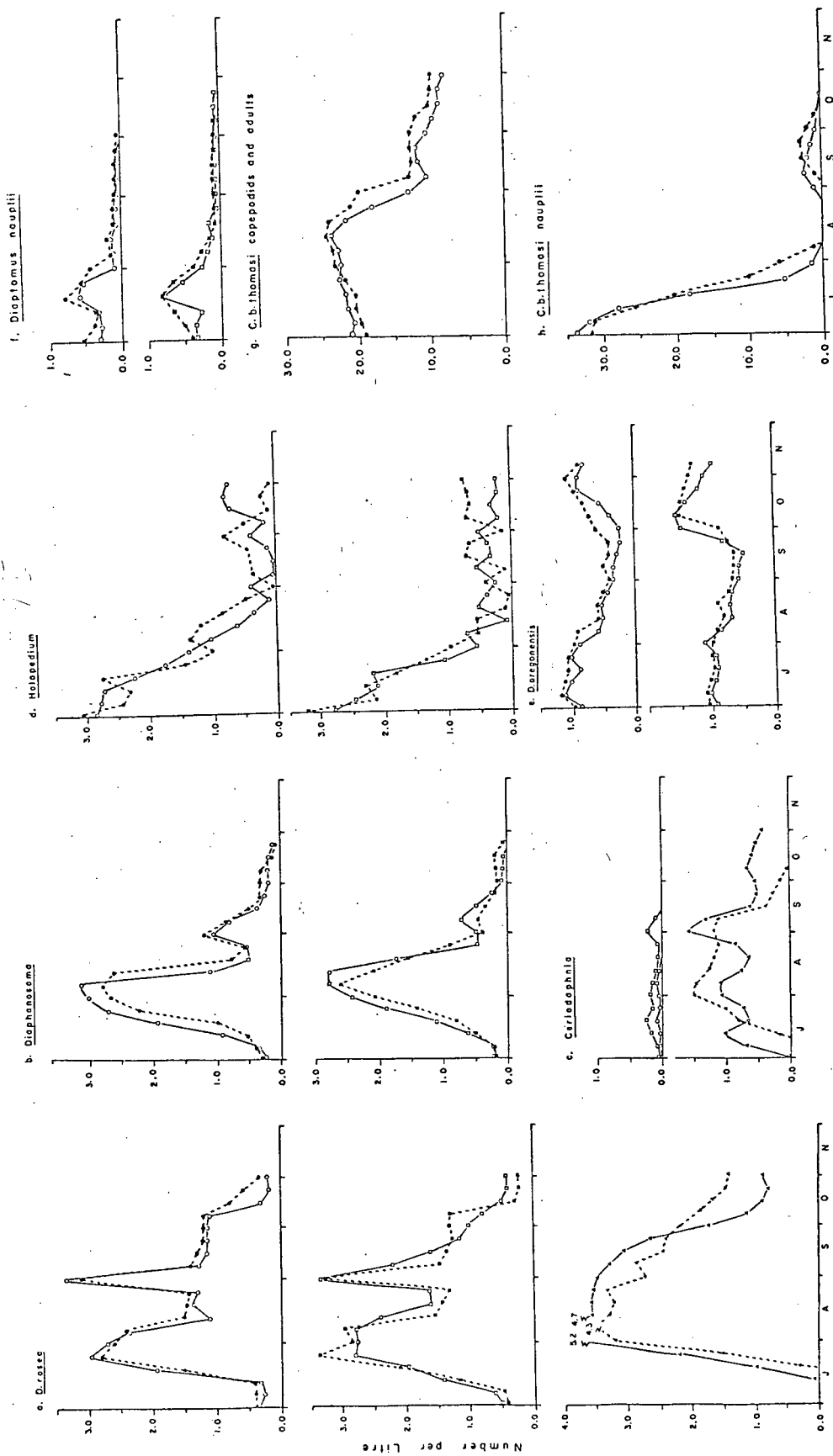


Figure 28. Changes in the standing crop of Placid Lake zooplankton showing seasonal variation of the numerically important zooplankton in replicate enclosures in 1976. Circles represent the treatment with C.b.thomasi, squares represent the treatment without C.b.thomasi, and triangles indicate the T.prasinus alone treatment. Open and solid symbols are replicates of the same treatment.



numbers were Polyphemus, Bosmina, Chydorus and solitary rotifers. Although Polyphemus is described as carnivorous, eating protozoans, rotifers and "minute crustaceans" (Brooks, 1959), Anderson (1970a) found no evidence of predation on diaptomid or cyclopoid nauplii by this species and the numbers in my enclosures were always too low to have a significant impact on crustacean prey (maximum of 0.13 per litre). Mites and chironomids were also occasionally sampled. By late September-October, chironomids were regularly sampled in all enclosures at about 0.7 to 1 animal per litre. I collected Ceriodaphnia in all replicates of all treatments but always in low numbers with the exception of the T.prasinus alone treatment. In spite of the fact that I individually pipetted the T.prasinus for introduction to this treatment, contaminating cladocerans Ceriodaphnia and D.rosea became abundant (Fig.28). Variation between replicates was much greater in the T.prasinus alone treatment than in either of the other two treatments and the variation was caused by appearance of these two cladocerans. This variation was probably due to the accidental nature of the introduction - rather like the appearance of a garden 'weed'. D.rosea was a numerically dominant zooplankter in all the treatments but Ceriodaphnia was not. This latter species became abundant, relative to its density in the other four enclosures, only in the treatment where T.prasinus and D.rosea were the sole representatives of the crustacean plankton. There was a 5 to 10 fold increase in Ceriodaphnia abundance in this treatment and this enhancement occurred in both replicates, suggesting that competitive

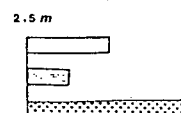
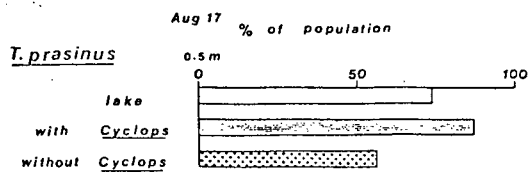
interactions might normally prevent Ceriodaphnia from increasing in number.

Enclosure does not appear to affect vertical distribution (Fig.29), suggesting that the enclosed crustacean populations probably interact in the same way as they do in the lake. There is one notable difference, however. T.prasinus seems to be over represented in the Cyclops absent treatment at 2.5 m. relative to the same depth in the Cyclops present treatment and in the lake. This result is typical of the August samples suggesting that T.prasinus is more vertically homogenous in the absence of C.b.thomasi, unlike either D.rosea or D.oregonensis. It is not clear, however, whether this 'expansion of territory' is due to C.b.thomasi / T.prasinus interaction or whether this result simply reflects the increased T.prasinus numbers in the Cyclops- free treatment.

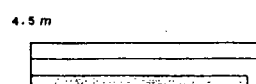
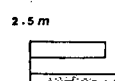
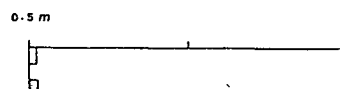
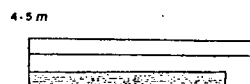
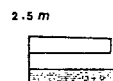
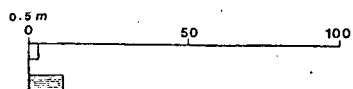
Effect of Competition

Neill (1978) showed that Daphnia rosea, one of the dominant grazers in the system, finds Placid Lake a poor food environment during the summer months. Bioassays of reproductive indicators are probably the best measures of changes in nutritional quantity and/or quality in the absence of any data on selectivity in feeding. Consequently, changes in the reproductive output of the two most important grazers in the lake, D.rosea and Diaptomus oregonensis, are probably the best measure of any differences between enclosures with respect to the food base. The proportion of ovigerous adult females of D.rosea and Diaptomus oregonensis (Fig.30) shows that the

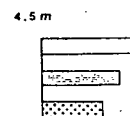
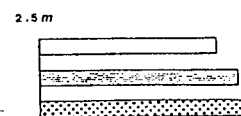
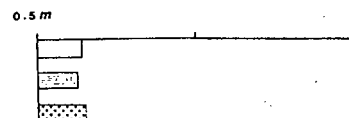
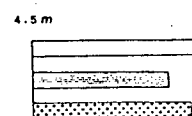
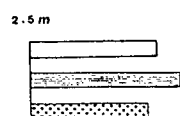
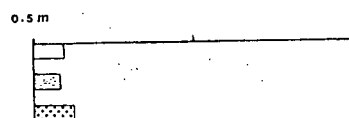
Figure 29. % of the abundant crustacean populations - the % of C.b.thomasi , D.orgonensis and D.rosea at 0.5, 2.5, and 4.5 m. in the C.b.thomasi enclosure, the enclosure without C.b.thomasi and Placid Lake on July 13th and August 17th, 1976. T.prasinus is shown only for August 17th as this species was not present in the plankton on July 13th, 1976.



July 13 C. b. thomasi



D. oregonensis



D. rosea

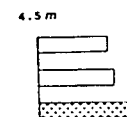
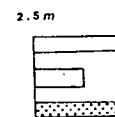
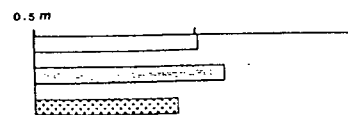
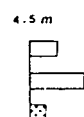
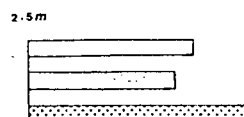
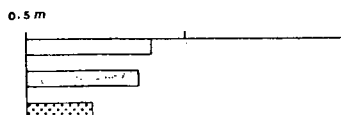
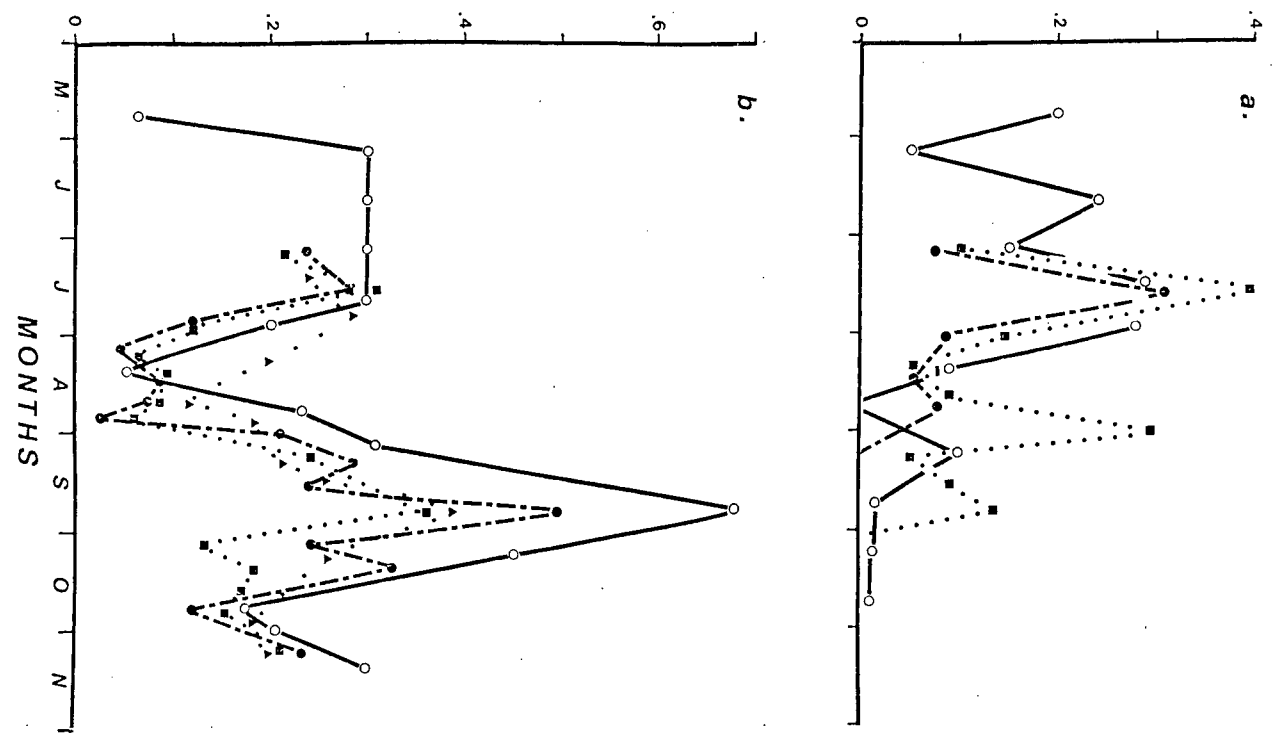


Figure 30. Proportion of ovigerous adult females of a) D.oregonensis and b) D.rosea during the summer of 1976. Symbols represent: circles - mean of the replicate enclosures with Cyclops , squares - mean of replicate enclosures without Cyclops , triangles - mean of replicate enclosures of the T.prasinus 'alone' treatment.

PROPORTION OVIGEROUS FEMALES



trends are the same between enclosures (analysis described in Appendix B). An analysis of variance on the eggs per female data for these two species show that there were no differences between enclosures or treatments (Table 7). Data for D.oregonensis include the enclosures with and without C.b.thomasi. The mean clutch size was 4.4 ± 0.2 ($\pm 1SE$), $n=122$. Data for D.rosea include all the enclosures as this species invaded the T.prasinus alone treatment and became abundant by the middle of August. There was no difference in clutch size between any of the enclosures (Mean= 1.8 ± 0.1 , $n=174$)

As T.prasinus can function herbivorously and Placid Lake is a low food environment, the effect of competition between this species and other herbivorous zooplankton was examined by comparing T.prasinus reproduction in the enclosures without predaceous zooplankton with the enclosures where only T.prasinus was added. There appeared to be no difference between these two treatments. The indicators of reproductive output, proportion of ovigerous females (Fig.31) and number of eggs per female (Table 8), show that T.prasinus experienced essentially the same food environment in the T.prasinus alone treatment as in the other treatments. This might have been an indication that food resources were not limiting T.prasinus. However, the ever-present 'weed' in the system, D.rosea, appeared in the T.prasinus alone enclosures and became numerous. Neill (1978) estimates that D.rosea contributes more than 75% of the summertime grazing pressure on lake seston. The appearance of D.rosea in the T.prasinus alone enclosures apparently eliminated any benefit T.prasinus gained

100
TABLE 7 One-way analysis of variance of the eggs per female of D.orgonensis in the enclosures in Placid Lake during July and August, 1976.

Source of variation	df	SS	MS	F
Between	5	5.6	1.1	0.7 ns
Within	116	197.7	1.7	

One-way analysis of variance of the eggs per female of D.rosea in the Placid Lake enclosures during July and August, 1976.

Source of variation	df	SS	MS	F
Between	5	3.1	0.6	0.8 ns
Within	168	228.3	1.3	

Figure 31. Proportion of ovigerous females of T.prasinus for the same time period and treatments as indicated in Fig. 30.

PROPORTION OVIGEROUS FEMALES

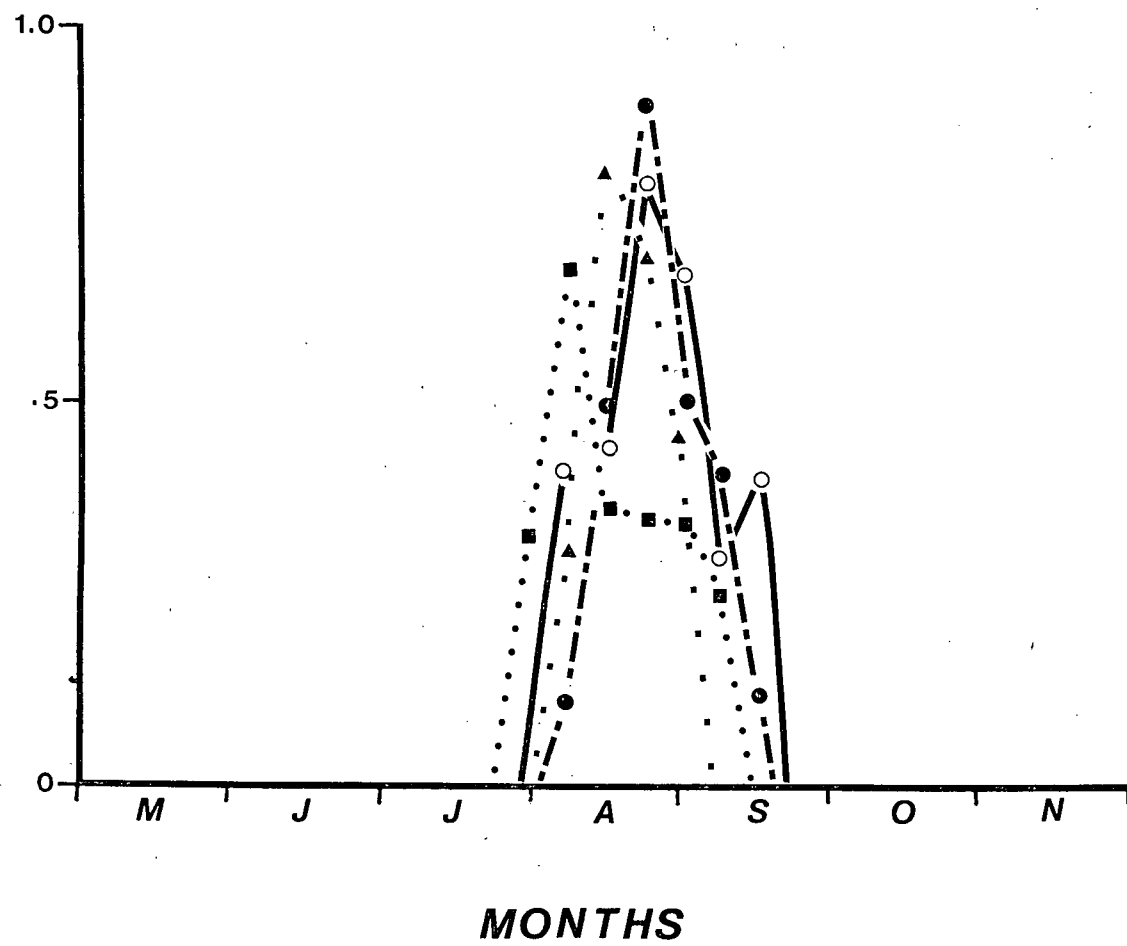


TABLE 8 Mean Clutch size (+ 1 SE) of T.prasinus in Placid Lake and in the experimental enclosures during August-September, 1976.

Cyclops	Without Cyclops	Tropocyclops alone	Lake
17.6 + 0.99	15.9 + 1.15	17.5 + 0.84	16.9 + 0.53
17.3 + 0.95	17.5 + 0.81	16.9 + 0.88	

analysis of variance

Source of variation	df	SS	MS	F
Between	6	38.5	6.4	0.4 ns
Error	133	2125.4	15.9	
Total	139	2163.9		

ns, not significant

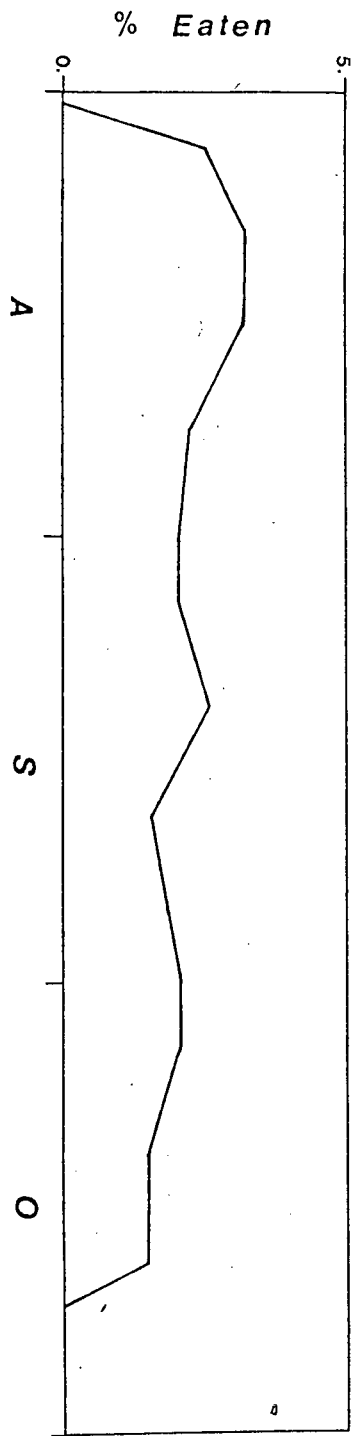
from the removal of the other grazers in the system, or food was never limiting in the enclosures.

Effects Of C.b.thomasi Predation

The predation mortality which could have been caused by C.b.thomasi in the lake was estimated by combining a laboratory estimated rate of predation with the field estimates of predator and prey standing stocks. With prey densities of 1 T.prasinus prey per litre, laboratory experiments showed that 0.05 T.prasinus nauplii could be eaten per C.b.thomasi predator per day. To extrapolate to lake densities, I used the equation $y=0.05X^{.33}$. The concentration of C.b.thomasi predators was estimated by taking the standing stock of C.b.thomasi found each sampling day above 3.5 m, as this was the deepest point at which T.prasinus was collected. Combining these estimates, I calculated the % of T.prasinus nauplii that could be removed daily by C.b.thomasi predators (Appendix C). From August 4th to Oct.18th, an average of about 2.6% per day could be lost to C.b.thomasi predation (Fig.32). The laboratory estimated residence time for T.prasinus nauplii was about 9.8 days at 1976 Placid Lake temperatures. If 2.6% per day could be lost to C.b.thomasi predation, newly hatched nauplii had about a 23-25% chance of being removed before reaching copepodid instar I. Clearly the predaceous instars of C.b.thomasi had the potential to inflict considerable mortality on T.prasinus nauplii, even at low Placid Lake densities.

McQueen (1969) estimated that 31% of the C.b.thomasi

Figure 32. Estimated daily predation of C.b.thomasi on T.prasinus nauplii for all C.b.thomasi copepodids IV, V, and adults above 3.5 m. on T.prasinus nauplii from Aug. 4th to Oct. 18th in Placid Lake in 1976.



nauplii standing stock and 30% of the diaptomid nauplii were eaten by the carnivorous instars of C.b.thomasi in Marion Lake. As C.b.thomasi in Placid Lake reaches densities comparable to that in McQueen's study area, the importance of this predator to the success of T.prasinus was tested in the field. Field testing is critical because small spatial/temporal discontinuities can severely bias results and predictions based solely on laboratory experiments. T.prasinus increased dramatically in both treatments where C.b.thomasi was excluded (Fig.33), confirming the indirect prediction that the presence of this cyclopoid predator was an important constraint on the success of T.prasinus in Placid Lake. The T.prasinus population expanded in a similar manner in both treatments where C.b.thomasi was excluded, suggesting that D.oregonensis had no significant impact on T.prasinus, because this calanoid copepod was absent from the T.prasinus alone treatment.

Laboratory feeding experiments indicated that the primary impact of C.b.thomasi predation was experienced by T.prasinus nauplii rather than the copepodid instars. I assessed the validity of this prediction by calculating survivorship curves (Fig.34) from field population data (Gehrs and Robertson, 1975) and laboratory estimated development times (Appendix D) using the mean abundance of the T.prasinus population in the Cyclops present and Cyclops absent treatments. The positive skew on the survivorship curves showed that the greatest mortality occurred in the early life stages. By the N3 instar about 70% of the nauplii had perished in both treatments, suggesting that these stages were not significantly affected by C.b.thomasi

Figure 33. Standing crop of T.prasinus in the experiments and lake for the summer of 1976. Symbols represent the treatments as explained for Figure 30 except that the open circles indicate the lake values.

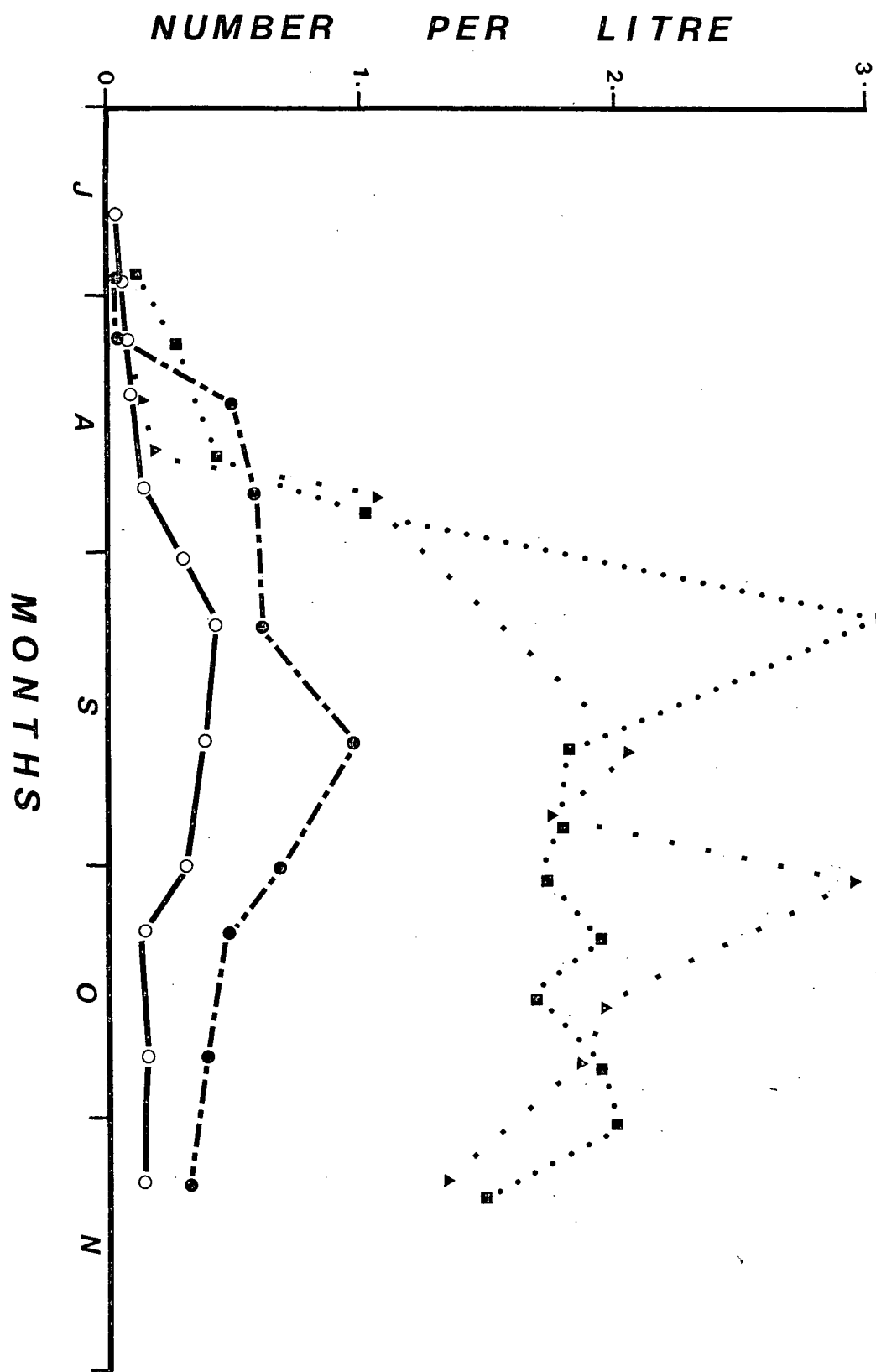
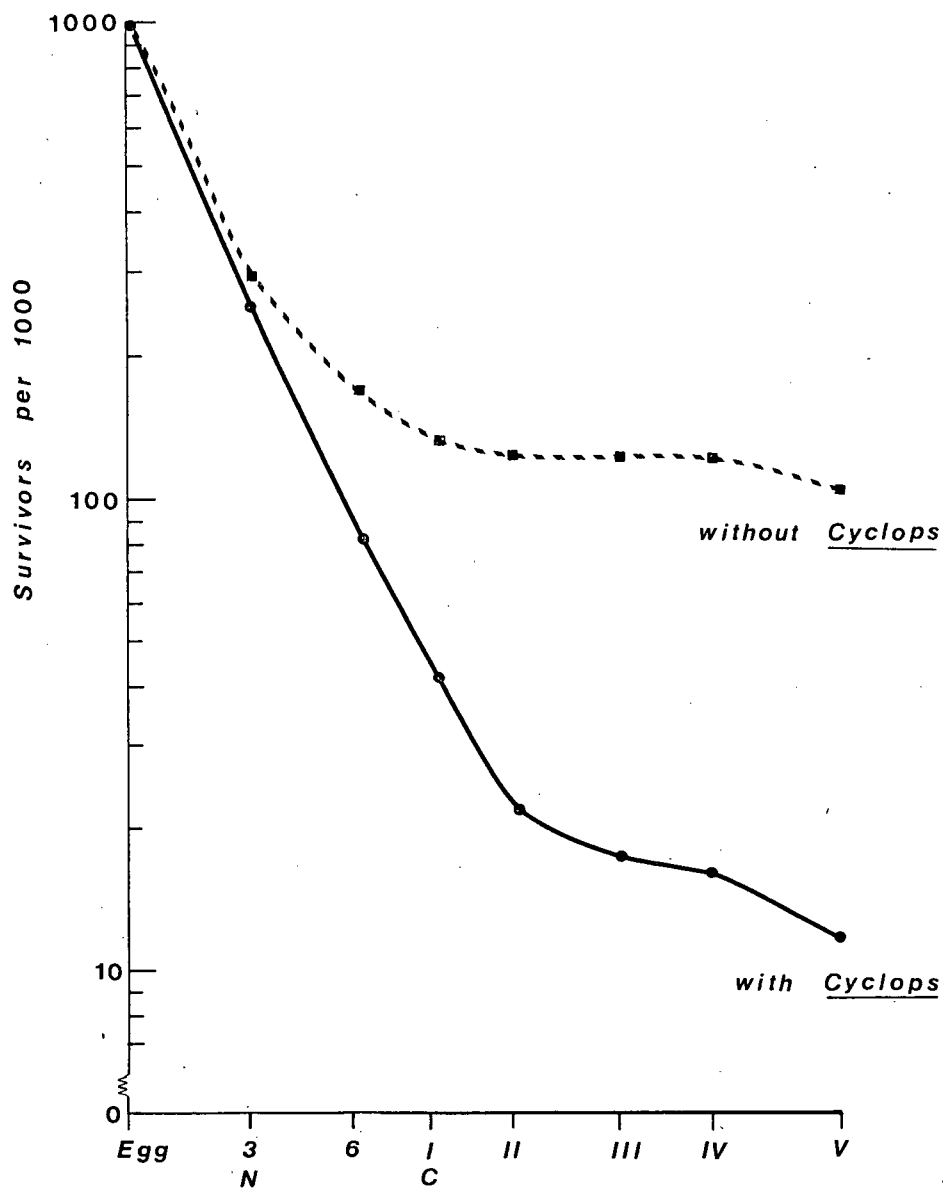


Figure 34. T.prasinus survivorship by instar in Placid Lake from August to October, 1977. Interval on the x-axis is scaled to represent the relative duration of each instar interval shown.



predation. T.prasinus survivorship was lower, however, by the N6 stage in the enclosures with Cyclops and this trend continued until instar CII. Contrasting this decline with the pattern in the treatment without Cyclops showed that the N3 to CI interval was the most sensitive to C.b.thomasi predation.

DISCUSSION

The greatest differences in zooplankton community composition between otherwise similar lakes is often in the relative abundance of species, especially the rare species. Many attempts have been made to correlate these patterns with biotic (Anderson, 1970a,b; Anderson, 1974; Anderson and Raasveldt, 1974; Pope and Carter, 1975; Northcote and Clarotto, 1975; Boers and Carter, 1978) or abiotic (Sprules, 1975; Patalas, 1971) features of the lakes under study, or to extrapolate from necessarily small scale laboratory experiments to spatially and temporally complex plankton communities (McQueen, 1969; Fedorenko, 1973; Confer and Cooley, 1977). However, the complexity of dynamic interactions often confounds both approaches in providing explanations for the causes of the observed patterns. This study used large scale in situ experimental enclosures to examine the factors limiting the population of T.prasinus in the context of the spatially, temporally complex community found in Placid Lake. T.prasinus is rare in Placid Lake, in contrast to its relative success in nearby Gwendoline, a lake with similar chemical characteristics and zooplankton community composition.

Laboratory feeding experiments showed that T.prasinus was able to ingest and assimilate phytoplankton efficiently even as adults. There was no evidence that T.prasinus cannibalized its own young or preyed on other living crustacean zooplankters. Consequently the predaceous instars of C.b.thomasi could not compete with T.prasinus. Competition between the two species could only occur during the early life stages, naupliar or early copepodid instar. However, the main egg pulse and naupliar development occur in August-September in T.prasinus, while in C.b.thomasi these events occurred in May-June. I therefore conclude that C.b.thomasi is not competing with T.prasinus for scarce food items.

Predation experiments show that, at low prey densities (1 per litre) and in the presence of alternative prey, predation rates are low. These experiments indicated that even though T.prasinus numbers were low in Placid Lake, the naupliar instars were not immune to predation. Calculations using the laboratory estimated predation rate and Placid Lake population data for T.prasinus and C.b.thomasi indicated that C.b.thomasi could inflict substantial mortality on T.prasinus, removing about 20-26% of the naupliar recruits. Laboratory experiments showed that, for T.prasinus copepodids in the presence of alternative prey, predation became negligible at concentrations below 5 prey per litre. This prey density was never reached in the lake and therefore predation mortality was probably not important to copepodid instars of T.prasinus. T.prasinus nauplii probably represented the 'bottleneck' most vulnerable to predation by C.b.thomasi.

Experimental enclosures placed in Placid Lake examined the causes for the population limitation of T.prasinus and showed that removal of T.prasinus by C.b.thomasi greatly enhanced recruitment in the T.prasinus population. This occurred even in the presence of non-predaceous zooplankters - possible competitors for small food particles. As the clutch-size and the number of ovigerous females was not significantly different between treatments, the larger populations of T.prasinus in the enclosures without C.b.thomasi could not be due to greater fecundity. Survivorship curves were constructed to evaluate the locations of major mortalities in the life history of T.prasinus. These curves showed that the NIV to CI interval was the most sensitive to mortality in the presence of C.b.thomasi.

Predaceous forms of C.b.thomasi eat the nauplii of calanoid copepods and cyclopoid copepods with no evidence of selection (McQueen, 1969; Smyly, pers.comm.; pers.obs.). Consequently T.prasinus emerges from diapause to face a non-discriminating predator with a developmental advantage due to an earlier positive numerical response to alternative food sources. Habitat heterogeneity in the limnetic region of an oligotrophic lake is probably minimal compared to littoral, benthic or terrestrial habitat. That which exists is principally the result of chemical gradients, temperature stratification and light attenuation (for visual predators). As predatory copepods hunt via mechanoreceptors (Kerfoot, 1978), the prey of such a predator cannot find a refuge by diel migration into the dark benthic area. By August the main body

of the C.b.thomasi population is found in the cooler deeper waters of the lake and the best strategy for T.prasinus is to remain near the surface. By remaining near the surface throughout the entire day, some segregation from the main body of the C.b.thomasi predator population is possible. Without this partial spatial refuge, all of the highly vulnerable T.prasinus nauplii recruiting during August can theoretically be eaten by C.b.thomasi. It is interesting that the depth distribution of T.prasinus changes in the absence of C.b.thomasi such that a greater % of the population is found at a deeper depth, although this is circumstantial, it is evidence of an interaction. Thus the tendency to remain near the surface may be the explanation for the continued persistence of T.prasinus in Placid Lake.

The numerical response of the T.prasinus population is the same in both treatments without C.b.thomasi in spite of the fact that only the filter-feeding cladocerans Ceriodaphnia and D.rosea are present in the T.prasinus 'alone' treatment. Consequently, D.oregonensis, present and abundant in the other treatment without C.b.thomasi, cannot be a significant mortality agent for T.prasinus although Lane (1978) reports that this species is predaceous. As there are no other potentially important predators, and no indication that food levels are different among treatments, food limitation may be the cause of the high NI to NIII mortality across all treatments. Although the stage at which naupliar feeding begins is not known, Rigler and Cooley (1974) report that food must be supplied to second instar calanoid nauplii if

significant mortality is to be averted. These authors conclude that only a few eggs contain sufficient stored energy to permit continued growth to N3 without externally provided food. Consequently, it appears that T.prasinus experiences a combined bottleneck of predator-induced mortality and food limitation during its early life stages. About 80% of the population perishes between the egg and copepodid I stages without any predator in the system. The invertebrate predator C.b.thomasi further reduces the already low survivorship through predation on the early naupliar instars. Consequently, the temporal strategy of T.prasinus leaves this warm water form vulnerable to the predaceous stages of C.b.thomasi while the spatial strategy separates T.prasinus from the greatest proportion of the predator population and permits the persistence of T.prasinus, at low densities, in this oligotrophic lake.

SUMMARY

1. T.prasinus is an omnivore but is not cannibalistic and does not prey on other microcrustaceans.
2. C.b.thomasi can remove about 3% of the T.prasinus nauplii daily during the peak period of naupliar production or about 2.2% daily averaged over the entire interval when T.prasinus nauplii are present in the plankton.
3. Predation by C.b.thomasi on the T.prasinus population in Placid Lake is reduced by vertical separation and low prey density.
4. Removing C.b.thomasi from the enclosure dramatically increases the standing stock of T.prasinus .
5. Survivorship curves suggest this increase is due to improved survivorship during the NIV to CI interval when C.b.thomasi is removed.

III. RESPONSES OF CYCLOPS BICUSPIDATUS THOMASI TO ALTERATIONS
IN THE FOOD AND PREDATOR ENVIRONMENT

INTRODUCTION

C.b.thomasi is a limnetic cyclopoid copepod, common throughout temperate North America (Carl, 1940; Rawson and Moore, 1944; Reed, 1964; Patalas, 1971; Patalas, 1972; Anderson, 1974). Although geographically widespread, C.b.thomasi generally exhibits a non-contagious distribution. Its presence in one lake does not predict its distribution or abundance in nearby lakes, or even in lakes within the same drainage system. This patchy distribution on a regional basis is characteristic of most freshwater limnetic crustacean species and Patalas (1971) concludes that the composition of the freshwater crustacean plankton community within a region is determined by lake morphology. However, Anderson (1974) reports that Acanthocyclops vernalis and C.b.thomasi are too widespread to be correlated with physical/chemical factors and suggests that competition and/or predation may be more important in explaining the distribution and abundance of these organisms. Zaret (1978) argues that predation is the principal organizing factor of freshwater zooplankton communities and that abiotic factors and food resources are comparatively insignificant.

A puzzling aspect of cyclopoid copepod distribution is the fact that a species which is abundant in one lake is often rare, although present, in a nearby apparently similar lake. In a study of 340 lakes and ponds, Anderson (1974) shows that when C.b.thomasi and Cyclops vernalis occur together, the latter is abundant only when the former is relatively low in number. The dynamics of the interaction may be complex

because Anderson (1972) suggests that the presence of fish may favour C.b.thomasi over Cyclops vernalis in these lakes. However, Smyly (1976a) reports that a reduction in Chaoborus flavicans predation in his experimental enclosures results in greater abundances of both C.bicuspidatus and C.vernalis. This paper examines the relative importance of these various explanations in maintaining a low abundance of C.b.thomasi in an oligotrophic montane lake in coastal British Columbia.

The 1976 experiments in Placid Lake indicated that the presence of a large C.b.thomasi population in a fish lake (Placid Lake) was an important causal factor restricting the success of the cyclopoid copepod T.prasinus. The relatively greater abundance of T.prasinus in nearby Gwendoline Lake (a lake without fish at the time of the study) seemed an improbable factor to be involved in limiting C.b.thomasi because the life histories of the two cyclopoid species were similar between Placid Lake and Gwendoline Lake. In the former lake, C.b.thomasi clearly had the advantage in the C.b.thomasi-T.prasinus interaction and there was no evidence that fish or Chaoborus flavicans were involved in maintaining the greater abundance of C.b.thomasi. C.b.thomasi was found in Gwendoline Lake at countable densities, even though the numbers were low, thus suggesting that dispersal was not a problem. Gwendoline Lake is deeper than Placid (mean of 13.4 m. compared to mean of 4.3 m. in Placid Lake) but several authors (Patalas, 1971; Sprules, 1977) associate C.b.thomasi with deeper colder lakes. Other authors, however, have found C.b.thomasi dominant under a wide range of conditions (Carl,

1940; Whittaker and Fairbanks, 1958; Anderson, 1974). In the Great Lakes, Patalas (1972) found an increasing abundance of C.b.thomasi associated with increasing nutrients. Patalas showed that C.vernalis is abundant only where C.b.thomasi is not but he attributes this result to depth and temperature preferences (C.b.thomasi preferring greater depth and colder temperature).

In Placid Lake the C.b.thomasi population experiences greatest mortality in the naupliar stages. McQueen (1969) estimated that 25-30% of the juveniles could perish through cannibalism in nearby Marion Lake. Other studies (Smyly, 1961; Anderson, 1970b) have suggested that cannibalism eliminates the naupliar and early copepodid instars which develop after the main pulse of recruits, resulting in a narrow distribution of instar stages and body sizes within a given lake. This cannibalistic behaviour could have a self-dampening effect on population size. Lane (1979) suggests that this species can effectively regulate its own population through intraspecific predation which becomes particularly intense at high densities. However, it seems possible that at low densities the cannibalistic habit of C.b.thomasi may exacerbate intraspecific mortality, already high in the early developmental stages, such that this species requires a greater food resource base to prosper numerically. Gwendoline Lake is, on average, slightly lower in organic carbon than Placid Lake (Walters, unpub.data). Even small differences in the available food may be critically important to the early life stages in such dilute environments and there is evidence that

some copepods require food early in their development. For example, in laboratory experiments with a calanoid copepod, Rigler and Cooley (1974) found that the duration of the second naupliar instar was variable and mortality was high unless some algal food was provided. These authors concluded that only a few eggs have enough stored food to carry them through to the third naupliar instar. If nutritional difficulties are encountered by C.b.thomasi nauplii in addition to intraspecific predation pressure, juvenile mortality may be so high that the population cannot increase in number even though the few surviving individuals may do very well.

One major difference between the two study lakes is that the Chaoborus species found in Gwendoline Lake are planktonic all day and some individuals are present throughout the year. In Placid Lake the Chaoborus species is C.flavicans, a species which is benthic by day and present in the plankton only at night. This difference may substantially increase the predation pressure on the C.b.thomasi population in Gwendoline Lake and result in a low abundance of C.b.thomasi. However, Anderson and Raasveldt (1974), in a survey of 50 lakes and ponds in Alberta and British Columbia, found that mean cyclopoid copepod densities were higher in communities which included a Chaoborus population, although they did not examine the mechanisms involved in producing the correlation.

Different stages in the life history of C.b.thomasi may be differentially susceptible to variations in competition, predation or changes in the physical/ chemical environment. All these factors can potentially play a part in determining

the ultimate success of C.b.thomasi in Gwendoline Lake. Specific hypotheses which emerge from the several alternative explanations are the following: 1) the physical or chemical environment in Gwendoline Lake is unfavourable to C.b.thomasi

2) food resources in Gwendoline Lake are too low to support C.b.thomasi whose cannibalistic behaviour is unsuited to an extremely oligotrophic environment 3) invertebrate predation by Chaoborus limits the C.b.thomasi population in Gwendoline Lake 4) predation by Chaoborus plus the low food levels limit the C.b.thomasi population but the effect of predation can be overcome by increasing food resources, particularly to the naupliar stages.

These hypothesis were tested experimentally to explain the way in which predation, competition and physical/chemical factors interact to determine the distribution and abundance of the cyclopoid copepod, C.b.thomasi.

MATERIALS AND METHODS

Field Experiments

To evaluate how competition and predation interface with nutrient levels in Gwendoline Lake, large in situ experiments were conducted from mid-May until late September. These enclosures were identical to those used in Placid Lake the year before. Therefore only the water and the zooplankton community differed from the previous experiments in Placid Lake where the C.b.thomasi population was abundant inside the enclosures. The bags were filled in the same way by pumping lake water through a 54 μ m mesh plankton net that removed all macrozooplankters but permitted grazable seston to pass through. C.b.thomasi, collected in Placid Lake and separated from the other crustaceans by a series of sieves, was added to the Cyclops-supplemented enclosures in Gwendoline Lake at Placid Lake densities. Natural lake densities of Gwendoline Lake crustacean macrozooplankton were added to all enclosures from pooled zooplankton samples

Six experimental disturbances were produced: three different communities and two nutrient levels. The three different communities were the following: one included Chaoborus, Gwendoline Lake crustaceans and Placid Lake densities of C.b.thomasi; one contained only Gwendoline Lake crustaceans; and one contained Gwendoline Lake crustaceans plus Placid Lake densities of C.b.thomasi but excluded

Chaoborus. Plastic screening was used to prevent egg-laying by adult Chaoborus in the four Chaoborus-free enclosures. Chaoborus adults were allowed to lay eggs in the remaining two enclosures. One enclosure of each community 'type' received a 'high' fertilizer treatment while one received no fertilizer. To produce the 'high' fertilizer condition, a phosphate-nitrate fertilizer (atomic ratio 1:10) was used (NaH_2PO_4 and KNO_3) at a phosphate concentration of $500 \mu\text{g l}^{-1} \text{ } 4\text{PO}_4$. Nutrients were added only once in mid-May, although partial mixing of the water within the enclosures was carried out via occasional bubbling during June, July and August. As high mortality occurred during the naupliar instars, the fertilizer addition was intended to enhance algal densities during naupliar production in May and June. The high nutrient concentration was not intended therefore to mimic any naturally occurring condition but rather to provide substantially increased food abundance to the herbivorous stages of C.b.thomasi.

Zooplankton sampling was done every 4-7 days in these enclosures and in the two lakes (Placid and Gwendoline) with an electric bilge pump. Each 100 litre sample was filtered through a 54 μm plankton net and preserved in sugar-formalin. For most species, samples were examined in toto under 25X magnification for species' abundances and reproductive condition. If visual examination suggested that a species' abundance exceeded 500 individuals, then the number of animals in the sample was estimated by counting all the animals in 1/10 to 1/5 of the sample. Temperature and oxygen profiles were occasionally monitored with a Yellow Springs Instruments

temperature/oxygen metre. Biweekly water samples were collected for determination of the ash-free dry weights of particles passing through a 30 μm mesh as previously described. This assessment of 'grazable seston' was combined with microscopic examination of algal size composition and category (colonial, filamentous, blue-green, etc.). Water samples fixed in 'Lugol's' solution for phytoplankton enumeration, had to be concentrated for counting. A subsample (100 ml of about 300 ml) was taken and allowed to settle for 24 hours. Seventy-five ml of the supernatant was then siphoned off and the remaining 25 ml allowed to settle for a further 20 hours prior to counting. Using an Utermohl's 'inverted' microscope, a minimum of 200 individuals (at least 100 of numerically important cells) was counted under 400X magnification. Measurements required for conversion to cell volume were taken for the most common types in each size and category. Where possible, phytoplankton was identified to species.

Length measurements of female cyclopoid copepods were made using an ocular micrometer in a dissecting scope, at 50X magnification. Metasomal length was measured to avoid inaccuracies caused by formalin induced contraction or expansion of the body segments (Smyly, 1976b).

Laboratory Predation Tests

Crop contents suggest Chaoborus trivittatus instar I feeds primarily on nauplii and rotifers (Neill and Peacock, 1980). As C.b.thomasi nauplii are abundant in Placid Lake during peak abundances of Chaoborus instar I in Gwendoline Lake, these larvae were offered C.b.thomasi nauplii from Placid Lake as prey in the presence of 4 alternative possible prey from Gwendoline Lake. All animals used were freshly collected. The experiments were conducted at Gwendoline Lake mid-June temperature at about 3 m. ($15 \pm 2^\circ\text{C}$) in seven 2 litre beakers and lasted 24 hours under a light:dark regime of 16 hours light and 8 hours dark. Predator and prey were added to sieved Gwendoline Lake water at normal lake densities with the exception of C.b.thomasi nauplii, which were added at Placid Lake densities. The number of prey killed per predator per day was deduced by comparing the number of living and dead prey retrieved in the Chaoborus beakers with those observed in 2 control beakers at the end of the 24 hour period. As there was no mortality in the control beakers, the dead prey were included in the number of prey killed per predator per day.

RESULTS

Effect of Introduction on the C.b.thomasi Population in the Absence of Chaoborus

As C.b.thomasi is rare in Gwendoline Lake, adults were introduced from Placid Lake to four experimental enclosures, at Placid Lake densities, to assess this species' ability to coexist with Gwendoline Lake zooplankters in Gwendoline Lake water. I eliminated the only predators sufficiently abundant to have an impact on C.b.thomasi, the phantom midge fly larvae Chaoborus, from two of these enclosures. In the absence of Chaoborus, C.b.thomasi had no difficulty surviving and recruiting in both the unfertilized and the fertilized 'Gwendoline Lake' treatment (Fig.35 a-c). Not only does the C.b.thomasi population survive and recruit but vertical distribution also follows a similar pattern in the Gwendoline Lake enclosure to that observed in Placid Lake (Fig.36). As in Placid Lake, adults are found throughout the water column, copepodid instars peak at approximately 2.5 m. and the majority of the nauplii are found below 2.5 m. Therefore introduction to the alien Gwendoline Lake environment does not affect the general pattern of development or spacing behaviour of the introduced C.b.thomasi population.

The contribution of each instar to the total population within the Gwendoline Lake enclosures was similar to the per cent composition observed in Placid Lake in June (Fig.37).

Figure 35. Changes in standing crop of C.b.thomasi in Placid Lake and in the fertilized and unfertilized 'Cyclops' enclosures in Gwendoline Lake from May to September, 1977.

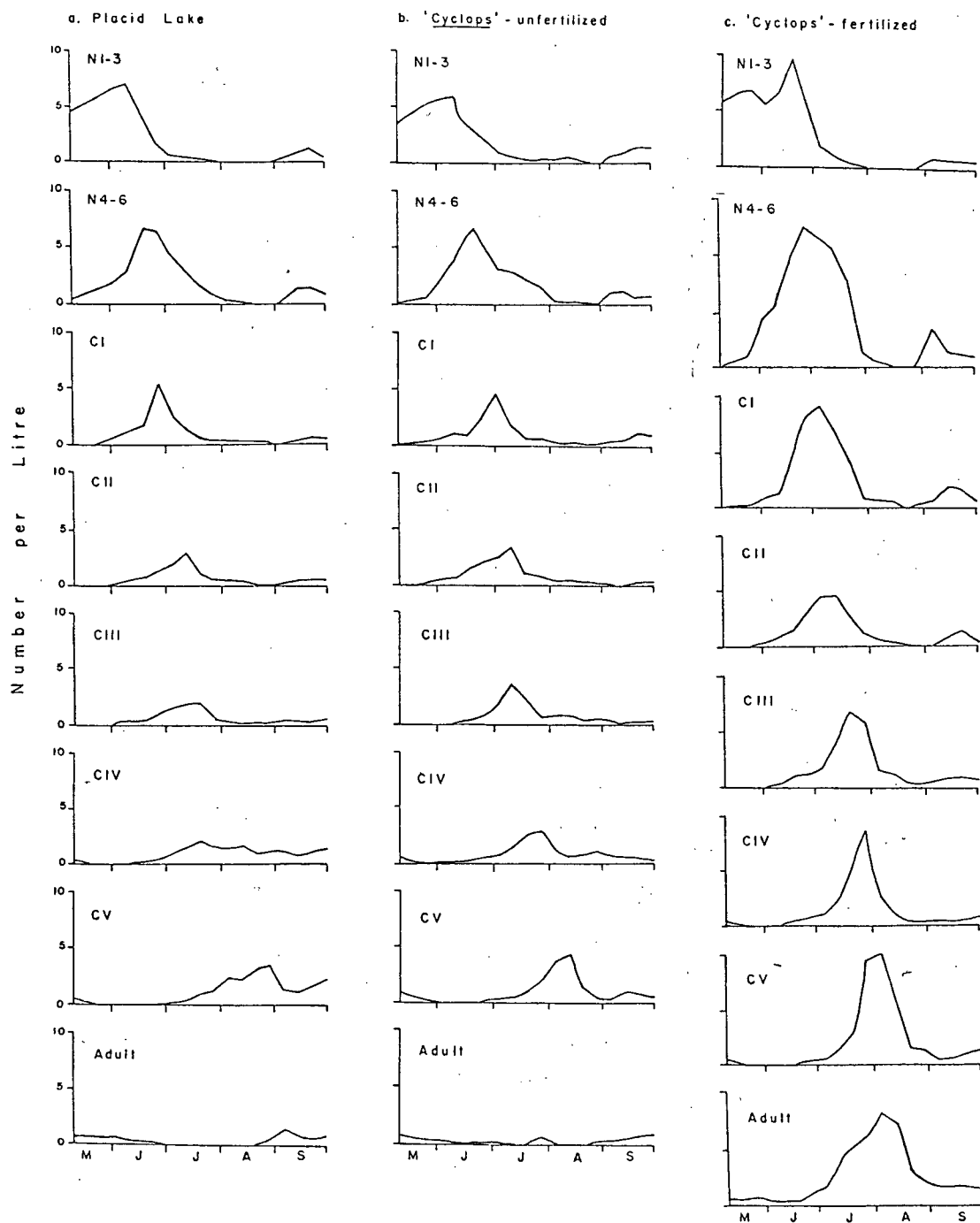
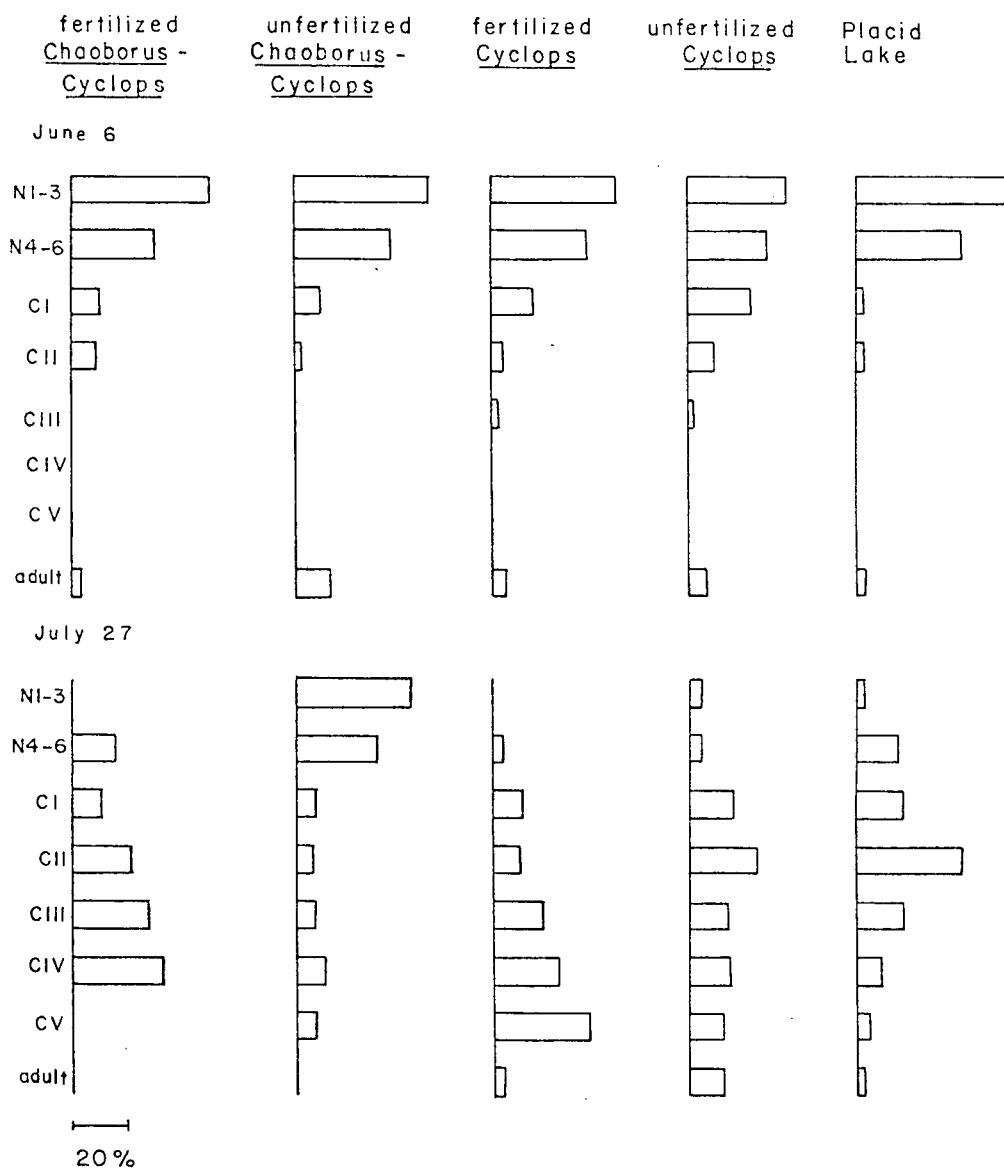


Figure 36. Depth distribution of C.b.thomasi for C.b.thomasi nauplii, copepodids and adults in Placid Lake and in the unfertilized 'Cyclops' treatment in Gwendoline Lake on June 7, 1977.

Figure 37. % composition of C.b.thomasi instars in the fertilized and unfertilized 'Chaoborus-Cyclops' treatment, the fertilized and unfertilized 'Cyclops' treatment (no Chaoborus in this treatment), and in Placid Lake in 1977.

% Composition of Cb.thomasi instars

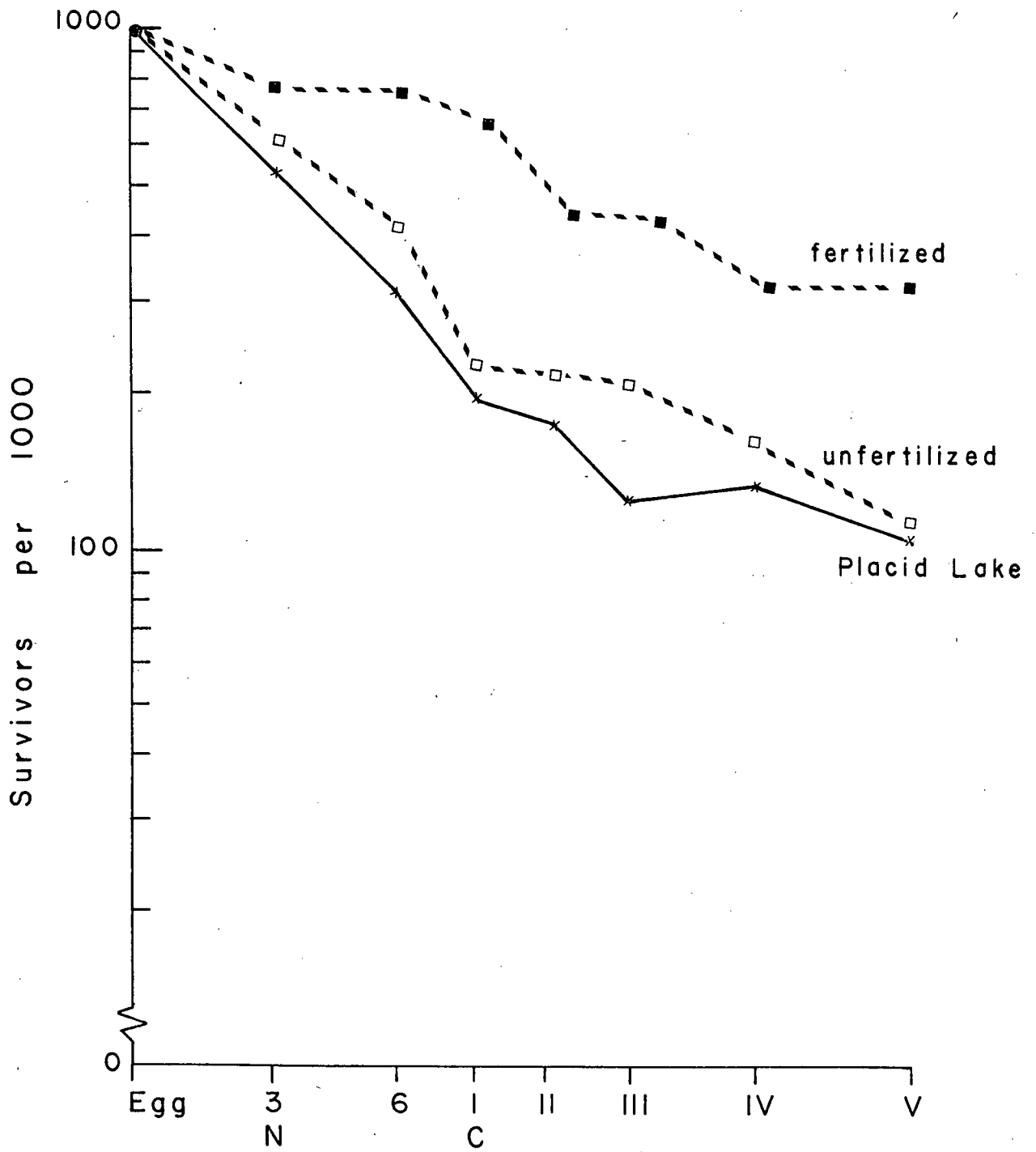


This similarity was maintained only in the unfertilized enclosure without Chaoborus by the end of July. As the Gwendoline Lake enclosures were identical in size and depth, and temperature did not differ between the enclosures, the different age structure observed in the fertilized Chaoborus-free enclosure was probably not related to abiotic factors but to the absence of Chaoborus.

Survivorship curves were calculated using the method of Gehrs and Robertson (1975) to permit a comparative assessment of mortality patterns between the Chaoborus-free enclosure populations and that in Placid Lake. Instar durations were derived from the spring/summer generation by using the interval between the first appearance of the first individual of instar $n+1$ and instar n (Comita, 1972). The difference approximates the duration of instar n in a population where overlap of successive generations is minimal. Instar durations (applicable to the spring/summer generation) used in developing these life tables are given in Appendix C. The main body of the C.b.thomasi population overwinters in copepodid IV and V stages. There are few adults in the fall plankton when compared with the spring densities, suggesting that only a small proportion of the 5th copepodid instars moult to the adult stage before the spring. Consequently, apparent mortality shown by the survivorship curves in the copepodid instars IV and V may be unrealistically high based on fall population sizes. However, survivorship curves are probably representative of real mortality patterns until the 4th copepodid interval. The resulting survivorship curves are

both positively skewed, signifying high early mortality for immature instars (Fig.38). Greatest mortality occurs in the egg to copepodid I interval in both populations. Naupliar stages are clearly the most vulnerable period; survivorship increases in the copepodid stages. Burgis (1971) also reports high mortality in the naupliar instars of a tropical cyclopoid copepod species. Substituting the Gwendoline Lake community for the Placid Lake community does not alter the pattern of naupliar mortality. This result suggests that the heavy naupliar mortality observed in Placid Lake is the result of diffuse or intraspecific competition for scarce food resources and/or intraspecific predation rather than an interaction with an abundant population of Diaptomus oregonensis, the only member of the Placid Lake crustacean plankton community which is not found in Gwendoline Lake. In any case, differential mortality in Chaoborus-free Gwendoline Lake environment is not the cause of the low abundance of C.b.thomasi in this lake.

Figure 38. C.b.thomasi survivorship by instar in the experimental enclosures without Chaoborus larvae in Gwendoline Lake and in Placid Lake for the spring generation of C.b.thomasi in 1977. Interval on the x-axis is scaled to represent the relative duration of each instar interval shown.



Effect of Fertilization in the Absence of Chaoborus

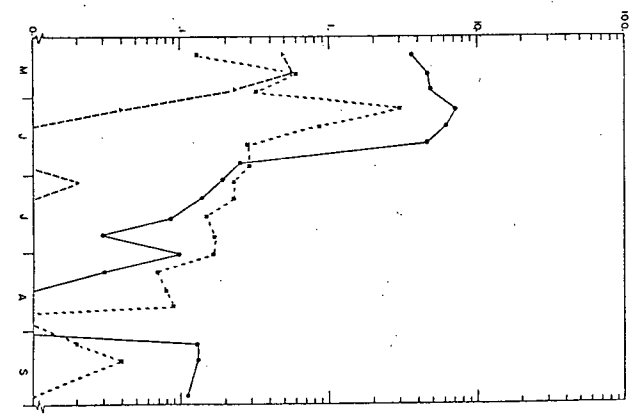
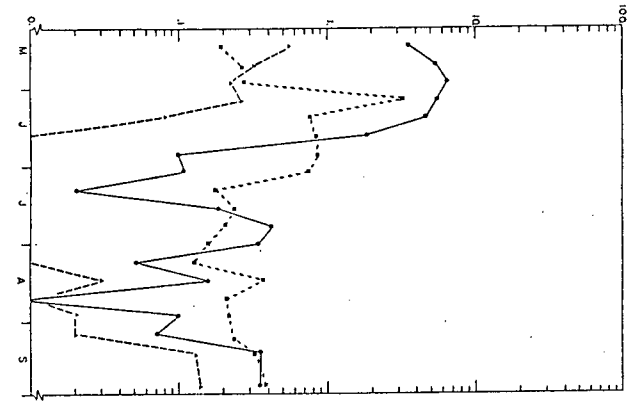
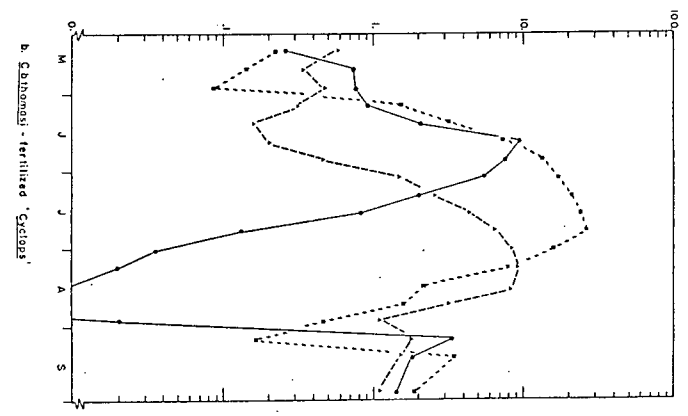
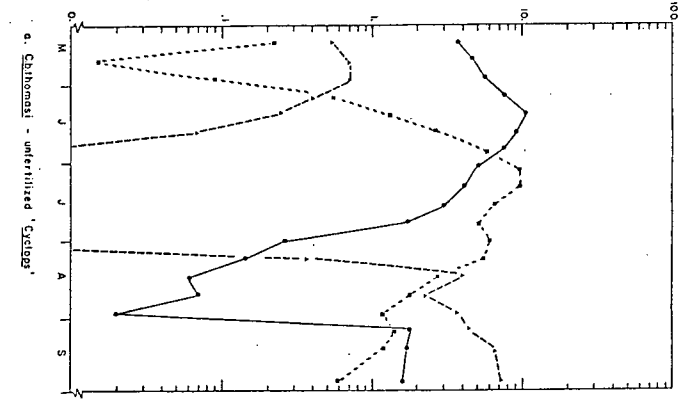
In the absence of Chaoborus, adding fertilizer to the Gwendoline Lake enclosure dramatically increased survivorship of C.b.thomasi (Fig.38, Fig.39 a,b). As observed in Placid Lake and the unfertilized treatment, mortality rates were highest in the egg to N3 interval although these rates were lower than in Placid Lake or in the unfertilized treatment. However, the fertilized enclosure experienced relatively little mortality in the N4-6 to CI interval compared to that observed in the unfertilized bag. In the latter environment, approximately 76% of the eggs produced failed to develop to the CI stage while in the fertilized environment only 32% perished by instar CI.

C.b.thomasi, known to be carnivorous and cannibalistic in the later copepodid and adult instars (McQueen, 1969; Anderson, 1970; Lane, 1976, 78, 79), was the only predator in these enclosures. However, losses to intraspecific predation should have been lower in the unfertilized enclosures as adults declined faster and disappeared by mid-June (as in Placid Lake) whereas adults were continuously present in countable numbers throughout the season in the fertilized treatment (Fig.39 a,b).

The high mortality associated with the naupliar instars might be the result of inadequate nutrition. As nauplii are herbivorous (Fryer, 1957b, Smyly, 1970), I compared particulate organic matter, phytoplankton volume biomass and type composition between the fertilized and unfertilized enclosures to assess available food resources. Phytoplankton cell counts were converted to cell volume by assuming the cell form to

Figure 39. Changes in the standing crop of the introduced C.b.thomasi (nauplii, copepodids, and adults) for the four Gwendoline Lake enclosures in 1977 from May to September. Circles represent nauplii, squares represent copepodids and triangles indicate adults.

NUMBER PER LITRE



correspond to simple geometrical solids (sphere, cone or cylinder) (Findenegg, 1969). Phytoplankton were assigned to the following groups based on extensive evidence of relative edibility (e.g. Burns, 1968; Arnold, 1971; Schindler, 1971; Porter, 1973; Gliwicz, 1975; Nadin-Hurley and Duncan, 1976; Gliwicz, 1977; Porter, 1977) : <2um (small, coccoid cells, mainly bacteria), 2-20 um (nannoplankton as defined by Gelin and Ripl(1978)) and >20 um (large, solitary cells, mainly diatoms), colonial and filamentous. McCauley and Briand (1979) treated all species larger than 50 um and all blue-green algae, irrespective of size, as inedible. Although this distinction might be valid for filter-feeders, such a definition seemed unwarranted for raptorial feeders. My criteria included size, shape and 'quality' based on the above literature. Consequently, I distinguish filamentous algae as a group because most species observed were blue-green, considered a poor nutritive source by some authors (e.g. Arnold, 1971), but not colonies, most of which were green algae. Colonies were relatively uncommon and therefore I combined this group with solitary >20 um cells (primarily 'edible' diatoms) because all of these species were probably available to raptorial feeders and many available to filter-feeders (Porter, 1977). Bacteria formed a group because, being <2 um, individuals cells probably presented handling problems; nannoplankton were grouped together because all these small green algal cells were probably desirable food items. Table 9 lists the most common groups encountered and their estimated cell volume.

Table 1

Some physical, chemical and biological characteristics of Placid and Gwendoline Lake.*

CHARACTERISTICS	Placid	Gwendoline
Elevation, m.	510	522
Drainage area, ha.	44	81
Surface area, ha.	1.6	13.0
Maximum depth, m.	7	27
Colour, Pt units	20-25	15
Transparency (Secchi depth, m.)	4-6	5-7
pH	6.6	6.6
Total Carbon (mg l ⁻¹)	5.0	3.0
Total Phosphorus (mg l ⁻¹)	0.006	0.003
Total Organic Nitrogen (mg l ⁻¹)	0.17	0.05
Total Dissolved Solids (mg l ⁻¹)	17-23	18

CRUSTACEAN ZOOPLANKTON SPECIES +

<u>Diartomus kenai</u>	A	A
<u>Diartomus oregonensis</u>	A	---
<u>Diartomus leptopus</u>	---	A
<u>Daphnia rosea</u>	A	A
<u>Holopedium gibberum</u>	A	A
<u>Diaphanosoma brachyurum</u>	A	A
<u>Rosina longirostris</u>	R	A
<u>Ceriodaphnia quadrangula</u>	R	R
<u>Polypheus radicularis</u>	A	A
<u>Cyclops bicuspidatus thomasi</u>	A	R
<u>Tropocyclops prasinus</u>	R	A

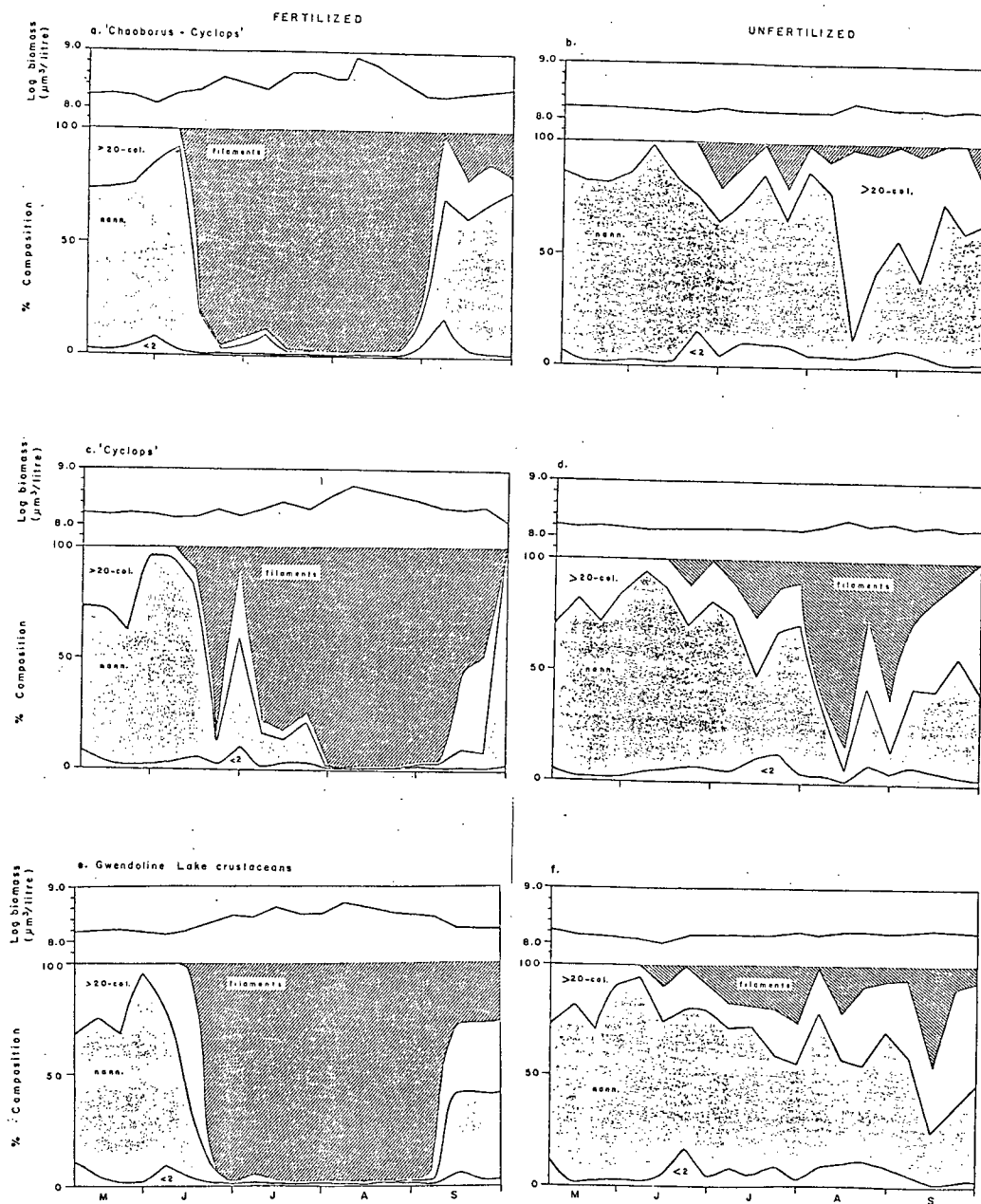
* adapted from Neill (1978)

+ Key to symbols: A = abundant R = rare --- = absent

Phytoplankton standing crop, as measured by cell volume did not differ between the high and low nutrient enclosures until the second week in June (Fig.40 a-g). At this point the standing crop in the fertilized enclosures increased relative to the low nutrient enclosures and remained higher throughout the summer months. The increase in volume biomass was accompanied by a substantial shift in algal composition from a predominance of nannoplankton to net plankton (here including >20 μm solitary cells, colonial and/or filamentous types) (Fig.40 a-g). By June 24th, the blue-green algae Oscillatoria and Lyngbya were the most common forms. This change in phytoplankton composition was not accompanied by increased mortality rates in the C.b.thomasi population. When the algal shift occurred, the majority of the C.b.thomasi population was in the N4-6 to CI stages.

Survivorship in the fertilized enclosure during this interval was high (Fig.38). Many authors (Arnold, 1971; Porter, 1973; Nadin-Hurley and Duncan, 1976) consider blue-green algae a poor quality food for filter-feeding cladocerans. The naupliar instars of copepods have generally been ignored in zooplankton feeding studies and it is possible that the raptorial mode of feeding common to cyclopoid copepods obviates the handling problems experienced by filter-feeders with large filaments (Gliwicz, 1975). Although blue-green algae are generally considered less nutritive food sources than other types of algae and some species (eg. Microcystis aeruginosa, Anabaena flos-aquae) may even be toxic (Gentile and Maloney, 1969; Gentile, 1971; Carmichael et al, 1975; Porter, 1977),

Figure 40. Variation in phytoplankton biomass and % composition. The total phytoplankton volume biomass is based on estimated cell volume and the % composition is composed of four groups as explained in the text. The groups are indicated by: <2 - less than 2 μm , nann - nannoplankton (2 - 20 μm), >20-col - greater than 20 μm cells and phytoplankton colonies, filaments - filamentous algae.



there appears to be considerable variation in the ability of zooplankton to assimilate different species of blue-green algae (Schindler, 1971). Lewis (1979) found that the production of an herbivorous cyclopoid copepod, Thermocyclops hyalinus, was positively correlated with the abundance of diatoms and of blue-green algae. Infante (1978) has also shown that cyclopoids in Lake Valencia, Venezuela, ingest and digest large amounts of Lyngbya limnetica. This is clearly an area which requires further investigation before generalizations can confidently be made.

I analyzed differences in fecundity by counting the eggs produced per female and the proportion of ovigerous females in the populations of both the high and low nutrient treatments over the egg-bearing period in May and June. A two-way analysis of variance was used to differentiate between the effect on clutch size due to fertilization and that due to predation (Table 10). Fertilization was the only factor that significantly affected clutch size ($p < 0.01$). Smyly similarly found that increasing available food increased the mean clutch size. Smyly was able to almost double the mean clutch size of female adult Cyclops abyssorum when he artificially fed these animals Artemia nauplii in excess of daily need.

In the absence of Chaoborus, the proportion of ovigerous female C.b.thomasi is also different between the fertilized and unfertilized enclosures (Fig.41, arcsin transformed data analyzed as described in Appendix B, $t=3.05$, $df=6$, $p < .01$). However, it is clear from Fig.41 that this difference is due to an extended period of egg production in the high nutrient

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Table 10 Clutch size (+1 SE) of C.b.thomasi in experimental enclosures in May-June 1977.

Unfertilized predator	Fertilized predator	Unfertilized	Fertilized
21.0 + 1.34	25.7 + 1.30	21.0 + 0.94	26.0 + 1.88

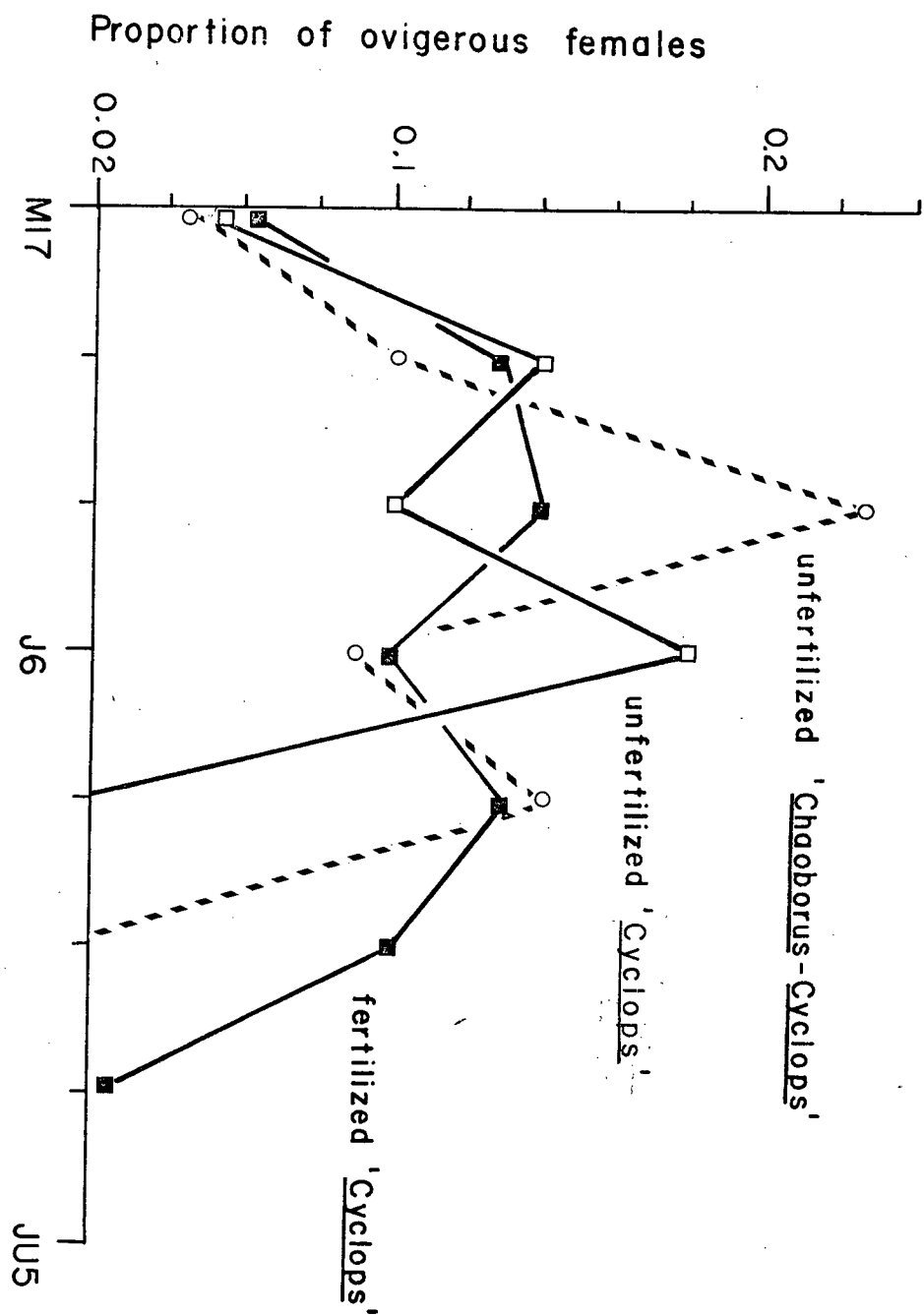
analysis of variance

Source of variation	df	SS	MS	F
Fertilization	1	140.16	140.16	14.06**
Predator	1	0.16	0.16	0.02 ns
Fertilization x Predator	1	0.18	0.18	0.02 ns
Error	20	199.33	9.97	
Total	23	339.83	14.78	

Note: Predator indicates presence of Chaoborus, fertilized/unfertilized as described in the text.

**P<0.01; ns, not significant

Figure 41. Proportion of ovigerous C.b.thomasi females for 3 treatment enclosures during May-June in Gwendoline Lake in 1977.



enclosure rather than a greater proportion of ovigerous females throughout the egg-bearing period. This is confirmed by a t-test on the proportion of ovigerous females during the first four weeks ($p=0.2$). Fertilization therefore enhances egg production in this population by increasing the number of eggs per clutch and possibly by extending the egg-producing period. Smyly (1973) has also suggested that increased food resources result in longer breeding periods.

Effect of Chaoborus at Low Nutrient Concentrations

The presence of Chaoborus in the unfertilized enclosure drastically reduced C.b.thomasi standing stock to a level where sampling became difficult (Fig.39d). The first sample of the enclosures showed the initial densities of adult female C.b.thomasi to be similar - $2.8 \times 10^2/\text{m}^3$ in the Chaoborus treatment compared to $2.4 \times 10^2/\text{m}^3$ in the Chaoborus-free enclosure. There might have been some predation by two year old 4th instar Chaoborus trivittatus on the adult female C.b.thomasi. However, I used a Mann-Whitney U test to analyze differences in the standing stock of adult C.b.thomasi females between the Chaoborus present and the Chaoborus absent unfertilized enclosures and there was no statistical difference ($p=.84$). In spite of this result and the previous finding that there was no difference in the number of eggs produced per female between Chaoborus and Chaoborus-free enclosures, there were fewer nauplii sampled in the presence of Chaoborus (Fig.39c). This result was not due to a lower proportion of ovigerous females (Fig.41). Copepodid instars were always

scarce in the Chaoborus enclosures when compared to the enclosure without Chaoborus. The critical period for the C.b.thomasi population appeared to be during the naupliar instars. To estimate the impact of Chaoborus on C.b.thomasi nauplii, first instar Chaoborus were exposed to C.b.thomasi nauplii in the presence of other prey at densities commonly found in Gwendoline Lake. Chaoborus instar I was chosen because nauplii and rotifers are common in crop contents (Neill and Peacock, 1980), Fedorenko (1973) observed that C.americanus instar II fed least efficiently on calanoid nauplii and C.b.thomasi naupliar declines coincided with the appearance of first instar Chaoborus in the plankton. Feeding rates of Chaoborus instar I are shown in Table 11. The fraction of the standing crop of C.b.thomasi nauplii that could be removed by instar I Chaoborus predation was calculated using predator standing stock values found in the Chaoborus unfertilized enclosure and the C.b.thomasi naupliar densities observed in the unfertilized Chaoborus -free enclosure (Fig.42). Calculations are described in Appendix C. The estimated mean percentage of C.b.thomasi nauplii that could be removed daily by Chaoborus instar I was 6.9%. As the estimated residence time for C.b.thomasi nauplii was 17.5 days, it was conceivable that all the C.b.thomasi nauplii could be eaten. Although a spatial refuge did not seem likely as 1st instar larvae were found in the 1-5 m. layers throughout the day (Fig.43), C.b.thomasi was not driven to extinction in the unfertilized enclosure, nor in the lake. However, it was clear that 1st instar Chaoborus had the potential to inflict drastic losses on

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Table 11 Predation rates of Chaoborus larval instar I on
C.b.thomasi nauplii in the presence of other prey
(Mean number eaten per litre per 24 hours). n=5

	Initial prey	Prey killed/litre	Prey killed /litre/predator/day
<u>C.b.thomasi</u>	10	4.4	2.2
<u>Diapatomus</u> nauplii	3	1.9	1.0
<u>Diapatomus</u> copepodids CI-CIII	2	0.0	0.0
<u>D.rosea</u> <1.0 mm	2	0.2	0.1
<u>Diaphanosoma</u> <1.0 mm	1	0.2	0.1

Figure 42. Estimated % of C.b.thomasi nauplii eaten by Chaoborus - the C.b.thomasi nauplii in the unfertilized 'Cyclops' enclosure which could be eaten by Chaoborus instar I larvae as found in the unfertilized 'Chaoborus-Cyclops' treatment.

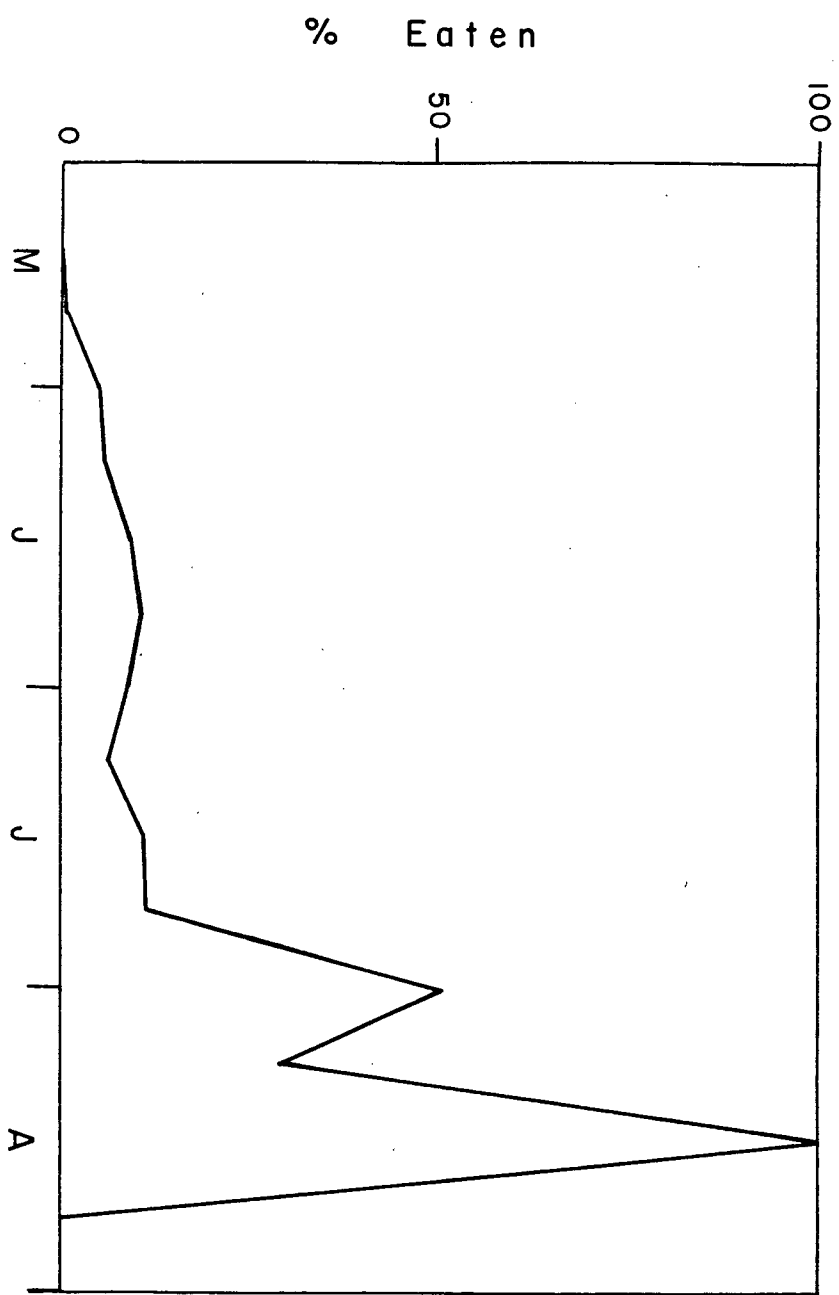
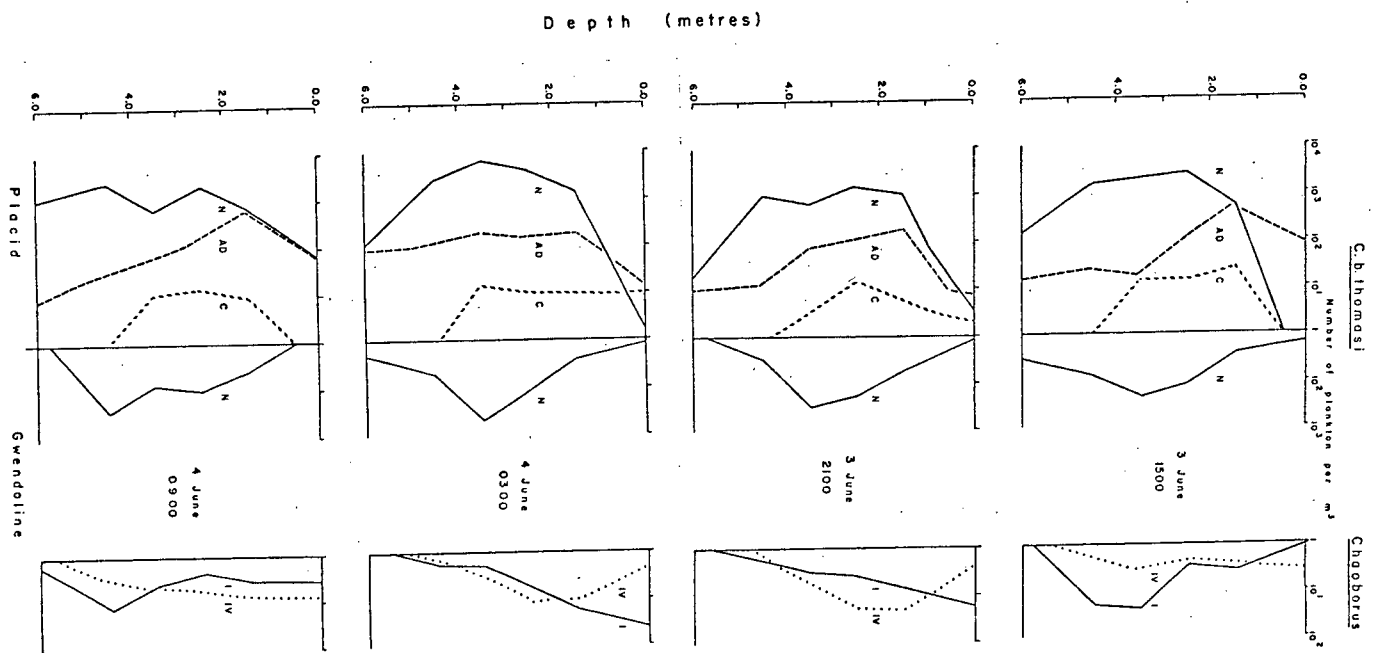


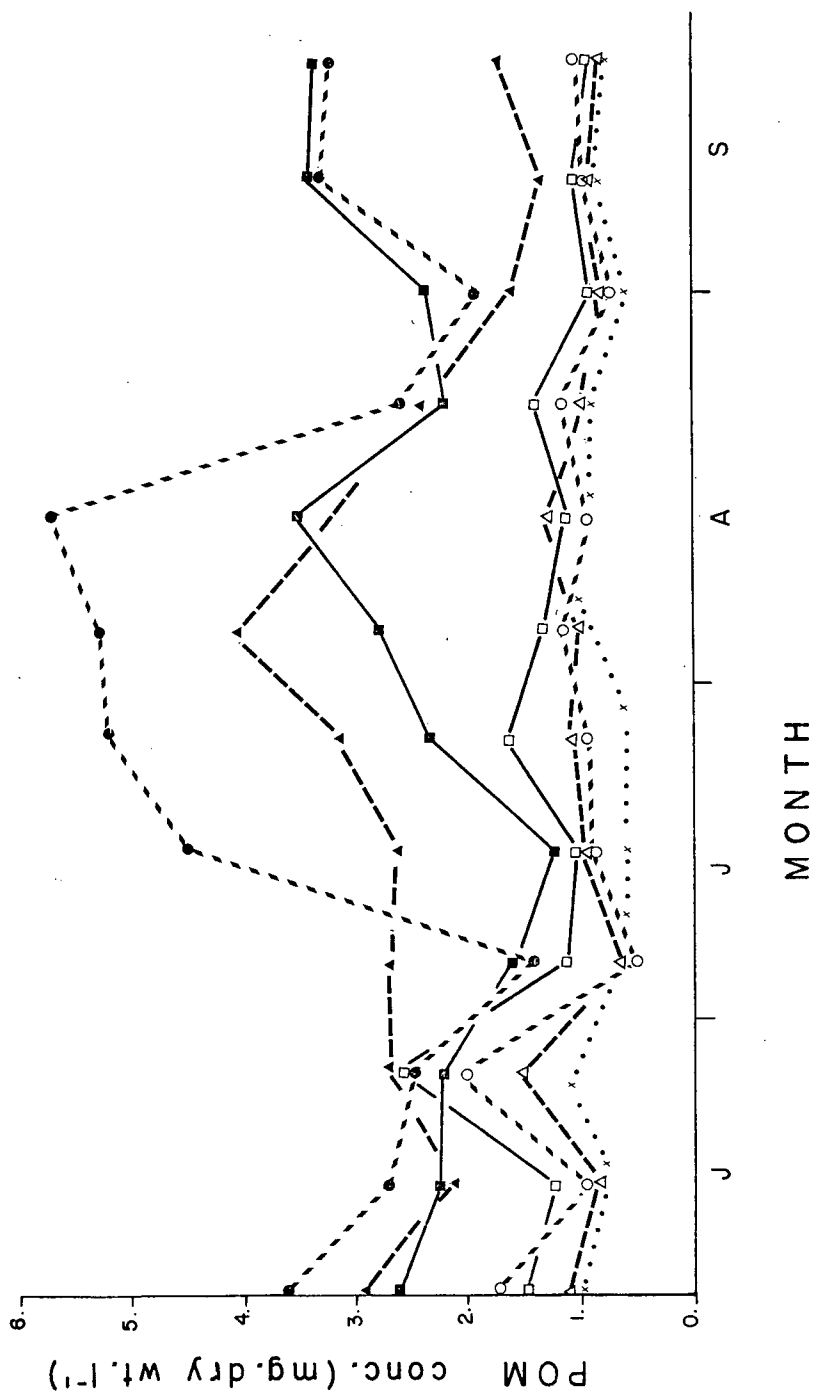
Figure 43. Vertical distribution of C.b.thomasi and Chaoborus - C.b.thomasi instars in Placid Lake and Gwendoline Lake (on left) and Chaoborus instars in Gwendoline Lake (on right) over a 24 hour period in June, 1978. Letters indicate the instar of the plankton shown: N - C.b.thomasi nauplii, C - C.b.thomasi copepodids, AD - C.b.thomasi adults. Roman numerals indicate the instars of Chaoborus.



the C.b.thomasi population, although when numbers became low, encounter rates might have become so rare that predation mortality might have been sufficiently reduced to allow some individuals to reach maturity. Fedorenko (1973) also observed that all 1st, 2nd and young 3rd instars of C.trivittatus larvae were found above the thermocline at all times of the day. As C.b.thomasi nauplii remained at about 2-5 m. during the entire day, there was clearly considerable spatial overlap between predator and prey.

Particulate organic matter and phytoplankton cell volume were similar between Chaoborus and Chaoborus-free enclosures (Fig.44). The percent composition of algal types was remarkably alike in pattern between the two treatments, although the chronology was slightly different (Fig.40 b,d). Net plankton became the dominant type in August, about a week earlier in the Chaoborus-free enclosure while the Chaoborus treatment developed large green colonies instead of the blue-green filaments which were dominant in the former enclosure. This development probably had little effect on the C.b.thomasi population as the bulk of the population had reached the carnivorous instars in both enclosures by August (Fig.39d).

Figure 44. Summer variation in particulate organic matter (POM) for Gwendoline Lake and the experimental enclosures. POM values are derived from pooled samples from the surface, 2.5 m., and 4.5 m. depths. Circles represent the 'Chaoborus-Cyclops' treatment, square represent the 'Cyclops' treatment, triangles represent the 'predator-free' enclosures and x indicates the lake values. Solid symbols represent fertilized treatments and open symbols represent unfertilized enclosures.



Effect of Fertilization and Chaoborus

First instar Chaoborus larvae were found in great numbers in both the fertilized and unfertilized enclosures (Fig.45). In the unfertilized conditions, however, relatively few developed into second instar larvae. This result was consistent with the observations of Fedorenko (1973) and Neill and Peacock (1980) that relatively few Chaoborus survived to the older instars in these oligotrophic lakes. The massive early juvenile mortality decreased significantly in the high nutrient enclosure as many more instar I developed into instar II and III. Neill and Peacock (1980) showed that this improved survivorship was due to solitary rotifer blooms at the high nutrient levels. Solitary rotifer numbers (Kellicottia, Keratella and Lecane spp.) increased dramatically in the fertilized enclosure (Fig.46) and this rotifer explosion was correlated with increasing Chaoborus instar I survivorship. The effect of this improved Chaoborus survivorship was to increase the rate of C.b.thomasi decline. In contrast to the Chaoborus-free high nutrient enclosure, few C.b.thomasi copepodid instars were recruited from the large naupliar standing stock and, unlike the unfertilized Chaoborus enclosure, no adults were sampled in August or September (Fig.39d).

This summer decline did not appear to be related to food resources. Adding nutrients to a Chaoborus enclosure resulted in changes paralleling that observed in the enriched Chaoborus-free enclosure in both particulate organic matter and phytoplankton standing crop. As in the unfertilized

Figure 45. Variation in the standing crop of Chaoborus larvae. Roman numerals indicate the larval instar (I, II and III are shown) of Chaoborus in fertilized and unfertilized 'Chaoborus-Cyclops' enclosures and in Gwendoline Lake during the summer of 1977.

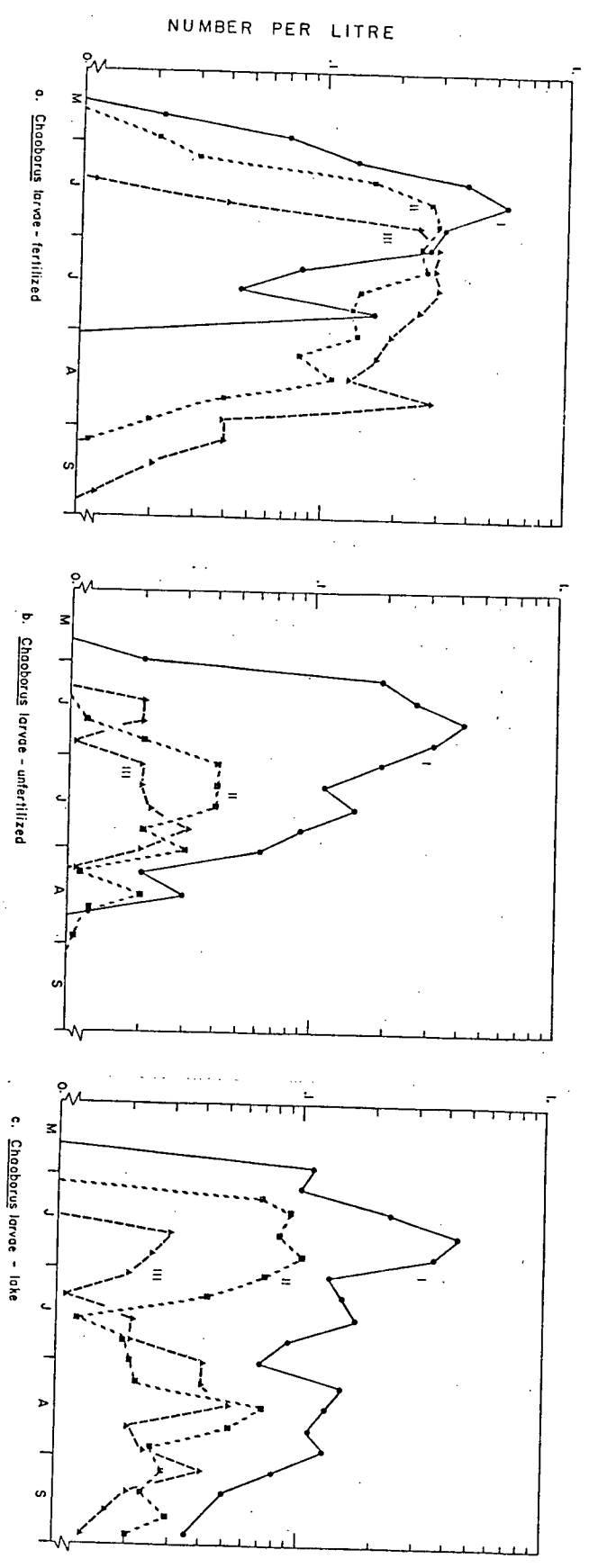
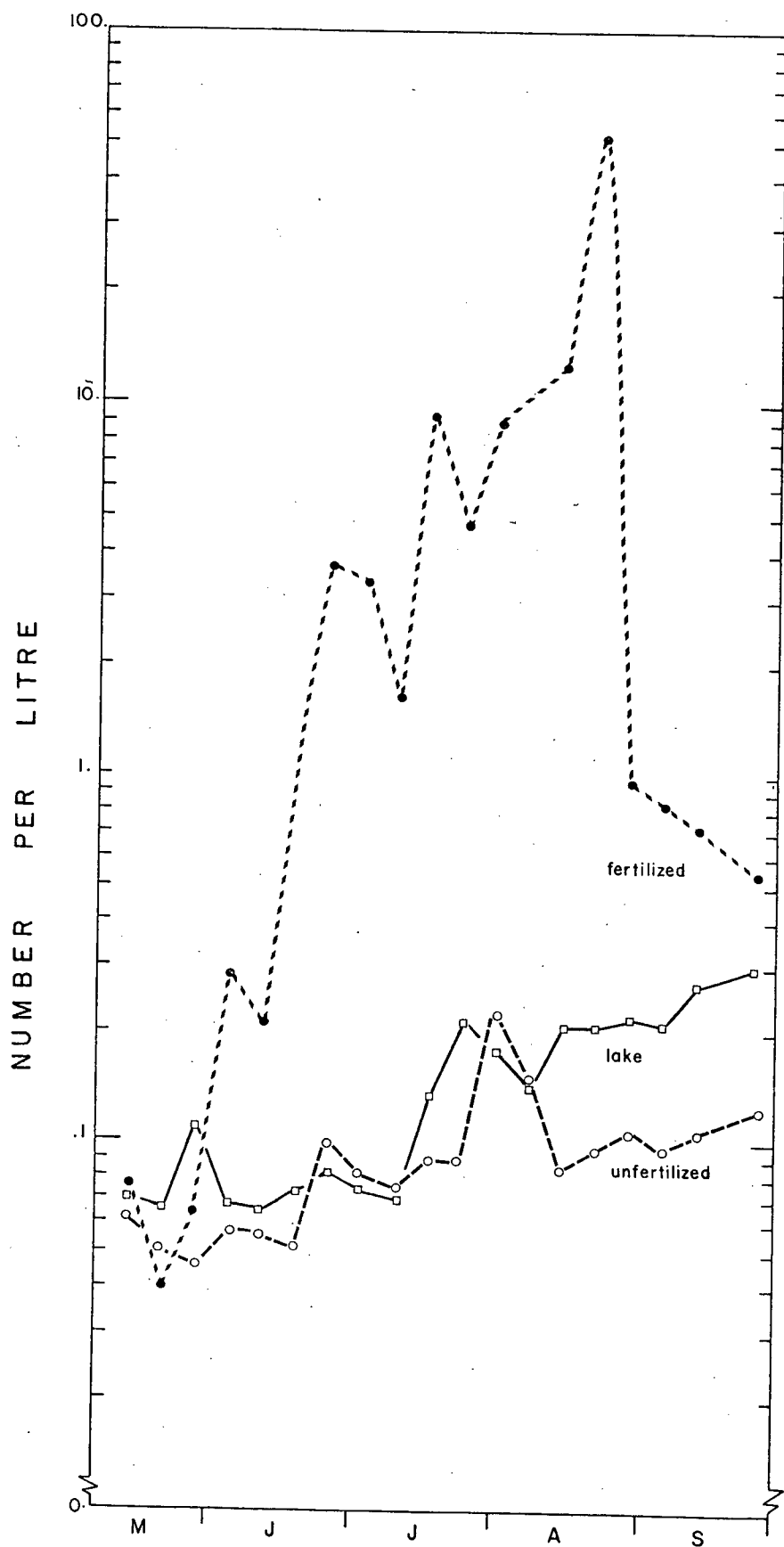


Figure 46. Variation in the standing crop of solitary rotifers observed in the 'Chaoborus-Cyclops' treatments and Gwendoline Lake during the summer of 1977.



enclosures, the pattern of change in percent composition of algal types was similar although the timing of events was slightly different. Filaments, mainly blue-greens, Oscillatoria and Lyngbya, became the overwhelming dominants in June, about a week earlier in the Chaoborus present enclosure and this dominance was maintained until late August (Fig.40 a,c).

DISCUSSION

C.b.thomasi is abundant in Placid Lake, a small montane lake with a resident population of cutthroat trout, and scarce in Gwendoline Lake, a nearby larger, deeper lake without a fish population. The experimental transplantation of C.b.thomasi from Placid Lake to an enclosure in Gwendoline Lake revealed that C.b.thomasi could survive and recruit in the fishless lake environment when the predaceous Chaoborus species present in this lake was removed. Consequently the low abundance of C.b.thomasi in Gwendoline Lake could not be explained by the hypothesis that physical/chemical differences between this lake and Placid Lake were unfavourable to C.b.thomasi.

There was no indication that food resources were too low to support an abundant population of C.b.thomasi, comparable to that found in Placid Lake. A measure of the 'grazable seston' - particulate organic matter - showed that the unfertilized enclosures were indistinguishable from Gwendoline Lake. Food resources were therefore probably similar to those experienced in the lake yet C.b.thomasi was always scarce in Gwendoline Lake and abundant in the enclosures without Chaoborus. C.b.thomasi was able to increase in the Chaoborus-free enclosures even though there was evidence that food was limiting in Gwendoline Lake. Adding nutrients to Gwendoline Lake water in the enclosures increased the number of eggs per clutch (mean of 25.7 compared to a mean of 21.0 per clutch, $p < .01$) and extended the period during which ovigerous females were present in the population. The latter effect suggested that the increase in the total number of eggs produced in the

fertilized enclosure might be due to a longer female adult life thus possibly permitting an increase in the number of broods per female. In Acanthocyclops viridis, Smyly (1970) found that the mean number of broods varied with the diet, from 1.5 broods on algae to 8.6 broods on Artemia nauplii. This author also found longevity varied with diet, from 67.9 days on Artemia to 106.4 days on Chydorus sphaericus. In Gwendoline Lake, Chydorus spp. increased in all the fertilized enclosures and may have served as an important food source for the later instars of C.b.thomasi.

C.b.thomasi survivorship in the unfertilized enclosure showed a mortality pattern similar to that observed in Placid Lake. The greatest mortality occurred in the egg to CII interval in both environments. Several authors (Gehrs and Robertson, 1975; Boers and Carter, 1978) have observed a similar pattern in calanoid populations, although Rigler and Cooley (1974) found that all five cohorts of Skistodiaptomus oregonensis shared a high survival to N3. Gehrs and Robertson (1975) suggest that the high mortality occurring in the N6 stage may be associated with morphological changes occurring as the organism moults from larval to copepodite form. There is evidence that the N5-N6 stages are more sensitive to environmental stress. Karanas et al. (1979) showed that the N5-N6 stages of Acartia clausii, a marine calanoid copepod, were unusually sensitive to midultraviolet radiation. Tolerance increased with age with the exception of stages N5-N6 which were even more sensitive than the N3-N4 instars.

I grouped nauplii by early (N1-N3) and late (N4-N6)

naupliar instars in this study and I found significant mortality occurred during both intervals. Burgis (1971) also found high naupliar mortality in the early stages of Thermocyclops hyalinus although Lewis (1979) concluded there was relatively little naupliar mortality in the same species. Gehrs and Robertson (1975) found that a laboratory population of Diaptomus clavipes had little mortality in the egg to N4 interval but in the field population 84% failed to develop to the N4 stage.

In spite of high naupliar mortality, the survivorship curves from the Chaoborus-free enclosures suggest that C.b.thomasi should not experience any more difficulty surviving and recruiting in the Gwendoline Lake environment than it does in Placid Lake, where this species is abundant. However, the predaceous midge fly larvae, Chaoborus differs in species and behaviour between the two lakes. C.flavicans, a small species which is benthic during the daylight hours, is found in Placid Lake. In Gwendoline Lake, C.trivittatus and C.americanus are the indigenous species, with the former the more abundant species. Both species are entirely planktonic and both are larger in size than C.flavicans, C.trivittatus being the largest. Fedorenko (1973) concludes that this predator can have a substantial impact on zooplankton communities, although Neill and Peacock (1980) found that Chaoborus does not have a major demographic effect on indigenous species in low nutrient environments. Similarly, Northcote et al. (1978) were unable to find any significant effect on species composition or on seasonal abundances of crustacean plankters when Chaoborus

was effectively eliminated from Eunice Lake by salmonid predation.

C.b.thomasi was introduced into enclosures in Gwendoline Lake without Chaoborus, identical to those described above, to test the hypothesis that Chaoborus prevented the expansion of the C.b.thomasi population in this lake. Alternatively, predation by Chaoborus might be an important factor limiting the success of C.b.thomasi only when food resources were low and C.b.thomasi juvenile mortality was already high. Although C.b.thomasi reproduced in the enclosures with Chaoborus, naupliar recruitment did not result in the copepodid recruitment observed in the enclosures without Chaoborus.

Smyly (1976b) found that instar IV larvae of C.trivittatus ate more C.b.thomasi adults than either the larger adult Diaptomus kenai or the smaller adult T.prasinùs when offered a choice, although densities used in the experiments were higher than those found in Gwendoline Lake. Adult numbers of C.b.thomasi decreased more rapidly in the Chaoborus enclosure suggesting that there might have been some loss of adult females to the overwintering fourth instar C.trivittatus larvae. However, the proportion of adult female C.b.thomasi producing eggs and the number of eggs per clutch were not significantly different between the two treatments and the number of females present during the reproductive period in May-June were not statistically different. This result showed that there was a similar potential for increase between the enclosures both with and without Chaoborus.

Algal standing crops in the unfertilized enclosures with

and without Chaoborus were remarkably similar, both in volume biomass and in the composition of algal types. Therefore, increased mortality in the Chaoborus treatment due to naupliar starvation was unlikely, and there was no reason to expect intraspecific predation to be greater in this situation.

Gwendoline Lake is a low food environment for Chaoborus. Greatest mortality occurs in the first and second instars (Neill and Peacock, 1980). Rotifer populations are low in the unfertilized enclosures, as they are in the lake. A laboratory experiment using alternative crustacean prey at realistic lake densities showed that first instar Chaoborus ate more C.b.thomasi nauplii than the alternatives - calanoid nauplii and immature cladocerans. This result may be due to size and/or behaviour. C.b.thomasi nauplii are smaller than the calanoid nauplii (D.leptopus and D.kenai) found in Gwendoline Lake and appear to swim in a quick jerky fashion rather than the smooth gliding motion of the calanoid nauplii. As Chaoborus locate prey via mechanoreceptors (Giguere and Dill, 1979), this behaviour may make them more vulnerable. In addition, D.leptopus may have a temporal refuge as this species produces eggs in March (in some years at least), reaching copepodite stages by June when 1st instar Chaoborus appear (M.A.Chapman,pers.comm.).

Gerritsen (1978) investigated the potential predatory impact of a Chaoborus sp. (he did not identify the species) on Cyclops scutifer nauplii. He argues that nauplii are cryptic to the vibration-sensitive Chaoborus predators because nauplii are less active than copepodids or adults. Fedorenko

(1973) also found that Chaoborus larvae instar II did not feed effectively on calanoid nauplii. However, it is clear that Chaoborus instar I can selectively remove rotifers (Neill and Peacock, 1980) and that this susceptibility cannot be predicted by examining swimming speeds alone. Clearly the developmental response and spatial/temporal interaction of predator and prey must be important factors in assessing prey vulnerability.

Furthermore, the spectra of prey items available to a small Chaoborus larva are extremely limited, particularly in oligotrophic lakes where rotifers are generally not abundant. Lewis (1979) notes the discrepancies between growth rates based on cohort development in the field and that possible based on published feeding rate data. He finds that even with high assimilation and growth efficiencies, laboratory estimates of prey intake are much too low. Lewis suggests that part of the problem may be explained by the tendency of most investigators to focus on the last instar, the instar he estimates to have the lowest growth rate.

Using C.b.thomasi population data from the Chaoborus-free enclosure and 1st instar Chaoborus from the Chaoborus enclosure, I estimated the C.b.thomasi naupliar population which could be removed by 1st instar Chaoborus larvae (Fig.46). It was clear that the probability of being eaten was extremely high over the entire 17.5 day residence time of an average naupliar C.b.thomasi copepod. As approximately 76% of the naupliar population perished before reaching the copepodid instars even in the absence of Chaoborus, the addition of this predator had catastrophic effects on C.b.thomasi copepodid

recruitment.

Lewis (1977) examined gut contents of all 4 instars of Chaoborus in tropical Lake Lanao and found cyclopoid nauplii seldom represented. This author concluded that some predator avoidance mechanism must be operating and suggested it may be behavioural - lack of motion causing the nauplii to be cryptic to Chaoborus larvae as suggested by Gerritsen (1978). However, the only rotifer commonly encountered in the gut contents was Keratella - a loricate rotifer. Fedorenko (1975) found that small, soft-bodied prey such as copepod nauplii and nonloricate rotifers were seldom detected in crop analysis and she attributed this result to rapid digestion of these food types in the larval crop. Lewis (1979) conceded that rapid processing in the crop might have contributed to his result.

Fertilization appeared to accelerate the elimination of C.b.thomasi nauplii, even though survivorship was greatly enhanced by the addition of fertilizer to Chaoborus-free enclosures. Adding nutrients caused a rotifer bloom and greatly improved juvenile Chaoborus survivorship. A similar response was observed by Neill (pers.comm.), such that even the r-strategist cladocerans were unable to survive the impact of Chaoborus predation. Chaoborus survivorship improved about 20-fold over low nutrient treatments in the 'intermediate' fertilizer additions (Neill and Peacock, 1978). As C.b.thomasi improved its survivorship only about 4-fold at the 'high' fertilizer level, it seemed unlikely that C.b.thomasi could numerically escape this predator even at less extreme nutrient levels.

These results indicate that the predator component of the biotic environment has more effect on the abundance of C.b.thomasi than lake depth, temperature or even nutrient level. The generality of this result is difficult to evaluate. Patalas (1971) examines only the crustacean plankton community in his study of 45 lakes in the Experimental Lakes Area. Anderson and Raasveldt (1974) found a weak positive correlation ($p < 0.30$) between mean cyclopoid densities and the presence of Chaoborus spp. but he does not differentiate between chaoborid species in grouping his communities. Both C.americanus and C.flavicans are found in his study area. Pope and Carter (1975) found that all the lakes in the Matamek River System were dominated by cyclopoid copepods, primarily Cyclops scutifer, during July and late August-September and they reported no difference between those lakes with high densities of Chaoborus spp. (mainly C.americanus in the fishless lakes) and no fish and those lakes with fish. However, Von Ende (1979), in a study of 4 bog lakes in the Upper Peninsula of Michigan, reports that C.b.thomasi is abundant only in a fish lake with a small, benthic-by-day species of Chaoborus, C.punctipennis.

If the principal impact of predation is on the naupliar instars, rather than the copepodid or adult, the results of Lynch (1979) may indicate an interaction between C.vernalis and C.americanus. Lynch concludes that C.vernalis is not influenced by Chaoborus predation but he does not provide any explanation for the large naupliar mortality observed in the presence of abundant Chaoborus. Naupliar abundance data also

suggest that the June decline of C. vernalis, identical in both high and low Chaoborus conditions, represents the end of a generation rather than evidence of immunity to Chaoborus predation. However, as cyclopoid and calanoid nauplii are not differentiated and no instar or reproductive data are presented, there are no data with which to discriminate between the two hypotheses. However, future studies should consider this possibility. Most planktonic invertebrate predators are organisms with limited functional and numerical responses (Hall et al, 1976), and this generalization is particularly true in oligotrophic systems where the predator exists in a very dilute food environment. This study shows that spatial/temporal interaction and the abundance of alternative prey must be evaluated before the efficacy of an invertebrate predator can be accurately assessed.

SUMMARY

1. C.b.thomasi can survive and reproduce in enclosures filled with Gwendoline Lake water and and Gwendoline Lake crustacean plankton.
2. The naupliar stages represent the developmental bottleneck for C.b.thomasi populations in Gwendoline Lake and this mortality pattern is similar to that observed in Placid Lake.
3. Fertilization of the Gwendoline Lake enclosures increases survivorship of C.b.thomasi about 22% over that observed in the unfertilized treatment.
4. Adding the midge fly larvae C.trivittatus and C.americanus to the Gwendoline Lake enclosures drastically reduces the abundance of C.b.thomasi.
5. In the presence of Chaoborus , fertilization

does not increase the abundance of C.b.thomasi but rather, improves the survivorship of Chaoborus and this results in the rapid decline of C.b.thomasi nauplii.

IV. EFFECT OF VARYING INVERTEBRATE PREDATOR ABUNDANCE AND
FOOD ON A CRUSTACEAN PLANKTON COMMUNITY

INTRODUCTION

Limnetic crustacean zooplankton live in a relatively unstructured habitat with little apparent protection from their predators. Yet the persistence and often high abundance of lacustrine prey species, even in oligotrophic systems, suggest an insensitivity to predator influence. This appearance of immunity might explain why there was little interest in the role of predators in determining the composition of freshwater prey communities until the classic papers of Hrbacek (1962) and Brooks and Dodson (1965). Since that time considerable evidence has been amassed to show that fish can alter the composition of crustacean prey (Hurlbert, Zedler and Fairbanks, 1972; Zaret, 1978; O'Brien, 1979). Fish plankivores selectively remove prey which are large in size or visible through pigmentation and/or conspicuous locomotion (Zaret, 1978). Thus the presence of fish predators favours prey species which have a small body-size, reduced pigmentation or reduced motion (Northcote and Clarotto, 1975; Zaret, 1975; Zaret and Kerfoot, 1975; Northcote et al., 1978; Lynch, 1979).

The role of invertebrate predators in causing changes in the composition and abundance of prey populations is more controversial but some researchers (e.g. Lane, 1979) suggest these predators are at least as important as fish in shaping prey dynamics. There are several reasons why the impact of invertebrate predators is difficult to define. Invertebrate predators, unlike fish predators, usually have a life expectancy only slightly longer than their prey. Thus there is little time, relative to fish, for invertebrate predators to

have an impact. There is also little flexibility in the prey type that they can locate and handle (Hall et al., 1976; Zaret, 1978). The prey characteristics which affect the success of an invertebrate predator are often difficult to define because they represent a complex function of size, shape, behaviour, tactile or chemical detectability (Li and Li, 1979), and spatial and temporal interactions (Lewis, 1977). Attempts to describe the predator-prey relations experimentally have been confounded by these problems (McQueen, 1969; Dodson, 1974; Fedorenko, 1975; Kerfoot, 1979; Lane, 1979; Lynch, 1979).

Predatory impact and the temporal availability of food for both predator and prey are interrelated and difficult to uncouple in examining communities composed of small, short-lived aquatic animals. However Lane (1979), using fluorescent labelling techniques, estimates that Cyclops bicuspidatus can crop 33% of the Daphnia population at 5 m during June and 69% of this population at 20 m. Although Lane estimates lower rates of prey consumption by this predator during July and August, it is clear that C.bicuspidatus has a major impact on Daphnia biomass in Gull Lake. However, Gull Lake is a relatively nutrient rich system and therefore may represent an environment where C.bicuspidatus can exercise high predation rates per predator with relatively little overall influence on prey abundance. Zaret (1978) suggests that if predation and competition are the main determinants of community species composition, nutrients will have their greatest effect on the numerical levels of species rather than on composition of species. Hall et al. (1976) conclude that invertebrate

predators rarely cause prey extinctions, unlike vertebrate predators, because they have poor functional and numerical responses relative to their prey. Lynch (1979) reports that the invertebrate predator Chaoborus reaches sufficiently high densities in Pleasant Pond to cause prey extinctions but that a smaller predator, the cyclopoid copepod Cyclops vernalis, does not. Therefore in a nutrient rich environment prey with high reproductive rates may numerically swamp a small predator with a poor functional response and low rates of recruitment such that no net impact on prey population numbers is detected. However, in an oligotrophic system these microcrustacean predators may have a significant numerical and/or compositional effect on prey populations because prey are already food-limited and abundance is low. Furthermore, it is also possible that the impact of predaceous cyclopoid copepods is altered by the presence of other invertebrate predators such that the combined effect is greater than that predicted from examining either population alone. Small invertebrate predators may influence relations between herbivorous crustacean species by reducing the number of competitors and thereby increasing scarce food resources. Alternatively, insufficient energy may be available to support a substantial predatory trophic level because prey density and productivity are low. Hence predation may be unimportant under oligotrophy and only become of consequence under more productive conditions.

In this study I examined the impact of C.b.thomasi on the relative and absolute abundances of herbivorous prey in large

in situ perturbations of nutrients, Cyclops and Chaoborus densities. By using field enclosures I was able to experimentally manipulate the initial composition of the zooplankton communities and track numerical responses through time while ensuring that environmental variables influenced all treatments in a similar manner. By fertilizing water bodies of identical size and shape, the manner in which competition and predation interface with nutrient levels could be monitored without the confounding effects of different lake morphologies. This approach also allows predator impact to be assessed without the problem of estimating predator effect with a technique which does not discriminate between prey killed by predation and those dying from other causes.

The experiments were therefore designed to 1) compare the impact of C.b.thomasi predation on the zooplankton community when Cyclops is the only predator with that when Cyclops is combined with another invertebrate predator which has a more impressive functional response 2) to compare these effects with those produced in the same communities by altering the nutrient environment in side-by-side enclosures 3) to compare crustacean community dynamics under the above conditions with the responses of the same grazer community when invertebrate predators are absent.

MATERIALS AND METHODS

Biomass estimates

Dry weights were determined for all cyclopoid copepods as described in section three. I estimated the biomass of all cladocerans and calanoid copepods by converting length measurements to dry weight. All measurements were made using a calibrated ocular micrometer in a dissecting microscope at 50X magnification. For Cladocera the distance between the anterior end of the head (excluding helmet projections if present) and the posterior margin of the valves (excluding spine) was measured. For calanoid copepods, the metasome plus urosome (excluding caudal rami) was considered body length. Means of at least 40 animals were converted to dry weight using equations derived from Research Forest Lake animals (Neill, unpub.data) or from Dumont et al.(1975). Phytoplankton cell volumes, estimated as described in Section Three, were converted to ash-free dry weight using the criteria of Vollenweider (1969).

Field experiments

The experimental design and sampling methods were also described in section three. All experiments were carried out in Gwendoline Lake. There were 6 treatments: 3 different communities and 2 levels of nutrients. I shall refer to the community with lake densities of the Gwendoline Lake crustaceans but no Chaoborus as 'predator-free' ; the community with the above plus added Placid Lake densities of C.b.thomasi as the 'Cyclops' treatment; and the latter community, including all the above plus Gwendoline Lake densities of Chaoborus as the 'Chaoborus-Cyclops' community. The 2 nutrient levels were created by fertilizing one half of the community treatment enclosures and leaving the other half with unaltered Gwendoline Lake water. A single large dose of a phosphate-nitrate fertilizer (NaH_2PO_4 and KNO_3 , at a ratio of 1:10) was added in mid-May at a phosphate concentration of $500 \mu\text{g PO}_4$ per litre. Partial mixing was carried out by occasional bubbling during June, July and August. The 'high' nutrient treatment was not designed to simulate any 'natural' condition but rather to substantially increase food resources during early June and thereby enhance spring crustacean recruitment.

Cluster analyses were performed on the data to describe the relative species abundances between treatments during two time intervals, May-June and August. The time periods were chosen to reflect initial conditions/ responses and the period of greatest divergence, respectively, thus facilitating the identification of species groupings through time and between treatments. The raw data matrix comprising the numerical

abundance of 21 species/stages was modified to make the treatment effects additive by application of the $\log(x+1)$ transformation (Sokal and Rolf, 1969). Pearson product-moment correlation coefficients were used as the basis for UPGMA clustering (unweighted pair-group method using the arithmetic average of the coefficients between a sample candidate for admission and that of members of an extant cluster (Sneath and Sokal, 1973)). This clustering technique yielded the best representation of relationships among matrices as measured by cophenetic correlation (Sneath and Sokal, 1973). The analyses were performed using the NT-SYS package of programs developed by F.J. Rohlf, J. Kispough and D. Kirk at the State University of New York at Stony Brook.

General Life Histories

The two major plankton invertebrate predators included in the experimental design are Chaoborus larvae and the cyclopoid copepod C.b.thomasi. Both predators are found in Gwendoline Lake although C.b.thomasi is rare.

Of the 2 Chaoborus species found in Gwendoline Lake, C.americanus is univoltine while C.trivittatus may take 2 years to mature. The latter comprises 90-95% of the Chaoborus larvae (Neill, 1980). Although pupation, emergence and reproduction occurs in late spring to early summer, the 2 year cycle of the most abundant species, C.trivittatus, results in a sustained abundance throughout the year of larger larvae that prey upon crustaceans. First and second instar larvae are present for a relatively short period from June through mid-

July and these instars prey upon small animals, rotifers and nauplii (Neill and Peacock, 1980).

Because C.b.thomasi was present but rare in Gwendoline Lake, I introduced C.b.thomasi to 4 enclosures at densities realistic for nearby Placid Lake. As described in section three, introduction to the Gwendoline Lake enclosures in the absence of Chaoborus did not appear to disrupt the seasonal dynamics of C.b.thomasi as observed in Placid Lake. Carnivorous instars of C.b.thomasi were present during May and June, when reproduction occurred. Adult mortality escalated by late June, leaving small particle-feeding nauplii to represent the species. The nauplii developed to copepodid instars by mid-July, becoming increasingly carnivorous with each molt. By August the C.b.thomasi population was again dominated by carnivorous instars.

The herbivorous prey species in Gwendoline Lake also reproduced in the spring - D.leptopus reproducing as early as March in 1977 (M.A. Chapman, unpub.data). By late May D.kenai was reproducing and the cladocerans, D.rosea and Holopedium gibberum, were common. Bosmina longirostris was present in low numbers. The only other cladoceran commonly encountered in Gwendoline Lake, Diaphanosoma brachyurum, was a summer species and appeared in the plankton in July. T.prasinus was the only relatively abundant cyclopoid copepod and did not appear in the plankton in countable numbers until late July. T.prasinus began reproduction in August and disappeared from the plankton again by early November.

The calanoid copepods usually produce no more than two

generations per year; T.prasinus produces only one. In contrast to slow copepod recruiters, the cladocerans are all multivoltine, producing parthenogenic young through the spring-summer period and resting eggs in late fall. Typically, cladoceran populations decline during late July and August and increase again in early September.

Body Size and Weight

The spectrum of zooplankton sizes observed within the enclosures in Gwendoline Lake are shown in Table 12. The adult mean length of both cyclopoid species was <1.0 mm. C.b.thomasi adults were slightly larger (max. of 1.1 mm) than those of T.prasinus (max. of 0.9 mm). T.prasinus nauplii were distinguished from C.b.thomasi nauplii by their green coloration. A huge cyclopoid copepod, Macrocylops albidus, (max.length 2.6 mm) was present in low numbers throughout the season in both nutrient treatments, although somewhat more abundant (but always <0.2 individuals/litre) in the fertilized enclosures. Mesocyclops edax was irregularly sampled, as were the cladocerans, Latona sp., Ceriodaphnia sp., and Schapholeberis sp. All these rare species were more common in the fertilized enclosures than the unfertilized treatments.

Cyclopoid nauplii and rotifers probably represented the smallest prey in the community, along with neonates of Chydorus and Bosmina. Although diaptomid nauplii and copepodids were not differentiated to species, the mean sizes of the copepodids corresponded to Fedorenko's (1973) 'small' group, perhaps suggesting that these instars were D.leptopus copepodids.

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TABLE 12. Mean length and dry weights of Gwendoline Lake zooplankton used in conversions to biomass.

Species	Length (mm)	Dry Weight (ug/animal)
<u>C.b.thomasi</u> adult	0.91	5.07
copepodid	0.55	1.66
nauplius	0.13	0.37
<u>T.prasinus</u> adult	0.70	2.57
copepodid	0.45	1.14
nauplius	0.10	0.24
<u>D.kenai</u> adult	2.41	49.78*
<u>D.leptopus</u> adult	1.60	23.02*
<u>Diaptomus</u> copepodid	1.33	14.96*
<u>Diaptomus</u> nauplius	0.36	0.71*
<u>D.rosea</u>	1.32	7.60**
<u>Holopedium</u>	1.23	12.62**
<u>Bosmina</u>	0.40	1.80*
<u>Chydorus</u>	0.35	1.48*
Rotifers		0.28**
Other cyclopoids	1.73	26.79*
Other cladocerans	0.98	2.95*

* from Dumont (1975)

** from length/weight regressions on Research Forest Lake animals (Neill, unpub.data)

Mean size of the calanoid nauplii in this study (0.36 mm) was similar to that of Fedorenko's (0.35 mm) in which both species of diaptomids were also grouped as calanoid nauplii. Consequently it was difficult to speculate on the relative representation of the two calanoid copepod species based on size, although poor representation of D.kenai adults in September in all treatments suggested that most surviving nauplii were D.leptopus.

RESULTS

Cluster Analyses of the Community

I observed crustacean zooplankton community responses to fertilization under different conditions of invertebrate predation during the period from mid-May to late September, 1977. Initial densities of all zooplankton but C.b.thomasi mimicked Gwendoline Lake densities. Because the enclosures were filled with the May assemblage of animals and T.prasinus did not appear in the plankton until mid-July, T.prasinus was added to all enclosures to equal summertime densities. The numerical abundance of 21 species/stages ($\log(x+1)$ transformed) was used to calculate a correlation matrix for 7 collection dates representing 49 samples during May-June to illustrate patterns of similar species abundances between treatments and the lake. The matrix of species/stages (representing sampling dates and treatments) was then subjected to cluster analysis to facilitate description of similarities between treatments and Gwendoline Lake. As C.b.thomasi and Chaoborus were experimental variables, these species were not included in the analysis which therefore represented only Gwendoline Lake grazers.

A cluster of 10 treatments is evident at the top of the dendrogram (Fig.47a). The first 7 of these represent the initial samples taken on May 17 from all 6 treatments and the lake (sampled to the same depth as the enclosures). Initial

Figure 47. Cluster analyses of the treatment enclosures in Gwendoline Lake.

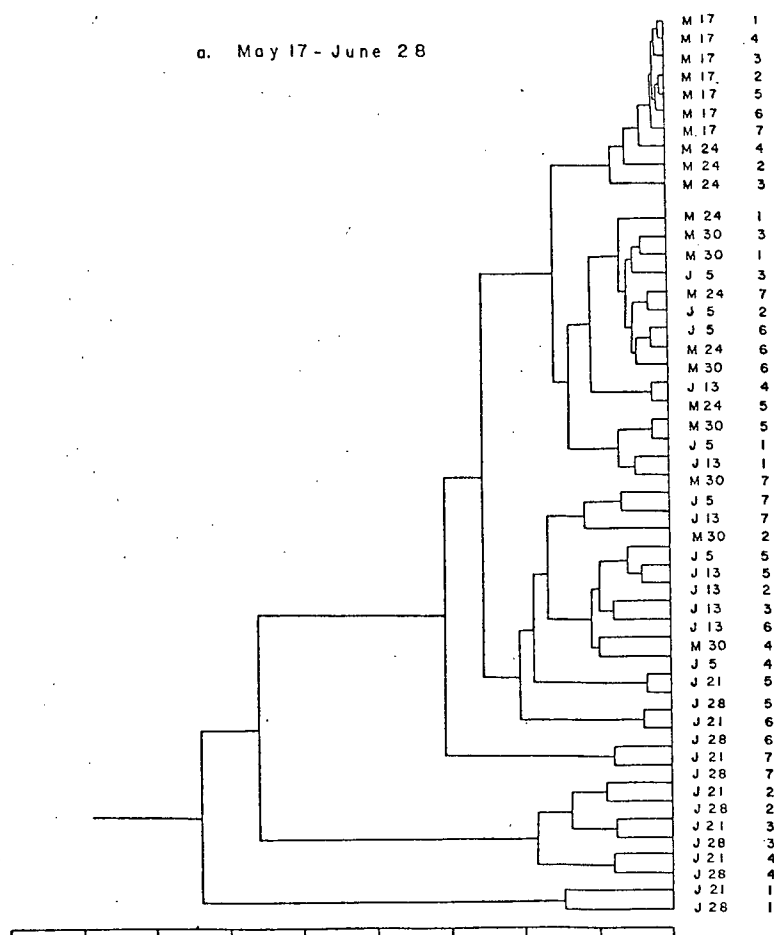
A. This figure shows the cluster analysis of the species abundance data from the treatment enclosures and the lake on 7 sampling dates from May 17 (M17) to June 28 (J28), 1977.

B. This figure shows the cluster analysis of the species abundance data for the treatment enclosure on 5 sampling dates in August. Treatment numbers represent: 1 - fertilized 'Chaoborus-Cyclops', 2 - fertilized 'predator-free', 3 - fertilized 'Cyclops', 4 - unfertilized 'Cyclops', 5 - unfertilized 'predator-free', 6 - unfertilized 'Chaoborus-Cyclops' .

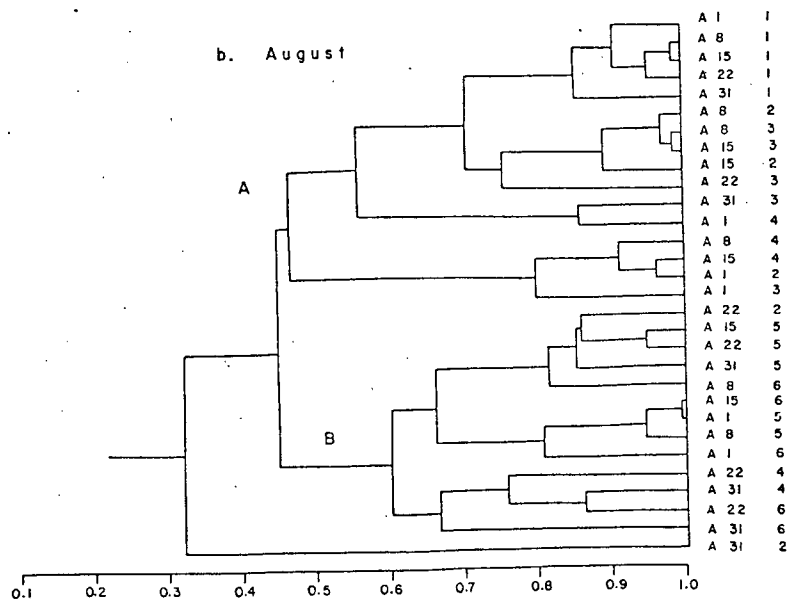
Sample

Date Treatment

a. May 17 - June 28



b. August



densities are clearly very similar between treatments and the lake. Similarity between enclosures decreases with time and the dendrogram indicates this chronological order from top to bottom. Early samples from all treatments are closely related but treatments increasingly differentiate into more distantly related groups as time progresses. By the latter two weeks in June, represented by J21 and J28, each treatment essentially forms a small cluster. However, the fertilized 'Cyclops' treatment is most similar to the fertilized 'predator-free' enclosure, both of which are quite distinct from the 'Chaoborus-Cyclops' treatment. Included in the former grouping is the unfertilized 'Cyclops' treatment, perhaps suggesting that the influence of C.b.thomasi in the unfertilized environment is to release more food resources for herbivores thus creating conditions more like the fertilized 'Cyclops' enclosure without Chaoborus.

The same analysis performed on 5 sampling dates and the 6 treatments in August indicates considerable divergence in prey zooplankton among treatments has occurred (Fig.47b). There appears to be two large clusters A and B with each group further split into 4 and 3 groups respectively. The August 31st sample from the fertilized 'predator-free' treatment at the bottom of the dendrogram appears to be quite distinct. With interesting exceptions, group A and B correspond to fertilized versus unfertilized enclosures. Within A, there is evidence of a clustering of all the August fertilized 'Chaoborus-Cyclops' samples. This is the only treatment wherein each sample remains most similar to its next

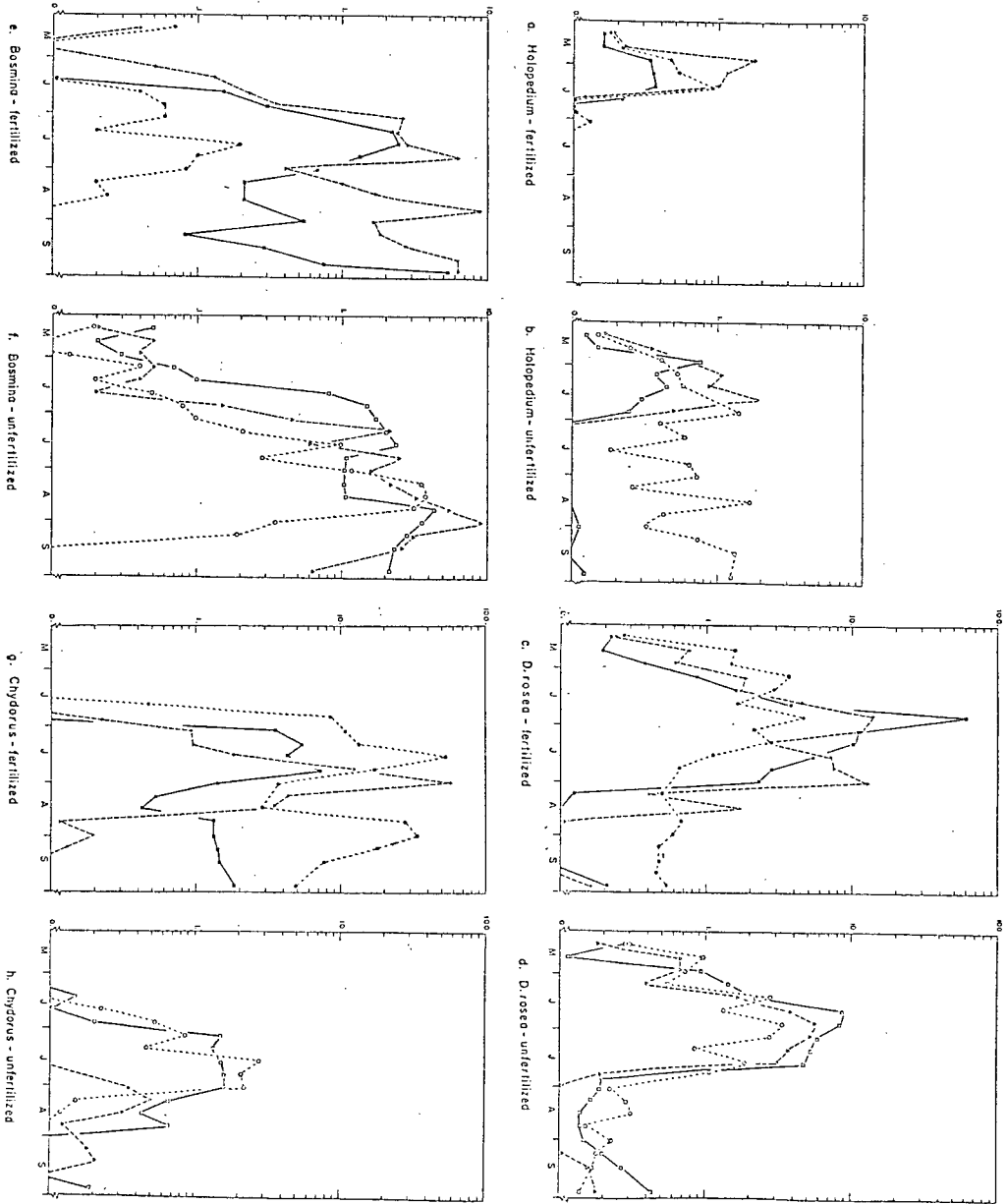
chronological sample throughout August, suggesting that community structure is most unique within this treatment. As in the late June samples, the samples from the fertilized 'Cyclops' and 'predator-free' treatments appear to cluster together and the only samples from an unfertilized enclosure included in cluster A are those from the 'Cyclops' enclosure. However, late August samples from this treatment are found in the B cluster with samples from all the remaining unfertilized treatments. In terms of the general pattern, the most aberrant samples are the A22 and A31 samples from the fertilized 'predator-free' treatment. The former clusters with the unfertilized 'predator-free' enclosure while the latter forms a distinct group.

Cladoceran numerical response

To understand the population abundances which give rise to the clustering patterns, a detailed description of prey dynamics in response to nutrient and predator manipulations is presented. Fig.48 (a-h) illustrates the trends in population densities of major cladoceran species observed in the experimental communities. With the notable exception of Holopedium, these fecund zooplankters responded to fertilization by initially increasing in number across all treatments. Holopedium increased in the fertilized enclosure where neither Chaoborus nor C.b.thomasi were present but rapidly disappeared from all the fertilized enclosures by mid-June - early July. I observed a similar pattern, although not so rapid a decline, in all treatments except the unfertilized

Figure 48. Variation in standing crop of cladoceran crustaceans in Gwendoline Lake, 1977. Circles represent the 'Chaoborus-Cyclops' enclosures, squares represent the 'Cyclops' treatments and triangles represent the 'predator-free' treatments. Open symbols represent the fertilized treatments and solid represent the unfertilized treatments.

NUMBER PER LITRE



'Chaoborus-Cyclops' enclosure. As Holopedium was usually found below the thermocline in Gwendoline Lake by July, and the enclosures mimic Placid Lake where the maximum depth is 7 m., this disappearance might reflect temperature stress. Neill (1980) found that during the cold spring of 1976, fertility was higher in this species (31% ovigerous with 2.61 ± 0.21 eggs/female) than in 1977. In my shallower enclosures, fertility was low in May (maximum of 13% with 2.1 ± 0.17 eggs/female) and reproduction effectively ceased in all treatments by mid-June, although ovigerous females were detected sporadically in the unfertilized 'Chaoborus-Cyclops' enclosure. The persistence of Holopedium in the latter treatment suggested an immunity to Chaoborus predation and possibly, the importance of this predator in relieving grazing pressure by cropping competitors.

Unlike Holopedium, D.rosea rapidly increased in abundance in all the high nutrient enclosures surpassing population densities observed in the unfertilized enclosures in June. Rates of fertility were similar in all the fertilized enclosures: 'Chaoborus-Cyclops' - 29% ovigerous females with 11.23 ± 0.06 (s.e.) eggs/female; 'predator-free' - 24% ovigerous females with 10.85 ± 0.80 eggs/female; 'Cyclops' - 26% ovigerous females with 11.20 ± 0.49 eggs/female. All the unfertilized enclosures were lower: 'Chaoborus-Cyclops' - 15% ovigerous females with 4.43 ± 0.14 ; 'predator-free' - 15% ovigerous with 3.12 ± 0.22 and 'Cyclops' - 14% ovigerous with 4.12 ± 0.17 eggs/female. The presence of Chaoborus appeared to moderate D.rosea population increases and a similar, although

less marked, effect was observed in the unfertilized 'Chaoborus-Cyclops' enclosure. While the presence of Chaoborus dampened numerical increases in June, the inclusion of this predator also appeared to moderate the August decline.

In contrast to Chaoborus, the presence of an abundant C.b.thomasi population neither blunted the June increase nor restrained the August population crash in the fertilized enclosure. However, in the unfertilized enclosure, D.rosea does not decline as drastically in the C.b.thomasi enclosure as this population does in the unfertilized 'predator-free' enclosure. Fertility declined in all enclosures in August but only in the 'predator-free' enclosure (both nutrient enhanced and unenriched) did fertility rates drop to zero. Thus food limitation was probably the cause of the population crashes in these treatments. In the 'Cyclops' unfertilized treatment there averaged about 15% ovigerous D.rosea females with 1.2 ± 0.23 eggs/female in August. In the similar community but fertilized treatment only 7% carried eggs with 1.0 ± 0.16 eggs/female. Consequently the presence of 'Cyclops' appeared to free up more resources for the D.rosea population in the unfertilized enclosure than in the high nutrient treatment. There were relatively more ovigerous females in both the 'Chaoborus-Cyclops' treatments and in the fertilized 'Cyclops' enclosure in August - 11% with 1.4 ± 0.79 and 13% with 1.2 ± 0.11 eggs/female in the fertilized and unfertilized treatments respectively.

In sum, D.rosea was unable to increase numerically in the fertilized 'Chaoborus-Cyclops' enclosure to the extent possible

in the other two treatments and this result appeared to be due to Chaoborus predation. In contrast C.b.thomasi had relatively little effect on D.rosea densities. D.rosea exhibited dynamics in the fertilized 'Cyclops' enclosure similar to that observed in the fertilized 'predator-free' treatment. However, in the unfertilized enclosure C.b.thomasi appeared to break the August decline in a manner equivalent to that observed in the unfertilized 'Chaoborus-Cyclops' treatment. Thus C.b.thomasi might be important to D.rosea in low food environments by relieving grazing pressure through predation on small herbivores. In high nutrient situations this effect seemed to be swamped by cladoceran reproduction.

Bosmina exhibited more oscillatory behaviour. This species did not increase markedly in the high nutrient enclosure over the unfertilized treatments in both enclosures without Chaoborus. In the fertilized Chaoborus enclosure Bosmina remained at much lower densities than in any of the unfertilized enclosures (Fig.48 e,f). During June, over 25% of the population were ovigerous in the fertilized 'Chaoborus-Cyclops' enclosure compared to 20% in the 'predator-free' and 17% in the 'Cyclops' fertilized treatment. This relatively high fertility yet low population number of Bosmina in the fertilized 'Chaoborus-Cyclops' enclosure was probably due to suppression by Chaoborus predation. Ovigerous females constituted about 12-15% of the population in all the unfertilized enclosures during this period and densities were only slightly lower than those in the fertilized treatments. The inability of Bosmina to significantly increase in number in

the fertilized 'predator-free' enclosure might be caused by competition from the other small cladoceran, Chydorus (Fig.48 g,h). By the end of July, 24% of the Bosmina population were ovigerous but over 31% of the Chydorus population carried eggs. Bosmina declined in early August while Chydorus numbers underwent a minor explosion, increasing almost 5-fold. The Chydorus bloom was short-lived, however, and ovigerous females dropped to 9%. As this decline occurred, Bosmina increased. Fertility rose until 23% of the population carried eggs. Bosmina abundance declined again at the end of August. This decrease was not as sharp and was unrelated to Chydorus abundance because the latter population never recovered from its early August decline in this enclosure.

Chydorus (Fig.48 g,h) densities struck a contrast to the Bosmina trends in all the fertilized enclosures. This species increased dramatically in all these enclosures when compared to population numbers in the unfertilized enclosures. Chydorus appeared in the fertilized 'Chaoborus-Cyclops' treatment in mid-June, about two weeks ahead of its appearance in the other fertilized treatments. Over 40% of the population was ovigerous during June although this high fertility decreased to about 15% in July. Fertility was lower in both 'predator-free' and 'Cyclops' fertilized enclosures, at 5% and 15% respectively in late June.

During August the proportion of ovigerous females in the fertilized 'Cyclops' enclosure rose to over 40%. This high production of young was not reflected in population increases, in spite of the fact that the number of eggs each female

carried was relatively invariant (2.0 ± 0.01) across all treatments. As previously described, Chydorus experienced a brief bloom in the fertilized 'predator-free' enclosure and probably encountered severe food shortages by mid-August because the fertility rates dropped to about 9%. In the 'Chaoborus-Cyclops' fertilized treatment only 20-25% of the population was ovigerous during August. Consequently, the lower Chydorus population numbers in the fertilized 'Cyclops' enclosure was probably caused by C.b.thomasi predation.

In sum, Bosmina was apparently not an effective competitor at either nutrient level and was very sensitive to Chaoborus predation in the fertilized treatment. In contrast Chydorus was able to increase dramatically in all fertilized enclosures. Chydorus seemed relatively immune to Chaoborus predation, possibly because Chydorus tended to concentrate near the water surface. The most abundant population of Chydorus was found in the fertilized 'Chaoborus-Cyclops' enclosure. Lowest Chydorus densities, among the fertilized treatments, were found in the 'Cyclops' enclosure, thus C.b.thomasi, unlike Chaoborus, apparently had a significant impact on Chydorus. At low nutrient levels Chydorus was least abundant in the 'predator-free' enclosure suggesting that Chydorus was a weak competitor and unable to sequester food resources in the absence of an invertebrate predator to release some grazing pressure.

Calanoid Copepod Response

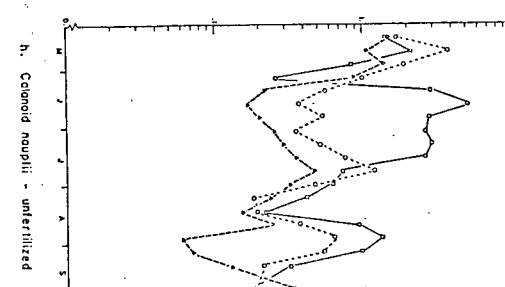
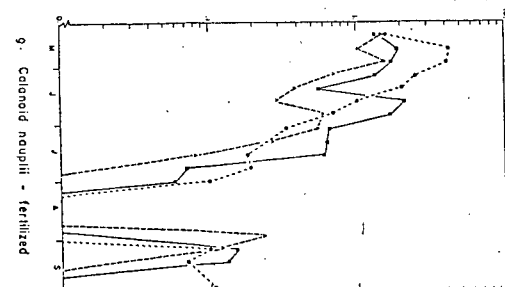
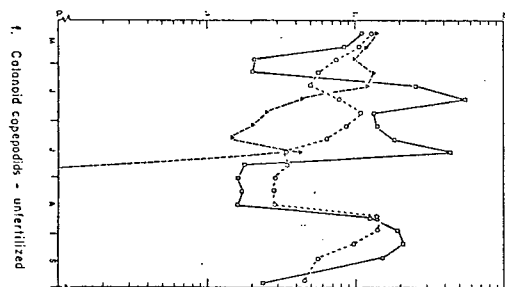
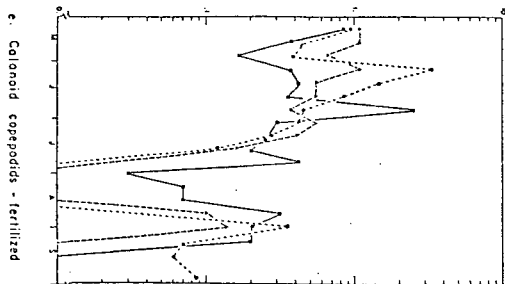
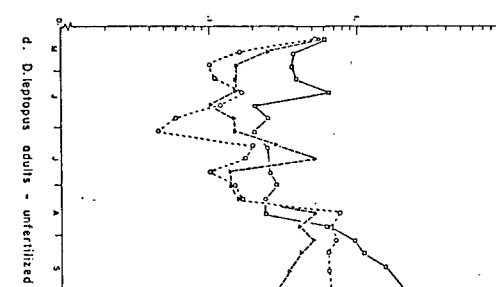
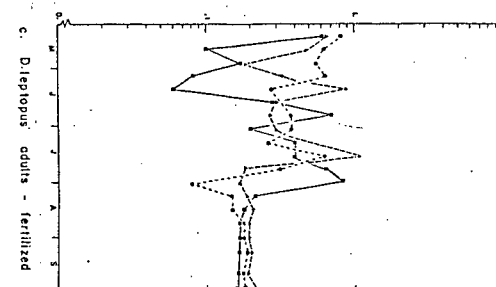
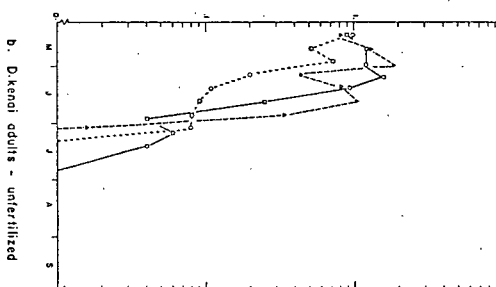
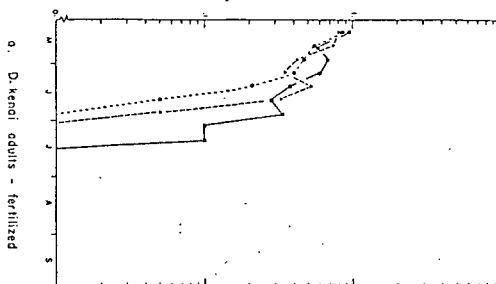
The Gwendoline Lake calanoid copepods did not increase numerically in response to fertilization of the enclosures (fig.49 a-h). D.kenai adults vanished from all treatments by late July and I did not sample adults again. This disappearance probably reflected temperature stress as D.kenai adults were sampled only below the thermocline in Gwendoline Lake during the summer months. In Placid Lake where maximum depth is the same as my enclosures, D.kenai adults also disappeared from the plankton during July and August. This phenomenon has been observed over many years (Walters, unpub.data).

Calanoid copepod nauplii were continuously present in all unfertilized enclosures but were not sampled during the mid-August period in all the high nutrient enclosures. Calanoid copepodids recruited from naupliar instars most successfully in the unfertilized C.b.thomasi enclosure (Fig.49 e,f). Copepodids decreased to low levels in all the fertilized enclosures by early August and disappeared from the samples in the unfertilized 'predator-free' enclosures by the same time. Again, calanoid copepodids seemed to recruit most effectively (of the fertilized treatments) in the 'Cyclops' fertilized enclosure. Only in this treatment were copepodids continuously present even though numbers were low. The weakest recruitment of copepodids was in the 'predator-free' enclosures in both nutrient treatments.

D.leptopus is commonly found in the epilimnion in summer (Walters, unpub.data). This tolerance for higher temperature

Figure 49. Variation in standing crop of calanoid copepods in Gwendoline Lake, 1977. The treatment enclosures in Gwendoline Lake are indicated as in Fig. 48.

NUMBER	PER	LITRE
1	1	1
2	2	2
3	3	3
4	4	4
5	5	5
6	6	6
7	7	7
8	8	8
9	9	9
10	10	10
11	11	11
12	12	12
13	13	13
14	14	14
15	15	15
16	16	16
17	17	17
18	18	18
19	19	19
20	20	20
21	21	21
22	22	22
23	23	23
24	24	24
25	25	25
26	26	26
27	27	27
28	28	28
29	29	29
30	30	30
31	31	31
32	32	32
33	33	33
34	34	34
35	35	35
36	36	36
37	37	37
38	38	38
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40	40	40
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90	90	90
91	91	91
92	92	92
93	93	93
94	94	94
95	95	95
96	96	96
97	97	97
98	98	98
99	99	99
100	100	100



may have contributed to the more positive numerical response of D.leptopus adults in the enclosures compared that of D.kenai. September values were higher in the unfertilized enclosures and there was little community treatment effect.

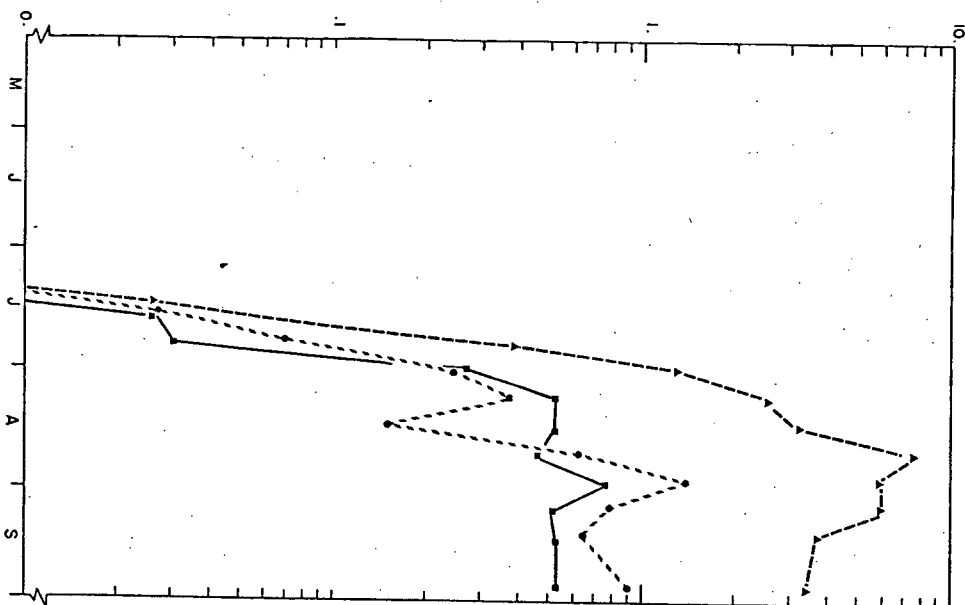
Cyclopoid Copepod Response

C.b.thomasi, described in section 3 (Fig.39), responded positively to fertilization in the absence of Chaoborus larvae. The interaction of both Chaoborus and C.b.thomasi clearly had a negative impact on the C.b.thomasi population. Thus the 'Chaoborus-Cyclops' enclosures became essentially Chaoborus enclosures. T.prasinus, the only other numerically important cyclopoid copepod in the system, increased dramatically in the fertilized treatment without either Chaoborus or C.b.thomasi (fig.50 a,b). However, in the presence of C.b.thomasi, the T.prasinus population was more abundant in the unfertilized enclosure. In the unfertilized 'Chaoborus-Cyclops' treatment T.prasinus densities were as high as in the unfertilized 'predator-free' enclosure. Thus, Chaoborus larvae were probably not important in restricting T.prasinus numbers in the unfertilized environment. There was a slight dampening effect in the fertilized 'Chaoborus-Cyclops' enclosure, however (Fig.50 a,b).

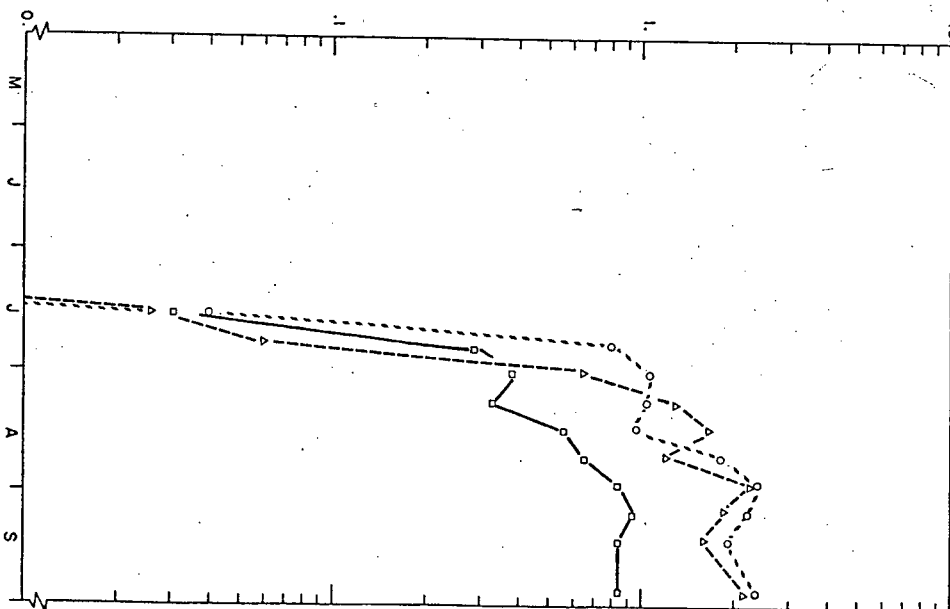
Figure 50. Changes in the standing crop of T.prasinus in Gwendoline Lake enclosures, 1977. Symbols are described in the Fig. 48 legend.

NUMBER PER LITRE

a. *T. prasinus* - fertilized



b. *T. prasinus* - unfertilized



Biomass Response of Phytoplankton and Prey Zooplankton

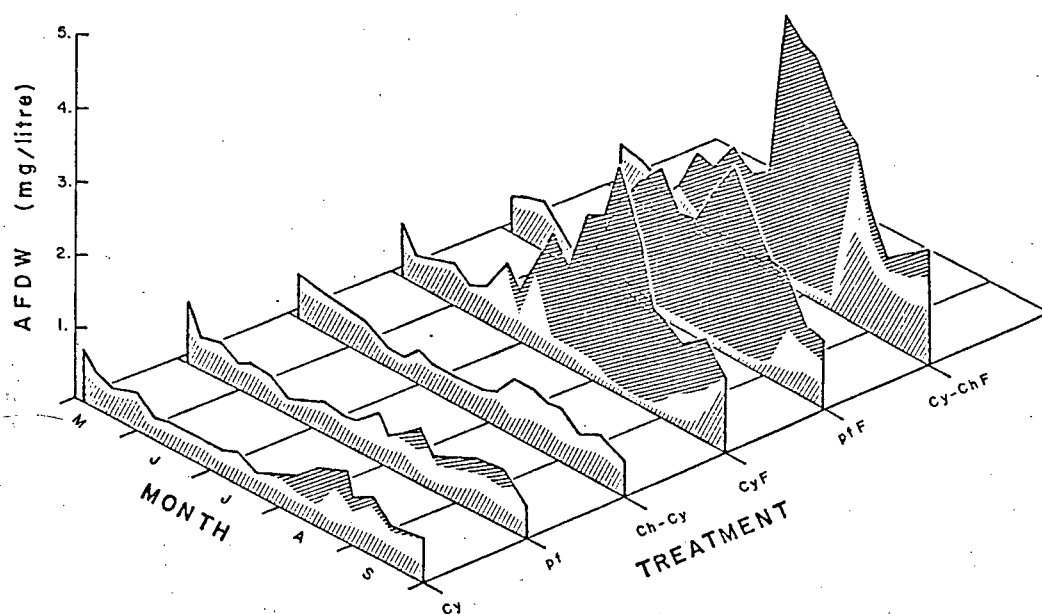
The effect of a zooplankton population on community food resources is closely correlated with biomass, which varies greatly between species and instar. Consequently, I examined the relative effect of the predator and nutrient treatments on phytoplankton and zooplankton biomass (fig.51 a,b). Chaoborus was not included in the total zooplankton biomass shown in Fig.51b because this zooplankter functioned exclusively, in terms of its interaction with other zooplankton species, as predator. However, because cyclopoid copepods were both prey and predator the biomass of these species was included in the analysis of total prey zooplankton biomass.

Adding nutrients to the Gwendoline Lake enclosures caused a significant increase in algal biomass (Fig.51a). In May and early June, all the fertilized enclosures had a higher biomass of nanoplankton (2-20 μm) and this resulted in higher zooplankton biomass in each fertilized treatment relative to its unfertilized equivalent. However, by July and August, blue-green filamentous algae were the phytoplankton group which experienced the most enhancement in the fertilized enclosures. Several authors (eg. Arnold, 1971; Gliwicz, 1975; Porter, 1977) argue that blue-green algae can not be utilized very effectively by zooplankton grazers, particularly the cladocerans. Fig 51b seems to at least partially support this view because the large July-August phytoplankton biomass does not, in general, translate into herbivore biomass. For most of this period in all fertilized enclosures the ratio of phytoplankton to zooplankton biomass was greater than 1.0.

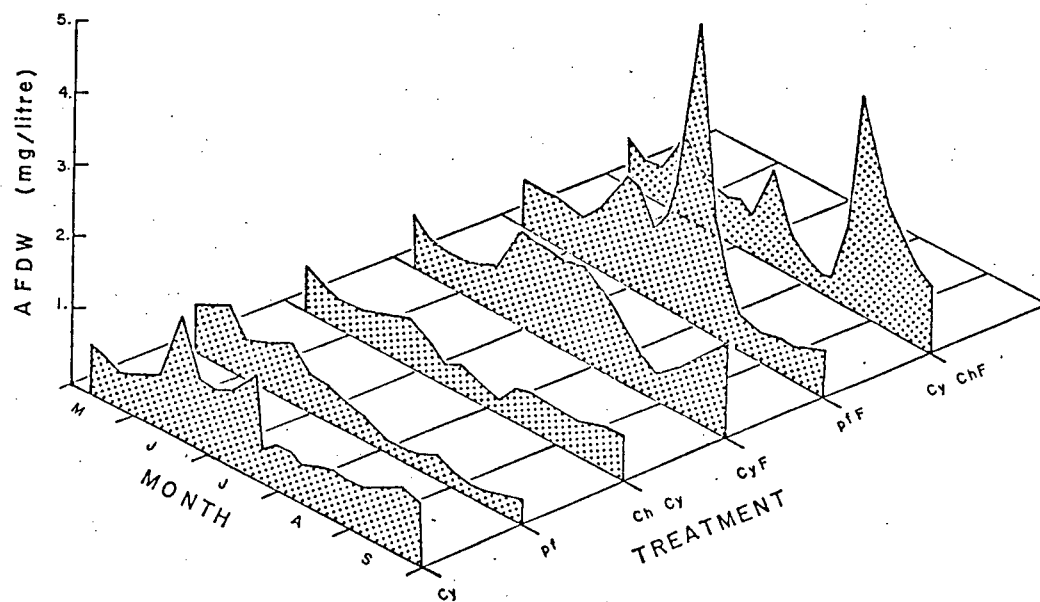
Figure 51. Ash-free dry weight of total phytoplankton and zooplankton biomass.

A. Ash-free dry weight (AFDW) of total phytoplankton biomass in each treatment from May to September, 1977. Nannoplankton, >20 μ m cells and colonies, and filaments indicated by light line, white and dark stripes respectively. Treatment letters represent: Cy - unfertilized 'Cyclops' treatment, pf - unfertilized 'predator-free' treatment, Ch-Cy - unfertilized 'Chaoborus-Cyclops' treatment, CyF - fertilized 'Cyclops' treatment, pfF - fertilized 'predator-free' treatment, Cy-ChF - fertilized 'Chaoborus-Cyclops' treatment.

B. Changes in the AFDW of the total crustacean-rotifer biomass in each Gwendoline Lake treatment from May to September, 1977. Letters for each treatment are the same as in a.



a. Phytoplankton



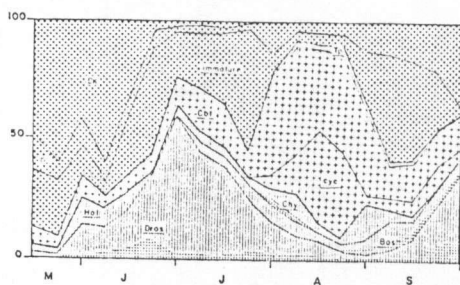
b. Zooplankton

Nevertheless, there were distinct differences between treatments. The zooplankton biomass in the fertilized 'Cyclops' treatment was most similar to its unfertilized counterpart throughout the summer season. There were differences in early June, when the zooplankton biomass in the unfertilized enclosure was slightly higher. This result was probably caused by the fact that adult D.kenai were relatively more numerous (Fig.49 a,b). A small numerical change in these large animals translated into significant biomass differences, although the numerical change was within the range of sampling error.

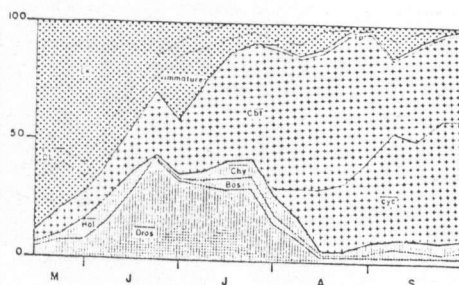
During July the fertilized 'Cyclops' enclosure maintained about 2.5X the zooplankton biomass of the unfertilized enclosure for several weeks after the latter experienced a sharp mid-July decline. There were two important factors which contributed to this difference: much greater C.b.thomasi copepodid recruitment in the fertilized treatment and a delay in the D.rosea decline until early August (Fig.52 a,b) coupled with a high D.rosea population (Fig.48 b,c). The proportion of the D.rosea biomass in reproductive condition was higher during July in the fertilized treatment (Fig.52 a,b) but declined in August. Apparently fertilization in the presence of 'Cyclops' prolonged the favourable food environment for the D.rosea population at least.

Both the 'predator-free' and 'Chaoborus-Cyclops' unfertilized enclosures exhibited lower total biomass throughout and a lower mid-summer decline than the unfertilized 'Cyclops' treatment. The 'predator-free' reached particularly

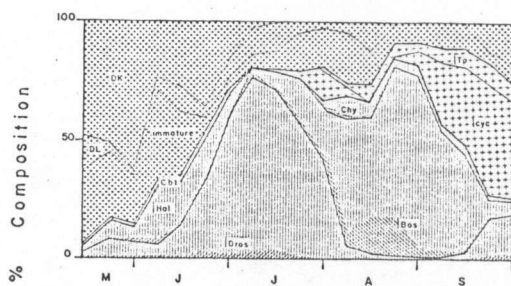
Figure 52. Changes in the % composition of crustacean-rotifer biomass in each treatment enclosure in Gwendoline Lake in 1977. Lettering indicates the zooplankton type and shading represents the following four groups: calanoid copepods, cyclopoid copepods, cladocerans and rotifers (latter shown as white). Lettering represents: DK - D.kenai adults, DL - D.leptopus adults, immature - immature calanoid copepods, Tp - T.prasinus population, cbt - C.b.thomasi population, cyc - cyclopoid copepods other than T.prasinus or C.b.thomasi, Hol - Holopedium, Dros - D.rosea, Chy - Chydorus and Bos - Bosmina. Cross-hatching on the cladoceran plankton indicates the % of the total in reproductive condition.



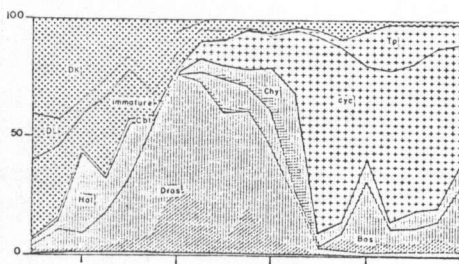
a. Unfertilized 'Cyclops'



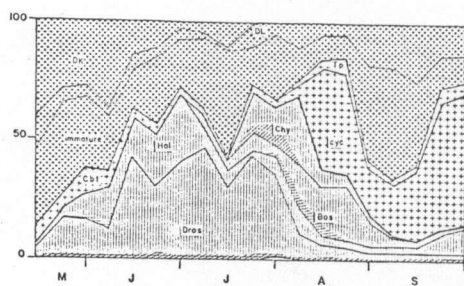
b. Fertilized 'Cyclops'



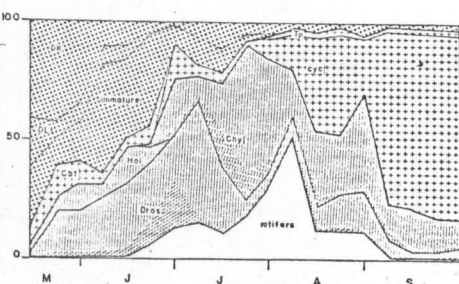
c. Unfertilized 'predator-free'



d. Fertilized 'predator-free'



e. Unfertilized 'Chaoborus-Cyclops'



f. Fertilized 'Chaoborus-Cyclops'

low levels by early August. However, the fertilized latter community achieved the highest total biomass of any treatment, reaching 4.3 mg/litre in July. The mean ratio of phytoplankton to zooplankton biomass (P/Z ratio) was 0.74 during July but reversed in August to 4.13. Clearly a high phytoplankton biomass was available in August but not utilized. D.rosea and Chydorus were the most abundant species causing the zooplankton peak at the end of July (Fig.48 c,g). Although Chydorus were extremely numerous, this species' relative contribution to total biomass was minor compared to D.rosea, reflecting its small size (Fig. 52d). Consequently the August zooplankton biomass decline (fig.51b) was almost exclusively a decline in the D.rosea population. This decrease was probably caused by starvation as the percent of the D.rosea biomass in reproductive condition was greatly reduced by August. Although T.prasinus increased in August and 2 large cyclopoid copepod, Macrocylops albidus and Mesocyclops edax became relatively more numerous, their combined biomass was low. Relative to the other two fertilized treatments, the total biomass in the fertilized 'predator-free' treatment remained low through September. The phytoplankton continued to be dominated by blue-green filaments and large green colonies; nannoplankton was slow to recover. Consequently by the end of September phytoplankton biomass was higher in the unfertilized 'predator-free' treatment but the D.rosea population (Fig.52d) remained low in number. In the unfertilized 'predator-free' treatment Chydorus was never able to become abundant (Fig.48 g,h) and Bosmina replaced D.rosea in

relative importance in the total biomass (Fig.52c).

In contrast to the fertilized 'predator-free' treatment, the high nutrient 'Chaoborus-Cyclops' enclosure maintained a lower total zooplankton biomass during July (from .66 to 1.23 mg/litre), experienced a late July - early August depression and increased most sharply in late August (Fig.51b). The P/Z ratio was higher during July and August than that in the fertilized 'predator-free' enclosure. However, blue-green filaments were dominant. The late July/early August zooplankton decline was correlated with the decline of D.rosea and the relative increase of Chydorus and solitary rotifers (Fig.52f). Although Chydorus remained extremely abundant, the D.rosea population increased in mid-August, coincident with a phytoplankton shift to nanoplankton. This return of nanoplankton occurred just when large Macrocyclus albidus became relatively more common and Chydorus decreased sharply. The decrease in Chydorus probably reflected food limitation because reproduction abruptly declined about the end of July (Fig.52f). Although there might have been some predation loss to Macrocyclus, these animals were never very numerous.

In general, fertilization enhanced phytoplankton biomass and this increase resulted in crustacean zooplankton biomass increases across all communities. However, by late summer this difference between fertilized and unfertilized enclosures was not so distinct. While mean total crustacean biomass values in September were higher in both fertilized treatments with invertebrate predators ('Chaoborus-Cyclops' - 1.21 mg/litre, 'Cyclops' - 0.94 mg/litre) than in the fertilized

'predator-free' treatment (0.49 mg/litre), zooplankton biomass in the latter treatment was lower than that in the unfertilized 'Cyclops' enclosure (0.88 mg/litre). This result was due to an increase in D.rosea, the presence of a considerable C.b.thomasi population in the 'Cyclops' treatment as well as the reappearance of adult D.leptopus and immature calanoid copepods (Fig.52a). None of these species was important in the fertilized 'predator-free' enclosure by September. The mean September crustacean biomass in the unfertilized 'Chaoborus-Cyclops' enclosure was also slightly higher (0.54 mg/litre) than in the fertilized 'predator-free' treatment and 2X that of the unfertilized 'predator-free' treatment (0.25 mg/litre). The higher September biomass in the community with higher levels of invertebrate predation was mainly due to the reappearance of D.leptopus. These calanoids were most successful in the unfertilized enclosures with invertebrate predators.

The percent composition of biomass in May in all treatments was dominated by the calanoid copepods. This biomass predominance was lost by the end of July in all treatments because the adults died and were replaced by nauplii. However, in all fertilized enclosures the calanoids continued to diminish in relative importance throughout the summer and were unable to make a September 'recovery', even in those enclosures with invertebrate predators (Fig.52 b,d,f). This result was in contrast to the return (mainly of D.leptopus) in both the unfertilized enclosures with C.b.thomasi and Chaoborus. Although the calanoid copepods did not dip to such

low levels of relative importance in the unfertilized enclosure as these animals did in all the fertilized enclosures, the recovery was weak relative to that observed in the 'predator' enclosures with Chaoborus and C.b.thomasi. The similarity of the percent composition configurations of the calanoid copepods in the unfertilized 'Chaoborus-Cyclops' and 'Cyclops' treatments strongly suggested that the presence of invertebrate predators was important for calanoid survival, perhaps by cropping competing microcrustaceans. In view of similar calanoid copepod recoveries in both these treatments, and the dissimilar pattern in the unfertilized 'predator-free' enclosures, a physical explanation, such as temperature stress, seemed to be too simple an interpretation, at least for D.leptopus densities.

Another general difference between fertilized and unfertilized enclosures was the rotifer abundance. In unfertilized enclosures, their contribution to total biomass was too low to depict (0.002 - 0.01 mg/litre) except for a brief bloom (0.10 mg/litre) in the 'Chaoborus-Cyclops' treatment (Fig.52f). In all fertilized enclosures the relative contribution of rotifers was higher (2 - 3%) and in the fertilized 'Chaoborus-Cyclops' treatment, rotifer biomass increased dramatically in August to 50% of the total zooplankton biomass. This result reflected both a great increase in solitary rotifers (Keratella, Kellicottia, Lecane) and a decrease in cladocerans, particularly D.rosea and Chydorus (Fig.52f).

As a group, cyclopoid copepods prospered in all the

fertilized enclosures relative to the unfertilized treatments. T.prasinus was most important, relative to other species, in both fertilized and unfertilized 'predator-free' enclosures, although numbers were about 2X higher in the former treatment.

DISCUSSION

Altering the abundance of the predaceous cyclopoid copepod, C.b.thomasi, had little compositional effect on the prey species although certain prey species abundances were altered by the presence of an abundant C.b.thomasi population. Cluster analyses showed that, by August, samples from fertilized enclosures were most different from unfertilized samples. The only treatment that consistently clustered with itself throughout August was the high nutrient 'Chaoborus-Cyclops' treatment. C.b.thomasi, although initially enhanced in this treatment to Placid Lake densities, was so low in abundance by July that estimates were unreliable. Consequently C.b.thomasi was not the perpetrator of this difference. Rather, improved survival of 1st and 2nd instar Chaoborus larvae (Neill and Peacock, 1980) appeared to cause a major change in predator impact. Under low nutrient conditions these developmental constraints prevented Chaoborus from responding numerically to increasing prey abundances.

Conversely, improved survivorship of C.b.thomasi under high nutrient conditions without Chaoborus larvae had relatively little effect on the structure of the community. There was no clear grouping of this treatment within the August

samples. While the community composition remained relatively invariant under different nutrient levels and C.b.thomasi abundance, there was evidence that C.b.thomasi had an effect on some prey species densities. Analysis of the total crustacean/rotifer biomass supported Lane's (1979) argument that C.b.thomasi had a dampening effect on zooplankton abundance. Even under the 'high' fertilizer treatment in the 'Cyclops' enclosure, zooplankton biomass was only 1.2X greater than that in the unfertilized 'Cyclops' treatment. The percent composition of algal types (Fig.40) was further evidence that C.b.thomasi dampens competition for scarce food types in June-July. All fertilized enclosures showed a shift from edible diatoms and greens (shown as 2-20 um, colonial and >20 um) to relatively undesirable filaments (mainly blue-green algae) in mid-June. However, in the fertilized 'Cyclops' enclosure there was a short recovery period in late June to a diatom-green dominated algal community. Thus, although C.b.thomasi was not a 'keystone' species in Paine's sense (1969), this species nevertheless appeared to reduce grazing pressure upon the more edible algae by removing some of the competing grazers.

This interpretation is supported by a comparison of the population dynamics of Chydorus in the 'Cyclops' versus the 'Chaoborus-Cyclops' treatments. The small-sized Chydorus never reached the numerical abundance in the former treatment that it did in the latter and in the 'predator-free' treatment. Chydorus became abundant only when the dominant grazer, D.rosea, declined. The inability of the Chydorus population to

increase in density in the fertilized 'Cyclops' treatment might be due to C.b.thomasi predation in addition to competition from D.rosea. Lynch (1979) provides indirect evidence that Cyclops vernalis influences the abundance of the small cladoceran Ceriodaphnia, although data from my 1976 experiments suggest that C.b.thomasi has no significant numerical impact on Ceriodaphnia. At low nutrient levels there is no indication that C.b.thomasi has a negative impact of Chydorus. In fact, the presences of C.b.thomasi appears to have a beneficial effect on population size when densities of Chydorus in this treatment are compared to the unfertilized 'predator-free' treatment.

Although C.b.thomasi predation in June appears to increase edible food types by lowering grazer densities, there is no evidence that T.prasinus functions in this manner. Blue-green filaments dominate the algal community longer in August in the fertilized 'predator-free' enclosure than in either of the other fertilized treatments. T.prasinus increases significantly in this enclosure but the prolonged predominance of blue-green algae and the fact that the catastrophic decline in zooplankton biomass begins in July, long before T.prasinus appears in the plankton, suggest that edible food shortage is the cause of the zooplankton decline. There is no evidence that T.prasinus ever prey on living microcrustaceans, in spite of numerous laboratory observations, although T.prasinus clearly does consume protozoans.

T.prasinus population size is lower in the unfertilized 'Cyclops' enclosure than in either of the other two

unfertilized treatments. In spite of the fact that T.prasinus is able to sequester sufficient food resources to increase in the fertilized 'predator-free' enclosure, this species is unable to sustain even the density possible in the low nutrient 'Cyclops' enclosure in the fertilized 'Cyclops' treatment. These data confirm the Placid Lake studies showing that T.prasinus recruits poorly in the presence of C.b.thomasi. Thus cyclopoid interactions can be an important factor in determining the relative abundance of cyclopoid copepod species.

Fertilization increases the abundance of all the cladocerans except Holopedium. The inability of Holopedium to numerically increase (this species was not observed in any samples after July in all fertilized enclosures) may be due to poor competitive abilities in the higher temperature epilimnion environment of the enclosures. Only in the unfertilized 'Chaoborus-Cyclops' treatment does Holopedium maintain a population large enough to sample throughout the summer season.

The rapid increase in numbers of the dominant cladoceran grazer, D.rosea, suggests that food availability is an important factor limiting the population density of this species in the low nutrient waters of Gwendoline Lake. The presence of C.b.thomasi appears to release more food resources in June but the effect is weak and transitory. The number of eggs per female doubles in the fertilized treatments and the percent of the population carrying eggs is about 1.5 X higher. Although reproductive output is greatest in the fertilized 'Chaoborus-Cyclops' treatment, D.rosea numbers peak at only 1.4

X higher than in the unfertilized enclosure. However, there is a 5-fold increase in abundance in the fertilized 'Cyclops' treatment and a 3-fold increase in the high nutrient 'predator-free' enclosure. The high Chaoborus population, about 40X over the unfertilized enclosure, clearly has a significant impact on D.rosea abundance. In both nutrient conditions, however, Chaoborus has the general effect of dampening D.rosea increases but also moderating the August decline.

In contrast to Chaoborus, C.b.thomasi appears to have this effect only in the low nutrient enclosure. In the fertilized enclosure the population dynamics of D.rosea resemble the fertilized 'predator-free' treatment in pattern - a rapid increase followed by a sharp decline. Reproduction drastically decreases about 2-3 weeks before the crash suggesting the decline in both these enclosures may be attributed primarily to resource depletion. There may be also be a predator effect on young D.rosea neonates in the fertilized 'Cyclops' enclosure in early August. The proportion of the population reproducing remains at about 7% in this treatment but drops to zero in the fertilized 'predator-free' enclosure, yet numbers decline faster in the former. However, the general pattern of population increase and crash is similar between the two treatments, suggesting that C.b.thomasi has little capability to relieve grazing pressure in the high nutrient situation. When abundances are lower, as in the low nutrient treatment, the losses to C.b.thomasi have a relatively greater effect. This conclusion is supported by the greater D.rosea fertility rates in the latter treatment

(15% or about 2X the fertilized enclosure) during August.

Bosmina is clearly depressed by the large Chaoborus population in the fertilized Chaoborus treatment. Neill (1980) reports significant suppression of Bosmina populations by Chaoborus predation in two years of experiments in unfertilized enclosures. Bosmina numbers are slower to increase in the unfertilized 'Chaoborus-Cyclops' treatment and this result may be due to predation. There is a definite suppression of C.b.thomasi by Chaoborus and T.prasinus by C.b.thomasi. However, long term density effects on other species by either C.b.thomasi or Chaoborus are difficult to identify.

The responses of the cladocerans, calanoid and cyclopoid copepods to fertilization are notably different, representing distinctly different strategies within the zooplankton community. In general, the calanoid copepods (represented in Gwendoline Lake by D.kenai and D.leptopus) respond like K-strategists in the enclosures. They are unable to turn short bursts of high food levels into increased population numbers. In contrast, the high reproductive potential of the cladocerans allows rapid expansion of this group until resources are drastically depleted, at which point the populations crash. This response, best exemplified by D.rosea , is that of the classical r-strategist. Allan (1976) concludes that the three major taxa of freshwater zooplankton can be ranked with respect to opportunism in this order: rotifers > cladocerans > copepods. However, my results suggest that intermediate between the cladoceran strategy and the calanoid strategy is

that of the cyclopoid copepods. Both C.b.thomasi and T.prasinus are clearly capable of increasing reproductive output in the fertilized treatments. Although the population increase is slow relative to the cladocerans, reproductive output is significantly higher than the calanoid copepods. However, like the latter, cyclopoid copepods are less susceptible to resource depletion than are the cladocerans. Hence T.prasinus increases numerically throughout August, when most cladoceran populations are in decline, and C.b.thomasi experiences no decrease in numbers during this period. The omnivorous habit, coupled with the ability of both T.prasinus and C.b.thomasi to feed on dead crustacean zooplankters, probably allows this group to sustain high populations under a relatively broad spectrum of conditions. Cyclopoids may even utilize the seemingly inedible blue-green algae. Lewis (1979) concludes that Thermocyclops hyalinus is using blue-green filamentous algae in Lake Lanao, and Infante (1978) similarly reports digestion of filamentous blue-greens by cyclopoid nauplii. Thus cyclopoid copepods may occupy the generalist role within the zooplankton community, scavenging whatever is available.

In summary, C.b.thomasi does appear to dampen the numerical response of certain prey species through predation. Under high fertilizer conditions Chaoborus has the capability to alter community composition, as well as abundance. In contrast to Chaoborus, C.b.thomasi has a greater net effect on most prey species abundance when nutrients are low. At high nutrient levels, C.b.thomasi has virtually no impact on the

dynamics of the dominant grazer, D.rosea. At low nutrient levels both C.b.thomasi and Chaoborus appear to improve conditions for the calanoid copepod, D.leptopus. Finally, although C.b.thomasi cannot effect a compositional change in the zooplankton community, even when food is scarce, this invertebrate predator does appear to be instrumental in relieving grazing pressure such that zooplankton population fluctuations are dampened.

SUMMARY

1. Even at high nutrient levels, C.b.thomasi does not cause a compositional change in the zooplankton community.
2. C.b.thomasi decreases the numerical response of certain species to fertilization, e.g. Chydorus and T.prasinus.
3. The presence of C.b.thomasi has little effect on the D.rosea population in the fertilized treatment but under low nutrient conditions, the presence of C.b.thomasi appears to release scarce food resources - this effect is similar to that of Chaoborus at low nutrient levels.
4. At low nutrient levels the presence of C.b.thomasi and Chaoborus appears to be essential for the continued presence of calanoid copepods during the summer months.
5. An abundant C.b.thomasi population seems to reduce fluctuations in total crustacean biomass at both high and low nutrient levels.

GENERAL DISCUSSION

The feeding structures of adult T.prasinus and C.b.thomasi are remarkably alike, although adult diets are quite dissimilar. T.prasinus is omnivorous in the later instars, eating algae, protozoans and probably dead macrozooplankters, while C.b.thomasi is markedly carnivorous in the copepodid and adult instars. Seasonal abundance peaks reveal a temporal separation of the naupliar instars in both lakes studied. Consequently, T.prasinus and C.b.thomasi do not compete. Large scale enclosure experiments in Placid Lake show that lake densities of C.b.thomasi limit the numerical increase of T.prasinus. This impact is caused by two important factors: enormous naupliar mortality in the T.prasinus population, probably caused by starvation, and C.b.thomasi predation on these T.prasinus instars. The ability of T.prasinus to persist in Placid Lake in spite of these difficulties is attributed to behaviour which results in spatial separation from the principle part of the carnivorous C.b.thomasi population. Consequently, C.b.thomasi is unable to cause population extinction. Hall et al. (1976) suggest that this result is generally characteristic of the impact of invertebrate predators on prey populations.

I carried out a transplant experiment to explain why C.b.thomasi, obviously successful in Placid Lake, is extremely rare in nearby fishless Gwendoline Lake. By permitting the Chaoborus species common to Gwendoline Lake (C.trivittatus and

C.americanus) to lay eggs in two enclosures, I showed that the presence of Chaoborus was critical in restricting C.b.thomasi population numbers. Vulnerability to Chaoborus predation was caused by limited alternative prey and spatial/temporal overlap of C.b.thomasi nauplii with 1st instar Chaoborus. Adding nutrients to the enclosures simply exacerbated the predator impact by greatly improving Chaoborus survivorship. Although C.b.thomasi responded to fertilization by increasing the number of eggs per clutch and extending the egg-bearing period, this response was not sufficient to permit C.b.thomasi to outstrip the numerical response of Chaoborus. In contrast to C.b.thomasi, r-selected rotifers achieved the highest densities in the fertilized 'Chaoborus-Cyclops' enclosure - in spite of high predator abundance. The temporal overlap and prey developmental response are essential factors in determining prey sensitivity. Rapid development and parthenogenic reproduction allow the rotifers to increase numerically in August, when Chaoborus predation is reduced. These larvae molt to a size at which rotifers are no longer an attractive prey item. By August, C.b.thomasi numbers are low due to earlier Chaoborus predation and this species' developmental response is such that there are no reproductive individuals available to take advantage of the opportunity. As a consequence, the C.b.thomasi population cannot recover and population numbers remain low.

The impact of C.b.thomasi on other zooplankters was examined in large side-by-side enclosures in Gwendoline Lake with different levels of food abundance and invertebrate

predation. The presence of C.b.thomasi appeared to have a dampening effect on total zooplankton biomass in treatments without a Chaoborus population. However, while Chaoborus reached a point at high nutrient levels at which early instar survival was high and predatory impact enormous, C.b.thomasi was unable to track prey demographic responses in the high fertilizer enclosure. C.b.thomasi caused no major compositional changes in the crustacean community at either nutrient level. Paradoxically, D.rosea and D.leptopus were numerically more successful in treatments with C.b.thomasi than in those enclosures without an invertebrate predator. Thus by dampening small grazer numbers, C.b.thomasi might be responsible for maintaining a sufficient food supply for D.rosea and D.leptopus.

While the numerical abundance of any species is at least partially dependent upon the success of its most mortality-prone stage, identification of the crucial period requires analysis of the spatial/temporal dynamics within the context of the community species assemblage. The tendency to attribute similar responses to different species of the same genera or even different instars of the same species, often across different communities, has caused considerable confusion about the mechanisms which govern zooplankton seasonal abundance fluctuations and biogeographical patterns. It is clear from this study that Chaoborus predation far outweighs food availability as an important variable limiting the recruitment of C.b.thomasi in Gwendoline Lake. This predator's impact cannot be predicted by applying only feeding rates and

preference data from observations on 3rd and 4th instar Chaoborus larvae. It is evident that the predatory impact of Chaoborus upon the C.b.thomasi population is also dependent upon the particular spatial and temporal interaction of predator and prey instars, as well as the scarcity of alternative prey. Neill (1980) shows that calanoid copepods in Gwendoline Lake are vulnerable to Chaoborus in the spring, when calanoid densities are low and alternative prey scarce. If reproduction is delayed, summertime recovery from springtime predation mortality is difficult and long-term demographic effects are possible. However, during most years predation impact is negligible. The fact that C.b.thomasi is rare in Gwendoline Lake suggests that the negative effect of Chaoborus on the C.b.thomasi population observed in this study is a common event in Gwendoline Lake.

While both cyclopoid and calanoid copepods were unable to match cladoceran numerical response to increased nutrients, there were important differences between the two copepod groups. Fertilization of the enclosures increased the densities of both C.b.thomasi and T.prasinus (in the absence of predators) and decreased the abundance of both D.kenai and D.leptopus. Patalas (1972) observed that a "declining proportion of diaptomids and an increasing abundance of cyclopoids (C.b.thomasi and T.prasinus mexicanus) and cladocerans" were characteristic trends related to increasing nutrients in the St. Lawrence Great Lakes. Similarly, Hillbrecht-Ilkowska and Weglenska (1973) found increased cladoceran and cyclopoid copepod production and a decrease in

calanoids in response to increased food resources.

Cyclopoid copepods have two obvious advantages over filter-feeding calanoids in responding to increased nutrients: cyclopoid copepods are capable of a greater numerical response than calanoid copepods (eggs/clutch range over 100 while eggs/clutch in calanoids are generally <30 (Hutchinson, 1967)); and the omnivorous habit allows cyclopoids to exploit increases in both primary and secondary production. In addition, some cyclopoid copepods are apparently capable of utilizing even blue-green algae (Infante, 1978; Lewis, 1979). Thus a greater variety of algal types can be utilized directly by naupliar instars and indirectly by copepodid and adult stages cropping increased herbivore biomass. Increasing nutrients characteristically decreases calanoid copepod abundance (McNaught, 1975), a group predominantly adapted to the exploitation of low nutrient, nutritionally dilute environments (Allan, 1976). By contrast, cyclopoid copepods are able to capitalize on increased nutrients yet are also able to endure long periods of starvation (Smyly, per.comm.; pers.obs.). Consequently cyclopoids are abundant in high nutrient environments but are also important components of oligotrophic lakes. These animals seem to be the generalists of the lacustrine plankton community. However, in spite of the above, cyclopoid copepod species are generally underrepresented relative to calanoid copepod species in ultraoligotrophic environments, such as those found in the arctic (Rylov, 1963; Tash, 1971; Moore, 1978). The 'generalist' strategy seems to fail under these extreme

conditions.

The feeding structures of C.b.thomasi and T.prasinus and their relative densities in oligotrophic waters may provide some insight into the general problem cyclopoid copepods have in living in an extremely dilute environment. Fryer (1957a) argues convincingly that the herbivorous habit in Cyclopoida represents a more recently evolved taste than the carnivorous diet. Late copepodid and adult C.b.thomasi are probably obligate carnivores on microcrustaceans (McQueen, 1969), while the same instars in T.prasinus can utilize algae or protozoans but probably no living animal larger than a small rotifer. According to Fryer's reasoning, C.b.thomasi belongs to a more primitive group, while the genus Tropocyclops represents a more recently evolved condition. The small structural changes observed in adult mouthparts can then be said to approximate the small changes observed in other animal groups like, for example, finches, grasshoppers, bees, etc. (Lack, 1947; Isley, 1944; Brian, 1957), in which minor changes in the mouthpart structure lead to very large differences in the type of food taken. Further, the observation that the guts of all cyclopoid copepods are short like those of carnivorous animals (Fryer, 1957a), suggests that herbivorous cyclopoid copepods are not very efficient at digesting plant matter. Consequently, species which exploit plant food sources throughout their life history require a superabundance of food to be numerically successful because they are not very efficient food processors. The omnivorous habit, like that of T.prasinus (which can feed on microzooplankters as well as

algae) may represent a transitional stage from carnivory to herbivory. However, this species possesses feeding apparatus remarkably similar to that of C.b.thomasi, a species which gathers much larger animal food items. It seems unlikely that T.prasinus, with such relatively coarse feeding equipment, can be very efficient at collecting fine food particles. Thus T.prasinus probably functions best on protozoans, rotifers and large algae. In oligotrophic systems, protozoan populations are often low, rotifers and large algae are scarce much of the year and the food environment is very dilute. Consequently, unproductive lakes may represent marginal habitat for T.prasinus, a species whose feeding habits evolved in more productive systems. The fact that T.prasinus is never very abundant in oligotrophic Gwendoline Lake (an essentially predator-free system for T.prasinus) relative to C.b.thomasi densities in Placid Lake, yet increases significantly when Gwendoline Lake water is fertilized, suggests that the food environment is not ideal for T.prasinus.

Assuming that copepodid and adult feeding structures are relevant indicators of 'food niche' and that the food environment is important to the 'success' of cyclopoid copepods, some biogeographical patterns emerge. In general, species which are herbivorous/omnivorous as adults should be most abundant in productive lakes and rare or absent in oligotrophic systems. Carnivores, on the other hand, should be the only abundant cyclopoid copepods to thrive in extremely low nutrient lakes. If the herbivorous habit evolved in systems with high food abundance, warm to moderate temperatures are probably a

concomitant requirement. Pejler (1964) states that arctic and subarctic lakes are almost always oligotrophic while tropical lakes usually have a good deal in common with the eutrophic lakes of the temperate zone. On a broad geographic scale, carnivorous species, but not adult herbivores, should be common in arctic or subarctic lakes where productivity and temperature is low (Moore, 1978; Patalas, 1975). Herbivorous species should be most common in warmer climates. There is some evidence in the literature to support this qualitative generalization, although the distribution and abundance of microcrustaceans relative to lake trophic status is still incompletely known. Eucyclops and Tropocyclops are not found in tundra and taiga regions, although both genera have cosmopolitan southern distributions (Rylov, 1963). Several authors (Burgis, 1971; Infante, 1978; Lewis, 1979) have found that herbivorous species are the only abundant cyclopoids in tropical lakes. Rylov (1963) considers the Arctic species complex to consist primarily of the genus Cyclops - all adult carnivores. More recent surveys have not contradicted this generalization (e.g. Tash, 1971; Moore, 1978).

In North America, Patalas (1975) found Tropocyclops prasinus mexicanus only in the St. Laurence Great Lakes communities with relatively high total zooplankton abundance (48-184 individuals/l and 0.68-3.81 mg/l wet weight biomass). C.b.thomasi, however, was found in deep subarctic lake communities (2.7 individuals/l and 0.07 mg/l wet weight biomass) and in the St. Laurence Great Lakes, - often achieving numerical dominance. Moore (1978) found only 2 cyclopoid

copepod species in his study of 18 lakes in the Canadian arctic and subarctic - C.b.thomasi and Cyclops scutifer. Both species are carnivores in the later instars. Like C.b.thomasi, C.scutifer is also common in some temperate lakes (Elgmork, 1967). Sprules (1975) suggests that pH has a major effect in the industrially acidified lakes of La Cloche Mountains, Ontario. However, the relationship between food resources and pH is complex and many cyclopoid species, in particular T.prasinus and C.b.thomasi, are euryionic (Rylov, 1963; Fryer, 1980). Thus the primary effect with respect to the cyclopoids may be food limitation. Carter et al. (1980) conclude that postglacial dispersal is important in explaining crustacean plankton distributions in eastern North America. However, their speculations are based on one sample from each lake collected over a variety of time intervals. In the University of British Columbia Research Forest Lakes, June samples may not detect T.prasinus and August samples in Gwendoline Lake are unlikely to collect C.b.thomasi. Rare species, essential for any assessment of species dispersal, are also less likely to be collected by 'once-only' sampling when a large mesh net is used as in the Carter et al.(1980) study (158 μ m - 239 μ m) because nauplii can pass through the mesh. Gurney (1931) cautions that "although in some cases present distribution is probably due to the influence of the glacial period, the great possibilities of passive transport must always be borne in mind, and speculation founded on geographical distribution must be accepted with caution."

In summary, by experimentally studying the mechanisms operating on a local scale, biogeographical patterns may be more easily interpreted. This study demonstrates that the naupliar instars of both T.prasinus and C.b.thomasi are very sensitive to predation and food limitation. While the naupliar stages contribute little to species biomass, mortality experienced by these life stages sets an upper bound on later instar abundances. Unfortunately, little is known about naupliar feeding structures or feeding behaviours of these instars. However, it appears that explanations for distribution and abundance patterns of cyclopoid copepods require some knowledge of the relative sensitivity of all instars to various community interactions.

The ability of cyclopoid nauplii to utilize 'unpalatable' algal types such as filamentous blue-green algae needs further investigation. This study suggests that C.b.thomasi and T.prasinus nauplii are more sensitive to low food densities than to changes in algal types. Phytoplankton seasonal shifts to blue-green algae may favour cyclopoid copepod species over other herbivores, such as filter-feeding cladocerans, because the latter appear to have difficulty utilizing these algal forms (Gliwicz, 1975; Porter, 1977).

The relative abundance of both C.b.thomasi and T.prasinus in Placid Lake and Gwendoline Lake is maintained by predation pressure on the vulnerable stages of the less numerically important species in each lake. However, both Gwendoline Lake and Placid Lake are probably marginal habitats for T.prasinus because microzooplankters and algae are relatively low in

abundance. I have suggested that, in dilute food environments, a cyclopoid species will need to be carnivorous in the later instars to become a numerically significant member of the plankton. However, within a lake, the species which becomes dominant will probably be determined by predation, either through intracyclopoid interactions as suggested by Smyly (1978) or by other vertebrate or invertebrate predator effects (e.g. Dodson, 1970; Hurlburt and Mulla, 1980). In any case, it is clear that biotic interactions can be critically important in explaining regional inter-lake differences in cyclopoid copepod species' abundance.

Within the crustacean community, C.b.thomasi (and Chaoborus in a low nutrient environment) appears to enhance the numerical importance of the large grazers in the lake, D.rosea and D.leptopus, possibly by reducing the abundance of competitors. Unlike Chaoborus, C.b.thomasi does not seem capable of causing prey extinctions. The reason for this difference probably lies in the small functional and numerical response of C.b.thomasi relative to its prey. The prey can escape predator impact both by swamping C.b.thomasi numerically through high rates of reproduction and by increasing in size beyond that which C.b.thomasi can attack successfully. By cropping small zooplankters, cyclopoid copepods may act as community 'stabilizers' preventing large fluctuations in community biomass. This role is probably most important in low nutrient environments where food is scarce most of the year.

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APPENDIX A

An "index of assimilation" was calculated according to the formula (Sorokin, 1968):

$$Ca/C = \frac{R \cdot Cr \cdot 100 \cdot 24}{W \cdot t} \quad \text{in \%}$$

where

Ca = amount of food assimilated

C = mean carbon content of the consumers

R = radioactivity (disintegrations per minute) in the bodies of the consumers

Cr = content of organic carbon in a definite portion of labelled food, or
ugC/disintegrations per minute.

W = mean content of organic carbon in the consumers

t = duration of feeding with labelled food (in hours)

APPENDIX B

The principle employed in this analysis is to analyse differences in proportion of ovigerous females between treatments on each sampling date thereby eliminating the ups and downs. As the populations in the different treatments were not the same, it was necessary to weight the proportion according to the sample size in each treatment.

Differences between the 2 treatments in which D.oregonensis was present were analyzed in the following way:

$$t_x = (n_x / N_x) N_x$$

where t_x = proportion of ovigerous females on each sampling date in treatment x weighted according to sample size

n_x = no. of females with eggs in treatment x

N_x = total no. of females in treatment x

arcsine transformation was taken of t and t

where t_1 = treatment with C.b.thomasi

t_2 = treatment without C.b.thomasi

Then $t_1 - t_2 = p$ for each sampling date

using a two-tailed t-test the trends between the two treatments were compared ($H_0 = p = 0$).

For D.oregonensis, the period tested was July 7 to August 22, after which time this species produced ovigerous females only in the treatment without C.b.thomasi. The July-August time interval

represented the period when food shortages were most likely to occur, and when food shortages were most likely to have a negative impact on the reproducing T. prasinus ; however, there was no difference between the two treatments ($t = 0.4$, $df = 7$, $p < 0.05$).

D. rosea and T. prasinus were present in all 3 treatments. The same principle was applied to the data and an analysis of variance was employed. The difference in the number of ovigerous females of D. rosea and T. prasinus between treatments were analyzed in the following way:

For each treatment, $p_x = n_x / N_x$

where p_x = proportion of ovigerous females
 n_x = no. of females with eggs
 N_x = total no. of females

An arcsine transformation was performed on p_1 , p_2 and p_3 where

p_1 = treatment with C. b. thomasi
 p_2 = treatment without C. b. thomasi but with other Placid Lake crustacean plankton
 p_3 = treatment with T. prasinus 'alone'

The weighted average proportion of ovigerous females across all treatments (P) was then calculated:

$$P = \frac{w_1 p_1 + w_2 p_2 + w_3 p_3}{w_1 + w_2 + w_3}$$

where $w_x = N_x$ and calculations were checked to ensure that: $w_1 (p_1 - P) + w_2 (p_2 - P) + w_3 (p_3 - P) = 0$ for each sample.

A weighted analysis of variance of the directions ($p_x - P$) with weights (w_x) was then performed, with the following result:

one-way weighted analysis of variance on arcsine transformed values of the proportion of ovigerous females of *D. lugens* from July 1 to November 1, 1976.

SOURCE OF VARIATION	DF	SS	MS	F
BETWEEN	2	0.07	0.04	0.01 NS
WITHIN	42	209.5	6.89	
TOTAL	44	286.5		

NS=not significant

one-way weighted analysis of variance on arcsine transformed values of the proportion of ovigerous females of *I. trispinosus* in Placid Lake from July 29 to Sept. 13, 1976.

SOURCE OF VARIATION	DF	SS	MS	F
BETWEEN	2	0.01	0.01	0.02 NS
WITHIN	21	2.24	0.11	
TOTAL	23	2.25		

NS=not significant

APPENDIX C

The duration time of the various instars of T. prasinus from Placid Lake, 1976, at $16 \pm 2^\circ\text{C}$ was determined in the laboratory as described by Smyly (1970) except that lake water was used and the nauplii were checked by placing them in a very small drop of water. I did not apply a Krogh curve to the data as the temperature in Placid Lake only varied from 14.5 to 18.5°C during August-September, the period when T. prasinus juveniles were developing. The only exception to this generalization was one week in early September when the temperature dropped to 11.5°C . The results for 20 animals were as follows:

STAGE	DURATION (IN DAYS)
EGG TO HATCH	5.1
N - III	3.0
NIV - VI	6.8
CI	5.2
CII	5.1
CIII	7.0
CIV	6.2
CV	8.1
ADULT	38.4

The development time of the various instars of C. b. thomasi in Placid Lake and Gwendoline Lake enclosures 1977, was estimated from field population data. Column A refers to Placid Lake and the unfertilized Gwendoline enclosure populations, column B indicates the development time in the fertilized Gwendoline enclosure. Both enclosures in Gwendoline Lake were Chaoborus- free.

STAGE	DURATION (IN DAYS)	
	A	B
EGG TO HATCH	5.0	5.0
N - III	7.0	7.0
NIV - VI	10.5	10.5
CI	7.0	7.0
CII	7.0	7.0
CIII	7.0	7.0
CIV	10.0	9.0
CV	14.0	12.0

The abundance of each instar for a particular generation was calculated using the following model (Gehrs and Robertson, 1975):

$$\sum_{x=j}^k (l_{ix} + l_{i,x+1}/2) (w_{x,x+1}/D_i) = N_i$$

l = number of individuals alive

i = instar designation

x = collection designation

j = first collection prior to the appearance of instar i

k = collection following the last collection in which instar i appears

D_i = duration of instar i in days

w = interval in days between collection x and collection $x+1$

N = net number of individuals of instar i observed in the interval $x = j$ to $x = k$ or the estimated number of individuals of instar i in a particular generation.

Survivorship of *T. prasinus* in the Placid Lake enclosures in 1976.

	With <i>C. b. thomasi</i> *	Without <i>C. b. thomasi</i> †
Stage	Number at the BEGINNING OF AGE interval (lx)	Number at the BEGINNING OF AGE interval (lx)
Egg	1000	1000
NIII	295.2	294.4
NVI	87.5	164.7
CI	42.7	132.2
CII	21.2	127.4
CIII	17.9	127.4
CIV	17.6	127.6
CV	11.9	107.8

* original lx = 5.18×10^2

† original lx = 5.46×10^2

Survivorship of *C.b.thomasi* in Placid Lake and the Gwendoline enclosures without the midge larvae Chaborus in 1977.

	Lake*	Unfertilized**	Fertilized***
	Number at the beginning of age interval	Number at the beginning of age interval	Number at the beginning of age interval
Stage	(lx)	(lx)	(lx)
Egg	1000	1000	1000
NIII	549.5	609.8	790.0
NVI	322.7	406.8	780.3
CI	199.4	238.3	680.7
CII	174.8	227.1	450.2
CIII	126.5	221.4	440.4
CIV	145.9	166.3	320.9
CV	116.5	119.3	340.6

*original lx = 6.4×10^3

**original lx = 5.1×10^3

***original lx = 5.7×10^3

Survivorship of *C.b.thomasi* in Placid Lake and the Gwendoline
enclosures without the midge larvae Chironomus in 1977.

	Lake*	Unfertilized**	Fertilized***
	Number at the beginning of age interval (lx)	Number at the beginning of age interval (lx)	Number at the beginning of age interval (lx)
Egg	1000	1000	1000
NIII	540.5	609.8	790.0
NVI	322.7	406.8	730.3
CI	199.4	238.3	680.7
CII	174.8	227.1	450.2
CIII	126.5	221.4	440.4
CIV	145.9	166.3	320.9
CV	116.5	119.3	340.6

*original $lx = 6.4 \times 10^3$

**original $lx = 5.1 \times 10^3$

***original $lx = 5.7 \times 10^3$

APPENDIX D

Predation of *C. b. thorasi* on *T. prasinus* nauplii in Placid Lake, 1976, assuming the predation rate $(PR) = 0.05X^{0.67}$, where X = no. prey per litre.

Date	Prey standing crop		Prey killed / Predator		Predator standing crop		Total Prey removed		Prey standing crop removed	
	(#/litre)	/litre/day	/litre/day	(#/litre)	(#/litre)	(#/litre)	(#/litre)	(#/litre)	(#/litre)	(#/litre)
Aug 4	0.04	0.003	0.003	0.41	0.001	0.001	2.5			
11	0.15	0.01	0.01	0.49	0.005	0.005	3.3			
18	0.30	0.02	0.02	0.40	0.01	0.01	3.3			
22	0.48	0.03	0.03	0.38	0.01	0.01	2.1			
30	0.50	0.03	0.03	0.34	0.01	0.01	2.0			
Sept 7	0.46	0.03	0.03	0.30	0.009	0.009	2.0			
13	0.46	0.03	0.03	0.34	0.01	0.01	2.5			
20	0.39	0.02	0.02	0.28	0.006	0.006	1.5			
27	0.15	0.01	0.01	0.31	0.003	0.003	2.0			
Oct 4	0.02	0.001	0.001	0.39	0.001	0.001	2.0			
11	0.02	0.001	0.001	0.30	0.001	0.001	1.0			
18	0.02	0.001	0.001	0.30	0.001	0.001	1.0			

0.24 0.19 4.24 0.22 26.2

Mean # prey removed from August to October = 2.2

Mean residence time of *T. prasinus* nauplii = 9.8 days; therefore,

C. b. thorasi predators can potentially remove about 22% of the

nauplii recruited during this period in 1976 (or about 20% if one assumes an exponential decay in the number of nauplii).

Predation of Chaoborus larvae instar I on C.B.thomasi nauplii calculated using

the standing crop of Chaoborus in the unfertilized enclosure and the standing crop of C.B.thomasi in the unfertilized

Chaoborus-free enclosure in Gwentolite Lake, 1977. Predation rate is assumed constant at 2.2 prey per predator per litre per day.

Date	Prey standing crop		Predator standing crop	Total prey removed		% prey standing crop removed
	(#/litre)	(#/litre)	(#/litre)	(#/litre)	(#/litre)	
May 24	4.97		0.01	0.02		0.4
31	5.84		0.02	0.04		0.6
June 6	7.91		0.19	0.42		5.3
13	10.20		0.26	0.57		5.5
21	9.28		0.38	0.84		9.1
28	7.38		0.30	0.66		8.9
July 5	4.90		0.18	0.40		8.1
11	4.17		0.11	0.24		5.0
19	3.15		0.15	0.33		10.5
25	1.71		0.09	0.20		11.7
Aug 3	0.26		0.06	0.13		50.0
8	0.14		0.02	0.04		28.5
15	0.06		0.03	0.07		100.0
22	0.07		0.01	0.02		28.7

Mean % prey removed calculated for the period from May 17th to

July 25th (nauplii are scarce in August, hence the constant

Predation rate is unrealistic during this period) = 6.5

Mean residence time of C.B.thomasi nauplii = 17.5 days and

therefore Chaoborus first instar larvae can potentially remove all the nauplii recruited in the Gwentolite Lake enclosure, 1977.