THE ENERGETICS OF PREDATION: A COMPONENTS STUDY OF *CHAOBORUS TRIVITTATUS* LARVAE

by

Louis A. Giguère

B.A. Université Laval 1967

B.Sc. Université Laval 1971

M.Sc. University of British Columbia 1974

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in the Department

of

Biological Sciences

SIMON FRASER UNIVERSITY

July 1981

Approval

Name: Louis A. Giguère

Degree: Doctor of Philosophy

Title of Thesis: The energetics of predation: a components study of *Chaoborus trivittatus* larvae

Examining Committee:

Chairman: Dr. Robert C. Brooke

Dr. L. M. Dill, Senior Supervisor

Dr. P. Belton

Dr. E. B. Hartwick

Dr. M. Mackauer

Dr. Glen H. Geen, Professor, Public Examiner

Dr. E.E. Werner, Assoc. Professor, Zoology Dept.
Michigan State University,
External Examiner

Date approved

Title of Thesis/Project/Extended Essay

The energetics of predation: a components study of *Chaoborus trivittatus* larvae

Author:

(signature)

Louis A. Giguère

(name)

Aug. 17, 1981

(date)

ABSTRACT

The objectives of this study of the rate of transfer of energy between a predator and its prey were to explore ways that body size affects the process, alters the pattern of resource utilization of foragers, and influences the structure of animal communities. The 4th instar larva of *Chaoborus trivittatus*, an ambush predator, was studied. I analyzed several components of predation:

Encounter with prey. I designed an encounter model which assumes a cylindrical attack field for the predator. Measurements of reactive distances between ´hungry´ predators (i.e. un-fed for at least 24 hours) and prey indicated that copepods (0.9-2.6 mm in length) are liable to be attacked whenever they come within 2.2 mm of the center of the body of the elongate larva. The model was corroborated by observations in the laboratory.

Components of prey capture. Data were collected in the laboratory to show the effect of prey size and temperature on components of prey capture in a ´hungry´ larva. Prey size was inversely related to the proportion of successful attacks, which was higher at 13 C than at 6 or 24 C. The components were combined to predict predation rates for a ´hungry´ *Chaoborus* larva. An effect of predator size on feeding rates was also documented.

Respiration. The energy consumption (in mJ/larva/hr) of small and large 4th instar larvae were 8.6 and 20.5 at 13 C and 21.2 and 30.6 at 21 C respectively. The cost of processing food was also estimated. It equals the standard metabolic rate times 0.369. The energy costs of one swimming and one attacking movement were 0.07 and 0.57 mJ/motion respectively.

Digestion. The efficiency of food assimilation was determined by labelling copepods radioactively and feeding known numbers to Chaoborus larvae. At 24 C efficiency was nearly constant at about 80% for all meal sizes, but at other temperatures it was 91.2% to 86.5% for meal sizes of 0.10 to 0.50 µl, and varied from 75.8% at 16 C to 52% at 6 C for a meal size of about 0.90 µl. The instantaneous rate of digestion (expressed as mg dry weight of meal/thousand mg dry weight of Chaoborus/hour) was -0.09, -0.22 and -0.35 at 6, 13 and 22 C respectively. There were no significant effects of meal size or predator size on digestion rates.

I also investigated quantitatively the effect of underwater sound on attack distance by Chaoborus. The larva attacked a needle vibrating at frequencies between 350 and 2050 Hz, maximum attack distance occurring with a signal of approximately 1100 Hz. Increasing ´hunger´ significantly decreased the minimum effective frequency by 11%. Average distances for attack were estimated at 1.9 mm for larvae with food in their crops and 2.25

mm for larvae with empty crops. The sounds produced by three species of prey were analyzed. Significant differences in frequency at maximum sound pressure level occurred within the range of frequencies where ´hunger´ significantly affected the response of Chaoborus. This could result in selective feeding by larvae which have food in their crop.

Next I use a model to explore possible energetic advantages to vertical migrants which alternate between warm surface layers and cold deeper layers where digestion may be more efficient, but assimilation efficiency is reduced. Energy budgets were computed for larvae given a fixed amount of food, and then either assumed to migrate to cool (5 C) deep water for a sixteen hour ´resting´ period, or to continue feeding in the warm (16 C) food-rich surface layers. Larvae derived maximal energy benefits by migrating when the density of Diaptomus kenai, their principal prey, was <0.2 animal/liter, and by feeding near the surface otherwise. A comparison of these findings with field data indicates that seasonal changes in vertical migration patterns can provide energetic benefits.

In the GENERAL DISCUSSION, I combine the components of predation and examine the mechanisms underlying size-selective predation by Chaoborus. The size and swimming speed of prey influence the encounter process substantially and cause passive size selection. I propose a null hypothesis to test for behavioural (active) size selection by larvae. I also compare

their size-selective feeding to that of fish, and discuss potential competitive interactions between fish and invertebrate predators.

DEDICATION

À mes parents,

QUOTATION

"We felt it was a rice-night, and the chiefs of the Abu Tayi came to sup with us. Afterwards, with the embers of our coffee-fire pleasantly red between us against the cool of this upland north-country, we sat about on the carpets chatting discursively of this remote thing and that.

Nasir rolled over on his back, with my glasses, and began to study the stars, counting aloud first one group and then another; crying out with surprise at discovering little lights not noticed by unaided eye. Auda sent us on to talk of telescopes -of the great ones- and of how man in three hundred years had so far advanced from his first essay that now he built glasses as long as a tent, through which he counted thousands of unknown stars. ´And the star -what are they?´ We slipped into talk of suns beyond suns, sizes and distance beyond wit. ´What will now happen with this knowledge?´ asked Mohammed. ´We shall set to, and many learned and some clever men together will make glasses as more powerful than ours, as ours than Galileo´s; and yet more hundreds of astronomers will distinguish and reckon yet more thousands of now unseen stars, mapping them, and giving each one its name. When we see them all, there will be no night in heaven.´ "

T. E. Lawrence (1926), Seven Pillars of Wisdom, (P. 288-289)

ACKNOWLEDGEMENTS

First I want to express my gratitude to Larry Dill for his continuous support throughout the years. His expertise always found its mark and his criticism, particularly at the writing stage of this study, contributed much to my development as a scientist.

Special recognition goes to A. Delâge, R. Jaremovic, D. Morley and P. Belton who helped with the research material presented in Chapters 1, 2, 4 and 5 respectively. R. Dunbrack also provided many hours of enjoyable discussion which influenced my outlook on biology. R. Dunbrack, R. Koopman and M. Stephens provided statistical advice at various stages of the study. T. Northcote and W. Neill gave me access to the U.B.C. Research Forest facilities for the purpose of collecting biological materials in Gwendoline Lake. I thank them as well as the staff at U.B.C. Research Forest in Haney, British Columbia. Many other people have contributed directly or indirectly to this study: V. Bourne, J. Brett, A. Duncan, G. Geen, J. Gerritsen, S. Halford, B. Hartwick, L. Jaremovic, K. Lee, R. Long, M. Mackauer, K. Nair, W. Neill, L. Palmer, R. Pastorok, M. Swift, T. Taylor, T. VanderSar and E. Werner.

This work would not have been possible without the very generous financial assistance accorded to me by Simon Fraser University, the Quebec Department of Education, and Dr. and Mme. P. Audet. I also acknowledge the support of NSERC grant #A6869 to L. Dill.

I thank my family, W. Donnely, L. Druehl and K. Puckett who provided moral support in the final stages of this study.

Finally, I salute all the folks in the Dillery who kept the stellar invaders at bay ---most of the time---.

TABLE OF CONTENTS

Approval ii

Abstract ....iii-vi

Dedication vii

Quotation viii

Acknowledgements ....ix-x

List of Tables ....xv-xx

List of Figures ....xx-xxv

A. GENERAL INTRODUCTION 1

The *Chaoborus* larva as a simple model organism 6

Thesis outline 8

B. MATERIALS AND GENERAL METHODS 11

C. AN EXPERIMENTAL COMPONENT STUDY OF THE FEEDING OF CHAOBORUS LARVAE 14

1. AN ENCOUNTER MODEL FOR ZOOPLANKTON 15

INTRODUCTION 15

Section I- THE STRIKE FIELD OF A CHAOBORUS LARVA 17

Methods 17

Results 18

Section II- DESIGNING THE ENCOUNTER MODEL 23

A general model of encounter 23

A simple model of encounter 28

Model parameters 30

Section III- TESTING THE MODEL 32

Methods 32

Results 34

DISCUSSION 40

2. THE COMPONENTS OF PREDATION 46

INTRODUCTION 46

MATERIALS AND METHODS 49

Section I- The effect of prey size, prey density and temperature on components of predation ...50

Section II- The effect of predator body size on Pr(capture) and some components of predation .54

RESULTS 55

Section I- The effect of prey size, prey density and temperature on components of predation ...55

Section II- The effect of predator body size on Pr(capture) and some components of predation .60

DISCUSSION 64

3. RESPIRATION AND ENERGETICS 69

INTRODUCTION 69

MATERIALS AND METHODS 70

RESULTS 77

Resting metabolism 77

Active metabolism 82

DISCUSSION 84

4. DIGESTIVE PROCESSES 89

INTRODUCTION 89

MATERIALS AND METHODS 92

Assimilation efficiency 92

Rate of emptying of the crop 96

RESULTS 98

Assimilation efficiency 98

Rate of emptying of the crop 101

DISCUSSION 103

Effect of meal size on AE 103

Cause of the decrease in AE 104

Consequences for optimal foraging 105

5. ACOUSTICS IN ZOOPLANKTON 110

INTRODUCTION 110

MATERIALS AND METHODS 113

RESULTS 117

Section I- The response of the predator 117

Frequency response 117

Effect of amplitude 119

Effect of hunger 119

Section II- The stimulus from the prey 125

DISCUSSION 130

6. ENERGETICS OF VERTICAL MIGRATION 137

INTRODUCTION 137

SCENARIO FOR THE MODEL 138

THE MODEL 141

THE PREDICTION 144

COMPARISON WITH FIELD DATA 147

DISCUSSION 151

D. GENERAL DISCUSSION 154

Section I- DETERMINING REACTIVE DISTANCES 157

Materials and methods 157

Results 158

Section II- PREDICTING ENCOUNTER RATES WITH PREY 160

Section III- SIZE-SELECTIVE PREDATION BY 4th INSTAR LARVAE OF *C. TRIVITTATUS* 164

Section IV- FORAGING, SIZE, AND COMMUNITY STRUCTURE . 168

Size-selective predation 168

Energetics and evolutionary significance 173

Competition between planktivorous fish and invertebrates 175

CONCLUSIONS 181

Appendix I 184

LIST OF REFERENCES 185

LIST OF TABLES

Table Page

I Apparent attack distance at seven different intervals along the body of 'hungry' 4th instar larvae of *Chaoborus trivittatus* (see Fig. 1) feeding on *Diaptomus kenai* (a copepod). 20

II Frequency of attack on copepods by the 4th instar larva of *C. trivittatus* as a function of apparent attack distance (see Fig. 1). 21

III Weighted estimates for the volume of space within which a sphere will contact a cylinder during the next short time interval Δt if it is moving at speed v towards the surface of the cylinder using an exact formula (Vw1 from Model 1, Chapter 1 Section II) and an approximate formula (Vw2 from Model 2, Chapter 1 Section II). This was carried out for several cylinder radii (H+d= 1, 3, 5 mm) and two prey speeds (v= 0.5 and 5.5 mm). L+d was set equal to 15 mm. The number of points used in the calculations are given in column 6. Kr and Kz represent the number of radial and axial intervals respectively. 27

IV Summary of data used to compute a correction factor (CF) which takes into account uneveness in predator and prey distributions within experimental arenas, and restrictions on the directions from which prey can approach a predator when Plexiglas walls are present (see Chapter 1 Section III for explanation). 35

V D-statistic (from the Kolmogorov-Smirnov test) for goodness of fit between expected encounter frequencies during 1 min intervals assuming a random (Poisson) process and data collected in the laboratory for copepods and 4th instar larvae of *C. trivittatus*. Data were collected at 13 C for prey size categories I to IV and at a density of 6 prey/arena. For $n = 24$ one minute intervals, $p \geq 0.20$ when $D \leq 0.212$ (Zar 1974). 36

VI Encounter parameters between copepods and the attack field of the 4th instar larva of *C. trivittatus* for four prey size categories (see MATERIALS AND GENERAL METHODS) and two prey densities (3 and 6 prey/arena).
m= mean encounter rate in #/min (± 95% C.L.)
m*= Probability that at least one encounter occurs in one minute (see Chapter 2 for explanation). 56

VII The percentage of copepods that enter the attack field of the 4th instar larva of *C. trivittatus* and are attacked by a ´hungry´ larva (i.e. Pr(strike), see Eqn. 5 Chapter 2). The total number of encounters observed is shown in parentheses. Data were collected for four prey size categories at three temperatures. Data were first pooled with respect to prey density. The probability estimates (p) are from a contingency X^2 test. 58

VIII Summary of the data available for strike efficiency (with the total number of strikes observed) for the 4th instar larva of *C. trivittatus*, as a function of temperature and prey size. Data were pooled with respect to prey density. 59

IX Probability that a 'hungry' 4th instar larva of *C. trivittatus* will capture a copepod in one minute determined from the product of individual components of predation (see Eqn. 5, Chapter 2). This was done for four prey size, three temperature, and two prey density treatments. 61

X Probability that a 'hungry' 4th instar larva of *C. trivittatus* will capture a copepod in one minute (with sample size) determined from the geometric probability distribution for four prey size and three predator size categories (see Chapter 2 and Appendix I for explanation). The data were first pooled with respect to temperature. The probability estimates (p) were obtained from the extension of the median test (Siegel 1956). 62

XI Mean metabolic expenditures (in mJ/larva/hr) ± SE (with sample size) of young and old 4th instar larvae of *C. trivittatus* that fed on one copepod at 13 and 21 C. 78

XII Analysis of variance of mean metabolic expenditures of 4th instar larvae of *C. trivittatus* as a function of temperature and age of larvae. 79

XIII Mean metabolic expenditures (in mJ/larva/hour) ±SE (with sample size) as a function of starvation period for young 4th instar larvae of *C. trivittatus* at 21 C. Each ´starved´ group (i.e. not fed for 1-2, 4, 6 days) is compared statistically with a control group using a two-tailed t-test. Percentage increases in energy consumption represent metabolic costs of processing food (SDA). 81

XIV Unit cost of swimming and attacking (in mJ per motion) ± SE (with sample size) of 4th instar larvae of *C. trivittatus*. Young and old larvae are compared statistically with a two-tailed t-test. 83

XV Instantaneous rates of digestion (expressed as mg dry weight of meal/thousand mg dry weight of *Chaoborus*/hour) as a function of meal volume and temperature (T) for two size categories of the 4th instar larva of *C. trivittatus*. Sample sizes are indicated in parentheses. 102

XVI Sound pressure level and sound frequency analysis for three species of zooplankton attached to a probe. Sound pressure level is the mean of the maximum values recorded for individuals of each species. 126

XVII Maximum attack distance of 4th instar larvae of *C. trivittatus* responding to a vibrating probe (all frequencies examined), and to natural prey (*D. kenai*). 133

XVIII Summary of studies of aquatic predators′ responses to a vibrating probe, including effective frequency, effective amplitude, and attack distance. 135

XIX Energy budget for *Chaoborus* larvae undergoing vertical migration after eight hours of feeding near the surface. 145

XX Energy budget (J/day) for *Chaoborus* larvae staying near the surface for 24 hours, at various *D. kenai* densities. 146

XXI Mean apparent attack distances (mm, with sample sizes in parentheses) for 3rd (∼10 mm) and 4th (∼15 mm) instar larvae of *C. trivittatus* feeding on copepods at three temperatures. The data are based on high speed films of predator-prey interactions (see MATERIALS AND GENERAL METHODS). A summary of statistics is also provided. 159

LIST OF FIGURES

Figure Page

1 Position of copepods (projected onto the horizontal plane through the predator when filmed from above) at the moment of attack by the 4th instar larva of Chaoborus trivittatus. The data (left and right sides pooled) are grouped at 2 mm intervals (1 to 7) along the larval body. Apparent attack distance is measured perpendicularly from the long body axis to the nearest position of the prey at the time of attack. The hatched and dotted lines circumscribe areas which include about 93% of all observations. 19

2 Representation of the general encounter problem between spheres and a cylinder assuming that spheres are uniformly distributed and moving in random directions. ´A´, the area extending from the z and r axes and delimited by the dashed line represents in a plane the volume of space within which the center of a sphere can contact the surface of the cylinder during a short time interval (Δt) if it is moving at speed v towards the cylinder. Only one half of ´A´ is shown here for simplicity. By rotating ´A´ around the z axis, one obtains the contact volume Vc (see Chapter 1 Section II

for explanation). The points represent a grid of 22 x 10 uniformly distributed points from which one can determine $\Omega(r,z)$, the solid angle subtended by the cylinder and a sphere of radius $v \ \Delta t$ (volume B), and determine the likelihood that a sphere is moving towards the cylinder. This allows numerical evaluation of Model 1. 25

3 Representation of a simplified encounter problem between spheres and a cylinder assuming that spheres move along axes perpendicular to the symmetry of the cylinder (see Chapter 1 Section II for explanation). ´A´ represents the volume of space within which a sphere can contact the surface of the cylinder during a short time interval (Δt) if it is moving at speed v towards the end of the cylinder. ´B´ defines this volume for a sphere moving towards the side of the cylinder. 29

4 Graphic representation of observed vs expected encounter rate values of Chaoborus-copepod interactions based on visual data collected in the laboratory and predictions generated from Model 2 (Chapter 1 Section II) respectively. The solid line represents a perfect fit. I show results for copepod size categories I to IV (see MATERIALS AND GENERAL METHODS) at two prey densities (unfilled circles: 3 prey/arena; filled circles: 6 prey/arena). 38

5 Diagram of apparatus used to measure energetic cost of attack in Chaoborus larvae. The acoustic signal is provided by an oscillator. The transducer is an insect pin glued onto a transistor radio earphone. A screen keeps the larva near the vibrating needle. 76

6 Time sequence of appearance of ^{32}P (mean±SE) in lake water in which 4th instar larvae of C. trivittatus were kept after feeding upon one copepod (about 1.8 mm long) at 13 C (n= 8). 95

7 Efficiency of food assimilation as a function of meal volume for the 4th instar larvae of C. trivittatus fed labelled copepods at four different temperatures. Unfilled circle: n= 2. Vertical bars: 95% C.L. 99

8 Schematic digestion curves of 1 mg C. trivittatus larvae at 4 temperatures. The crop volume threshold (TH= 0.50 μl) above which food leakage is presumed to occur is indicated by the horizontal line. This line intersects the digestion curves at four points from which one can determine t_{TH}(filled circles), i.e. the time necessary for crop volume to reach TH. 106

9 Side view of a 4th instar larva of C. trivittatus mounted for an experiment. Larval length: 13.3 mm. 111

10 Mean probe vibration frequency (±SE) to which 4th instar C. trivittatus larvae with an empty crop responded at various distances. D= decreasing stimulus.

I= increasing stimulus. 118

11 The effect of voltage setting on mean probe vibration frequency to which 4th instar C. trivittatus larvae responded at various distances. The larvae had food in their crops. Top three curves: decreasing stimuli. Bottom three curves: increasing stimuli. 120

12 The effect of ´hunger´ on the distance of attack of 4th instar C. trivittatus larvae in response to a probe vibrating at different frequencies (type I stimulus only, see Chapter 5 for explanation). 122

13 Percent positive responses to a vibrating probe as a function of distance from 4th instar larvae C. trivittatus with or without food in their crop. 123

14 Sona-Gram for Diaptomus leptopus attached to a probe. 128

15 Cross-sections of Sona-Grams showing sound pressure level as a function of frequency for two copepod species and one daphnid. The noise level fluctuates around 15-25 dB. 129

16 Relative capture rate as a function of ´hunger´ for 4th instar larvae of C. trivittatus. Capture rates are expressed as a percentage of capture rate of 1-2 day ´starved´ larvae at each temperature. Unfilled circles: 13 C. Filled circles: 24 C. 142

17 Vertical distribution of zooplankton in Eunice Lake in 1972 (from Fedorenko 1973, 1975a). The dotted line

represents prey density above which the simulation model (see Chapter 6) predicts ´no migration´ for 4th instar larvae of *C. trivittatus*. MT= midnight. 148

18 Plot of % overlap of *Chaoborus* depth distribution at noon and at midnight versus the area under the curve of noon depth distribution of *D. kenai* lying above the critical density threshold predicted by the simulation model (see Chapter 6 and Fig. 17). 150

19 Summary of data on assimilation efficiency of copepods by 4th instar larvae of *C. trivittatus* (from Fig. 7). Unfilled circles: small meal (~0.5 µl). Filled circle: large meal (~0.9 µl). 153

20 Encounter rate between spheres (representing copepod prey) and a cylinder representing the attack field of 3rd and 4th instar *C. trivittatus* (based on measurements of mean attack distances) given an equal density of prey of each length. Parameter values are given in the text. The details of the model are in Chapter 1 Section II. 161

21 Encounter rate between spheres (representing copepod prey) and a cylinder (see Fig. 20 above) given equal biomass or volume of prey for each prey length category. 165

22 Rate of successful encounter with prey of different length by 4th instar larvae of *C. trivittatus*. It is defined as the product of the rate at which prey encounter the strike field of the predator (Fig. 20)

times the strike efficiency of the larva. The data are expressed relative to the most vulnerable prey size. 167

23 Relative rate of successful encounter as a function of the size of zooplanktonic prey for a Chaoborus larva (A) and a facultative planktivorous fish (B) (from O´Brien 1979). See GENERAL DISCUSSION for explanation. 171

A. GENERAL INTRODUCTION

"One of the chief factors limiting the choice of food in these polyphagous forms appears to be size. ... This sort of relation between the sizes of predators and the animals they prey upon is very important in splitting up the animal community into food niches. The limitations placed by size of food on feeding together with other special food-preferences give rise to ´food-chains´, leading usually from smaller to larger forms, ..."

C. Elton (1933), The Ecology of Animals (p. 29)

Body size plays an important role in determining rates of biological processes and, recently, a considerable amount of attention has been given to various ways in which this affects the outcome of competitive and predatory interactions and hence influences the structure of aquatic and terrestrial communities (Brooks and Dodson 1965, Pianka 1973). Although some aspects have been given theoretical treatment and some descriptive data can be interpreted as fitting predicted schemes of community organization through size (e.g. species packing), ecologists have yet to quantify satisfactorily how size and morphological features of foragers determine utilization on the prey size dimension of the niche (Werner 1977).

I approached this problem by developing a computer model of predation which served as the focus of the investigation while I measured various components of predation in the laboratory. Holling (1963, 1964) was the first to suggest this comprehensive approach to predation. In this study, I divided that process into various components (proximate factors) linking an organism to its environment in terms of energetic contributions to fitness (ultimate factors). My first step consisted of identifying some of the pitfalls inherent in such analyses.

First, many studies often become increasingly involved in working out the fine details and the intricacies of the mechanics of predation rather than in attempting to achieve a broad synthesis (Holling 1964), and some doubts can be raised about the possibility of achieving a synthesis of such a large number of components at the level of precision proposed by Holling. Secondly, faced with the prospect of including a very large number of components (as well as their possible interactions) in their studies, other experimenters either concentrate on the most easily studied components and/or restrict the study to a simplified set of environmental conditions. Consequently their models are based on fragments tied together with many simplifying assumptions that sometimes originate from theoretical frameworks similar to the theories they purport to test. This greatly limits their usefulness. Thirdly, such studies are usually carried out in artificial laboratory universes (often the prey itself is restrained from escaping) that may have no bearing on the problems confronting the predator in its natural setting (particularly in the case of ´searchers´ living in a complex environment) or which may alter its behaviour radically. Unfortunately, whereas modern ecologists recognize the need to understand the selective pressures acting upon organisms in their natural environments, field studies often do not lend themselves to a precise quantification of components of foraging.

Much of the problem resides therefore in finding an organism for which a sufficiently accurate description of foraging could be attempted in the laboratory without getting entangled unnecessarily in a large number of detailed components or losing too much realism. Consequently I established three criteria that I considered essential if this study were to attain some of its objectives. The ideal system must (a) have the lowest possible level of complexity, so that the number of components to be studied could be kept at a manageable level, (b) be one which keeps discrepancies between laboratory findings and field situations to a minimum, and (c) be one which can be quantified easily.

Aquatic invertebrate predators are particularly well suited for this purpose. They live in a relatively uniform environment and many attack in response to acoustic stimuli produced by their prey. Since the propagation of these signals in water is not altered greatly by biotic or abiotic factors in the environment, much of the complexity of the interactions between predator and prey which is encountered in studies of visual predators is eliminated, and the task of developing component-based models of predation that can be translated to field situations is thus greatly simplified. These predators are also simple to obtain, are easily manipulated in the laboratory, and have respiration rates which are directly related to body mass (Harding 1977, Banse and Mosher 1980) and the temperature of their environment (Ivleva 1980, Clarke 1980). They are thus extremely convenient to work with.

Other desirable attributes are: That the predator's behaviour should be stereotyped, that it engage in few activities besides foraging, and that it use a sit-and-wait feeding tactic. With these considerations in mind, I undertook a bioenergetic study of Chaoborus larvae (Diptera: Chaoboridae) feeding on copepod prey.

Chaoborus spp. are common in lakes and ponds throughout the world and are an important element of many zooplankton communities (Welch 1968, Sprules 1972, Fedorenko 1973, Lewis 1975, Smyly 1978, Pastorok 1980b). Their impact on their prey populations can be substantial (Fedorenko 1975b, Pastorok 1978, Lewis 1979, Lynch 1979, Pastorok 1980a) and they are thought to affect the structure of freshwater communities significantly (Dodson 1970, Sprules 1972, Allan 1973, Anderson and Raasveldt 1974, Smyly 1976, Lynch 1979, Pastorok 1980b, Smyly 1980, Neill and Peacock 1980).

The ultimate objective of this study is to determine how body size affects net rate of transfer of energy between predator and prey, using prey which vary in size but possess a uniform body plan.

The Chaoborus larva as a simple model organism

The 4th instar larva of Chaoborus trivittatus Loew is an ideal subject for a component study on size-selective predation. Most of the two year life cycle of this dipteran is spent in the 4th instar, the stage in which most growth takes place. The reproductive function is confined to an aerial (non-feeding) adult stage. It has no known major predators in the study area (Gwendoline Lake, British Columbia, a fishless lake, Neill and Peacock 1980). Thus all of its activities have feeding or feeding-related functions whose unit cost could be estimated.

Most importantly Chaoborus is an ambush predator whose feeding success depends upon sudden attacks when prey come close to its body. This presents two advantages. First, the negative terms of the energy budget of ambush predators can be obtained directly by combining data on basal or standard metabolic rates with estimates for unit cost of activity weighted by the appropriate intensity levels of activity (e.g. while attacking prey or migrating vertically). Secondly, by mapping the positions of the prey relative to the body of the predator when attacks occur (from high-speed films of predator-prey interactions), it is possible to circumscribe a cylindrical field surrounding a 'hungry' larva within which a prey is liable to be attacked, and to develop a working definition of encounter to be used in the laboratory (an 'encounter' was scored whenever prey came within 2 mm of a larva). By defining an encounter with respect to a target volume rather than the sensory system of the predator, I created an arbitrary separation of encounter and attack parameters which was simple, provided all the necessary information to construct a descriptive model of Chaoborus predation, and limited the components to be studied.

Because a component study deals with several important but distinct aspects of feeding and energetics (behaviour, digestion, assimilation, respiration), I present the results in five self-contained experimental studies. These components are then brought together in a simulation model in which I consider energetic consequences of a strategy of vertical migration to this predator. Although each chapter has a discussion which deals with specific aspects of the feeding of Chaoborus , I conclude the thesis with a GENERAL DISCUSSION in which I summarize results on the effects of body size on the foraging strategy of size-selective planktivores, and consider their importance to the structure of zooplankton communities.

Thesis outline

Chapter 1: *An Encounter Model for Zooplankton*. I develop a collision model which assumes that a predator possesses an effective encounter field which is cylindrical. Its size and shape is determined by measurements taken from high-speed films of *Chaoborus*-copepods interactions (Giguère *et al*. submitted). The encounter model represents the framework on which other components of predation (Chapter 2) can be grafted.

Chapter 2: *A Component Study of Predation*. I present data showing the effect of prey density, prey size, predator size and temperature on the components of prey capture in a ´hungry´ *Chaoborus* larva.

Chapter 3: *Respiration and Energetics*. Standard metabolic rates and costs of processing food are determined in a respirometer. The energy costs of swimming and attacking prey are also measured experimentally (Giguère 1980). These estimates cover the negative terms of the energy budget of the *Chaoborus* larva.

Chapter 4: Digestive Processes. Larval food assimilation efficiency and digestion rates are determined under different temperature and meal size conditions (Giguère 1981). Given supplementary information on effects of ´hunger´ on components of predation (Giguère in prep.), all results can be combined to generate estimates of the net rate of transfer of energy between predator and prey varying in size.

Chapter 5: Acoustics in Zooplankton. The first quantitative study of the relationship between the attack behaviour of a predator and the distance of the source of an underwater acoustic signal is undertaken (Giguère and Dill 1979). This study provides background information necessary to design a predation model for Chaoborus.

Chapter 6: Energetics of Vertical Migration. I reexamine McLaren´s (1963) metabolic efficiency hypothesis regarding energy savings accrued to vertically migrating animals in temperate latitudes. I combine several components of the feeding of Chaoborus larvae, and I compare energy budgets based on two alternative migratory tactics. I then determine which tactic permits a maximization of net energy returns per unit time. Based on these results, I consider whether observed patterns of larval Chaoborus vertical migration can be accounted for on an energetic basis (Giguère and Dill 1980).

GENERAL DISCUSSION: I examine size selective predation in Chaoborus larvae by breaking down the process into a passive component (prey size dependent encounter rates and strike efficiency) and an active component (behavioural choice mediated by ´hunger´). I compare the feeding pattern of invertebrate predators with that of fishes based on a facultative planktivore from O´Brien´s (1979) review. I assess their respective impact on zooplankton populations, consider their competitive interactions and their importance to the structure of zooplankton communities.

B. MATERIALS AND GENERAL METHODS

Animals were collected from Gwendoline Lake, British Columbia (see Northcote and Clarotto 1975 or Neill and Peacock 1980 for a brief description of some lake characteristics). They were stored in an aquarium at 13 C under a 12:12LD cycle. Because 4th instar larvae of Chaoborus trivittatus undergo extensive diel vertical migration in the field, they were expected to be pre-adapted to a wide range of temperature conditions and acclimation was felt to be unnecessary. The average length of larvae used in most experiments (with standard error) was 14.8 (0.95±SE) mm based on photographic estimates obtained in the laboratory. When necessary, larvae were separated into ´old´ (at least one year old, ~16 mm long) and ´young´ (a few weeks old, ~13 mm) individuals (categories from Fedorenko and Swift 1972).

Diaptomus copepods were used as prey. They were visually separated into 4 approximate size categories (unless otherwise indicated): I- D. leptopus (S.A. Forbes) 1.00-1.29 mm in length; II- D. kenai (M.S. Wilson) 1.30-1.59 mm; III- D. kenai 1.60-1.89 mm; and IV- D. kenai 2.00-2.39 mm. Prey volume was determined from a formula in Edmondson and Winberg (1971). This range of copepod sizes covers the bulk of the diet of the 4th instar larva of C. trivittatus in coastal lakes and ponds near Vancouver, British Columbia (Fedorenko 1975a, Swift 1976, Giguère 1979). Swift and Fedorenko (1975) have also shown that this larva cannot capture prey much longer than 2.2 mm.

Available facilities (growth chambers with temperature controls) permitted four temperature treatments for most experiment (6, 13, 16 and 24 C). Respiration rates were determined in a constant temperature bath at 13 and 21 C, and digestion rates at 6, 13 and 22 C.

High-speed films of _Chaoborus_-copepod interactions were taken with a Ciné-8 camera (Visual Instrumentation Corp., Burbank, California). Larvae were not fed for at least one day (i.e. were ´starved´ or ´hungry´), and offered copepods as prey (_D. kenai_ and _D. leptopus_, 0.9-2.6 mm in length). Each larva was filmed (45-150 frames/s) from above a small rectangular Plexiglas container filled with 6-8 ml of lake water (at 6, 13 and 24 C).

All statistical tests (viz. t-test and analysis of variance) were performed under the assumption of two-tailed distributions (unless otherwise indicated) and the rejection level was set at 0.05.

Details of specific techniques are provided in the relevant sections of the thesis.

C. AN EXPERIMENTAL COMPONENT STUDY OF THE FEEDING OF CHAOBORUS LARVAE

1. AN ENCOUNTER MODEL FOR ZOOPLANKTON

INTRODUCTION

The 4th instar larva of Chaoborus trivittatus feeds primarily on crustacean zooplankton by hovering in the water and striking at prey which come close to its body (≤ 3.8 mm, Giguère and Dill 1979; Chapter 5). Since (a) a larva does not pursue or lunge at prey, (b) prey move in more or less unpredictable directions, and (c) predator and prey live in a relatively uniform aquatic environment, stochastic collision models could be used to quantify their encounter process accurately. To do so, one must imagine a suitable patch in space within which prey are uniformly or randomly distributed, and view prey as particles moving in random directions. These will encounter a target volume (the ambush predator) according to a function which will depend on their size and speed, and the size and shape of the strike field of the predator.

Unfortunately encounter models presently available were developed for spherical objects (i.e. the encounter radius of the predator extends in every direction from a central point, e.g. Gerritsen and Strickler 1977), a simplistic representation which does not apply to many predators (including the Chaoborus larva) and restricts the use of these models. The objectives of this chapter are therefore three-fold: first, to delimit the effective strike field of a Chaoborus larva (the larva is elongate and attacks prey along its whole body); second, to propose a mathematical formulation describing the rate at which prey encounter this strike field (i.e. the encounter process between randomly moving spheres and a stationary cylinder); and third, to demonstrate the suitability of this model for making accurate quantitative predictions by comparing its output with encounter data collected in the laboratory (using copepods as prey). I also discuss applications of the model to field situations.

Section I- THE STRIKE FIELD OF A CHAOBORUS LARVA

Methods

I attempted to determine the configuration of the strike field of a ´starved´ 4th instar larva of *Chaoborus* by filming predator-prey interactions at 45-150 frames/s (see MATERIALS AND GENERAL METHODS for details). The shortest distance between copepod prey (*Diaptomus* species) and the centre of the predator at the moment of attack was measured on film perpendicularly to the main body axis of the predator. Since these measurements are of a projection of the position of the prey onto the two-dimensional horizontal plane through the predator, they underestimate true attack distances and are referred to as apparent attack distances.

Results

Apparent attack distances did not vary significantly between temperature treatments (ANOVA, F= 1.034; d.f.= 2,188; p= 0.36) and the data were pooled. Prey size was regressed on attack distance but the coefficient of determination was not significant (r^2= 0.0006; d.f.= 1,189; slope= -0.05; p= 0.62). I grouped observations at 2 mm intervals along the larval body (the first and last interval are open) and plotted all cases where apparent attack distance was > 1 mm (Fig. 1). In this way, biases due to the effect of the contour of the body of the larva on apparent attack distances were eliminated. It was then possible to carry out statistical comparisons for data collected towards the outside of the attack field of the larva and determine its configuration. The mean values from the seven different regions did not vary significantly (Table I; F= 0.71; d.f.= 6,96; p= 0.64), a fact suggesting that *Chaoborus* attacks extend at comparable distances along the entire body. Attack frequencies showed a marked decrease at distances greater than 2.2 mm from the center axis (Table II); this may represent a threshold value set by physiological and morphological limitations of the capture mechanism; other observations suggest that larvae can detect prey at much greater distances. Since visual observations in the laboratory indicate that a larva will attack prey above or below its body as well as to the side

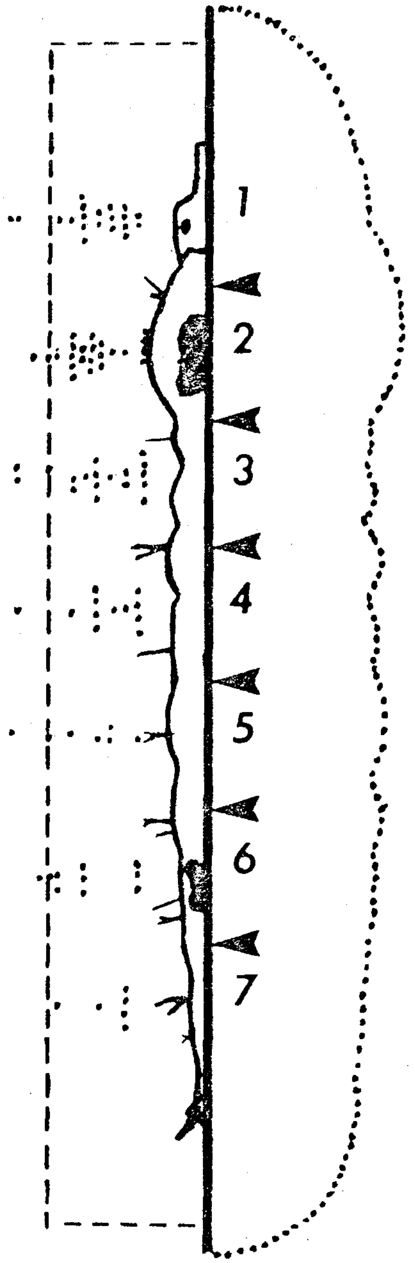


Fig.1 Position of copepods (projected onto the horizontal plane through the predator when filmed from above) at the moment of attack by the 4th instar larva of <u>Chaoborus trivittatus</u>. The data (left and right sides pooled) are grouped at 2 mm intervals (1 to 7) along the larval body. Apparent attack distance is measured perpendicularly from the long body axis to the nearest position of the prey at the time of attack. The hatched and dotted lines circumscribe areas which include about 93% of all observations.

Table I Apparent attack distance at seven different intervals along the body of ´hungry´ 4th instar larvae of _Chaoborus trivittatus_ (see Fig. 1) feeding on _Diaptomus kenai_ (a copepod).

Interval #	1	2	3	4	5	6	7
Mean (mm)	1.80	1.79	1.76	1.74	1.94	2.12	1.60
Variance	0.29	0.29	0.32	0.37	0.32	0.69	0.16
Sample size	20	25	19	14	8	11	6

Table II Frequency of attack on copepods by the 4th instar larva of _C. trivittatus_ as a function of apparent attack distance (see Fig. 1).

Apparent attack distance (mm)	Number of observations
0.00-0.20	29
0.21-0.40	12
0.41-0.60	17
0.61-0.80	19
0.81-1.00	15
1.01-1.20	27
1.21-1.40	17
1.41-1.60	9
1.61-1.80	11
1.81-2.00	4
2.01-2.20	13
2.21-2.40	4
2.41-2.60	1
2.61-2.80	1
2.81-3.00	3
3.01-3.20	2
3.21-3.40	0
3.41-3.60	0
> 3.61	2

(except for dead spaces directly behind, and directly in front and just above its head), this threshold value determines a roughly cylindrical effective strike field for the Chaoborus larva (the area inside the hatched line in Fig. 1 encloses 93% of all attacks observed on film).

A functional definition for ´encounter´ can then be developed to collect visual observations of predator-prey interactions in the laboratory, and to test the model (Section III). I scored an ´encounter´ whenever prey entered the volume of space found within 2 mm of the surface of the body of a larva (represented in a horizontal plane by the dotted line in Fig. 1), i.e. not with respect to the sensory apparatus of the predator but rather with respect to a volume of space within which prey become vulnerable to attack (whether or not prey detection occurred). It is simple and easily ascertained with a millimetric grid affixed to the bottom of experimental arenas (see Section III of this Chapter and Chapter 2).

Section II- DESIGNING THE ENCOUNTER MODEL

A general model of encounter

Having outlined a cylindrical strike field in the *Chaoborus* larva, I will derive a general formulation of the encounter problem for a stationary cylinder of length L and diameter H centered around the coordinates z= r= 0, and spheres of diameter d which are uniformly distributed and move at constant velocity (v) in random directions.

My aim is to calculate the encounter rate (E) that will serve as the input parameter for a Poisson distribution (to yield exact probability of capture). This rate can be evaluated by considering the probability of encounter (P) between N spheres and the cylinder over a small interval of time Δt:

$$E = N \times P / \Delta t \qquad (1)$$

However P will depend on the position of the spheres in the space around the cylinder and the probabilities will have to be integrated over the entire available space (Vtot) to evaluate E. Furthermore, since P= 0 when the spheres are located at greater distances than v Δt from the cylinder (they cannot reach the cylinder during Δt), this defines (a) a volume of space outside of which the chance of encounter during Δt is nil, and (b) a volume of space next to the cylinder (Vc) where a sphere will contact the cylinder during the next short time interval Δt if it is moving in the right direction. In Fig. 2, half of this volume is represented in a plane by the area enclosed by the dashed lines.

The probability of encounter P(r,z) inside Vc is given by $\Omega(r,z)/4\pi$, where $\Omega(r,z)$ represent solid angles subtended by the volume resulting from the intersection of the cylinder and a volume of radius v Δt centered on r,z. One solid angle is illustrated in a (r,z) plane on Fig. 2. By integrating over these small portions of volume dV, the rate E is then:

$$E = \frac{1}{\Delta t} \cdot n \int_{Vtot} P \cdot dV = \frac{n}{\Delta t} \frac{\Omega(r,z)}{4 \cdot \pi} \qquad \text{Model 1}$$

where n= N/Vtot or the density of spheres. The last integral can be considered as an equivalent volume Vw1 equal to Vc weighted by the probability that a sphere can contact the cylinder during Δt.

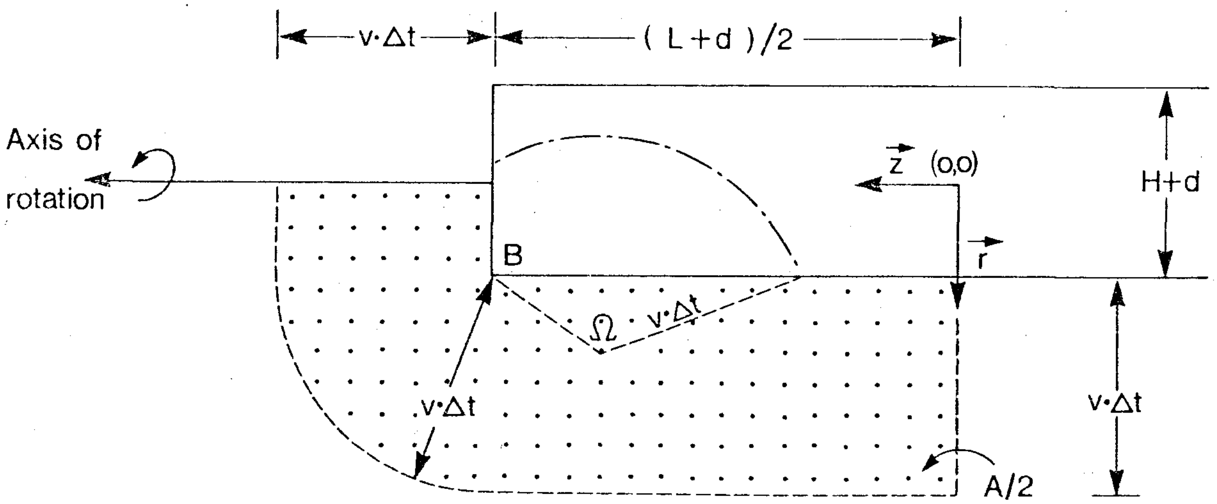


Fig. 2 Representation of the general encounter problem between spheres and a cylinder assuming that spheres are uniformly distributed and moving in random directions. ´A´, the area extending from the z and r axes and delimited by the dashed line represents in a plane the volume of space within which the center of a sphere can contact the surface of the cylinder during a short time interval (Δt) if it is moving at speed v towards the cylinder. Only one half of ´A´ is shown here for simplicity. By rotating ´A´ around the z axis, one obtains a contact volume Vc (see text for explanation). The points represent a grid of 22 x 10 uniformly distributed points from which one can determine $\Omega(r,z)$, the solid angle subtended by the cylinder and a volume of radius v Δt (volume B), and determine the likelihood that a sphere is moving towards the cylinder. This allows numerical evaluation of Model 1.

Vwl has been numerically evaluated[1] for a normal range of prey speeds (see Eqn. 4 below), predator strike diameters (H) (from Section I above, Giguère and Dill 1979; Chapter 5) and sphere diameters (d). In such a geometric model, the size of prey is taken into account by considering a cylinder whose dimensions are increased by the diameter of the sphere ($H' = H + d$, $L' = L + d$), in interaction with dimensionless prey.

This numerical solution (Table III, column 3) can be obtained for example by computing the solid angles for 22x10 uniformly distributed points within the area A/2 as shown in Fig. 2. The integration over Vc is then calculated in polar coordinates. The solid angles are given by: $\iint \sin\theta \, d\theta \, d\phi$. When $v \Delta t$ is tangent to the cylinder, there is agreement with solid angle tables based on an integration formula (Guest 1961 and Masket and Rodgers 1962); elsewhere, the limits of integration must be modified accordingly. The accuracy of the estimate of Vwl obviously improves with the number of points used in the calculations (Kr and Kz in Table III represent the number of radial and axial intervals respectively). For example, in the case of a spherical model for which both analytical and numerical solutions are presently available, the % error introduced by using a numerical solution is ≤0.5% using ten radial intervals.

---

[1] An analytical solution has since been proposed (J. Gerritsen, pers. comm.). It yields estimates which are within 0.3% of my numerical solution.

Table III Weighted estimates for the volume of space within which a sphere will contact a cylinder during the next short time interval t if it is moving at speed v towards the surface of the cylinder using an exact formula (Vw1 from Model 1) and an approximate formula (Vw2 from Model 2). This was carried out for several cylinder radii (H+d= 1, 3, 5 mm) and two prey speeds (v= 0.5 and 5.5 mm). L+d was set equal to 15 mm. The number of points used in the calculations are given in column 6. Kr and Kz represent the number of radial and axial intervals respectively.

H+d mm	v mm/s	Vw1 mm^3	Vw2 mm^3	Vw1/Vw2	Kr x Kz
1	0.5	6.1	5.1	1.183	20 x 32
1	5.5	66.8	56.4	1.183	24 x 26
3	0.5	19.4	16.2	1.198	16 x 32
3	5.5	213.2	178.0	1.198	14 x 26
5	0.5	34.3	28.3	1.214	18 x 32
5	5.5	377.0	311.0	1.212	16 x 26

A simple model of encounter

The procedure outlined above is cumbersome, and I was interested in finding an alternate formulation of the model which possesses a simple analytical solution and yet produces realistic estimates of encounter rate. For simplicity's sake, assume that spheres are moving exclusively along a set of three axes that are perpendicular to the symmetry of the system (i.e. the cylinder). The prey can then approach the cylinder from six orthogonal directions (+x, -x, +y, -y, +z, -z) with equal likelihood.

Once more, it is possible to delimit a contact volume (from $v \Delta t$, the dimensions of the cylinder and the spheres moving along perpendicular axes) within which a sphere can contact the surface of a cylinder during a short time interval. To find this contact volume (V), let us recognize 2 characteristic directions from which prey may approach a predator: from the ends of the cylinder (yielding volume A in Fig. 3) or else from the sides, above or below (yielding volume B in Fig. 3). V is then equal to:

$$V = v \;\Delta t \;[\; 4\;(d+L)\;(H+d) + 2\pi \;\left(\frac{H}{2} + \frac{d}{2}\right)^2 \;] \qquad (2)$$

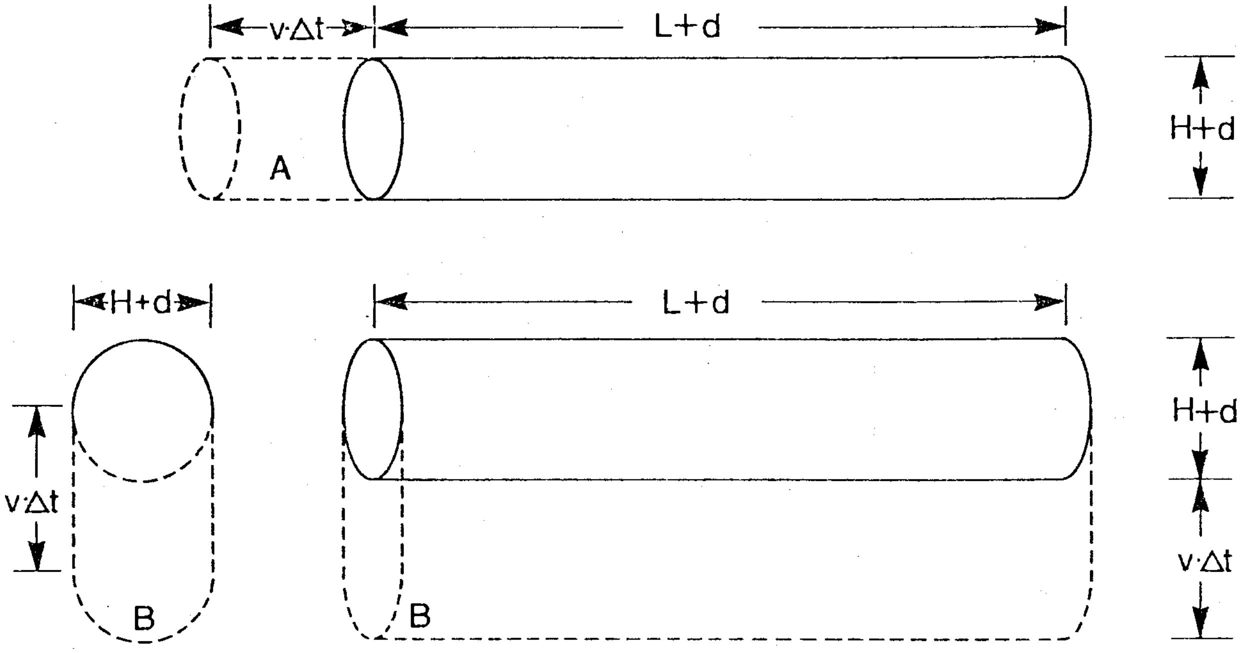


Fig. 3 Representation of a simplified encounter problem between spheres and a cylinder assuming that spheres move along axes perpendicular to the symmetry of the cylinder (see text for explanation). ´A´ represents the volume of space within which a sphere can contact the surface of the cylinder during a short time interval (Δt) if it is moving at speed v towards the end of the cylinder. ´B´ defines this volume for a sphere moving towards the side of the cylinder.

The probability that the prey is moving towards the predator is 1/6, and Vw2= V·(1/6). The encounter rate is then:

$$E= \frac{N \cdot v}{Vtot} \left[\frac{2}{3} (d+L) (H+d) + \frac{\pi}{12} (H+d)^{2} \right] \qquad \text{Model 2}$$

As desired, this analytical formula is simple, and based on experimental parameters (v, d, H, L, N, Vtot) which are easily measured. To ensure that it yields good results numerically, I compare Vw1 and Vw2 (columns 3 and 4 respectively) in Table III (column 5). The results show that Model 2 underestimates the exact values obtained from Model 1. The error remains consistently around 20% (over a wide range of possible combinations for prey speed and predator strike diameter). Estimates derived from Model 2 can thus be corrected by a simple multiplicative factor (~1.2).

Model parameters

In order to compare the output of the model to encounter data collected in the laboratory (i.e. Chaoborus-copepod interactions), I must choose appropriate parameters values for the model. The characteristic dimensions of the cylinder representing the strike field of the predator are: L= 18 mm and H= 4.4 mm (see Fig. 1). Vtot was set equal to 75 ml, (see Section III of this Chapter).

The diameter of the spheres was set equal to the maximum width (w, in mm) of a copepod measured in the cephalic area under a binocular microscope. For D. kenai and D. leptopus, this relates to length (l, in mm) as follows ($r^2 = 0.98$, $n = 24$, $p < 0.01$):

$$w = 0.3456\, l^{.8354} \qquad (3)$$

The speed of copepods (D. kenai only) was determined from high speed films (see MATERIALS AND GENERAL METHODS). Measurements were taken from individuals travelling along straight path segments, their primary mode of locomotion in the laboratory. The data were grouped according to prey size at 0.2 mm intervals, and a polynomial equation was fitted by a least squares method to the mean of each group. Since group sizes were unequal, this was preferred to fitting individual data points. The relationship was:

$$v\ (\mathrm{mm/sec}) = -0.53 + 2.15\, l - 0.153\, l^2 \qquad (4)$$

This formula is approximate since it ignores stops and quick bursts of speed exhibited by diaptomid copepods. Nevertheless it represents the overall conditions prevalent in this system, and is consistent with the data of Swift and Fedorenko (1975) for the same species.

Section III- TESTING THE MODEL

Methods

One predator was presented with 3 or 6 (N) prey of any of four size categories (I to IV, MATERIALS AND GENERAL METHODS) inside rectangular experimental arenas containing 75 ml of lake water (Vtot). All prey size categories were presented at 13 and 24 C unless otherwise indicated. An ´encounter´ was scored whenever a part of the body of a prey (excluding antennae) came within 2 mm of the surface of the body of the predator or an attack occurred. More details are given in Chapter 2.

Two separate tests were carried out: (1) I compared the frequency of encounters per minute in 24 consecutive 1 min intervals to that expected from a Poisson distribution (Sokal and Rohlf 1969) to determine whether they were distributed randomly over time (13 C and 6 prey/arena). Goodness of fit was checked with the Kolmogorov-Smirnov test (Siegel 1956); (2) I compared the encounter data to predicted values derived from Model 2. Since predator and prey tend to aggregate near a water-Plexiglas interface, and the Plexiglas surface blocks prey from approaching the predator from that particular direction, I had to assess the importance of these factors in order to correct for potential biases.

Given a predator of cylindrical attack field of 2.2 mm radius and the assumptions of Model 2, and assuming furthermore that prey need a space equivalent to their own body length for turning and manoeuvering purposes, I considered that a Plexiglas wall within 6 mm of the long body axis of a larva prevented prey from approaching the predator from that particular direction and produced a shadow effect (this value is for a copepod 1.9 mm long; a slight bias results with respect to prey size). I marked the inside of the arenas 6 mm away from each wall, and delineated three zones according to whether they were bounded by one wall (zone b), two walls (c) or none (a). Their volumes were assessed graphically and expressed as % of total volume (CFO). Everything else being equal, the number of encounters in each zone should be proportional to their volume, and the expected number of encounters in each zone would equal CFO times the total number of encounters for an arena. To take into account unevenness in the distribution of predator and prey among zones and shadow effects by Plexiglas walls, I designed a correction term (CF) for each zone as follows. First I estimated: CF1/CF0, where CF1= the proportion of prey found in each zone as determined from photographs (top and side view) taken at 1 min intervals for 14 mins from 6 arenas (prey size categories I and III, 24 C); CF2/CF0 where CF2= the proportion of time spent by predators in each zone, i.e. where at least 50% of its body lies, during feeding experiments (from event recorder charts; prey size categories III and IV only); and CF3, a term which represents the proportion of the cylinder which is not ´shadowed´ by the presence of Plexiglas walls for each zone (a value of one indicates no ´shadow´ effect). I then multiplied these factors and CF0 together for each zone, and summed them to obtain a global correction factor for bias in the laboratory experiments (CF= 1.035; Table IV). This value suggests that the extent to which predator and prey aggregate near Plexiglas walls (these trends are significant) is nearly compensated for by the fact that a wall prevents prey from approaching a predator from a particular direction (for these arenas).

Results

The agreement of observed encounter frequencies during 1 min intervals with predicted values from a Poisson distribution was good ($p \geq 0.20$, Table V). Large prey may have encountered the

Table IV Summary of data used to compute a correction factor (CF) which takes into account uneveness in predator and prey distributions within experimental arenas, and restrictions on the directions from which prey can approach a predator when Plexiglas walls are present (see text for explanation).

Zone Bounded by	a no wall	b 1 wall	c 2 walls	Sum
CF0: % of total volume in zone	44.7	47.7	7.5	
CF1: % of prey in zone	23.1	60.0	16.9	
CF2: % of time spent by predator in zone	3.2	39.0	57.8	
CF3: Correction for encounter in presence of wall(s)	1.0	0.72	0.50	
$\frac{CF1 \times CF2 \times CF3}{CF0 \times 100}$	0.017	0.368	0.650	1.035

Table V D-statistic (from the Kolmogorov-Smirnov test) for goodness of fit between expected encounter frequencies during 1 min intervals assuming a random (Poisson) process and data collected in the laboratory for copepods and 4th instar larvae of <u>C. trivittatus</u>. Data were collected at 13 C for prey size categories I to IV and at a density of 6 prey/arena. For n=24 one minute intervals, $p \geq 0.20$ when $D \leq 0.212$ (Zar 1974).

Replicate	Prey size categories			
	I	II	III	IV
1	0.046	0.100	0.071	0.188
2	0.033	0.200	0.058	0.204

strike field of the larvae in a somewhat clumped manner. Since this could be related to some form of sexual behavior enhanced by very high densities of adult copepods used in these experiments, more data were obtained at low densities (two replicates at 13 C with 1, 2 and 3 prey/arena). None of the data (Kolmogorov-Smirnov test, $D \leq 0.12$; $n=24$; $p >> 0.50$) indicate that copepods encounter the strike field of a Chaoborus larva in a non-random fashion over time. Note that although this finding increases the plausibility of the model, it is not a test of the assumption that prey swim in random directions (viz. this pattern could occur even if prey swim predominantly in one plane).

There were no significant differences between the rate at which prey encountered the strike field of a Chaoborus larva at 13 vs 24 C (paired t-test; $t= 0.02$; d.f.= 7; $p \geq 0.90$). The data therefore were pooled and analyzed in a two-way Analysis of variance (Sokal and Rohlf 1969). There was no interaction between prey size and prey density ($F= 1.32$; d.f.= 3,48; $p= 0.28$) but there were significant effects of prey size ($F= 6.34$; d.f.= 1,48; $p \leq 0.0001$) and prey density ($F= 40.07$; d.f.= 3,48; $p= 0.001$) on E. The data were multiplied by 1.035 (to correct for bias in this system, see Methods) and compared to the predictions derived from Model 2 (times 1.2; Table III) for the same density and prey size categories (Fig. 4). The fit is striking when one considers that the theoretical model was

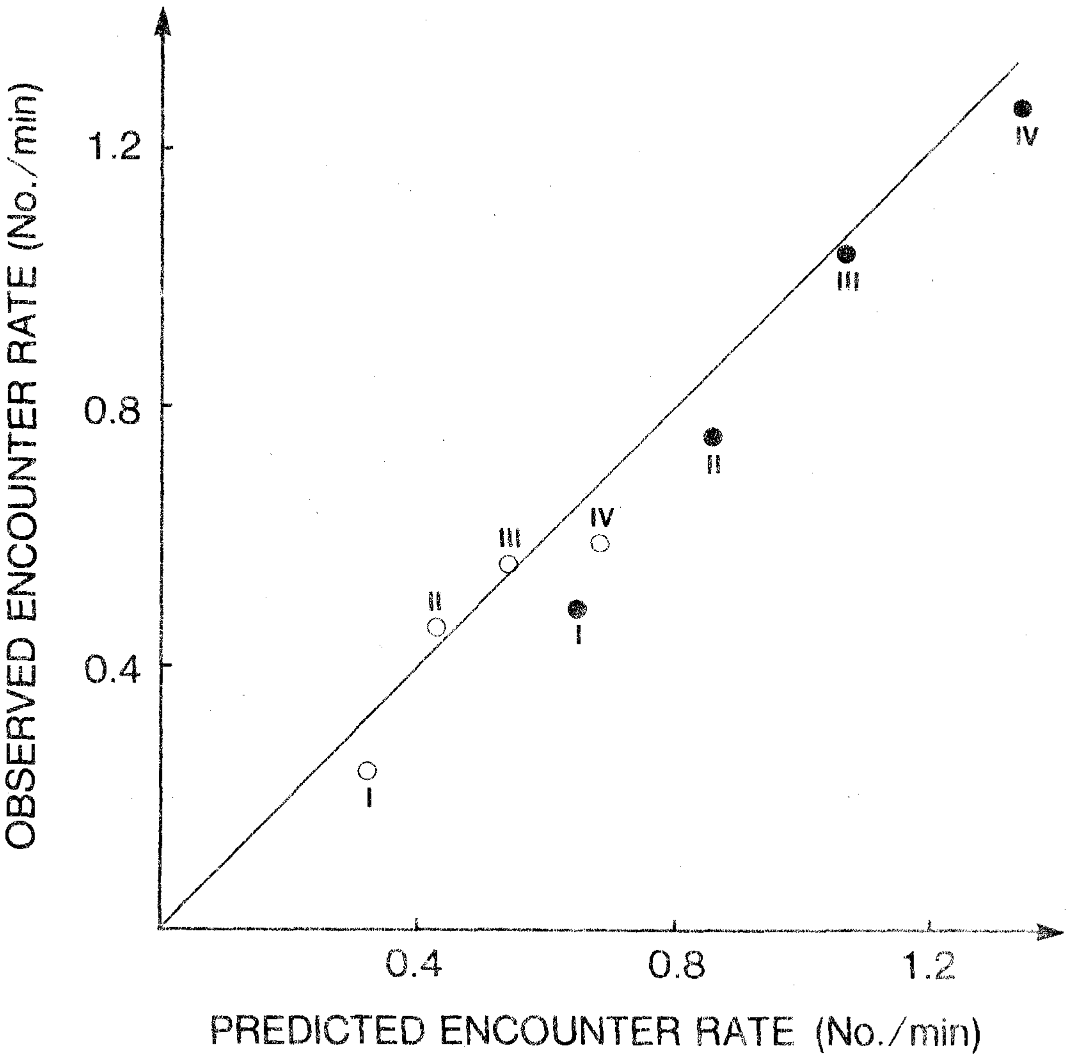


Fig. 4 Graphic representation of observed vs expected encounter rate values of Chaoborus-copepod interactions based on visual data collected in the laboratory and predictions generated from Model 2 respectively. The solid line represents a perfect fit. I show results for copepod size categories I to IV (see MATERIALS AND GENERAL METHODS) at two prey densities (unfilled circles: 3 prey/arena; filled circles: 6 prey/arena).

derived independently. The error varied from -6.3 to 17.2% for categories II, III and IV, but values as high as 20.1 and 37.0% were obtained for category I. Since the latter category refers to *D. leptopus* and Eqn. 4 (for copepod speed) applies to *D. kenai* only, the estimates for swimming speed may have been erroneous. I conclude that the model is consistent with laboratory data given proper input parameter values.

Note that an ´encounter´ refers to the entry of prey within the strike field of a predator regardless of prey detection by the predator. By determining empirically what proportion of ´encounters´ result in an attack by the larva, it is possible to generate descriptive estimates of predation rates in chaoborines. For example, I show in Chapter 2 that 46% of copepods entering the strike field of the 4th instar larva of *C. trivittatus* are attacked regardless of prey length (0.9-2.6 mm), prey density (1, 3, 4 or 6 prey/arena) or temperature (6, 13 or 24 C). A similar value was also obtained using *Daphnia rosea* as prey. A wider range of prey sizes (i.e. smaller prey) will have to be used in future experiments to cover adequately the potential range of food items accessible to this larva.

DISCUSSION

An analytical formula was derived which yields estimates for the encounter rate between moving spheres and a stationary cylinder. This approximate solution was congruent with an ´exact´ solution obtained from a general formula solved with a numerical method (where I estimate the angles subtended by a solid). Since these techniques can be applied to volumes of different shapes (e.g. cone, ellipsoid, etc.; Masket and Rodgers 1962), this method could be applied to solve encounter problems for other organisms living in a fluid environment. Many predators lie in ambush until a prey comes within a short distance and then launch an attack to subdue it (e.g. some chaetognaths in the marine environment, Feigenbaum 1979). The size and shape of their strike field will depend on the morphology and physiology of the capture mechanism, and non-spherical collision models will often be necessary.

In the case of the Chaoborus larva, I have shown that it possesses a strike field which is approximately cylindrical, and that it is possible to derive a simple collision model to take this into consideration. The model predictions agree well with observations collected in the laboratory (i.e. the rate at which copepods approach within 2 mm of the body of the larva).

Furthermore, the data indicated a random pattern of distribution of ´encounters´ over time when copepods were used as prey. These experimental verifications lend support to the model, at least for simplified laboratory universes. To determine whether the proposed model accurately represents the opportunities of Chaoborus larvae to feed on zooplankton in their natural environment, I must examine the plausibility of its underlying assumptions.

(1) The predator is stationary. Whether the movements of the larva will affect predicted rates of encounter will depend on the intensity levels of displacement. Observations in the laboratory suggest two principal modes of locomotion in the Chaoborus larva: a jack-knife motion while traveling rapidly from place to place (i.e. swimming), and a slow sinking motion resulting from changes in buoyancy mediated by the tracheal sacs (see Teraguchi 1975). Whereas the former is not accompanied by strike movements upon encountering prey, the latter is and it may be considered as a form of searching and/or stalking. Observations in the field and the laboratory suggest that 4th instar larvae of Chaoborus do not ´search´ or ´stalk´ extensively and that relatively low speeds (< 1 mm/s) are involved (if prey change direction frequently in more or less unpredictable fashion, this tactic would have a limited success).

On the other hand, if larvae ´search´ or ´stalk´ while vertically migrating (when prey are expected to come predominantly from a particular direction, see below), substantial increases in encounter rates may be possible. According to Pastorok (1978), larval migration of 4th instar C. trivittatus at realistic speeds of about 0.9 mm/s will increase encounter rate with prey by less than 10%. His estimate is based on the assumption that the encounter field of the predator is a sphere (its size was set equal to the volume of the strike field based on observations of predator-prey interactions). Although this method is inexact and underestimates encounter rates by 28-42% relative to the present model, it indicates clearly that a larva cannot greatly affect its encounter rate with prey through this behavior.

(2) Prey are spherical. Whereas this approximation appears to hold for copepods, prey of different shapes may not be so easily incorporated into the model. Unfortunately it may be difficult to determine the effective size of spherical prey objects which are equivalent to real prey over a wide range of prey size or length. Two factors mitigate this problem: (a) prey are very small relative to the strike field of the predator, and the latter will be more important in determining the encounter process; (b) prey swimming speeds are often strongly positively correlated with prey size (Eqn. 4 above, Swift and Fedorenko

1975) and the model will be most responsive to changes in swimming speed of prey as prey size increases. Small errors in estimating the effective size of prey will be negligible by comparison. It should also be noted that the model ignored the presence of antennae in copepods and that large individuals may use their antennae to detect predators before the main part of their body comes within striking distance of the predator. This possibility needs further study.

(3) Prey swim at constant speed and in random directions. Movement patterns of copepods include rolls, loops, sudden jumps, sprints for fast escape, chases related to sexual behaviour, etc. Based on observations in the laboratory, their most predominant locomotory behaviour consists of relatively slow displacements along straight path segments (while ´filter-feeding´) interspersed with sudden jumps or changes of direction of short duration. This pattern of behaviour is consistent with the model since it generally involves movement at constant speed, and frequent changes in swimming direction may result in prey approaching the strike field of the predator from random (or unpredictable) directions.

Unfortunately, it is not likely that this pattern holds under all circumstances. For example D. kenai which is the favored prey of this larva (see MATERIALS AND GENERAL METHODS and Chapter 6) undergoes regular vertical migration (viz.

directional swimming). It is therefore important to assess the importance of preferential swimming directions by prey to the encounter process by looking at the symmetry of the strike field of the predator (i.e. compare the encounter rates for prey which move in a vertical vs a horizontal plane where a prey can approach the predator not only from two sides but from the ends as well). For copepods 1.7 mm long at a density of 0.04 prey/ml, and other parameter values given on the section on model parameters, I predict 0.0039 encounter/s in the former case and 0.0047 encounter/s in the latter. Therefore a difference of 20% exists under the worst possible assumption, i.e. the prey are moving exclusively in one plane. If copepods move more generally in both planes in various proportions as suggested by laboratory observations, a smaller error would result.

(4) Prey are uniformly distributed within a patch. This condition can be relaxed to include cases where the prey are randomly distributed, but the major problem consists of defining an appropriate time scale and the patch size while taking into account the tendency of prey to aggregate in specific areas. A patch must be sufficiently small to yield a fairly uniform distribution of prey (in spite of the fact that on a large scale, prey are unevenly distributed in natural environments, particularly so on a vertical scale) but not so small that a significant number of prey move in and out of it over short

periods of time. In other words, one must define an instantaneous rate of encounter for a predator entering a new patch, and apply the model successively as the predator travels from patch to patch over time. The relevant scale of predation dynamics should be determined by potential directional movements of the predator or the prey, e.g. vertical travel.

The time scale should depend on the amount of time necessary for a copepod to pass through a patch while swimming in a straight line. Given speeds ≤ 6 mm/s (Eqn. 4 above, Swift and Fedorenko 1975) and a patch size of 1 m^3 (Gerritsen and Strickler 1977), a value of 2 1/2 min is obtained. If swimming generally occurs in a more random fashion (few species migrate extensively and those that do only do so for 1 or 2 hours daily), this estimate could be revised upwards considerably.

In conclusion, the assumptions proposed for the model seem adequate to represent prevailing conditions encountered by Chaoborus larvae in natural systems. Because (1) predator and prey live in a relatively uniform environment, and (2) the larvae attack in response to acoustic stimuli produced by their prey and the propagation of these signals in water is not altered greatly by biotic or abiotic factors in the environment, the model can be directly transposed to solve encounter problems for larvae in a field situation. However, this will first require extensive knowledge of predator and prey distribution in the field.

2. THE COMPONENTS OF PREDATION

INTRODUCTION

Body size plays a central role in the ecology of aquatic predators. Food size or ration size affects the growth and/or reproduction of aquatic consumers (Nakamura and Kasahara 1956, Parker and Larkin 1959, Le Cren 1958, Paloheimo and Dickie 1966, Gliwicz 1969, Kerr 1974, Galbraith 1975, Petrova _et al_. 1975, Hillbricht-Ilkowska 1977, Morgan _et al_. 1978, Sprules and Holtby 1979, Vermeer _et al_. 1979, Wańkowski and Thorpe 1979, Vidal 1980a,b,c,d) and hence competitive processes (i.e. the size-efficiency hypothesis, Brooks and Dodson 1965, Dodson 1974a; see Hall _et al_. 1976 for a review). Size selective predation by visual predators (Ivlev 1961, Hrbáček _et al_. 1961, Hrbáček 1962, Brooks and Dodson 1965, Galbraith 1967, Houde 1967, Brooks 1968, Dodson 1970, Hall _et al_. 1970, Wells 1970, Hutchinson 1971, Zaret 1972, Nilsson and Pejler 1973, Kerfoot

1975, O´Brien 1975) and non-visual ´invertebrate´ predators (McQueen 1969, Anderson 1970, Dodson 1974a, Kerfoot 1975, Smyly 1976, Confer and Cooley 1977, Kerfoot 1977, Lynch 1979, Neill and Peacock 1980) has also been shown to have a substantial impact on the size and species composition of pelagic zooplankton assemblages.

In spite of the fact that size selective predation affects major ecological processes in aquatic communities, and has played a major role in the development of ecological theory (feeding niche and optimal foraging), ecologists have not satisfactorily apportioned the size selective process to individual components of predation. The efficiency of prey capture will vary with the relative sizes of the antagonists (this has rarely been quantified accurately, Werner 1977; see DISCUSSION for some exceptions), and encounter rates with prey will often depend on predator and prey sizes, because reactive distances are often size-dependent, and speeds of movement of animals are often correlated with body size. Yet simple prey-density-dependent predation functions are generally used in ecological studies (e.g. functional response, Solomon 1949, Holling 1965; for a review of other models see May 1976 and Hassell 1978) and significant features of the dynamics of predator-prey interactions can be lost in the process of simplification.

Detailed studies of components of fish predation have been carried out. Several prey detection models are available (e.g. Ware 1973, Confer and Blades 1975, O'Brien et al. 1976, Confer et al. 1978, Eggers 1977) and fish metabolism has been extensively studied (see Elliott 1979). Unfortunately comprehensive detailed studies are lacking for invertebrate predators. Because predation by small invertebrates occurs at a different scale of predation dynamics than that of relatively large fishes, component studies are needed to reveal the nature of the interactions of invertebrate predators with zooplanktonic prey.

Therefore I undertook quantification of the feeding of the 4th instar larva of *C. trivittatus* on copepods, emphasizing the effects of size on the components of predation. Little detailed information is available concerning predation rates in chaoborines. Body size is known to affect prey selection (Allan 1973, Swüste et al. 1973, Swift and Fedorenko 1975, Smyly 1980, Vinyard and Menger 1980, Winner and Greber 1980), but none of these studies (except for Swift and Fedorenko) used prey which had uniform body plans, comparable escape abilities (Kerfoot 1978) or known swimming speeds (Smyly 1980). Thus they have limited usefulness.

MATERIALS AND METHODS

Fourth instar larvae of _C. trivittatus_ were allowed to attack prey (_D. leptopus_ and _D. kenai_) inside rectangular arenas in the laboratory. A trial consisted of a 12-60 min confrontation (usually 24 or 36 min). The duration was pre-fixed (in 12 min increments) according to prey density. This procedure was repeated until a sufficient sample size was achieved for one treatment category (i.e. one particular combination of predator size, prey size, prey density and temperature). Detailed visual observations of predator-prey interactions were recorded to quantify components of predation as follows (where Pr= probability of):

$$\mathrm{Pr(capture)} = \mathrm{Pr(encounter)} \times \mathrm{Pr(strike)} \times \text{Strike efficiency} \qquad (5)$$

To estimate Pr(encounter), encounter rates (m, in #/min) were estimated (see below) and used as input parameters for a Poisson probability distribution. Pr(strike) and strike efficiency were expressed as proportions of total numbers of encounters and strikes respectively.

I scored an ´encounter´ whenever a part of the body of a prey (excluding antennae) entered a cylindrical volume of space within 2.0 mm of the surface of the body of the larva (this value included 93% of the total number of attacks observed on high-speed films, see Chapter 1), or an attack occurred. Thus an ´encounter´ was usually scored regardless of prey detection by the predator. This division of the space around a larva was chosen for practical reasons (see GENERAL INTRODUCTION). It provides all the necessary information to construct a descriptive model of Chaoborus predation.

I report here the results pertaining to first prey capture by a ´hungry´ larva; the effects of ´hunger´ on the components of predation will not be considered at the present time.

Section I- The effect of prey size, prey density and temperature on components of predation

Observations and data analysis. Predator-prey interactions were monitored by looking down into two juxtaposed arenas. Observations were noted with the help of event recorders running at minimum speed of 3 cm/min (Esterline Angus models A620X and minigraph). Events were coded and decision rules established to deal with some rare but potentially confusing situations in a consistent manner (e.g. a prey moving more or less parallel to the encounter volume is scored only once). The observer prepared the apparatus, assigned predators to treatment cells ´randomly´ (see below) and introduced prey into the arenas. Since deciding that an encounter had occurred involved judgment on the part of the observer (similar to an umpire calling strikes in baseball), an initial training period of 33 hrs was needed until consistent observations were obtained. Grids were glued to the bottom of the arenas to help in making this decision.

Because of various constraints in running these experiments, predators were re-used for periods of 1-3 weeks. Consequently, the data lack independence in a stastistical sense although randomization (by dice throw) was carried out whenever possible. A stastical analysis (F-test) comparing variances in time to first capture within and between individuals indicated no significant differences ($p \geq 0.25$ for all treatment categories tested). Consequently statistical bias due to a lack of independence should be slight.

Experimental arenas. Small containers were assembled out of 0.6 cm Plexiglas. The inside dimensions of each chamber were: height= 4.5, width= 5.0 and depth= 4.0 cm. They were calibrated for volume and a fill line was drawn to show 75 ml. These small dimensions avoided excessive heterogeneity in patterns of distribution of prey without affecting the strike efficiency of the predator in any appreciable manner (strike efficiency within

0.6 mm of Plexiglas vs away from it, $X^2 = 0.46$ and 0.12 for two prey size categories at 13 C; d.f.= 1; $p \geqslant 0.50$). Moreover I have already shown (Chapter 1 Section III) that increases in rates of encounter due to the tendency of the predator and the prey to aggregate in the vicinity of a Plexiglas wall are nearly compensated by a ´shadow´ effect since prey cannot approach the predator from this particular direction. Consequently relatively unbiased encounter rates are presumed to occur within these arenas.

Predator handling. Very small and very large larvae were individually removed from field samples to ensure uniformity of size (mean length= 14.8 mm ±0.95 SE), and individuals were placed singly into an arena. This eliminated the possibility of predator interference. The larvae were given 3 days to become familiar with their new surroundings and fed 2-3 times in a simulated experiment. They remained permanently in a particular arena to keep disturbances to a minimum. Individuals were generally ´starved´ 1-3 days before being used in a trial (depending on convenience) since early results showed that time to first capture did not vary significantly for starvation periods upwards of 1-2 weeks. All individuals tested had an empty crop.

Prey handling. Inter-specific differences with respect to vulnerability to predation were assumed not to exist, except for those that are reflected in body size (see results below). To start a trial, a number of prey of a given size category were put inside an arena using a piece of plastic window screening. Individuals showing signs of damage were immediately replaced. This method of introduction resulted in slightly higher levels of prey activity at the beginning of a trial, but an otherwise stable pattern of activity seemed to hold for at least one hour.

Treatments. Four treatment factors were initially considered, but early results showed that light did not significantly affect time to first capture ($t= -0.99$; $d.f.=39$; $p \geq 0.30$) and a standard setting of 1600 Lux was adopted thereafter. Treatments comprised four levels of prey size (categories I to IV, see MATERIALS AND GENERAL METHODS), three levels of temperature (6, 13 and 24 C) and six levels of prey density (1, 2, 3, 4, 6 and 9 prey/arena). Not all possible combinations of these levels were investigated, and two densities were most commonly used throughout (3 or 6 prey/arena). All but the lowest prey density represent food concentrations greater than normally encountered in the lake. This was necessary to generate a sufficient number of observations over short time periods. It was assumed that there was no effect of density on Pr(strike) or strike efficiency (see results below).

Section II- The effect of predator body size on Pr(capture) and some components of predation

The experiments described above did not include a complete range of larval sizes. I investigated separately how predator body size affects prey capture by running one series of experiments (13 C, 6 prey/arena) using three predator length categories (11-12, 13-14 and 15-16 mm). Pr(capture) was determined directly for all four prey size categories using the geometric distribution (Appendix I). Some visual observations were also collected to quantify components of predation (right hand side of Eqn. 5) according to the methods previously described in Section I above. However, since sample size was small (n= 8) and these data are incomplete (I have visual observations for prey size categories I, II and III only), the individual components of predation are dealt with summarily.

RESULTS

Section I- The effect of prey size, prey density and temperature on components of predation

1. Pr(encounter). To obtain a uniform composition of prey sizes, and in order to ensure consistency in scoring encounters, the encounter data were collected over a short period (10 days) in June 1977. Mean encounter rate values (m) are summarized at the top of Table VI. Significant effects (see statistics on p. 37, Chapter 1) of prey density and prey size (but not temperature) on m were found. These values were converted to a probability estimate by making use of the Poisson distribution. Since the larva can only capture one prey at a time, the opportunities for capture can be best described by adding up the probabilities that there occur one, two, three, etc. prey within the strike field of the predator (one minus the zero term of the Poisson distribution, $m^* = (1 - e^{-mt})$. These values are also given in Table VI.

Table VI Encounter parameters between copepods and the attack field of the 4th instar larva of C. trivittatus for four prey size categories (see MATERIALS AND GENERAL METHODS) and two prey densities (3 and 6 prey/arena). m= mean encounter rate in #/min (± 95% C.L.) m*= Probability that at least one encounter occurs in one minute (see text for explanation).

Parameter	m		m*	
Prey density (#/ml)	0.04	0.08	0.04	0.08
Prey size categories				
I	0.227(.056)	0.519(.184)	0.203	0.405
II	0.443(.089)	0.737(.136)	0.358	0.522
III	0.492(.164)	1.000(.152)	0.389	0.632
IV	0.557(.092)	1.214(.296)	0.427	0.703

2. Pr(strike). There was no significant effect of density on the proportion of ´encounters´ which resulted in a strike (X^2; d.f.=3; p= 0.74, 0.15, 0.73 and 0.49 for 4 treatment categories tested). The data were pooled over this variable and are summarized in Table VII. There was no significant effect of temperature or prey size on Pr(strike) (contingency X^2; $p \geq 0.34$). The pooled value for Pr(strike) on copepods is therefore 0.459. An estimate obtained for Pr(strike) on *Daphnia rosea* (~2 mm), a different type of prey also found in Gwendoline Lake, was nearly identical (0.472).

3. Strike efficiency. There was no significant effect of prey density on the proportion of strikes which were successful (X^2; d.f.= 1-4; $p \geq 0.32$ for five treatment categories tested). The data were therefore pooled over this variable and are summarized in Table VIII, along with results from Swift and Fedorenko (1975) and Pastorok(1978). Their results are similar to my findings at 6 and 24 C, but data collected at 13 C clearly indicate a positive effect of temperature on strike efficiency (roughly a 50% increase). It is presumed that this results from different effects of temperature on speeds of attack and escape in the predator and prey respectively. Confirmation awaits the analysis of high-speed films of predator-prey interactions.

Table VII The percentage of copepods that enter the attack field of the 4th instar larva of *C. trivittatus* and are attacked by a ´hungry´ larva (i.e. Pr(strike) see Eqn. 5). The total number of ´encounters´ observed is shown in parentheses. Data were collected for four prey size categories at three temperatures. Data were first pooled with respect to prey density. The probability estimates (p) are from a contingency X^2 test.

Temperature (C)	6	13	24	
Prey size categories				
I		0.373(51)	0.450(20)	0.55
II		0.443(194)	0.483(118)	0.49
III		0.456(217)	0.444(162)	0.82
IV	0.493(138)	0.435(389)	0.474(880)	0.34
		0.67	0.90	p

Table VIII Summary of the data available for strike efficiency (with the total number of strikes observed) for the 4th instar larva of *C. trivittatus*, as a function of temperature (T) and prey size. Data were pooled with respect to prey density.

T	Approximate copepod sizes					
(C)	0.6	1.0	1.2	1.4-1.5	1.8	2.1-2.2
6						0.033(92)
10	0.396(187)	0.242(66)		0.198(116)	0.143(154)	0.022(180)
13			0.287(28)+	0.287(87)	0.314(236)	0.143(328)
15				0.240(55)*		
24			0.226(40)+	0.204(54)	0.174(161)	0.092(500)

*= *Diaptomus franciscanus* += *D. leptopus* Otherwise *D. kenai*

10 C= Swift and Fedorenko (1975) 15 C= Pastorok (1978)
6, 13 and 24 C= This study (except 1.2 mm prey, Pastorok 1978)

This temperature effect may have been confounded by an acclimation factor since larvae were kept at 13 C when brought into the laboratory. I investigated this possibility by estimating strike efficiency over time for larvae kept at 24 C. No trends towards an increase in strike efficiency were apparent after three weeks. It is thus likely that the temperature effect on strike efficiency is real.

To estimate Pr(capture), I multiplied the individual components of predation (right hand side terms of Eqn. 5). This simple computation is justified because there were no effects of prey density on Pr(strike) or strike efficiency, and because the two prey species did not seem to differ with respect to their vulnerability to predation except as expected on the basis of their differences in body size alone (e.g. see Table VIII). The results are presented in Table IX.

Section II- The effect of predator body size on Pr(capture) and some components of predation

Pr(capture) determined from the geometric distribution varied with predator body size (Table X) and the differences were significant for prey size categories I and IV (extension of

Table IX Probability that a ´hungry´ 4th instar larva of C. trivittatus will capture a copepod in one minute determined from the product of individual components of predation (see Eqn. 5). This was done for four prey size, three temperature, and two prey density treatments.

Temperature (C)	6		13		24	
Prey density (#/ml)	0.04	0.08	0.04	0.08	0.04	0.08
Prey size categories						
I	0.020	0.039	0.026	0.051	0.021	0.040
II	0.033	0.048	0.047	0.069	0.034	0.049
III	0.026	0.041	0.056	0.089	0.031	0.050
IV	0.006	0.007	0.032	0.045	0.020	0.030

Table X Probability that a ´hungry´ 4th instar larva of *C. trivittatus* will capture a copepod in one minute (with sample size) determined from the geometric probability distribution for four prey size and three predator size categories (see text and Appendix I for explanation). The data were first pooled with respect to temperature. The probability estimates (p) were obtained from the extension of the median test (Siegel 1956).

Predator sizes	Prey size categories			
	I	II	III	IV
Small	0.079(8)	0.109(16)	0.047(16)	0.008(8)
Medium	0.040(8)	0.056(16)	0.056(16)	0.015(7)
Large	0.024(8)	0.034(16)	0.056(8)	0.056(8)
p	0.03	0.40	0.64	<0.01

the median test, Siegel 1956). It is clear that small predators are more successful at capturing small prey than are large predators and *vice versa*. Pr(strike) data did not exhibit any recognizable trend with respect to predator body size, but strike efficiency data showed the same significant trends as Pr(capture). The last two sets of data were significantly correlated ($r^2 = 0.50$; d.f.= 7; $p \leq .05$); body size dependent strike efficiency is thus a major determinant of patterns of Pr(capture) in these larvae.

Prey size had a positive effect ($p \leq .01$) on Pr(encounter); these encounter values were collected in June 1978 and are somewhat higher than those reported in Table VI. Predator size had no significant effect ($p = 0.09$), although the trend was in the expected direction. High-speed films of *Chaoborus*-copepod interactions (see GENERAL DISCUSSION) show that attack distances of 'hungry' 4th instar larvae of *C. trivittatus* are not affected by larval length within an instar. An effect of predator size on encounter rates therefore may have been difficult to detect given my sample size and methods.

DISCUSSION

Prey size had a strong positive effect on encounter rate values. A collision model based upon theoretical considerations of the size and speed of randomly moving particles has been developed independently in an attempt to describe this process accurately. It showed good agreement with the present data (Table VI) obtained in the laboratory (Giguère *et al.* submitted; Chapter 1).

The larvae generally responded to 46% of prey coming within 2.0 mm of their body regardless of prey length (over a 0.9-2.6 mm range) or experimental conditions. Pastorok (1980) reported non-selective feeding by 3-day ′starved′ *C. trivittatus* 4th instar larvae when offered the choice between two types of prey (1.5 mm *Diaptomus franciscanus* and *Daphnia pulicaria*). My results also suggest opportunistic feeding (with respect to prey size or type) in ′hungry′ *Chaoborus* larvae. However, since an encounter with prey was not defined with respect to prey detection by the predator, these results must be interpreted cautiously. A broader range of prey sizes will have to be included in future experiments. Copepods as small as 0.6 mm are not uncommon in the lake, and there must exist a lower prey size threshold below which prey will elicit relatively few attacks.

Strike efficiency tends to decrease as prey size increases, although the trend obtained at 13 C is not linear like the data of Swift and Fedorenko (1975) at 10 C. Similar results have been presented by Kerfoot (1978) for two species of cyclopoid copepods feeding on Bosmina. This effect of prey size on strike efficiency (along with prey size dependent encounter rate values, see Chapter 1, and GENERAL DISCUSSION) will be critical in determining patterns of food size selection of larval chaoborines.

Strike efficiency also exhibited patterns of variation as a function of the size of the 4th instar larva. It is clear that predator and prey size interact to determine patterns of feeding efficiency in this predator. This had been previously demonstrated for one aquatic invertebrate predator using prey of uniform body plan (Cloarec 1980). Similar data have been published for non-aquatic predatory insects (Dixon 1959, 1970, Wratten 1973, Glen 1975, Evans 1976). There are also several studies on aquatic invertebrates which deal with this problem at the interspecific level (Brown 1974, Kerfoot 1978, Gittelman 1978, Williamson and Gilbert 1980). Clearly the relative size of a predator and its prey is an important variable to control for in feeding or growth experiments. Detailed information on the effect of body size on individual components of predation is thus necessary to predict accurately the rate of transfer of energy between a predator and its prey.

For the *Chaoborus* larva, one could argue that the size of prehensile antennae and other parts of the trophic apparatus is adapted to grasp prey of a particular size and that this determines patterns of strike efficiency. An important factor militates against this morphological interpretation: whereas body size varies considerably with growth within an instar, head length remains constant (although a variable degree of chitinization with age, Swift and Fedorenko 1975, and possibly of muscularization as well, could affect strike efficiency). The most significant factor contributing to a variable strike efficiency is therefore body size *per se*, through the effects of drag, viscosity, etc. on speed of attack. Visual observations suggest an attraction between the predator and the prey when prey are very small and close to the body of the predator. Prey can be entrained by the attack movements of the predator and remain at a safe distance from the predator's head throughout the attack cycle. This suggests a much closer coupling between predator and prey sizes than was previously assumed.

An effect of temperature on strike efficiency is also relevant in the context of the energetics of vertical migration. McLaren (1963) suggested that migrants can derive an energy boost by alternating between warm, food rich surface water layers (where feeding occurs) and cold deeper layers (where digestion is more efficient). Swift (1976) could not demonstrate the existence of such an energy bonus for migrating 4th instar

C. trivittatus larvae in Eunice Lake (British Columbia), but he suggested that diel variation in prey vulnerability could affect his findings (although his model called for a considerable change in prey vulnerability to alter his conclusions). Since strike efficiency (at least for copepods) is temperature dependent, and since D. kenai also undergoes diel vertical migration in the field (roughly in the opposite direction to that of the larvae), predators could maximize food intake by timing their movements to encounter ′preferred′ prey in the appropriate temperature zone where strike efficiency is highest. On the other hand digestion rates (Fedorenko 1975a; Chapter 4) and respiration rates (Swift 1976, Giguère 1980; Chapter 3) are also temperature dependent in this organism, and food assimilation efficiency is temperature and meal size dependent (Giguère 1981; Chapter 4). Consequently more detailed models must be used to determine: (1) if an energy boost is possible under simulated field conditions, (2) the net magnitude of this possible gain, and (3) what factors or combination of factors are mainly responsible for it. Some of these factors are considered in Chapter 6 (Giguère and Dill 1980).

Ultimately I hope to obtain similar data to examine the effect of body size on capture efficiency for smaller instars. It should then be possible to determine if there exists a continuum of resource utilization throughout the life cycle of Chaoborus, or whether feeding occurs through discrete phases or stanzas as suggested for fishes (Parker and Larkin 1959). This information would be useful in order to understand growth and development patterns in chaoborines. Before doing so, the present methods will be applied to describe the effects of ´hunger´ on the components of predation (Giguère in prep.). A comprehensive energetic model of predation by the 4th instar larva of C. trivittatus on copepods will then be assembled.

3. RESPIRATION AND ENERGETICS

INTRODUCTION

Two of the major problems encountered in component studies of predation consist of evaluating what proportion of the predator´s time is spent in foraging vs non-foraging activities (and the various costs associated with these), and what the actual rate of successful search is in a natural environment. The problems are particularly acute when dealing with a vertebrate predator searching for prey in a relatively heterogeneous environment and engaging in any number of non-feeding behaviours (e.g. social, reproductive and anti-predatory behaviours).

To circumvent these problems, I undertook an energetics study of an ´ambush´ type of predator, living in a relatively simple and uniform environment, and whose behavioural repertoire consisted of a few activities whose frequencies and unit costs could be estimated. In Gwendoline Lake, the 4th instar larva of C. trivittatus has no known major predator (Neill and Peacock 1980), and all of its activities (sitting in ambush, swimming vertically and attacking prey) have feeding or feeding-related functions. Moreover, it attacks primarily in response to acoustic stimuli produced by its prey (Giguère and Dill 1979; Chapter 5), and the propagation of these signals in water should not be altered greatly by biotic or abiotic factors in the environment. In this way, much of the complexity of the interaction between predator and prey which is encountered in component studies of visual predators is eliminated, and laboratory results can be translated easily to a field situation. In this chapter, I present results on respiration rates pertaining to the negative terms of the energy budget of the 4th instar larva of C. trivittatus, and describe a new technique which permits measurement of the cost of attacking prey by exploiting the tendency of the larvae to attack a needle vibrating at high frequency.

MATERIALS AND METHODS

Chaoborus handling. Chaoborus larvae were kept in 75 ml containers at the experimental temperature for at least 24 hours before an experiment. This allowed them to become accustomed to confinement. To minimize the possibility of activity due to light-controlled diel rhythms, the respirometer bath was covered with a black plastic sheet and the larvae were kept under dark conditions. Periodic observations ensured that the larvae remained motionless. Oxygen comsumption by young (~13 mm in length) and old (~16 mm in length) larvae was estimated separately. Based on samples dried in an oven for 3 days at 80 C, they weighed 1.30± 0.05(26) and 1.84± 0.17(11) mg dry weight respectively. (All data presented in this chapter are means ± SE(with sample size)).

<u>Apparatus and data conversion</u>. All measurements were obtained with a manometric technique using a Gilson differential respirometer (Gilson 1963) and standard operating procedures. The unit possesses a constant temperature bath and 14 individual 16 ml flasks. I used 6-8 ml of lake water per flask (with 6-8 ml of air space) to avoid declining oxygen tensions in the water for long (24 hour) respiratory runs (I assumed that diffusion maintained the gas equilibrium between air and water). The apparatus was located in a growth chamber and the temperature regulated (±1.5 C) to obtain more accurate readings. After a two hour equilibration period, initial readings were taken. Larval oxygen consumption was then estimated from a set of readings taken after a fixed period of time and converted to energy by multiplying by the constant 0.0202 Joule/μl oxygen. Although the

respirometer is calibrated to show very small differences in volume (0.2 μl), external sources of variation (mainly small differences in temperature) do not permit such accuracy. Therefore I relied on statistical measures to identify significant differences between treatments ($p \leq 0.05$).

The number of larvae in each vial was increased from one to four individuals to facilitate readings at low levels of oxygen consumption for young larvae, since it did not result in a marked increase in their activity or consumption of energy (for fed young larvae at 21 C, energy consumption in mJ/larva/hour was 23.9± 2.08(8) for one larva, 19.0± 1.76(7) for two larvae, and 19.5± 0.78(15) for four larvae; F= 3.31; d.f.= 2,27; $p > 0.05$).

Resting metabolism. Starved individuals should consume less oxygen than recently fed ones since the latter are engaged in processing, absorbing and transporting food metabolically. Therefore I had to establish two sets of experiments to determine metabolic expenditures in recently fed animals, and metabolic expenditures for larvae 'starved' for a fixed period of time using recently fed animals as controls. In the first case, all larvae were fed copepods (D. kenai) just prior to the start of an experiment, and 1-2 individuals (either old or young) were placed in each vial. This was repeated at 13 and 21 C and resulted in four treatment groups. Given that a short period of starvation does not reduce oxygen consumption and that larval feeding occurs on a fairly regular basis, these data approximate metabolic expenditures at rest for larvae in the field. In the second case, three groups of young larvae were ´starved´ for 1-2, 4 and 6 days respectively. In each group, at least half the larvae were fed copepods in a tray at 21 C just prior to being introduced into the respirometer flask.

By comparing the metabolic rate of ´starved´ larvae (SMR) to that of those recently fed, one may obtain an estimate of ´specific dynamic action´ or SDA, i.e. the increase in metabolism due to processing of a meal (Wigglesworth 1965). According to Warren and Davis (1967) this method is valid as long as the activity of the animals studied is minimal, a condition which appeared to hold in these experiments.

Active metabolism. I attempted to estimate the energy cost of swimming and attacking prey by stimulating larval Chaoborus confined in a respiratory flask at 21 C, either with a bright light flash or a brief acoustic signal. By substracting the measured levels of active metabolism from the resting metabolism of the immobile larvae, the cost of their swimming or attacking motions can be evaluated. This assumes that respiration rates do not vary according to a circadian rhythm independent of external conditions and that any increase above the basal rate can be attributed to the activity of the larva (such as for

C. punctipennis, Sigmon *et al*. 1978). According to observations made on Odonata (Lawton 1971), this is most likely to occur in organisms in which the eyes are less important in prey detection. This would apply to the *Chaoborus* larva (Giguère and Dill 1979; Chapter 5).

For the energy cost of swimming, all larvae were ´starved´ for 24 hours and four individuals were put into each of 9 flasks. Larval respiration rates were measured for 3 hours, following which the flasks were exposed to a bright source of light to which the larvae responded by swimming (presumably an avoidance reaction). It consists of a jack-knife motion followed by a glide. This 70 s exposure alternated with a 70 s rest period, and the sequence was repeated 21 times for a total of 49 min. The total number of swimming motions of the larvae was counted in one or two vials each time and for four or five periods per vial. The larvae were then left alone for 71 min to reclaim any oxygen debt, and a final reading was taken. By comparing larval oxygen consumption at rest (first 3 hours) with that during the period which included swimming (last 2 hours) for each vial, I determined the consumption due to swimming activity. This was divided by the estimate of the total number of swimming motions for each vial and converted into Joules.

For the energy cost of attacking, a single larva was placed in each vial and the stimulus for attack was provided by an acoustic signal. The transducer consisted of a transistor radio earphone with a shortened insect pin affixed to its diaphragm (Giguère and Dill 1979; Chapter 5). The unit was placed inside a flask and the electrical wires run through a previously broken side arm and sealed with epoxy glue. The larva was kept in the vicinity of the vibrating needle by a plastic screen (Fig. 5). Signals were produced at 1,000 Hz, and at a volume of 3 v. Short (<1 s) signals were used, and the number of attacks generated was limited to a maximum of 300 to prevent the accumulation of an excessive oxygen debt. As in the previous experiment, each trial ended with a period of at least 60 min during which no activity was elicited.

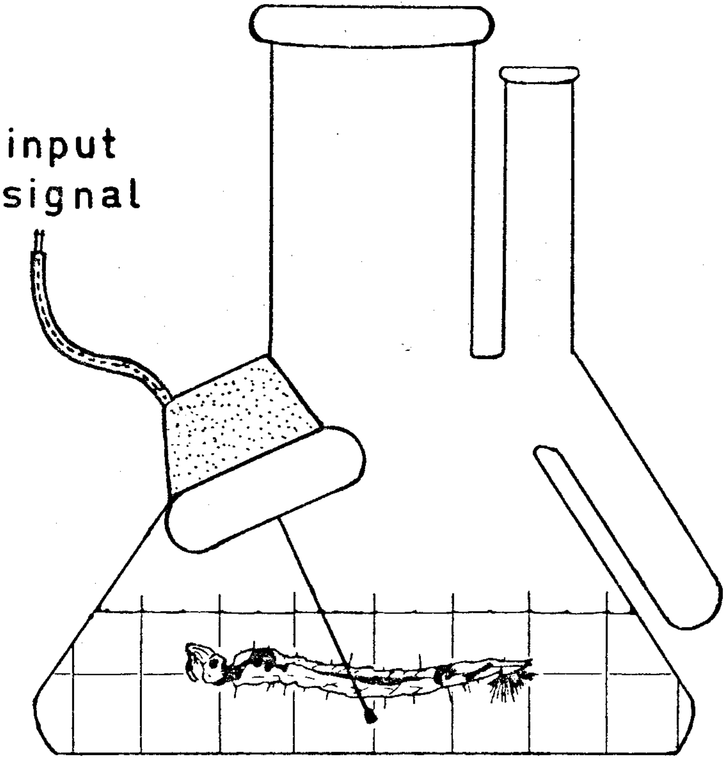


Fig. 5 Diagram of apparatus used to measure energetic cost of attack in Chaoborus larvae. The acoustic signal is provided by an oscillator. The transducer is an insect pin glued onto a transistor radio earphone. A screen keeps the larva near the vibrating needle.

RESULTS

Resting metabolism

Energy consumption of fed larvae is shown in Table XI. An analysis of variance was performed on these data, and there was a highly significant effect of temperature and age (or size) on energy consumption. Although the data also suggest an interaction between age and temperature (i.e. old larvae show a greater degree of temperature independence relative to young ones), this effect was not significant (Table XII). On the other hand, Q_{10} values calculated (according to a formula in Hoar 1966) from these data were 3.1 and 1.7 for young and old larvae respectively and very similar to those derived from Swift´s (1976) figures (2.9 and 1.7) over the same range of temperature. Therefore our joint data suggest clearly an interaction between temperature and the age of a larva on respiration rates. Since larvae do not interact with one another in the confines of the respirometer flasks (both Swift and I used one old larva and two young ones in our experiments), the effect cannot be attributed to differences (with respect to age) in temperature dependent levels of behavioural interaction between larvae. Rather it is

Table XI Mean metabolic expenditures (in mJ/larva/hr)± SE (with sample size) of young and old 4th instar larvae of *C. trivittatus* that fed on one copepod at 13 and 21 C.

Age of larva	Temperature (C)	
	13	21
Young	8.6± 1.28(13)	21.2 ± 1.83(7)
Old	20.5± 0.85(30)	30.6 ± 1.78(15)

Table XII Analysis of variance of mean metabolic expenditures of 4th instar larvae of C. trivittatus as a function of temperature and age of larvae.

Source of variation	Sum of squares	d.f.	Mean square	F	p
Temperature	3.52	1	3.52	51.9	<0.001
Age	3.90	1	3.90	57.5	<0.001
Interaction	0.05	1	0.05	0.7	0.40
Residual	4.14	61	0.07		
Total	12.41	64			

likely to reflect previous temperature regimes experienced by larvae in the field. Old larvae exhibit vertical migration patterns of wider amplitude than young ones. This could expose them to cold temperatures for longer periods of time and induce acclimatization.

On the other hand, although the pattern of my data is consistent with Swift's data, my estimates are greater than one would predict from his figures (by 33%, 33%, 43% and 22%). Since his measurements apply to larvae which had no food in their crop, more detailed information on SDA is needed to interpret this difference correctly.

Fed individuals consumed energy at a higher rate than 'starved' individuals and the differences were found to be statistically significant after periods of 4 and 6 days (Table XIII). By averaging the statistically significant values, one finds that SDA causes a 37.3% increase in energy consumption relative to un-fed young 4th instar larvae of C. trivittatus. This value would account for the differences observed between Swift's results and my data in Table XI (assuming that SDA is independent of body size (or age?) as shown for fishes, Kerr 1971). This value is also comparable to the 40% value determined by Gourévitch (1928) for another insect, the cockroach, at 15°C.

Table XIII Mean metabolic expenditures (in mJ/larva/hr)±SE (with sample size) as a function of starvation period for young 4th instar larvae of *C. trivittatus* at 21 C. Each ′starved′ group (1-2, 4, 6 days) is compared statistically with a control group using a t-test. Percentage increases in energy consumption represent metabolic costs of processing food (SDA).

Days starved	Treatment groups not fed		Treatment groups fed		% increase	No. of larvae per flask	t	p
1-2	19.8	2.48(8)	21.6	1.48(15)	9.1	1-2	0.68	0.50
4	13.3	1.20(5)	18.9	0.69(9)	42.1	4	4.36	<0.001
6	15.5	0.49(6)	20.4	1.70(6)	31.6	4	2.74	0.02

Active metabolism

Young and old 4th instar larvae do not differ significantly with respect to their energy consumption due to swimming or attacking (Table XIV). Since these larvae differ in body size, this finding is somewhat surprising. However, sample sizes are small and only small changes in body size are found within an instar. The difference may be too small to be detected using a Gilson apparatus. The pooled estimates are 0.07 and 0.57 mJ/motion for swimming and attacking respectively. To determine if a bias is inherent to these estimates because of the accumulation of an oxygen debt (measured energy expenditure would decline at high levels of activity) I regressed the estimates for expenditures while active on the number of motions in each case.

The correlation was not significant for cost of swimming (r^2= 0.06; d.f.= 7; p= 0.87; y-intercept= 0.07) but some effect (albeit not significant) was indicated for cost of attacking (r^2= 0.41; d.f.= 16; p= 0.09). The y-intercept (1.2 mJ) suggests a unit cost value double that shown in Table XIV.

Table XIV Unit cost of swimming and attacking (in mJ per motion) ± SE (with sample size) of 4th instar larvae of *C. trivittatus*. Young and old larvae are compared statistically with a two-tailed t-test.

Unit cost of	Young larva	Old larva	t	d.f.	p	Pooled value
swimming	0.08± 0.021(6)	0.05± 0.007(3)	1.00	7	0.35	0.07± 0.014(9)
attacking	0.68± 0.277(12)	0.34± 0.114(6)	0.83	16	0.42	0.57± 0.189(18)

DISCUSSION

Before examining these estimates of metabolic expenditures in the context of the feeding ecology of the Chaoborus larva, the unit cost estimates must be weighted by considering appropriate intensity levels of activity for a larva living in its natural environment.

The energy cost of attacking (0.57 mJ/attack) is about 2.8 and 6.6% of the hourly metabolic rate at 13 C for old and young larvae respectively. If an attack occurred every 100 s, it would double the metabolic expenditure of an old larva. However, since a larva can generally capture a copepod in 3 to 8 attacks, the cost of capture represents only 0.3 to 3.9% of the energy contents of a copepod over a copepod size range of 1.2-2.3 mm (from Fedorenko 1973). A daily meal of 2-3 copepods (Fedorenko 1975b) can then be secured at an attack cost less than 2.8% of the daily resting metabolic expenditure of an old larva at 13 C.

The energy cost of swimming is about eight times lower than the cost of attacking, but its total contribution could be significant because the larvae exhibit considerable vertical displacements in the field. Since a larva covers roughly 2.5 cm vertically per swimming motion (based on observations in an artificial column in the laboratory), it will cost a larva 17 mJ to actively swim a distance of 6 m. If one assumes that (a) a larva migrates from a temperature of 6 to 20 C and that the respiration rate at 13 C represents the average metabolic expenditure during this period, (b) the unit swimming cost is constant regardless of temperature (i.e. the effect of drag due to temperature dependent changes in viscosity are considered to be negligible), and (c) the active vertical migration of 6 m lasts about 1 hour (as for C. flavicans in Lochan Dubh, Goldspink and Scott 1971), an old larva would approximately double its metabolic rate during this period. This result is in line with various estimates published on active vertical migration in planktonic crustaceans (see review by Klyashtorin 1978).

The daily cost of migration can be calculated in another way. If we accept a resting metabolic expenditure of 490 mJ/day at 10 C (from Swift 1976), the cost of a 20 m active migration (i.e. 10 m in each direction) represents 11.6% of the daily expenditure at rest. This is much greater than the less than 3% estimated by Swift (1976) for the same vertical displacement. His estimate is based upon friction coefficients, sinking rates, and the metabolic efficiency of the animals, and may well represent a theoretical minimum cost for displacement in Chaoborus larvae. Such an estimate might apply in the case of a larva which migrates vertically by adjusting its buoyancy with the help of its tracheal sacs. On the other hand my estimate would be applicable in a situation where vertical migration occurs by active swimming. If one assumes that a larva uses both methods in equal proportions, an intermediate cost value of 7.3% of the daily metabolic expenditure at rest would be appropriate. While there is no direct evidence to support this assumption, Fedorenko and Swift's (1972) data do show that larvae in the field exhibit a rapid dusk rise (active swimming?) followed by a gradual descent throughout the night (passive sinking?; see Pearre 1979, p. 30). However, to obtain a realistic value for the daily cost of vertical migration for 4th instar _C. trivittatus_ in Gwendoline Lake, this estimate must be corrected to include SDA and to account for the fact that the amplitude of migration is no more than 6 m. This results in an increase of 2.8% to the daily resting metabolic expenditure at 10 C.

In short, the portion of metabolic expenditures attributable to the activity of the larvae is quite small (< 5-10% of the daily resting metabolic expenditures). On the other hand SDA (36.9% of SMR) could play a very significant role in affecting the balance of the energy budget of this ambush predator. Whereas good estimates are now available for SMR (Swift 1976) and SDA (this chapter), it remains difficult to assess the importance of the latter since one also would need to know how SDA varies as a function of meal volume, and the time spent between feeding bouts relative to the total duration of SDA following meal intake (presumably about 3 days). Although the experiments above refer to individuals that captured a single prey, a sufficient number of young larvae (at 21 C) captured two prey to warrant a comparison, and hence evaluate the effect of meal volume on SDA. The difference in energy consumption of individuals catching two prey or one prey (25.9± 3.52(10) and 23.9±2.08(8) mJ/larva/hour respectively) was not significant (t= -0.46; d.f.= 16; p= 0.67).

The lack of an effect of meal size on SDA (expressed as an instantaneous rate or % of SMR) suggests that the metabolic processes involved in the assimilation, transportation, storage of food, etc. can be described as being switched ´on´ or ´off´. Thus the larvae can be characterized according to two fundamental physiological states. Since it is obvious that SDA must depend somehow on the size of the meal ingested, one has to consider the length of time during which SDA is expressed in relation to the time necessary to complete digestion of a meal of a particular size. Although these data are not available for Chaoborus, crop emptying takes longer for large meals than small ones (Chapter 4).

The question then becomes how often do starvation periods of 2-4 days occur for individuals living in their natural environments? Is this critical starvation interval attained periodically (in which case SDA would be a major determinant of total expenditures), or is feeding occurring in a sufficiently regular manner that only one physiological state is possible (SMR+SDA) except under very specific circumstances (such as in the winter)?

According to crop content analyses performed by Fedorenko (1975a) and Swift (1976) on *C. trivittatus* larvae from neighbouring Eunice Lake, at most 40% of larvae collected had food in their crop, a rough value of 30% being generally more representative of their data. On the basis of this observation as well as information on the diel feeding pattern of the larvae, Swift (1976) suggested that only a small proportion of the larval population feeds on a given day. Therefore SDA is a significant factor that must be considered in energetics studies of *Chaoborus* larvae.

4. DIGESTIVE PROCESSES

INTRODUCTION

Optimal foraging theory says that an animal should feed efficiently because (a) it may be in competition with other animals for a limited resource, and/or (b) this allows more time to be spent in other important activities (Davies 1977). On these grounds, optimal feeding strategies based on the interaction of behavioural and morphological adaptations have been proposed and tested experimentally. One prediction is that predators should rank prey according to profitability (i.e. net energy content/'handling' time, or the time spent pursuing, subduing and eating prey) and feed only upon the most profitable items still allowing them to meet their energetic requirements (see Pyke _et al_. 1977).

An underlying assumption of this theorem is that prey can be assigned a fixed net energy content regardless of the predator´s previous hunting success. For example, it may be assumed that assimilation efficiency remains the same whether or not the gut is partly full. However, it appears quite unlikely that organisms possess an unlimited capacity for assimilation; rather it is reasonable to expect that under normal circumstances it should be bounded, and that foraging should be carried out in such a way that physiological capacity for absorption is rarely exceeded. Having meal size regulated by gut fullness (i.e inversely related to ´hunger´) would serve this purpose. However, many organisms feed upon fairly large food items (i.e. whole prey) and it is unlikely that ´hunger´ will always succeed in adjusting meal size optimally. Similarly, food items may become available in various temporal patterns that force meal size to vary considerably. It is therefore possible that assimilation efficiency will vary as well, and to imagine various ways that this might depend on meal size and influence optimal diet significantly. Assimilation efficiency, while included as a component in some models, is usually assumed to be constant.

Preliminary observations suggested a decrease in assimilation efficiency for large meal sizes in the Chaoborus larva. The mid-gut (where absorption occurs) has a limited volumetric capacity relative to the maximum volume of the crop (which liquefies and pumps the food into the mid-gut), and since crop volume decreases in roughly exponential fashion after feeding, the initial rate of transfer of food materials from the crop into the mid-gut is high relative to the latter's storage capacity. This could create a nutrient loss in the faeces and result in lowered assimilation efficiency (AE).

The purpose of the present study was to determine empirically the rate of emptying of the crop (or rate of digestion) and the efficiency of assimilation for prey or meals varying in size at different temperatures. Little is known about the latter in predatory zooplankton (Cosper and Reeve 1975), but it is usually found to be constant over a wide range of feeding rates in invertebrate predators (Lawton 1970). If assimilation efficiency could be shown to vary as a function of meal volume, it would be of considerable importance for studies on growth, production and optimal foraging of invertebrate predators.

MATERIALS AND METHODS

Assimilation efficiency

In order to evaluate AE at various temperatures while controlling temperature effects on feeding rates, I fed a known number of radioactively labelled prey to individual 4th instar larvae of Chaoborus, monitoring the appearance of radioactive materials in the water in which they were kept. Copepods were labelled by allowing them to feed for 3 days in 300 ml of lake water to which 50 µC of ^{32}P orthophosphate (Amersham) were added. They were washed and re-suspended for 24 hours in natural lake water to eliminate short term loads of ^{32}P (e.g. in the gut, or adhering to the carapace), rinsed twice more and divided into three approximate prey size categories: I- D. leptopus, 1.3 mm in length, 0.10 µl by volume; II- D. kenai, 1.8 mm, 0.30 µl; III- D. kenai, 2.2 mm, 0.50 µl. They were offered to Chaoborus larvae for a period of up to 45 min, and the larvae that fed were individually placed in vials containing 12 ml of lake water. Five meal size (or volume) treatment groups resulted: 0.10 (I), 0.20 (2xI), 0.30 (II), 0.50 (III) and 0.90 µl (2xIII). The latter category was set arbitrarily at 0.90 µl rather than

$\sim$ 1.0 µl to compensate for the tendency of the larvae to obtain a somewhat smaller prey on their second capture. Sample size generally varied between 7 and 92 (mean= 17.6).

Following feeding, the larvae were kept without food and transferred to a new vial at least three times during the experiments (including the first and last day in every case) to avoid direct uptake of ^{32}P from the water (Marshall and Orr 1955). After 5-10 days (depending on temperature and convenience), the larvae were measured, transferred to 2 ml Protosol, and digested at 60 C for at least 6 hours. In this way, self absorption biases were kept to a minimum. The amount of ^{32}P in each larva was then estimated using standard procedures (toluene cocktail, quench on background corrections) on a scintillation counter. All vials (4-5/larva) containing waste water were assayed using Cerenkov's method (Kobayashi and Maudsley 1974) and all results were converted to disintegrations per minute (dpm). Percent assimilation was then estimated for each larva (as 100 X (dpm larva)/(dpm waste water + dpm larva) and the arc-sin square-root transformation applied for statistical treatment. These experiments were carried out at 6, 13, 16 and 24 C. There were therefore twenty meal volume-temperature combinations.

To ensure that excretion of ^{32}P by the larvae did not significantly reduce the estimates of assimilation, I observed the sequence of appearance of ^{32}P in the water over 8 days for 8 larvae fed a meal volume of 0.50 µl at 13 C, transferring the animals to new vials daily. The dpm values showed a rapid decline with time, were low after 6 days, and equalled 0 for 5 of the 8 animals after 8 days (Fig. 6) . If we use the mean value from the last set of vials to provide an estimate for daily loss due to excretion (assuming that this value remains constant throughout), excretion represents less than 1% of the total dpm over 8 days. Therefore, AE will be estimated fairly accurately as long as (1) phosphorus is fairly evenly distributed in all parts of the body of the copepod (as for *Calanus finmarchicus*, Marshall and Orr 1955), or (2) all body parts are assimilated in the same proportion, regardless of their phosphorus content. While this has not been demonstrated experimentally, Marshall and Orr's results obtained with ^{32}P were consistent with results obtained with a weight method, suggesting that the ^{32}P radio-tracer method provides an adequate approximation of global AE.

In another set of experiments, two groups of larvae were fed a supplementary copepod (labelled or unlabelled, $\sim$0.50 µl in volume, 13 C, n= 16 and 14 respectively) after 48 hours from the start of the experiment. The feeding was limited to a 15 min period and occurred in a separate tray. Following feeding, the animals were immediately returned to fresh vials to continue the experiment. Reduced AE was expected in this case because larvae often appeared to flush part of their gut shortly after the

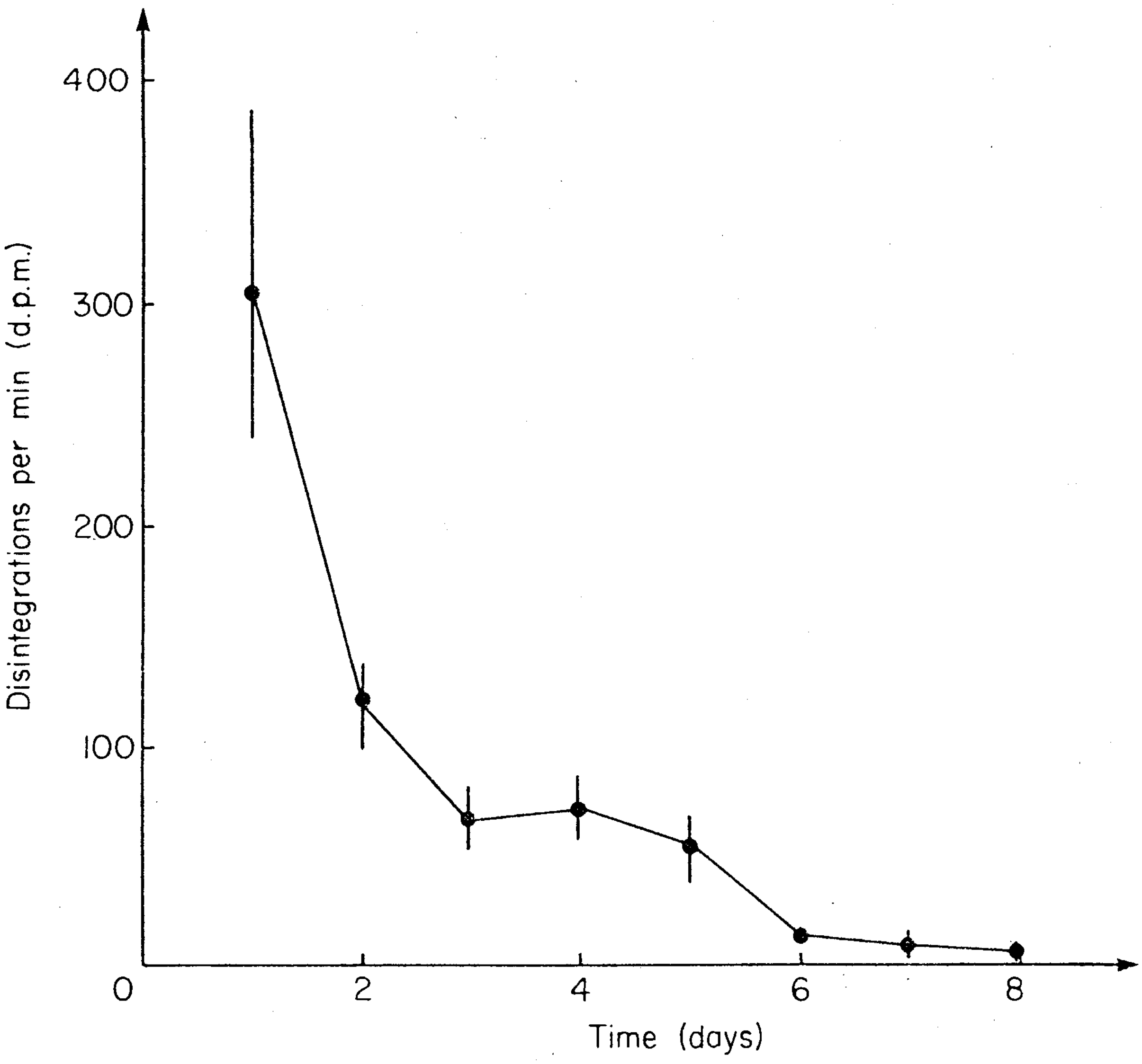


Fig. 6 Time sequence of appearance of ^{32}P (mean ±SE) in lake water in which 4th instar larvae of C. trivittatus were kept after feeding upon one copepod (about 1.8 mm long) at 13 C (n= 8).

successful capture of prey. The food material (which has a bright red colour) was exuded posteriorly, diffusing rapidly in the water. These experiments were designed to provide a quantitative estimate of the amount of food wastage involved.

A few larvae regurgitated most of their food shortly after feeding, but this problem was not identified early enough to allow separate treatment of these data. However, since the frequency distribution of AE values was bimodal with a large gap intervening between the two modes, I ignored all low values (AE < 26%). This resulted in the rejection of less than ten data points, and 2-3% of the total sample size over all experiments.

Rate of emptying of the crop

In order to compare the rate of emptying of the crop to mid-gut capacity, and to evaluate the net rate of energy intake for various feeding rates at different temperatures, digestion rates were estimated at 6, 13 and 22 C for young and old 4th instar larvae of *C. trivittatus*. Each group was allowed to feed on small *D. leptopus* or large *D. kenai*. The larvae ($n > 5$) were then periodically observed and the crop volume visually estimated until all were empty. After the larvae captured a prey, there was a short initial period during which crop volume remained constant (presumably while digestion and liquefaction began), but it decreased in roughly exponential fashion thereafter. However it was assumed that an exponential decline prevailed throughout, and rate of crop emptying was estimated according to Brett and Higg´s (1970) graphical method (originally used for rate of gastric digestion of salmon). The data were expressed as mg dry weight of meal/thousand mg dry weight of Chaoborus/hour and the following relationship determined:

$$\ln V_t = \ln V_i - Rt \tag{6}$$

where V_i = initial meal volume in the crop, V_t = meal volume in the crop at time t and R= the instantaneous rate of digestion (i.e. the slope of the straight line describing the crop emptying process). This method is relatively straightforward and accurate, and does not necessitate serial slaughter. Dry weight of prey was estimated by multiplying prey volume (or wet weight since 1 gr $\sim$ 1 ml) by 0.06 (W. Neill, U.B.C., pers. comm.), and dry weight of larvae was obtained from Fedorenko and Swift (1972).

RESULTS

Assimilation efficiency

Multiple regression analysis revealed the following statistically significant ($p \leq 0.05$) effects (by order of importance): meal size(-), temperature(-), a temperature x meal size interaction(-), and predator size(+). The poor fit of the model ($r^2 = 0.26$) was due partly to a lack of linearity in the trends observed (Fig. 7). At 24 C, AE was nearly constant (~80%). At all other temperatures tested, AE decreased significantly from 91.2% to 86.5% for meal sizes up to 0.50 µl:

$$AE = 0.92 - 0.118\ V_i \tag{7}$$

It was much lower for the largest meal size (from 76% at 16 C to 52% at 6 C).

Temperature or size are not the only factors that reduce AE. Animals that were allowed to feed 48 hours after the start of an experiment yielded relatively low AE values of 81.9 and 80.3% for labelled and unlabelled copepods respectively. The difference between these two groups is not statistically significant ($t = -0.63$; d.f.= 29; $p = 0.53$) but their pooled value

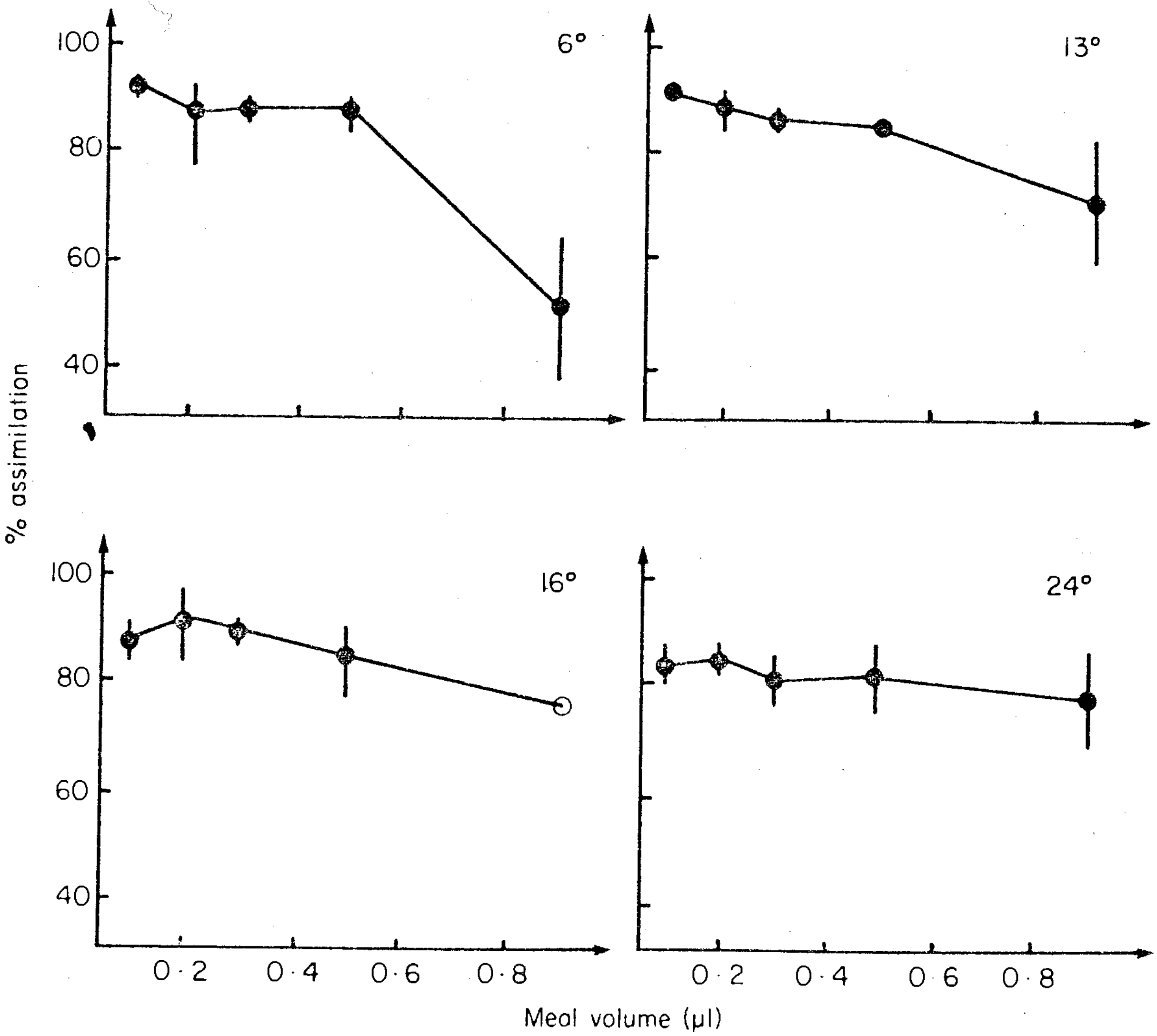


Fig. 7 Efficiency of food assimilation as a function of meal volume for the 4th instar larvae of C. trivittatus fed labelled copepods at four different temperatures. Unfilled circle: n= 2. Vertical bars: 95% C.L.

differs significantly from that of individuals that were not fed a supplementary copepod (87.6%) ($t = 6.67$; d.f.= 131; $p < 0.0001$). Part of this loss may be due to phosphorus turnover and excretion, but it is presumed that this 6.5% food loss resulted from the gut ´flushing´ behaviour exhibited by the larvae since it agrees well with the volume of food present in the gut at that time (by comparison with photographic estimates). A similar phenomenon was inferred by Clarke (1979) for _Glyptonotus antarcticus_. Upon resuming feeding after a two day starvation period, this isopod increased faeces production by a factor of 5-8 with a concomitant 3-7% reduction in AE (defaecation strategies are discussed by Calow 1975). It is therefore possible that AE values lower than 80% are normal for _Chaoborus_ larvae if feeding occurs frequently and faeces are produced regularly. Swift (1976) obtained an AE estimate of 76.4% at 10 C in the 4th instar larva of _C. trivittatus_ feeding on copepods, using a radiocarbon method and allowing feeding on unlabelled prey after an initial feeding on labelled prey. The best estimate AE must then be about 76-82%, but it can be very much lower for large meals and low temperatures.

Rate of emptying of the crop

The instantaneous rates of crop emptying (Table XV) are fairly similar across meal sizes or larval body sizes, even though a difference appears between young and old larvae at 6 C. A pairwise comparison with respect to meal size (t= -0.96; d.f.= 5; p= 0.40) and larval size (t= -0.27; d.f.= 5; p= 0.80) indicates no statistically significant overall differences. The results were therefore pooled and tested for a temperature effect which was found to be significant (F= 21.5; d.f.= 2,9; p= 0.0004). These results are compatible with those on rate of gastric digestion in fishes (Brett and Higgs 1970), although some effects of meal size on the instantaneous rate of digestion have been reported elsewhere (Steigenberger and Larkin 1974, see Elliott and Persson 1978, and Jobling and Davies 1979).

Although there is no significant effect of larval size on digestion rate, the results are expressed as percentages of the dry body weight of the larvae. Therefore, a young larva did take longer to digest a meal of a given size than did an older one. In contrast Fedorenko (1973) reported no such difference in the digestion rate of copepods between 3rd and 4th instar larvae of _C. americanus_ and _C. trivittatus_, although she mentions that the variability between larvae was considerable. This variability could be attributed to variation in body size within an instar.

Table XV Instantaneous rates of digestion (expressed as mg dry weight of meal/thousand mg dry weight of *Chaoborus*/hour) as a function of meal volume and temperature (T) for two size categories of the 4th instar larva of *C. trivittatus*. Sample sizes are indicated in parentheses.

T (C)	Small larvae		Large larvae		Grand mean
	Small meal	Large meal	Small meal	Large meal	
6	-0.59(6)	-0.054(9)	-0.119(6)	-0.167((5)	-0.09
13	-0.278(9)	-0.240(8)	-0.112(7)	-0.241(9)	-0.22
22	-0.316(6)	-0.361(8)	-0.382(6)	-0.351(8)	-0.35

DISCUSSION

Effect of meal size on AE

Whereas some authors have not detected an effect of meal size or feeding rate on AE (e.g. Cosper and Reeve 1975, Lawton 1970), Corner *et al*. (1976) obtained a 10-20% decrease in AE for *Calanus helgolandicus* feeding on barnacle nauplii over a 4-7 fold increase in the ration ingested. An even greater meal size dependent decrease in AE was recorded for *Macrocyclops albidus* feeding on *Paramecium* (Klekowski and Shushkina 1966). The experimental curves presented here show a substantial decline in AE (up to 42%) as a function of meal volume, and the magnitude of the reduction and its interaction with temperature coincides well with *C. trivittatus* growth data published by Swift (1976), although temperature-dependent feeding and digestion rates may have played a role in producing Swift´s results. These data therefore strongly suggest that the capacity for assimilation in *Chaoborus* larvae can be exceeded and that AE can vary considerably.

Cause of the decrease in AE

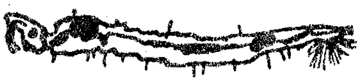
At 22 C, the rate of crop emptying can be quite high (0.41 μl/hour for a 1 μl meal and a 1.5 mg larva, ln V_i = 3.69, see Eqn. 6) compared to the volume of the mid-gut (~0.1 μl by photographic estimates). However, since the greatest reduction in AE occurred at low temperatures, we need to know the exact rates of assimilation and digestion with respect to temperature to determine if an overloading of the mid-gut is possible. In the absence of physiological data on maximum assimilation rate in the midgut of a Chaoborus larva, it is not possible to provide a model which would permit a correct interpretation of the AE data and the factor(s) underlying the decrease in AE cannot be identified with certainty.

One mechanism which might partially explain the effects of temperature and meal volume on AE is food wastage though the mouth. Thomson (1975) has demonstrated that malfunctions of muscular valves in the gut of the blowfly, Phormia regina (Diptera: Callophoridae) occur when the crop is greatly distended. The proventricular valve acts as a regulator and prevents an excess of food from reaching the mid-gut, forcing it back anteriorly where regurgitation may occur. In Chaoborus, it is possible that the pro-ventriculus regulates food transfer as suggested for Phormia. The crop contents could thus leak out anteriorly when the crop is full and/or closing of the mouth opening is partially obstructed. Multiple prey capture often results in parts of the body of prey projecting outside the mouth of Chaoborus and liquid egesta can be seen to escape.

If this is the case, the amount of food wasted should be a function of the amount of time (t_{TH}) that the crop volume remains above a critical threshold where AE begins to decline sharply (say TH= 0.50 µl from Fig. 7). If we express crop volume as a function of time for a 1 mg larva which has secured a meal 0.90 µl in volume as shown in Fig. 8, we can easily obtain values for t_{TH}: these are 6.1, 2.8, 2.3 and 1.5 hours for 6, 13, 16 and 22 C respectively. A regression of food loss (measured as reduced AE from an expected value of 0.81 from Eqn. 7) on these values of t_{TH} is highly significant ($y = -7.14 - 5.93\ t_{TH}$; $r^2 = 0.987$; $p < 0.01$). This suggests a direct linear relationship between t_{TH} and the amount of food lost. Although not a critical test of the above hypothesis, these results are congruent with an interpretation involving leakage of crop contents through the mouth opening.

Consequences for optimal foraging

AE decreased from 91.2% to 86.5% from the smallest prey size ingested to the largest one, a small but significant effect which will affect predicted values of optimal prey size when included in the calculation of net energy content. However the



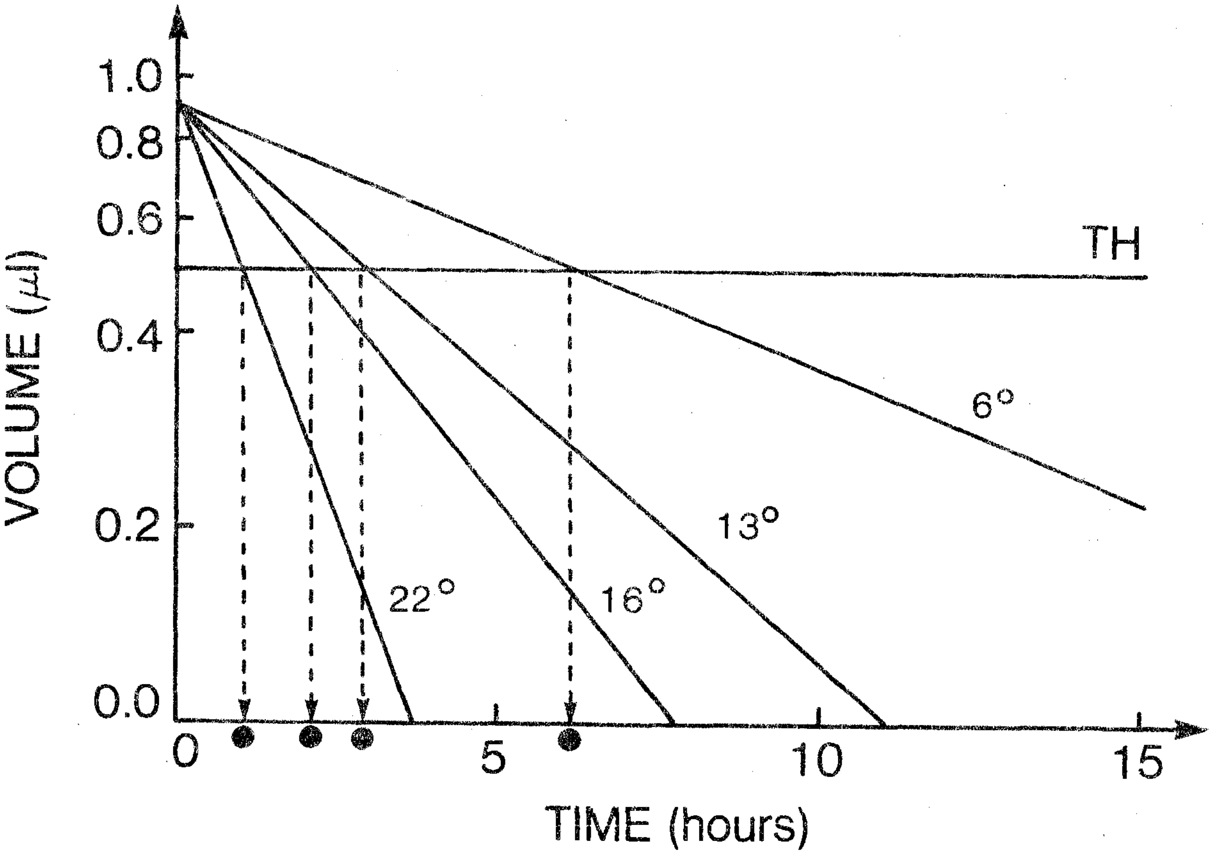


Fig. 8 Schematic digestion curves of 1 mg C. trivittatus larvae at 4 temperatures. The crop volume threshold (TH= 0.50 μl) above which food leakage is presumed to occur is indicated by the horizontal line. This line intersects the digestion curves at four points from which one can determine t_{TH} (filled circles), i.e. the time necessary for crop volume to reach TH.

most important reduction in AE occurs for the largest meal (achieved by multiple prey capture). This result implies that it is not possible to assign prey a specific net energy content as this depends also on the physiological state of the predator (i.e. the extent of fullness of its crop). In other words, there is an interaction occurring between prey ingested which determines the overall AE of a particular meal (a similar argument could be made for some species of fish where AE is known to vary, see Elliott 1976). The problem of optimal foraging in these organisms must therefore be approached from the point of view of optimal meal size (rather than optimal prey size) and more attention must be paid to spatio-temporal patterns of feeding and the concomitant functioning of the gut.

For example, two alternative tactics can be envisaged in cases where AE decreases as a function of meal size: (a) an organism can maintain a high feeding rate and allow AE to decrease accordingly, or (b) it can curtail feeding and maintain AE at a high value. This decision should depend on the rate and cost of feeding (a function of food distribution and availability), the rate of digestion and the extent to which AE decreases as a function of meal volume (or feeding rate). In *Chaoborus* larvae, all these rates are also temperature dependent and detailed simulation modelling will be necessary to predict which is the ´best´ tactic from an energetic standpoint.

Although this problem has not been investigated in invertebrate predators, studies on suspension-feeding mussels have described cases of these two alternative tactics: Tactic (a) for *Mytilus edulis* (Thompson and Bayne 1972, 1974; Widdows 1978), and *Aulacomya ater* (Griffiths and King 1979), and tactic (b) for *Modiolus modiolus* and *Arctica islandica* (Winter 1969). While the ecological factors which dictate the tactic adopted by a species are not known, it may be assumed that the gut is limited in its capacity for assimilation and that natural selection results in highest assimilation efficiencies for meal sizes which are secured most frequently. Consequently it would be interesting to attempt to relate the patterns of food abundance and availability for these species in their natural habitat to their respective feeding tactics (see Winter 1969). Specific hypotheses could be tested by comparing, for example, two populations of the same species living in geographical areas varying in their tidal cycles (thus imposing different resource utilization patterns).

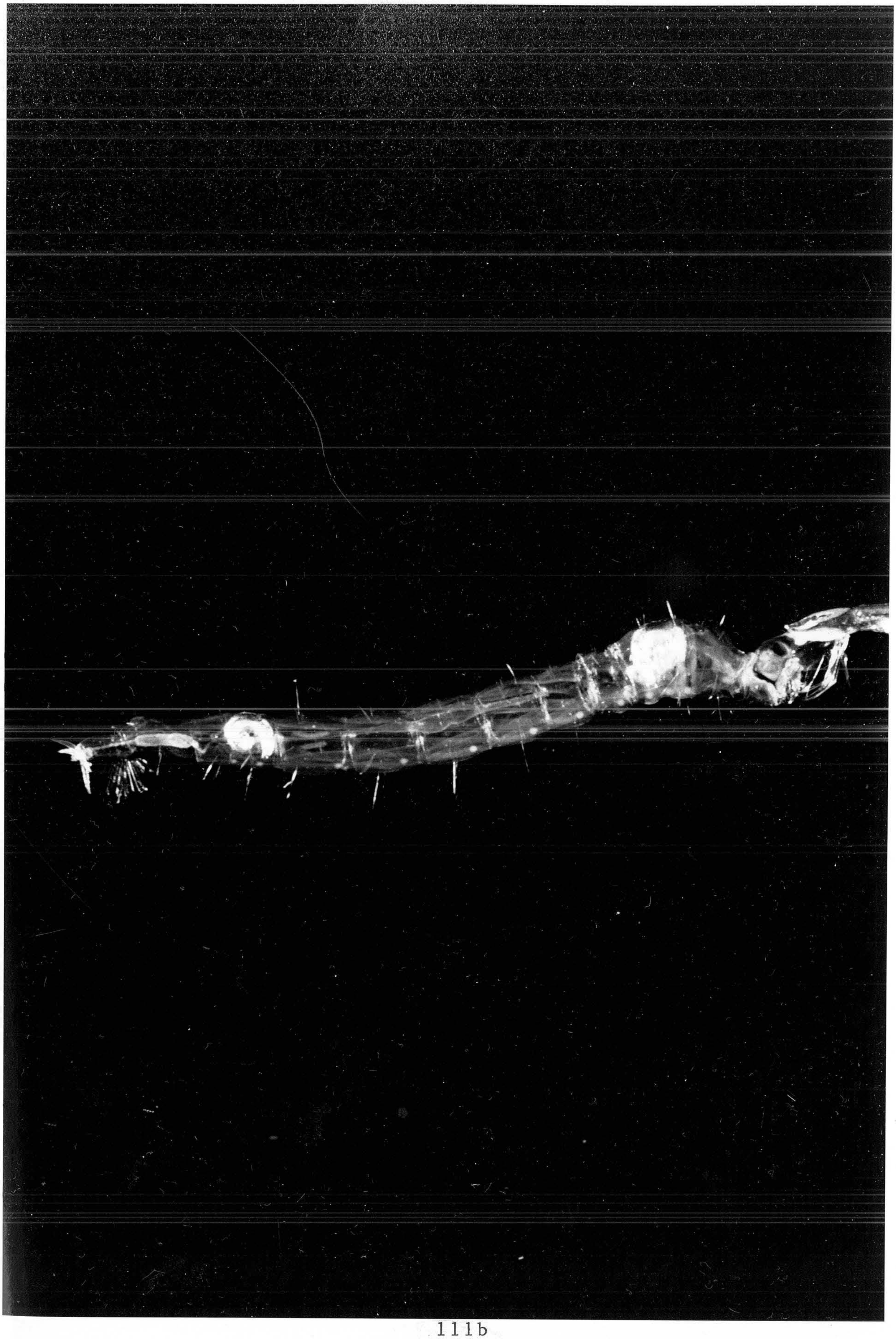
Besides ´optimal diet´, another fundamental aspect of foraging which will be affected by meal size and temperature dependent AE is ´optimal foraging space´ (Schoener 1971). In *Chaoborus*, given that prey abundance and temperature both decrease as a function of depth in Gwendoline Lake (except in the winter), and that there are no other major selective forces determining where a larva should be at a particular time (such as predator avoidance), an individual could vary its net rate of energy intake by foraging at different depths. Some of the consequences of a variable assimilation efficiency to an energy maximizing strategy of vertical migration have been explored elsewhere (Giguère and Dill 1980; Chapter 6).

5. ACOUSTICS IN ZOOPLANKTON

INTRODUCTION

Studies of aquatic invertebrates that respond to acoustic stimuli are relatively few. Most deal with responsiveness of predators to stimuli of various frequencies, or attempt to identify the site and structure of the sensory receptors involved. No quantitative study of the relationship between attack behaviour and the distance of the source of an underwater signal has been published. Brief mentions of attack distances in response to a vibrating probe have been made for chaetognaths (Horridge and Boulton 1967, Feigenbaum and Reeve 1977) and a chaoborid (Horridge 1966). I studied the response of the 4th instar larva of *C. trivittatus* (Fig. 9) to a probe vibrating at various frequencies and intensities, and determined attack distances at different ´hunger´ levels. I also analyzed the stimuli originating from its natural prey species (one daphnid

Fig. 9 Side view of a 4th instar larva of *C. trivittatus* mounted for an experiment. Larval length: 13.3 mm.



111b

and two copepods). The results should prove useful in understanding the behaviour of other aquatic predators which detect their prey in response to mechanical disturbances in a fluid environment, particularly the chaetognaths which bear many resemblances to Chaoborus larvae ecologically. Both are abundant and important predators in their respective communities (Feigenbaum and Reeve 1977; Fedorenko 1973, Lewis 1975), and have a diversified diet of zooplankton comprising a substantial amount of copepods (Reeve and Baker 1975; Fedorenko 1975a, Swift 1976, Giguère 1979). They both are transparent, rest motionless in the water and strike at prey at close quarters (Horridge 1966, Newbury 1972, Feigenbaum 1979; Fedorenko 1973, Giguère pers. obs.), and appear to carry out most feeding activities at night (Pearre 1973, Nagasawa and Marumo 1976; Fedorenko 1975a, Swift 1976).

MATERIALS AND METHODS

Animals were collected from Gwendoline Lake except for Daphnia, which came from a laboratory culture. The larvae were prepared for the experiments by gluing their head capsule to the tip of a 1 ml syringe with Super-Glue 3 (Woodhill Chemical Co.). The needle had previously been bent at approximately a 45 angle (Fig. 9). The syringe was mounted on a micromanipulator and the animal positioned horizontally inside a 15 cm rectangular container. The transducer consisted of a transistor radio earphone, with a shortened insect pin (14 mm in length) affixed to its diaphragm with epoxy glue. The pin´s rounded tip was 0.80 mm in diameter, and it was placed in a position adjacent to the head capsule of the larva with a second manipulator. The unit was moved towards or away from the head of the Chaoborus, at fixed distance intervals (d= 0, 0.375, 0.75 mm, etc.) on the larva´s right side. For each new larva, the tip of the needle was first placed in a position adjacent to the head capsule of the larva and the micro-manipulator was set at d= 0. The unit was powered by an audio oscillator (Hewlett-Packard 200AB) and produced small localized disturbances to which a larva responded. The same unit with the insect pin removed failed to elicit any response. The experiments were carried out at room temperature, on the top of an anti-vibration table, and at light intensities around 900 lx. Prior to an experiment, each larva was presented with a short stimulus (1000 Hz, d= 1.125 mm, 3 v, 1 s) to ensure that it was responsive after being manipulated. This resulted in the rejection of less than 5% of the larvae.

A positive response consisted of a sudden ´strike´ movement of the larva, but also included (less than 10% of the time) any detectable feeding motions, including those of the mandibular apparatus, which sometimes preceded an attack. The equivalence between positive responses and attack behaviour can only be inferred from independent observations made on non-immobilized larvae. The stimuli presented were of two kinds: (a) a rising frequency stimulus (Type I) obtained by slowly rotating the frequency dial of the generator from 200 to 2100 Hz or until the larva responded, and (b) a decreasing frequency stimulus (Type D) obtained by reversing the procedure. The first values at which the larvae responded were recorded in each case. An alternative method produced similar results: short stimuli of constant frequency were presented to the larvae at 50 Hz intervals. More importantly, this procedure demonstrated that a larva will respond to frequencies intermediate between the values referred to above (i.e. type I and D stimuli), suggesting that these define the boundaries of the range of effective frequencies to which a Chaoborus larva will respond. However the first method was preferred for convenience. A correction factor was applied to compensate for the tendency of the experimenter to overshoot the effective frequency while watching the larva.

For the determination of the range of effective frequencies as a function of amplitude, I used two type I stimuli followed by two type D stimuli at each distance, as the probe was moved in. Starting at d= 0 and moving the probe step-by-step outward produced the same results; thus the larvae were not being sensitized to the stimuli as the probe was moved in. For all other experiments, two type I stimuli were presented at each distance as the probe was moved in, and two type D stimuli as the probe was moved out. When the larva responded to both of the type I (or D) stimuli at a given distance, the variation between readings was small and significantly smaller than the variation between individuals. To determine standard errors, one of the replicates was selected at random. The rate of presentation of stimuli was limited to a maximum of 3/min, and generally 2/min. No evidence of habituation was detected, even in trial runs where much higher rates of presentation were utilized.

The amplitude at the tip of the needle was determined using a stroboscope. It was small (∿10 μm) but not constant at any voltage. It increased slowly as the frequency rose from 200 to 1400 Hz where resonance occurred and amplitude suddendly tripled before declining again at higher frequencies. However, larvae presented with a type D stimulus often did not respond until the frequency fell below this area of resonance, suggesting that

Chaoborus response is primarily frequency specific. Nevertheless, since the amplitude at the tip of the needle is somewhat confounded with frequency in these experiments, the results should be interpreted with caution, particularly those pertaining to attack distance, until more results are obtained with an amplitude regulator.

The acoustic signal from the prey was recorded on a magnetic tape cassette using a similar transducer and a Pioneer CT-F2121 recorder. The rounded tip of the insect pin was removed and the prey glued on the end at approximately a 45 angle. The recording was later analyzed for frequency and sound pressure level on a Sona-Graph model 6061B (Kay Electric Co.). Because of inherent noise (60 cycles) at high amplification, only frequencies above 400 Hz were analyzed.

The prey were *D. leptopus*, *D. kenai* and *Daphnia pulex*. The last were used instead of the normal prey, *Daphnia rosea*, which was rare in the lake at the time of the experiments. Prey lengths were ~1.5 mm, ~2.0 mm and 1.5-2.2 mm respectively.

RESULTS

Section I- The response of the predator

Frequency response

The range of effective frequencies was determined as a function of distance for larvae without food in their crop (n= 19) at a volume setting of 3 v. The results are presented in Fig. 10. At the farthest point away from Chaoborus, both kinds of stimuli elicit a positive response at similar frequencies. This appears to be an ´optimal´ frequency (1100 Hz) since it results in the greatest attack distance. As the probe is moved in, type I produces a positive response at a lower frequency, and type D at a higher one. In this way, roughly symmetrical curves are described and the maximum range of effective frequencies is found at d= 0. The lower and upper mean values are 675 and 1500 Hz respectively (range 550-2050 Hz).

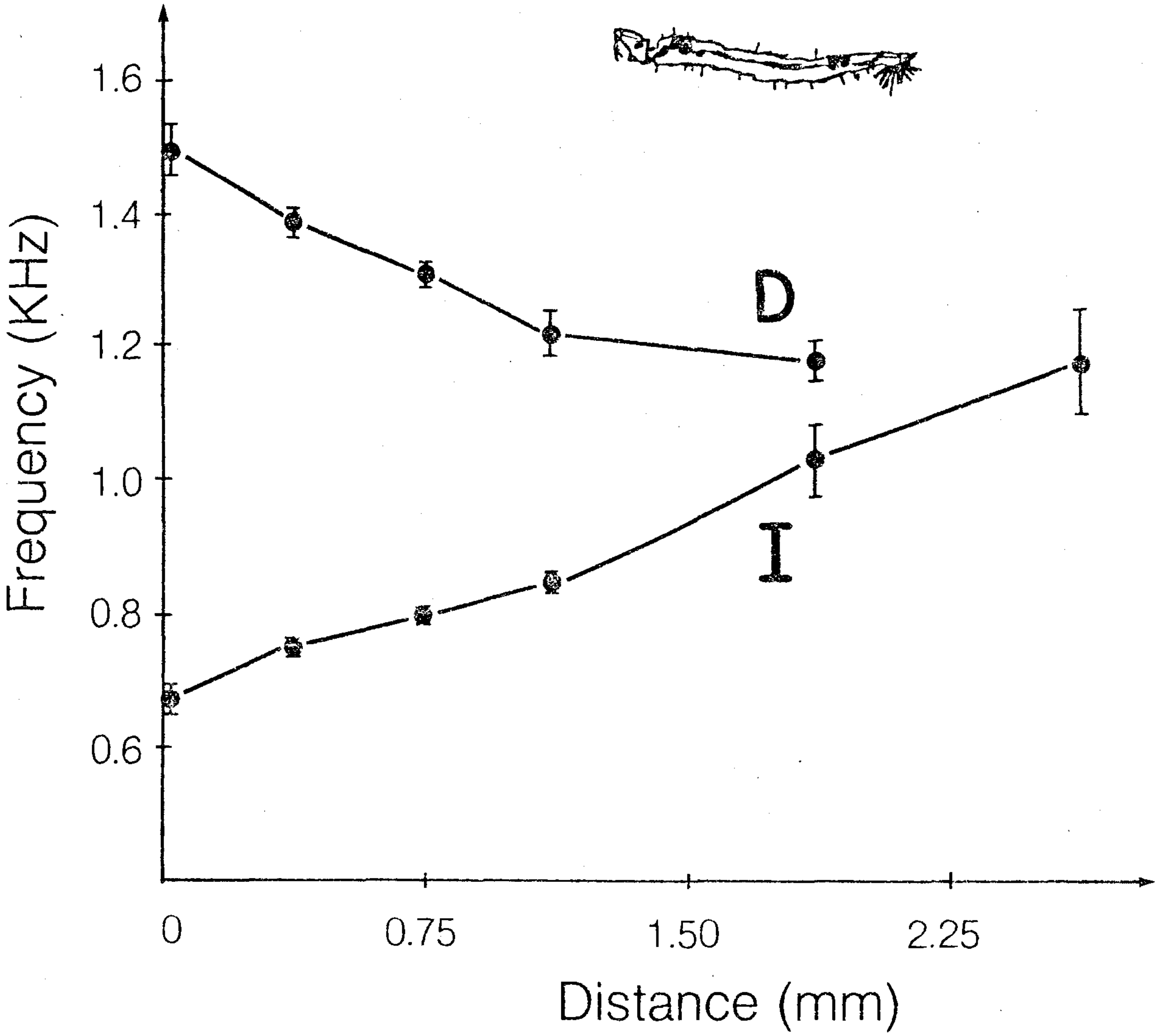


Fig. 10 Mean probe vibration frequency (±SE) to which 4th instar C. trivittatus larvae with an empty crop responded at various distances. D= decreasing stimulus. I= increasing stimulus.

Effect of amplitude

In this experiment, the range of effective frequencies was determined as a function of distance for three groups of larvae (n= 5 to 6) with some food in their crop at three different volume (2, 3 and 10 v). The results are depicted in Fig. 11. For any given amplitude, I observe an ´optimal´ response around 970 Hz and louder signals elicit positive responses at greater distance away from the predator at each frequency. Consequently, each curve envelops all the other curves of lower amplitude. The loudness of the signal is clearly important in determining attack distance. The distances at which least 50% of the larvae respond (at any frequency) to a stimulus of type I are 0.75, 1.5 and 4.5 mm for 2, 3 and 10 v stimuli respectively. The mean lower and upper values for effective frequencies are 400 and 1575 Hz respectively (range 350-1850 Hz).

Effect of hunger

Assuming that stimulus frequency is prey species (and perhaps size) specific, and given that ´hungry´ predators will frequently take a wider range of prey types than ´satiated´ ones (i.e. those with some food in their crop) (e.g. Ivlev 1961), one

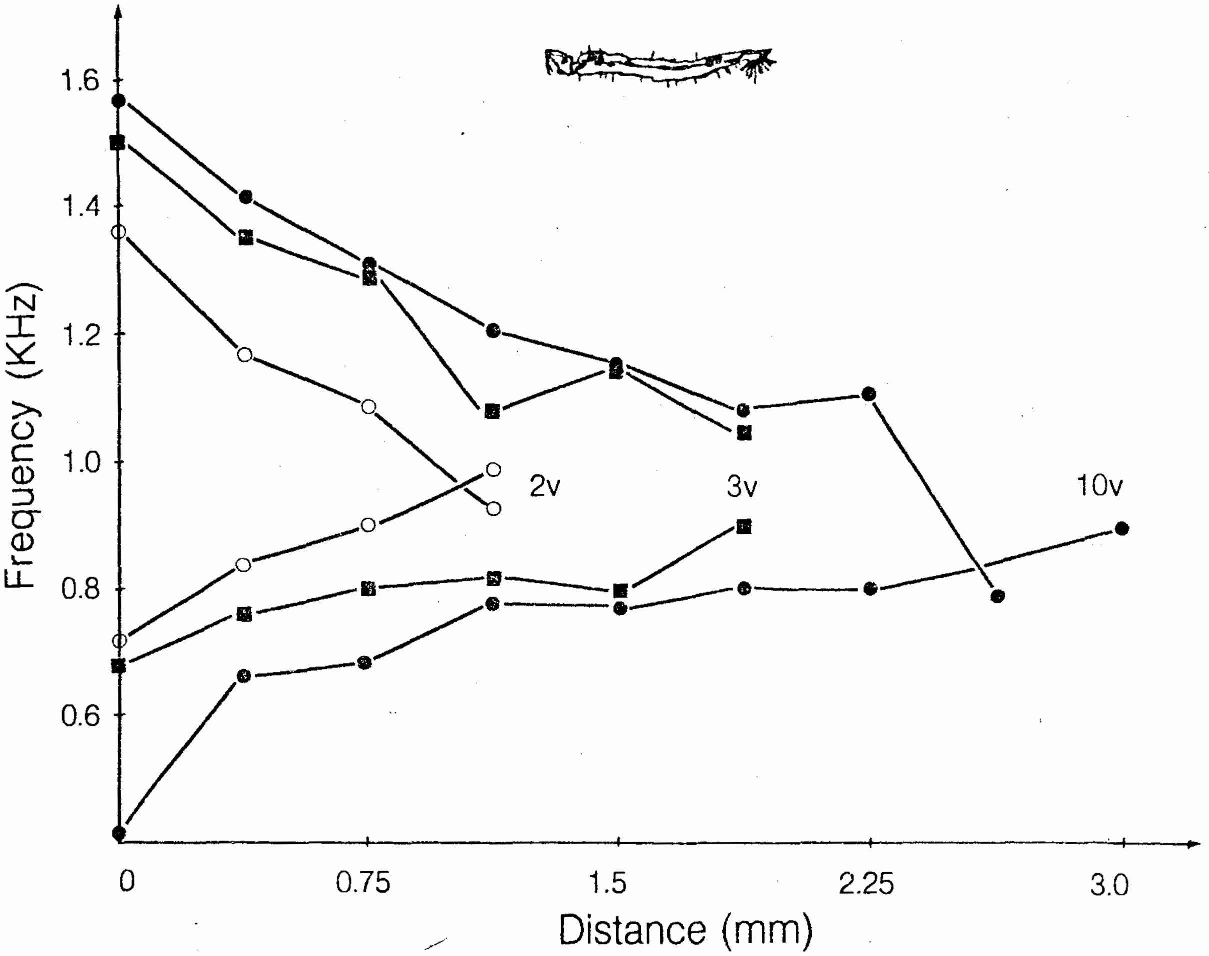


Fig. 11 The effect of voltage setting on mean probe vibration frequency to which 4th instar C. trivittatus larvae responded at various distances. The larvae had food in their crops. Top three curves: decreasing stimuli. Bottom three curves: increasing stimuli.

might predict that a ´hungry´ larva should respond to a wider range of frequencies than a ´satiated´ one. I therefore conducted an experiment to test the null hypothesis that ´hunger´ has no effect on the range of effective frequencies in Chaoborus. I used one volume setting (3 v), an increased sample size (n= 10 to 13), and four levels of ´hunger´. Since Chaoborus larvae are transparent, I was able to establish two groups of ´satiated´ larvae (H1= crop volume > 0.5 µl, H2= crop volume between 0 and 0.4 µl). Two other groups were ´starved´ for 1-3 days (H3) and 6-8 days (H4) respectively, and had no prey remaining in their crops.

The results are summarized in Fig. 12. These groups were presented with both I and D stimuli at all distances, but significant effects (ANOVA) were observed only with the type I stimulus at short distances (d= 0 and 0.375 mm). The effect of ´hunger´ is small (∼11%), but larger crop volumes are possible (0.8-1.0 mm) than were actually used. A predator keeping its crop full for an extended period of time may thus be expected to exhibit a restricted diet (again, assuming some species-specific frequency stimulus).

To test the null hypothesis that ´hunger´ has no effect on attack distance in Chaoborus, the % positive responses of larvae with partly full (H1, H2) and empty (H3, H4) crops were plotted as a function of distance (Fig. 13). The difference was statistically significant (sign-test, Siegel 1956). Attack

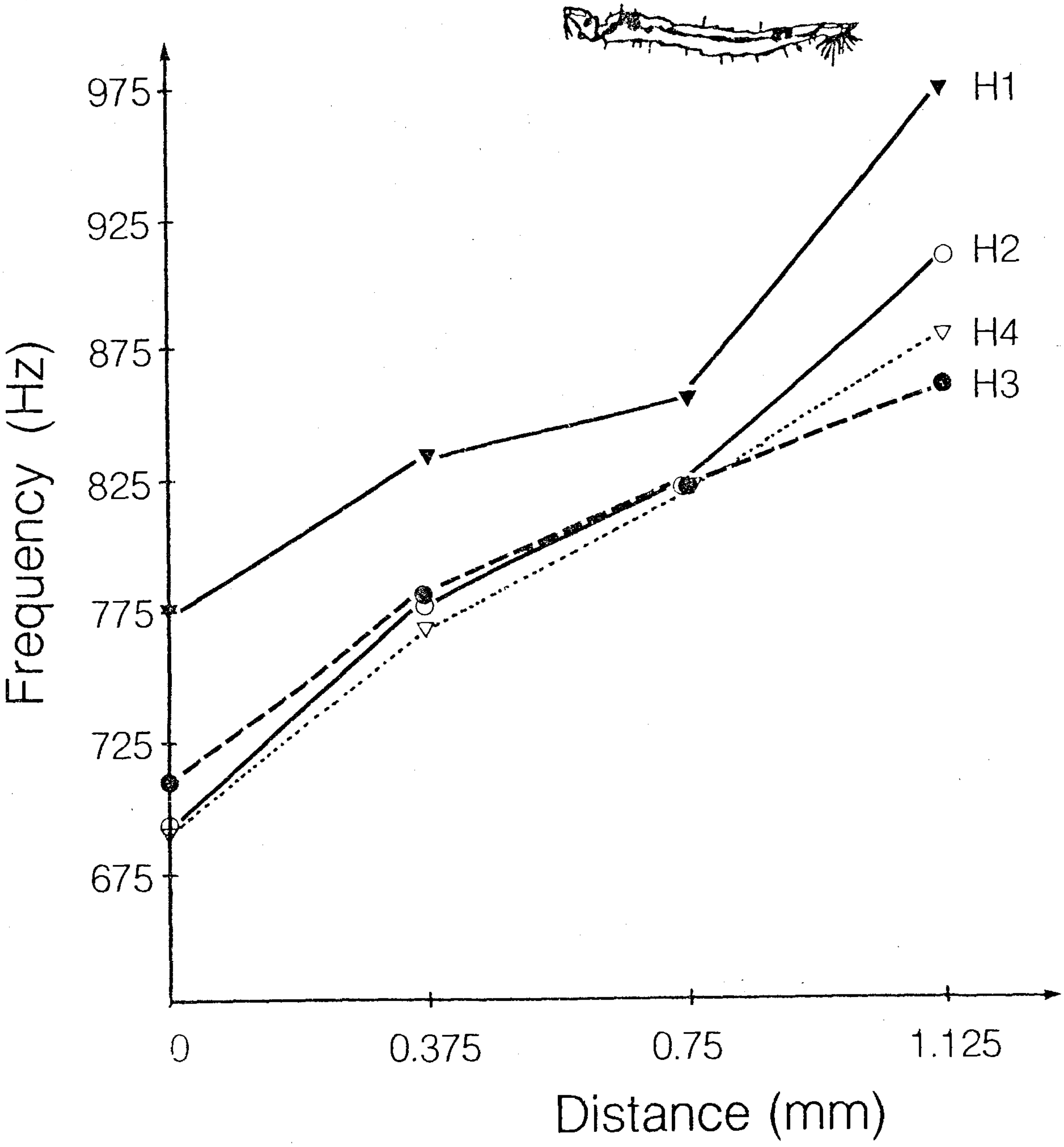


Fig. 12 The effect of ´hunger´ on the attack distance of 4th instar *C. trivittatus* larvae in response to a probe vibrating at different frequencies (type I stimulus only, see text for explanation).

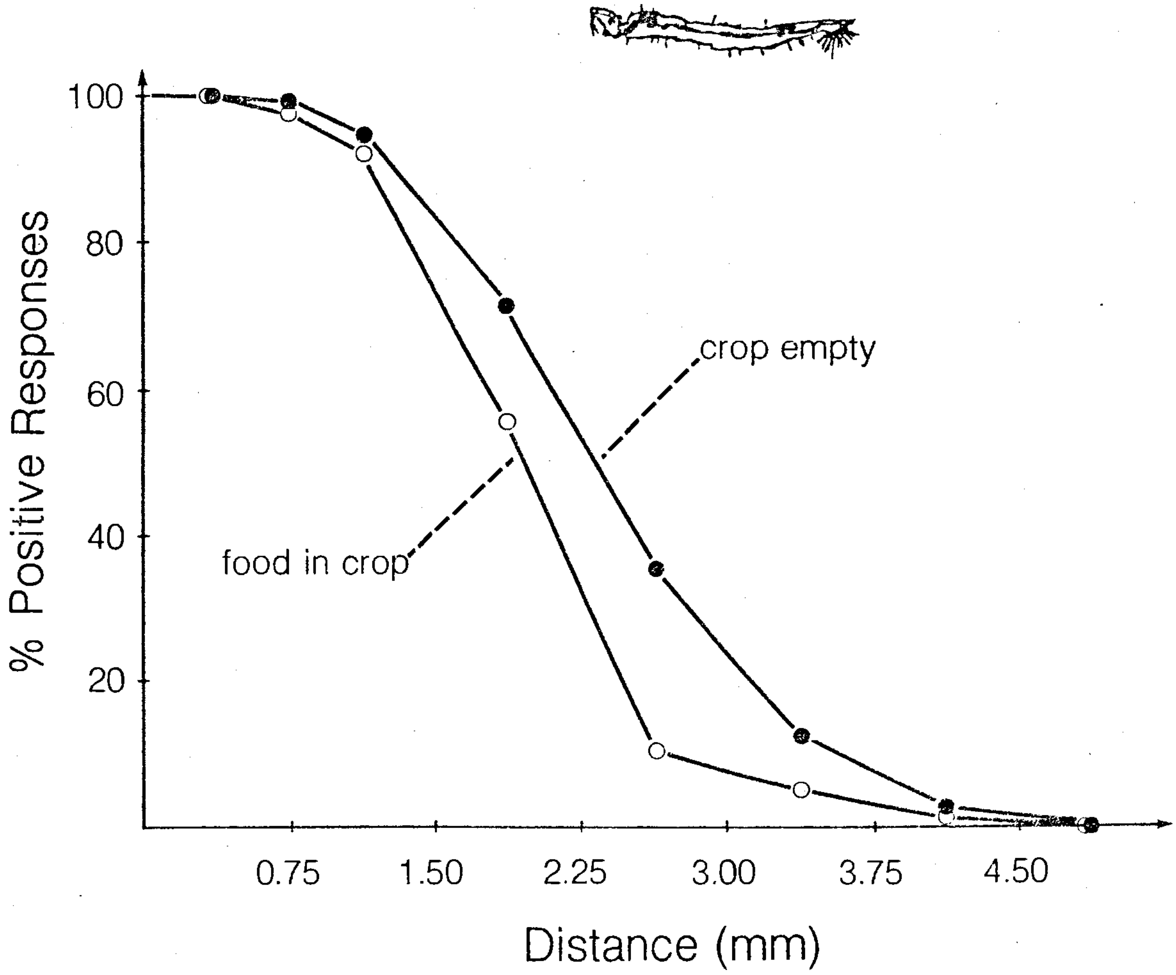


Fig. 13 Percent positive responses to a vibrating probe as a function of distance from 4th instar larvae C. trivittatus with or without food in their crop.

distances (at the 50% response level) were 1.9 and 2.25 mm for ´satiated´ and ´hungry´ larvae respectively (an 18.4% increase). Assuming a cylindrical reaction field around a 1.5 cm larva, this would yield a reaction volume 32.8% greater for a ´hungry´ larva than for a larva with food in its crop. These findings can be compared with other results obtained from high speed films of predation on *Diaptomus kenai*. Distances were measured by drawing a straight line from the nearest part of the body of the prey to the head of the predator. This was carried out for positive responses to prey near the anterior (1/3) portion of the body of the larvae, except in cases where the prey actually made contact with the predator. Attack distance increased by 30.8% from 1.43 to 1.87 mm over the same range of ´hunger´ and at the same temperature as for the vibrating needle experiments. Although the increase is not statistically significant (p= 0.35, Mann-Whitney U-test, Siegel 1956) the trend is in the same direction. Thus ´satiated´ *Chaoborus* do not respond to prey until they come quite close, but may then select species on the basis of their signal frequency.

Section II- The stimulus from the prey

Various behaviours of the three species of prey were recorded and analyzed for their sound pressure level and frequency characteristics. No significant differences in the former were detected between species (mean= 33.5 dB). I also compared (ANOVA) maximum and minimum frequencies, and frequency at the highest sound pressure level but only the last two proved to differ significantly (Table XVI). The results suggest that copepods generate sound with a wider range of frequencies than Daphnia, and that in D. kenai highest sound pressure level occurs at around the frequency (1080 Hz) which elicits positive responses at maximum distance in Chaoborus (1100 Hz). Also, the frequency at the highest sound pressure level in D. leptopus (685 Hz) and Daphnia (830 Hz) lie near the range where ´hunger´ significantly affected responses in Chaoborus. Consequently, selective feeding might be expected for a predator operating with a partially filled crop. This condition should occur at high food densities. Lewis (1977) and Pastorok (1978) (in the field and laboratory respectively) both report selective feeding occurring in Chaoborus when food density is relatively high.

The origin of the sound produced by zooplankton is not known but I believe it to be caused by friction of the cuticle

Table XVI Sound pressure level and sound frequency analysis for three species of zooplankton attached to a probe. Sound pressure level is the mean of the maximum values recorded for individuals of each species.

Variable	Prey species			ANOVA	
	D. leptopus	*D. kenai*	*Daphnia*	d.f.	F
FREQUENCY (Hz):					
-maximum	1104	1204	1094	2,7	1.31
-at highest sound pressure level	684	1081	830	2,5	11.29*
-minimum	515	575	703	2,7	6.66*
SOUND PRESSURE LEVEL (dB):	32.5	33.5	34.2	2,6	3.40

* = significant, $p \leqslant 0.05$

of the jointed appendages, as well as by the action of these appendages against one another and against the carapace. An observer equipped with earphones can correlate sounds with particular motions of the animal. The swimming motions of D. leptopus sound like ´drumming´ (see Figs. 14 and 15) and the rapid downward action of the abdomen of D. kenai results in a ´pop´. The antennal beat of Daphnia was heard as a ´flutter´ and movements of the postabdomen produce a loud ´crack´. On the other hand, the overlap in frequencies emitted between species is extensive (Fig. 15).

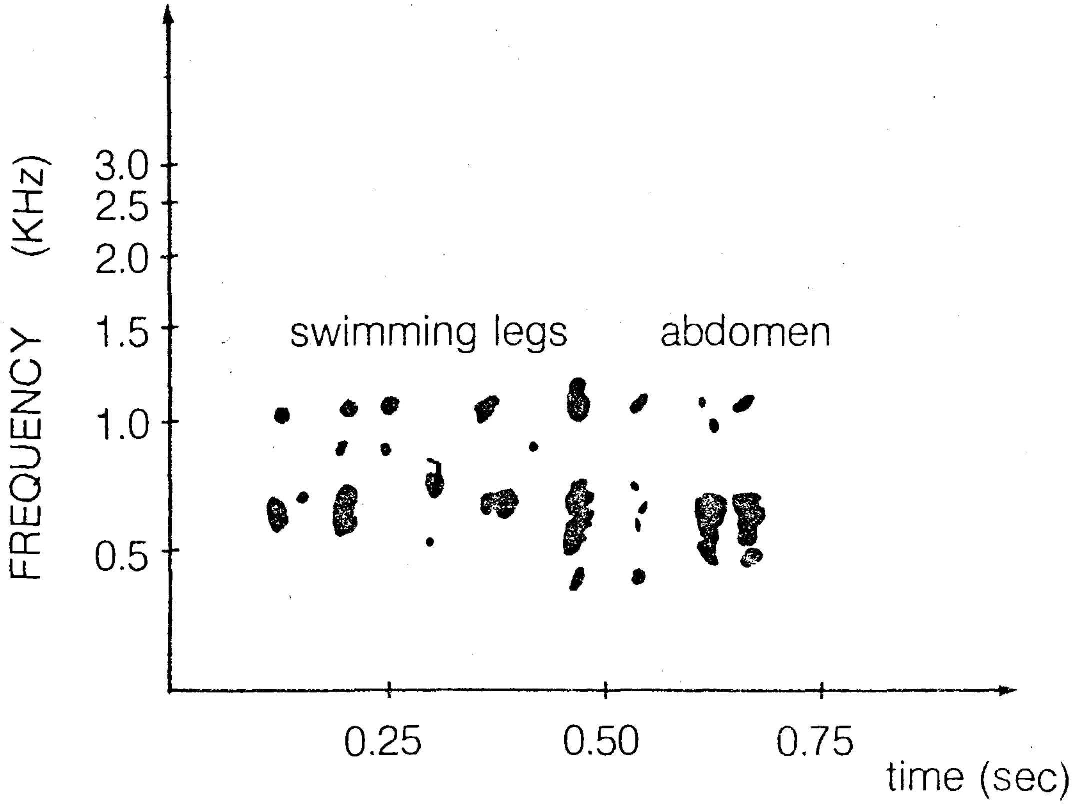


Fig. 14 Sona-Gram for Diaptomus leptopus attached to a probe.

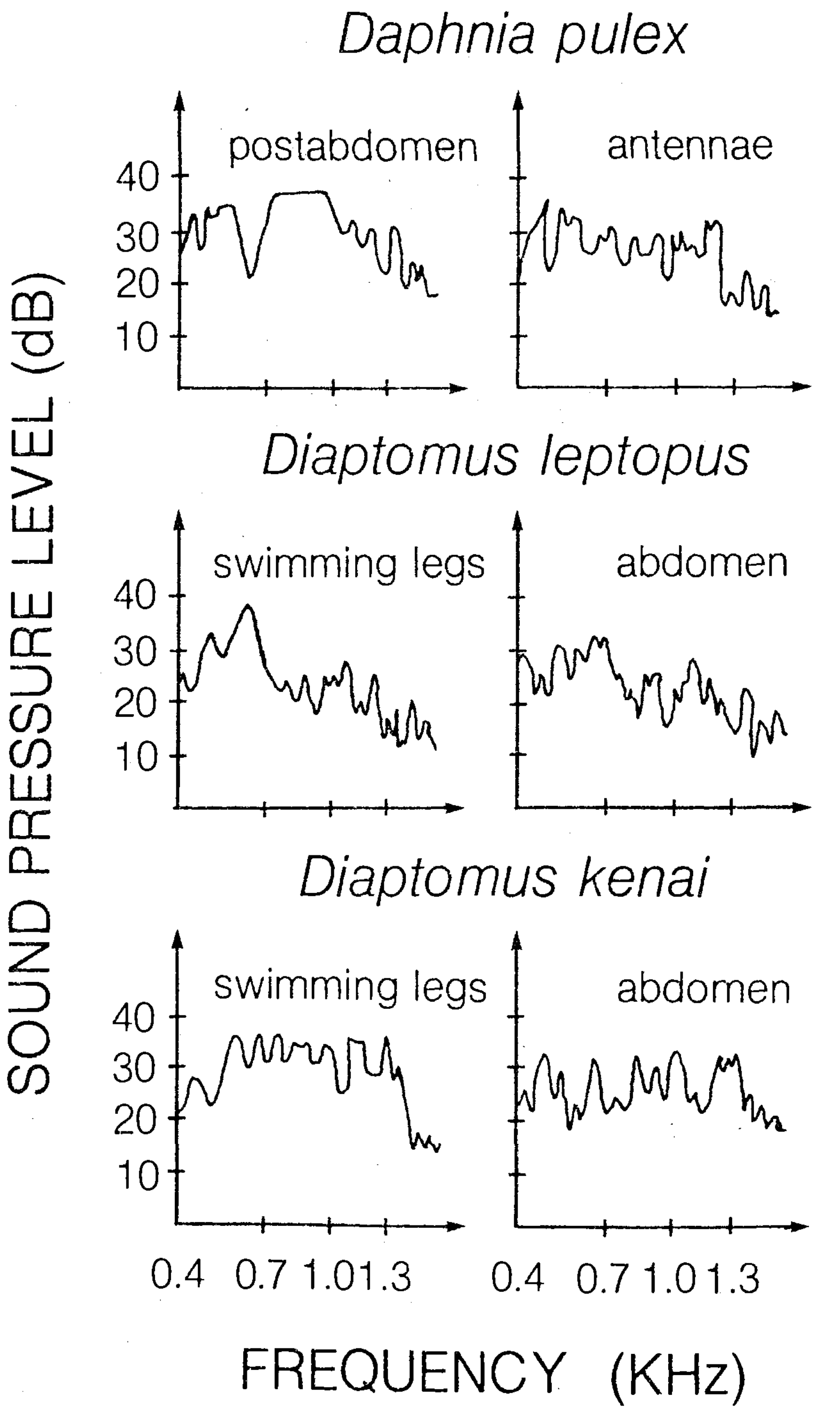


Fig. 15 Cross-sections of Sona-Grams showing sound pressure level as a function of frequency for two copepod species and one daphnid. The noise level fluctuates around 15-25 dB.

DISCUSSION

Aquatic invertebrate predators are known to carry out such essential activities as feeding and mating in total darkness (Chaoborus larva, Dühr 1955; chaetognath, Parry 1944, Reeve 1964; water strider, Wilcox 1972) and non-visual sensory mechanisms must be postulated to account for these abilities. Perception of vibration with motile cilia (Horridge 1966) is the most plausible hypothesis. Although chemical communication has also been demonstrated (Katona 1973), the speed of diffusion of chemicals in water is less than the speed of planktonic animals (Strickler 1975), and olfaction is not likely to be functional in locating prey for an accurate strike at close quarters (Feigenbaum and Reeve 1977).

Mechano-receptors (setae) have been described in chaetognaths (Horridge and Boulton 1967, Feigenbaum 1978) and in cyclopoid copepods by Strickler and Bal (1973). The latter suggested that animals may create signals "of discrete frequencies for individual species and could be recognized by setae of characteristic length" (p. 2658). Newbury (1972) determined that appendages of copepods move at characteristic frequencies which correspond to the frequencies at which chaetognaths attack a vibrating probe, and suggested that selective predation may be accounted for in that way. However, Feigenbaum and Reeve (1977) found that chaetognaths responded positively at all frequencies tested (8-480 Hz). Moreover, only in two species out of four studied to date (review by Feigenbaum and Reeve) does the frequency with peak positive response coincide with Newbury's data on copepods. Strickler (1975) verified the assumption that disturbances created around the moving body of zooplankton is species-specific, but found the wake to be specific only to the various orders. My study looked at the frequencies of the sound produced by prey of Chaoborus (range 425-1300 Hz), and revealed correspondence with the range of frequencies to which the predator responds (range 350-1850 Hz). But since all three species of prey studied overlap considerably in the frequencies produced, and since Chaoborus responds strongly to artificial signals with a narrow frequency band anywhere within the frequency range common to all three species, I would argue against selective predation on the basis of discrete species-specific frequencies. However, 'hunger' significantly reduced the range of effective frequencies in Chaoborus, and frequency at the highest sound pressure levels in D. leptopus lies in the area where this effect occurs. This would result in reducing the effective encounter field between the predator and this prey and possibly diminish the relative contribution of this item in the diet of a 'satiated' predator.

In order to determine how the experimental results compare to a situation involving a natural prey, I compiled (Table XVII) maximum attack distances for Chaoborus larvae in response to acoustic signals of various intensities and to the copepod D. kenai (high speed film). These included 100% and 90% of observations (the latter to eliminate outliers). First, it should be noted that experiments using a vibrating probe can overestimate maximum attack distance in acoustic predators considerably, depending on the volume used. Second, it appears that a volume setting between 2 and 3 v would result in ´normal´ maximum attack distances. My regular setting at 3 v clearly overestimated (by 10-15%) maximum attack distance relative to the situation involving natural prey.

Therefore, the best estimate for mean attack distance in the 4th instar larva of C. trivittatus is about 1.4-1.9 mm. Comparatively, Feigenbaum and Reeve (1977) estimated an attack radius of 0.88 mm for the chaetognath Sagitta hispida in the laboratory, based upon a mathematical model fitted with data from feeding experiments at various prey densities. However, since (a) Sagitta exhibits sink-and-swim behaviour (Feigenbaum and Reeve 1977) which should increase encounter rate with the prey, and (b) the percentage of attacks resulting in successful capture of copepods is low in Chaoborus (5-35% depending on size and temperature, Chapter 2) compared to Sagitta (83%, Feigenbaum and Reeve 1977), greater feeding rates should be possible in the

Table XVII Maximum attack distance of 4th instar larvae of *C. trivittatus* responding to a vibrating probe (all frequencies examined), and to natural prey (*D. kenai*).

Stimulus	Number of individuals tested	Maximum attack distance(mm), including:	
		90% of observations	100% of observations
Probe			
2.0 v	10	1.7	2.3
3.0 v	8	2.2	3.8
3.5 v	8	2.6	4.1
6.0 v	13	3.0	4.5
10.0 v	8	4.5	6.0
D. kenai	22	1.9	3.4

chaetognath.

Despite the striking ecological similarities between Chaoborus larvae and chaetognaths, the former attack at higher frequencies and lower amplitudes than the latter (Table XVIII). This is surprising, particularly in view of the fact that their diets are similar (mainly copepods). However Sagitta feeds on fish larvae as well as zooplankton. Intuitively I would associate low frequencies and high amplitudes with swimming fish larvae. Therefore the chaetognath might possess a response reflecting a compromise to a diet including two very different types of food. Moreover Spadella, a benthic chaetognath, responds to probes at even lower frequencies than Sagitta. Presumably it feeds on a diversified diet of benthic organisms as well as some zooplankton.

It is possible that the planktonic mode of life of a variety of aquatic crustacea results in the production of similar sounds (high frequency, low amplitude) when feeding, mating or moving, and that the range of effective frequencies for acoustic predators reflects the extent to which they rely upon this food source. This hypothesis could be tested in chaoborine larvae since they feed in the muddy substrate of ponds and lakes to various degrees. The only example available for comparison (Horridge 1966; see Table XVIII) was collected in shallow ponds where larvae are likely to utilize the substratum for feeding, and to eat insects and insect larvae (Parma 1971).

Table XVIII Summary of studies of aquatic predators´ responses to a vibrating probe, including effective frequency, effective amplitude, and attack distance.

Species	Frequency (Hz)		Amplitude (μm)	Attack distance (mm)	
	normal	range		normal	maximum
Spadella cephaloptera		8-21	300	1	$\leqslant 3$
Spadella schizoptera	30	8-140	100-300		$\leqslant 3$
Sagitta hispida	150	8-480	100-300	0.88	$\leqslant 3$
Chaoborus sp.	200		5		$\leqslant 5$
Chaoborus trivittatus	1100	350-2050	$\leqslant 10$	$\leqslant 1.9$	$\leqslant 3.8$

S. cephaloptera: Horridge and Boulton (1967)
S. schizoptera: Feigenbaum and Reeve (1977)
S. hispida: Feigenbaum and Reeve (1977)
Chaoborus sp.: Horridge (1966)
C. trivittatus: This study, 3v.

Chaoborus from Gwendoline Lake rarely do either. Therefore, respective values of 200 and 1080 Hz fit the hypothesis. More data collected with the same probe will be needed to draw firm conclusions.

6. ENERGETICS OF VERTICAL MIGRATION

INTRODUCTION

In fishless lakes near Vancouver, the predatory 4th instar larvae of Chaoborus trivittatus demonstrate striking changes in seasonal patterns of vertical migration. In June most larvae remain near the surface throughout the day and night and exhibit migrations of small amplitude (based on depth distribution profiles from Fedorenko 1975a; see Pearre 1979). Later on, in the summer and the fall, however, the larvae undergo migrations of increasing amplitude. My purpose here was to investigate whether this pattern could be the result of individuals attempting to maximize their net rate of energy intake (ENET). I investigated this possibility by computing daily energy budgets for larvae using the two contrasting tactics (migratory and non-migratory) and by comparing the resulting ENET.

The data required to calculate daily energy budgets under various temperature and prey size conditions were collected in the laboratory, using larvae from Gwendoline Lake. In this paper, I generate a prediction about a migratory tactic based on a simulation model with a few simplifying assumptions. This prediction is then compared to field data collected in another fishless lake in the same vicinity (Eunice Lake) by another researcher (Fedorenko 1973, 1975a). Both lakes are situated in the U.B.C. Research Forest and contain a similar set of crustacean zooplankton species (except that *Diaptomus leptopus* in Gwendoline Lake is replaced in Eunice Lake by *D. tyrelli*, a species which is similar in size).

SCENARIO FOR THE MODEL

Let us consider a hypothetical fishless lake with a simplified temperature stratification in two layers (16 C for 0-5 m and 6 C from 5 m down). Moreover, let us assume that most prey are found in the top 5 m of the lake during the daytime. *D. kenai* for example is usually rare below that depth during the day (< 0.05 ind/l). We can imagine the following scenario, based on the timing and usual migratory pattern of the 4th instar: *Chaoborus* larvae come up at dusk to feed in the upper layers for a period of 8 hours. If we grant the larvae a composite meal of 0.8 J for this period (based on data in Fedorenko 1973), what is the ´best´ migratory tactic, i.e. the one permitting maximization of ENET over the next 16 hours? At dawn, an animal can either cease feeding and return toward the bottom of the lake, or forego vertical migration and continue feeding for the remainder of the day (16 hours). In the former case, greater metabolic efficiency (McLaren 1963) may be possible (at the cost of vertical migration and a potentially reduced assimilation efficiency). Non-migratory larvae, on the other hand, can count on greater opportunities to capture prey, provided that they are not fully satiated and that there is a sufficient number of easily ´handled´ energy-rich items available to compensate for higher metabolic rates at high temperature. For several reasons, I expect that this depends on the availability of the prey *D. kenai*. First, it ranks first or second in terms of relative contribution to the total biomass of crustacean zooplankton in these lakes. Second, it constitutes the bulk of the diet of 4th instar *C. trivittatus* in coastal lakes and ponds near Vancouver, British Columbia (Fedorenko 1975a, Swift 1976, Giguère 1979). Copepods are also almost always considered among the most important *Chaoborus* foods (Deonier 1943, Main 1953, Lewis 1977), and although other cladocerans are generally preferred (*Bosmina* and *Diaphanosoma*, Lewis 1977), these are not dominant members of the zooplankton community in these lakes (see Northcote and Clarotto 1975). *Daphnia rosea* on the other hand is important numerically and by biomass, but daphnids rank the lowest in prey choice experiments conducted with *Chaoborus* larvae (Lewis 1977). For example, Swüste *et al*. (1973) and Pastorok (1980a) found a preference for copepods over daphnids. Copepods are also more easily ´handled´ than daphnids because of their body shape (Swift and Fedorenko 1975, see also Swüste *et al*. 1973). *Chaoborus* ingestion time (Swift and Fedorenko 1975) and digestion time (Fedorenko 1973, Giguère pers. obs.) for *Daphnia* are greater than for the prey *Diaptomus*. Moreover, the % energy assimilated by *Chaoborus* is greater for copepod prey than for *Daphnia* prey (Swift 1976). Parma (1969) has published data showing greater growth for *C. crystallinus* larvae fed with a copepod diet that those fed mainly *Daphnia pulex*. Similar results were also obtained with 4th instar *C. trivittatus* feeding on *D. franciscanus* and *Daphnia rosea* (Pastorok 1980a). Therefore *D. kenai* could make an energy boost possible for non-migratory 4th instar larvae. The following model attempts to compare the magnitude of this energy boost, given various densities of *D. kenai*, to the boost accrued from vertical migration.

THE MODEL

Data were collected in the laboratory and the details of methods are presented in Chapters 2-4. The following data were included in the model:

(1) Capture rate. The rate of capture of a relatively large copepod (1.8 mm long, ~ 0.3 μl by volume) per unit time (CAP) was obtained from data in Chapter 2. This particular prey size was chosen because it is about an average size *D. kenai* in Gwendoline Lake. At a given density, the capture rate for a larva having food in its crop is lower than for larvae 'starved' for 1-2 days (crop volume= 0) (Fig. 16). This is caused by fewer attacks being triggered under partly satiated conditions and by a lower probability that an attack will be successful once launched. These data allow calculation of feeding rates, if it is further assumed that CAP increases linearly as a function of *D. kenai* density. This is not an unrealistic assumption considering the low prey density found in these oligotrophic lakes and the relatively short 'handling' time of copepods by *Chaoborus* (103.6 sec for 1.8 mm length prey; Swift and Fedorenko 1975).

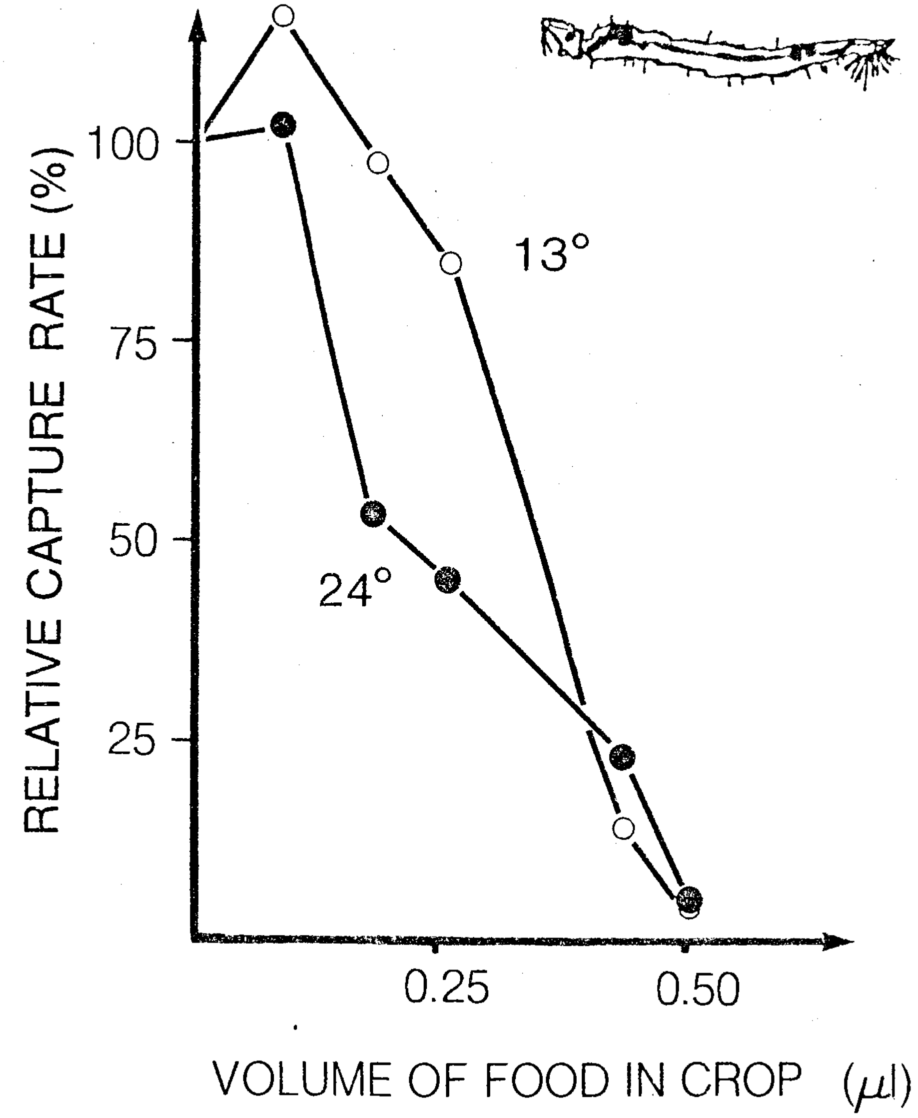


Fig. 16 Relative capture rate as a function of ´hunger´ for 4th instar larvae of <u>C. trivittatus</u>. Capture rates are expressed as a percentage of capture rate of 1-2 day ´starved´ larvae at each temperature. Unfilled circles: 13 C. Filled circles: 24 C.

(2) *Metabolic costs*. The energetic costs of three behaviours of the 4th instar larvae are required in the model. These are the metabolic rates at rest (0.008 J/hour at 5 C and 0.020 J/hour at 16 C, from Swift 1976 and corrected for SDA, Giguère 1980; Chapter 3), the metabolic cost while swimming[1] (0.07 mJ per swimming motion) and while attacking (0.057 mJ/attack, Giguère 1980; Chapter 3). The cost of vertical migration can then be estimated since vertical displacement is generally of the order of 5 m in these lakes and a larva covers roughly 2.5 cm vertically per swimming motion (based on observations in an artificial column in the laboratory). If we assume active swimming, an average roundtrip therefore represents an expenditure of 0.028 J.

(3) *Assimilation efficiency*. Using a radio-tracer technique, I evaluated the % assimilation of copepods by *Chaoborus* under four temperature conditions and five different meal volumes (Giguère 1981; Eqn. 7 and Fig. 7 in Chapter 4). It was nearly constant over the complete range of possible meal volumes (up to 0.9 µl) at 24 C. At lower temperatures, it was constant up to a meal volume of 0.5 µl but decreased for larger

---

[1] These values as well as those given in Table XIX and XX differ from those found in Giguère and Dill (1980). The data given in this chapter have been revised (larger sample sizes), and the model includes more details on the processes of respiration (including SDA) and digestion. The general conclusions remain the same.

meals (two large *D. kenai* ingested), particularly at low temperature.

(4) Digestion rate. The rate of emptying of the crop was studied at three different temperatures and the data are presented in Chapter 4 (Eqn. 6). Values for the instantaneous rate of digestion at 16 C were obtained by linear interpolation from the mean values shown in Table XV.

THE PREDICTION

What is the migratory tactic that will result in a maximum amount of net energy being secured by a 4th instar larva in a day? In the case of a larva choosing vertical migration, I obtain the value 0.13 Joule for ENET/day (Table XIX gives a complete breakdown). Some feeding is allowed on the low *D. kenai* density found below 5 m. In the case of no vertical migration, I computed the number of further captures by simulating predation hourly over a period of 16 hours at a given prey density and ´hunger´ level (also updated each hour). The results suggest that vertical migration should cease to occur at *D. kenai* densities above about 0.20/litre if individuals attempt to maximize ENET/day (Table XX).

Table XIX Energy budget for *Chaoborus* larvae undergoing vertical migration after eight hours of feeding near the surface.

	Joule/day
Meal assimilation	0.56
Vertical migration	-0.03
Respiration	-0.40
TOTAL:	0.13

Table XX Energy budget (J/day) for *Chaoborus* larvae staying near the surface for 24 hours, at various *D. kenai* densities.

Prey density (no./l):	0.1	0.2	0.3	0.4	0.5
Meal assimilation	0.76	0.80	0.85	0.90	0.95
Respiration	-0.66	-0.66	-0.66	-0.66	-0.66
Cost of attacks	-0.01	-0.02	-0.03	-0.04	-0.05
TOTAL:	0.09	0.12	0.16	0.20	0.24

Moreover, I found that larvae cannot increase ENET/day by staying near the surface until one more prey is captured and then migrating. This can be attributed to two factors: The CAP value in the early part of the 16-hour period is low and is combined with a lowered assimilation efficiency for all prey, including those captured previously; and any potential savings due to a lowered respiration rate following capture late in the period will be outweighed by the cost of vertical migration.

COMPARISON WITH FIELD DATA

Data on vertical distribution of zooplankton in Eunice Lake are available from Fedorenko (1973, 1975a). I reproduce here the information on vertical distribution of old 4th instar larvae of C. trivittatus at noon and midnight, as well as the noon distribution of D. kenai on four dates in 1972 (Fig. 17). The dotted line represents the density above which I predicted cessation of vertical migration based on the simulation model above. I would expect that fewer larvae would migrate as the density of D. kenai increases above this threshold. This is because a greater number of larvae will capture copepods as the density of the latter increases, up to a point where presumably most Chaoborus larvae can secure one or two more prey items and should remain near the surface ´en masse´. Chaoborus daytime and

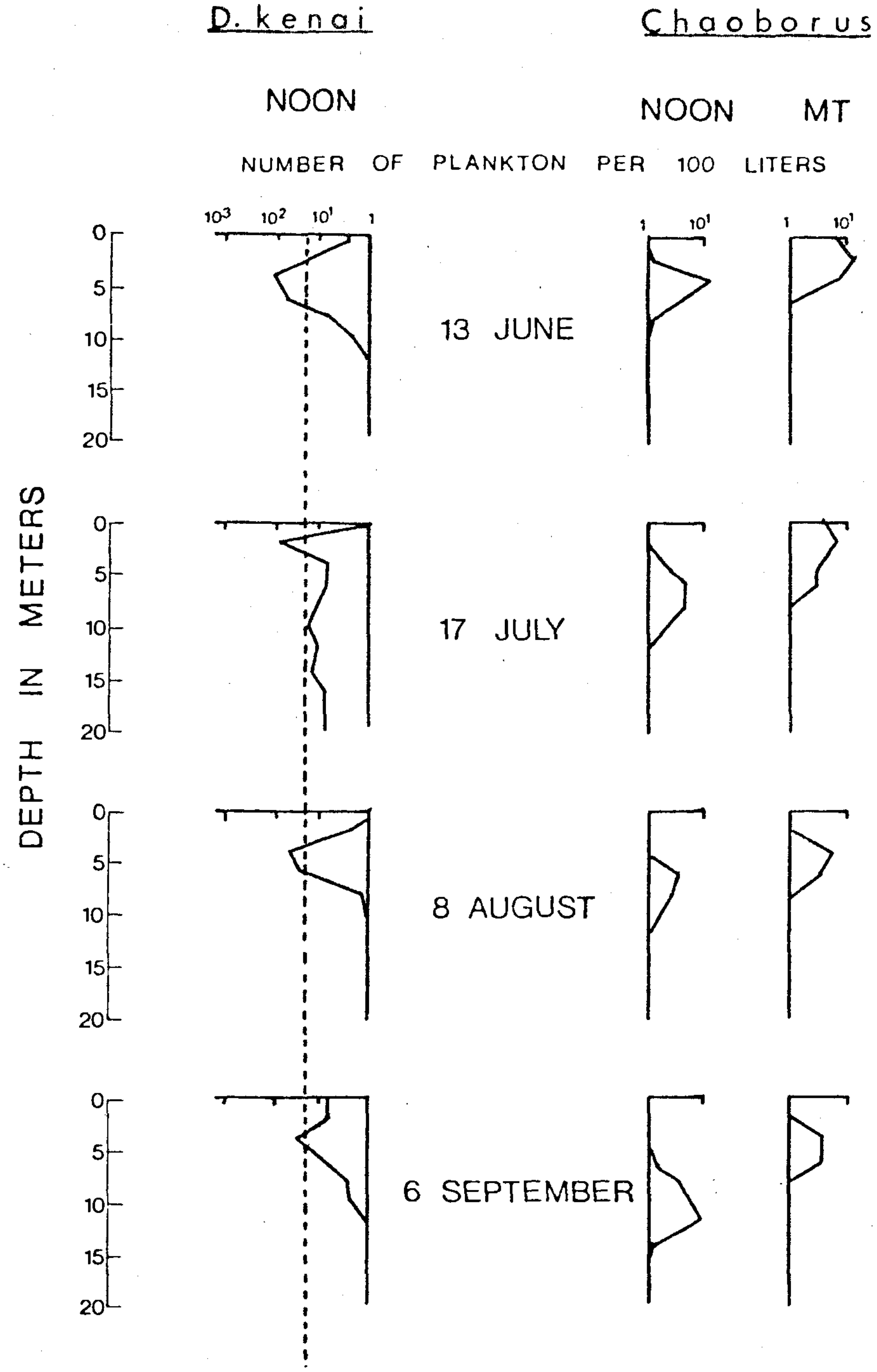


Fig. 17 Vertical distribution of zooplankton in Eunice Lake in 1972 (from Fedorenko 1973, 1975a). The dotted line represents prey density above which the simulation model (see text for explanation) predicts ´no migration´ for 4th instar larvae of C. trivittatus. MT= midnight.

nighttime distribution overlap should then be maximal, i.e. little or no vertical migration should occur. To examine this relationship quantitatively, I plotted the area under the *D. kenai* curve above the critical threshold against the % overlap in *Chaoborus* density curves at noon and at midnight (all data were first converted from a logarithmic to a linear scale). The results confirm the predicted pattern of vertical migration (Fig. 18).

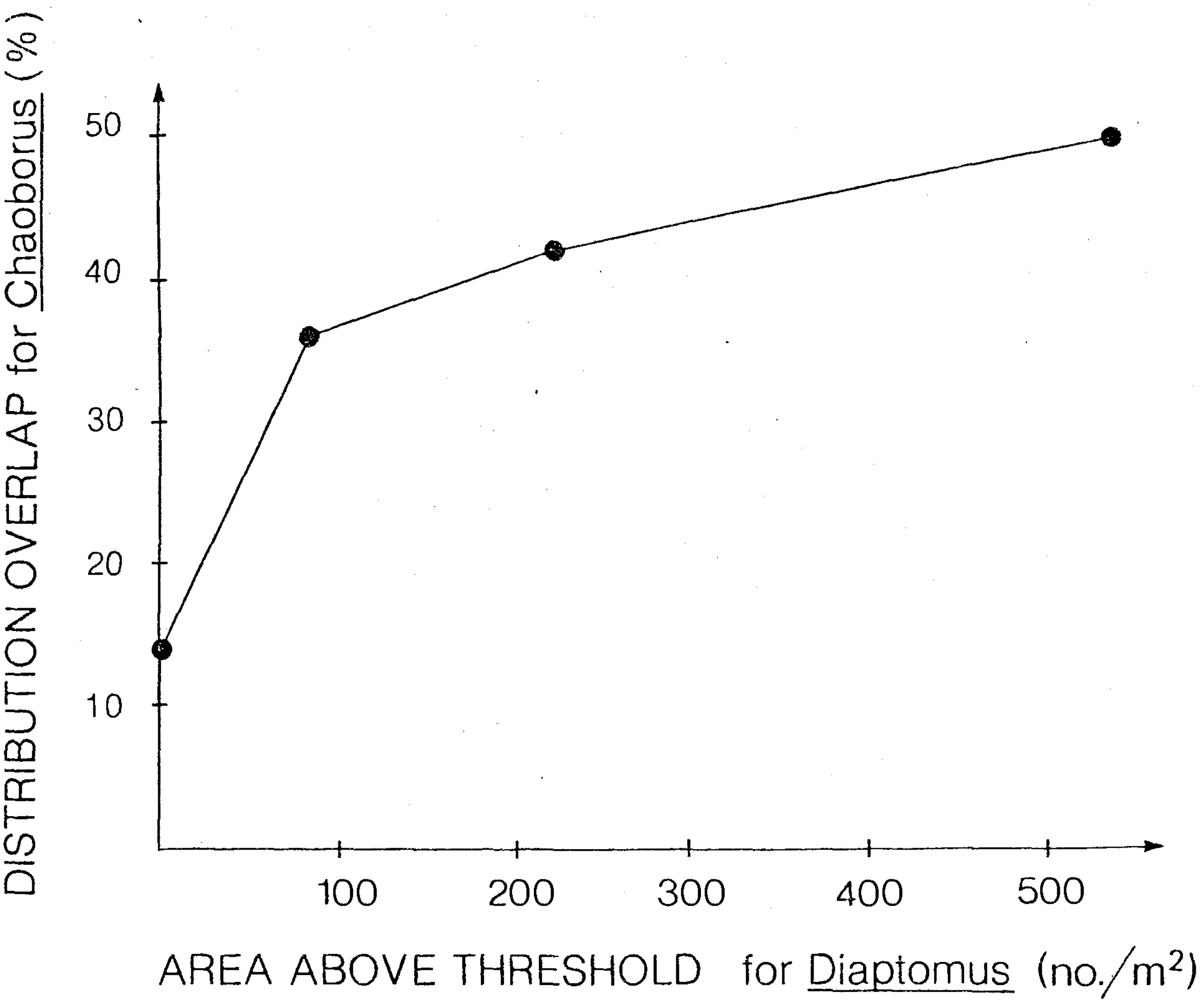


Fig. 18 Plot of % overlap of Chaoborus depth distribution at noon and at midnight versus the area under the curve of noon depth distribution of D. kenai lying above the critical density threshold predicted by the simulation model (see text and Fig. 17 for explanation).

DISCUSSION

The agreement between the field data and the model prediction is encouraging considering the simplifying assumptions under which the latter was derived. The next step will consist of testing the robustness of the model by relaxing the assumption of a fixed copepod size and using a more realistic temperature profile that matches field data on each date. Capture efficiency is known to vary with temperature, prey size, prey type and predator size (see Chapter 2), and all prey species should be included to obtain a complete picture of *Chaoborus* predation.

This energy-efficiency hypothesis is an expansion of the metabolic efficiency hypothesis of McLaren (1963), who suggested that increasingly extensive migrations will be valuable as surface temperatures increase, since an animal can gain an energy bonus by feeding efficiently at high temperature (near the surface) and resting at low temperature (greater depth) while maintaining a low metabolic rate. Swift (1976) studied the energetics of *C. trivittatus* and his simulations demonstrated that a larva would maximize growth either by feeding near the surface or by migrating according to its own physiological rhythm. According to Swift, his conclusion differs from

McLaren's because of different assumptions about the effect of temperature on digestion rate. However, both Swift and McLaren assume that assimilation efficiency is constant. My data suggest that assimilation efficiency is temperature dependent and that the effect is very much dependent on meal size (Giguère 1981; Fig. 19, Chapter 4). Over a 24-hour period, *Chaoborus* assimilation decreases by 0.037 J/ C for larger meals (0.9 µl) compared to a 0.025 J/ C decrease in respiration. There is actually an increase of 0.003 J/ C in assimilation for smaller meals (0.5 µl). The next step will consist of testing the effect of meal volume on migratory behaviour of *Chaoborus* by pre-feeding known amounts of food to larvae before introducing them into thermally stratified water columns in the laboratory. If the present model is confirmed, I would predict vertical migration of low amplitude for *Chaoborus* in the summer since one would tend to associate high crustacean zooplanton production (and hence larger meals for *Chaoborus*) with higher surface temperature in temperate waters. This prediction is contrary to McLaren's.

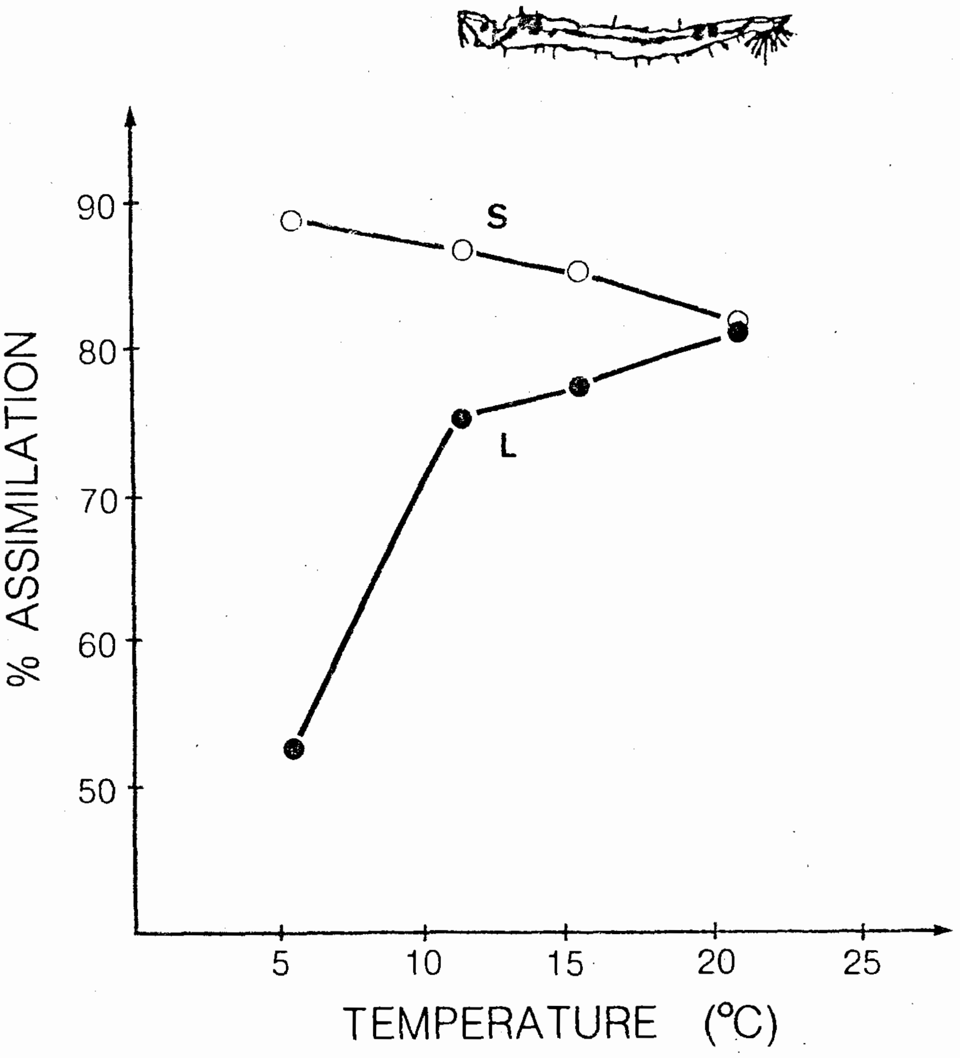


Fig. 19 Summary of data on assimilation efficiency of copepods by 4th instar larvae of *C. trivittatus* (from Fig. 7). Unfilled circles: small meal (~0.5 µl). Filled circle: large meal (~0.9 µl).

D. GENERAL DISCUSSION

To this point in the thesis, several components of the feeding of Chaoborus larvae have been studied and reported upon in detail (Chapters 1-5). I have also illustrated how they can be combined in a simulation model to investigate one aspect of predator-prey interactions among pelagic zooplankton (i.e. vertical migration, Chapter 6). A similar approach will now be used to achieve a synthesis and emphasize the importance of size-selective predation to the structure of zooplankton communities. First, some additional information is provided, and the components of the feeding of Chaoborus are brought together to reveal mechanisms underlying size-selective predation. I then discuss competitive interactions between fish and invertebrate predators.

Aquatic invertebrate predators are believed to have a substantial impact on zooplankton populations, partly because they are abundant (relative to fish), and partly because they select prey of specific sizes (Dodson 1974b). Yet ecologists have not attempted to unravel the dynamic properties of these interactions by carrying out comprehensive studies of the predation process. For example reactive distances to prey have rarely been measured (for exceptions see Kerfoot 1978, Cloarec 1979, 1980), and quantitative studies on size-dependent encounter rates between predator and prey are lacking. This information is essential since size and speed of predator and prey (the major determinants of encounter) are generally not much different. Thus prey characteristics can affect substantially the encounter process and the availability of prey to the predator.

Since crustacean zooplankton move more or less randomly in a relatively uniform environment, the encounter problem can be approached by designing stochastic models of their interactions. I proposed a model (Chapter 1) to predict encounter rates for an ambush predator feeding on zooplankton which was based on realistic assumptions concerning the size and cylindrical shape of the strike field of the predator (the 4th instar larva of _C. trivittatus_). Here I will use this model to determine the effect of size of predator and prey on encounter rate values.

First, I measure from high speed films the mean apparent attack distances for 3rd and 4th instar _C. trivittatus_ feeding on preferred prey (copepods). These values will differ from the distances reported in Chapter 1, which enclose 93% of observed attacks. Second, I combine these data with the encounter model and generate realistic estimates of encounter rates. Third, I combine this information with other components of predation (Chapters 2-4) to investigate the size-selective nature of the feeding of _Chaoborus_. I break down the problem in two parts: (a) effects of prey-size-dependent encounter rates and strike efficiency, which determine the vulnerability of different sized prey to the predator (passive size selection), and (b) effects of hunger that influence selection through the behaviour of the larvae (active size selection; Pastorok 1978, 1980b).

Finally, I compare the size-selective feeding of invertebrate predators with that of visual planktivores (mainly fish), whose impact on size and species composition of natural freshwater zooplankton assemblages is firmly established (Dodson 1974b, Hall *et al*. 1976). I describe patterns of utilization on the prey size dimension of the niche (other differences between prey types are ignored for simplicity) for both fish and invertebrate predators, and I discuss their competitive interactions. I also examine their feeding strategies in a bioenergetic context and consider their importance to the structure of zooplankton communities.

Section I- DETERMINING REACTIVE DISTANCES

Materials and methods

I measured from high-speed films the distance at which *Chaoborus* larvae begin to attack copepods (for details see Chapter 1 and MATERIALS AND GENERAL METHODS). I used 3rd and 4th instar larvae of *C. trivittatus* ´starved´ at least 24 hours. *D. kenai* and *D. leptopus* were used as prey since they are preferred by *Chaoborus* (see Chapter 6) and they provide a large number of prey with a uniform body plan.

Results

Apparent attack distances did not vary significantly between temperature treatments, and the data were pooled (Table XXI). I then regressed prey length (0.9-2.6 mm) on attack distance for all observations for each larval instar but the coefficients of determination were not significant for either 3rd (r^2= 0.026; slope= 0.27; n= 42; $p \geq 0.30$) or 4th instar larvae (r^2= 0.001; slope= -0.05; n= 192; $p \geq 0.65$). I then tested for an effect of predator size by computing a mean value for each individual predator, and regressing those on individual larval body size within each instar. The coefficients of determination were not significant for either 3rd (r^2= 0.004; slope= 0.01; n= 11; $p \geq 0.85$) or 4th instar larvae (r^2= 0.074; slope= -0.10; n= 20; $p \geq 0.24$). However, mean apparent attack distances varied significantly between instars (means in Table XXI; F= 7.79; d.f.= 1,29; $p < 0.01$). Although predator body size-dependent attack distances in invertebrate predators have been inferred from estimates of their area of discovery (Nicholson 1933, Thompson 1975), direct evidence comes from only a few previous studies (Gittelman 1978, Cloarec 1980, Jamieson and Scudder 1979).

Table XXI Mean apparent attack distances (mm, with sample size in parentheses) for 3rd (~10 mm) and 4th (~15 mm) instar larvae of C. *trivittatus* feeding on copepods at three temperatures. The data are based on high speed films of predator-prey interactions (see MATERIALS AND GENERAL METHODS). A summary of statistics is also provided.

Instar	Temperature (C)			F	p	d.f.	Grand mean
	6	13	24				
3rd		0.72(18)	0.92(25)	0.80	>0.20	1,41	0.84
4th	1.04(82)	1.10(82)	1.10(81)	1.03	>0.20	2,188	1.17

Section II- PREDICTING ENCOUNTER RATES WITH PREY

The collision model assumes a cylindrical attack field for a *Chaoborus* larva (details and rationale are presented in Giguère *et al*. submitted; Chapter 1). The target cylinder is stationary, and spherical prey are assumed to be uniformly or randomly distributed, and moving in random directions. Mean apparent attack distances (Section I above) for 3rd and 4th instar larvae (last column in Table XXI) were used to determine appropriate cylinder radii. They were corrected to true three-dimensional attack distances by dividing by 0.62, based on a Monte Carlo simulation for the projection of randomly chosen radii onto the horizontal plane passing through the center of a circle. The radii of the cylinders were thus set at 1.3 and 1.9 mm, and their lengths (based on sample measurements) at 11.4 and 14.9 mm for 3rd and 4th instar larvae respectively.

The model predicts that a 4th instar larva encounters prey 2.4 mm long 9.07 times more often than it encounters 0.5 mm prey (Fig. 20), although attack distances in *Chaoborus* larvae are independent of prey length (at least over a 0.9-2.6 mm range). This very substantial bias, which will surely affect prey selection, is due to the contribution of prey characteristics (viz. size *per se* and size-dependent swimming speed) to the encounter process. The same pattern holds for a 3rd instar

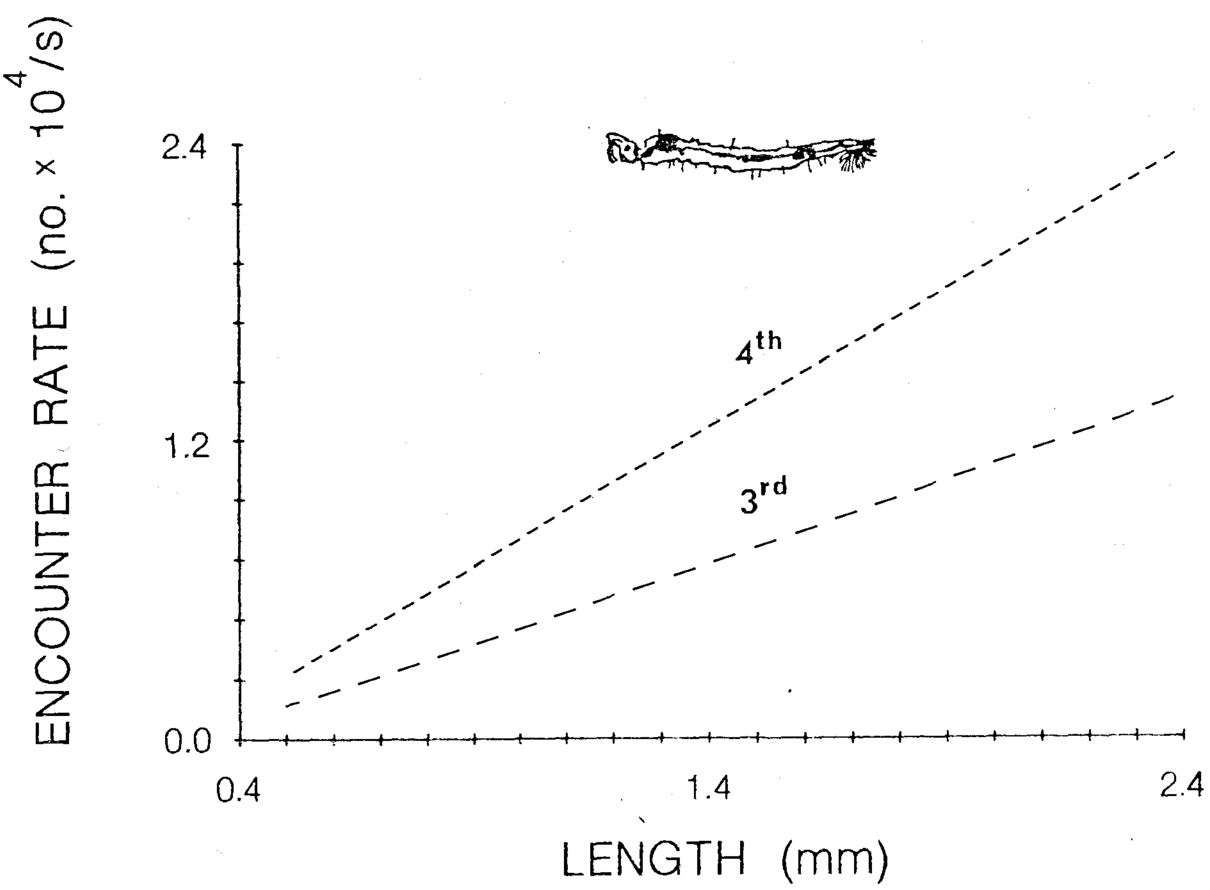


Fig. 20 Encounter rate between spheres (representing copepod prey) and a cylinder representing the attack field of 3rd and 4th instar C. trivittatus (based on measurements of mean attack distances) given an equal density of prey of each length. Parameter values are given in the text. The details of the model are in Chapter 1 Section II.

larva, although encounter values are lower than in the previous case. Differences in the slope of the relationship between larval instars indicate the presence of an interaction between predator and prey sizes. The encounter value ratio (2.4/0.5 mm prey) for a 3rd instar larva is 9.78 (cf. 9.07 for a 4th instar larva, a difference of 7.8%). Thus these characteristics of the prey are relatively more important in the encounter process when the predator is small. This conclusion should not be restricted to ambush predators like Chaoborus; zooplankton are highly mobile and the speed of prey often exceeds that of predators.

Factors which influence the swimming speed of prey (see Section III below) will affect feeding by predators considerably. This finding is relevant to the controversy concerning the feeding of larval marine fishes, which show a great deal of resemblance to such small planktivorous predators as chaoborids and chaetognaths (see Section IV below). Recently, researchers have attempted to determine the minimum prey density necessary to sustain growth of fish larvae, because ´good´ and ´bad´ years in larval survival seem to be correlated with plankton density (Rosenthal and Hempel 1970, Houde 1978). Some authors claim that normal growth of larval fish cannot be supported at average natural prey densities, and invoke patchiness in prey distribution to account for the fishes´ survival (Blaxter 1965, Parsons and LeBrasseur 1970, Werner and Blaxter 1980), while others maintain that this latter condition is not necessary (see Houde 1978, and Werner and Blaxter 1980 for a review).

Much of the controversy is based on laboratory experiments using brine shrimp (Artemia spp.) as food. Unfortunately, brine shrimp nauplii have low swimming speeds (Rosenthal and Hempel 1970), and these may be decreased further at low temperatures (most experiments are carried out around 10 C). Artemia typically inhabit shallow water bodies and develop under relatively warm conditions. They are unlikely to acclimatize to low temperatures, and their respiration and activity rates must decrease sharply with temperature. Experiments using Artemia may therefore overestimate the minimum prey densities needed to sustain fish growth. More experiments should be carried out using natural zooplankton, because fast swimming prey (such as copepods) may allow larval fish to grow normally at lower food densities.

The argument to this point has assumed that the rate of encounter is determined solely by prey size and speed. However, small prey are generally large ones in natural communities. For example, Sheldon et al. (1972) found roughly equal biomass at all sizes of organisms in marine pelagic communities. It therefore is of interest to determine encounter rates with prey while holding total prey volume (biomass) constant for each size. I arbitrarily set total prey volume equal to 0.0067 ml, computed the number of prey needed to make up this volume, and carried out simulations as before. Greater encounter rate values are predicted for smaller prey (Fig. 21). Thus a fixed amount of biomass packaged in many small prey produces a greater number of encounters with the predator than an equivalent biomass of large prey. Clearly, number of prey carries more weight than prey size (and/or speed) from a strict encounter point of view. On the other hand prey of different sizes are not equally available because capture efficiency is also prey-size-dependent in _Chaoborus_ larvae (Chapter 2; Swift and Fedorenko 1975; Giguère in prep.). Other components of the predation process therefore must be included to examine size-selective predation.

Section III- SIZE-SELECTIVE PREDATION BY 4th INSTAR LARVAE OF C. TRIVITTATUS

Prey of different sizes are not equally available to a 4th instar larva of _C. trivittatus_. For example, prey larger than 2.3 mm in length cannot be ingested because their diameter exceeds that of the mouth opening of the larva (Fedorenko 1973, Swift and Fedorenko 1975). In addition strike efficiency decreases more or less linearly as a function of prey size (Swift and Fedorenko 1975). By combining the results in Fig. 20 with Swift and Fedorenko's data, I determined a relative rate of

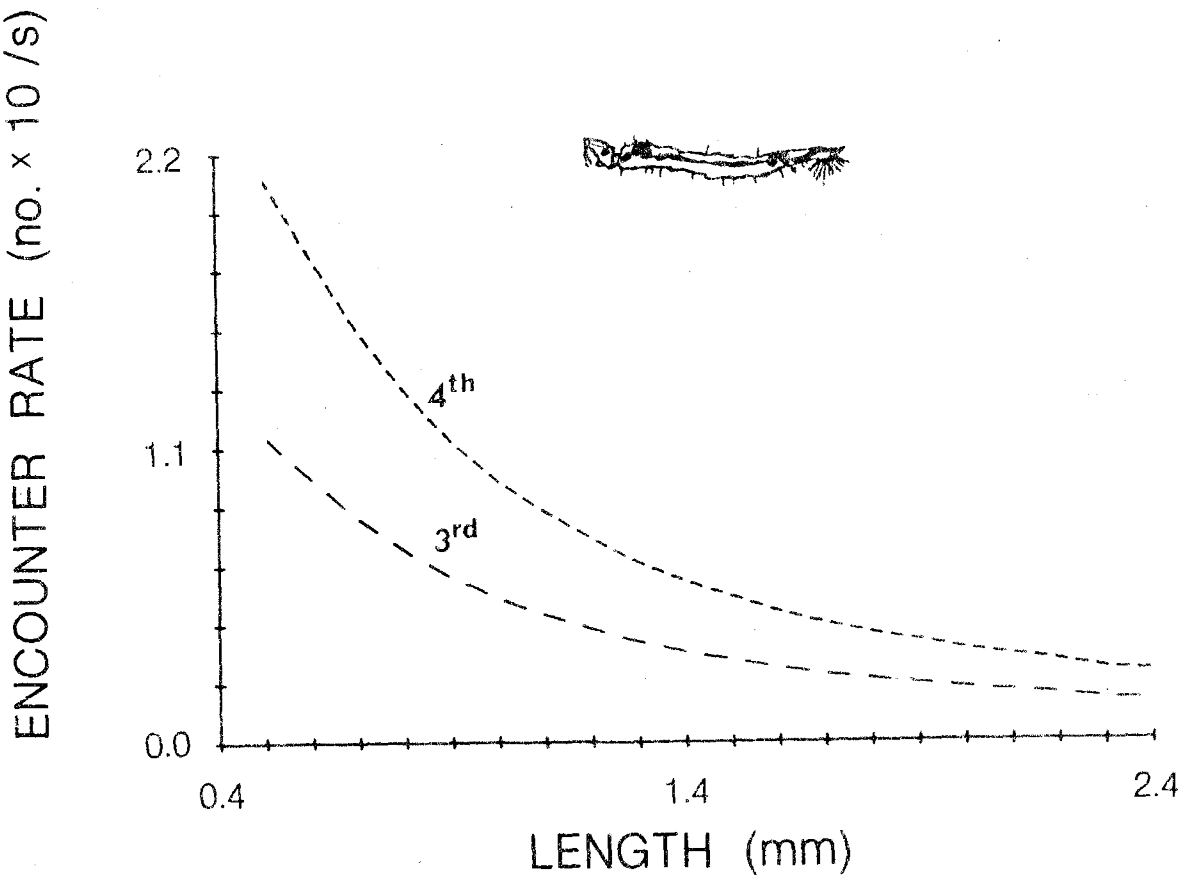


Fig. 21 Encounter rate between spheres (representing copepod prey) and a cylinder (see Fig. 20 above) given equal biomass (volume) of prey for each prey length category.

successful encounter with prey of different sizes. It shows (Fig. 22) that prey 1.3-1.4 mm long are most vulnerable to a 4th instar *Chaoborus*; everything else being equal (including density), they should appear most frequently in the diet. This kind of baseline information on passive size selection is essential in order to assess preference in *Chaoborus* larvae. Fig. 22 provides a valid quantitative null hypothesis for tests of behavioural or active size-selective predation in laboratory situations where prey are offered in equal proportions.

Note that since (a) copepod swimming speeds have been reported to be sex dependent in some species (Katona 1973, Gerritsen 1980) and to vary in response to other ecological conditions (ambient pressure, light quality and intensity, Champalbert 1975, 1978), and (b) strike efficiency is affected by temperature and predator body size to some extent (Chapter 2), Fig. 22 reflects only the general conditions found in this system.

The feeding patterns described above will also be modified by active (behavioural) selection (Swüste *et al.* 1973, Giguère and Dill 1979, Pastorok 1980b, Smyly 1980, Vinyard and Menger 1980, Winner and Greber 1980). However this should have only a minor impact on prey populations (see below).

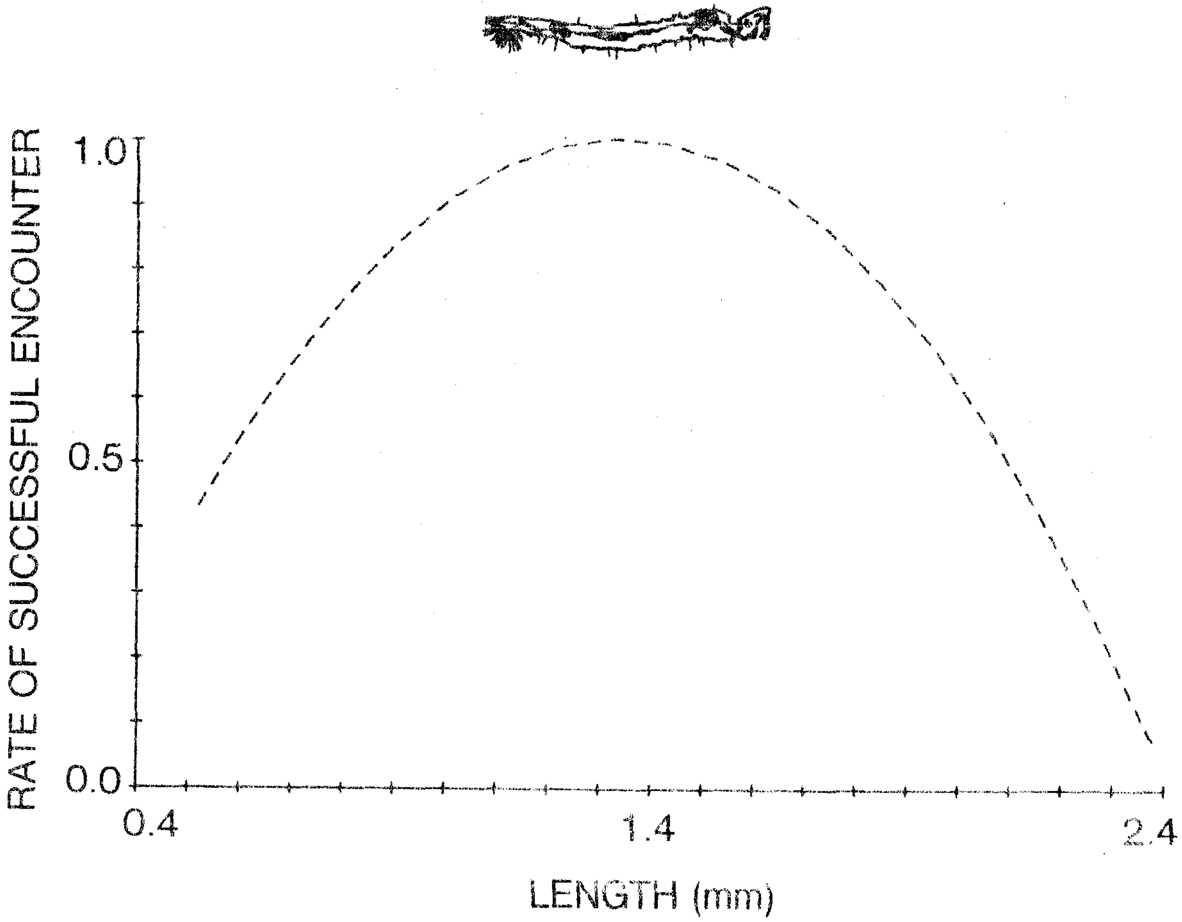


Fig. 22 Rate of successful encounter of prey of different length by 4th instar larvae of C. trivittatus. It is defined as the product of the rate at which prey encounter the strike field of the predator (Fig. 20) times the strike efficiency of the larva. The data are expressed relative to the most vulnerable prey size.

Section IV- FORAGING, SIZE, AND COMMUNITY STRUCTURE

Size-selective predation

Recently, aquatic ecologists (e.g. Dodson 1974a,b) have taken a closer look at the effect of invertebrate predators on the size and species composition of natural freshwater zooplankton communities (the impact of visual predators is firmly established, Dodson 1974a, Hall *et al*. 1976). Experimental field studies have indicated that larval chaoborids can affect the competitive balance between prey population and shift prey species composition (Allan 1973, Sprules 1972, Smyly 1976, Lynch 1979). Unfortunately, estimates of predation pressure vary widely (see Pastorok 1980a for a review), and little is known about the selective nature of their feeding (data have been collected using prey which vary greatly in body plan, swimming speed, or both).

The present study, on the other hand, provides the basis for a comprehensive treatment of the effect of body size on predation by a non-visual invertebrate planktivore. It is based on an encounter model which was shown to be adequate in the laboratory, and on size-dependent attack distances measured from high-speed films of predator-prey interactions. Strike efficiencies that depend on prey size were also determined empirically (Swift and Fedorenko 1975; Chapter 2). I will therefore review patterns of size-selective predation in the 4th instar larva of *C. trivittatus*, and compare them to those of a prototype adult[1] freshwater facultative planktivorous fish as pictured by O'Brien (1979)in his recent review. This will permit me to assess the potential impact of these two types of predators on zooplankton populations, and evaluate the scope for competitive interactions.

Passive size-selection

Size relationships will affect the relative availability of prey to a predator (encounter rate x capture efficiency), and *Chaoborus* larvae and fish are likely to differ markedly in this respect. Because of its small size and low speed, the 4th instar larva of *C. trivittatus* encounters large prey at a greater frequency than small prey (the former swim faster), while the efficiency of prey capture decreases rapidly with size, partly because of the size of the predator's mouthparts. Passive prey selection is thus bounded by a maximum size around 2.3 mm, with a peak efficiency for prey 1.3-1.4 mm long (Fig. 22).

---

[1] This distinction is historical (e.g. Galbraith 1967 and Brooks 1968 showed that adult fish select prey larger than 1 mm) but is arbitrary. I retain it for convenience, and for contrasting small invertebrates to large visual predators. Juvenile and larval fishes also feed on zooplankton, and the latter are considered below.

Planktivorous fish, on the other hand, have a large reactive field compared to the size of zooplankton, and search for prey at relatively high speeds. Although movements of prey may be an important factor in locating prey, they do not contribute significantly to the encounter process. Therefore encounter rates will be determined mainly by the inherent characteristics of visual detection systems of the predator. Assuming that prey are distributed uniformly (i.e. aggregations are not detected as super-organisms, Eggers 1977), reactive distance should increase with the size of the prey (O´Brien 1979). Thus encounter rate will be biased towards large prey. For example, assuming a spherical reactive field for planktivorous fish, O´Brien (1979) estimated that a 2 mm Daphnia is 27 times more likely to be located than a 1 mm Daphnia (over the same range of copepod lengths my model yields a factor of 2.4 for the 4th instar Chaoborus larva). Since the efficiency of prey capture by fish predators is not likely to vary much over this small range of sizes, passive prey selection by fishes will be strongly biased towards large items (Fig. 23).

Active size-selection

Active selection should not substantially affect the size distribution within populations of prey fed upon by Chaoborus

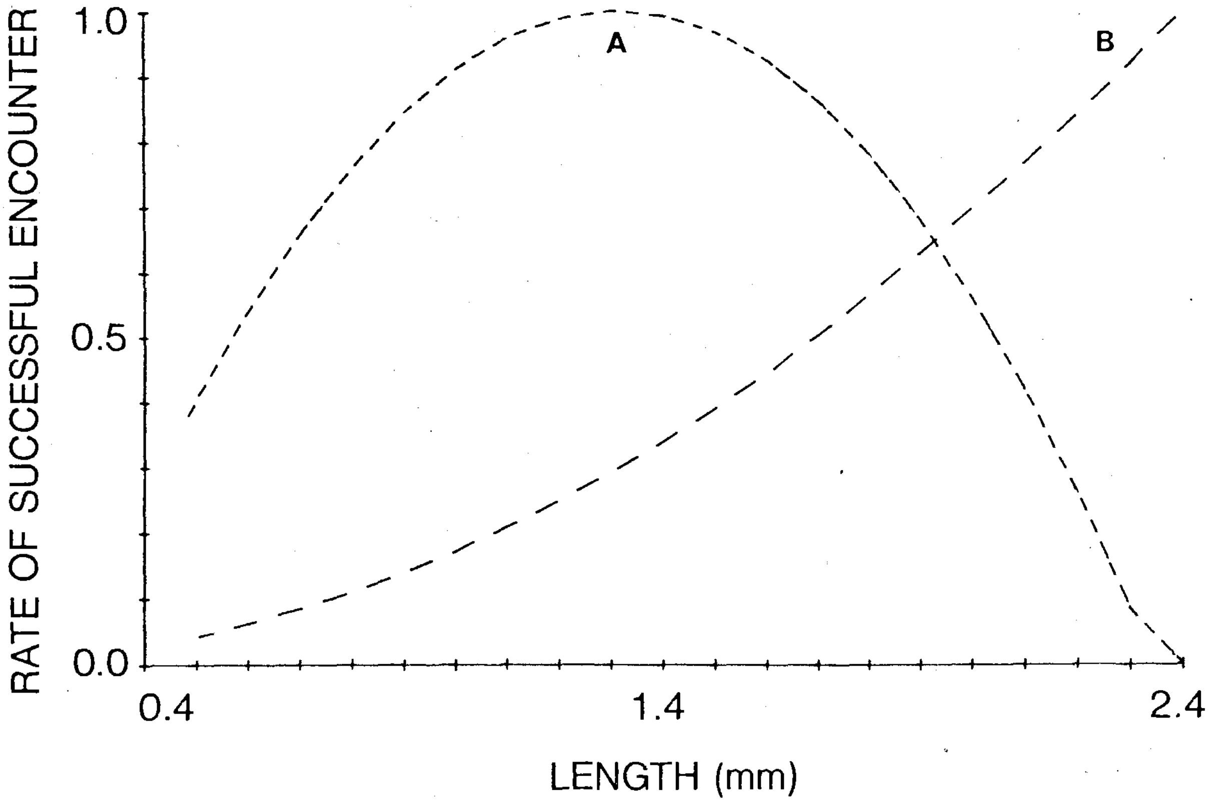


Fig. 23 Relative rate of successful encounter as a function of the size of zooplanktonic prey for a *Chaoborus* larva (A) and a facultative planktivorous fish (B) (from O'Brien 1979). See text for explanation.

larvae, for the following reasons: (a) Selective feeding is associated with low ´hunger´ levels, and thus with feeding rates which are lower than those of ´starved´ animals (Fig. 16); (b) low ´hunger´ levels in predators are associated with an abundance of food, the very circumstance in which only a small percentage of the prey population should be affected. Moreover low hunger levels, and thus selective feeding, are unlikely to be common in natural situations. Fedorenko´s (1973) field studies clearly demonstrated that the growth of 4th instar larvae of C. trivittatus was limited by food availability in Eunice Lake (British Columbia) in 1972. Analyses of crop content also revealed that generally fewer than 30% of larvae collected from coastal lakes and ponds near Vancouver, British Columbia, had food in their crop (Fedorenko 1975, Swift 1976, Giguère 1979).

Active size-selection by fish is also expected to have little impact on zooplankton. Fish feed until their gut is completely full with little or no apparent change in behaviour, and they rarely pass by detected prey (O´Brien 1979). One study (Hall et al. 1979) investigated size-selection in a field situation by appropriately correcting for biases in encounter rates due to the effect of prey size on the reactive distance of fish (using Egger´s 1977 visual detection model). It was found that the golden shiner (a facultative planktivore) did not actively select for large Daphnia on 7 sampling dates out of 8.

The exception corresponded to the highest density of Daphnia. Therefore active selection by planktivorous fish is not likely to modify considerably their impact on zooplankton, and passive selection is probably more important for both types of predators.

Energetics and evolutionary significance

The feeding success of a predator (and hence its growth and perhaps reproduction rate) is determined primarily by the frequency with which it meets suitable prey. In aquatic predators, I have argued that this depends on a few basic components which are a function of the relative sizes of the antagonists. Since body size has a large genetic component, these interactions are presumably under the influence of natural selection. The job of the evolutionary ecologist consists of unravelling the ultimate factors which govern these interactions. I will attempt to do so by comparing their feeding tactics (described above) in a bioenergetic context.

Planktivorous animals feed on small mobile prey that must be encountered and captured at a minimum rate to satisfy the metabolic demands of the predator. For a predator to be large, it must be able to encounter many relatively large prey (smaller zooplankters may represent an energy gain which is disproportionate to the cost of capture). This is exemplified by fishes which have (a) visual systems permitting long reactive distances that depend on the size of the prey, (b) high swimming speed relative to that of the prey, and (c) relatively high and constant capture efficiencies over the size range of most zooplankton. Thus they scan relatively large volumes of water, encountering many prey with a strong bias towards easily captured highly profitable items. Under these circumstances, they can maintain the high feeding rates (in terms of net energy gain per unit time) necessary to meet their metabolic demands. This strategy will result in a diet which differs greatly from the food spectrum available in their environment (i.e. what Griffiths (1975) calls an ´energy maximizer´).

Small predators do not feed in the same manner: (1) prey are difficult to pursue and a predator is best to launch sudden attacks at short distances to capture them successfully (i.e. they cannot select larger prey just because they might detect them at greater distances); prey are highly mobile, and the predator can maintain a positive energy budget without incurring large costs of searching for and pursuing prey at high drag coefficients. As a consequence of these two factors, prey characteristics should generally contribute substantially to the rate of encounter, and encounter with prey will be relatively unpredictable (although predators can reduce the variability by increasing their swimming speed).

This unpredictabilty is compounded by another factor. Gut size is quite small (e.g. three 1.8 mm copepods fill most of the crop of a 4th instar C. trivittatus), and a predator might be expected to satisfy its metabolic demands (or fill its crop) by feeding selectively on a few large prey. Large prey are rare and encountered quite unpredictably, and failure to capture one of the three individual prey necessary to fill the gut entails a 33.3% energy loss. The benefits of capturing large prey must therefore be weighed against the risk of multiple failures, which is high compared to an equivalent meal of smaller prey. A predator should therefore hedge its bets by taking smaller but more frequently encountered prey which represent substantial energy gains to small predators. Hence small invertebrates should feed opportunistically and maximize capture rates under most circumstances (cf. Griffiths' 'number maximizer'). This has been reported for a score of aquatic predators including Chaoborus (Dodson 1970, Dodson and Dodson 1971, Fedorenko 1975a, Lewis 1977, Pastorok 1978). This strategy would be particularly advantageous when continuous feeding is possible, as is the case for several aquatic invertebrate predators (chaoborids, chaetognatha, see Giguère and Dill 1979; mysids, Sameoto 1980).

Competition between planktivorous fish and invertebrates

Larval stages of fish feed primarily on small zooplankton and are subject to the same ecological constraints as invertebrate predators (e.g. small size, low mobility, etc., see below). Therefore, the potential for competitive interactions with invertebrate predators is greater than for non-larval fish, and I will consider them separately.

Larval fish

Larval fish exhibit feeding tactics and strategies similar to those discussed for small planktivorous invertebrate predators. First of all, many larval fishes do not feed visually. Houde (1978) states that they possess non-functional eyes at birth, and they attack only prey coming within a few mm (Rosenthal and Hempel 1970). They often feed continuously (Werner and Blaxter 1980). It is not surprising then to find that larval fish (and juveniles as well) are ´number maximizers´ (Griffiths 1975). Since many adult fishes are ´energy maximizers´ (Griffiths 1975; there are exceptions), fish growth should be accompanied by progressive changes in behavioural, physiological and morphological characteristics that will reflect these changes in feeding strategy (Ross 1978, Houde and

Schekter 1980). In larval fishes, vision comes into play early to aid in prey detection, and reactive distances increase progressively with larval size (Rosenthal and Hempel 1970). The fishes´ movements also become more directional (Kawamura and Hara 1980) and more rapid (Rosenthal and Hempel 1970). At the same time, their feeding efficiency increases. This is correlated with the growth of the mouth and fins, and faster darting behaviour in some larvae (Rosenthal and Hempel 1970, Blaxter and Staines 1971, Hunter 1972).

These larvae show other resemblances to the freshwater chaoborines and the marine chaetognaths. Not only are they comparable in size and feeding habits, but they possess transparent bodies and undergo diel vertical migrations. Competition for food between aquatic invertebrate and larval fishes could thus be intense and invertebrate predators could create ´bottlenecks´ in the reproductive cycle of fishes by depressing food density below levels necessary for fish survival or growth. The fish strategy may therefore consist of producing fewer larvae which are larger and more advanced in their development. By hatching with better vision and greater swimming ability (and probably greater feeding efficiency as well), the larvae would do better at low critical food densities (small slow moving larvae require a higher minimum food density to sustain growth than large fast moving ones, Houde 1978).

Such an adaptation would also help fishes to cope with variations in zooplankton production. In small temperate fresh-water bodies or at high latitudes in marine environments for example, seasonal and annual fluctuations in plankton numbers are considerable and very low food densities may occur from time to time. This situation would favour large larval size at hatching. Comparisons could be carried out along latitudinal gradients or among water bodies varying greatly in size.

Juvenile and adult fish

The patterns of prey size selection shown in Fig. 23 indicate the possibility of competitive interactions between large vertebrate and small invertebrate aquatic predators. By weighting the curves with appropriate prey densities and feeding intensities, one can determine utilization rates and obtain a better understanding of the dynamics of competitive interactions. Visual predators can also limit the spatial or temporal distribution of invertebrate predators and even induce their vertical migrations (Zaret and Suffern 1976, Wright *et al*. 1980) but this form of competition will not be considered here.

Competition results from the use by individuals of similar resources in limited supply (Birch 1957). The magnitude of the competition therefore will depend upon the abundance of the resource as well as the rates of food utilization by the competitors. In the case of planktivores, competition will be affected by the availability of alternate food resources to the competing predators. Freshwater fish are facultative planktivores, whereas many invertebrates are obligate planktivores (however Chaoborus larvae will sometimes ingest benthic materials; Parma 1971, Pastorok 1980a). As a result, there exists an asymmetry (Werner and Hall 1977) in the nature of the competitive relationship between small invertebrate and large visual predators living in fresh water. Since plankton may not contribute the most substantial portion of the diet of many planktivorous fishes (from an energetic standpoint), fish abundance may not always be related to their zooplankton food base. For example, Eggers et al. (1978) studied the ecology of fishes inhabiting Lake Washington and found that fish growth did not correlate well with zooplankton abundance. Moreover, fishes did not appear to reduce the abundance of zooplankton significantly. Predation pressure by planktivorous fish may therefore vary considerably from one situation to another and one should be cautious when interpreting data on competitive interactions.

If feeding by visual planktivores is low, competition will not be significant because fish feed mainly on large prey (Fig. 23), and small prey are relatively abundant. The feeding niche of the invertebrate predator will then be complementary to that of the vertebrate predator (Dodson 1970, Giguère 1979). If feeding pressure by visual planktivores is high, (e.g. obligate planktivores, large numbers of juvenile fish, or in small lakes with extensive margins of emergent vegetation supporting many facultative planktivores), the feeding niche of the invertebrate predator will be included inside that of the vertebrate predator. Coexistence may then depend upon patterns of resource abundance and various mechanisms of temporal or spatial segregation. For example, feeding in fishes is restricted to certain hours of the day during which light intensity is favourable; aquatic invertebrates respond to acoustic stimuli generated by zooplankton (Horridge 1966, Strickler and Bal 1973, Giguère and Dill 1979) and can feed continuously. Moreover the *Chaoborus* larva is resistant to low oxyen concentrations and can feed in the oxygen depleted hypolimnion. This can provide a refuge from vertebrate predation (Frey 1964, Stahl 1966, Hongve 1973). Thus, even when the feeding niche of *Chaoborus* is included within that of the fishes', coexistence may be possible.

CONCLUSIONS

I have explored ways that body size affects the rate of transfer of energy between 4th instar larvae of Chaoborus trivittatus (an ambush predator) and copepod prey. The method used was that of experimental components analysis (Holling 1964). The results given in the thesis provide only partial answers to the questions raised (e.g. only larvae starved at least 24 hours were used), but the following can be concluded:

(1) Larvae attack 48% of the prey which come within 2.2 mm from the central axis of their body, regardless of the size of the prey (0.9-2.6 mm) or the ambient temperature (6, 13, 16 or 24 C). Therefore, the swimming speed of prey, which is positively correlated with their length, influences encounter rates substantially.

(2) The proportion of successful attacks (i.e. the strike eficiency) is inversely related to prey length, and higher at 13 C than at 6 or 24 C. A small larva is more successful at capturing small prey than a large larva is, and *vice versa*.

(3) By combining the results on encounter rate and strike efficiency, I determined a relationship for the rate of successful encounter with prey (passive selection) as a function of prey size. It is a monotonic function which reaches a maximum for copepods 1.3-1.4 mm in length. This provides a null hypothesis to test for active or (behavioural) size selection by larvae that have food in their crops (i.e. are not ´hungry´).

(4) Although no effect of meal size on metabolic rate is apparent, the presence of food in the gut of a larva increases metabolic rate (SMR) by 36.9% (specific dynamic action or SDA). Large larvae (~16 mm in length) have a higher total SMR than small ones at 13 and 21 C. The total cost of prey capture represents only 0.3-3.9% of the energy content of copepods over the size range 1.2-2.3 mm, and metabolic expenditures attributable to the activity of the larvae are less than 10% of the daily expenditures. I conclude that SDA should be an integral part of energetic studies of predation.

(5) The efficiency of food assimilation (AE) can vary by as much as 33% depending on meal volume and temperature conditions. Predator size also had a small positive effect on AE. I conclude that the problem of optimal foraging should be approached from the point of view of optimal meal size, which will be related to prey size. More attention should be paid to spatio-temporal patterns of feeding since the capacity for food assimilation can be exceeded substantially.

(6) There was no significant effect of meal size or predator size on the instantaneous rate of digestion (expressed as mg dry weight of meal/thousand mg dry weight of *Chaoborus*/hour).

(7) In the general discussion, I summarized patterns of size selection in the *Chaoborus* larva, and considered its effects on the structure of aquatic communities. Ignoring other

differences between prey types, I argued that the feeding success of aquatic predators depends on a few basic components which are a function of the relative sizes of the antagonists. Competition for food between aquatic invertebrate predators and larval fish could be intense. In the case of juvenile or adult fishes, which visually select the largest prey sizes, the intensity of competition could be less severe. However, freshwater fishes are facultative planktivores (whereas many invertebrate predators are more exclusively planktivorous), and their abundance may not be directly related to the zooplankton food base. Fish predation pressure could thus vary considerably from one situation to another. Depending upon the abundance of the resource and the rates of food utilization by the competitors, the feeding niche of a non-visual invertebrate predator like Chaoborus could be complementary to that of the fish, or included within it.

Appendix I

Given that p equals the probability of capturing one prey in one minute, and that this value remains constant throughout a given period (i.e. ´hunger´ effects on p are negligible over short periods of time), the probability that an individual will capture its first prey in the ith minute is $p \times (1-p)^{t_i-1}$. In other words, it is the product of the probability that it will capture it, say, in the fifth minute (p) times the probability that it did not capture any in the first four minutes $(1-p)^4$. Thus, $n \times (1-p)^{24}$ represents the number of predators that should remain unsuccessful at the end of a 24 min period. This equation can easily be solved for p. I carried out this procedure for the 5 treatment categories for which sample size was largest in my experiments (Chapter 2), and used these values to generate a distribution for the number of predators expected to have captured their first prey at various times (up to 24 minutes). Predicted and observed distributions never differed significantly (X^2; $p \geqslant 0.25$, d.f.= 23).

LIST OF REFERENCES

Allan, J.D. 1973. Competition and the relative abundances of two cladocerans. Ecology 54: 484-498.

Anderson, R.S. 1970. Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48: 1229-1240.

Anderson, R.S. and L.G. Raasveldt. 1974. *Gammarus* and *Chaoborus* predation. Canadian Wildlife Service, Occasional Paper No. 18. Information Canada, Ottawa. 23 pp.

Banse, K. and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50: 355-379.

Birch, L.C. 1957. The meanings of competition. Am. Nat. 91: 5-12.

Blaxter, J.H.S. 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest. 10: 79-88.

Blaxter, J.H.S. and M.E. Staines. 1971. Food searching potential in marine fish larvae, p. 467-485. In Crisp, D.J. (Ed.). Fourth European Marine Biology Symposium. Cambridge Univ. Press, Cambridge.

Brett, J.R. and D.A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka* J. Fish. Res. Board Can. 27: 1767-1779.

Brooks, J.L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17: 273-291.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Brown, H.D. 1974. Defensive behavior of the wheat aphid, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae), against Coccinellidae. J. Ent. (A) 48: 157-165.

Calow, P. 1975. Defaecation strategies of two freshwater gastropods *Ancyclus fluviatilis* Mull. and *Planorbis contortus* Linn. (Pulmonata) with a comparison of field and laboratory estimates of food absorption rates. Oecologia 20:

51-63.

Champalbert, G. 1975. Répartition du Peuplement Animal de l'Hyponeuston. Etude Expérimentale de la Physiologie et du Comportement des Pontellidés. Ph.D. Thesis. Centre Universitaire de Marseille Luminy, Marseille. 312 pp.

Champalbert, G. 1978. Rythmes d'activité natatoire de quelques copépodes hyponeustoniques en fonction des conditions d'éclairement et de pression. J. exp. mar. Biol. Ecol. 35: 233-249.

Clarke, A. 1979. Assimilation efficiency of the antarctic marine isopod *Glyptonotus antarcticus*. Mar. Biol. 52: 157-160.

Clarke, A. 1980. A reappraisal of the concept of metabolic cold adaptation in polar marine invertebrates. Biol. J. Linnean Soc. 14: 77-92.

Cloarec, A. 1979. Hit distance estimation by *Ranatra*. Biol. Behav. 4: 173-191.

Cloarec, A. 1980. Ontogeny of hit distance estimation in *Ranatra*. Biol. Behav. 5: 97-118.

Confer, J.L. and P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571-579.

Confer, J.L. and J.M. Cooley. 1977. Copepod instar survival and predation by zooplankton. J. Fish. Res. Board Can. 34: 703-706.

Confer, J.L., Howick, G.L., Corzette, M.H., Kramer, S.L., Fitzgibbon, S. and R. Landesberg. 1978. Visual predation by planktivores. Oikos 31: 27-37.

Corner, E.D.S., Head, R.N., Kilvington, C.C. and L. Pennycuick. 1976. On the nutrition and metabolism of zooplankton. X. Quantitative aspects of *Calanus helgolandicus* feeding as a carnivore. J. Mar. Biol. Assoc. U.K. 56: 345-358.

Cosper, T.C. and M.R. Reeve. 1975. Digestive efficiency of the chaetognath *Sagitta hispida* Conant. J. exp. mar. Biol. Ecol. 17: 33-38.

Davies, N.B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46: 37-57.

Deonier, C.C. 1943. Biology of the immature stages of the Clear

Lake gnat (Diptera: Culicidae). Ann. Entomol. Soc. Amer. 36: 383-388.

Dixon, A.F.G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle Adalia decempunctata (L.). J. Anim. Ecol. 28: 259-281.

Dixon, A.F.G. 1970. Factors limiting the effectiveness of the coccinellid beetle, Adalia bipunctata (L.), as a predator of the sycamore aphid, Drepanosiphum platanoides (Schr.). J. Anim. Ecol. 39: 739-751.

Dodson, S.I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15: 131-137.

Dodson, S.I. 1974a. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. Ecology 55: 605-613.

Dodson, S.I. 1974b. Adaptive change in plankton morphology in response to size-selective predation: A new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721-729.

Dodson, S.I. and V.E. Dodson. 1971. The diet of Ambystoma tigrinum larvae from Western Colorado. Copeia 1971: 614-624.

Dühr, B. 1955. Uber Bewegung, Orientierung und Beutefang der Corethralarva (Chaoborus crystallinus De Geer). Zool. Jb. Physiol. 65: 378-429.

Edmondson, W.T. and G.G. Winberg. (Eds.) 1971. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No. 17. Blackwell Scientific Publications, Edinburgh. 358 pp.

Eggers, D.M. 1977. The nature of food selection by planktivorous fish. Ecology 58: 46-59.

Eggers, D.M., Bartoo, N.W., Richard, N.A., Nelson, R.E., Wissmar, R.C., Burgner, R.L. and A.H. Devol. 1978. The Lake Washington ecosystem: The perspective from the fish community production and forage base. J. Fish. Res. Board Can. 35: 1553-1571.

Elliott, J.M. 1976. Energy losses in the waste products of brown trout (Salmo trutta L.). J. Anim. Ecol. 45: 561-580.

Elliott, J.M. 1979. Energetics of freshwater teleosts. Symp. zool. Soc. Lond. 44: 29-61.

Elliott, J.M. and L. Persson. 1978. The estimation of daily rates of food consumption. J. Anim. Ecol. 47: 977-991.

Elton, C. 1933. The Ecology of Animals. Chapman and Hall, London. 97 pp.

Evans, H.F. 1976. The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum*. Ecological Entomology 1: 85-90.

Fedorenko, A.Y. 1973. Predation Interactions Between Zooplankton and Two Species of *Chaoborus* (Diptera: Chaoboridae) in a Small Coastal Lake. M.Sc. Thesis, Univ. of British Columbia, Vancouver. 123 pp.

Fedorenko, A.Y. 1975a. Instar- and species-specific diets in two species of *Chaoborus*. Limnol. Oceanogr. 20: 238-249.

Fedorenko, A.Y. 1975b. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. Limnol. Oceanogr. 20: 25-258.

Fedorenko, A.Y. and M.C. Swift. 1972. Comparative biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. Limnol. Oceanogr. 17: 721-730.

Feigenbaum, D.L. 1978. Hair-fan patterns in the Chaetognatha. Can. J. Zool. 56: 536-546.

Feigenbaum, D. 1979. Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. Mar. Biol. 54: 75-82.

Feigenbaum, D. and M.R. Reeve. 1977. Prey detection in the Chaetognatha: Response to a vibrating probe and experimental determination of attack distance in large aquaria. Limnol. Oceanogr. 22: 1052-1058.

Frey, D.G. 1964. Remains of animals in quaternary lake and bog sediments and their interpretation. Ergebn. Limnol. 2: 1-114.

Galbraith, M.G., Jr. 1967. Size selective predation on *Daphnia* by rainbow trout and yellow perch. Trans. Am. Fish. Soc. 96: 1-10.

Galbraith, M.G., Jr. 1975. The use of large *Daphnia* as indices of fishing quality for rainbow trout in small lakes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2485-2492.

Gerritsen, J. 1980. Adaptive responses to encounter problems, p. 52-62. In Kerfoot, W.C. (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, Amer. Soc. Limnol. Oceanogr. Univ. Press New England, Hanover.

Gerritsen, J. and J.R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. J. Fish. Res. Board Can. 34: 73-82.

Giguère, L.A. 1979. An experimental test of Dodson's hypothesis that Ambystoma (a salamander) and Chaoborus (a phantom midge) have complementary feeding niches. Can. J. Zool. 57: 1091-1097.

Giguère, L.A. 1980. Metabolic expenditures in Chaoborus larvae. Limnol. Oceanogr. 25: 922-928.

Giguère, L.A. 1981. Food assimilation efficiency as a function of temperature and meal size in larvae of Chaoborus trivittatus (Diptera: Chaoboridae). J. Anim. Ecol. 50: 103-109.

Giguère, L.A., Delâge, A., Dill, L.M. and J. Gerritsen. Submitted. Predicting encounter rates for zooplankton: A model assuming a cylindrical encounter field. Can. J. Fish. Aquat. Sci.

Giguère, L.A. and L.M. Dill. 1979. The predatory response of Chaoborus larvae to acoustic stimuli, and the acoustic characteristics of their prey. Z. Tierpsychol. 50: 113-123.

Giguère, L.A. and L.M. Dill. 1980. Seasonal patterns of vertical migration: A model for Chaoborus trivittatus, p. 122-128. In Kerfoot, W.C. (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, Amer. Soc. Limnol. Oceanogr. Univ. Press of New England, Hanover.

Gilson, W.E. 1963. Differential respirometer of simplified and improved design. Science 141: 531-532.

Gittelmamn, S.H. 1978. Optimum diet and body size in backswimmers (Heteroptera: Notonectidae, Pleidae). Ann. Entomol. Soc. Amer. 71: 737-747.

Glen, D.M. 1975. Searching behaviour and prey-density requirements of Blepharidopterus angulatus (Fall.) (Heteroptera: Miridae) as a predator of the lime aphid, Eucallipterus tiliae (L.) and the leafhopper, Alnetoidea alneti (Dahlbom). J. Anim. Ecol. 44: 115-134.

Gliwicz, Z.M. 1969. Studies on the feeding of pelagic zooplankton in lakes with varying trophy. Ekol. Pol. Ser. A: 663-708.

Goldspink, C.R. and D.B.C. Scott. 1971. Vertical migration of *Chaoborus flavicans* in a Scottish Loch. Freshwat. Biol. 1: 411-421.

Gourévitch, A. 1928. L'action dynamique spécifique chez les blattes. Compt. Rend. Acad. Sci. 187: 65-67.

Griffiths, D. 1975. Prey availability and the food of predators. Ecology 56: 1209-1214.

Griffiths, C.L. and J.A. King. 1979. Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. Mar. Biol. 51: 141-149.

Guest, P.G. 1961. The solid angle subtended by a cylinder. The Review of Scientific Instruments 32: 164-165.

Hall, D.J., Cooper, W.E. and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839-928.

Hall, D.J., Threlkeld, S.T., Burns, C.W. and P.H. Crowley. 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. Ann. Rev. Ecol. Syst. 7: 177-208.

Hall, D.J., Werner, E.E., Gilliam, J.F., Mittelbach, G.G., Howard, D., Doner, C.G., Dickerman, J.A. and A.J. Stewart. 1979. Diel foraging behavior and prey selection in the Golden Shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Can. 36: 1029-1039.

Harding, G.C.H. 1977. Surface area of the euphausiid *Thysanoessa raschii* and its relation to body length, weight, and respiration. J. Fish. Res. Board Can. 34: 225-231.

Hassell, M.P. 1978. The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton. 237 pp.

Hillbricht-Ilkowska, A. 1977. Trophic relations and energy flow in pelagic plankton. Pol. Ecol. Stud. 3: 3-98.

Hoar, W.S. 1966. General and Comparative Physiology. Prentice-Hall, Englewood Cliffs, New Jersey. 848 pp.

Holling, C.S. 1963. An experimental component analysis of population processes. Mem. ent. Soc. Can. 32: 22-32.

Holling, C.S. 1964. The analysis of complex population processes. Can. Ent. 96: 335-347.

Holling, C.S. 1965. The functional response of invertebrate predators to prey density. Mem. ent. Soc. Can. 48: 1-86.

Hongve, D. 1973. On the ecology and distribution of *Chaoborus* from the upper Romerike district, south east Norway. Norw. J. Ent. 22: 49-57.

Horridge, G.A. 1966. Some recently discovered underwater vibration receptors in invertebrates, p. 395-405. In Barnes, H. (Ed.). Some Contemporary Studies in Marine Science. G. Allen and Unwin Ltd., London.

Horridge, G.A. and P.S. Boulton. 1967. Prey detection by Chaetognatha via a vibration sense. Proc. R. Soc. Lond. Ser. B 168: 413-419.

Houde, E.D. 1967. Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York. Trans. Amer. Fish. Soc. 96: 17-24.

Houde, E.D. 1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28: 395-411.

Houde, E.D. and R.C. Schekter. 1980. Feeding by marine fish larvae: Developmental and functional responses. Env. Biol. Fish. 5: 315-334.

Hrbáček, J. 1962. Species composition and the amount of zooplankton in relation to the fish stock. Roypr. Cesk. Akad. Ved. Rada. Mat. Prir. Ved. 72: 1-116.

Hrbáček H., Dvořakova, M., Kořínek V. and L. Procházkóva. 1961. Demonstrations of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Int. Ver. Theor. Angew. Limnol. Verh. 14: 192-195.

Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull. U.S. 70: 821-838.

Hutchinson, B.P. 1971. The effect of fish predation on the zooplankton of ten Adirondack lakes with particular reference to the alewife, Alosa pseudoharengus. Trans. Am. Fish. Soc. 100: 325-335.

Ivlev, V.S. 1961. Experimental Ecology of the Feeding of Fishes. Yale Univ. Press, New Haven. 302 pp.

Ivleva, I.V. 1980. The dependence of crustacean respiration rate on body mass and habitat temperature. Int. Revue ges. Hydrobiol. 65: 1-47.

Jamieson, G.S. and G.G.E. Scudder. 1979. Predation in Gerris (Hemiptera): Reactive distances and locomotion rates. Oecologia 44: 13-20.

Jobling, M. and P.S. Davies. 1979. Gastric evacuation in plaice, Pleuronectes platessa (L.): Effects of temperature and meal size. J. Fish. Biol. 14: 539-546.

Katona, S.K. 1973. Evidence for sex pheromones in planktonic copepods. Limnol. Oceanogr. 18: 574-582.

Kawamura, G. and S. Hara. 1980. The optomotor reaction of milkfish larvae and juveniles. Bull. Jap. Soc. Sci. Fish. 46: 929-932.

Kerfoot, W.C. 1975. The divergence of adjacent populations. Ecology 56: 1298-1313.

Kerfoot, W.C. 1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316-325.

Kerfoot, W.C. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnol. Oceanogr. 23: 1089-1102.

Kerr, S.R. 1971. Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Board Can. 28: 801-809.

Kerr, S.R. 1974. Theory of size distributions in ecological communities. J. Fish. Res. Board Can. 31: 1859-1862.

Klekowski, R.Z. and E.A. Shushkina. 1966. Ernährung, Atmung, Wachstum und Energie-Unformung in Macrocyclops albidus. Int. Ver. Theor. Angew. Limnol. Verh. 16: 399-418.

Klyashtorin, L.B. 1978. A study of the energy expenditure of planktonic crustaceans on active swimming and vertical migrations. Okeanologiya 18: 143-148. (Fisheries and Marine Service, Dartmouth, N.S., Translation Series #4358).

Kobayashi, Y. and D.V. Maudsley. 1974. Biological Applications of Liquid Scintillation Counting. Academic Press, New York. 196 pp.

Lawrence, T.E. 1926. Seven Pillars of Wisdom. Penguin Books Ltd., New York. 700 pp.

Lawton, J.H. 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). J. Anim. Ecol. 39: 669-689.

Lawton, J.H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. 40: 385-423.

Le Cren, E.D. 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of T and changes in population density. J. Anim. Ecol. 27: 287-334.

Lewis, W.M., Jr. 1975. Distribution and feeding habits of a tropical *Chaoborus* population. Int. Ver. Theor. Angew. Limnol. Verh. 19: 3106-3119.

Lewis, W.M., Jr. 1977. Feeding selectivity of a tropical *Chaoborus* population. Freshwat. Biol. 7: 311-325.

Lewis, W.M., Jr. 1979. Zooplankton Community Analysis: Studies on a Tropical System. Springer-Verlag, New York. 163 pp.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. Limnol. Oceanogr. 24: 253-272.

Main, R.A. 1953. A Limnological Study of *Chaoborus* (Diptera) in Hall Lake, Washington. M.Sc. Thesis, Univ. of Washington, Seattle. 106 pp.

Marshall, S.M. and A.P. Orr. 1955. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation and excretion in adult and stage V *Calanus*. J. Mar. Biol. Assoc. U.K. 34: 495-529.

Masket, A.V.H. and W.C. Rodgers. 1962. Tables of solid angles. U.S. Atomic Energy Commission, Report TID-14975. 476 pp.

May, R.M. 1976. Models for single populations, p. 4-25. In May, R.N. (Ed.). Theoretical Ecology. Saunders Co. Toronto.

McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. 20: 685-727.

McQueen, D.J. 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. J. Fish. Res. Board Can. 26: 1605-1618.

Morgan, M.D., Threlkeld, S.T. and C.R. Goldman. 1978. Impact of the introduction of Kokanee (*Oncorhynchus nerka*) and opossum shrimp (*Mysis relicta*) on a subalpine lake. J. Fish. Res. Board Can. 35: 1572-1579.

Nagasawa, S. and R. Marumo. 1976. Further studies on the feeding habits of *Sagitta nagae* Alvarino in Suruga Bay, central Japan. J. Oceanogr. Soc. Jap. 32: 209-218.

Nakamura, N. and S. Kasahara. 1956. A study of the phenomenon of the tobi-koi or shoot carp. II. On the effect of particle size and quality of the food. Bull. Jap. Soc. Sci. Fish. 21: 1022-1024.

Neill, W.E. and A. Peacock. 1980. Breaking the bottleneck: Interactions of invertebrate predators and nutrients in oligotrophic lakes, p. 715-724. In W.C. Kerfoot (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, Amer. Soc. Limnol. Oceanogr., Univ. Press of New England, Hanover.

Newbury, T.K. 1972. Vibration perception by chaetognaths. Nature 236: 459-460.

Nicholson, A.J. 1933. The balance of animal populations. J. Anim. Ecol. 2: 132-178.

Nilsson, N. and B. Pejler. 1973. On the relation between fish fauna and zooplankton composition in North Swedish lakes. Inst. Freshwater Res. Drottningholm Rep. 53: 51-77.

Northcote, T.G. and R. Clarotto. 1975. Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2378-2393.

O'Brien, W.J. 1975. Some aspects of the limnology of the ponds and lakes of the Noatak drainage basin, Alaska. Int. Ver. Theor. Angew. Limnol. Verh. 19: 472-479.

O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Amer. Sci. 67: 572-581.

O'Brien, W.J., Slade N.A. and G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (Lepomis macrochirus). Ecology 57: 1304-1310.

Paloheimo, J.E. and L.M. Dickie. 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23: 1209-1248.

Parker, R.R. and P.A. Larkin. 1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16: 721-745.

Parma, S. 1969. The life cycle of Chaoborus crystallinus (DeGeer) (Diptera: Chaoboridae) in a Dutch pond. Int. Ver. Theor. Angew. Limnol. Verh. 17: 888-894.

Parma, S. 1971. Chaoborus flavicans (Meigen) (Diptera: Chaoboridae): an Autecological Study. PhD. Thesis, Univ. of Groningen, Groningen. 128 pp.

Parry, D.A. 1944. Structure and function of the gut in Spadella and Sagitta. J. Mar. Biol. Assoc. U.K. 26: 16-36.

Parsons, T.R. and R.J. LeBrasseur. 1970. The availability of food to different trophic levels in the marine food chain, p. 335-338. In Steele, J.H. (Ed.). Marine Food Chains. Oliver and Boyd, Edinburgh.

Pastorok, R.A. 1978. Predation by Chaoborus Larvae and its Impact on the Zooplankton Community. Ph.D. Thesis, Univ. of Washington, Seattle. 238 pp.

Pastorok, R.A. 1980a. Selection of prey by Chaoborus larvae: a review and new evidence for behavioral flexibility, p. 538-554. In Kerfoot, W.C. (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, Amer. Soc. of Limnol. Oceanogr. Univ. Press of New England, Hanover.

Pastorok, R.A. 1980b. The effects of predator hunger and food abundance on prey selection by Chaoborus larvae. Limnol. Oceanogr. 25: 910-921.

Pearre, S., Jr. 1973. Vertical migration and feeding in Sagitta elegans Verrill. Ecology 54: 300-314.

Pearre, S., Jr. 1979. Problems of detection and interpretation of vertical migration. J. Plankton Res. 1: 29-44.

Petrova, M.A., Yelagina, T.S., Spiridinov, V.K. and T.A.

Filtakina. 1975. Production of planktonic crustaceans of two secondary oligotrophic lakes. Gidrobiol. Zh. 11: 61-65.

Pianka, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53-74.

Pyke, G.H., Pulliam, H.R. and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Reeve, M.R. 1964. Feeding of zooplankton with special reference to some experiments with *Sagitta*. Nature 201: 211-213.

Reeve, M.R. and L.D. Baker. 1975. Production of two planktonic carnivores (chaetognath and ctenophore) in South Florida inshore waters. Fish. Bull. U.S. 73: 238-248.

Rosenthal, H. and G. Hempel. 1970. Experimental studies in feding and food requirements of herring larvae (*Clupea harengus* L.), p 344-364. In Steele, J.H. (Ed.). *Marine Food Chains*. Oliver and Boyd, Edinburgh.

Ross, S.T. 1978. Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pisces: Triglidae). Fish. Bull. U.S. 76: 225-234.

Sameoto, D.D. 1980. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (Crustacea Euphausiacea). J. Plankton Res. 2: 129-143.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 11: 369-404.

Sheldon, R.W., Sutcliffe, W.H., Jr. and M.A. Paranjape. 1977. Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board Can. 34: 2344-2353.

Siegel, S. 1956. Non-parametric Statistics for the Behavioral Sciences. McGraw-Hill, Toronto. 312 pp.

Sigmon, C.F., Tombes, A.S. and L. Tilly. 1978. Diel oxygen uptake in *Chaoborus punctipennis* (Diptera: Culicidae). Hydrobiologia 61: 69-73.

Smyly, W.J.P. 1976. Some effects of enclosure on the zooplankton in a small lake. Freshwat. Biol. 6: 241-251.

Smyly, W.J.P. 1978. Further observations on limnetic zooplankton in a small lake and two enclosures containing fish. Freshwat. Biol. 8: 491-495.

Smyly, W.J.P. 1980. Food and feeding of aquatic larvae of the midge *Chaoborus flavicans* (Meigen) (Diptera: Chaoboridae) in the laboratory. Hydrobiologia 70: 179-188.

Sokal, R.R. and F.J. Rohlf. 1969. Introduction to Biostatistics. W.H. Freeman, San Francisco. 368 pp.

Solomon, M.E. 1949. The natural control of animal population. J. Anim. Ecol. 18: 1-35.

Sprules, W.G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53: 375-386.

Sprules, W.G. and L.B. Holtby. 1979. Body size and feeding ecology as alternatives to taxonomy for the study of limnetic zooplankton community structure. J. Fish. Res. Board Can. 36: 1354-1363.

Stahl, J.B. 1966. The ecology of *Chaoborus* in Myers Lake, Indiana. Limnol. Oceanogr. 11: 177-183.

Steigenberger, L.W. and P.A. Larkin. 1974. Feeding activity and rates of digestion of northern squawfish (*Ptychocheilus oregonensis*). J. Fish. Res. Board Can. 31: 411-420.

Strickler, J.R. 1975. Intra- and interspecific information flow among planktonic copepods: Receptors. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2951-2958.

Strickler, J.R. and K. Bal. 1973. Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): Their structure and importance. Proc. Nat. Acad. Sci. U.S.A. 70: 2656-2659.

Swift, M.C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology 57: 900-914.

Swift, M.C. and A.Y. Fedorenko. 1975. Some aspects of prey capture by *Chaoborus* larvae. Limnol. Oceanogr. 20: 418-425.

Swüste, H.F.J., Cremer, R. and S. Parma. 1973. Selective predation by larvae of *Chaoborus flavicans* (Diptera: Chaoboridae). Int. Ver. Theor. Angew. Limnol. Verh. 18: 1559-1563.

Teraguchi, S. 1975. Detection of negative buoyancy in the phantom larva, Chaoborus americanus. J. Insect Physiol. 21: 1265-1269.

Thompson, D.J. 1975. Towards a predator-prey model incorporating age structure: The effects of predator and prey size in the predation of Daphnia magna by Ischnura elegans. J. Anim. Ecol. 44: 907-916.

Thompson, R.J. and B.L. Bayne. 1972. Active metabolism associated with feeding in the mussel Mytilus edulis L. J. Exp. Mar. Biol. Ecol. 9: 111-124.

Thompson, R.J. and B.L. Bayne. 1974. Some relationships between growth, metabolism and food in the mussel Mytilus edulis. Mar. Biol. 27: 317-326.

Thomson, A.J. 1975. Synchronization of function in the foregut of the blowfly Phormia regina (Diptera: Calliphoridae) during the crop-emptying process. Can. Ent. 107: 1193-1198.

Vermeer, K., Cullen, L. and M. Porter. 1979. A provisional explanation of the reproductive failure of tufted puffins Lunda cirrhata on Triangle Island, British Columbia. Ibis 121: 348-354.

Vidal, J. 1980a. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of Calanus pacificus and Pseudocalanus sp. Mar. Biol. 56: 111-134.

Vidal, J. 1980b. Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of Calanus pacificus and Pseudocalanus sp. Mar. Biol. 56: 136-146.

Vidal, J. 1980c. Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size on the metabolic rate of Calanus pacificus. Mar. Biol. 56: 195-202.

Vidal, J. 1980d. Physioecology of zooplankton. IV. Effects of phytoplankton concentration, temperature and body size on the net production efficiency of Calanus pacificus. Mar. Biol. 56: 203-211.

Vinyard, G.L. and R.A. Menger. 1980. Chaoborus americanus predation on various zooplankters; functional response and behavioral observations. Oecologia 45: 90-93.

Wánkowski, J. and J. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic Salmon (*Salmo salar* L.). J. Fish. Biol. 14: 351-370.

Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 787-797.

Warren, C.E. and G.E. Davis. Laboratory studies on the feeding bioenergetics and growth of fish, pp. 175-214. In Gerking, S.D. (Ed.). The Biological Basis of Freshwater Fish Production. Wiley and Sons, San Francisco.

Welch, H.E. 1968. Energy Flow through the Major Macroscopic Components of an Aquatic Ecosystem. Ph.D. Thesis, Univ. of Georgia, Athens. 97 pp.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556-565.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111: 553-578.

Werner, E.E. and D.J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58: 869-876.

Werner, R.G. and J.H.S. Blaxter. 1980. Growth and survival of larval herring (*Clupea harengus*) in relation to prey density. Can. J. Fish. Aquat. Sci. 37: 1063-1069.

Widdows, J. 1978. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. Mar. biol. Assoc. U.K. 58: 109-124.

Wigglesworth, V.B. 1965. The Principles of Insect Physiology. Chapman and Hall, London. 827 pp.

Wilcox, R.S. 1972. Communication by surface waves: Mating behavior of a water strider. J. comp. Physiol. 80: 255-266.

Williamson, C.E. and J.J. Gilbert. 1980. Variation among zooplankton predators: The potential of *Asplanchna*, *Mesocyclops*, and *Cyclops* to attack, capture, and eat various rotifer prey, p. 509-517. In Kerfoot, W.C. (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3, Amer. Soc. Limnol. Oceanogr. Univ. Press of New Hampshire, Hanover.

Winner, R.W. and J.S. Greber. 1980. Prey selection by *Chaoborus* punctipennis under laboratory conditions. Hydrobiologia 68: 231-233.

Winter, J.E. 1969. Über den Einfluss der Nahrungshonzentration und anderer Faktoren auf Filtrierleistung und Nahrungaushutzung der Muscheln Arctica islandica und Modiolus modiolus. Mar. Biol. 4: 317-328.

Wratten, S.D. 1973. The effectiveness of the coccinellid beetle, Adalia bipunctata (L.), as a predator of the lime aphid, Eucallipterus tiliae L. J. Anim. Ecol. 42: 785-802.

Wright, D., O´Brien, W.J. and G.L.K. Vinyard. 1980. Adaptive value of vertical migration: A simulation model argument for the predation hypothesis, p. 138-147. In Kerfoot, W.C. (Ed.). Evolution and Ecology of Zooplankton Communities. Special Symposium Volume 3. Amer. Soc. Limnol. Oceanogr. Univ. Press of New England, Hanover.

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, 620 pp.

Zaret, T.H. 1972. Predator-prey interaction in a tropical lacustrine ecosystem. Ecology 53: 248-257.

Zaret, T.M. and J.S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21: 804-813.