THE RELATIVE IMPORTANCE OF FOOD AVAILABILITY AND PREDATION TO THE JUVENILE SURVIVAL OF DIACYCLOPS THOMASI

by

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We accept this thesis as conforming to the required standard

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In situ enclosure experiments were conducted in Placid Lake, British Columbia to determine the effect of food availability and predation on the naupliar survival of *D. thomasi*. These experiments revealed that food limitation due to competition from the grazing assemblage, interspecific predation by *D. kenai* and intraspecific predation by *D. thomasi* adults could all substantially affect the survival of *D. thomasi* nauplii. Subsequent feeding studies showed that *D. kenai* at lake densities were capable of preying on nauplii at a rate of 20% of nauplii per predator per day and this seemed to account for most of the mortality of *D. thomasi* nauplii in enclosures with *D. kenai*.

When these results were extrapolated to two oligotrophic montane lakes, cannibalism was judged to be the major mortality agent. In the Placid Lake community, the effect of interspecific predation and competition acted only earlier and later in the season respectively, and the magnitude of their effect was influenced by year to year variation in weather. In Eunice Lake, in which *D. thomasi* has recently become a community dominant, experimental results suggested that *D. kenai* had previously limited *D. thomasi* in the lake. The introduction of cutthroat trout and a mild winter seemed to be responsible for the decline in *D. kenai* and concurrent increase in *D. thomasi*. 
# TABLE OF CONTENTS

ABSTRACT .......................... ii

LIST OF TABLES ...................... v

LIST OF FIGURES ..................... vi

ACKNOWLEDGEMENTS ................... vii

GENERAL INTRODUCTION ................ 1

CHAPTER 1 ................................ 8

  Materials and methods ................. 8

  Study area .......................... 8

  Placid Lake Community ................. 9

  Experimental Methods .................. 14

  Experimental design .................... 19

  Analysis ................................ 20

Results .................................. 23

  Precision of sample data .............. 23

  Set up of enclosures .................... 26

  Results of survivorship calculations ... 28

Discussion ............................. 49

CHAPTER 2 ................................ 55

  Materials and methods ................. 55

  Experimental methods .................. 55

  Experimental design .................... 56

Results .................................. 62

Discussion ............................. 67

GENERAL DISCUSSION .................. 71
LIST OF TABLES

Table I  Some physical, chemical and biological characteristics of Placid and Eunice Lakes in the UBC Research Forest .............................................. 12
Table II Stocking densities of zooplankton in the enclosures ............................................. 16
Table III Precision of zooplankton data ................................. 24
Table IV Precision of phytoplankton data ................................. 25
Table V Dynamics of zooplankton in enclosures ................. 27
Table VI The effect of surfaces on D. kenai predation on Diacyclops nauplii .............................. 66
Table VII Predation rates of carnivorous copepods on nauplii .............................................. 69
Table VIII Effect of fertilizer on chlorophyll content .... 92
Table IX Effect of fertilizer on phytoplankton size classes ......................................................... 93
Table X Effect of fertilizer and grazers on total chlorophyll content ........................................ 95
Table XI Effect of fertilizer and grazers on phytoplankton size classes ........................................ 96
Table XII Results for estimation of stage duration of immature Diacyclops thomasi ....................... 100
LIST OF FIGURES

Figure 1 Spring zooplankton community composition in Eunice Lake from 1975-1982 ........................................ 4
Figure 2 Location of study area ........................................ 10
Figure 3 Experimental design ........................................... 21
Figure 4 Effect of the grazing assemblage, fertilization, Diaptomus kenai and Diacyclops thomasi alone on naupliar survival (Integration) ........................................ 31
Figure 5 Effect of the grazing assemblage, fertilization, Diaptomus kenai and Diacyclops thomasi alone on naupliar survival (Curve fitting) ........................................ 33
Figure 6 Effect of the successive addition of mortality agents on naupliar survival (Integration) ......................... 35
Figure 7 Effect of the successive addition of mortality agents on naupliar survival (Curve fitting) ......................... 37
Figure 8 Summary of the effect of a single factor on survival to the end of the naupliar stages (Integration) ........ 40
Figure 9 Summary of the effect of a single factor on survival to the end of the naupliar stages (Curve fitting) ........ 42
Figure 10 Summary of the effect of a single factor on survival to the beginning of the third copepodite stage (Integration) ........................................ 44
Figure 11 Summary of the effect of a single factor on
survival to the beginning of the third copepodite stage
(Curve-fitting) ................................................. 46
Figure 12 Design of experimental cages ..................... 60
Figure 13 Functional response of *Diaptomus kenai* to
naupliar densities ............................................ 63
Figure 14 Graphical representation of Gehrs and Robertsons
method of survivorship calculation .......................... 104
Figure 15 Graphical representation of fit obtained from
curve fitting procedure ....................................... 111
Figure 16 Graphical representation of error in survivorship
curves ................................................................. 113
Figure 17 Temperature and precipitation during the
experimental period (May-June, 1982) ......................... 117
Figure 18 Survivorship calculated using integration ....... 120
Figure 19 Survivorship calculated using curve fitting ....... 125
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GENERAL INTRODUCTION

Systems ecology, like other systems-oriented disciplines, is concerned with the constraints which act on systems to keep them within certain boundaries. Unlike most systems in other disciplines however, stochastic events play a much larger role in ecosystems. Because of the complicated nature of ecosystems, the large influence of stochastic events and difficulties associated with quantifying behaviour, systems theory for ecology has not been well developed.

Holling (1973) suggested that because of the above problems, a qualitative rather than a rigorous quantitative approach might be more useful in studying ecosystems, and he began to examine the general qualitative behaviour of some systems. He observed that ecosystems often persisted in one configuration for many years and then suddenly appeared to change in behaviour and community structure, sometimes even when no large perturbation had occurred. He attributed this phenomenon to the presence of a "domain of attraction" in which the system usually existed. However once the boundary to this domain of attraction was reached, the system could quickly change to another configuration. This way of viewing systems also explained why no large perturbation was needed to change the system. A small perturbation, applied over a number of years might push a system closer and closer to the boundary of the domain of attraction until only a small additional perturbation would be needed to push the system into a different configuration.
Several systems which appear to exhibit this sort of behaviour have been examined in detail. Analysis of outbreaks of spruce budworm (Ludwig et al. 1978), transitions between grass and woody vegetation in African semi-arid grazing savannas (Walker et al. 1981) and the collapse of many of the Great Lakes fisheries (Beeton 1969 in Holling 1973) have revealed that the sudden changes in configuration are the result of surpassing the threshold value of some critical variable. In plankton communities, eutrophication has been found to cause sudden algal blooms and shifts in zooplankton community composition, however, little work has been done to examine changes in zooplankton communities in detail and determine the causes of these changes.

Recently, Eunice Lake in the University of British Columbia Research Forest has shown a dramatic shift in community structure (Walters unpubl. data). In the years 1975 through 1980, the Eunice Lake zooplankton community was dominated by the herbivorous cladoceran *Daphnia rosea* and the mostly herbivorous calanoid copepods *Diaptomus kenai*. In 1981, the community suddenly became dominated by the carnivorous cyclopoid copepod *Diacyclops thomasi* and the herbivorous cladoceran *Holopedium gibberum* and seems to have continued in this configuration until the present (Figure 1). No large perturbation was applied directly to this lake during the transition period although cutthroat trout were introduced in 1974 (Hume 1978) and upstream Gwendoline Lake was fertilized in 1979 (Hay 1981). The fertilization of Gwendoline Lake resulted in greatly increased biomass of Cladocera in that year, both in Gwendoline and Eunice Lakes. However, this increase in biomass occurred only during
the year of fertilization and Gwendoline Lake regained its former community structure (Walters unpubl. data). In order to gain insight into the constraints acting on an oligotrophic montane lacustrine community and the mechanisms mediating such shifts in structure, this situation was examined in greater detail. *Diacyclops thomasi* changed from being rare to being a community dominant. This radical change in number and importance in the community suggests that the examination of the population dynamics of this organism may reveal the causes of the shift in community structure in Eunice Lake.

Peacock (Neill and Peacock 1980, Peacock 1981) found that the period of highest mortality for *Diacyclops* seemed to occur in the naupliar stages, particularly in the early naupliar stages. This pattern of mortality in the Copepoda has been found both in freshwater (Burgis 1971, Rigler and Cooley 1974, Gehrs and Robertson 1975, Confer and Cooley 1977, Peacock 1981) and marine systems (Heinle 1966, Parsons et al. 1969, Mullin and Brooks 1970 in Landry 1978b, Landry 1978a). The uniformity of this pattern suggests that the major portion of the mortality of many species of copepods occurs during the naupliar stages and that the significant factors influencing population regulation and therefore the community structure of communities dominated by copepods may act during these early stages.

There are a number of factors which hypothetically could influence the survival of nauplii in general. Nauplii appear to be exceptionally vulnerable to food limitation. In the calanoid copepod *Calmoecia lucasi*, Green (1975) found that the balance of assimilated food intake and respiratory output was negative only
Figure 1 Spring zooplankton community composition in Eunice Lake from 1975-1982. Zooplankton biomasses are averaged from those found from mid-May to early July. The total zooplankton biomass is divided into the categories shown below. Samples were collected with a 200 μm net. (Walters (unpubl. data)

- all nauplii and calanoid copepodites
- small calanoid copepods (*Diaptomus leptopus*, *D. tyrrelli*)
- *Diaptomus kenai*
- small Cladocera (*Bosmina longirostris*, *Diaphanosoma brachyurum*, *Polyphemus pediculus*)
- *Daphnia rosea*
- *Holopedium gibberum*
- *Diacyclops thomasi*
for the naupliar stages. This result, combined with the observation that a stronger correlation between size and metabolic rates exists for cyclopoid and calanoid nauplii than for adults (Epp and Lewis 1979, 1980) suggests that nauplii are treading a thin line between starvation and successful survival to the copepodite stages. Little is known about the actual diet and feeding responses of nauplii in nature although the smaller stages of some marine copepods have been found to graze more efficiently on small algae than the larger stages (Mullin and Brooks 1970, Paffenhoffer 1971, Poulet 1977). However it is possible that nauplii are poor competitors for the food resources and are out-competed by larger cladoceran and copepod grazers. It is also possible that nauplii do not overlap in their food requirements with larger grazers and there is a deficiency of the appropriate size of food due to other factors such as an inappropriate nutrient regime or competition for nutrients from larger algae.

Predation is frequently suggested to play a strong role in structuring zooplankton communities and invertebrate predators in particular have been suggested to be major mortality agents for smaller animals (Dodson 1974, Kerfoot 1977, Lane 1978, 1979, Zaret 1980). Much of the work on invertebrate predation has involved predation on cladocerans. However several studies which have examined predation rates on nauplii and extrapolated their effect on community structure have found that predation can substantially affect naupliar survival (McQueen 1969, Confer and Cooley 1977, Landry 1978b). Intraspecific predation has also been found to be a major mortality factor for copepod
nauplii in several circumstances (McQueen 1969, Landry 1978a).

It therefore seems that both food availability, due either to competition or other non-competitive factors, and predation, either inter- or intraspecific, have the potential to exert a large influence on the survival of nauplii. The role these factors play in influencing the naupliar survival of *D. thomasi* in an oligotrophic montane lake was examined in a set of enclosure experiments described in Chapter 1. In these experiments, I hypothesized that nauplii were dying because of a lack of available food. There were two possible explanations for this: 1. nauplii utilized the same sizes of phytoplankton as other grazers in the system and were out-competed; 2. nauplii did not use the same sizes of 'cells as other zooplankton but the abundance of the sizes which were used was low. These two hypotheses were tested by (1) adding the grazing assemblage to an experimental enclosure and (2) adding fertilizer to increase the food supply. An alternative set of hypotheses was that nauplii were being heavily affected by predation. There were two possible sources of predation: 1. intraspecific predation by *Diacyclops thomasi* and 2. interspecific predation by *Diaptomus kenai*. These two hypotheses were tested by (1) adding *Diacyclops thomasi* adults to the enclosures and (2) adding adult *Diaptomus kenai* to the enclosures. Interspecific predation by *Diaptomus kenai* on *Diacyclops thomasi* nauplii was examined in more detail in Chapter 2.
CHAPTER 1

Naupliar survival is suspected to be the major bottleneck in the life history of D. thomasi (Neill and Peacock 1980). Food limitation and predation appear to have the potential to act as major mortality agents during this developmental period. The relative importance of food limitation, due both to competitive and non-competitive factors, and predation, both inter- and intraspecific was examined in a set of enclosure experiments.

Materials and methods

Study area

This study was conducted in Placid Lake in the University of British Columbia Research Forest located approximately 40 km east of Vancouver in the Coast Range Mountains (Fig. 2). Lakes in the Research Forest have been described in detail elsewhere (Efford 1967, Northcote and Clarotto 1975, Neill 1978), but they are mostly small oligotrophic lakes. Diacyclops thomasi is abundant in Placid Lake, although it is much less abundant than in nearby Eunice Lake. Consequently in Placid Lake, other zooplankters would be more likely to play a major role in limiting the population, thus more closely approximating conditions in Eunice Lake prior to 1979. Enclosure experiments to examine the relative importance of food availability and predation on the naupliar survival of D. thomasi were conducted
in Placid Lake in May and June 1982. Due to its small size and large watershed in comparison to its volume (Table I), this lake undergoes relatively sudden and drastic changes of temperature and water level. Nevertheless Placid Lake shows a similar zooplankton community with comparable dynamics to other lakes in the Research Forest (Walters, unpubl. data). Both Placid and Eunice Lakes support populations of cutthroat trout (*Salmo clarki clarki*). The population in Placid Lake is presumed to be native, however the population in Eunice Lake was introduced from nearby Loon Lake in 1974 and 1975.

**Placid Lake Community**

In order to affect the naupliar survival of *D. thomasi*, other zooplankton in Placid Lake would have to overlap at least temporally with the nauplii. *Diacyclops* is univoltine with the major burst of production occurring in early spring. It enters the water column from a winter diapause in late April as stage 4 and 5 copepodites and molts to reproductive adults. These adults produce nauplii during May and June with a peak in production occurring at the end of May. The nauplii occur mainly in the upper 2 meters of the water column. Examination of the seasonal patterns in Placid Lake reveals one species of cyclopoid copepod, two species of calanoid copepods and several species of cladocerans which occur in significant densities at the same time as *Diacyclops* nauplii. The most common species of Cladocera present are *Holopedium gibberum* and *Daphnia rosea*. The cladoceran species *Bosmina longirostris*, *Ceriodaphnia quadrangulara* and *Polyphemus pediculus* are also present but occur
Figure 2 Location of study area. (from Neill, 1978)
Table I  Some physical, chemical and biological characteristics of Placid and Eunice Lakes in the UBC Research Forest. (modified from Neill, 1978)

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Placid</th>
<th>Eunice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation, m</td>
<td>510</td>
<td>480</td>
</tr>
<tr>
<td>Drainage area, ha</td>
<td>44</td>
<td>191</td>
</tr>
<tr>
<td>Surface area, ha</td>
<td>1.6</td>
<td>18.2</td>
</tr>
<tr>
<td>Maximum depth, m</td>
<td>7</td>
<td>42</td>
</tr>
<tr>
<td>Mean depth, m</td>
<td>4.3</td>
<td>15.8</td>
</tr>
<tr>
<td>Colour, Pt units</td>
<td>20-25</td>
<td>15</td>
</tr>
<tr>
<td>Transparency (Secchi depth, m)</td>
<td>4-4.5</td>
<td>6-10</td>
</tr>
<tr>
<td>Total dissolved solids, mg/l</td>
<td>17-23</td>
<td>16</td>
</tr>
<tr>
<td>Maximal epilimnetic depth, m</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Crustacean-zooplankton species</td>
<td></td>
<td>-1981</td>
</tr>
<tr>
<td>Diaptomus kenai</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Diaptomus tyrrelli</td>
<td>-</td>
<td>A</td>
</tr>
<tr>
<td>Diaptomus oregonensis</td>
<td>A</td>
<td>-</td>
</tr>
<tr>
<td>Diaptomus leptopus</td>
<td>-</td>
<td>R</td>
</tr>
<tr>
<td>Daphnia rosea</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Diaphanosoma brachyurum</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>R</td>
<td>A</td>
</tr>
<tr>
<td>Ceriodaphnia quadrangula</td>
<td>R</td>
<td>-</td>
</tr>
<tr>
<td>Polyphemus pediculus</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Dicacyclops thomasi</td>
<td>A</td>
<td>R</td>
</tr>
<tr>
<td>Tropocyclops p. prasinus</td>
<td>R</td>
<td>A</td>
</tr>
</tbody>
</table>

A indicates abundant
R indicates rare
- indicates absent
in low numbers and are unlikely to significantly influence naupliar survival. *Holopedium* peaks in density toward the end of May, often contributing the majority of the biomass in the lake at this time. *Daphnia* is generally in low numbers in the spring but begins increasing in biomass at the end of May and peaks in the summer. The two species of calanoid copepods in the lake are *Diaptomus oregonensis* and *D. Kenai*. *D. oregonensis* is a comparatively small copepod (1.25 - 1.5 mm adult length) which occurs in high densities from the beginning of October to the end of June, dropping in density during the summer. *D. oregonensis* produces nauplii in the spring starting later than *D. thomasi* and probably peaking in July. *Diaptomus kenai* is a large copepod (1.8 - 3.0 mm adult length) which occurs in high densities in Placid lake only during very early spring when small numbers occur in the upper water column. The majority of the *D. kenai* population remains deeper although it migrates to the surface at night. *D. kenai* retreats completely to the lower depths of the water column in early June and disappears completely during the summer. *D. thomasi* adults are also present and occur in the upper water column during the period of naupliar production.

These species can be grouped together according to their possible effect on naupliar mortality. The Cladocera present are herbivorous except for *Polyphemus* and could compete with the nauplii for food. Some calanoid copepods have been found to be carnivorous and Lane (1978) suggested that *D. oregonensis* was a predator. The small size of *D. oregonensis* in Placid Lake seems to make this possibility unlikely so it can also be regarded as
a competitor. The above animals were grouped together and are hereinafter collectively referred to as the "grazing assemblage". D. *kenai* has also been considered to be strictly herbivorous but its large size allows for the possibility of predation. Krause (unpubl. data) has found some evidence for its predatory ability. D. *thomasi* is known to be cannibalistic on its own nauplii and has been calculated to be capable of consuming 31% of its own yearly production (McQueen, 1969).

**Experimental Methods**

*In situ* enclosure experiments were conducted from May 25 until June 16, 1982 to test the 4 hypotheses potentially involved in limiting naupliar survival. The experimental enclosures used were similar to those described by Neill (1981). A floating collar consisting of styrofoam and plywood was divided in frames approximately 45 cm square. The frame was then anchored to the bottom with cement blocks at each of the corners. 4 mil clear polyethylene plastic bags slightly over 1 m deep were suspended from these frames. This arrangement provided enclosures which were approximately 300 l in volume. The bags were initially filled with lake water which had been pumped through a 54 μm net to remove all crustaceans while allowing grazable seston to pass. The water used was taken from a depth of several meters in the lake to allow for an adequate nutrient supply for the duration of the experiment. Since larvae of the phantom midge, *Chaoborus*, have been found to exert considerable predation pressure on invertebrate communities (Lynch 1979, Neill and Peacock 1980), 2 mil, clear polyethylene
plastic tents were constructed over the experimental enclosures to prevent Chaoborus from laying eggs in the enclosures yet allow maximal light penetration. The tents could easily be removed for sampling. The ends of the tents were covered by plastic screening to allow for air circulation.

The enclosures were stocked with lake densities of crustacean zooplankton, determined by sampling the lake with a Clarke-Bumpus sampler 3 days earlier. Since the mesh size on the sampling apparatus was too large to collect nauplii, vertical hauls were made over the same depth range that the Clarke-Bumpus sample was taken. The number of nauplii was calibrated by assuming that the proportion of D. oregonensis in the vertical haul was representative of the proportion of D. oregonensis in the Clarke-Bumpus sample. The starting densities of animals in the enclosures may be found in Table II. Since D. kenai occurs deeper in the water column during the day and migrates vertically upwards at night, it was stocked at a slightly higher density than found during the day to average out the density over a 24 h period.

The animals used in the study were collected from the lake on the day the enclosures were set up. They were sorted for addition to the enclosures using a combination of sieving and pipetting. Nauplii were obtained by filtering out all of the larger animals using a 153 μm sieve. D. thomasi and D. kenai adults were individually pipetted out. The grazing assemblage was considered to be those animals which remained after nauplii and all Diacyclops and D. kenai copepodites were removed. To obtain the desired densities in the experimental enclosures,
Table II Stocking densities of zooplankton in the enclosures.

<table>
<thead>
<tr>
<th>Species</th>
<th>Lake Density (l⁻¹)</th>
<th>Enclosure Density (l⁻¹)</th>
<th>Number in Enclosure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diacyclops thomasi</td>
<td>1.0</td>
<td>1.0</td>
<td>300</td>
</tr>
<tr>
<td>Diaptomus kenai</td>
<td>.06</td>
<td>.22</td>
<td>66</td>
</tr>
<tr>
<td>Diaptomus oregonensis</td>
<td>3.6</td>
<td>3.5</td>
<td>1050</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>.6</td>
<td>.6</td>
<td>180</td>
</tr>
<tr>
<td>Nauplii</td>
<td>3.6</td>
<td>3.5</td>
<td>1050</td>
</tr>
</tbody>
</table>
D. kenai and D. thomasi were counted individually. The desired densities of nauplii and the grazing assemblage were obtained by adding the required amount of a calibrated concentrated zooplankton "soup".

To enhance potentially limiting food abundance for nauplii, some of the enclosures were fertilized with 6 μg/l P in a 30:1 N:P atomic ratio using NH₄Cl and (NH₄)₂HPO₄. Fertilizer was added to the enclosures twice during the course of the experiment, once while the bags were being filled and subsequently after the experiments had been running 12 days. The amount of fertilizer added approximately doubled the amount of phosphorus in the water. A large N:P ratio and the use of ammoniacal nitrogen was chosen to try to increase the growth of edible algae without shifting the algal composition excessively and, in particular, without unduly favouring the growth of large nitrogen-fixing blue green algae (Neill pers. comm.).

All of the enclosures were sampled at four day intervals for zooplankton, starting the day after set-up. The zooplankton community was sampled by removing the animals from 15 l collected from several depths and areas in each enclosure using a battery-operated bilge pump. Animals were preserved in a sucrose-5% formaldehyde solution (Haney and Hall 1973) and all samples were later counted in toto. All nauplii and immature copepodites were counted under 50X on a binocular dissecting microscope. Cyclopoid nauplii and copepodites were identified following Torke (1974) and staged under 50X. Larger animals were counted under 25X.

Chlorophyll and phytoplankton were also sampled at 4 day
intervals. However the first sample was taken on the day of set-up prior to the addition of animals to the enclosures. After the first sampling period, sampling was done in synchrony with zooplankton sampling. Chlorophyll and phytoplankton were sampled by withdrawing approximately 700 ml of water from each enclosure using a piece of hose approximately 3 cm in diameter and extending 1 m into the enclosure. An 80 ml aliquot of the well-mixed sample was fixed with Lugol's solution for later enumeration of phytoplankton cells. A 250 ml aliquot was filtered through a Whatman GF/C glass fibre filter, folded and immediately put in the dark on ice. After transport back to the lab, these samples were stored at approximately -20 °C for 4 to 6 months.

Chlorophyll a measurements were made on the frozen samples following a method modified from Strickland and Parsons (1965) using a Turner Design Model 10 fluorometer. Magnesium carbonate was not added to the samples. Correction for phaeophytin, inactive chlorophyll, was made by measuring the sample both before and after several drops of 1% HCl was added. Calculation of the amounts of live chlorophyll and phaeophytin was done using the equations:

\[
\text{live chlorophyll} = \frac{r(\text{BA}-\text{AA})}{r-1}
\]

\[
\text{phaeophytin} = r(\text{BA} - \text{live chlorophyll})
\]

Where

- BA = fluorescence before acid
- AA = fluorescence after acid
- \( r \) = conversion factor

Phytoplankton cell counts were made by settling 50 ml of
preserved samples for 48 hours, transferring the residue to a counting chamber and settling for an additional 24 hours. Phytoplankton cells were then counted under 400X and divided into the size classes <2 µm, 2-5 µm, 5-9 µm, 9-13 µm, 13-18 µm, >18 µm, colonies and filaments. The minimum of 200 cells or 30 fields was counted for each size class for each sample. This criterion has been found to be the most efficient in reducing sample variance (D. Robinson, E. Krause pers. comm.).

Experimental design

Four factors were hypothesized to significantly affect naupliar survival. These were: (1) food limitation due to competition from other grazers, (2) food limitation due to non-competitive factors, (3) intraspecific predation by D. thomasi adults and (4) interspecific predation by D. kenai. These hypotheses were tested by (1) adding the grazing assemblage to an experimental enclosure, (2) adding fertilizer to an enclosure, (3) adding adult D. thomasi to an enclosure and (4) adding D. kenai to an enclosure.

Eighteen experimental enclosures were set up with sixteen different experimental treatments. The sixteen treatments included every possible combination of the four factors mentioned above. Figure 3 provides a summary of these treatments. Nauplii were added to every experimental enclosure. The two additional experimental enclosures were set up to be replicates of the treatment of fertilizer and nauplii only. Since it was not feasible to replicate all experimental treatments, these 3 replicates were used as an estimate of
between enclosure variability. Since fertilizer is known to increase variance between bags (Neill, pers. comm.) and these treatments would have few organisms to stabilize this effect, the treatment with fertilizer and nauplii only was considered a priori to have the greatest potential for experimental variability. On the final day of sampling, three zooplankton samples were taken from each enclosure and 3 chlorophyll and phytoplankton samples were taken from 5 enclosures. These replicates were used to obtain an estimate of sample variance within enclosures.

Analysis

Analysis of variance was the most commonly used statistical technique and was done either using a pocket calculator or the computer program UBC GENLIN (Grieg and Bjerring 1977). In either case, Bartlett's test for homogeneity of variance was conducted. If the variance was not homogeneous, the data were log-transformed and the test re-applied. In most cases, the lack of homogeneity was not significant once the data were transformed. Simulation analyses were all performed on an Apple II microcomputer. Curve fitting was performed using the package N2SNO found in UBC CURVE (Moore 1981). Unless the use of a packaged program is explicitly stated, I wrote and performed all simulations and analyses.
Figure 3 Experimental design. Four factors were used in the experiment to examine their effect on *Diacyclops thomasi* naupliar survival:

1. fertilization
2. presence of the grazing assemblage
3. presence of *Diaptomus kenai*
4. presence of *Diacyclops thomasi*.

Every possible combination of these 4 factors was included in the experimental design. In this representation, every box represents an enclosure and the symbols in it indicate the treatments it contains. For example, the box in the upper left hand corner represents the enclosure which contains fertilizer and grazers.

G Grazers
K *Diaptomus kenai*
D *Diacyclops thomasi*
F fertilizer
<table>
<thead>
<tr>
<th></th>
<th>Present Grazers</th>
<th>Absent Grazers</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DIAPTORUS KENAI</strong></td>
<td>Pres  F G  D G  K F  K F  D G  K F  K D</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Absent F  G  D  K  G</td>
<td></td>
</tr>
</tbody>
</table>

**FERTILIZER**
Results

Precision of sample data

Coefficients of variation were calculated from the three replicate zooplankton samples taken from all enclosures at the end of the experiment. A fairly consistent coefficient of variation between 40 and 50 % is shown for all zooplankton (Table III). If samples to which the tested treatment was not added are excluded, the coefficient of variation is consistently lower. This would be expected if the variance increased with decreasing abundance.

The precision of the phytoplankton data can be seen in Table IV. Phytoplankton cell counts were probably more variable although this is difficult to judge since all samples were counted from only one of the enclosures from which replicates were taken. The chlorophyll measurements showed that estimates of live chlorophyll were considerably more variable than those for either phaeophytin or total chlorophyll.

The coefficients for both the zooplankton and phytoplankton data are larger than those found by Marmorek (1983). The increased variation is probably due to the small volume of the samples taken. However, the variation is similar to that reported by Wiebe and Holland (1968) in their study of sampling error.
Table III Precision of zooplankton data

<table>
<thead>
<tr>
<th>Organism</th>
<th>No. of Enclosures</th>
<th>Mean Coefficient of Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daphnia rosea</td>
<td>18</td>
<td>48.5</td>
</tr>
<tr>
<td></td>
<td>8 *</td>
<td>42.6</td>
</tr>
<tr>
<td>Diacyclops thomasi</td>
<td>18</td>
<td>72.1</td>
</tr>
<tr>
<td></td>
<td>8 **</td>
<td>44.6</td>
</tr>
<tr>
<td>Diaptomus oregonensis</td>
<td>18</td>
<td>54.0</td>
</tr>
<tr>
<td></td>
<td>8 *</td>
<td>46.9</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>18</td>
<td>50.9</td>
</tr>
<tr>
<td></td>
<td>8 *</td>
<td>40.8</td>
</tr>
<tr>
<td>Calanoid nauplii copepodites</td>
<td>18</td>
<td>52.3</td>
</tr>
<tr>
<td>Calanoid nauplii and copepodites</td>
<td>84 ***</td>
<td>42.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>48.0</td>
</tr>
</tbody>
</table>

* - calculated from only enclosures containing the grazing assemblage.
** - calculated from only enclosures containing D. thomasi.
*** - calculated over all stages.
Table IV Precision of phytoplankton data

<table>
<thead>
<tr>
<th>No. of Enclosures</th>
<th>Mean Coefficient of Variation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Chlorophyll measurements</strong></td>
<td></td>
</tr>
<tr>
<td>live chlorophyll</td>
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</tr>
<tr>
<td>phaeophytin</td>
<td>5</td>
</tr>
<tr>
<td>total chlorophyll</td>
<td>5</td>
</tr>
<tr>
<td><strong>Cell counts</strong></td>
<td></td>
</tr>
<tr>
<td>&lt; 2 µm</td>
<td>1</td>
</tr>
<tr>
<td>2 - 5 µm</td>
<td>1</td>
</tr>
<tr>
<td>5 - 9 µm</td>
<td>1</td>
</tr>
<tr>
<td>9 - 13 µm</td>
<td>1</td>
</tr>
<tr>
<td>13 - 18 µm</td>
<td>1</td>
</tr>
<tr>
<td>18 - 30 µm</td>
<td>1</td>
</tr>
<tr>
<td>Mean of size classes</td>
<td></td>
</tr>
</tbody>
</table>
Set up of enclosures

Count data of zooplankton and phytoplankton from the enclosures were examined to confirm proper set up of the experimental enclosures. Details of the statistical analysis may be found in Appendix A. In general, treatment differences were observed for all treatments after set up and these differences continued for the duration of the experiment. All zooplankton treatments appeared to suffer extensive mortality associated with set up and were much lower in density than the lake at the beginning of the experimental period. This difference increased during the course of the experiment for adult D. thomasi and the grazing assemblage since densities in the lake rose due to animals breaking diapause. The differences decreased for Cladocera at the end of the experimental period. Nauplii were at lake density at the beginning of the experiment. These results are summarized in Table V.

Fertilizer treatments resulted in significant increases in total chlorophyll a after the first sampling period. This increase in total chlorophyll was largely made up of increases in phaeophytin since live chlorophyll showed significant increases only during 2 sampling periods. Examination of size classes of phytoplankton showed that fertilization resulted in significant increases in plankton of the 5-18 μm range for the second and third sample periods. Phytoplankton data were also examined to determine if the grazing assemblage had a significant impact on the food availability. This analysis showed that the grazing assemblage decreased total chlorophyll a starting in the third sampling period and continuing to the end
Table V Dynamics of zooplankton in enclosures.

<table>
<thead>
<tr>
<th>Organism</th>
<th>Effect of Treatment</th>
<th>Effect of Time</th>
<th>Density in Enclosures (l⁻¹) (Percentage of Lake Density)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Beginning</td>
</tr>
<tr>
<td>Diacyclops thomasi</td>
<td>***</td>
<td>ns</td>
<td>0.75</td>
</tr>
<tr>
<td>Diaptomus kenai</td>
<td>p</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>Diaptomus oregonensis</td>
<td>***</td>
<td>***</td>
<td>0.72</td>
</tr>
<tr>
<td>Daphnia rosea</td>
<td>***</td>
<td>***</td>
<td>0.13</td>
</tr>
<tr>
<td>Holopedium gibberum</td>
<td>***</td>
<td>***</td>
<td>0.47</td>
</tr>
<tr>
<td>Nauplii</td>
<td>-</td>
<td>-</td>
<td>3.58</td>
</tr>
</tbody>
</table>

*** - indicates significance at the level .001.
ns - indicates non-significance.
p - indicates that no statistical test was done but visual inspection assured the presence in enclosures.
of the experiment. An interaction between fertilizer and the grazing assemblage occurred during the last two sampling periods. Examination of the abundance of phytoplankton size classes on the third sampling period revealed that the grazing assemblage decreased phytoplankton biomass in the 5-13 μm range and an interaction between fertilizer and grazers occurred in the 5-9 μm range.

Results of survivorship calculations

Two methods for the calculation of survivorship were examined in detail (Appendix B). Integration under the population abundance curve is the method which has been most frequently used to examine copepod survivorship. The other method investigated involved constructing a simulation model of conditions in the enclosures and fitting the simulated curve to the actual population abundance curve by minimizing the sums of squares. These investigations revealed that both methods had some difficulties but both seemed fairly robust and consistent within themselves. Survivorship was therefore calculated using both techniques and results compared. The results from integration under the curve are presented in Appendix D, Figure 19. Examination of these results on a very general level indicated that all the factors tested had some effect on naupliar survival. Fertilizer increased survival whereas all other factors, to a greater or lesser extent, decreased survival. Results from curve fitting are shown in Appendix D, Figure 20. These results also show an effect of all factors on naupliar survival. The general effects of these factors on
overall survival to the third copepodite stage was the same as the results from integration.

When the results of the calculation of survivorship are examined, the shortcomings of the methods of analysis and the sampling technique must be considered. These effects, examined in detail in Appendix B, are summarized below:

1. Integrating under the population curve underestimates survivorship and this effect becomes more noticeable when reproducing adult *D. thomasi* are present. This technique is also vulnerable to slight differences in developmental rates between enclosures.

2. Curve fitting underestimates survivorship when adult *D. thomasi* are present in the enclosures. This technique is vulnerable to inadequacies in the model used for generating the curve.

3. Sampling error results in a 10% variation in daily survival rate. This variation resulted in approximately a 25% variation in every point on the survival curve. Differences between enclosures containing the same treatment seemed to show an error of approximately the same magnitude as the sampling error.

Because of the large variability in the calculated curves and the relative similarity of the results of the survivorship calculations, no statistical analyses were performed. Instead, general trends were observed. The most confidence was placed in
trends which (a) appeared in the results from both methods of survivorship calculation, (b) were consistent in their effect (i.e. always increased or decreased survival when added to an enclosure) and (c) differed from other treatments by more than the sample and within treatment variation.

The accuracy of the results from the two methods could not be compared. Although it was possible to perform simulations to test the accuracy of the method of integration under the curve, it was not possible to do this for the curve-fitting method since there was no way to estimate the effect of inadequacies of the model used.

The results from both methods showed that all factors tested had a negative effect on naupliar survival by themselves. (Figures 4 and 5). In both cases, fertilizer showed a slight negative effect. Adult *D. thomasi* showed a stronger negative effect. *D. kenai* and grazers showed still stronger negative effects than the other two factors. Adult *D. thomasi*, *D. kenai* and grazers seemed to be additive in their effect in both methods of analysis. An example of this additivity can be seen in Figures 6 and 7.

An estimation of the overall strength of these factors in influencing survivorship can be made by comparing survivorship between treatments which only differ by one factor. Summaries of these comparisons are shown in Figures 8-11. From these summaries it can be seen that fertilizer has a very mixed effect until the beginning of the copepodite phase. The net effect of this factor is positive using the method of integration and sightly negative using curve fitting. If the net effect of
Figure 4 Effect of the grazing assemblage, fertilization, *Diaptomus kenai* and *Diacyclops thomasi* alone on naupliar survival (Integration). The distance on the x-axis between developmental stages is proportional to the duration of the stages.

- Nauplii alone
- *Diacyclops thomasi*
- *Diaptomus kenai*
- Grazing assemblage
- Fertilizer
Figure 5 Effect of the grazing assemblage, fertilization, \textit{Diaptomus kenai} and \textit{Diacyclops thomasi} alone on naupliar survival (Curve fitting). The distance on the x-axis between developmental stages is proportional to the duration of the stages.

- Nauplii alone
- \textit{Diacyclops thomasi}
- \textit{Diaptomus kenai}
- Grazing assemblage
- Fertilizer
Figure 6 Effect of the successive addition of mortality agents on naupliar survival (Integration). The distance on the x-axis between developmental stages is proportional to the duration of the stages.

- Nauplii alone
- Diacyclops thomasi
- Diacyclops thomasi and grazers
- Diacyclops thomasi, grazers and Diaptomus kenai
Figure 7 Effect of the successive addition of mortality agents on naupliar survival (Curve fitting). The distance on the x-axis between developmental stages is proportional to the duration of the stages.

- Nauplii alone
- Diacyclops thomasi
- Diacyclops thomasi and grazers
- Diacyclops thomasi, grazers and Diaptomus kenai
fertilizer is examined over all stages up to the third copepodite stage, the effect of fertilizer additions becomes more positive.

The most consistent negative effect appeared to be that of the grazing assemblage. Both methods of analysis showed the same pattern and effects did not change over the developmental stages. The curve fitted results gave a consistent large negative effect while the integrated results showed more variation both in magnitude and direction of effect. *D. kenai* also showed a consistent negative net effect in both methods although this effect seemed to increase in the copepodite stages of the curve-fitted results.

*Diacyclops* showed inconsistent effects in the two methods of analysis. The curve-fitted results showed a slight positive effect over all developmental stages, whereas the integrated results showed a strong negative effect on all developmental stages. The strong negative effect of cannibalism in the integrated results may largely be due to the underestimation of survival which is known to occur with this method. The slight positive effect in the curve-fitted results is somewhat suspect. Because it is known that *D. thomasi* are cannibalistic, one would expect a decrease in survivorship in the enclosure with only *D. thomasi* adults and nauplii since there would be nothing else for the adults to eat. A positive effect of adult *D. thomasi* on treatments containing grazers could be explained if the adults reduced competition for juveniles by preying on competitors. However McQueen (1969) found that the predation rate of adult *D. thomasi* on nauplii was not affected by the presence of
Figure 8 Summary of the effect of a single factor on survival to the end of the naupliar stages (Integration). This table shows a summary of comparisons between treatments which only differ by one factor.

\( \uparrow \) indicates a positive effect less than the sample variance.

\( \uparrow \uparrow \) indicates a positive effect greater than the sample variance.

\( \downarrow \) indicates a negative effect less than the sample variance.

\( \downarrow \downarrow \) indicates a negative effect greater than the sample variance.

\( \boxed{\text{---}} \) indicates no effect

An example of the interpretation of this table is as follows:

The upper left hand box shows that fertilizer causes a negative effect less than the sample variance when added to an enclosure containing nauplii only.

A summary of the net effect of each factor is provided at the bottom of each column. Solid arrow are considered to be worth twice as much as hollow arrows.

- F  Fertilizer
- K  Diaptomus kenai
- D  Diacyclops thomasi
- G  Grazers

NB Arrows which result from comparisons involving treatment KG (eg. column 4, row 2) must be treated with caution as unusually low numbers of nauplii reduced the precision of the calculated survivorship in this treatment.
<table>
<thead>
<tr>
<th>Nauplii Only</th>
<th>F</th>
<th>K</th>
<th>D</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>▼</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K</td>
<td></td>
<td>▼</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
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<td></td>
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<td>G</td>
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<tr>
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</tr>
<tr>
<td>6</td>
<td></td>
<td>5</td>
<td>8</td>
<td>4</td>
</tr>
</tbody>
</table>
Figure 9 Summary of the effect of a single factor on survival to the end of the naupliar stages (Curve fitting). This table shows a summary of comparisons between treatments which only differ by one factor.

- indicates a positive effect less than the sample variance.

↑ indicates a positive effect greater than the sample variance.

↓ indicates a negative effect less than the sample variance.

↓↓ indicates a negative effect greater than the sample variance.

- - indicates no effect

An example of the interpretation of this table is as follows:

The upper left hand box shows that fertilizer causes a negative effect less than the sample variance when added to an enclosure containing nauplii only.

A summary of the net effect of each factor is provided at the bottom of each column. Solid arrow are considered to be worth twice as much as hollow arrows.

F Fertilizer
K Diaptomus kenai
D Diacyclops thomasi
G Grazers
### ADDED TREATMENT

<table>
<thead>
<tr>
<th>Nauplii Only</th>
<th>F</th>
<th>K</th>
<th>D</th>
<th>G</th>
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<td>4</td>
<td>11</td>
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</table>
Figure 10 Summary of the effect of a single factor on survival to the beginning of the third copepodite stage (Integration). This table shows a summary of comparisons between treatments which only differ by one factor.

- indicates a positive effect less than the sample variance.
- indicates a positive effect greater than the sample variance.
- indicates a negative effect less than the sample variance.
- indicates a negative effect greater than the sample variance.
- indicates no effect.

An example of the interpretation of this table is as follows:

The upper left hand box shows that fertilizer causes a negative effect less than the sample variance when added to an enclosure containing nauplii only.

A summary of the net effect of each factor is provided at the bottom of each column. Solid arrow are considered to be worth twice as much as hollow arrows.

F  Fertilizer
K  Diaptomus kenai
D  Diacyclops thomasi
G  Grazers

NB Arrows which result from comparisons involving treatment KG (eg. column 4, row 2) must be treated with caution as unusually low numbers of nauplii reduced the precision of the calculated survivorship in this treatment.
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<thead>
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<th>BASELINE TREATMENT</th>
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<th>D</th>
<th>G</th>
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Numbers at the bottom of the table:
- F: 7
- K: 5
- D: 11
- G: 4
Figure 11 Summary of the effect of a single factor on survival to the beginning of the third copepodite stage (Curve-fitting). This table shows a summary of comparisons between treatments which only differ by one factor.

↑ indicates a positive effect less than the sample variance.

↑↑ indicates a positive effect greater than the sample variance.

↓ indicates a negative effect less than the sample variance.

↓↓ indicates a negative effect greater than the sample variance.

— indicates no effect.

An example of the interpretation of this table is as follows:

The upper left hand box shows that fertilizer causes a negative effect less than the sample variance when added to an enclosure containing nauplii only.

A summary of the net effect of each factor is provided at the bottom of each column. Solid arrow are considered to be worth twice as much as hollow arrows.

F  Fertilizer
K  Diaptomus kenai
D  Diacyclops thomasi
G  Grazers
### Baseline Treatment

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</tr>
</tbody>
</table>

**ADDED TREATMENT**
alternate prey. An indirect benefit due to reduced competition also does not explain the increase in survival when adult *D. thomasi* were added to treatments containing *D. kenai* or fertilizer. These observations indicate an error in the modelling of recruitment in enclosures containing adult *D. thomasi*. This conclusion is further supported by observations made while calibrating the model. When initial conditions were adjusted to minimize negative mortality (Appendix B), results remained relatively consistent when examined with one factor held constant (i.e. examining the results from all enclosures containing adult *Diacyclops* as shown in Figure 19c). However *Diacyclops* results as a group seemed to shift down as negative mortality was minimized. These difficulties obscure the importance of cannibalism in influencing the juvenile survival of *D. thomasi*. However it is probable that it falls somewhere between the extremes shown in the results from integration and curve-fitting.
Discussion

In the experimental enclosures, it appeared that the grazing assemblage and *D. kenai* had a larger and more consistent effect on juvenile survival than other factors although difficulties in estimating survivorship in enclosures containing adult *D. thomasi* make its status uncertain. There is however an indication that this species may also substantially affect survival. *D. thomasi* is known to be carnivorous and cannibalistic and to prey preferentially on nauplii (McQueen 1969). Therefore it is probable that the effect of adult *D. thomasi* on naupliar survival was due to cannibalism. *D. kenai* is known to be a filter feeder and capable of feeding on small food particles (Buckingham 1978, Chapman 1982, Krause unpubl. data). However it seems unlikely that its effect on survivorship was due entirely to competition since its density and biomass were so much lower than that of the grazing assemblage, which had overall a similar effect. This observation suggests that predation may have been occurring. This prediction was later confirmed (Chapter 2) and a predation rate of 20% of the nauplii per predator per litre per day was found. It therefore seems likely that the main effect of *D. kenai* on naupliar survival was due to predation on nauplii.

The interpretation of results relating to food limitation is more difficult. The grazing assemblage seemed to decrease survivorship and fertilizer appeared in general to increase it. However fertilizer did not show consistent effects within either method of analysis. In enclosures containing nauplii alone, fertilizer did not appear to have any effect. This result could
be explained if nauplii ate the smallest sizes of phytoplankton which were not stimulated by the application of fertilizer. Comparison of small phytoplankton between fertilized and unfertilized enclosures containing nauplii alone showed that there was no significant difference between them, indicating that the lack of response on the part of the small phytoplankton was not due to the larger grazers consuming any increased production. The grazing assemblage showed a consistent net reduction in naupliar survival. The probable explanation for this is competition for food from the larger cladocerans and copepods. These grazers did not show any detectable effect on the smaller algal size classes which nauplii are presumed to eat, despite feeding studies which have shown that these organisms are capable of eating the smaller size classes (Buckingham 1978, Krause unpubl. data). Another possible explanation for reduced survival in the presence of grazers is competition from other nauplii. Enclosures with grazers also contained *D. oregonensis* nauplii. When fertilizer was present in enclosures containing grazers or adult *D. thomasi*, more nauplii were also present. If food resources were not increased (as indicated by examination of the phytoplankton size data), the survival of nauplii in fertilized conditions would actually decrease due to an increase in the number of nauplii. This appeared to be the case only in about one quarter of the enclosures. Naupliar competition would also imply a reduction in food supply, which was not noted. Changes in the smaller algal classes have occurred but been undetectable with my phytoplankton sampling program. It is therefore difficult to
draw any specific conclusion about the source of competition however it appears that competition does have substantial effect on naupliar survival.

In summary, it appeared that in the experimental enclosures interspecific predation from D. kenai and competition either from large cladoceran grazers and calanoid copepods or from other nauplii had the largest effects on naupliar survival. Although difficulties existed in assessing its importance, intraspecific predation by D. thomasi also seemed to have a substantial effect. It is not possible to comment on the importance of a shortage of food from non-competitive sources since the smaller phytoplankton, which nauplii probably eat, were not stimulated by the application of fertilizer.

Predation has previously been suggested to play a major role in naupliar mortality. Confer and Cooley (1977) found that predation by omnivorous zooplankton could account for most of the naupliar mortality of Diaptomus minutus. McQueen (1969) suggested that up to 30% of the calanoid naupliar production in Marion Lake could be eaten by D. thomasi. Landry (1978b) suggested that Labidocera trispinosa could inflict population mortalities of 54%, 18% and 15% on Calanus pacificus, Paracalanus parvus and Acartia tonsa, respectively.

Competition has not been previously suggested as a major cause of naupliar mortality, however there has been some indication that competition may affect survival. Olenick (1982) working in Eunice Lake found that competition from Diaptomus tyrrelli seemed to affect primarily the naupliar stages of Diaptomus leptopus. Neill (in press), also working in the UBC
Research Forest, has found that competition from *Daphnia rosea* can limit populations of rotifers suggesting that competition with cladocerans may indeed have a significant effect on smaller organisms in these lakes.

In extrapolating the results from the enclosures to Placid Lake both the difficulties experienced in setting up the enclosures and the seasonal dynamics of the Placid Lake community must be considered. The condition in the enclosures (i.e. low grazers, high *D. kenai* and low adult *D. thomasi*) probably reflect fairly accurately conditions which occur in early May, near the beginning of the reproductive period of *D. thomasi*. Although densities of competitors changed greatly during the experimental period, the majority of nauplii had passed into the copepodite stage by the time the large increases occurred and these changes would have had little effect on naupliar survival. Survivorship of the young copepods was not greatly affected by the change either since they are probably not as vulnerable to competition and they start to become carnivorous. As the season in the lake proceeds, *D. kenai* decrease in number and therefore in importance as a factor in *D. thomasi* naupliar survival. Both grazing biomass and the number of nauplii increase and therefore the importance of competition to naupliar survival would increase, presuming that algal productivity does not increase proportionally. The importance of both interspecific predation and competition depend to some extent on year to year climatic variation. During cooler years when nauplii develop more slowly and *D. kenai* remain in the upper water column for a longer period of
time, *D. kenai* would assume more importance as a mortality agent. During warm springs when cladocerans are likely to rise early in the year and increase rapidly, competition is likely to be more important. Cannibalism would be most important at the beginning and particularly at the end of the reproductive period when the ratio of older copepodites to nauplii is the highest. However intraspecific predation would continue to have an effect throughout the reproductive period.

There are other potential sources of mortality which are present in Placid Lake but were not included in the enclosure experiments. Both *Chaoborus* and *Polyphemus* are known to be predators. Larger *Chaoborus trivittatus* and *C. americanus* have been found to be capable of controlling community structure (Lynch 1979, Neill and Peacock 1980, Neill 1981) but do not prey heavily on nauplii (Fedorenko 1975). Smaller *Chaoborus flavicans*, which is the species resident in Placid Lake, only rises in the water column at night. Although this species probably eats smaller organisms, it would probably still have a small effect on nauplii since it would only overlap spatially with the nauplii for a short period of time each day. Nauplii are also extremely slow swimmers (Gerritson 1979) and are therefore relatively invulnerable to ambush predators due to low encounter rates. The inclusion of *Chaoborus* in the experiment would probably have affected naupliar survival indirectly by decreasing the abundance of predators and competitors. In addition, since fish prey heavily on *Chaoborus*, it is often reduced in importance in lakes with fish. *Polyphemus* is mainly littoral in Placid Lake and would be unlikely to greatly affect
naupliar survival of the limnetic *D. thomasi*.

From the pattern of seasonal dynamics observed in Placid Lake, it would appear that cannibalism is the most important mortality agent over the season. Therefore, in the Placid Lake community, it would seem that *D. thomasi* is limited mostly by cannibalism although predation by *D. kenai* early in the season could have an effect. Competition from either larger grazers or other nauplii could have a substantial effect later in the season. Cannibalism has been previously implicated as a major mortality agent in aquatic ecosystems (McQueen 1969, Landry 1978a). However there is some suggestion that the population of Placid Lake may exist at a level lower than could be accounted for by cannibalism alone. McQueen (1969) found that 25-30% of the yearly production of *D. thomasi* could be cannibalized by the adults. However Peacock (1981) found that mortality of nauplii in Placid Lake was approximately 75-80%. The results from my enclosure experiments, although calculated survival rates were much lower, indicated that competition from other grazers and predation by *D. kenai* could significantly affect survival and these additional factors may account for the discrepancy in these reported mortality rates.
CHAPTER 2

Results from enclosure experiments (Chapter 1) indicated that \textit{D. kenai} could substantially influence the survival of \textit{D. thomasi} nauplii. The proposed mechanism for this influence was predation. Because \textit{D. kenai} has previously been assumed to be totally herbivorous, confirmation of its predatory ability was required to substantiate this hypothesis.

\textbf{Materials and methods}

\textbf{Experimental methods}

Experiments on the predation of \textit{D. kenai} on nauplii were conducted both in October, 1982 and May, 1983. All animals for the experiments were obtained from the University of British Columbia Research Forest. In October, the \textit{D. kenai} used were collected from Gwendoline Lake. Nauplii of \textit{D. thomasi} were collected from Eunice Lake and water for the experiments was also taken from Eunice Lake. In May, all the animals and water were collected from Placid Lake.

All feeding experiments were conducted in a controlled environment chamber set to 8 °C with a 16:8 h light:dark cycle to simulate spring light conditions unless otherwise specified. On the day of collection, 3.5 l lake water was filtered through a 54 \textmu m sieve into identical 4 l purple plastic containers. \textit{D. kenai} were pipetted into the experimental containers immediately after filtering was completed and allowed to equilibrate for 24 h. On the following day nauplii were individually pipetted into small formalin-free jars of filtered
lake water. Cyclopoid nauplii were always used unless otherwise specified. The contents of all the jars were then added to the experimental containers and the jars rinsed with filtered lake water within a total of about 15 minutes. The containers were then left 24 ± 2 hours. At the end of this time all the D. kenai were removed into small jars within 15 minutes using a 406 μm sieve. The water from each experimental container was filtered through a 54 μm sieve using a siphon and the remaining animals collected, added to the appropriate jar containing D. kenai and then immediately fixed using concentrated formalin. These samples were later counted under 50 X on a binocular dissecting microscope to determine the remaining number of nauplii. The gut contents of some D. kenai were examined by dissecting out the gut in a drop of water under a dissecting microscope. The gut was squashed under a coverslip and the contents examined.

**Experimental design**

Since the experiments were designed to provide information about possible interactions in lake conditions, all experiments were conducted with densities of animals which were naturally found at lake conditions. A duration of 24 h was chosen since a preliminary series of experiments indicated that a significant decrease did occur when D. kenai were added to experimental containers but that the duration of the experiment (24-96 h) did not have a significant effect on the number eaten. This lack of effect is probably due to keeping D. kenai in relatively small containers since there has been some evidence that the feeding
response may change with holding time for animals from the Research Forest lakes (Buckingham, 1978). No time shorter than 24 h was used since this duration allowed the containers to go through one complete light cycle. Experiments were always started between 1600 and 1800.

A set of experiments was conducted in October, 1982 to determine the functional response of *D. kenai*. Prey densities of 5, 10, 15, 25 and 50 nauplii/container (125, 250, 375, 625, and 1250 per 100 l) were chosen. A density of 375/100 l corresponds approximately to the naupliar density at the time the field experiments were set up. A density of 1250/100 l corresponds to the highest density found in the enclosure experiments. The predator density chosen was 1 per container (25/100 l) which was the approximate density used in the enclosure experiments. Each treatment was replicated 4 times. Four containers were set up containing 15 nauplii only to serve as controls for background mortality and counting error.

After I found that *D. kenai* did, in fact, prey on nauplii, I was concerned that they might trap their prey against a surface. *Neomysis* have been observed to do this (Johnston 1981, Johnston and Lasenby 1982) and *D. kenai* has been observed to repeatedly come up and hit the surface of the lake in calm water (Neill, pers. comm.). If *D. kenai* trapped their prey against a surface, their effect on the mortality of nauplii in small enclosures would be artificially inflated. In order to determine whether trapping occurred, an experiment was devised using cages made of NITEX netting (Fig. 12). The cages were designed to eliminate as much as possible the area available to
the *D. kenai* for entrapment by allowing an escape area for nauplii. These cages were constructed out of 471 µm mesh which was large enough to be easily permeable to nauplii but small enough that *D. kenai* were unable to pass through. This net size was tested beforehand and I found that while *D. kenai* could not pass through, both *D. thomasi* and *D. oregonensis* adults could and therefore I assumed that the smaller nauplii could also. Although the cages were constructed to minimally decrease the volume available to the *D. kenai*, some reduction in volume occurred (1-1.5 l). To control for this decrease in volume, similar-sized cages were constructed of 54 µm mesh. Nauplii were added to the cages in densities such that at the beginning of the experiment, the average number available to *D. kenai* was the same in cages of both large and small mesh, assuming an even distribution of nauplii.

It was also possible that *D. kenai* trapped against a water surface and not against container sides. In this case enclosure experiments would not overestimate the impact of predation. In order to test this hypothesis, both large and small mesh cages were divided into two groups: one completely submerged and one where the surface of the water was just below the top of the cage. Twenty experimental containers were set up. Five containers had large mesh cages completely submerged, 5 containers had small mesh cages completely submerged, 5 containers had large mesh cages with a water surface and the remaining 5 had small mesh cages with a water surface. In each of these 4 treatments, 1 container contained no *D. kenai* and was used as a control. Twenty-five nauplii were added to containers
with small mesh cages and 35 nauplii were added to containers with large mesh cages to correct for the difference in volume available to nauplii the two types of cages. All animals were added to the inside of the cages regardless of treatment.

A comparison was done between the feeding rate of *D. kenai* on calanoid and cyclopoid nauplii. In this experiment 16 experimental containers were set up: 8 with calanoid nauplii and 8 with cyclopoid nauplii. *D. kenai* were not added to 3 containers of each type. Twenty-five nauplii were added to each container. A comparison was also done on the effect of temperature on the predation rate of *D. kenai*. This experiment was set up in a similar manner to the previous one with only cyclopoid nauplii being used. One group was held at 8 °C while the other group was held at 16 °C.
Figure 12 Design of experimental cages.
Results

The determination of the functional response of *D. kenai* showed a highly significant linear regression (F=93.678, p < .01) with an equation of Y= (0.198 ± 0.062(SE))X - 0.514. An analysis of variance showed that the linear regression accounted for 72.8% of the total variation. The calculated regression equation is shown in Figure 13. There appeared to be no losses in controls associated with naupliar mortality or counting error.

The linear response of prey disappearance to prey density suggested that it was in fact predation that caused a decline in the prey number. To confirm this, the gut contents of ca. 25 *D. kenai* were examined and animal remains were found in 8% of the guts although the majority of the gut contents were phytoplankton.

When the results of the experiments designed to examine the effect of surfaces on predation rate were examined, there was a loss in controls associated with naupliar mortality, counting and handling error. In order to distinguish whether there were any additional losses associated with predation, an analysis of variance was performed on appropriate sets of controls and experimental treatments. If these proved significant, the results of each experimental container were subtracted from the mean of the appropriate controls and any further analysis was performed on the resultant data (number eaten). These results are shown in Table VI. An analysis of variance showed no significant difference in predation between *D. kenai* contained in small mesh cages and those contained in large mesh cages.
Figure 13 Functional response of *Diaptomus kenai* to naupliar densities.
This result gives no indication that *D. kenai* use surfaces to trap nauplii and thus the predation effect observed in the *in situ* experiments was probably not an artifact of enclosure. A comparison of predation rates of caged *D. kenai* with those of uncaged *D. kenai* conducted at similar densities also showed no significant difference, suggesting that the reduction in container volume did not affect the feeding rates of *D. kenai*.

Comparisons between predation rates on cyclopoid and calanoid nauplii and between different temperatures were made in a similar manner to those described above (controls and treatments compared and treatments subtracted from mean of controls) These results showed no significant difference in predation rates either on calanoid vs. cyclopoid nauplii (*F* = .29, *P* < .75) or between different temperatures (*F* = 1.23, *P* < .50). A comparison of results obtained in the spring to those obtained in the fall also showed no difference (*F* = 1.29, *P* < .50).

A comparison was also made between predation rates for females and those for males. To increase sample size and allow comparison between different prey densities, these results are expressed as proportion of nauplii eaten per predator per day. Since the functional response was determined to be linear, this procedure did not introduce bias. The mean proportion of nauplii consumed by females was 0.225 ± 0.105(SE, *n*=16) and the mean for males was 0.254 ± 0.137(SE, *n*=32). This comparison showed no difference in feeding rates between males and females (*F*=.224, *P* > .75).
Table VI The effect of surfaces on D. kenai predation on Diacyclops nauplii. A cage with 471 μm mesh represents the least surface available for entrapment. Numbers represent the number of nauplii eaten in 24 h.

<table>
<thead>
<tr>
<th>471 μm +water surface</th>
<th>471 μm +water surface</th>
<th>54 μm</th>
<th>54 μm</th>
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<td>9</td>
<td>9</td>
<td>2.7</td>
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<td>6.0</td>
<td>6.0</td>
<td>6.3</td>
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Discussion

*D. kenai* has been previously regarded as totally herbivorous in the coastal montane lakes around Vancouver (Olenick 1982), and Krause (in prep.) has found that they are capable of eating a wide range of size classes of phytoplankton. A recent study of the mouthparts of *D. kenai* (Chapman 1982) from the University of British Columbia Research Forest showed that *D. kenai* has mouthparts typical of those found for other *Diaptomus* species. Chapman suggested that *D. kenai* is likely to be usually a filter-feeder and capable of ingesting very small particles due to the density of the labral and labial setae. She also suggested that *D. kenai* may be incapable of capturing very large algal cells and stronger bodied animals since it lacks the robust armature of the maxilipeds found in *D. shoshone* but conceded they may be capable of capturing some larger algal cells and soft-bodied animals. Nevertheless, there has been some indication that *D. kenai* may be omnivorous. Gerritson (1980) has suggested that *D. kenai* may be a predator although he provides no evidence for his classification and he does not list it as an omnivore. A series of experiments by E. Krause (unpubl. data) showed that *D. kenai* seemed to produce extremely large mortality rates of calanoid nauplii over a relatively short period of time. This study has confirmed these suggestions. The functional response of *D. kenai* predation was found to be linear with a slope of 0.20. These experiments were done at extremely low densities when compared with other feeding studies (Table VII) which may account for the linear response. However, since this study was set up with densities that were
found in the lake and in the enclosures, this type of response probably occurs naturally. Other studies have also found a linear response when densities were low. Peacock (1981) found a linear response for *D. thomasi* feeding on *T. prasinus* copepodites and the majority of feeding studies on *Mesocyclops edax* done by Jamieson (1980b) showed a linear response. Ambler and Frost (1974) found that at low densities, the feeding response of the marine calanoid copepod *Tortanus discaudatus* did not differ significantly from a straight line.

The predation rate found in this study was approximately 0.20 at lake densities expressed as the proportion of nauplii eaten per predator per day. This rate is well within the feeding rates recorded for other studies. (See Table VII). It is higher than predation rates recorded for cyclopoid predators on nauplii but consistent with the lower end of the feeding rates recorded for calanoid predators. Most feeding studies with calanoid predators on nauplii have been done with marine zooplankton however the two predation rates recorded for freshwater calanoid copepods, *Epischura lacustris* and *D. kenai*, are consistent with these values.

In this study, there was no indication that temperature influenced the predation rates on nauplii. This result is surprising since Buckingham (1978) considered *D. kenai* a "cold water" species and found that their filtering rates on seston declined as temperature increased above 8 °C.

Calanoid and cyclopoid nauplii also seemed to be taken at the same rate. Lonsdale et al. (1979) found that *Acartia tonsa* showed a much lower predation rate on its own nauplii while
Table VII A comparison of predation rates of cyclopoid and calanoid copepods on copepod nauplii. All predation rates are expressed as proportion of nauplii eaten per predator per day. Where the response was linear, the range of values over which the rate was studied is shown. If the response was non-linear, the rate and density shown are those of maximum slope.

<table>
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<tr>
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<th>Predation Rate</th>
<th>Reference</th>
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<td>500</td>
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<td>Landry, 1978a</td>
</tr>
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<td>Acartia tonsa</td>
<td>A. tonsa (N1-3)</td>
<td>280</td>
<td>.06</td>
<td>Lonsdale et al. 1979 *</td>
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<tr>
<td></td>
<td>(N4-6)</td>
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<td>.03</td>
<td></td>
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<td>canadensis (N1-3)</td>
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<td>.16</td>
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<td>Diaptomus kenai</td>
<td>Diacyclops thomasi</td>
<td>1-1.5</td>
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<tr>
<td>Tortanus discaudatus</td>
<td>Calanus pacificus</td>
<td>N3</td>
<td>.55</td>
<td>Ambler and Frost 1974</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N5</td>
<td>.78</td>
<td></td>
</tr>
</tbody>
</table>

* - rates measured at one density only
Jamieson (1980b) found that *M. edax* preferred calanoid to cyclopoid nauplii. The similarity of predation rates at different temperatures and different prey types found in this study may be due to my inability to distinguish between treatments because of the large variability in the results. This variability is common in many studies of crustacean feeding (Buckingham 1978, Landry 1978, Jamieson 1980b, Peacock 1981) and may reflect physiological differences among individual animals.

The majority of studies on copepod predation have found that the predation rate is higher on smaller animals (McQueen 1969, Confer 1971, Ambler and Frost 1974, Wong 1980, Peacock 1981). From the point of view of the predator, the higher capture rate of small prey may be a result of requiring more individuals to make up their daily ration. From this standpoint it may be useful to look at predation rates as the proportion of dry weight consumed. When viewed in this way, the large predation rates of calanoid copepods in Table VII are easily explainable since most of the calanoid copepods listed there are larger than the cyclopoid copepods. However when the dynamics of the prey population are being examined, these considerations are interesting but irrelevant. From the prey's standpoint, it makes very little difference why the predator acts as it does. The sole consideration is that as an individual becomes larger, it has a smaller chance of being eaten.
GENERAL DISCUSSION

Food limitation and predation were considered to be potentially important in affecting the naupliar survival of Diacyclops thomasi. In situ enclosure experiments in Placid Lake using natural densities of zooplankton revealed that food limitation due to competition, interspecific predation by D. kenai and intraspecific predation by adult D. thomasi had strong negative effects on the survivorship of juvenile D. thomasi. Extrapolation of these results to Placid Lake, taking seasonal dynamics into consideration, suggested that cannibalism was the major mortality agent over the whole season although both interspecific predation by D. kenai and competition from the grazing assemblage exerted a substantial effect at the beginning and end of the reproductive period, respectively. With these results, it is now possible to construct a scenario for the shift in community structure in Eunice Lake (Fig 1).

Cutthroat trout were introduced into Eunice Lake in 1974 and 1975 (Hume 1978) and have since increased to the point where they can now be considered to be at their "carrying capacity" (J. Andrew, pers. comm.). Several years after the trout were introduced, D. kenai began to decrease until they are now rare in the lake. This decline is probably due to trout predation since trout are known to prey on D. kenai, particularly during the winter and spring (Hume 1978). The D. kenai population would be particularly vulnerable to predation since it is univoltine. In 1978, after D. kenai had declined for several years, D. thomasi began to appear in regular zooplankton samples
in consistent but low numbers during the late fall and early winter. Before their decline, D. kenai in Eunice Lake had occurred in much higher densities than in Placid Lake and they remained in the water column for a much longer period of time. These observations, combined with the knowledge that D. kenai are capable of substantially influencing naupliar survival, suggest that D. kenai had limited the population of D. thomasi in Eunice Lake to the point where it was extremely rare in regular zooplankton samples. In 1979, upstream Gwendoline Lake was fertilized and this resulted in an increase in the biomass of Daphnia rosea in Eunice Lake during that summer. D. thomasi continued to increase in number in Eunice Lake while D. kenai continued to decline. The winter of 1980-1981 was warm and the lake never froze. D. thomasi increase in number until it dominated the community. D. kenai disappeared almost entirely from the lake and the grazing assemblage increased in density late in the spring and was greatly reduced in number compared to previous years.

One possible explanation for these events is as follows. The warm winter with open water allowed wind to mix the lake well, releasing into the water column nutrients from the sediment. The level of nutrients in the sediment had probably been increased by the fertilization which had occurred fifteen months previously in an upstream lake and therefore the nutrients released into the water column were probably also increased. D. thomasi is known to increase its clutch size and lengthen its reproductive period in response to fertilization (Peacock 1981). Increased naupliar production combined with
increased survival due to reduced interspecific predation from *D. kenai* and reduced competition from other grazers were probably responsible for the large increase in *D. thomasi*. Cyclopoid copepod predators have been found to preferentially attack smaller prey (McQueen 1969, Brandl and Fernando 1975, 1978, Jamieson 1980b). By the time the Cladocera began their spring increase, there may have been enough *Diacyclops* copepodites to have a significant impact on the smaller neonate cladocerans. Although this effect cannot be confirmed, the idea is supported by the shift in the dominant cladoceran from *Daphnia rosea* to the relatively inedible *Holopedium gibberum*.

The combination of a warm winter and cool spring with increased nutrient levels probably hastened what would have been a gradual increase in *D. thomasi* in the lake, although it probably would have equilibrated at a much lower level if the spring had not been cool. The present configuration appears relatively stable and should persist.

Prior to 1979, it appeared that *D. thomasi* in Eunice lake was limited by predation from *D. kenai*. Some possible evidence for population limitation by *D. kenai* has also been found in Lake Findley, Washington. Pederson and Litt (1976), in examining the congeneric occurrence of *Diaptomus franciscanus* and *D. kenai*, found large year to year variation in the abundance of *D. franciscanus* nauplii but relatively little variation in the abundance of adults. They offered no explanation for this phenomenon but, after examining the life cycles of both organisms, concluded that they did not compete since they were temporally separated. However, examination of
their life cycles reveals that *D. kenai* adults and copepodites reach peak densities during the same period of time as *D. franciscanus* nauplii are present. One explanation for the variation in the abundance of nauplii is limitation by predation from *D. kenai*.

The current population of *D. thomasi* in Eunice Lake is probably almost entirely limited by cannibalism and may have actually increased its carrying capacity by the large incidence of cannibalism. Fox (1975) suggested that low food availability may increase rates of cannibalism. Polis (1981) suggested that cannibalism can increase the population carrying capacity by making use of immature animals to transform food resources unavailable to the adult. The required conditions for this to occur are: (1) immature animals feed on resources inaccessible to the adults; (2) adults feed on immature animals and thus indirectly incorporate previously unavailable resources and (3) food is limiting to the adult population (Polis 1981). These conditions seem to hold in Eunice Lake. McQueen (1969) found that adults were completely carnivorous while nauplii are known to be herbivorous.

Eunice Lake thus appears to have shifted from one "domain of attraction" to another. In the former community configuration *D. thomasi* appeared to be limited by interspecific predation by *D. kenai*. The change in configuration was mediated by a decrease in predator density, probably caused by vertebrate predation and unusual weather conditions which delayed competition from grazers and allowed for an increase in the fertility of *D. thomasi*. In the present configuration
D. thomasi appears to be limited by intraspecific predation.
REFERENCES


Hay, T. 1981. Responses of zooplankton communities in four small lakes to change in predation patterns. BSc Thesis, University of British Columbia


APPENDIX A. SET UP OF ENCLOSURES

Zooplankton

The count data of the enclosures were examined to confirm that proper set-up of the experimental conditions had been achieved. Comparisons were done between those enclosures to which a particular treatment had been added (e.g. *D. thomasi*) and those to which it had not. Comparisons with the lake were made at the beginning of the experimental period between the initial average density of all enclosures to which the treatment in question had been added and the stocking density. The effect of enclosure was examined by comparing the behaviour of zooplankton populations in the upper 2 m of the lake with those in the enclosure which contained the same conditions as those of the lake (i.e. fertilizer absent and *D. thomasi*, *D. kenai* and the grazing assemblage present). This comparison was made at the middle and end of the experimental period. All comparisons were made using numerical densities since enclosure samples were too small to allow an accurate measurement of length for biomass calculations. These comparisons are summarized in Table V.

*Diacyclops thomasi*

Analyses of variance of the difference in numbers of *D. thomasi* adults between treatments containing *D. thomasi* and those without showed an extremely significant difference (*P << .001* in all but one case, *P < .005* in the fifth sampling period)
that was maintained throughout the experimental period. When a 2-way analysis of variance was done using treatment and time as the 2 factors, the results showed an extremely significant effect of treatment (P << .001) but insignificant effects of either time or the interaction between treatment and time. This result is to be expected when dealing with animals with a life cycle longer than the experimental period. When compared to lake data, the densities of adult *D. thomasi* in enclosures were 25% lower at set-up and this difference increased to 50% as numbers in the lake rose. There appeared to be mortality associated with handling since the numbers of *D. thomasi* in the bags decreased after the first sampling period and thereafter held constant. Since the increase in the lake was associated with the breaking of diapause and entry into the water column of overwintering animals, the increasing difference between the lake and the enclosures is expected.

**Diaptomus kenai**

No statistical analyses were done on the numbers of *D. kenai* captured since they occurred in very low densities in the enclosures. If perfect capture efficiency is assumed, only 3 *D. kenai* could be expected to be caught in each sample. In fact, capture efficiency is much less than this since *D. kenai* are strong swimmers. However, *D. kenai* was captured at some time during the experiment from every enclosure to which it had been added and never captured from those to which it had not been added. Visual inspection at each sampling period assured
that *D. kenai* were still present. Replicate sampling during the last sampling period gave an estimate of .07 /l compared to .22 /l which were originally added.

**Grazing assemblage**

The grazing biomass of both the lake and the enclosures was almost entirely made up of the three species: *Diaptomus oregonensis*, *Daphnia rosea* and *Holopedium gibberum*. These species were examined in detail. *Bosmina longirostris*, *Ceriodaphnia quadrangula* and *Polyphemus pediculus* were found infrequently. *Bosmina* seemed to occur both in enclosures with and without grazers whereas *Ceriodaphnia* and *Polyphemus* occurred more in enclosures with grazers. The wide-spread, albeit low density of *Bosmina* is probably due to its small size. Because of its size, it is more likely to be picked up in a pipette and remain undetected and loose eggs are more likely to pass through the nauplius sieve.

**Diaptomus oregonensis**

*D. oregonensis* showed a similar pattern to that of *D. thomasi*. Analyses of variance showed significant differences (*P << .001* except for sampling period 5 where *P < .005*) between treatments containing the grazing assemblage and those without for the duration of the experiment. A two-way analysis of variance showed significant effects of both time, treatment (*P << .001*) and the interaction term (*P < .01*) but the
F of the treatment term was 15 X as large as that of time (Ftrt = 168.16, Ftime = 10.24) indicating that the treatment effect was much larger than that of time. When compared to lake data, D. oregonensis were 80% lower in density in the enclosures at the beginning of the experimental period and were much more variable in density. In the middle of the sampling period, densities were approximately 50% of those in the lake. However at the end of the experiment, densities in the enclosures were higher since most D. oregonensis in the lake had moved lower in the water column and numerical densities in the lake had also decreased.

Daphnia rosea

Daphnia also showed consistent significant differences between treatments with grazers and those without grazers for the entire experimental period although the significance of the differences was in general not so great (P < .001 in 3 cases, P < .01 in 3 cases). A two-way analysis of variance again showed significant effect of treatment, time and the interaction term although the interaction was an order of magnitude smaller than the other two terms (Ftrt = 111.94 (P < .001), Ftime = 30.33 (P < .001), Ftxt = 3.42 (P < .01)). The significance of time is to be expected since the enclosures were set up during the spring growth phase. The Daphnia in the enclosures showed a steady increase in number during the experimental period. Those in the lake also showed an increase although numbers in the lake peaked during the middle of the experimental period.
rather than at the end. The density of Daphnia was 33% lower in the enclosures after set-up and the magnitude of this difference increased to 90% with recruitment from overwintering eggs in the lake during the middle of the experimental period but became equal at the end of the experimental period.

Holopedium gibberum

Holopedium behaved in a fairly similar manner to Daphnia. There were consistent differences between treatments with and without grazers during the course of the experiment. These were once again less significant than those shown by the copepods (P < .001 in 4 cases, P < .025 in 1 case, P < .05 in 1 case). A two-way analysis of variance showed significant effects of treatment, time and the interaction term, all with P < .001, although the treatment effect was again the largest. The Holopedium showed a peak of abundance at the middle of the experimental period. The Holopedium in the lake also showed this pattern. Densities in the lake were 25% higher than those in the enclosures after set-up but became almost equal at the peak and were actually 30% higher than lake density at the end.

Nauplii

The densities of nauplii were examined at the first sampling period to check setup densities and check for differences between treatments. No differences were found between those treatments without adult D. thomasi and those with
(ones where nauplii could have theoretically been recruited). In contrast to the other zooplankton added to the enclosures, the average density of nauplii in enclosures was not significantly different from the stocking density (i.e. lake density) \((z = -0.43, p = 0.33)\). Approximately 50% of the nauplii were cyclopoid \((D. \text{thomasi})\) and the rest were calanoid \((D. \text{oregonensis})\).

**Phytoplankton**

**Fertilizer**

The effect of fertilizer on the phytoplankton in the enclosures was estimated by measuring the amount of chlorophyll \(a\). This estimate of phytoplankton abundance was supplemented by counts of phytoplankton size classes for the second two experimental periods, since this time was considered to be critical for naupliar growth. The results of the first sampling period showed all treatments to be virtually identical in live chlorophyll \(a\), phaeophytin \(a\) and total chlorophyll \(a\). This is exactly what was expected since the samples were taken immediately after the bags had been filled and before the phytoplankton had a chance to respond to the fertilizer. Live chlorophyll \(a\) has previously been used as a measure of available food for zooplankton (Marmorek 1983) since phaeophytin \(a\) can consist of degraded or digested chlorophyll \(a\) (Daley 1973, Daley and Brown 1973). In this experiment however, the density of grazers was low and it seems likely that most of the phaeophytin
measured was degraded rather than digested. This is especially true for those cases where no grazers were added to the enclosures. Some of the largest increases in phaeophytin occurred in enclosures in which only nauplii were present. These results suggest that fertilization caused the phytoplankton to grow rapidly during the first few days and then maintain a fairly high biomass but grow at a slow rate with the majority of the cells being senescent. Since phaeophytin in this case was not digested and was available as food, total chlorophyll would probably be a better measure of food availability. The greatest correlation was also found between total chlorophyll and total algal biomass (r = .76). This conclusion is supported by the examination of the phytoplankton sizes classes (Table VIII). Analyses of variance showed a significant difference (P < .005) between fertilized and unfertilized enclosures in the 2-5 μm, 5-9 μm, 9-13 μm and 13-18 μm classes in the second sampling period. In the third sampling period, the same analysis showed a significant difference in the abundances of the same size classes (P < .05 in 2-5 μm, P < .001 in others mentioned above), although there was no significant difference in the live chlorophyll. Total chlorophyll would not be an effective measure of food availability if the majority of the increase in phytoplankton biomass in fertilized enclosures was due to an increase in inedible algae. This did not seem to be the case. The differences in large inedible algae between fertilized and unfertilized enclosures were not significant in the samples
examined \( (F < 1) \). Visual inspection of data from a fertilized and an unfertilized enclosure seemed to indicate that this result held until the end of the experimental period. Analyses of variance showed significant differences in live chlorophyll in the second \( (F = 136.4, P << .001) \) and sixth \( (F = 6.4, P < .025) \) sampling periods. However, there were consistent and significant \( (P < .025) \) differences between the amount of phaeophytin and total chlorophyll present in fertilized and unfertilized treatments from the second sampling period on (Table IX).

In summary, fertilizer significantly increased total chlorophyll and phaeophytin from the second sampling period on. Live chlorophyll was significantly increased only during the second and sixth sampling periods. Phytoplankton biomass was significantly increased in the second and third sampling periods in the size range 2-18 \( \mu m \).

Grazing assemblage

The phytoplankton data can also be examined to determine if grazers had a significant impact on the food available. Since the hypothesis was that the grazing assemblage might compete with nauplii for food, it is important to show that there was a difference in available food in enclosures with grazers and those without. When the total chlorophyll content was examined (Table X), two way analyses of variance, which pools all treatments containing the factor of interest, showed that in the second sampling period, fertilizer increased the total
Table VIII  Effect of fertilizer on chlorophyll content. Chlorophyll content is expressed as µg/l.

<table>
<thead>
<tr>
<th>Sampling Period</th>
<th>Live Chlorophyll No Fertilizer</th>
<th>Live Chlorophyll No Fertilizer</th>
<th>Phaeophytin No Fertilizer</th>
<th>Phaeophytin No Fertilizer</th>
<th>Total Chlorophyll No Fertilizer</th>
<th>Total Chlorophyll No Fertilizer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.836</td>
<td>0.844</td>
<td>0.511</td>
<td>0.493</td>
<td>1.336</td>
<td>1.337</td>
</tr>
<tr>
<td>2</td>
<td>3.367</td>
<td>0.969</td>
<td>1.413</td>
<td>0.484</td>
<td>4.675</td>
<td>1.453</td>
</tr>
<tr>
<td>3</td>
<td>1.004</td>
<td>0.538</td>
<td>2.046</td>
<td>0.433</td>
<td>2.962</td>
<td>0.972</td>
</tr>
<tr>
<td>4</td>
<td>0.910</td>
<td>0.411</td>
<td>1.574</td>
<td>0.323</td>
<td>2.323</td>
<td>0.734</td>
</tr>
<tr>
<td>5</td>
<td>0.928</td>
<td>0.185</td>
<td>2.328</td>
<td>0.618</td>
<td>3.035</td>
<td>0.803</td>
</tr>
<tr>
<td>6</td>
<td>2.168</td>
<td>0.356</td>
<td>2.678</td>
<td>0.606</td>
<td>4.097</td>
<td>0.948</td>
</tr>
</tbody>
</table>
Table IX  Effect of fertilizer on phytoplankton size classes. All biomasses are expressed as μg/l.

<table>
<thead>
<tr>
<th>Size classes</th>
<th>Sampling Period 2</th>
<th>Sampling Period 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fertilizer</td>
<td>No Fertilizer</td>
</tr>
<tr>
<td>&lt; 2 μm</td>
<td>7.6</td>
<td>9.3</td>
</tr>
<tr>
<td>2 - 5 μm</td>
<td>4.7</td>
<td>15.2</td>
</tr>
<tr>
<td>5 - 9 μm</td>
<td>40.6</td>
<td>79.0</td>
</tr>
<tr>
<td>9 - 13 μm</td>
<td>43.3</td>
<td>106.8</td>
</tr>
<tr>
<td>13 - 18 μm</td>
<td>23.3</td>
<td>60.9</td>
</tr>
<tr>
<td>&gt; 18 μm</td>
<td>12.8</td>
<td>24.1</td>
</tr>
</tbody>
</table>
chlorophyll ($F = 148.8$, $P < .001$). The effect of fertilizer continued to be strong until the end of the experimental period ($P < .001$ except sampling period 4 where $P < .005$), however grazers significantly decreased the total chlorophyll during the third sampling period ($F = 7.6$, $P < .025$) and this effect also continued to the end of the experiment. During the fifth sampling period, the interaction between fertilizer and grazers became significant ($F = 8.0$, $P < .025$) and the interaction effect increased during the last sampling period ($F = 17.4$, $P < .005$).

Examination of phytoplankton size classes (Table XI) showed that fertilizer significantly increased size classes 5-9 µm ($F = 65.7$, $P < .001$) 9-13 µm ($F = 22.4$, $P < .001$) and 13-18 µm ($F = 11.0$, $P < .005$). The presence of grazers significantly decreased size classes 5-9 µm ($F = 61.1$, $P < .001$), 9-13 µm ($F = 10.9$, $P < .005$) and the interaction between fertilizer and grazers had a significant effect on the size classes 5-9 µm ($F = 50.5$, $P < .001$).
Table X Effect of fertilizer and grazers on total chlorophyll content. Chlorophyll is shown as μg/l.

<table>
<thead>
<tr>
<th>Sampling Period</th>
<th>No Fertilizer or Grazers</th>
<th>Fertilizer</th>
<th>Grazers</th>
<th>Fertilizer and Grazers</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.374</td>
<td>1.394</td>
<td>1.299</td>
<td>1.278</td>
</tr>
<tr>
<td>2</td>
<td>1.535</td>
<td>5.197</td>
<td>1.370</td>
<td>4.153</td>
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<td>1.245</td>
<td>3.402</td>
<td>0.698</td>
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<tr>
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<td>1.021</td>
<td>3.129</td>
<td>0.447</td>
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<td>0.931</td>
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<td>6</td>
<td>0.842</td>
<td>5.870</td>
<td>1.054</td>
<td>2.323</td>
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</table>
Table XI Effect of fertilizer and grazers on phytoplankton size classes. All biomasses are expressed as μg/l.

<table>
<thead>
<tr>
<th>Size Classes</th>
<th>No Fertilizer or Grazers</th>
<th>Fertilizer</th>
<th>Grazers</th>
<th>Fertilizer and Grazers</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 2 μm</td>
<td>5.8</td>
<td>6.3</td>
<td>6.3</td>
<td>8.8</td>
</tr>
<tr>
<td>2 - 5 μm</td>
<td>5.8</td>
<td>17.8</td>
<td>3.0</td>
<td>14.5</td>
</tr>
<tr>
<td>5 - 9 μm</td>
<td>39.0</td>
<td>114.5</td>
<td>15.8</td>
<td>52.0</td>
</tr>
<tr>
<td>9 - 13 μm</td>
<td>37.0</td>
<td>145.3</td>
<td>8.8</td>
<td>69.0</td>
</tr>
<tr>
<td>13 - 18 μm</td>
<td>20.5</td>
<td>75.3</td>
<td>4.3</td>
<td>80.8</td>
</tr>
<tr>
<td>&gt; 18 μm</td>
<td>5.0</td>
<td>15.0</td>
<td>15.0</td>
<td>11.3</td>
</tr>
</tbody>
</table>
APPENDIX B. EVALUATION OF METHODS FOR CALCULATION OF SURVIVORSHIP

Since the analysis of survivorship was critical to the enclosure experiments, methods of survivorship calculation were investigated to determine their behaviour and reliability.

Duration of naupliar stages

Estimates of the duration of the naupliar stages are critical to the calculation of survival estimates. The duration of stages is the link between static estimates of age composition in a population and its dynamics.

The effect of various factors on naupliar development has been well reported in the literature. Most of these reports investigated the effect of temperature on developmental rates (Auvrey and Dussart 1966, Spindler 1971, Munro 1974, Landry 1975, George 1976, Jacobs and Bowhuis 1979, Sarvala 1979, Jamieson 1980a, Vijverberg 1980). Increasing temperature often rapidly increases the developmental rate. There is some debate in the literature about whether this increase is proportional throughout the life history (Landry 1975) or whether these increases are disproportionate (Munro 1974). Some attention has also been given to the quality of diet (Auvrey and Dussart 1966, Smyly 1970, Whitehorse and Lewis 1973, Jamieson 1980a) and to the effect of light (Auvrey and Dussart 1966, Spindler 1971). Increasing light intensity and duration appeared to increase the developmental rate (Spindler 1971). Increasing food quality also seemed to increase the developmental rate. Some species
seemed more sensitive than others (Auvrey and Dussart 1966) and mixtures of food also seemed to produce better results. Food quantity has also been found to increase developmental rate of copepods. Weglenska (1971) found that increasing concentrations of natural seston from a eutrophic lake significantly increased the developmental rate of *Eudiaptomus graciloides*. Klekowski and Shushkina (1966), working with different concentrations of a single food source found that although there was a slight increase, *Mesocyclops albidus* was relatively insensitive to differences in food concentration over the range tested.

Most of these factors are of little significance in estimating developmental rates in my enclosures. The effect of temperature is important only when comparing estimated durations with previously reported ones. However, if quantity of food significantly influences development rates, this could influence the results of enclosures with fertilizer.

Estimates of the durations of the developmental stages of *D. thomasi* in the enclosures were initially made using the method outlined by Rigler and Cooley (1974). Because copepods reproduce over a discrete time interval, graphs of the abundance of each developmental stage vs time show distinct peaks in abundance. The method of Rigler and Cooley involves setting the difference between the peaks to half the duration of the two instars involved. The initial stage of this calculation involved examining juvenile copepods from those enclosures without adult *Diacyclops* to find when these peaks in abundance
occurred. Because of the uncertainty surrounding the effects of food quantity on developmental rate, enclosures with and without fertilizer were examined separately. The means of enclosures within each of these groups were pooled after no significant difference was found between them (Table XII). The overall mean was used for further calculations.

One of the problems with Rigler and Cooley's method is that one of the variables must always be estimated since the number of unknowns is always one greater than the number of equations. When this was done, there was always one duration which ended up very low. The initial estimates obtained from this method are shown in Table XII. These, of course, failed when used to calculate survivorship. Comparisons with other estimates for developmental rates including those made by Peacock (1981) for D. thomasi and Tropocyclops prasinus in the same lake showed that the estimate for the duration of stages n1-3 was badly underestimated. In order to obtain a more reasonable value for the durations, a combination of values obtained by Peacock (1981) and those obtained from the enclosures were fitted using simulation modelling to the results from enclosures containing only nauplii so that the peaks corresponded to those found in the enclosures. These fitted values are also shown in Table XII. The difference between the fitted durations and the calculated durations is due to the short persistence time of each stage and the infrequent sampling relative to the durations. The difference between fitted values and previously calculated values are probably due to difference in temperature.
Table XII Results for estimation of stage duration of immature *D. thomasi* in enclosures

a) Appearance of Peak in Abundance Curves

<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>Unfertilized (day in experiment) (± S.E.)</th>
<th>Fertilized (day in experiment) (± S.E.)</th>
<th>Pooled (day in experiment) (± S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>nauplius 1-3</td>
<td>1.0 ± 2.0</td>
<td>0.8 ± 1.8</td>
<td>0.9</td>
</tr>
<tr>
<td>nauplius 4-6</td>
<td>5.0 ± 5.8</td>
<td>6.8 ± 1.8</td>
<td>6</td>
</tr>
<tr>
<td>copepodite 1</td>
<td>13.3 ± 2.3</td>
<td>11.2 ± 1.8</td>
<td>12</td>
</tr>
<tr>
<td>copepodite 2</td>
<td>17.2 ± 2.3</td>
<td>12.8 ± 3.4</td>
<td>14.5</td>
</tr>
<tr>
<td>copepodite 3-4</td>
<td>18.7 ± 2.3</td>
<td>18.0 ± 2.0</td>
<td>18.3</td>
</tr>
</tbody>
</table>

b) Calculated Durations

<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>Calculated **</th>
<th>Fitted</th>
<th><em>Diacyclops thomasi</em></th>
<th><em>Tropocyclops prasinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>nauplius 1-3</td>
<td>1</td>
<td>5</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>nauplius 4-6</td>
<td>9</td>
<td>7</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>copepodite 1</td>
<td>3</td>
<td>2</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>copepodite 2</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>copepodite 3-4</td>
<td>5</td>
<td>-</td>
<td>7</td>
<td>6</td>
</tr>
</tbody>
</table>

As the temperature during the experiment varied frequently and was for a large portion of the time later in the experiment much higher (Appendix C) than those at which Peacock's work was done (13 - 18 °C), the results are reasonable. It is worthy of note that neither my enclosures nor previous estimates by Peacock (1981) give any indication that food quantity had a significant effect on the naupliar duration of *D. thomasi*.

**Analysis of naupliar survival**

Methods to analyse the survival of zooplankton seem to be divided into two categories: 1. those for populations with continuous recruitment (usually Cladocera) and 2. those for populations which reproduce in discrete cohorts (usually Copepoda). The method used for one category is in general unsuitable for the other. Continuous recruitment methods of analysis often assume a stable age structure, or at least one which does not change rapidly (Edmondson 1968, Argentesi et al. 1974, Seitz 1979, Taylor and Slatkin 1981). Many of the models also assume constant mortality rates throughout the life history of the organism being investigated (Edmondson 1968, Taylor and Slatkin 1981). On the other hand, most work which has been done with copepods with discrete generations has used the technique of integrating under the curve of abundance vs time as outlined in Southwood (1966). Both Rigler and Cooley (1974) and Gehrs and Robertson (1975) have introduced this technique in the zooplankton literature and several others have since used it to estimate survivorship (Confer and Cooley 1977, Neill and
Peacock 1980, Peacock 1981). Since in the majority of cases in the enclosure experiments, continuous recruitment was not taking place and since continuous recruitment methods often contained untenable assumptions (i.e. constant mortality rate), the discrete generation method of analysis was examined.

This method is outlined by Rigler and Cooley (1974) and Gehrs and Robertson (1975). In this method, the total number of animals occurring in each instar for the whole generation is calculated using the trapezoidal method for integrating under a curve and corrected for the duration of each instar. The equation for this method is given in Gehrs and Robertson (1975) and is listed below.

\[
N = \frac{1}{2} \sum_{i=x=j}^{k} \left( \frac{(1 + \frac{1}{2})}{W/D} \right) \cdot \frac{W}{D}
\]

Where

- \( l \) = number of individuals alive
- \( i \) = instar designation
- \( x \) = collection designation
- \( j \) = first collection prior to the appearance of instar \( i \)
- \( k \) = collection following last appearance of instar \( i \)
- \( W \) = interval in days between collection \( x \) and \( x+1 \)
- \( D \) = duration of instar \( i \)
- \( N \) = number of individuals of instar \( i \) produced in the interval \( x=j \) to \( x=k \), that is the number of individuals of instar \( i \) produced in a particular generation.
A geometric illustration of this method of integration is shown in Fig 14. There are some inherent problems with this approach which are associated with numerical integration. In the case shown in Fig 14a, this method estimates the area well. The curve is relatively gentle and sampling interval short in comparison with the length of time the instar persists. However if the sampling interval is relatively long in comparison with the persistence time of the instar or if the peak is missed during sampling, the estimation becomes much poorer (See Fig 14b,c & d). The consequences of this behaviour when evaluating the survivorship of a population through a number of instars can be profound if the instars do not have peaks exactly in phase with the sampling times. This effect is particularly important if the persistence of each instar is short. The effect of the duration of the instars can either damp or accentuate this phenomenon depending on the relative magnitude of the duration and the sampling interval. If the sampling interval is small relative to the duration, the error is damped; when the sampling interval is large, the error is accentuated. If instar durations are of unequal length, the chances of sampling exactly on the peak are diminished. The error of the survivorship estimate then becomes greater due to varying differences in the relative magnitudes of the sampling interval and the duration.

When the equation was used with simulated field conditions, I found it to be quite accurate. The accuracy of the equation increased with decreasing sample width \((W)\), however the \(x, x+1\)
Figure 14 Graphical representation of Gehrs and Robertsons method of survivorship calculation. The total number in each stage (only one shown here) is calculated by numerically integrating under the curve using contiguous trapezoids. Each trapezoid has an area of \((W, x, x+1)(1 + 1)/2\). In this example, the duration of the stages is assumed to be one and thus drop out of the calculation. The sampling interval is represented by \(W\). Lx represents the abundance a sampling period \(x, x+1\) of x.

a) Integration under a gentle curve with a relatively short sampling period.

b) Integration under a gentle curve where the peak is missed.

c) Integration with a long sampling interval.

d) Integration with a long sampling interval where the peak is missed.
error was only 1% even when W was twice as long as the shortest duration (and slightly longer than all the others). The exception to this was when the W coincided with the length of several successive durations. In this case, the accuracy increased. The accuracy of the equation dropped dramatically as the length of time each stage persisted decreased. If the fastest stage persisted in the water for more than 20 days, sampling at weekly intervals gave an error of < 1%. However if the stage persisted only 12 days, the error was 8% and if the same stage persisted only 8 days the error was 190%.

This result has severe consequences for examining the survival of nauplii in enclosures. Anytime the effect of cannibalism on nauplii needs to be separated out, nauplii as a group with no adults present will necessarily persist in the water column for a shorter time than in situations where there is recruitment. Additional nauplii cannot be distinguished unless the adults do not produce any eggs until the original nauplii have developed to the next stage. This means that if integration is performed under the entire curve, the calculation of background mortality of other factors will be less accurate than that for mortality associated with presence of adults, if the complete development of a cohort is examined. Unfortunately this means that a much longer time span is required for the experiment which in turn means that the development of the cohort where the adults are present will in situ be subject to different environmental conditions and it will be impossible to separate this effect from the effect of
adults. Enclosure experiments also have the added problem that the whole area under the curve cannot be integrated for the first stage because adding nauplii to enclosures essentially sets the peak at the beginning of the experiment. This problem can be adjusted by halving the developmental rate of the first instar and assuming an even age distribution within the first instar.

In simulations of enclosure conditions, I found that survival rates were consistently underestimated once the duration of the first instar was corrected. In spite of its lack of accuracy however, the technique was fairly robust to errors in the data. A Monte Carlo simulation to determine the effect of variation in data drawn from a log-normal distribution on the calculation of survival rates showed that a 40\% coefficient of variation in the data was reduced to an 8\% variation in the daily survival rate.

The effect of egg production on the calculated survival rates was examined by integrating under the same region of the curve as was used in the other simulations, i.e. ignoring later nauplii production by the adults. This technique overestimated survivorship for stages with short durations and underestimated it for stages with long durations because of the difference in length of the developmental stages. This effect is more noticeable when large numbers of nauplii are produced. In order to understand the reason for this, it is helpful to think of an analogy. Imagine a freeway which goes from the centre of town to the suburbs. Suppose everyone works in the center of
town and lives in the suburbs so that during the evening rush hour, the number of cars getting on the freeway in the suburbs is negligible. Now suppose one wants to estimate the number of cars getting off at each exit and one decides to do this by flying over the freeway and taking an aerial photograph at several different points. If the traffic is moving at the same speed at all points along the way, this method will give a good estimate of the "mortality". However, if one of the photographs is taken where an accident has occurred and traffic is backed up, the number of cars estimated to have left the freeway at the previous exit will be underestimated (i.e. those which stayed on will be overestimated) but subsequent "mortality" will be overestimated. If the aerial photograph was taken of a large area, and the accident significantly slowed the traffic these effects would increase with the volume of traffic.

Because of the difficulties with this method, I investigated another approach which involved modelling the dynamics of immature *D. thomasi* in the enclosures and using a least squares method of curve fitting to estimate survival parameters. The curves of abundance of immature *D. thomasi* vs time were fit to simulated curves using the routine N2SNO (Moore 1981) for non-linear parameter estimation. This method uses a numerical approximation of the derivative and has three methods for determining convergence of the fitted curve. Variability convergence was used in these calculations. This method also has some problems associated with the technique. Least squares
is known to be susceptible to outliers (Moore 1981). As with other models, the accuracy of the results will be dependent on the structure of the model and can also be sensitive to the initial conditions. The initial conditions of the model were fitted by examining the simplest conditions (i.e. those enclosures with nauplii alone) and adjusting the set-up conditions so that negative mortality was minimized. Negative mortality (spontaneous generation) is clearly impossible and the presence of this phenomenon indicates a deficiency in the model. One of the most obvious and easily adjustable areas for this deficiency to occur is in the set-up conditions. Although initial number in each stage were known, the age (rather than stage) distribution was unknown and had to be estimated. It is these estimates which were adjusted to minimize negative mortality. In most cases, these changes did not affect the relative results. A graphical representation of the fit obtained is shown in Figure 15. When the initial conditions were tested by fitting model-generated data, I found that the technique in fact underestimated copepodite survival. The values were not adjusted further since adjustment of conditions so the technique was accurate for model-generated data caused negative mortality in the real data, probably due to some unknown deficiency in the model. Since it is more important that survival rates within the experiment be comparable, this underestimation should not significantly affect the ranking of mortality factors. The precision of the curve fitting was also tested by fitting curves to model-generated data which had
been drawn from a log-normal distribution with a coefficient of variation of 40%. This procedure showed that this variation was reduced to 8% variation in daily survival rate. The effect of a 40% variation in the data (assuming a log-normal distribution) on survivorship curves is shown in Fig 16.

There was also a problem with this technique with enclosures containing adult *Diacyclops*. Since the water temperature fluctuated and was considerably warmer towards the end of the experimental period, the duration of developmental stages became shorter. This is reflected in the progressively larger difference between values recorded by Peacock (1981) and values from my enclosures (Table XII). Unfortunately this increase in temperature also caused nauplii which hatched later in the experiment to develop faster than those at the beginning of the experiment - those for which the durations were calculated. The change in developmental rate over time was not incorporated in the model since I felt that the additional assumptions which would have been made and the extra parameters needed would not have improved the accuracy. The probable effect of this increase in temperature is underestimation of the survival of the younger naupliar stages and overestimation of the survival of the later naupliar stages. As with the trapezoidal method of integration, this effect will become more severe as more nauplii are added to the system. This effect can be more easily understood by again referring to the freeway analogy. Consider the same freeway and use the same technique for estimation of "mortality". This time however, the freeway
Figure 15 Graphical representation of fit obtained from curve fitting procedure.

——— estimated abundance

_____ actual abundance
Figure 16 Graphical representation of error in survivorship curves. Each curve was generated from a model drawing data from a lognormal random distribution with a coefficient of variation of 40% (variance of 0.4). The figure shows the approximate amount of variation expected in calculated survivorship curves with the variation found in the data.
has been updated to a system of express lanes and feeder lanes for a certain distance. One also has the additional information of the posted speed limit. It is well known that the posted speed limit has very little to do with the actual speed, particularly in the express lanes. Using this technique one will underestimate the number of cars going through the express lanes because they are moving faster. However, when the data are examined at a later point where there are no express lanes, one will imagine that fewer cars left the freeway than actually did because some of the cars missed while they were in the express lanes will show up.
APPENDIX C.  TEMPERATURE AND PRECIPITATION DURING THE EXPERIMENTAL PERIOD (MAY-JUNE, 1982)
Figure 17 Temperature and precipitation during the experimental period (May-June, 1982). Water temperature of Placid Lake is marked when it was taken.

- S  water temperature at the surface.
- B  water temperature 1 m below surface.
- ------ daily maximum temperature
- ----- daily minimum temperature
- --- total daily precipitation
APPENDIX D. RESULTS OF SURVIVORSHIP CALCULATIONS
Figure 18 Survivorship calculated using integration. This method calculates survivorship by integrating the area under the abundance curve of each instar. The distance on the x-axis between developmental stages is proportional to the duration of the stages. The survivorship curves are presented in four graphs:
(a) enclosures containing fertilizer
(b) enclosures containing Diaptomus kenai
(c) enclosures containing Diacyclops thomasi
(d) enclosures containing the grazing assemblage.
The survivorship of nauplii from the enclosure containing nauplii alone is shown in each group. The treatment is marked at the end of each curve.

- nauplii alone
- F Fertilizer
- K Diaptomus kenai
- D Diacyclops thomasi
- G Grazing assemblage
a)

SURVIVORSHIP PER 1000

DEVELOPMENTAL STAGE

N4  C1  C2  C3
Figure 19 Survivorship calculated using curve fitting. This method calculates survivorship by minimizing the sum of squares between the actual population curves and simulated curves. The distance on the x-axis between developmental stages is proportional to the duration of the stages. The survivorship curves are presented in four graphs:
(a) enclosures containing fertilizer
(b) enclosures containing Diaptomus kenai
(c) enclosures containing Diacyclops thomasi
(d) enclosures containing the grazing assemblage.
The survivorship of nauplii from the enclosure containing nauplii alone is shown in each group. The treatment is marked at the end of each curve.

nauplii alone
F  Fertilizer
K  Diaptomus kenai
D  Diacyclops thomasi
G  Grazing assemblage