### THE UNIVERSITY OF MANITOBA

Population Dynamics and Feeding Ecology of <u>Chaoborus flavicans</u> (Meigen) (Diptera:Chaoboridae) in Relation to <u>Chaoborus</u> Productivity in

West Blue Lake

### WALTER LYSACK

by

### A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

> DEPARTMENT OF ZOOLOGY WINNIPEG, MANITOBA

> > AUGUST, 1976

"POPULATION DYNAMICS AND FEEDING ECOLOGY OF <u>CHAOBORUS FLAVICANS</u> (MEIGEN) (DIPTERA:CHAOBORIDAE) IN RELATION TO <u>CHAOBORUS</u> PRODUCTIVITY IN WEST BLUE LAKE"

by

#### WALTER LYSACK

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

#### © 1976

Permission has been granted to the LIBRARY OF THE UNIVER-SITY OF MANITOBA to lend or sell copies of this dissertation, to the NATIONAL LIBRARY OF CANADA to microfilm this dissertation and to lend or sell copies of the film, and UNIVERSITY MICROFILMS to publish an abstract of this dissertation.

The author reserves other publication rights, and neither the dissertation nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

### TABLE OF CONTENTS

	PAGE	
INTRODUC	CTION 1	
LITERATU	JRE REVIEW	
	General Biology of Chaoborus sp 8	
	Population Dynamics and Productivity 13	
•	of <u>Chaoborus</u> 13	
	Vertical Migration of Chaoborus Larvae 18	
	Respiration and Feeding Ecology of	
•	Chaoborus Larvae 22	
METHODS	AND MATERIALS 27	
•	Description of Study Area 22	
	Life History, Population Dynamics and	
· · ·	Production of <u>C</u> . <u>flavicans</u> 27	
	Respiration and Feeding of <u>C</u> . <u>flavicans</u> 33	
	Calculations 36	
RESULTS		
	Life History and Population Dynamics of	
	<u>C. flavicans</u> 38	
	Production of <u>C</u> . <u>flavicans</u> in West Blue Lake 50	
	Respiration and Feeding of <u>C</u> . <u>flavicans</u> 61	
DISCUSS	ION	
•	Life History and Population Dynamics of	
•	C. flavicans in West Blue Lake	
· .	Growth, Feeding and Respiration of C. flavicans	
	in West Blue Lake86	
	Productivity of <u>C</u> . <u>flavicans</u> in West Blue Lake1	00

(i)

· · · ·	. · · · · · · · · · · · · · · · · · · ·	P	AGE
LITERATURE	CITED	• • • • • • • • • • • • • • • • • • • •	117
APPENDICES	••••••	• • • • • • • • • • • • • • • • • • •	133

(ii)

## LIST OF FIGURES

FIGURE	<u> </u>	AGE
1.	Map of West Blue Lake showing sampling stations	28
2.	Head capsule length	31
3.	Vertical distribution of <u>C</u> . <u>flavicans</u> larvae during	39
	1974	39
4.	Temporal changes in density of <u>C</u> . <u>Flavicans</u> larvae	•
	at three stations during 1974-75	40
5.	Temporal changes in benthic density of <u>C</u> . <u>flavicans</u>	
•	larvae during 1974	42
6.	Diel vertical migration of <u>C</u> . <u>flavicans</u> larvae	43
7.	Head capsule length histograms of <u>C</u> . <u>flavicans</u>	•
	larval instars, 1974	45
8.	Instar succession of <u>C</u> . <u>flavicans</u> larvae, 1974	46
9.	Temporal changes in emergence rate of <u>C</u> . <u>flavicans</u>	
· · · ·	adults	48
10.	Horizontal distribution of adult emergency across	
•	station 1	49
11.	Presence or absence of <u>C</u> . <u>flavicans</u> and amphipods	• .
	at station 1 transect	51
12.	Growth curve (irrespective of instar) of	
	overwintered 1973-74 generation and 1974-75	
	generation of <u>C</u> . <u>flavicans</u>	52
13.	Instar-specific growth curves	53

(iii)

FIGURE		PAGE
14.	Growth in terms of carbon content of <u>C</u> . <u>flavicans</u>	
	larvae and pupae, 1975	. 55
15.	Allen curve production of 1974-75 generation of	
	<u>C. flavicans</u> larvae	. 56
16.	Effect of temperature on $O_2$ consumption rate of	
•	<u>C. flavicans</u> larvae and pupae	. 65
17.	Effect of body size on 02 uptake per unit weight of	£
	C. <u>flavicans</u> larvae and pupae at five temperatures	66
18.	Food selection by <u>C</u> . <u>flavicans</u> instars I - IV	. 68
19.	Effect of food concentration on ingestion rates	
	of <u>C</u> . <u>flavicans</u>	69
20.	Feeding intensities of <u>C</u> . <u>flavicans</u>	72
Al.	Rearing tanks	134
Bl.	Transparent PVC feeding chamber	136
В2.	Rope cradle	. 137
вз.	Feeding chamber suspended in the water	. 138
C1.	Effect of predator density on ingestion	143

### LIST OF TABLES

TABLE		PAGE
1.	Temporal changes in pelagic densities (no. $m.^{-2}$ )	
	of <u>C</u> . <u>flavicans</u> during 1974-75	41
2.	Pechen-Shuskina production of the 1974-75	•
• .	generation of <u>C</u> . <u>flavicans</u> in West Blue Lake	57
3.	Carbon and caloric conversions of Pechen-Shuskina	
	production	62
4.	P/B ratios	63
5.	Feeding curve parameters and significance tests	70

(v)

# LIST OF APPENDICES

•	APPENDI	<u>×</u>	PAGE
	A.	Rearing Tanks	133
ļ	Β.	Feeding Chambers	135
(	С.	Trial Feeding Experiment	139
· . ]	D.	Benthic Densities of Chaoborus Larvae, 1974	144
]	Ε.	Depth-weighted Peaks of Vertical Migration of	
	• ,	C. flavicans, D. pulicaria and C. bicuspidatus	145
]	F.	Emergence and Sex Ratio of <u>C</u> . <u>flavicans</u> Adults	148
(	<b>G</b> .	Numbers of <u>C</u> . <u>flavicans</u> and Amphipods Caught in	
		Submerged Traps at Station 1	149
1	Η.	Dry Weights of <u>C</u> . <u>flavicans</u> Larvae and Pupae	150
-	I.	Instar-specific Growth Data	151
i	J.	Calorific Content of <u>C</u> . <u>flavicans</u> Larvae and Pupae.	153
]	Χ.	Carbon Content of <u>C</u> . <u>flavicans</u>	1,56
]	L.	Hatching Success of <u>C.</u> <u>flavicans</u> Eggs	159
1	4.	C. flavicans Respiration Data	160
1	N .	Allen Curve Production	163
(	р.	Feeding Experiment Results	165
. ]	<b>D</b> .	Authors of Species	171

(vi)

#### ACKNOWLEDGMENTS

I wish to express my sincere gratitude to Dr. F. J. Ward , professor , Department of Zoology , University of Manitoba , for his valuable counsel and support during this study. I greatly appreciate the advice and critical review of the manuscript by Dr. K. W. Stewart , professor , Department of Zoology , University of Manitoba , Dr. O. A. Saether , Scientist, Fisheries Research Board of Canada and Dr. K. Patalas , Principal Scientist , Fisheries Research Board of Canada.

Special thanks are due to Dr. K. Patalas for advice and encouragement. Assistance in the field by Mr. and Mrs. A. Ternowski is greatly appreciated. I would like to thank my parents and Mr. and Mrs. J. Wood for encouragement and support.

This work received support from grants to Dr. Ward from the National Research Council of Canada (A2604) and from the Department of Mines, Resources and Environmental Nanagement, Province of Manitoba.

#### ABSTRACT

The life cycle, population dynamics, respiration and feeding ecology of <u>Chaoborus flavicans</u> (Meigen) (Diptera: Chaoboridae) in West Blue Lake were examined over a two year period. The new generation began in early July. Larvae grew into fourth instars before winter. Fourth instars overwintered in the mud in a state of diapause, emerged next spring and metamorphosed into pupae. Adults emerged, mated and produced floating egg rafts during late June and early July. Larval abundance declined rapidly after they hatched and remained low for the rest of the season. Younger instars remained nearer the surface while older instars moved to deeper daytime depths and exhibited more extensive diel vertical migrations.

Developmental times of <u>C</u>. <u>flavicans</u> instars I-IV were: 10, 12, 12, and 142 days respectively. Biweekly weight increments were larger in successive instars. Maximum dry weights of instars I-IV were: 0.0193, 0.0493, 0.1543 and 0.9354 mg. respectively. Caloric content per unit weight (5.864 kcal. gm.<sup>-1</sup>dry weight) was not different among larvae and pupae. Carbon content per unit weight of instars I-IV and pupae was: 661.3, 602.8, 623.6, 468.1, and 389.8 ug. C mg.<sup>1</sup>dry weight respectively. Net productivity of <u>C</u>. <u>flavicans</u> larvae was 1982 mg. dry weight m.<sup>2</sup>year<sup>-1</sup> (1.09 x 10 ug. C m.<sup>2</sup>year<sup>-1</sup>, 11.625 kcal. m.<sup>2</sup>year<sup>-1</sup> according to the Allen curve and 2074 mg. dry weight m.<sup>2</sup>year<sup>-1</sup>according to the

(viii)

Pechen-Shuskina formula.

Oxygen uptake rates of fourth instars and pupae increased exponentially with temperature. In younger instars, oxygen uptake rates increased linearly with temperature. In Oxygen uptake per unit weight was significantly higher in pupae than in larvae. In situ incubation experiments showed that diversity in size and type of prey increased in successive instars. First instars fed on rotifers and nauplii and second instars added larger <u>Cyclops bicuspidatus</u> Thomasi to their diet. Third instars began feeding on small <u>Daphnia</u> <u>pulicaria</u> Leydig. Fourth instars preferred <u>C</u>. <u>bicuspidatus</u> and consumed all other types of prey. Feeding rates of all instars were lower in the hypolimnion than in the epilimnion. Feeding intensity increased with food concentration and temperature and decreased as larvae grew older.

### INTRODUCTION

Research at West Blue Lake is aimed at quantitatively describing energy exchanges and pathways in this freshwater ecosystem. To help attain this goal, information about food web components is required. Life cycles, population dynamics, productivity and feeding parameters are pertinent in describing an organism's place in the food web and its contribution to the productivity of the whole ecosystem.

<u>Chaoborus</u> larvae play an important role in freshwater ecosystems. They contribute significantly to the total biomass and productivity of the ecosystem. <u>Chaoborus</u> larvae exert significant predatory pressure on freshwater zooplankton. In turn, <u>Chaoborus</u> larvae are an important food source for amphipods and fish.

<u>Chaoborus</u> larvae occur in large numbers. Densities of over 50,000 m.<sup>-2</sup> are reported (Borutzky 1939, Bonomi 1962). <u>Chaoborus</u> larvae can attain a dry weight of 1.3 mg. (Parma 1971). Parma (1971) estimated biomass of benthic <u>Chaoborus</u> larvae to be 57.5 kg. ha.<sup>-1</sup> (wet weight) and 6.5 kg. ha.<sup>-1</sup> (dry weight). In Lake Mendota, winter biomass of <u>Chaoborus</u> larvae was 558 kg. ha.<sup>-1</sup> (Juday 1921). Borutzky (1939) found a maximum biomass in November of 17.5 kg. ha.<sup>-1</sup>

(dry weight). Deevey (in Brooks and Deevey 1963) estimated productivity of <u>Chaoborus</u> larvae to be 15 to 28 kg. (dry weight) ha.<sup>-1</sup> year<sup>-1</sup>. Thus <u>Chaoborus</u> larvae contribute substantially to total biomass and productivity of the freshwater ecosystem.

<u>Chaoborus</u> larvae exert significant predatory pressure on zooplankton. Kajak and Ranke Rybicka (1970) found that 7% and 13% of the zooplankton population were removed daily by <u>Chaoborus</u> in two Polish lakes. Fedorenko's (1975) estimated mean percentages of standing crop of prey eaten by <u>Chaoborus</u> were: 2% for copepod nauplii, 3% for <u>Diaptomus</u> <u>tyrelli</u>, 9% for <u>D. kenai</u>, and 4% for <u>Diaphanosoma</u>. Dodson (1972) found that <u>Chaoborus</u> predation accounted for 93% of <u>Daphnia</u> mortality in Leechmere Pond, Colorado. Dodson stated that the population growth rate of <u>Daphnia</u> was significantly influenced by this predation pressure.

<u>Chaoborus</u> larvae and pupae are a substantially important food source for amphipods and fish. Anderson (1970, 1974) observed many <u>Gammarus lacustris</u> feeding on <u>C</u>. <u>americanus</u> in many Alberta lakes. He stated that amphipod predation on chaoborids is the reason why amphipods and chaoborids rarely coexist. <u>G. lacustris</u> and <u>Hyallela</u> <u>azteca</u> are present in West Blue Lake. Biette (1969) observed a maximum density of 223 <u>Gammarus</u> per m.<sup>2</sup> in late June and 334 <u>Hyallela</u> per m.<sup>2</sup> in late July. However feeding of amphipods on <u>Chaoborus larvae</u> was not examined. In West Blue Lake, Chaoborus is not an important food source for walleye (Kelso 1971) or for yellow perch fry (Wong 1972). However, Chaoborus larvae and pupae occur regularly in older yellow perch throughout the summer. Falk (1971) found that Chaoborus comprised 21% (by weight) of perch stomach contents in early June and 60% on June 22. In other lakes, Chaoborus are more important as fish food. Chaoborus larvae occur frequently in Kokanee (Northcote and Lorz 1966) and irregularly in stomachs of cutthroat trout (Dimick and Mote 1934), rainbow trout (Crossman and Larkin 1959), brook trout (Ricker 1932), and lake trout (Martin 1954). Campbell (1935) found that Chaoborus larvae comprised 50% of white suckers' stomach contents. Mills (per. com.) found that Chaoborus comprise 40 - 80% of the whitefish diet in the Experimental Lakes Area, Ontario.

The observations stated above led to the belief that a study of <u>C</u>. <u>flavicans</u> relative to the West Blue Lake ecosystem would be important in attaining the general goals of the West Blue Lake research program. A study of <u>Chaoborus</u> productivity and feeding would reveal a new energy pathway, help explain discrepancies between secondary and fish production estimates and provide new information about <u>Chaoborus</u> predation on West Blue Lake zooplankton.

The objectives of this study are: (1) to describe the life history of <u>C</u>. <u>flavicans</u> in West Blue Lake, (2) to quantitatively describe population dynamics of Chaoborus

aquatic stages and to estimate larval productivity, (3) to monitor diel vertical migration of <u>C</u>. <u>flavicans</u> larvae and their prey, (4) to describe effects of temperature and food concentration on ingestion rates of <u>C</u>. <u>flavicans</u> larvae, (5) to describe effect of temperature on respiration of <u>C</u>. <u>flavicans</u> larvae, and (6) to relate ingestion rates, respiration and vertical migration patterns of C. <u>flavicans</u> larvae to their productivity.

It is necessary to describe the life history of <u>C</u>. <u>flavicans</u> because subsequent studies of productivity and feeding are based on information obtained from knowledge of the life cycle. Parma (1971) described the life history of <u>C</u>. <u>flavicans</u> in a Dutch man-made pond. I was interested in comparing the life cycle of <u>C</u>. <u>flavicans</u> in West Blue Lake to the life cycle described by Parma as well as life cycles of <u>C</u>. <u>trivittatus</u> and <u>C</u>. <u>americanus</u> described by Fedorenko and Swift (1972).

Estimates of population parameters such as abundance, growth, fecundity, population structure, etc., are necessary to estimate production. Net production of a specific population for a given time period is the sum of the growth increments of all members of the population. The Allen curve was the first method chosen to calculate production of <u>C</u>. <u>flavicans</u> larvae in West Blue Lake. This method is applicable because <u>C</u>. <u>flavicans</u> is univoltine. Using the Allen curve, number in a cohort is plotted against mean weight of an individual. The area under this curve is the productivity of the cohort. The Pechen-Shuskina formula was the second method chosen to calculate production of <u>C</u>. <u>flavicans</u> in West Blue Lake. This method is also applicable because <u>Chaoborus</u> larvae pass through four identifiable instars, each of which provide one term in the Pechen-Shuskina production formula.

The Pechen-Shuskina formula differs from the Allen Curve because it takes into account the population structure (i.e. frequency of occurrence of various life history stages at different times). I was interested in comparing and evaluating the production values estimated by the two methods. The main reason for calculating productivity was to estimate the contribution of the <u>Chaoborus</u> population to the total productivity of the ecosystem.

Knowledge of diel vertical migration patterns of  $\underline{C}$ . <u>flavicans</u> and their prey was deemed important in this study. This knowledge would reveal whether or not <u>Chaoborus</u> larvae were maximizing their exploitation of prey populations by sychronizing their migratory patterns with the migratory patterns of their prey.

As <u>Chaoborus</u> larvae migrate daily through the water column, they encounter different temperatures and different prey densities. Studies of prey type selection and the effect of temperature and food concentration on <u>Chaoborus</u> ingestion rates would help reveal the nature of Chaoborus

feeding ecology. Oxygen uptake estimates by <u>C</u>. <u>flavicans</u> larvae at different temperatures would reveal whether or not the larvae spend much or little of their assimilated energy in respiration.

Observations on the feeding ecology of <u>Chaoborus</u> larvae have been mostly qualitative and limited in scope. Parma (1971) stated that <u>Chaoborus</u> larvae will ingest all crustacean zooplankters, rotifers, oligochaetes, chironomid larvae, mosquito larvae, algae and other <u>Chaoborus</u> larvae. Deonier (1943) and Main (1953) reported that different instars ingest different food types. First and second instars eat small zooplankters such as rotifers and nauplii. Older larvae eat larger copepods and cladocerans. Sikorowa (1973) confirmed that differences in food of <u>Chaoborus</u> larval instars exist. She pooled crop contents of <u>Chaoborus</u> collected from different locations at various times of the year and quantitatively analyzed diets of all four instars of <u>C. flavicans</u> and <u>C. crystallinus</u>. Roth's (1971) radioisotope approach was indirect and time-consuming.

Kajak and Ranke-Rybicka (1970) used a somewhat unrealistic method. They compared prey numbers before and after <u>in situ</u> incubations with <u>Chaoborus</u>. The accuracy of their method relied on a very high prey density. Fedorenko (1975) also used the differences in prey numbers before and after <u>in situ</u> incubation experiments. However prey numbers do not indicate the energy value of the consumed food. "Dry

.

weight and its calorific equivalent eaten per unit time by individual predators of known size are the best means of expressing the food intake and are easily incorporated into further calculations of the energy budget" (Edmonson and Winberg, 1971).

Thus, studies of ingestion, respiration and diel vertical migration patterns of <u>Chaoborus</u> would help explain the magnitude of <u>Chaoborus</u> productivity in West Blue Lake. For instance, if ingestion rates were low, oxygen uptake high, and if there were much temporal and spatial segregation of <u>Chaoborus</u> and their prey, one would expect <u>Chaoborus</u> productivity to be relatively low.

In this study, population dynamics of one generation of <u>C</u>. <u>flavicans</u> (1974-75) were monitored at three stations in West Blue Lake. Counts of <u>Chaoborus</u> larvae and zooplankton do not necessarily represent true abundance in the lake. Wind-generated currents may have altered horizontal distribution. Counts made at a few stations in a multibasin lake may not be representative of the whole lake. Average abundance may have been overestimated by counts made at a deep station especially if animals were concentrated near the bottom (Ward and Robinson 1974). Sampling was confined mainly to the ice-free season. Winter sampling was not deemed critically important in this study because <u>Chaoborus</u> larvae overwinter in the mud in a state of diapause.

#### LITERATURE REVIEW

General Biology of Chaoborus sp.

The Chaoborinae (Corethrinae), once considered to be a subfamily of the Culicidae, are now considered to be a separate family which is closely related to the Culicidae and Dixidae (Dyar 1905, Stone 1956, Freeman 1962, Cook 1965, Peus 1967). The family contains eight genera of which <u>Chaoborus</u> Lichtenstein 1800 is best known.

All palaearctic and nearctic species of <u>Chaoborus</u> may occur in ponds, puddles and bogs (Peus 1934, Remm 1957). All the nearctic species except <u>C</u>. <u>crystallinus</u> and <u>C</u>. <u>nyblaei</u> have also been found in relatively deep lakes while <u>C</u>. <u>flavicans</u> is the only European species known to occur outside the littoral zone of lakes deeper than 5 m. (Stahl 1966). <u>C</u>. <u>flavicans</u>, <u>C</u>. <u>crystallinus</u> and <u>C</u>. <u>nyblaei</u> are all holarctic species. Only <u>C</u>. <u>flavicans</u> is common throughout Europe, Siberia and North America. <u>C</u>. <u>crystallinus</u> is common in Europe and Siberia but in North America it has been reported only from northcentral Canada. <u>C</u>. <u>nyblaei</u> is known only from Norway, Finland and Baffin Island. <u>C</u>. <u>obscuripes</u> and <u>C</u>. <u>pallidus</u> are known from all over Europe (Saether 1972).

Chaoborus larvae are not restricted to eutrophic and

dystrophic waters (Stahl 1966, Parma 1971). <u>C. flavicans</u> has been found in large oligotrophic lakes (Brundin 1949, Fedorenko and Swift 1972). <u>C. obsuripes</u> is very common in high mountain lakes of Fennoscandia (Saether 1970). <u>Chaoborus</u> distribution probably depends more on zooplankton densities than on physical and chemical factors (Saether 1972). Highest densities of <u>Chaoborus</u> larvae have been found in eutrophic and dystrophic waters. Eggleton (1931) found 71,000 m.<sup>-2</sup> in Third Sister Lake.

The hardiness and transparency of Chaoborus larvae have made them a favorite subject of anatomical and physiological studies. Perttunen and Lagerspetz (1956) found that heart pulse rate of Chaoborus increases with temperature and that the anterior part of the heart pulses slower than the posterior part. At 5°C, the anterior end pulses 10 times in 273-351 seconds while the posterior part pulses 10 times in 176-269 seconds. At 40°C, the anterior part pulses 10 times in 28-75 seconds and the posterior part pulses 10 times in 12-13 seconds. The digestive system of Chaoborus has been studied by Montshadsky (1945), Gersch (1952, 1955), Duhr (1955) and Schonfeld (1957). The first digestion of food occurs in the pharynx. Indigestable parts are expelled through the mouth. Only fluid substances reach the gut. Chaoborus excretion and osmoregulation were studied by Staddon (1962) and Schaller (1949) respectively. In hypotonic solution, water diffuses through the anal tubuli walls

which are at the same time actively taking up ions. In hypertonic media, water leaves via the anal tubuli, causing the animal to drink. Superfluous ions are expelled through the rectum. Frolowa (1929) and Rai (1963) described the four pairs of chromosomes of C. crystallinus. Meinert (1886) and von Frankenburg (1915) described the anal apparatus of Chaoborus. Peus (1934) suggested that the retractile anal apparatus functions in stabilization and adherence. Juday (1921) showed that 67% of the dry weight of C. punctipennis is protein and 9.5% is fat. Juday (1921), Berg (1937) and Wesenberg-Lund (1943) stressed the importance of Chaoborus as a food source for other organisms. Prokesova (1963) showed that during anoxia, the percentage of glycogen increased in C. crystallinus and C. flavicans larvae while the percentage of fat increased only in C. flavicans. The completely closed tracheal system functions as a hydrostatic apparatus. Respiration occurs through the cuticle. Krogh (1911) found that pressure changes did not alter the 84% nitrogen : 16% oxygen content of the tracheal sacs of Chaoborus larvae. Von Frankenberg (1915) suggested that the stiff-walled sacs are elastic enough to be influenced by pressure changes and that air diffuses in when pressure is increased. Bardenfleth and Ege (1916) found that the air sac walls of lake forms of Chaoborus were twice as thick as those of pond forms. (References from Saether 1972).

The life cycle of <u>C</u>. <u>flavicans</u> was described in

detail by Parma (1971). He found that adults emerge mostly at dawn. However Berg (1937) stated that <u>Chaoborus</u> emerge at night. Jonasson (1972) used floating emergence traps and found that <u>C. flavicans</u> adults emerged over a six week period from July to mid-August. Parma (1971) observed an adult life span of 1.5 - 6 days. Mating swarms of <u>Chaoborus</u> have been reported for several species both in tropical and temperate regions (Wesenburg-Lund 1914, Muttkowski 1918, Juday 1921, MacDonald 1956, Verbeke 1957). These swarms occur along lakeshores.

Lindquist and Deonier (1942) observed a two to three day pre-oviposition period in laboratory cultures of <u>C</u>. <u>astictopus</u>. Parma (1971) observed deposition of unfertilized eggs one hour after <u>C</u>. <u>crystallinus</u> emergence. <u>C</u>. <u>flavicans</u> produced one egg raft per female. Each egg raft contained a mean of 449 eggs (Parma 1971). <u>C</u>. <u>crystallinus</u> egg rafts contain 351 eggs (Parma 1969). Parma (1971) observed that 100% of the egg rafts of <u>C</u>. <u>flavicans</u> hatch and that 97% of eggs in each raft hatch. Parma (1969) estimated developmental time of <u>C</u>. <u>flavicans</u> eggs to be 2-4 days.

<u>C. flavicans</u> first instar larvae are always limnetic and positively photoactic. Berg (1937) speculated that this keeps the larvae in surface waters so that they are dispersed from the littoral area by wind-generated currents. Berg (1937) and Lindquist and Deonier (1942) observed higher densities of first instars inshore where oviposition occurred.

Later, young larvae were observed in deeper water. <u>C</u>. flavicans second instar larvae are also strictly limnetic. Parma (1971) found only one second instar in several thousand benthic samples. The third instar of <u>C</u>. <u>flavicans</u> is dualistic in its behaviour. Parma (1971) found third instars in the water column and in benthos during day and night. He observed that the fourth instar larvae are benthic during the day and that some fourth instars migrate towards the surface at night. Roth (1968) observed the same phenomenon in <u>C</u>. <u>flavicans</u> larvae in Frains Lake, Michigan. However, fourth instar <u>C</u>. <u>flavicans</u> larvae in Corbett Lake, B.C., were never benthic but remained in the hypolimnion during the day (Teraguchi and Northcote 1966). <u>C</u>. <u>trivittatus</u> and <u>C</u>. <u>americanus</u> larvae in Eunice Lake, B.C., also did not occur in the benthos (Fedorenko and Swift, 1972).

Parma (1971) observed that <u>C</u>. <u>flavicans</u> pupae are buried in the mud during the day and migrate toward the surface at night.

In North America, <u>C. flavicans</u> fourth instar larvae overwinter in or near the benthos and pupate after the ice melts (Roth 1968, Stahl 1966). In Lake Esrom, Denmark, <u>C. flavicans</u> larvae remained in the mud all winter long (Jonasson 1972). The overwintering stage of <u>C. crystallinus</u> is the third and/or fourth instar (Parma 1969, Roth 1968, Malueg 1966, Stahl 1966). In Eunice Lake, B.C., <u>C. trivitta</u>tus has a two year life cycle. The fourth instar over-

winters twice before it pupates (Fedorenko and Swift 1972).

Population Dynamics and Productivity of Chaoborus

<u>Chaoborus</u> life cycle duration is correlated with the biotope. Shallow pond species may be plurivoltine while species living in stratified lakes may be univoltine. Also within one species such as <u>C</u>. <u>flavicans</u> or <u>C</u>. <u>punctipennis</u>, voltinism varies according to latitude and biotope. Both species occur separately or coexist in small shallow ponds (Judd 1957, 1961) and in deep stratified lakes (Stahl 1966, Malueg 1966, Roth 1968).

Von Frankenberg (1915) and Deonier (1943) showed that generation time can be as short as one or two months under favorable laboratory conditions. In nature, plurivoltinism has been observed for <u>C. crystallinus</u>, <u>C. punctipennis</u>, <u>C. astictopus</u> and <u>C. anomalus</u> (Meinert 1886, Peus 1934, Miller 1941, Lindquist and Deonier 1942, MacDonald 1956, Snell and Hazeltine 1963, Parma 1969). In stratified 1akes, <u>C. flavicans</u> is always univoltine (Lundbeck 1926, Lang 1931, Valle 1936, Borutzky 1939, Berg and Petersen 1956, Judd 1960, Parma 1971).

Parma (1971) estimated mean body length of overwintering fourth instar larvae of <u>C</u>. <u>flavicans</u> to be 9.64 mm. Mean wet and dry weights of these larvae were 3.61 mg. and 0.405 mg. respectively. Mean wet and dry weights of third instar larvae were 1.22 mg. and 0.085 mg. respectively.

Parma (1971) did not estimate mean length of <u>C</u>. <u>flavicans</u> third instar larvae or the mean lengths and weights of the first and second instars. Mean wet and dry weights of pupae were 5.18 mg. and 0.79 mg. respectively. Mean wet and dry weights of adult male and female <u>C</u>. <u>flavicans</u> were: 1.50 mg., 0.455 mg. (male) and 2.61 mg., 0.795 mg. (female).

Parma (1969) found that mean cephalic capsule lengths of C. flavicans instars I to IV were: 0.227, 0.419, 0.744 and 1.152 mm. respectively. Teraguchi and Northcote (1966) used probit analysis to distinguish the following C. flavicans cephalic capsule length classes: instar I : 0.1 -0.3, instar II : 0.3 - 0.5, instar II : 0.6 - 0.9, instar Iv: 0.9 - 1.5 mm. Instead of measuring total body length as Parma (1971) did, Teraguchi and Northcote (1966) measured "inter-bladder" lengths. Their inter-bladder length classes for C. flavicans instars I - IV were: 1.00 - 1.75 mm., 1.75 -3.00 mm., 3.00 - 4.50 mm., and 4.50 - 6.50 mm. respectively. Teraquchi and Northcote did not perform weight analyses of C. flavicans larvae. Roth (1968) examined preserved overwintered fourth instars of C. flavicans and found that their total body length ranged from 10 - 13 mm. McGowan (1974) determined instars of C. anomalus and C. ceratopogones in Lake George, Uganda, by measuring antennal base lengths. She expressed sizes of various life history stages in terms of carbon content. For C. anomalus and C. ceratopogones, mean carbon content was: instar II : 4 µg, 2 µg; instar III : 23 µg, 21 µg; instar IV : 143 µg, 139 µg; pupae : 105 µg,

111 µg respectively. Other estimates of <u>Chaoborus</u> carbon or calorific content are not reported in the literature. Fedorenko and Swift (1972) stated that the mean cephalic capsule lengths of <u>C</u>. <u>americanus</u> and <u>C</u>. <u>trivittatus</u> were instar I : 0.4 mm.; instar II : 0.5, 0.7 mm.; instar III : 1.0, 1.3 mm.; instar IV : 1.6, 2.2 mm. respectively. Fedorenko and Swift did not weigh larvae according to instar type.

Fedorenko and Swift (1972) plotted growth curves of C. americanus and C. trivittatus larvae irrespective of They found that C. americanus grew faster than C. instar. trivittatus. In the first year of their two year life cycle, C. trivittatus larvae grew to a maximum of 0.5 mg. (dry weight). In their second year, C. trivittatus grew from 0.7 to 1.9 mg. C. americanus larvae grew to a maximum of 0.8 mg. Parma (1971) used changes in weight frequency histograms to calculate biweekly growth increments of benthic fourth instar larvae of C. flavicans. He did not state these growth increments. In Lake Esrom, Denmark, C. flavicans larvae weighed 0.53 mg. before the beginning of winter diapause. Overwintered larvae grew guickly to 0.71 mg. in May and final mean weight in June was 0.97 mg. (dry weight) (Jonasson 1972).

Estimates of developmental times of <u>Chaoborus</u> instars are rare. Fedorenko and Swift (1972) estimated duration of <u>C. americanus</u> and <u>C. trivittatus</u> instars II, III and

IV to be 12 and 23 days, 17 and 48 days, 318 and 635 days respectively. Fedorenko and Swift did not estimate duration of first instars. Parma (1971) experimentally determined duration of C. flavicans instars by culturing larvae in an artificial food suspension at 20°C and constant daylight. Parma estimated duration of instars I, II and III to be 9 days, 20 days and 14 days respectively. Parma did not estimate fourth instar duration. However he stated that temperature, quantity and quality of food, photoperiod and presence or absence of burrowing behaviour influence fourth instar duration. The life span of Chaoborus pupae ranges from one day (Muttkowski 1918) to 10 - 12 days (Reaumur This variation can be attributed to different tem-1740). peratures. Parma (1969) showed that C. crystallinus pupae last 3 days at 20<sup>°</sup>C and 12 days at 10<sup>°</sup>C. Parma (1971) showed that C. flavicans pupae last 3 - 4 days at 20°C and 10 - 15 days at 10<sup>°</sup>C. Meinert (1886) reported the possibility of pupal diapause under culturing conditions.

Parma (1971) recorded a sex ratio of 1.22:1.0 to for <u>C</u>. <u>flavicans</u> adults raised in the laboratory. Parma (1969) found a decreasing percentage with time of males in a <u>C</u>. <u>crystallinus</u> population. He experimentally showed that males developed faster from pupae in laboratory cultures.

Reported estimates of <u>Chaoborus</u> abundance vary with latitude and lake type. In tropical Lake Lanao, Lewis

(1975) found that larval densities of Chaoborus ranged from 3800 to 19,000 individuals  $m^{-2}$ . McGowan (1974) recorded a maximum planktonic density of 31.7 x  $10^2$  m.<sup>-2</sup> and a maximum benthic density of 79.9 x  $10^2$  m.<sup>-2</sup> for C. anomalus and C. ceratopogones in Lake George, Uganda. Eggleton (1931) found a maximum density of 71.0 x  $10^3$  Chaoborus larvae m.<sup>-2</sup> in a eutrophic lake. Roth (1968) estimated total benthic population (comprised of three chaoborid species) to be 27.2 x  $10^{17}$ larvae in an oligotrophic lake with a surface area of 8.3 hectares. Dodson (1972) found 1230 larvae m.<sup>-3</sup> in Leechmere Pond, Colorado. Fedorenko (1975) found maxima of 1100 C. trivittatus m.<sup>-2</sup> and 200 C. americanus m.<sup>-2</sup> in Eunice Lake, B.C. Parma (1971) reported a maximum benthic density of 13.0 x  $10^3$  m.<sup>-2</sup>. In Lake Esrom, Denmark, density of <u>C</u>. <u>flavicans</u> larvae varied from 600 m.<sup>-2</sup> to 5000 m.<sup>-2</sup> (Jonasson 1972).

Few estimates of <u>Chaoborus</u> biomass and productivity are reported in the literature. Biomass of benthic <u>C</u>. <u>flavicans</u> larvae in Lake Vechten, Netherlands, was 57.5 kg. ha.<sup>-1</sup> (wet weight) and 6.5 kg. ha.<sup>-1</sup> (dry weight) (Parma 1971). In Lake Mendota, winter biomass of <u>Chaoborus</u> larvae was 558 kg. ha.<sup>-1</sup> (Juday 1921). Borutzky (1939) found a maximum biomass in November of 17.5 kg. ha.<sup>-1</sup> (dry weight). Deevey (in Brooks and Deevey 1963) estimated productivity of benthic <u>Chaoborus</u> larvae to be 15 to 28 kg. (dry weight) ha.<sup>-1</sup> year<sup>-1</sup> in some American lakes. Above estimates were calculated using Allen curves (Allen 1951). Jonasson (1972)

calculated biomass and productivity of <u>C</u>. <u>flavicans</u> larvae in Lake Esrom, Denmark. Jonasson's biomass estimates were based on monthly samples. Biomass of overwintering larvae  $(300 - 3000 \text{ mg. dry weight m.}^{-2})$  was, in general, lower than spring biomass estimates  $(373 - 4927 \text{ mg. dry weight m.}^{-2})$ . Summer biomass was lowest in Lake Esrom. It ranged from  $39 - 252 \text{ mg. dry weight m.}^{-2}$ . Jonasson (1972) found that <u>C</u>. <u>flavicans</u> productivity was, in general, lower in winter  $(-5.15 - 92 \text{ mg. dry weight m.}^{-2} \text{ month}^{-1})$  than in summer  $(35 - 457 \text{ mg. dry weight m.}^{-2} \text{ month}^{-1})$ .

#### Vertical Migration of Chaoborus Larvae

In most lakes, <u>Chaoborus</u> is benthic during the day and planktonic at night (Juday 1921, Eggleton 1932, Berg 1937). In some lakes, <u>Chaoborus</u> are continuously planktonic, moving from deep water during the day to surface waters at night (Hunt 1958, Northcote 1964, Fedorenko and Swift 1972).

MacDonald (1956) and Teraguchi and Northcote (1966) observed that <u>Chaoborus</u> larval instars differ in their migratory behaviour. MacDonald (1956) observed that younger instars remain in the limnetic zone while the older instars inhabit it only temporarily at night. Teraguchi and Northcote (1966) found that <u>C</u>. <u>flavicans</u> first instars showed no migration into surface waters. They were concentrated at 2 to 6 m. in June. Second instars were also abundant between 2 and 6 m. Teraguchi and Northcote observed a weak vertical migration of second instars into surface waters

during the night. Third instars occurred between 1 and 11 m. and exhibited a stronger diel vertical migration. During the day, third instars were concentrated at 9 to 11 m. At midnight, third instars were concentrated at 3 - 5 m. The most pronounced vertical migration was exhibited by fourth instars. During the day, they were concentrated at 8 to 13 m. Ascent by fourth instars was progressively earlier in the evenings as the season advanced and descent occurred later in Teraguchi and Northcote (1966) noted Cushing's the mornings. (1951) "midnight sinking" phase in the diel migration patterns of fourth instars. Midnight sinking occurred at 12 p.m. (two hours after ascent) in July. Later in the season, midnight sinking began at 11 p.m. Teraguchi and Northcote (1966) postulated that light intensity influences vertical migration. Fedorenko and Swift (1972) monitored diel vertical migration patterns of C. trivittatus and C. americanus in Eunice Lake, B.C. Seasonal changes in noon vertical distribution of these larvae were similar to those found by Teraguchi and Northcote (1966). The first two instars of both species and C. americanus larvae were found above the thermocline. As the season progressed, C. trivittatus third instars moved below the thermocline. Young and old C. trivittatus fourth instars occurred below the thermocline. Spatial overlap between the two species occurred for first, second and young third instars.

Fedorenko and Swift (1972) recorded marked differences in diel migration of instars of the two species. <u>C. americanus</u>

fourth instars began migrating at about 7 p.m., completed ascent by 9 or 10 p.m. and remained concentrated at 1 m. until C. trivittatus third instars had a migration pattern 6 a.m. similar to that of C. trivittatus young fourth instars. с. trivittatus old fourth instars began evening ascent at 6 p.m., completed ascent by 9 p.m. and began midnight sinking at midnight. During the day, C. trivittatus third and young fourth instars were spatially isolated from all other instars of both species. Roth (1968) found that C. flavicans were concentrated deeper than C. punctipennis and C. albatus in Frains Lake, Michigan. All three species exhibited similar migration Roth (1968) suggested that slight differences in patterns. morphology and distribution were sufficient to explain their coexistence. Migration patterns of C. punctipennis and C. flavicans in Myers Lake, Indiana were found to be alike in all respects (Stahl 1966).

Cushing's (1951) general scheme for migration patterns of all vertically migrating zooplankton was based on light as the initiating and controlling factor. The four phases of Cushing's migration patterns were: (1) dawn rise, (2) sharp descent to day depth, (3) ascent from day depth, and (4) midnight sinking. Cushing developed this pattern from observations of marine zooplankton. Hutchinson (1967) stated that the migration pattern was applicable to freshwater zooplankton.

Many theories hypothesizing adaptive values of

vertical migration have been proposed. These theories are as follows: escape from predators (Manteifel 1959, Pearre 1973), horizontal transport (Hardy and Gunter 1935, Hardy 1956, David 1961), social control of population size (Wynne-Edwards 1962), energy gain (McLaren 1963, Kerfoot 1970), combination of the above theories (Hutchinson 1967, Mauchline and Fisher 1969), and demographic effects (McLaren 1974).

McLaren's (1963) theory concerning adaptive value of vertical migration is the only one that considers the energy budget of the migrating animal. McLaren concluded that migrating animals accrue an energy gain from the more efficient partitioning of energy to growth at low temperatures and that this energy gain can be used for fecundity, growth, etc.

Swift (1974) stated that McLaren's (1963) theory on the energetic advantage of temperature alternation depends on assumptions which are not justified. Considering energetics only, animals should stay at the surface or follow a physiological migration pattern in order to maximize growth. Swifts's simulation model of the energetics of vertical migration in <u>C</u>. trivittatus larvae confirmed that, on an energetics basis, the two migration patterns cited above are better for larval growth than McLaren's (1963) migration pattern.

La Row (1968, 1969) demonstrated a persistent

diurnal rhythm in emergence of <u>Chaoborus</u> larvae from sediments. He also demonstrated a 24 hour periodicity of larvae kept under constant light conditions in sediment cores. When light intensity was low, larvae emerged from sediments and became planktonic. When light intensity was high, larvae re-entered sediments. In darkness, larvae maintained a 24 hour rhythm. At 5<sup>o</sup>C, diurnal activity ceased.

Respiration and Feeding Ecology of Chaoborus Larvae

Chaoborus larvae respire through the cuticle. The tracheal system has no respiratory function (Saether 1972). Swift (1974) measured 0, consumption of C. trivittatus fourth instars. He used constant pressure respirometers and the micro-Winkler technique to measure respiration and found significant differences in results of the two methods. Using constant pressure respirometers, Swift found that 0, consumption at 5, 10, 15, 20 and 25<sup>o</sup>C was 0.48, 0.95, 1.0, 1.25 and 2.0  $\mu$ l. larva<sup>-1</sup> hour<sup>-1</sup>. Swift stated that 0<sub>2</sub> consumption of Chaoborus larvae increases linearly with temperature. Berg et al. (1962) and Berg and Jonasson (1965) used a dropping mercury electrode to monitor 0, consumption of C. flavicans larvae. They found that 0, consumption increased linearly with temperature and with animal activity. A larva that remained still, consumed 1 - 2  $\mu$ 1 0 hour<sup>-1</sup> while a larva that moved 1 or 2 times per second at the same temperature consumed 10  $\mu$ l hour<sup>-1</sup>. At 8<sup>o</sup>C, 0<sub>2</sub> consumption rate was 6.0  $\mu$ l 0<sub>2</sub> gm.<sup>-1</sup> hour<sup>-1</sup>. At 20<sup>o</sup>C, it was 21.4  $\mu$ l

gm.<sup>-1</sup> hour<sup>-1</sup>. Berg and Jonasson (1965) also found that <u>C</u>. <u>flavicans</u> larvae have a higher  $0_2$  consumption rate in welloxygenated water than in anoxic water. No other reports of <u>Chaoborus</u> respiration exist in the literature.

<u>Chaoborus</u> adults and pupae do not feed. <u>Chaoborus</u> adults have short piercing - sucking mouthparts (Cook 1956) but no observations of adult feeding have been reported.

Crops of <u>C</u>. <u>flavicans</u> larvae from Lake Vechten, Netherlands, contained cladocerans (<u>Bosmina</u> sp. and <u>Leydigia</u> sp.), copepods (<u>Cyclops vicinus</u> and <u>Cyclops fimbriatus</u>), copepodids, and rotifers (<u>Notholca squamula</u> and <u>Keratella</u> <u>quadrata</u>) (Parma 1971). <u>Chaoborus</u> predation on larvae of culicid genera, <u>Culex</u>, <u>Aedes</u>, and <u>Anopheles</u> has been observed (Twinn 1931, James and Smith 1958, Skierska 1969). <u>Chaoborus</u> fourth instar larvae also prey on ephemerid larvae (Miall 1903, Sikorowa 1968) and dixid larvae (Meinert 1886). Parma (1971) observed cannibalism among all larval stages of <u>C</u>. <u>flavicans</u> and <u>C</u>. <u>crystallinus</u>. Felt (1904) observed <u>Chaoborus</u> ingesting newly hatched fish larvae.

Benthic <u>Chaoborus</u> larvae feed on harpacticoids (Lundbeck 1926, Sladecek 1952), oligochaetes (Parma 1971) and chironomid larvae (Alverdes 1926, Tubb and Dorris 1965).

Fish are the main predators of <u>Chaoborus</u> larvae and pupae. Lindquist, Deonier and Hancey (1943) found <u>Chaoborus</u> eggs and larvae in <u>Cyprinus carpio</u> stomachs. <u>Chaoborus</u> larvae occur frequently in Kokanee (Northcote and Lorz 1966),

cutthroat trout (Dimick and Mote 1934), rainbow trout (Ricker 1932) and lake trout (Martin 1954). Campbell (1935) found that <u>Chaoborus</u> larvae comprise 50% of white suckers' stomach contents. Mills (per. com.) revealed that <u>Chaoborus</u> larvae may comprise 40 - 80% of the whitefish diet in the Experimental Lakes Area, Ontario. Parma (1971) observed **C**oleoptera larvae eating <u>Chaoborus</u> larvae in the field. In laboratory experiments, Parma (1971) found that one <u>Cyclops</u> sp. ingests 25 <u>Chaoborus</u> first instars per day. Anderson and Raasveldt (1974) stated that there is heavy predation of <u>Chaoborus</u> larvae by <u>Gammarus lacustris</u> in some Alberta lakes.

<u>Chaoborus</u> larvae prefer copepods over cladocerans (Deonier 1943, Main 1953, Swuste <u>et al</u>. 1973, Anderson and Raasveldt 1974). First and second instars prey on small organisms such as nauplii, copepodids and rotifers (Kolmer 1904, Deonier 1943, Prokesova 1959, Sikorowa 1968). The above food preferences are based on laboratory studies.

There have been few quantitative studies of <u>Chaoborus</u> predation. Deonier (1943) stated that one <u>Chaoborus</u> larva can ingest 12 <u>Cyclops</u> in 45 minutes. Sikorowa (1973) pooled crop contents of chaoborids collected from different Polish lakes at various times of the year. She found that first and second instars preferred small zooplankters such as rotifers and nauplii while third and fourth instars preyed more on larger copepods and cladocerans. Kajak and Ranke-Rybicka (1970) performed in situ feeding experiments with

<u>C. flavicans</u> larvae in two Polish lakes. Experiments lasted 6 hours. Predator density was 3.3 fourth instars  $1.^{-1}$ . Incubation chambers containing various known mixtures of copepods and cladocerans were suspended at 1.5 and 6 m. depth. Kajak and Ranke-Rybicka found that <u>Chaoborus</u> larvae consumed 0.81 - 0.88 crustaceans larva<sup>-1</sup> hour<sup>-1</sup>. Maximum daily food consumption of larvae was 12.5% of their body weight.

Fedorenko (1975) performed in situ feeding experiments with second, third and fourth instars of C. americanus and C. trivittatus. She used various densities of predators and prey and suspended the feeding containers at various depths for 24 hours. Fedorenko found that C. americanus second and third instars preferred Bosmina sp. Diaptomus tyrelli was the major prey of C. trivittatus second and third instars. Second and third instars of both species also consumed some rotifers. C. americanus fourth instars showed no obvious food preference. They consumed rotifers, Bosmina, Holopedium, Diaptomus kenai and Diaptomus tyrelli. Young and old fourth instars of C. trivittatus also ingested most types of available zooplankton. C. trivittatus young fourth instars seemed to prefer Holopedium and D. tyrelli. C. trivittatus old fourth instars preferred D. kenai. Fedorenko (1975) stated that prey size determined diets of the first three instars of both species and that "spatial availability" of prey determined diets of fourth instars.
Kajak and Ranke-Rybicka (1970) observed that  $\underline{C}$ . <u>flavicans</u> fed mostly at night. Ten percent of larvae caught at night had full guts while 0.9% to 2.8% of larvae caught during the day had full guts. Fedorenko (1975) observed feeding activity peaks at dawn and dusk for <u>C</u>. <u>trivittatus</u> fourth instars feeding on <u>D</u>. <u>kenai</u>.

Fedorenko (1975) reported that feeding rate of second instar <u>C</u>. trivittatus was 2 <u>D</u>. tyrelli per day; third instars ate 6 - 7 <u>D</u>. tyrelli per day. These experiments had an initial food concentration of 5 D. tyrelli 1.<sup>-1</sup>. Fourth instar larvae of <u>C</u>. trivittatus and <u>C</u>. americanus ate 20 <u>D</u>. tyrelli larva<sup>-1</sup> day<sup>-1</sup> at an initial concentration of 70 <u>D</u>. tyrelli 1.<sup>-1</sup>. Experiments were not performed on second and third instars of <u>C</u>. americanus. Fedorenko stated that feeding rates of young instars increased directly with temperature and food concentration. Feeding rates of fourth instar <u>C</u>. trivittatus were independent of temperature.

Fedorenko's (1975) estimated mean percentage of standing crop of prey eaten by <u>Chaoborus</u> was: 2% for copepod nauplii, 3% for <u>D. tyrelli</u>, 9% for <u>D. kenai</u> and 4% for <u>Diaphanosoma</u>. Kajak and Ranke-Rybicka (1970) estimated that <u>C. flavicans</u> daily removed 7% and 13% of the zooplankton standing crop in two Polish lakes. Dodson (1972) estimated that <u>Chaoborus</u> predation accounted for 93% of <u>Daphnia</u> mortality in Leechmere Pond, Colorado.

Authors of some of the above species are listed in appendix P.

#### METHODS AND MATERIALS

Description of Study Area

West Blue Lake is located in west central Manitoba (fig. 1). The lake is 4.8 km. long and is narrow and steepsided. Maximum and mean depths are 31 m. and 11.3 m. respectively. There are no permanent inlet or outlet streams. Bell and Ward (1970) and Ward and Robinson (1974) presented detailed descriptions of West Blue Lake and its dominant flora and fauna.

Life History, Population Dynamics and Production of  $\underline{C}$ . <u>flavicans</u>

Stations 1, 2 and 5 (fig. 1) were used throughout this study. Stations 1, 2 and 5 were 17, 31 and 20 m. deep respectively. All stations were in the pelagic zone.

Larval and pupal densities were sampled weekly at stations 1, 2 and 5. Sampling was carried out from May 20, 1974, to August 26, 1974, and from May 14, 1975 to June 25, 1975. Additional samples were taken on Sept. 16, 1974 and Oct. 16, 1974. Samples were collected at 0, 1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 25 and 30 m. depth at station 2. At stations 1 and 5, samples were collected at 0 meters and two meter intervals from top to bottom. Triplicate samples at each depth were obtained with a 29 1. Schindler-Patalas





plankton trap. Sampling began at 9:30 a.m. on each sampling date.

The water column was sampled from top to bottom. This decreased disturbance of <u>C</u>. <u>flavicans</u> about to be sampled. Each sample was funneled into a 35 ml. labelled bottle. Two ml. of 100% formalin were added to each sample. Samples were counted at 20 x or 40 x under an Olympus binocular microscope.

Weekly benthic samples were taken at Stations 1, 2 and 5 from May 20, 1974, to August 12, 1974. Additional samples were collected on Oct. 16, 1974. A multiple corer (Hamilton <u>et al</u>. 1971) was used to obtain triplicate samples on each sampling date. Cores were washed in a 500  $\mu$  mesh bucket and contents were labelled and preserved in 5% formalin solution. Benthic <u>Chaoborus</u> larvae were sorted and counted under an Olympus binocular microscope at 20 x or 40 x.

Diel vertical migrations of first, second, third and fourth instar larvae of <u>C</u>. <u>flavicans</u> were monitored on July 6, July 20, August 7, and June 5, 1974, respectively at station 5. Samples were taken at three meter depth intervals from 0 to 21 m. One sample was collected at each depth with a 29 1. Schindler-Patalas plankton trap. Sampling began at 10:00 a.m. and continued at four-hour intervals for 24 hours on each sampling date. Each sample was labelled, preserved in a 5% formalin solution and counted at 20 x or 40 x under a

#### binocular microscope.

Imago emergence of <u>C</u>. <u>flavicans</u> was monitored in 1975. Conical floating transparent polyethylene traps constructed according to Sublette and Dendy (in Edmondson and Winberg 1971) were used. Five traps were evenly spaced on a shore to shore transect across station 1. Traps were monitored once a day from June 25 to July 9, 1975. Imagines were sexed and counted after removal from traps.

30

Five series of submerged conical traps evenly spaced on a shore to shore transect across station 1 were used to monitor long term movements of <u>C</u>. <u>flavicans</u> larvae and pupae and amphipods. Traps were submerged at 5 m. depth intervals from the top to the bottom of each vertical series. Submerged traps were monitored once at the end of a 24-hour period every week from June 28 to July 19, 1975. <u>Chaoborus</u> larvae and pupae were removed and preserved in 5% formalin solution. They were counted at 20 x or 40 x under a binocular microscope.

Instar succession of <u>C</u>. <u>flavicans</u> larvae was monitored weekly from May 20, 1974, to August 12, 1974, and on Sept. 16 and Oct. 16, 1974. Once each week, a series of vertical tows was taken from the bottom to the top of the water column at station 5. A large Wisconsin plankton net (mesh size : 243  $\mu$ ) was used. Cephalic capsule lengths (fig. 2) of 100 - 150 live larvae were measured weekly. Larvae were placed on a water film in a petri dish. Their

### Fig. 2. Head capsule length.



cephalic capsule lengths were measured at 10 x, 20 x, 30 x or 40 x (depending on larval size) under an Olympus binocular microscope equipped with an ocular micrometer. The micrometer was calibrated into 10  $\mu$  divisions.

Growth of C. flavicans larvae and pupae was monitored weekly from May 20, 1974, to August 26, 1974; on Sept. 16, 1974, Oct. 16, 1974, and weekly from May 14, 1975 to June 25, 1975. Instar-specific growth was monitored from July 1, 1975, to Aug. 12, 1975. Growth was measured in terms of dry weight, carbon content and calories. Larvae and pupae were caught in long vertical tows with a 243  $\mu$ plankton net. In 1974, larvae from tows were picked randomly (i.e. irrespective of instar) for the purpose of constructing an Allen curve (Allen 1951). Lots of 10 - 100 larvae (depending on larval size) were dried at 105 °C for two days. Dry weight of each lot was determined on a CAHN electric microbalance. Caloric content of dried larvae and pupae was determined by combustion in a Phillipson Microbomb Calorimeter (Phillipson 1964). If the weight of a lot of dried larvae or pupae was too light to be used as a caloric sample (< 2.0 mg.), then lots were combined. To determine carbon content, fresh larvae and pupae were placed on GFA precombusted glass fiber filters. These samples were dried at 105°C for two days. Carbon content of each sample was determined in a Perkin-Elmer Model 240 Elemental Analyzer. In 1975, estimates of instar-specific dry weight, caloric

content and carbon content were determined as above except that larvae were sorted according to instar, and dry weight samples were obtained every 3 or 4 days.

In June 1974, <u>C</u>. <u>flavicans</u> fourth instar larvae and pupae were caught in a plankton net and were placed in outdoor rearing tanks (appendix A). After adult <u>C</u>. <u>flavicans</u> emerged, mated and laid eggs, they were removed from the tanks and were sexed and counted. Thirty-three egg rafts collected from the tanks were placed in petri dishes containing well-oxygenated water. Numbers of eggs per raft were counted at 60 x under a binocular microscope. After counting, each raft was placed in a 500 ml. jar of welloxygenated water. Jars were stored in the rearing tank shelter for 3 to 6 days. Numbers of unhatched eggs in each raft were counted to determine hatching success.

### Respiration and Feeding of <u>C</u>. <u>flavicans</u>

A series of respiration experiments using second, third and fourth instar larvae and pupae of <u>C</u>. <u>flavicans</u> were performed in the laboratory during 1975. <u>Chaoborus</u> larvae and pupae were collected with a plankton net. They were sorted according to instar type and were held at experimental temperatures of 2 - 3 hours before each experiment. Oxygen consumption of <u>Chaoborus</u> larvae and pupae was measured with a Scholander respirometer according to methods of Scholander <u>et al</u>. (1952). Nine test chambers and one control chamber were used in each experiment. Experiments

were performed at 5, 10, 15, 20 and 25<sup>o</sup>C. Each experiment lasted one hour. For each instar, the same larvae were used for each temperature.

In 1975, a series of <u>in situ</u> feeding experiments was conducted on <u>C</u>. <u>flavicans</u> larvae to determine food type and food size preferences and the effect of temperature and food concentration on ingestion rates of <u>C</u>. <u>flavicans</u> larvae.

Transparent polyvinyl chloride (PVC) 15 1. feeding chambers (appendix B) and opaque 10 1. plastic bottles were used as incubation chambers for feeding experiments.

A trial experiment to determine predator density needed to produce optimum feeding in the chambers and to test relative efficiencies of the two types of chambers was conducted (appendix C).

Experiments to determine size and type of prey selected by <u>C</u>. <u>flavicans</u> larvae were performed on each instar in 1975. Each experiment was executed as follows: Two equal lots of an instar were starved for 24 hours. Three vertical tows taken with a 73  $\mu$  plankton net were individually strained through 1050  $\mu$  and 73  $\mu$  filters. This removed <u>C</u>. <u>flavicans</u> and large <u>D</u>. <u>pulicaria</u> but retained prey organisms 73  $\mu$  - 1050  $\mu$  in size. Contents of one tow were retained as a control sample. Each of the remaining two tow contents were individually placed in a PVC feeding chamber. One lot of starved instars (appendix D) was placed

in each chamber. Chambers were suspended at 5 m, depth in the lake and were incubated for 24 hours. At the end of the incubation period, <u>Chaoborus</u> larvae and remaining prey were removed from the chambers. <u>Chaoborus</u> larvae were sorted out of these test samples. Test and control samples were diluted to 15 l. (volume of feeding chamber). Two one liter subsamples from test and control samples were strained through a graduated set of filters (783  $\mu$ , 500  $\mu$ , 243  $\mu$ , and 73  $\mu$ ). Numbers and types of prey organisms from each filter were counted in a Sedgewick-Rafter cell at 100 x under a compound microscope.

In situ experiments to determine effects of food concentration and temperature on ingestion rates of C. flavicans larval instars were performed at station 5 during 1975. Four experiments per instar were performed. Each experiment was executed as follows: Eight equal lots of an instar were collected with a plankton net and were starved for 24 - 48 hours. Thirteen vertical tows were taken with a 73  $\mu$  plankton net on station 5 and were strained through a set of filters (500  $\mu$  - 73  $\mu$  for instar I, 783  $\mu$  - 73  $\mu$  for instar II, 1050  $\mu$  - 73  $\mu$  for instars III and IV) to eliminate large Daphnia and Chaoborus larvae. Contents of three tows were retained as control samples. Food from the remaining tows was diluted by either a half, once, one and a half times or twice the natural density using lake water filtered through a 73  $\mu$  filter. Each portion of diluted food was placed in a feeding chamber along with one lot of

starved larvae. Four chambers containing the above series of diluted food were suspended at four meters depth in the epilimnion. A duplicate set was suspended at 12 meters in the hypolimnion. Temperature at 4 and 12 meters was monitored with a thermistor. After 24 hours, contents of feeding chambers were removed. <u>Chaoborus</u> larvae were picked out of these samples. Test and control samples were filtered through pre-combusted GFC glass fiber filters and were dried for two days at 105 C. Test and control samples were analyzed in a Perkin-Elmer Model 240 Elemental Analyzer to determine carbon content. Calculations

No. larvae  $m.^2$  were calculated by multiplying no. larvae  $1.^{-1}$  by 1000 to obtain no. larvae  $m.^3$ . No. larvae  $m.^3$  between sampling depths was interpolated so that no. larvae  $m.^3$  for every one meter depth were obtained. These values were added to yield no. larvae  $m.^2$ . Benthic densities of <u>Chaoborus</u> larvae were not used in the calculation of no. larvae m. because benthic and pelagic densities were based on samples collected with different sampling devices. Density data from two different samplers are not comparable due to different efficiencies of the samplers.

Depth-weighted peaks of vertical migration polygons were calculated by multiplying no. larvae at each sampling depth by the sampling depth and adding the products. this no. larvae x depth was then divided by the total

number of larvae caught to yield a depth-weighted peak in the vertical distribution of larvae. Data on copepod and cladoceran vertical migration in West Blue Lake were provided by Patrick (unpublished) and Ward (unpublished) respectively.

The Allen curve method for determining productivity is based on the concept that, as a cohort grows older, the animals grow, but their numbers decrease because some die. The Allen curve represents the product of the age-specific growth function and the age-specific survivorship curve of a cohort. Actual net production is the product of mean density of animals and the mean individual weight increment divided by an appropriate time interval. The first point on the Allen curve in this study was obtained by applying fecundity and sex ratio data to the density of fourth instar larvae that survived until the end of the generation (appendix N). The first point on the Allen curve represents mean density of first instars that have just hatched, i.e., larvae at 0 weight.

In the calculation of Pechen-Shuskina production, instar densities were obtained by multiplying the per cent frequency of a given instar at a given time by the mean density of all larvae at that given time. Biomass at a given time was calculated by multiplying the mean density of an instar by the mean individual weight of that instar at that time.

#### RESULTS

Life History and Population Dynamics of C. flavicans

<u>C. flavicans</u> larvae rarely occurred above 5 m. in the lake. In early summer, <u>Chaoborus</u> larvae were most dense at 7 and 9 m. depth at all stations. Towards late summer and autumn, highest larval densities occurred deeper, at 9 to 15 m. (fig. **3**).

Highest densities of <u>Chaoborus</u> larvae occurred at station 5 throughout the growing season (fig. 4). Table 1 summarizes larval density changes during the study period. Numbers per square meter were obtained by extrapolating densities shown in fig. 3 to numbers per cubic meter and integrating the curve thus obtained. The highest mean density occurred on July 8, 1974, and declined steadily until June 25, 1975 (table 1).

Benthic densities of <u>C</u>. <u>flavicans</u> larvae were relatively high in spring, 1974, decreased in summer and increased again in fall, 1974 (fig. 5). <u>Chaoborus</u> larvae were never found in benthos from station 2. Appendix D lists numbers of larvae per square meter of benthos.

Fig. 6 illustrates vertical migration patterns of <u>C</u>. <u>flavicans</u> larvae and shows depth-weighted peaks (appendix E) in the migrating populations of <u>D</u>. <u>pulicaria</u> and <u>C</u>. <u>bicus-</u> <u>pidatus</u>.





ուսու հանությունը համաներին է հենուր և է հենուր և ենչել է հերումի է երկրությունը հետությունը։ հետությունը հետո





Date	1	Station 2		mean density	standard deviation
May 20, 1974	1912.02	544.18	935.92	1130.7	704.42
May 27, 1974	2103.47	1804.645	1316.09	1741.4	397.48
June 3, 1974 larvae pupae	1729.90 281.61	1307.35 948.18	1063.0 247.83	1366.7 492.5	337.40 394.96
June 10, 1974 larvae pupae	1701.14 264.36	155.16 91.95	942.54 114.94	932.9 157.1	773.04 93.61
June 17, 1974 larvae pupae	68.95 229.89	68.96 137.94	68.92 45'.97	68.9 137.9	0.02 91.96
June 24, 1974 larvae pupae	114.93 68.96	68.96 22.99	68.96 22.99	84.3 .38.3	26.54 26.54
July 1, 1974	0	• 0	0		•
July 8, 1974	5603.4	6953.7	10994.27	7850.5	2805.09
July 15, 1974	4135.0	3578.5	10608.81	6107.4	3908.22
July 22, 1974	3574.5	2342.0	11427.0	5781.2	4928.12
July 30, 1974	5477.0	3874.0	6007.5	5119.5	1110.77
Aug. 5, 1974	4117.0	4053.0	7587.0	5252.3	2022.13
Aug. 12, 1974	3949.0	5754.75	5772.25	5158.6	1047.64
Aug. 19, 1974	.3189.3	4096.92	4343.5	3876.6	607.83
Aug. 26, 1974	2931.5	3898.5	2970.0	3266.6	547.52
Sept. 16, 1974	2701.5	2183.0	2468.5	2451.0	259.69
Oct. 16, 1974	2453.5	18,96.0	2097.4	2148.97	282.30
May 14, 1975	2316.14	1028.77	2074.74	1806.55	684.31
May 21, 1975	2161.0	724.13	902.36	1262.49	783.21
May 28, 1975	996.46	806.36	2187.45	1330.09	748.56
June 4, 1975	1373.65	1482.7	1137.96	1331.44	176.20
June 11, 1975 larvae pupae	666.68 431.03	298.84 68.96	2195.42 603.45	1053.65 367.81	1005.76 272.81
June 18, 1975 larvae pupae	76.84 84.97	59.36 94.32	60.44 146.25	65.55 108.51	9.79 33.01
June 25, 1975 larvae pupae	120.49 47.82	43.68 34.48	68.96 34.48	77.71 38.93	39.15 7.71

Table 1. Temporal changes in pelagic densities (no. m.<sup>-2</sup>) of <u>C. flavicans</u> during 1974-75.

Fig. 5. Temporal changes in benthic density of  $\underline{C}$ . <u>flavicans</u> larvae during 1974.



Diel vertical migration of <u>C</u>. <u>flavicans</u> larvae. Depth-weighted peaks of <u>C</u>. <u>flavicans</u>, <u>D</u>. <u>pulicaria</u> and <u>C</u>. <u>bicuspidatus</u> indicated by <u>\_\_\_\_\_\_</u>, <u>D</u>\_\_\_\_\_, and <u>C</u>\_\_\_\_\_\_ respectively. Total numbers of <u>Chaoborus</u> larvae caught are below each polygon.

Fig. 6.



<u>Chaoborus</u> fourth instar larvae of the 1973-74 generation migrated 5.52 meters between 7.06 and 12.58 m. depth (fig. 6). <u>Chaoborus</u> first instar larvae of the new 1974-75 generation migrated 3.47 m. between 5.29 and 8.76 m. depth (fig. 6). <u>Chaoborus</u> second instar larvae migrated 3.3 m. between 5.33 and 8.63 m. depth (fig. 6). <u>Chaoborus</u> third instar larvae migrated 3.73 m. between 7.6 and 11.33 m. depth (fig. 6). Depth-weighted peaks of vertical migration of successive <u>Chaoborus</u> instars occurred deeper in the lake. Migrating distances of successive instars were, in general, greater than those of previous instars.

Depth-weighted peaks in migrating populations of  $\underline{D}$ . pulicaria and  $\underline{C}$ . <u>bicuspidatus</u> did not often coincide with depth-weighted peaks of  $\underline{C}$ . <u>flavicans</u> (fig. 6).

<u>C. flavicans</u> first instars had a head capsule length between .1 and 0.3 mm. Head capsule length of second instars was between 0.3 and 0.6 mm. Third instar head capsule length was between 0.6 and 1.0 mm. Head capsule length of fourth instars was between 1.0 and 1.5 mm. (fig. 7).

Fig. 8 illustrates instar succession and population structure changes. The overwintered fourth instar of the 1973-74 generation of <u>Chaoborus</u> occurred with 100% frequency until June 17. Pupae occurred until June 24. Adult emergence, mating and egg-laying during late June gave rise to the new 1974-75 generation. The frequency of first instars rose to 87% on July 8 and then declined sharply to 0% on July 30. The second instar appeared on July 8. Its occurrence

45

Fig. 7. Head capsule length histograms of <u>C. flavicans</u> larval instars, 1974.

11 Ħ IV 1007 11 Ш I۷ MAY 20 JULY 15 I 1 50 I I ł • I I I ۰ 100-MAY 27 JULY 22 50-1 1 ł 0 -100 JUNE 3 JULY 30 ı 1 50 I I. 1 I I ŀ 1 L Q. 100 JUNE 10 AUG. 5 ı 1 50 T I. I L ٥ 100 JUNE 17 ł AUG.12 Į . 50 1 1 1 ł 1 I 1 1 0. 100 JULY I SEPT. 16 ۱ 1 I I 50 ł I 1 ľ l I I I ł 100-JULY 8 ост. 16 I 50 1 I F 1 1.0 1.6 ... .6 1,0 1.6 ò HEAD CAPSULE LENGTH (mm.)

PERCENT FREQUENCY

## Fig. 8. Instar succession of <u>C</u>. <u>flavicans</u> larvae, 1974.



rose to 81% on July 22, declined and ended on August 12. Instar III appeared on July 15. Its occurrence rose to 72% on August 15. The fourth instar appeared on August 5 and its occurrence increased steadily to 100% on September 16.

In general, instar succession curves showed decreasing height and increasing width with time.

Imago emergence of the 1974-75 generation began on June 26, 1975, slowly increased to a maximum of 7.8 adults  $trap^{-1} day^{-1}$  on July 5, 1975, and ended on approximately July 11 or 12, 1975 (fig. 9, appendix F).

Most of the <u>Chaoborus</u> adults emerged near the lakeshores. The least amount of emergence occurred in the middle of the lake (fig. 10, appendix F).

The sex ratio of <u>Chaoborus</u> adults caught in emergence traps was  $0.91:1.0 \circle{2}: \circle{d}$  (appendix F).

In the outdoor rearing tanks (appendix A) 109 females and 101 males occurred after adult emergence. The  $\sigma^{1}: Q$ sex ratio of adults in the rearing tanks was 0.92:1.0. This sex ratio closely approximates the sex ratio of adults caught in emergence traps.

A few cases of multiple insemination of females were observed in the rearing tanks. Females laid eggs 24 to 36 hours after emerging. Each female produced one egg raft. Mean number of eggs per raft was 216.606. Mean number of first instar larvae hatching from each egg raft was 211.73. Hatching success was 97.73% (appendix L).

During the first week of July, newly hatched Chaoborus

Fig. 9. Temporal changes in emergence rate of <u>C</u>. <u>flavicans</u> adults.

17452) 17452) 186758



# Fig. 10. Horizontal distribution of adult emergence across station 1.



an Anna an an an an an an an an an Anna an Anna an an

first instar larvae (75-76 generation) occurred at 5 and 10 m. depth in all five submerged trap series. During the second and third weeks of July, new <u>Chaoborus</u> instars moved deeper and away from the shores (fig. 11).

<u>C. flavicans</u> pupae of the old 74-75 generation occurred at 0 to 10 m. depth in all five trap series. Overwintered fourth instar larvae of the 74-75 generation were trapped at 10, 15, and 20 m. depth. They occurred in all five trap series mostly at 10 m. depth (fig. 11, appendix G).

Amphipods were present only from '0 to 5 m. depth in all five trap series throughout the sampling season (fig. 11).

Production of C. flavicans in West Blue Lake

The growth curve of the 1974-75 generation of <u>C</u>. <u>flavicans</u> (irrespective of instar) shows a relatively faster growth rate during the ice-free season (fig. 12). Overwintered fourth instar larvae attained a weight of 0.9354 mg. (dry weight) in spring 1975. Average weekly growth increment of the overwintered 1973-74 generation was .0243 mg. Average weekly growth increment of the 1974-75 population was .0318 mg. (appendix H). Negative growth occurred in pupae of the 1973-74 and 1974-75 generations (fig. 12).

Instar specific growth curves of the 1975-76 generation show relatively slow growth in larval instars I and II and a faster growth rate in instar III larvae (fig. 13).

Differences in caloric content per unit weight of different <u>Chaoborus</u> instars and pupae were statistically insig-




Growth curve (irrespective of instar) of overwintered 1973-74 generation and 1974-75 generation of <u>C. flavicans</u>. Fig. 12.

950







nificant (appendix J). The mean caloric content of one mg. (dry weight) of <u>Chaoborus</u> is .0058638 kcal.

Growth in terms of carbon content (fig. 14) of <u>Chaoborus</u> instars I, II, and III showed trends similar to dry weight growth curves (fig. 13). Carbon content of fourth instar larvae and pupae varied irregularly during spring 1975 (fig. 14, appendix K). Carbon content per unit dry weight decreased from the beginning to the end of the growth periods of larval instars I, II, and III. Differences in carbon content per unit dry weight of the four larval instars and pupae were significant (appendix K).

The growth curve shown in fig. 12 was used to construct an Allen curve (fig. 15). From July 8, 1974, to June 25, 1975, the Allen curve production was 1982.55 mg. dry weight m.  $^{-2}$  year  $^{-1}$ . Production under the hassured line is 2094.70 mg. m.  $^{-2}$  week  $^{-1}$ . This represents production between the time of oviposition (July 1, 1974) and July 8, 1974 (appendix N).

Allen curve production of larvae from July 8, 1974 to June 25, 1975 in terms of calories and carbon content was 11.6253 kcal. m.<sup>-2</sup> year<sup>-1</sup> and 1.09 x 10<sup>6</sup>  $\mu$ g. C m.<sup>-2</sup> year<sup>-1</sup> respectively (appendix N).

Instar specific growth curves (fig. 13) were used to calculate Pechen-Shuskina production (table 2). Total production of larvae calculated according to the Pechen-Shuskina method was 2074 mg. dry weight m.<sup>-2</sup> year<sup>-1</sup>. This estimate is 91 mg. m.<sup>-2</sup> year<sup>-1</sup> higher than the Allen curve production

Fig. 14. Growth in terms of carbon content of  $\underline{C}$ . <u>flavicans</u> larvae and pupae, 1975.



## Fig. 15. Allen curve production of 1974-75 generation of <u>C</u>. <u>flavicans</u> larvae.



and any advantage of the state of the

	- ekly)	 1						· · · · · ·	· .•	•				
	P/B 2) (we	.9730	.7710	.3014	.1385	=.5460	·	2.000	1.4167	0.7345	0.5970			
t Blue Lake.	biomass (mg. m	12.6355	49.8828	34.8867	4.1696	١X		.6363	3.9366	42.3706 (	84.7014 (			
C. flavicans in Wes	daily production (mg.m. <sup>-2</sup> day <sup>-1</sup> )	1. 7563	5 • 49 39	1.5020	0.0825			0.1818	0.7967	4.4462	7.2240		•	
74-75 generation of	weekly production (mg. m. <sup>-2</sup> week <sup>-1</sup> )	12.294	38.4572	10.5138	0.5775	$\Sigma = 61.8425$ $\overline{X} = 15.4606$		1.2726	5.5769	31.1232	50.5680			
of the 19	w (mg.)	•0036	.0069	•0044	.0025			• 0036	.0051	.0101	.0160	· · · ·	• •	
production	<u>ы</u> (по.ш. <sup>-2</sup> )	3415	5573.5	2389.5	231			353.5	1093.5	3081.5	3160.5			
-Shuskina	N (no.m. <sup>-2</sup> )	5 0	6830	4317	462	0	0	707	1480	4683	) )			
Pechen	date	ly 1,197	Ly 8	ly 15	ly 22	Ly 30	ly 1	y 8	y 15	v 22			•	
Table 2.	Instar	I Jul	Jul	Ju]	Ju L	JuJ	II Jul	Jul	Jul	Ju1		•		
								•		•		•		

•

																				•			
	0.3276		0.0649		ζ = .8568		2.0		0.5983		0.8367		0.5933		0.4034		0.0363	•	0.0425		= 0.6444	•	
	41.2902		17.5481				0.7503		7.7220	•	65.6992		256.7919		385.1358		266.1604		44.7432	•	ıM		
	1.9323		0.1628	•		•	.2144		.6600		7.8533	:	21.7650	•	22.1963		1.3805	•	0.2715	· .	•	r r	· · · · · · · · · · · · · · · · · · ·
÷	13.5261	•	1.1393		$\frac{\Sigma}{X} = 103.2060$ $\frac{1}{X} = 17.2010$	•	1.5006	•	4.6200		54.9728		152.3547		155.3741		9.6635		<b>1.</b> 9005		$\overline{\Sigma} = 380.3862$ $\overline{X} = 54.3409$		
•	.0114		.0031			•	.0123		.0105	• •	•0328		.0469	-	.0518		• 00 70		• 00 10				
•	1186.5		367.5	· · ·	•	•	122		440		1676		3248.5		2999.5		1380.5		271.5	- 	•	•	· .
1638	•	735	• •	0		0		244	·	636		2716		3781		2218		543		0	•		
July 30		Aug. 5		Aug. 12		July 8		July 15		July 22		July 30		Aug. 5		Aug. 12		Aug. 19		Aug. 26			•
						III							•								•		

Table 2 (cont'd)

58

.

ue.       5       735 $10.1.3$ $10.421$ $1.5.4713$ $1.1.0477$ $116.0467$ $0.6664$ ue.       12       2941       2749.77 $0420$ $115.4903$ $16.4986$ $289.2071$ $0.3993$ ue.       19       2558.54 $2749.77$ $0420$ $115.4903$ $16.4986$ $289.2071$ $0.3993$ ue.       19 $2558.54$ $2749.77$ $0421$ $105.4298$ $15.0614$ $368.6912$ $0.3993$ ue.       2450.17 $0146$ $35.7724$ $5.1103$ $430.1877$ $0.0832$ apt. $2^+$ $2450.49$ $0147$ $36.0220$ $5.1460$ $46.1454$ $0.0713$ apt. $2^+$ $2415.76$ $01046$ $35.1821$	July 30	0	3 5 7 5	F 66 0	C F F L F		1	
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ې ئو	735	c•/ 0£	• 0.321	L5.4718	2.2103	7.7359	2.0
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			1838	.0421	77.339	11.0477	116.0467	0.6664
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ıg. 12	2941			•	•		
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		•	2749.77	.0420	115.4903	16.4986	289.2071	0.3993
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ıg. 19	2558.54						
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	•••	•	2504.27	.0421	105.4298	15.0614	368.6912	0.2860
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	1g. 26	2450						
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			2450.17	.0146	. 35.7724	5.1103	430.1877	0.0832
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	ept. 2 <sup>†</sup>	2450.33	• • •			· ·		
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$			2450.49	.0147	36.0220	5.1460	466.1454	0.0773
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	ept. 9 <sup>†</sup>	2450.66		•				•
$ pt. 16 2415 \\ pt. 23^{\dagger} 2380.53 \\ pt. 23^{\dagger} 2380.53 \\ pt. 30^{\dagger} 2310.03 \\ 2345.29 0.0190 \\ 44.5605 \\ 6.3658 \\ 6.3658 \\ 564.2181 \\ 0.0790 \\ 42.9940 \\ 6.1420 \\ 590.3716 \\ 0.0728 \\ 1.420 \\ 590.3716 \\ 0.0728 \\ 1.0682 \\ 1.825 \\ 5.9832 \\ 613.8541 \\ 0.0682 $			2450.83	.0146	35.7821	5.1117	502.1138	0.0713
$ \begin{array}{c} {} {} {} {} {} {} {} {} {} {} {} {} {}$	pt. 16	2415	. •	•				
$ pt. 23^{\dagger} 2380.53 \\ pt. 30^{\dagger} 2310.03 \\ tt. 30^{\dagger} 2310.03 \\ tt. 7^{\dagger} 2239.58 \\ tt. 7^{\dagger} 2239.58 \\ tt. 7^{\dagger} 2239.58 \\ tt. 7^{\dagger} 2204.34 \\ tt. 8825 \\ tt. 8825$			2415.76	.0189	45.6579	. 6.5226	535.3937	0.0853
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	pt. 23 <sup>†</sup>	2380.53	•		•	• •	•	
pt. $30^{\dagger}$ 2310.03 2274.82 .0189 42.9940 6.1420 590.3716 0.0728 t. $7^{\dagger}$ 2239.58 2204.34 .0190 41.8825 5.9832 613.8541 0.0682			2345.29	.0190	44.5605	6.3658	564.2181	0.0790
t. $7^{\dagger}$ 2239.58 2204.34 0.070 42.9940 6.1420 590.3716 0.0728 2239.58 2204.34 0.090 41.8825 5.9832 613.8541 0.0682	pt. 30 <sup>†</sup>	2310.03	•		•	· · ·		•
t. $7^{\dagger}$ 2239.58 2204.34 .0190 41.8825 5.9832 613.8541 0.0682			2274.82	.0189	42.9940	6.1420	590.3716	0.0728
2204.34 .0190 41.8825 5.9832 613.8541 0.0682	t. 7 <sup>†</sup>	2239.58						
			2204.34	.0190	41.8825	5.9832	613.8541	0.0682
					• • • •	•		
				•		•	•	

Table 2 (cont'd)

Table 2 (cont'd)

.

60

.

÷

estimate. Carbon and caloric conversions are presented in table 3. Instar III showed the highest production rate (54.34 mg.  $m^{-2}$  week<sup>-1</sup>) followed by instar IV (50.94 mg. m.<sup>-2</sup> week<sup>-1</sup>. Instar I showed lowest production (15.46 mg. m.<sup>-2</sup> week<sup>-1</sup>) (table 2).

Mean P/B ratios of larval instars I - IV were .5460, .8568, .6444 and .2278 respectively (table 2). The P/Bratio of the entire population was highest at the beginning of the new generation and declined slowly and irregularly until the end of the 1974-75 generation '(table 4).

Respiration and Feeding of C. flavicans

Oxygen uptake by larval instars II, III and IV and pupae of <u>C</u>. <u>flavicans</u> increased with an increase in temperature (fig. 16). Oxygen uptake increased faster per unit change in temperature in pupae and fourth instar larvae than in instars III and III (fig. 16).

Oxygen uptake of pupae differed significantly from larval oxygen uptake (F = 55.356, d.f. = 3, 12, P < 0.05). No significant differences occurred between oxygen uptake per unit weight of different larval instars. Oxygen uptake rates per unit weight of larvae and pupae (fig. 17) were significantly different (F = 4.386, d.f. = 3, 12, P < 0.05) (appendix M).

Successive instars of <u>C</u>. <u>flavicans</u> showed a tendency to choose larger and different prey types than previous instars. First instar <u>C</u>. <u>flavicans</u> fed mainly on rotifers and

61

Instar type m	g. dry weight m. <sup></sup> week <sup>-I</sup>	Production <sup>2</sup> ug.C m. <sup>-2</sup> week <sup>-1</sup> *	kcal. m. <sup>-2</sup> week <sup>-1</sup>
	•		
I	15.4606	10223.7546	.09066
II	17.2010	10368.8488	.10086
III	54.3409	33888.6155	.31864
IV	50.9425	23844.1975	•29872
total production	2073.71 mg. m. <sup>-2</sup> year <sup>-1</sup>	II38697.939 ug.C m2 year-1	12.1598 kcal. m. <sup>-2</sup> year <sup>-1</sup>

Table 3. Carbon and caloric conversions of Pechen-Shuskina production.

\* See appendix K for conversion.

' See appendix J for conversion.

$1_{y}$ $P/_{B}$			•	1.022		. 8344	·	.5443		.6865		• 59 30	•	.4652		.2254		.2596	.0832						
week	4	<del>ρ.</del>				· .	• • •	:				15.4718		77.3339	•	115.4903		105.4298	35.7724		6/CO.C4			•	
		<del>р</del>		•	•							7.7359	-	1,16.0467		289.2071		368.6912	430.1877		10,40,000	•		•	
	ε	Ê-		•	•	1.5006		4.62		54.9728		152.3547		155.3741		9.6635		1.9005	•						
Instar type		Ω.			•	. 7503		7.722	· · · ·	65.6992		256.7919		385.1358		266.1604		44.7432							
		گر		1.2726		5.5769		31.1232	•	50.5680	•.	13.5261		1.1393	۰.								•	Le	
	7	е Д		.6363		3.9366		42.3706	• •	84.7014	•	41.2902	•.	17.5481			•		•				•		وليتواجز والمتعالم والمتعادين والمتعادين
		Ωi	•	12.294	•	38.4572	· · ·	10.5138		0.5775			-		• •	•			•						ta magazi a sa s
		<b>д</b>	1974	12.6355		49.8828	•	34.8867		4.1696							•					•		•	
Date		•	July 1, 1		July 8		July 15		July 22	•	July 30		Aug. 5		Aug. 12		Aug. 19		Aug. 26	Sept. 16			•		

		•						64		
	.0242	•0144	.0926	.0373 0807	.0904	.0734		,		
	562.945	13.9642	80.2405	35.3875 80 8543	42.0816	4.7418	· • •			
	911.6979 6	971.5448	866.7339	948.3790 906 4208	465.3060	64.6282		• • •	•	
							•			
•			•							
	• • • •									
				• •			•			
â		· · ·							··· · · · · · · · · · · · · · · · · ·	
ible 4 (cont t. 16	y 14, 1975	y 21	y 28	me 4	me 11	me 18	C7 91		•	
	Ma	Ma	Ma	Ω	Ju	Γ, Υ	5			

Fig. 16. Effect of temperature on O<sub>2</sub> consumption rate of <u>C</u>. <u>flavicans</u> larvae and pupae. Bars indicate standard deviation.

65



Fig. 17. Effect of body size on 0<sub>2</sub> uptake per unit weight of C. flavicans larvae and pupae at five temperatures.

بويا وتشري المرار



nauplii. The second instar began feeding on copepods (<u>C</u>. <u>bicuspidatus</u>) to a small extent. However, instar II still showed a preference for rotifers and nauplii. Instar III was the first larval stage to feed on small (500 - 783  $\mu$ ) <u>D</u>. <u>pulicaria</u>. Instar III also showed an increased preference for copepods. Instar IV fed mainly on copepods and nauplii. Instar IV also ingested rotifers and some small and large (783 - 1050  $\mu$ ) <u>D</u>. <u>pulicaria</u>. Size range and diversity of food eaten by <u>Chaoborus</u> larvae increased from one instar to the next (fig. 18, appendix 0).

Ingestion rates of all instars increased with an increase in food concentration up to various asymptotes (fig. 19, table 5). Successive instars had higher ingestion rates at the same initial food concentration than previous instars. All instars incubated in the hypolimnion fed slower than the same instars incubated in the epilimnion (fig. 20). Multiple regression analysis of ingestion as a function of food concentration and temperature in the epilimnion and in the hypolimnion showed that temperature was not significant in the regressions for all instars (eg.: for instar II, F (d.f. = 1, 12, P < 0.01) = 4.89. Therefore for each instar, a simple regression of ingestion rate, I, on food concentration, x, in the epilimnion and in the hypolimnion was calculated (table 5). These simple curves showed high r values. An analysis of covariance performed on the epilimnetic and hypolimnetic feeding curves of each instar showed differences in slopes to be non-significant

68 Food selection by <u>C</u>. <u>flavicans</u> instars I - IV. R - rotifers, N - nauplii, C - <u>Cyclops bicuspidatus</u>, Dl - small <u>Daphnia pulicaria</u>, D2 - large <u>Daphnia pulicaria</u>. Fig. 18.

<u>[36363</u>



Effect of food concentration on ingestion rates of <u>C</u>. flavicans larval instars I - IV incubated in the epilimnion (------) and in the hypolimnion (-----). Fig. 19.



المشجر المستحر المحر المحر المحر المحر المحر

tests		Instar ty	Zpe	
	П	II	III	IV
epilimnetic equation	Y=9598-5.0847x	Y=.5863-5.001x	Y=.0794-4.1527	⊻=1081-3.2753x
hypolimnetic equation	Y=1.2937-6.0790x	Y=.6234-5.0780	Y=.3769-4.8138x	Y=2506-3.8318x
r <sub>epilimnion</sub>	.931	. 891	.891	. 879
r hypolimnion	106.	.903	. 880	• 760
вр Вр	• 8503	• 0083	1.36	.0763
ں 8 4	72.04	28.03	50.54	6.52
common b	-5.5821	-5.0395	-4.4834	-3.5535
Kd epilimnion	.00642	.0131	.0468	.0616
<sup>K</sup> hypolimnion	.00580	.0120	.0423	.0485

X = initial food concentration Critical F (1,26 d.f., P < 0.01) = Critical F (1,27 d.f., P < 0.01) =</pre> asymptote <sup>8</sup>2 β2 11 11 ช่ á ll C 0

4.21

שי

70

(table 5). Common b values decreased in successive instars. Analysis of covariance also showed a significant temperature effect on the feeding curves for all instars. Feeding curve asymptotes were always higher in the epilimnion than in the hypolimnion for a given instar (table 5).

71

Feeding intensity (in terms of amount eaten per unit body weight of larva) of successive instars was lower than feeding intensity of previous instars. Feeding intensities of all instars were highly variable at all food concentrations. In general, feeding intensities of all instars were higher in the epilimnion than in the hypolimnion (fig. 20, appendix 0).

Feeding intensities of <u>C</u>. <u>flavicans</u> instars I - IV at various food concentrations in the epilimnion (-----) and in the hypolimnion (----). Fig. 20.



## DISCUSSION

Life History and Population Dynamics of <u>C</u>. <u>flavicans</u> in West Blue Lake

<u>C. flavicans</u> fourth instar larvae overwintered in the mud of West Blue Lake in a state of diapause. As fall approached, benthic density increased from about 250 larvae m.<sup>-2</sup> to about 6000 larvae m.<sup>-2</sup>(fig. 5). Roth (1968) found that overwintered larvae of <u>C. flavicans</u>, <u>C. punctipennis</u>, and <u>C. albatus</u> were benthic during the day and planktonic at night.

<u>C. flavicans</u> larvae occurred in benthos of stations 1 and 5 but not in station 2 benthos. Stations 1 and 5 were 17 and 20 m. deep respectively, while station 2 was over 30 m. deep. Anoxia at 30 m. (Ward and Robinson 1974) probably prohibited <u>Chaoborus</u> larvae from inhabiting station 2 benthos.

After the ice melted in spring, <u>C</u>. <u>flavicans</u> fourth instars began emerging from the mud. Borutsky (1939) speculated that shoreward benthic migrations are temperatureregulated and that pupation is favoured in shallower, warmer zones.

<u>C. flavicans</u> pupae occurred in plankton samples for four weeks (June 3 - June 24) in 1974 and for 3 weeks (June 11 - June 25) in 1975. Parma (1969, 1971) found that <u>C.</u> <u>flavicans</u> pupae last 10 - 15 days at 10<sup>°</sup>C and 3-6 days at 15<sup>°</sup>C. <u>C. crystallinus</u> pupae last 12 days at 10<sup>°</sup>C and about 30 days at 5<sup>°</sup>C. Pupal life span of <u>C. flavicans</u> in West Blue Lake is longer than that observed by Parma (1971) probably because lower temperatures decrease developmental rate of pupae.

The univoltine nature of the <u>C</u>. <u>flavicans</u> population in West Blue Lake is partly reflected by one fairly short period of adult emergence per year. Imagines of the 1974-75 generation began emerging during late June. Emergence lasted 13 days (fig. 7). Emergence of <u>C</u> <u>flavicans</u> adults from Lake Esrom, Denmark lasted much longer. Jonasson (1972) observed that adult emergence occurred from early July to mid-August. More <u>Chaoborus</u> adults emerged near the shores of West Blue Lake than in the center of the lake (fig. 10). This indicates that pupae probably migrated shoreward before metamorphosis. Ultimately, this littoral emergence would increase the probability of successful mating by concentrating adults in one place.

Sex ratio of adult <u>C</u>. <u>flavicans</u> emerging in rearing tanks  $(.92:1 \sigma^{1}: Q)$  and caught in emergence traps (.90:1 Q: $\sigma^{*}$ ) indicate a 1:1 sex ratio in the West Blue Lake population of <u>C</u>. <u>flavicans</u>. Parma (1971) also found a 1:1 sex ratio in the <u>C</u>. <u>flavicans</u> population of Lake Vechten, Holland. Parma (1969) observed a temporal decrease in the proportions of male <u>C</u>. <u>crystallinus</u> and experimentally showed that this decrease was due to a faster developmental rate of males.

C. flavicans adults formed mating swarms along the

74

shores of West Blue Lake during early July. Swarming of Chaoborus has been reported for several tropical and temperate species (Wesenberg-Lund 1914, Muttkowski 1918, Berg 1937, MacDonald 1956, Verbeke 1957). Assuming each pair of adults mates once, a short emergence period in which all adults emergence at once would increase probability of reproduction since adult Chaoborus have a relatively short life span. Parma (1971) experimentally showed that adult life span of <u>C</u>. flavicans is 1.5 - 6 days. Adult life span of <u>C</u>. crystallinus is 1 - 3 days (Parma 1969). I observed a few cases of multiple insemination of C. flavicans females in the rearing tanks. Multiple insemination is a behavioural mechanism that would increase probability of successful oviposition by females of the population. Herms (1937) observed C. astictopus males copulating with many females and females copulating with many males.

I found <u>C</u>. <u>flavicans</u> egg rafts in the rearing tanks about two days after adults had begun to emerge. This disagrees with Berg's (1937) observation that oviposition occurs in a few hours after emergence. The two day preoviposition period of <u>C</u>. <u>flavicans</u> is similar to the 36-48 hour pre-oviposition period of <u>C</u>. <u>astictopus</u> (Lindquist and Deonier 1942). Ultimately, a long pre-oviposition period would reduce the number of eggs laid by a <u>Chaoborus</u> population since the probability of death or wind dispersal of females away from the lake would be higher. Each <u>C.flavicans</u> female laid one egg raft on the water surface of the rearing tank. The mean number of eggs per raft (217) that I observed was lower than the 449 eggs per raft counted by Parma (1971). The mean number of eggs per raft differs interspecifically and intraspecifically. Intraspecific differences may be due to different food conditions during the larval period. Wesenberg-Lund (1914) counted 200-300 eggs per raft of  $\underline{C}$ . flavicans.

I observed that floating egg rafts of <u>C</u>. <u>flavicans</u> were occasionally suspended under water or stuck to littoral vegetation above water, due to wave action. Parma (1971) observed the same mishaps with <u>C</u>. <u>flavicans</u> and <u>C</u>. <u>crystallinus</u> eggs. Insect eggs require a constant supply of oxygen (Chapman 1969). Presumably, floating egg rafts are advantageous to survival because oxygen is more readily available at the lake surface than at the lake bottom.

The 1974-75 generation of <u>C</u>. <u>flavicans</u> larvae began in early July (fig.9). Newly hatched first instars seemed to move away from shore and deeper into the lake (fig. 11). I chose to use presence or absence data from submerged traps rather than numerical abundances since the numbers of larvae caught in submerged traps were much lower than numbers of larvae caught by the Schindler-Patalas plankton trap. First instar larvae hatching from eggs pushed to shore by the wind probably drifted or migrated lakeward in search of food and to escape predation by littoral animals. Carnivorous copepods such as <u>Cyclops</u> (Parma 1971), amphipods (Anderson and Raasveldt 1974) and perch (Falk 1971) prey on <u>Chaoborus</u> larvae. Amphipods occurred only from 0 to 5 m. depth in all five submerged trap series and probably preyed on newly hatched <u>C</u>. <u>flavicans</u> larvae occurring in this depth zone. First instars were also probably preyed on by perch (Falk 1971) which migrate inshore in the evening in search of food (Wong and Ward 1972). By moving away from shore and deeper into the lake, young <u>Chaoborus</u> larvae would avoid predation by littoral and epilimnetic animals. Saether (1972) stated that young <u>Chaoborus</u> larvae are positively phototactic and remain near the lake surface. They are carried lakeward by wind-generated currents.

First instar larvae occurred in surface waters to a small extent for one to two weeks after hatching. Three weeks after hatching, no larvae occurred from 0 to 5 m. depth (fig. 3).

As <u>C</u>. <u>flavicans</u> larvae passed through the four instar stages, they moved deeper into the lake from 9 m. in early July to about 15 m. in late August (fig.3). Larvae seemed to prefer the water stratum just below the thermocline. Teraguchi and Northcote (1966) observed the same downward shift from 4 m. to 10 m. in the <u>C</u>. <u>flavicans</u> population of Corbett Lake, B.C. Fedorenko and Swift (1972) observed that
<u>C. americanus</u> and <u>C. trivittatus</u> larvae "... moved deeper with age." Light intensity seems to be a critical factor in determining vertical movements and distribution of <u>Chaoborus</u> larvae (Berg 1937, LaRow 1968, 1969, Chaston 1969).

78

Highest larval densities near the bottoms of sampling stations occurred in October (fig.3). Benthic larval densities in October were also high compared to benthic densities during the summer (fig.5). These two observations indicate that, as winter approached, <u>C. flavicans</u> larvae moved into the benthos to overwinter in a state of diapause. Jonasson (1972) observed that as winter approached, <u>C.</u> <u>flavicans</u> larvae moved into the benthos of Lake Esrom, Denmark and remained in the sediments until the following spring.

Highest mean larval density occurred on July 8, 1974, after new instars had hatched (table 1). From July to September, larval densities decreased quickly and somewhat irregularly. From September 1974 to May 1975, larval densities remained low and showed little temporal change(fig. 4). Densities of overwintered fourth instars showed a great deal of temporal and spatial variation during spring, 1975 (fig.3, table 1). This variation could have been caused by windgenerated currents during isothermal conditions and by great motility of fourth instar larvae. All density estimates of <u>C. flavicans</u> larvae from West Blue Lake are conservative because larvae could have been avoiding sampling devices and some larvae (especially first instars) could have been lost due to their becoming lodged in the screens of samplers.

Highest larval density (11427 m.<sup>-2</sup>) occurred at Station 5 on July 22, 1974. Highest mean larval density  $(7851 \text{ m.}^{-2})$  is, in general, lower than those occurring in tropical or eutrophic lakes and ponds. In tropical Lake Lanao, Lewis (1975) recorded a maximum of 19000 larvae m. $^{-2}$ in a 45 m. water column. In Lake George, Uganda, maximum density of Chaoborus larvae was only 3170' m. -2 (McGowan 1974). However Lake George has a maximum depth of only 3 m. Eggleton (1931) recorded a maximum density of 71000 larvae m.<sup>-2</sup> in a eutrophic temperate lake. Maximum larval density in Leechmere Pond, Colorado was 1230 m.<sup>-3</sup> (Dodson 1972). Maximum larval densities of C. flavicans in West Blue Lake were much higher than those of <u>C</u>. trivittatus (1100 m.<sup>-2</sup>) and C. americanus (200 m. $^{-2}$ ) in Eunice Lake, B.C. which is an oligotrophic lake whose mean depth is 15.8 m. (Fedorenko and Swift 1972). Possibly low Chaoborus densities in Eunice Lake were due to intraspecific competition between the two coexisting Chaoborus species.

Most of the horizontal variation in station densities occurred immediately after the new first instar larvae hatched (fig.4). This variation can be explained by the oviposition behaviour of female <u>Chaoborus</u> and the nature of the eggs in the littoral zone (Saether 1970, McGowan 1974).

<u>C. flavicans</u> eggs are laid in the form of floating rafts. Dispersion of egg rafts by wind from the littoral zone to other areas of West Blue Lake could have given rise to the large differences in station densities.

Absence of major peaks in larval density curves (fig.4) after early July reflects the univoltine nature of the <u>Chaoborus</u> population in West Blue Lake. Other <u>Chaoborus</u> populations in Canada are also univoltine (Teraguchi and Northcote 1966, Fedorenko and Swift 1972).

Estimates of pupal density were, in general, low and variable. Validity of these estimates is doubtful since <u>C. flavicans</u> pupae were highly motile and probably avoided capture. McGowan (1974) also experienced difficulty in capturing pupae.

Estimates of <u>C</u>. <u>flavicans</u> abundance do not necessarily represent their true abundance in the lake. Ward and Robinson (1974) stated that ". . . horizontal distribution can be affected by wind-produced currents. Counts made at a single station in a multibasin lake may not be representative of the whole lake. Estimates made at a single deep station may overestimate average abundance in the lake when the animals are concentrated near the bottom." Sampling error was at least partly decreased by collecting triplicate samples at each sampling depth at each station. Ward (unpublished) found a high correlation of D. pulicaria density and station depth. A correlation analysis of <u>Chaoborus</u> density and station depth did not reveal any relationship probably because <u>Chaoborus</u> larvae are more motile than <u>D</u>. <u>pulicaria</u>.

As C. flavicans larvae grew older, the depth range of their diel vertical migration patterns deepened (fig.6). In early July, most first instar larvae occurred in the epilimnion at all times of the day. Based on changes in depthweighted density peaks (fig.6), first instars migrated the least distance of all instars. Similarly, C. flavicans first instars in Corbett Lake, B.C. remained in the upper 6 m. and exhibited no diel vertical migration (Teraguchi and Northcote 1966). First instars began evening ascent at 10 p.m. and began morning descent between 2 a.m. and 6 a.m. (fig.6). Second instars migrated further and began evening ascent earlier than first instars. Teraquchi and Northcote (1966) noted a weak migration of second instars. However, Teraguchi and Northcote could not determine ascent and descent times because they monitored vertical migration patterns only three times per day. C. flavicans third instars migrated a greater distance than second instars and began evening ascent later than second instars. In Corbett Lake, C. flavicans third instars began evening ascent earlier than third instars in West Blue Lake.

Overwintered Chaoborus fourth instars showed the

most pronounced vertical migration of all instars in West Blue Lake. They migrated the greatest distance. The migration range of fourth instars was deeper than migration ranges of instars I to III (fig.6).

In Corbett Lake, <u>C</u>. <u>flavicans</u> overwintered fourth instars moved from 10 m. depth during the day to 3 m. depth at 11 p.m. Evening ascent of fourth instars in Corbett Lake began about two hours earlier than it did in West Blue Lake. Teraguchi and Northcote observed a midnight sinking phase of fourth instars in Corbett Lake which was not observed in West Blue Lake. Morning descent times (3-6 a.m.) were comparable in both lakes. Cushing's (1951) "dawn rise" phase was not observed in Corbett Lake or in West Blue Lake.

Validity of vertical migration comparisons between the <u>C</u>. <u>flavicans</u> populations of West Blue Lake and Corbett Lake is confounded by differences in (1) sampling times during the day and year, (2) sampling depths, (3) plankton traps employed in the studies and (4) multimodal vertical distributions of larvae in Corbett Lake as opposed to unimodal distributions in West Blue Lake.

Vertical migration patterns of <u>Chaoborus</u> larvae in West Blue Lake were based on only one sample per sampling depth and four hour sampling intervals at only one station. More precision and more information could have been gained by collecting triplicate samples more frequently at more

## sampling depths.

Some Chaoborus larvae always occurred near the surface of Eunice Lake during the day (Fedorenko and Swift There were no carnivorous copepods, amphipods or 1972). fish present in Eunice Lake. Fewer larvae inhabited the surface waters of Corbett Lake during the daytime (Teraguchi and Northcote 1966). Some rainbow trout and brook trout were present in Corbett Lake. In West Blue Lake, C. flavicans larvae did not inhabit surface waters except for a very short time after hatching. Cyclops, amphipods and fish are present in West Blue Lake. These animals are known predators of Chaoborus larvae (Parma 1971, Anderson and Raasveldt 1974). These observations lead me to believe that the presence of invertebrate and fish predators of Chaoborus in epilimnetic waters cause Chaoborus larvae to avoid surface waters during the day.

In West Blue Lake, the growing season of <u>C</u>. <u>flavicans</u> is restricted to the ice-free period from mid-May to mid-November. Consequently, durations of the first three instars of <u>C</u>. <u>flavicans</u> were relatively short while the fourth instar lasted from early August of one year to late June of the following year.

Temporal changes in the population structure of  $\underline{C}$ . <u>flavicans</u> larval instars were determined by measuring head capsule lengths (fig.2). This method is most frequently used

(Teraguchi and Northcote 1966, Parma 1969, 1971, Fedorenko and Swift 1972, MacDonald 1956) although some researchers measure antennal base lengths (McGowan 1974). The head capsule length classes used to determine the four instars of <u>C. flavicans</u> in West Blue Lake (fig.7) were very similar to those used by Teraguchi and Northcote (1966). Teraguchi and Northcote (1966) found that instars could be determined by measuring inter-bladder lengths (distance between anterior and posterior air bladders). The use of inter-bladder lengths to determine instars is tedious and time-consuming because larvae flex rapidly when they are being examined under the microscope.

84

First instars of <u>C</u>. <u>flavicans</u> in West Blue Lake were present for five weeks from June 24 to July 30. Successive instars were present for longer periods. Instars II, III and IV occurred for 6 weeks, 8 weeks and 11 months respectively (fig.8). These durations are much longer than those reported by Parma (1971). Parma cultured larvae in an artificial food suspension at 20<sup>°</sup>C under constant light. Parma estimated durations of instars I, II and III to be 9 days, 20 days and 14 days respectively. These estimates are not realistic because, in the natural situation, <u>Chaoborus</u> larvae experience daily and seasonal changes in temperature, food type, food size, food density, and photoperiod. These factors must influence duration of larvae to some degree.

Therefore, one would expect different durations of instars from different lakes and from the same lake at different Fedorenko and Swift (1972) estimated duration of C. times. americanus and C. trivittatus instars II, III and IV to be 12 and 23 days, 17 and 48 days and 318 and 635 days respectively. Developmental times of C. flavicans instars I - IV were 10 days, 12 days, 12 days, and 142 days respectively. These developmental times were estimated by calculating  $T_{1+i} - T_i$  where T is the date on which the median of the percent frequency curve of a given instar occurred. The developmental times of the first three instars in West Blue Lake were similar to the developmental times of C. americanus instars I - III in Eunice Lake (Fedorenko and Swift 1972). However the developmental time of <u>C</u>. <u>flavicans</u> instar IV is about half of the mean duration stated for C. americanus instar IV in Eunice Lake. I suspect that Fedorenko and Swift (1972) used width of instar frequency curves rather than the distance between medians of curves to estimate mean duration times. If this is not the case, then they confused duration with developmental time. For instance, in West Blue Lake, duration of instar IV is much longer than its developmental time.

<u>C. flavicans</u> pupae occurred for 3-4 weeks in West Blue Lake (table 1). Variation in pupal life span can be attributed to temperature since <u>Chaoborus</u> pupae do not feed.

Parma (1971) showed that <u>C</u>. <u>flavicans</u> pupae last 3-4 days at  $20^{\circ}$ C and 10-15 days at  $10^{\circ}$ C. These durations are not comparable to the lengths of time pupae occurred in West Blue Lake because in the natural situation, pupae experience a wide range of temperatures daily and seasonally. Also the length of time pupae occurred in samples was partly a function of differential developmental rates of overwintered fourth instars and pupae.

Growth, Feeding and Respiration of <u>C</u>. <u>flavicans</u> in West Blue Lake

Growth of C. flavicans larvae in West Blue Lake was monitored irrespective of instars during 1974 in order to construct an Allen curve for the purpose of calculating productivity. Mean weekly growth increment of the 1974-75 generation was 0.032 mg. dry weight (appendix H). Mean individual weights of larvae increased regularly in spite of the fact that they were based on samples composed of varying proportions of different instars (fig. 12). Similarly, the growth curve of C. americanus in Eunice Lake increased regularly until November when the mean dry weight was about 0.7 mg. (Fedorenko and Swift 1972). This weight was much higher than that of West Blue Lake larvae in October (fig.12). During the winter months, dry weight of C. americanus larvae decreased about 0.1 mg. (Fedorenko and Swift 1972). This is expected since Chaoborus larvae overwinter in a state of

diapause and do not feed (Fedorenko 1975). Although larval weights of Chaoborus were not monitored in West Blue Lake during the winter, they probably remained constant or decreased slightly. Jonasson (1972) observed that C. flavicans larvae grew to 0.53 mg. dry weight during the summer and that larval weight remained constant all winter until spring when larval weight increased rapidly to 0.71 mg. dry weight. In spring 1975, overwintered larvae grew faster than smaller larvae did during the previous summer. Overwintered larvae attained a maximum dry weight of 0.9 mg. which is the same as the mean dry weight of overwintered C. flavicans larvae in Lake Vechten (Parma 1971). Pupal growth curves fluctuated irregularly because some pupae in the weight samples contained developing adults while others had recently pupated from larvae. Pupae were slightly heavier than fourth instars (fig.12) because they contained developing adults in addition to their own weight. Maximum dry weight of Chaoborus pupae in West Blue Lake was 0.2 mg. higher than the dry weight of pupae from Lake Vechten (Parma 1971).

The amount of information obtained by monitoring growth of larvae irrespective of instar is limited and does not allow further calculations of the biomass and productivity of various instars. The major source of error in measuring growth of larvae irrespective of instar is that larvae are not selected randomly from tow samples, i.e., bigger larvae are more easily chosen than smaller larvae because they are easier to see. Thus when the population is composed of many small instars and relatively fewer large instars, mean individual weight will be overestimated. The only advantage of monitoring larval growth irrespective of instar is that a great deal of time is saved by eliminating the sorting of larvae according to instar.

Growth of instars I, II and III (fig.13) and overwintered fourth instars (fig.12) was monitored for use in calculating production according to the Pechen-Shuskina method (1964). C. flavicans instars I and II grew relatively slowly and showed the least weight increment of all instars. Instar III showed a greatly accelerated growth rate in August (fig. 13). The length of the field season did not permit a complete monitoring of third instar growth. Consequently, maximum weight of third instars is unknown. When second instars first occurred in the water column, their dry weight was less than that of first instars (fig.13). This discrepancy was due to loss of exuviae as first instars moulted. Parma (1971) showed that a Chaoborus exuvium contributes a maximum of 6% to the total dry weight of the Parma (1971) plotted water content of Chaoborus animal. instars versus their dry weight and found that an increase in dry weight of third and fourth instars was attended by a decrease in their water content. I did not measure fresh

weights of <u>C</u>. <u>flavicans</u> larvae because fresh weight is more variable than dry weight (Parma 1971). Dry weight is a more realistic indicator of the amount of <u>Chaoborus</u> flesh available as food for invertebrate and fish predators. Dry weight of <u>Chaoborus</u> larvae was a valuable factor because it was easily converted to carbon content and caloric content of larvae. Conversion of dry weight production to carbon production of <u>Chaoborus</u> larvae was especially useful in this study because it permitted comparison of <u>Chaoborus</u> production to production of other zooplankters and fish in West Blue Lake.

Caloric content per unit dry weight was not significantly different among <u>C</u>. <u>flavicans</u> instars and pupae. Slobodkin and Richman (1961) determined that caloric content of sixteen invertebrate species representing six phyla ranged between 5.4 and 6.9 kcal. gm. <sup>-1</sup>. Caloric content per unit dry weight of <u>C</u>. <u>flavicans</u> falls within the above range.

Growth curves in terms of carbon content of the first three <u>C</u>. <u>flavicans</u> instars (fig. 14) were similar to dry weight growth curves of instars I - III. Carbon content of fourth instars and pupae fluctuated irregularly with time (fig.14). In general, carbon content per unit dry weight decreased in successive instars and decreased with time within each instar. This trend is anomalous assuming that

carbon content reflects stored energy in <u>Chaoborus</u> larvae. One would expect carbon content per unit weight to increase with time and from one instar to the next. Fourth instars were expected to have the highest carbon concentration because this instar overwinters in diapause and a store of fat or lipids would be selectively advantageous during diapause.

McGowan's (1974) estimates of carbon content of second, third, fourth <u>Chaoborus</u> instars and pupae (4  $\mu$ g, 23  $\mu$ g, 143  $\mu$ g and 105  $\mu$ g respectively) are much lower than maximum carbon content of corresponding <u>C. flavicans</u> life stages in West Blue Lake (fig. 14).

These discrepancies are due to two factors: (1) McGowan analyzed carbon content of <u>Chaoborus</u> life history stages on only one date in August. It is not known whether carbon content of <u>Chaoborus</u> larvae and pupae increased after the time of McGowan's analysis, and (2) McGowan used a conductrimetric method to determine carbon content of live larvae and pupae whereas dry larvae and pupae were analyzed in this study. Use of dry samples in analyzing carbon content is more realistic than using wet samples. Ward and Robinson (1974) found that carbon values determined by a wet combustion procedure were lower than carbon values determined by using dry samples in an elemental analyzer. Ward speculated that wet combustion of some components of organisms is incomplete.

Relatively large error terms occurred in the estimation of mean carbon content of <u>C</u>. <u>flavicans</u> fourth instars and pupae. This error could have been inherent, i.e., real differences in carbon content of larvae and pupae were due to differential developmental rates and presence or absence of developing adults in pupae. The error could also have been caused by contamination of some samples during their preparation and analysis.

The use of carbon and caloric analyses in monitoring growth of <u>C</u>. <u>flavicans</u> larvae and pupae was not only tedious and time-consuming, but methodological errors were introduced in sample preparation and analysis. For instance, loss of even a small part of a calorific sample while transferring the sample from the balance to the calorimeter would result in underestimating caloric content per unit weight of sample. Although dry weights were easily and quickly determined, they were less useful in relating <u>Chaoborus</u> production to production of other zooplankters in West Blue Lake and in providing a food value of <u>Chaoborus</u> as fish and invertebrate food.

The increase in the size range and types of food consumed by <u>C</u>. <u>flavicans</u> larvae as they passed through the four instar stages (fig. 18) was similar to the increasing diversity of food type and size ingested by <u>C</u>. <u>trivittatus</u>

and C. americanus larvae in Eunice Lake, B.C. (Fedorenko 1975). Diet of first instar C. flavicans was restricted to rotifers and nauplii (fig. 18). This agrees with findings of Deonier (1943), Prokesova (1959) and Sikorowa (1968). C. flavicans second instars added Cyclops bicuspidatus copepodids to their diet but still consumed rotifers and nauplii to a great extent (fig. 18). In contrast, C. americanus second instars ingested more and larger prey types. They preferred Bosmina and ingested Daphnia, Holopedium and other cladocerans to a small extent. C. trivittatus second instars also preferred Bosmina but, in contrast to C. americanus second instars, they consumed Diaptomus tyrelli (Fedorenko 1975). Chaoborus second instars in Eunice Lake selected prey that was not only larger than the preferred prey of C. flavicans second instars in West Blue Lake, but of a different type. The first <u>C. flavicans</u> life history stage to begin ingesting small Daphnia pulicaria was the third instar while, in Eunice Lake, third instar C. americanus relied heavily on Bosmina and D. tyrelli and consumed some Holopedium. Third instar C. trivittatus preyed on more food types than <u>C</u>. <u>americanus</u> third instars or <u>C</u>. flavicans third instars ate. C. trivittatus third instars preyed on D. tyrelli, Bosmina, Daphnia, Holopedium and other cladocerans and on rotifers. <u>C</u>. <u>flavicans</u> fourth instars ingested the following prey in order of preference: Cyclops

nauplii, rotifers, small Daphnia and large Daphnia. с. americanus fourth instars in Eunice Lake seemed to revert back to consuming more rotifers and less Bosmina although they had grown large enough to ingest all prey types present in the lake. Perhaps this is an indication of the nutritional value of rotifers. Although they were much smaller than Bosmina, C. americanus larvae could have been selecting them because of their higher nutritional value. C. trivittatus fourth instars, in the first year of their two year life cycle, preferred <u>D</u>. tyrelli, rotifers, Bosmina, Holopedium and consumed a few D. kenai and Polyphemus. In their second year, C. trivittatus fourth instars showed a high preference for <u>D</u>. tyrelli and <u>D</u>. kenai and ingested all other available prey to a lesser extent (Fedorenko 1975). Fedorenko's analysis was performed by collecting Chaoborus larvae once a month and counting numbers of different prey types present in Chaoborus crops while the food preferences of <u>C. flavicans</u> in this study were determined from in situ incubation experiments. In spite of obvious differences in experimental approaches, in species of Chaoborus, and in prey types used in these two studies, it can be said that as Chaoborus larvae matured, they fed on wider ranges of food sizes and types.

In this study, species of rotifers consumed by <u>C</u>. <u>flavicans</u> larvae were not separately enumerated. <u>Keratella</u> <u>cochlearis</u>, <u>K</u>. <u>quadrata</u>, <u>Filinia longiseta</u>, and <u>Asplanchna</u> sp., the most common rotifers in West Blue Lake (Ward and Robinson 1974), are all possible prey of <u>C</u>. <u>flavicans</u>. Most of the <u>Cyclops bicuspidatus</u> pre-adult life history stages (except nauplii) were present on the 243-500 $\mu$  filter from which number of copepods eaten by <u>Chaoborus</u> larvae was determined. Thus, selection of specific copepod life history stages by <u>Chaoborus</u> larvae is unknown.

<u>Chaoborus</u> food preference experiments in this study were crude because they were based on counting numbers of prey before and after each experiment. Natural variations within control and test samples as well as errors induced by sampling and loss of prey organisms (especially rotifers and nauplii) during analysis obscured to some degree the true numbers and types of prey consumed by <u>C</u>. <u>flavicans</u> larvae. Fedorenko (1975) stated that second and third instars of both <u>Chaoborus</u> species could swallow all prey except large <u>Daphnia</u> and <u>Holopedium</u> and that larval size was not the primary factor determing their duet.

The majority of other <u>Chaoborus</u> feeding reports in the literature differed fundamentally from the food preference studies presented by Fedorenko (1975) and in this report because they were based on laboratory experiments in which predator and prey densities were artificially manipulated.

There have been very few quantitative studies of Chaoborus predation. Deonier (1943) observed that Chaoborus larvae ingest 12 Cyclops per larva in 45 minutes. Presumably, Deonier was working with fourth instars. Chaoborus feeding experiments of Kajak and Ranke-Rybicka (1970), Fedorenko (1975) and the experiments presented in this study are the only in situ Chaoborus feeding experiments reported in the literature. Kajak and Ranke-Rybicka (1970) performed in situ feeding experiments with C. flavicans fourth instars in two Polish lakes. Kajak and Ranke-Rybicka found that Chaoborus larvae consumed 0.81 - 0.88 crustaceans larva<sup>-1</sup> hour<sup>-1</sup>. Maximum daily food consumption of larvae was 12.5% of their body weight. Kajak and Ranke-Rybicka did not examine the temperature effect created by suspending feeding chambers at different depths. Kajak and Ranke-Rybicka sampled larvae during the day and during the night. Ten percent of larvae caught at night had full crops while 0.9% to 2.8% of larvae caught during the day had full crops.

Fedorenko (1975) concluded that <u>Chaoborus</u> larvae in Eunice Lake fed most intensely at dusk and dawn in spite of the fact that a  $X^2$  analysis showed no significant differences in proportions of larvae with full crops during the day and night. Fedorenko (1975) performed <u>in situ</u> feeding experiments with <u>C. trivittatus</u> instars II, III and IV and <u>C. americanus</u> instar IV. Prey was <u>D. tyrelli</u>, <u>D. kenai</u>

and Diaphanosoma. One larva was incubated with a known number of prey in 0.37 to 30.0 liter plastic bags. Difference in prey number before and after a 24 hour incubation at various depths was considered the feeding rate. Feeding rates on D. tyrelli increased with increasing prey density and, except for old C. trivittatus fourth instars, with increasing temperature. Maximum feeding rate of C. trivittatus second instars was 2 prey larva<sup>-1</sup> day<sup>-1</sup>. Third instars consumed 6-7 prey larva<sup>-1</sup> day<sup>-1</sup> at a concentration of 5 D. tyrelli 1.<sup>-1</sup>. These feeding rates are very similar to those of second and third C. flavicans instars feeding on copepods in West Blue Lake. Maximum feeding rates of fourth instars of both Chaoborus species in Eunice Lake were 20 prey larva<sup>-1</sup> day at a density of 80 <u>D</u>. tyrelli 1.<sup>-1</sup>. This feeding rate was much higher than that of C. flavicans fourth instars feeding on copepods. However, initial prey density was lower and several types of prey were offered to C. flavicans fourth instars in this study. Fedorenko (1975) assumed that second and third instars of C. americanus fed at the same rates as C. trivittatus second and third instars.

In Eunice Lake, maximum rates of <u>Chaoborus</u> feeding on <u>D</u>. <u>kenai</u> occurred at prey densities that were much lower than the <u>D</u>. <u>tyrelli</u> densities which elicited maximum feeding. Old <u>C</u>. <u>trivittatus</u> fourth instars consumed their maximum ration of 2.5 - 4.0 <u>D</u>. <u>kenai</u> per day at a prey density of 1 - 2 prey 1.<sup>-1</sup> (Fedorenko 1975).

In laboratory experiments performed to assess temperature effect on feeding rates of Chaoborus larvae, Fedorenko (1975) found that feeding rates increased linearly with temperature in all instars except old C. trivittatus fourth instars. Fedorenko (1975) extrapolated results of feeding experiments to estimate impact of Chaoborus predation on standing crops of prey in Eunice Lake. Estimated mean percentage of standing crop of prey eaten by Chaoborus 2% for copepod nauplii, 3% for Diaptomus tyrelli, was: 9% for Diaptomus kenai and 4% for Diaphanosoma. Fedorenko stated ". . . I have determined the effects of temperature, prey type and prey density on chaoborid feeding, evaluated the impact of larval predation on the zooplankton populations in Eunice Lake . . . " In reality, her experimental designs and results fell short of her objectives in some regards: (1) incubation experiments were performed at randomly selected depths and temperatures for different instars so it is difficult to compare feeding curves over a common temperature Perhaps an analysis of covariance would have been range. appropriate, (2) experiments on first instars of both Chaoborus species and C. americanus instars II and III were not performed. Fedorenko (1975) assumed that feeding rates of C. americanus instars II and III were similar to feeding rates of C. trivittatus instars II and III respectively,

(3) experiments on Chaoborus feeding on D. kenai were performed at prey densities of 1 - 10 prey 1.<sup>-1</sup> while experiments on Chaoborus feeding on D. tyrelli were performed at 0 - 200 prey 1.<sup>-1</sup>. Fedorenko (1975) assumed there was no interaction effect of mixed prey on Chaoborus feeding. Perhaps some experiments employing various proportions of the two experimental copepod species would have contributed some information about an interaction effect, (4) Fedorenko (1975) criticized Kajak and Ranke-Rybicka' (1970) for using high prey densities in their experiments but used 200 prey 1.<sup>-1</sup> in some of her own experiments, and (5) Fedorenko did not estimate interaction of temperature and prey density on feeding rates of Chaoborus larvae. This interaction presumably would be important in extrapolating feeding experiment results to determine impact of Chaoborus predation on zooplankton populations because Chaoborus larvae experience changes in both temperature and prey density and prey type during diel migrations.

Fischer and Lawton (in Edmondson and Winberg 1971) reviewed the different ways in which feeding rates can be expressed and stated that dry weight and its calorific equivalent eaten per unit time by individual predators of known size is the best means of expressing food intake. The <u>in situ</u> feeding experiments performed in this study monitored ingestion rates (in terms of carbon) of the four

instars of <u>C</u>. <u>flavicans</u> as affected by food concentration and temperature. Use of naturally occurring proportions of prey types in <u>in situ</u> incubations as opposed to single prey species experiments performed by Fedorenko (1975) hopefully provided more realistic estimates of natural feeding by <u>Chaoborus</u> larvae.

99

As found by Fedorenko (1975) ingestion rates of C. flavicans larvae were proportional to food concentrations (fig. 19). The fact that older instars ingested more food than younger instars at the same initial food density reflects their increasing body size and consequently, their increasing ability to consume more food. All instars were presented with a substantially wide range of prey sizes. Younger instars consumed only smaller prey organisms (fig.18). Consequently their ingestion rates were much lower than those of older instars at the same initial food concentration (fig. 19). Proportionately more feeding by instars III and IV occurred in the epilimnion than in the hypolimnion at the highest experimental food concentrations (fig. 19). At low food concentrations, differences between feeding rates in the epilimnion and hypolimnion for a specific instar were This implies that the slopes of the epilimnetic and lower. and hypolimnetic feeding curves of a particular instar should be different but an analysis of covariance revealed no difference in slopes (table 5). This means that differences in

epilimnetic and hypolimnetic feeding rates were equal at all experimental food concentrations. Temperature had a significant effect on feeding rates. Feeding rates of C. flavicans instars were consistently higher in the epilimnion than they were in the hypolimnion. However, the effect of temperature on feeding rates could not be quantified in this study due to the experimental design. Incubation experiments were performed either in the epilimnion or in the hypolimnion. In each case, temperature variation over the course of experiments on a particular instar was small but there was a large temperature difference between the epilimnion and hypolimnion. Consequently, a multiple regression analysis of ingestion rate on food concentration and temperature in each environmental situation showed that temperature was a non-significant factor. Hence a simple regression of ingestion rate on food concentration was calculated for the epilimnion and for the hypolimnion. However the temperature differences between the epilimnion and hypolimnion obviously caused differences between the feeding rates in the eipilimnion and hypolimnion. More information about Chaoborus feeding would have been acquired if feeding experiments had been conducted at more depths in the lake. This experimental design would have given rise to a multiple regression equation of ingestion rate on food concentration and temperature for each instar, allowing determination of

temperature X food density interaction. Bell and Ward (1970) conducted experiments relating incorporation rates of <u>Daphnia pulicaria</u> to food concentration and temperature. Their experimental design allowed them to determine whether or not the independent variables interacted. Bell and Ward's experimental design would have been more appropriate in this study.

Estimated a values in the epilimnetic and hypolimnetic feeding equations theoretically represent ingestion rates when food concentration is equal to 0. It is interesting to observe that a values were always higher in the hypolimnetic equation than they were in the epilimnetic equation for all instars except instar IV. These differences seem to imply that for instars I to III, a higher initial food concentration was required to initiate feeding at lower temperatures. In instar IV, feeding at a lower temperature was initiated by a food concentration lower than that required to initiate feeding at a higher temperature. Fourth instar C. flavicans occurred deeper in the lake during daytime than previous instars. Fourth instars also exhibited the most extensive diel vertical migrations. Since it would be energetically advantageous for fourth instars to maximize ingestion, initiation of feeding at lower food concentrations would be advantageous in spite of low hypolimnetic temperatures.

Because body size of C. flavicans instars increased

during the course of feeding experiments on each instar, feeding intensities of the four instars were calculated. Feeding intensities were highest in first instars and declined as age and size of larvae increased (fig.20). This trend reflects the adaptive strategy of Chaoborus feeding. Considerable numbers of first instars of a new generation must survive if the species is to continue its existence in the lake. By optimizing their feeding, Chaoborus first instars increase their developmental rate and thus are ready to become larger instars (capable of consuming a wider size range and types of food) sooner than they would if their feeding intensity was low. Higher feeding intensity of younger instars would tend to increase the probability of survival of the population and thus counteract probability of extinction reflected by high mortality rates of younger instars (fig. 15). Decreasing feeding intensities in older instars are due to the increasing diversity of food types and sizes that they consume. If older instars can consume more types and sizes of prey, then they do not have to feed as intensively as young instars whose diet is relatively restricted. Also the more extensive diel migrations of older instars will increase the numbers of prey that they encounter so they can afford to feed less intensively at specific depths.

The feeding experiments performed in this study

represent an initial attempt to estimate feeding rates of C. flavicans larval instars under natural conditions and thus are burdened with many errors. Natural variation in prey densities used to estimate initial and final food concentrations caused considerable deviations of many points on the feeding curves. Clumps of phytoplankton growing inside feeding chambers and retained during filtration could have caused underestimates of feeding rates. Contamination of glass fiber filters during processing and analysis, variations in feeding rates of individual C. flavicans larvae, growth, reproduction and death of prey organisms during incubations, crop eversion by experimental larvae during handling, sinking of prey to the bottom of feeding chambers and other factors are sources of error unaccounted for in this Replication of experiments would have improved prestudy. This vast array of possible sources of error miticision. gated against extrapolating the feeding data to estimate the impact of Chaoborus predation on the zooplankton populations of West Blue Lake as Fedorenko (1975) did.

<u>C. flavicans</u> first instars consumed a maximum of about 70% of their body weight per day at high food concentrations (fig.20). The amount of food ingested as a percentage of larval body weight declined in successive instars as well as with decreasing food concentrations within each instar. These estimates are higher than those observed by

Kajak and Ranke-Rybicka (1970). They estimated that maximum daily food consumption of fourth instar <u>C</u>. <u>flavicans</u> larvae was 12.5% of their body weight. However, Kajak and Ranke-Rybicka used a high predator density in their experiments. This could have increased competition between larvae, resulting in reduced feeding rates. Experiments performed by Kajak and Ranke-Rybicka lasted six hours during the day but Kajak and Ranke-Rybicka observed that <u>Chaoborus</u> larvae fed more at night. This could have caused an underestimate of daily food consumption.

Energy loss due to respiration is a major factor that affects <u>Chaoborus</u> production. Factors that increase respiration indirectly decrease net productivity.  $0_2$  uptake rates of West Blue Lake <u>Chaoborus</u> fourth instars (fig. 16) were substantially higher than  $0_2$  uptake rates of <u>C</u>. <u>trivittatus</u> fourth instars. <u>C. trivittatus</u> consumed 0.48, 0.95, 1.0, 1.25 and 2.0 µl  $0_2$  larva<sup>-1</sup> hour<sup>-1</sup> at 5, 10, 15, 20 and 25°C respectively (Swift 1974). Discrepancies may be due to different respirometers, different larval sizes and intraspecific differences.

 $0_2$  uptake rates of <u>C</u>. <u>flavicans</u> instars II and III increased linearly while  $0_2$  uptake rates of fourth instars and pupae increased exponentially with temperature (fig.16). Swift(1974) and Berg and Jonasson (1965) both stated that respiration of <u>Chaoborus</u> fourth instars increases linearly with temperature whereas respiration of fourth instars increased exponentially in this study (fig. 16). Swift (1974) indicated the possibility of a "plateau" in his graph of 0<sub>2</sub> uptake versus temperature. Because insects are poikilothermic, one would expect a linear relationship of their respiration and temperature as well as a linear relationship of their respiration rate and body weight. In this study, only the second and third instars showed a linearly increasing respiration rate with increasing temperature. The nonlinear increase of respiration rate of fourth instars and pupae could reflect a behavioural control of respiration. Perhaps at high temperatures, larvae and pupae are much more active than they are at low temperatures.

Berg and Jonasson (1965) determined that at  $8^{\circ}C$  and  $20^{\circ}C$ , <u>C</u>. <u>flavicans</u> larvae consumed 6.0 µl 0<sub>2</sub> gm.<sup>-1</sup> hour<sup>-1</sup> and 21.4 µl 0<sub>2</sub> gm.<sup>-1</sup> hour<sup>-1</sup>. These results are **a** bit higher than 0<sub>2</sub> uptake per unit body weight of <u>C</u>. <u>flavicans</u> fourth instars at comparable temperatures (fig.17).

It is difficult to relate the results of laboratory studies of respiration to the natural situation. <u>Chaoborus</u> larvae experience a wide daily and seasonal temperature change due to diel migrations and their respiration must alter accordingly. Duval and Geen (1975) demonstrated a diel circadian rhythm in the respiration rate of Eunice Lake zooplankton at various temperatures. Such factors must be

evaluated before one can include them in energy budget calculations.

106

Productivity of <u>C. flavicans</u> in West Blue Lake

The first major fraction of yearly production of  $\underline{C}$ . <u>flavicans</u> larvae that occurred in early July was due to the extremely high numbers of newly-hatched larvae. In spite of progressively larger weight increments in successive instars, production declined after early July because larval abundance quickly decreased.

Another major fraction of production seemed to occur during the winter (fig. 15). However, fourth instars overwinter in diapause and their weight remains constant or decreases slightly during this time (Jonasson 1972). Thus the large fraction of production that seemed to occur between October 6, 1974 and May 14, 1975 in reality probably occurred over a much shorter time interval in spring when larvae emerged from sediments and resumed feeding.

Pupal crop is represented by the area between the x - axis and an imaginary line drawn from the lowest larval density, parallel to the x - axis of the Allen curve (fig. 15) (Nees and Dugdale 1959). This area is insignificant compared to the rest of the area under the Allen curve. Low pupal productivity can be attributed to irregularly fluctuating pupal weights (fig. 12). Errors associated with estimating both density and weight of <u>Chaoborus</u> larvae are inherent in the Allen curve. The Allen curve may overestimate <u>Chaoborus</u> productivity because smaller instars are under-represented in dry weight samples. The Allen curve may also underestimate production due to avoidance of the plankton trap by larvae and loss of larvae, especially young instars, during the processing of samples.

Because instar densities and weights were monitored weekly, it was possible to calculate weekly production estimates according to the Pechen-Shuskina formula for all C. flavicans instars (table 2). Since no newly-hatched first instars occurred at sampling stations on July 1, the first density shown in table 2 was 0. In reality, there were many newly-hatched instars, but they were inshore and had not yet drifted out to the pelagic zone of West Blue Lake. If the density of newly-hatched first instars calculated from fecundity data to provide the first point on the Allen curve had been used in the Pechen-Shuskina calculation, weekly production of instar I between July 1 and July 8 on table 2 would have been 233 mg. dry weight  $m.^{-2}$  week<sup>-1</sup>. This would have increased the mean weekly production of instar I to 70.6 mg. dry weight m.<sup>-2</sup> week<sup>-1</sup>. Mean weekly production of third instar C. flavicans was relatively high (table 2). This was partly due to an accelerated growth rate of third

instars (fig. 13) and the aberrant numerical density estimated on Aug. 12 (fig.15). Assuming that the mortality rate of <u>C</u>. <u>flavicans</u> larvae was constant, the density of larvae recorded on Aug. 12 was too high. This could have been due to sampling a population whose distribution is highly contagious. The relatively high production value of fourth instars (table 2) probably overestimated their true production for the same reason stated in the discussion of the Allen curve. Relatively low productivity of second instars was due to rapidly declining abundance and relatively small weight increments.

The Pechen-Shuskina formula provided a production estimate that was only 91 mg. dry weight m.<sup>-2</sup> year<sup>-1</sup> higher than the Allen curve production estimate in spite of the fact that the two production estimates were based on different sampling schemes and different types of calculations.

Although the Pechen-Shuskina method is more tedious and time-consuming than the Allen curve method, it eliminates the under-representation of small instars associated with the Allen curve. Unlike the Allen curve, the Pechen-Shuskina formula provides information about production of each life history stage of a cohort. The calculation of production by each instar according to the Pechen-Shuskina method is exactly the same as plotting and calculating the area under an Allen curve for each instar. Presumably, if the relative proportions of different instars in dry weight samples had been similar to true relative proportions of different instars in the lake, Allen curve and Pechen-Shuskina production estimates would have been almost equal. Thus the discrepancy between the two production estimates is due to induced or methodological differences. Theoretically, there is no real difference between the Allen curve production and Pechen-Shuskina production of a cohort because the total production of a cohort (estimated by the Allen curve) is equal to the sum of production values of each life history stage of that cohort (estimated by the Pechen-Shuskina formula).

If the initial density of newly-hatched first instars shown on the Allen curve had been used in the Pechen-Shuskina calculations, first instars would have had the highest production: biomass ( $^{P}/_{B}$ ) ratio. The  $^{P}/_{B}$  ratio corresponds to the turnover rate and indicates what part of the biomass of a population will be replaced during a unit of time. Decreasing  $^{P}/_{B}$  ratios of successive <u>C</u>. <u>flavicans</u> instars (table 2) reflect slower developmental times of instars stated on page 16.

P/B ratios of the <u>C</u>. <u>flavicans</u> larval cohort irrespective of instar decreased during the first summer and winter of the 1974-75 generation and then increased in May as overwintering larvae emerged from sediments and began feeding (table 4). The slight decrease in P/B ratios after

the end of May probably represents to some degree the "loss" of larvae as they pupated.

Few estimates of Chaoborus biomass and productivity are reported in the literature. Parma (1971) calculated the biomass, production and <sup>P/B</sup> ratios of overwintering benthic C. flavicans larvae in Lake Vechten, Holland, for three years. Yearly biomass ranged from 2.9 kg. dry weight ha.<sup>-1</sup> to 3.8 kg. dry weight ha. -1 according to one of Parma's esti-According to Parma's Allen curve, biomass of benthic mates. Chaoborus larvae ranged from 5.3 to 7.3 kg. dry weight ha. -1. Parma did not explain the discrepancy between these two esti-Net production of overwintering fourth instars in mates. Lake Vechten was 70-90 kg. wet weight ha.<sup>-1</sup> year<sup>-1</sup>.  $P/_B$ ratios based on wet weights ranged from 2.1 to 2.4. Biomass of overwintering C. flavicans larvae in West Blue Lake was 911.7 mg. dry weight m.<sup>-2</sup> for the period from Oct. 16, 1974 to May 14, 1975 (table 2). When converted to Parma's units, this biomass estimate becomes about 90 kg. ha. -1 which is much higher than Parma's biomass estimates. However, converting the West Blue Lake estimate to kg. ha. $^{-1}$  is not valid because Chaoborus larvae were not distributed homogeneously throughout the lake. For instance, Chaoborus larvae did not occur in the benthos of station 2 (fig.5) and their densities varied from station to station (fig.4). Biomass and productivity estimates in this study were based on data from only

3 relatively deep stations. Extrapolation of these estimates to extensive areas of the lake is deemed unrealistic.

In Lake Mendota, winter biomass of Chaoborus larvae (558 kg. ha.<sup>-1</sup>) was five times greater than that of  $\underline{C}$ . flavicans in West Blue Lake (Juday 1921). Borutzky (1939) calculated Chaoborus biomass to be 17.5 kg. ha.<sup>-1</sup> for a one month period. Deevey (in Brooks and Deevey 1963) estimated that Chaoborus larvae produce 15-28 kg. ha. -1 year -1 in some American lakes. The above biomass and productivity estimates are based on different sampling intervals in different lakes and the use of different samplers and analytical methods. Thus, a comparison of the biomass and productivity of West Blue Lake C. flavicans to the above estimates is of little value. Parma (1971) stated ". . . I have no information about the rate of growth and mortality of the younger larval stages [instars I, II and III] and thus the production of [these] larvae is unknown." Parma's (1971) Allen curve contained four points whereas the Allen curve in this study contains 18 points. These types of differences make it difficult to objectively compare production parameters of different studies. Jonasson (1972) calculated biomass and productivity of C. flavicans larvae (irrespective of instar) based on monthly samples. Biomass of overwintering C. flavicans larvae in Lake Esrom ranged from 1878 to 2969 mg. dry weight m.<sup>-2</sup> except for one year in which the Chaoborus population decreased tremendously for unknown reasons.

Biomass of overwintering C. flavicans larvae in Lake Esrom was at least twice as large as that of overwintering larvae in West Blue Lake. Yearly production estimates of C. flavicans larvae in Lake Esrom were 1495.11, 262.93 and 2652.5 mg. dry weight m.  $^{-2}$  year  $^{-1}$  for 1953, 1954 and 1955 respectively. The production of Lake Esrom Chaoborus larvae during 1953 and 1955 was very similar to production of C. flavicans larvae in West Blue Lake. Because old Chaoborus generations in Lake Esrom ended in July, one of the highest production periods occurred in autumn when young larvae hatched and grew. From September to October, C. flavicans production in Lake Esrom was 241.24, 56.82 and 366.66 mg. dry weight m.<sup>-2</sup> month<sup>-1</sup> for 1953, 1954 and 1955 respectively. Winter production was negative during the three years of observations. In spring, production of Lake Esrom Chaoborus increased to 74 - 864 mg. dry weight m.<sup>-2</sup> month<sup>-1</sup>. No other estimates of Chaoborus production are reported in the literature although many workers (Fedorenko and Swift 1972, McGowan 1974, Lewis 1975) seem to have all the data necessary to plot Allen curves.

<u>Chaoborus</u> larvae are not distributed homogeneously; their distribution is highly contagious (McGowan 1974). Therefore caution should be exercised in extrapolating <u>Chaoborus</u> production parameters beyond areas greater than a few square meters.

Although C. flavicans larvae are among the largest

members of the zooplankton community in West Blue Lake, they contribute less net production to the ecosystem than copepods and cladocerans. Ward (unpublished) estimated that yearly production of Daphnia pulicaria ranged from 2530 mg. C  $m_{\star}^{-2}$ year<sup>-1</sup> to 4090 mg.  $C m.^{-2}$  year<sup>-1</sup> during 1972 to 1974. Thus, yearly production of Daphnia is 2 to 3.5 times greater than Chaoborus production in West Blue Lake. Patrick (unpublished) estimated that production of Cyclops bicuspidatus in West Blue Lake was 2650 mg.  $C m.^2 year^{-1}$  during 1974-75. Production of <u>C</u>. <u>bicuspidatus</u> was about 1500 mg. C m.<sup>2</sup> year<sup>-1</sup> higher than that of Chaoborus larvae. Production of D. pulicaria and C. bicuspidatus was expected to be higher than Chaoborus production because Chaoborus is strictly carnivorous and thus is in a higher trophic level. Conversely, Chaoborus production was higher than walleye production (25 mg. C  $m.^2$  year<sup>-1</sup>) in West Blue Lake (Ward and Robinson 1974) because walleye are in the highest trophic level of the West Blue Lake ecosystem.

Relatively low productivity of <u>C</u>. <u>flavicans</u> larvae can be attributed in part to some features of their life history strategy and feeding characteristics. Abundance of <u>C</u>. <u>flavicans</u> in West Blue Lake is partly limited by the fact that <u>Chaoborus</u> is univoltine. In other lakes and ponds, other <u>Chaoborus</u> species are plurivoltine (Meinert 1886, Peus 1934, Miller 1941, Lindquist and Deonier 1942, MacDonald 1956, Snell and Hazeltine 1963, Parma 1969). Abundance of
<u>C. flavicans</u> in West Blue Lake is also partly limited by the fact that each female reproduces only once a year and that the number of eggs laid by each female is much lower than the fecundity reported by Parma (1971). <u>C. flavicans</u> abundance would increase if there were proportionately more females than males. Each female would still have a high probability of being inseminated due to the multiple insemination behavior of males.

High mortality of younger instars reduced abundance greatly during the first few weeks of the new generation and the population remained at a low level of abundance for the rest of the year. High mortality of young Chaoborus larvae can be attributed to the fact that first instars hatched in the littoral zone, moved into the pelagic zone and showed extremely limited diel vertical migrations. This probably subjected them to constant predation from copepods (Parma 1971), amphipods (Anderson and Raasveldt 1974), and fish (Falk 1971). Because first instars remained in the warm epilimnion and fed most intensively, they developed in a relatively short time. Older instars were able to consume more types and sizes of prey and fed less intensively. Older instars avoided predation in the epilimnion to some degree by remaining deeper in the lake during the day and moving towards the surface at night to feed. Kajak and Ranke-Rybicka (1970) reported that Chaoborus larvae feed more at

night than during the day. However, because older instars moved deeper into the lake, they developed slower, fed less intensively and consumed less food than they would have consumed at higher temperatures. Large depth differences between depth-weighted density peaks of <u>Chaoborus</u> larvae and their prey, <u>Cyclops</u> and <u>Daphnia</u>, seem to indicate that predation of the whole population of <u>Chaoborus</u> on <u>Cyclops</u> and <u>Daphnia</u> populations was reduced by spatial and temporal segregation of predator and prey during diel vertical migrations (fig.6).

Respiration rates of <u>C</u>. <u>flavicans</u> larvae were substantially high especially at higher temperatures. Energy loss by respiration was the energy that larvae used in their metabolic processes and represented the cost of living. Jonasson (1972) converted oxygen consumption of benthic <u>C</u>. <u>flavicans</u> larvae to caloric values. He estimated that the average annual population respiration was 51.2 kcal. m. year . McNeill and Lawton (1970) showed that aquatic invertebrates respire 1.1 to 5.5 times more energy than they produce on a yearly basis. Thus a substantial amount of the potential productivity of <u>Chaoborus</u> is used in respiration, reducing their net production.

This study represents an initial attempt to relate <u>Chaoborus</u> productivity in West Blue Lake to the life history, population dynamics and feeding ecology of <u>Chaoborus</u>. Obvious refinements and additional information about Chaoborus

excretion, egestion, and assimilation would provide a complete energy budget of <u>C</u>. <u>flavicans</u> which could then be inserted into the energy flow and food web patterns of the West Blue Lake ecosystem.

#### LITERATURE CITED

Allen, K. R. 1951. The Horokiwi Stream, a study of a trout population. N.Z. Mar. Dept. Fish. Bull. 10: 231p.
Alverdes, F. 1926. Corethra - und Ephemeridenlarven nach

> Unterbrechung ihrer Bauchganglienkette. Z. Vergl. Physiol. 3: 558-594.

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

predation and the possible effects of <u>Gammarus</u> and <u>Chaoborus</u> feeding on the zooplankton composition in some small lakes and ponds in western Canada. Can. Wildl. Serv. Occas. Pap. 18: 26p.

- Bardenfleth, K. S., and R. Ege. 1916. On the anatomy and physiology of the air-sacs of the larva of <u>Corethra</u> <u>plumicornis</u>. Vidensk. Medd. Dansk naturhist. Foren. 67: 25-42.
- Bell, R. K., and F. J. Ward. 1970. Incorporation of organic carbon by <u>Daphnia pulex</u>. Limnol. Oceanogr. 15: 713-726. Berg, K. 1937. Contribution to the biology of <u>Corethra</u> Meigen (<u>Chaoborus</u> Lichtenstein). Biol. Meddr. 13:

1-101.

- Berg, K., and I. C. Petersen. 1956. Studies on the humic acid Lake Gribso. Folia Limnol. Scan. 8: 1-273.
- Berg, K., P. M. Jonassen, and K. W. Ockelmann. 1962. The respiration of some animals from the profundal zone of a lake. Hydrobiologia 19: 1-40.

- Berg, K., and P. M. Jonassen. 1965. Oxygen consumption of profundal lake animals at low oxygen content of the water. Hydrobiologia 26: 131-143.
- Biette, R. M. 1969. Life history and habitat differences between <u>Gammarus lacustris</u> Sars and <u>Hyallela azteca</u> (Saussure) in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 97p.
- Bonomi, G. 1962. La dinamica produttiva delle principali popolazioni macrobentoniche del Lago di Varese. Memorie Ist. Ital. Idrobiol. 15: 207-254.
- Borutzky, E. V. 1939. Dynamics of the total benthic biomass in the profundal of Lake Beloie. Trudy Limnol. Sta. Kosine. 22: 196-218.
- Brooks, J. L. and E. S. Deevey. 1963. New England in: Frey, Limnology in North America. Madison, The Univ. Wisconsin Press. 117-162.
- Brundin, L. 1949. Chironomiden und andere Bodentiere der sudschwedischen Urgebirgsseen. Rept. Inst. Freswater Res. Drottningholm. 30: 1-914.

Campbell, R. S. 1935. A study of the common sucker,

<u>Catostomus commersoni</u> (Lacepede) of Waskesiu Lake. M. A. Thesis. Dept. Biol. Univ. Saskatchewan, Saskatoon, Sask. 48p.

Chapman, R. F. 1969. The insects: structure and function. American Elsevier Publishing Co. New York. 819p. Chaston, I. 1969. The light threshold controlling the vertical migration of <u>Chaoborus punctipennis</u>

in a Georgia impoundment. Ecology 50: 916-920.

- Cook, E. F. 1956. The nearctic Chaoborinae (Diptera: Culicidae). Tech. Bull. Minn. agric. exp. Stn. 218: 1-102.
- Cook. E. F. 1965. Family Chaoboridae. In: A. Stone, <u>et al.</u>, A catalog of the Diptera of America north of Mexico. USDA agric. Handb. 276: 102-105.
- Crossman, E. J., and P. A. Larkin. 1959. Yearling liberations and change of food as affecting rainbow trout yield in Paul Lake, British Columbia. Trans. Amer. Fish. Soc. 88: 36-44.
- Cushing, D. H. 1951. The vertical migration of planktonic crustacea. Biol. Rev. Cambridge Phil. Soc. 26: 158-192. David, P. M. 1961. The influence of vertical migration on

speciation in the oceanic plankton. Syst. Zool.

10: 10-16.

- Deonier, C. C. 1943. Biology of the immature stages of the Clear Lake gnat. Ann. Entomol. Soc. Am. 36: 383-388.
- Dimick, R. E., and D. C. Mote. 1934. A preliminary survey of the food of Oregon trout. Oregon State Coll. Agric. Exp. Sta. Bull. 323: 23p.
- Dodson, S. I. 1972. Mortality in a population of <u>Daphnia</u> rosea. Ecology 53: 1011-1023.

- Duhr, B. 1955. Uber den chemischen Sinn, die Darmperistaltik und die Bildung der peritrophischen Membran der Corethralarve (<u>Chaoborus crystallinus</u> De Geer). Zool. Jb., Abt. Allg. Zool. Physiol. 65: 315-333.
- Duval, W. S., and G. H. Geen. 1975. Diel rhythms in the feeding and respiration of zooplankton. Verh. Internat. Verein. Limnol. 19: 518-523.
- Dyar, H. G. 1905. Our present knowledge of North American corethrid larvae. Proc. Entomol. Soc. Wash. 7: 13-16.
- Edmondson, W. T. and G. G. Winberg. 1971. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, Blackwell, Oxford. 358p.
- Eggleton, F. E. 1931. A limnological study of the profundal bottom fauna of certain freshwater lakes. Ecol. Monogr. 1: 231-332.
- Falk, M. R. 1971. Food habits, gastric digestion and food consumption rates of yellow perch, <u>Perca fluviathilis</u> <u>flavescens</u> (Mitchill) in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Manitoba 175p.
- Fedorenko, A. Y. 1975. Instar and species-specific diets
  in two species of <u>Chaoborus</u>. Limnol. Oceanogr.
  20: 238-249.

Fedorenko. A. Y. 1975. Feeding characteristics and predation

impact of Chaoborus (Diptera, Chaoboridae) larvae

in a small lake. Limnol. Oceanogr. 20: 250-258. Fedorenko. A. Y., and M. C. Swift. 1972. Comparative

biology of Chaoborus americanus and Chaoborus

trivittatus in Eunice Lake, British Columbia.

Limnol. Oceanogr. 17: 721-735.

Felt, E. P. 1904. Mosquitoes or Culicidae of New York State. Bull. N.Y. State Mus. 79: 241-400.

- Frankenberg, G. von. 1915. Die Schwimmblasen von <u>Corethra</u>. Zool. Jahrb. Physiol. 35: 505-592.
- Freeman, P. 1962. Notes on Chaoboridae (Diptera: Nematocera), with descriptions of a new genus and of two new species from Australia and Africa. Proc. Roy.

Ent. Soc. London. 31: 41-43.

Froldwa, S. L. 1929. Die Geschlechtschromosomen bei

Chaoborus plumicornis F. (Corethra plumicornis F.).

Z. Zellforsch. mikrosk. Anat. 9: 66-82.

Gersch, M. 1952. Experimentelle Untersuchen iiber den Verdauungstraktus der Larve von Chaoborus

(<u>Corethra</u>). Z. Vergl. Physiol. 34: 346-369.

Gersch, M. 1955. Untersuchungen iiber Auslosung und Steuerrung der Darmbewegungen bei der Larve von <u>Chaoborus</u> (<u>Corethra</u>). Biol. Zentralbl. 74: 603-628. Hamilton, A. L., W. Burton, and J. F. Flannigan. 1970.

A multiple corer for sampling profundal benthos. J. Fish. Res. Board Can. 27: 1867-1869.

Hardy, A. C. 1956. The open sea. Its natural history: the world of plankton. Collins, London. 335p. Hardy, A. C., and E. R. Gunther. 1935. The plankton

of the South Georgia whaling grounds and adjacent waters, 1926-1927. Discovery Rept. No. 11. 456p. Herms, W. B. 1937. The Clear Lake gnat, Bull. Calif. Agr. Exp. Sta. 607: 1-22.

Hunt, B. P. 1958. Limnetic distribution of <u>Chaoborus</u> larvae in a deep Florida lake (Diptera). Florida Entomologist 41: 111-116.

Hutchinson, G. E. 1967. A treatise on limnology. Vol. II. Introduction to lake biology and the limnoplankton. John Wiley and Sons, New York. 1115p.

James, H. G., and B. C. Smith. 1958. Observations on three species of <u>Chaoborus</u> Licht. (Diptera: Culicidae) at Churchill, Manitoba. Mosquito News 18: 242-248. Jonasson, P. M. 1972. Ecology and production of the

profundal benthos in relation to phytoplankton in Lake Esrom. Oikos Suppl. 14: 1-148.

Juday, C. 1921. Observations on the larvae of <u>Corethra</u> <u>punctipennis</u> Say. Biol. Bull. mar. biol. Lab., Woods Hold. 40: 271-286.

- Judd, W. W. 1957. A study of the population of emerging and littoral insects trapped as adults from tributary water of the Thames River at London, Ontario. Amer. Midland Natur. 58: 394-412.
- Judd, W. W. 1960. A study of the population of insects emerging as adults from South Walker Pond at London, Ontario. Amer. Midland Natur. 63: 194-210.
- Judd, W. W. 1961. Studies of the Byron Bog in southwestern Ontario. XII. A study of the opulation of insects emerging as adults from Redmond's Pond in 1957. Amer. Midland Natur. 65: 89-100.
- Kajak, Z., and B. Ranke-Rybicka. 1970. Feeding and predation efficiency of <u>Chaoborus flavicans</u> Meigen (Diptera, Culicidae) larvae in eutrophic and dystrophic lake. Pol. Arch. Hydrobiol. 17: 225-232.
- Kelso, J. R. M. 1971. Population parameters and bioenergetic demands of walleye, <u>Stizostedion vitreum</u> vitreum (Mitchell) in relation to their trophic dynamic ecology, West Blue Lake, Manitoba. Ph.D. Thesis. Univ. Manitoba, Winnipeg, Man. 146p.
- Kerfoot, W. B. 1970. Bioenergetics of vertical migration. Am. Nat. 104: 529-546.
- Kolmer, W. 1904. Eine Beobachtung iber vitale Farbung bei <u>Corethra plumicornis</u>. Biol. Zbl. 24: 221-223.

Krogh, A. 1911. On the hydrostatic mechanism of the <u>Corethra</u> larva with an account of methods of microscopical gas analysis. Skand. Arch. Physiol. 25: 183-203.

Lang, K. 1931. Faunistish-okologische Untersuchungen in einigen seichten ologotrophen bzw. dystrophen Seen in Sudschweden. Acta Univ. Lund. N.F. 27: 1-173.

- LaRow, E. J. 1968. A persistent diurnal rhythm in <u>Chaoborus</u> larvae. I. The nature of the rhythmicity. Limnol. Oceanogr. 13: 250-256.
- LaRow, E. J. 1969. A persistent diurnal rhythm in <u>Chaoborus</u> larvae. II. Ecological significance. Limnol. Oceanogr. 14: 213-218.
- Lewis, W. M. 1975. Distribution and feeding habits of a tropical <u>Chaoborus</u> population. Verh. Internat. Verein. Limnol. 19: 3106-3119.
- Lindquist, A. W., and C. C. Dednier. 1942. Flight and oviposition habits of the Clear Lake gnat. J. Econ. Entomol. 35: 411-145.

Lindquist, A. W., C. C. Deonier and J. E. Hancey. 1943. The relationship of fish to the Clear Lake Gnat in Clear Lake, California. Calif. Fish Game. 29: 193-202.

Lundbeck, J. 1926. Die Bodentierwelt Norddeutscher Seen. Arch. Hydrobiol., Suppl. 7: 1-470.

- MacDonald, W. W. 1956. Observations on the biology of chaoborids and chironomids in Lake Victoria and on the feeding habits of the "elephant-snout fish" (<u>Mormyrus kannume</u> Forsk.). J. Anim. Ecol. 25: 36-53. Main, R. A. 1953. A limnological study of Chaoborus (Diptera)
  - in Hall Lake, Washington. M.Sc. Thesis, Univ. Wash. 106p.
- Malveg, K. W. 1966. An ecological study of <u>Chaoborus</u>. Ph.D. dissertation, Univ. Wis., Madison. 255p.
- Manteifel, B. P. 1959. The adaptive significance of the periodic migrations of water organisms. [in Russian]. Vop. Ikhtiol. 13: 3-15.
- Martin, N. V. 1954. Catch and winter food of lake trout in certain Algonquin Park Lakes. J. Fish. Res. Board Canada. 11: 5-10.
- Mauchline, J., and T. R. Fisher. 1969. The biology of euphausiids. In F. S. Russell and C. M. Younge, [eds.]. Advances in marine biology. Vol. 7. Academic Press, London. 454p.
- McGowan, L. M. 1974. Ecological studies on <u>Chaoborus</u> (Diptera, Chaoborudae) in Lake George, Uganda. Freshwat. Biol. 4: 483-505.
- McLaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Bd. Can. 20: 685-727.

McLaren, I. A. 1974. Demographic strategy of vertical

migration by a marine copepod. Am. Nat. 108: 91-102.

McNeill, S., and J. H. Lawton. 1970. Annual production and

respiration in animal populations. Nature 225: 472-474. Meinert, F. 1886. De eucephale Myggelarver. Mem. Acad. Sci. Lett. Danemark. 3: 369-493.

Miall, L. C. 1903. The natural history of aquatic insects. London and New York: MacMillan. 395p.

Miller, R. B. 1941. Some observations on <u>Chaoborus</u> <u>punctipennis</u> Say (Diptera, Culicidae). Can. Entomol. 73: 37-39.

Montshadsky, A. S. 1945. On the mechanism of digestion in the larvae of <u>Chaoborus</u> (Diptera: Culicidae). [In Russ., Engl. summary.]. Zool. Zh. 24: 90-98.

Muttkowski, R. A. 1918. The fauna of Lake Mendota: a qualitative and quantitative survey with special reference to the insects. Trans. Wis. Acad. Sci. Arts Lett. 19: 374-482.

Nees, J., and R. C. Dugdale. 1959. Computation of production for populations of aquatic midge larvae. Ecology 40: 425-430.

Northcote, T. G. 1964. Use of a high-frequency echo sounder to record distribution and migration of <u>Chaoborus</u> larvae. Limnol. Oceanogr. 9: 87-91. Northcote, T. G., and H. W. Lorz. 1966. Seasonal and diel

changes in food of adult Kokanee (<u>Onchorhynchus</u> <u>nerka</u>) in Nicola Lake, British Columbia. J. Fish. Res. Board Canada. 23: 1259-1263. Parma, S. 1969. The life cycle of <u>Chaoborus</u> crystallinus (De Geer) (Diptera: Chaoboridae) in a Dutch pond. Verh. internat. Verein. Theor. angew. Limnol. 17: 888-894.

Parma, S. 1971. <u>Chaoborus falvicans</u> (Meigen) (Diptera, Chaoboridae): an autecological study. Ph.D. Thesis. University of Groningen, 128p.

Pearre, S. 1973. Vertical migration and feeding in <u>Sagitta</u> elegans Verrill. Ecology 54: 300-314.

Perttunen, V., and K. Lagerspetz. 1956. On the temperature acclimation of the heartbeat and of the onset of muscle tremor in <u>Corethra plumicornis</u> (Diptera, Culicidae) larvae. Archum Soc. Zool. Bot. Fenn. " "Vanamo". 11: 65-70.

Peus, F. 1934. Zur Kenntnis der Larven und Puppen der Chaoborinae (Corethrinae auct.). Arch. Hydrobiol. 27: 641-668.

Peus, F. 1967. Ptychopteridae, Chaoboridae, Dixidae. In: J. Illies (ed.), Limnofauna Europaea. 330-334. Phillipson, J. 1964. A miniature bomb calorimeter for small

biological samples. Oikos 15: 131-139.

Prokesova, V. 1959. Hydrobiological research of two

naturally polluted pools in the woody inundation area of the Elbe. Acta Soc. Zool. Bohemoslov. 23: 34-69.

Prokesova, V. 1963. Resistance adaptability of Chaoborus

larvae (Diptera) under anaerobic conditions in hydrogen sulfide. Acta Soc. Zool. Bohemoslov. 27: 178-184.

- Rai, K. S. 1963. A comparative study of mosquito karyotypes. Ann. Entomol. Soc. Amer. 56: 160-170.
- Reaumur, F. A. F. 1740. Memovies pour servir a l'histoire des Insectes. Histoire des Tipules. 5: 40-43.
- Remm, H. J. 1957. Zur Faunistik und Okologie der Culiciden (Diptera, Culicidae) der Estnischen SSR. Entomol. Obozr. 36: 148-160.
- Ricker, W. E. 1932. Studies of speckled trout (<u>Salvelinus</u> <u>fontinalis</u>) in Ontario. Univ. Toronto Stud. Biol. Ser. 36, Publ. Ont. Fish. Res. Lab. 44: 67-110.
- Roth, J. C. 1968. Benthic and limnetic distribution of three <u>Chaoborus</u> species in a southern Michigan lake (Diptera, Chaoboridae). Limnol. Oceanogr. 13: 242-249. Roth, J. C. 1971. The food of <u>Chaoborus</u>, a plankton predator, in a southern Michigan lake. Ph.D. Thesis, Univ. Mich. 94p.
- Saether, O. A. 1970. Nearctic and Palaearctic <u>Chaoborus</u> (Diptera: Chaoboridae). Bull. Bish. Res. Bd. Can. 174: 1-57.
- Saether, O. A. 1972. Chaoboridae. In: Das zooplankton der Binnengewasser. Binnengewasser. 26: 257-280.

Schaller, F. 1949. Osmoregulation und Wasserhaushalt der

- Larve von <u>Corethra plurnicornis</u>, mit besonderer Berucksichtigung der Vorgange am Darmkanal. Z. vergl. Physiol. 31: 684-695.
- Scholander, P. F., C. L. Claff, J. R. Andrews and D. F. Wallach. 1952. Microvolumetric respirometry. J. Gen. Physiol. 35: 375-395.
- Schonfeld, C. 1957. Histophysiologische Untersuchungen zur Verdauungstatigkeit der Muckenlarve <u>Chaoborus</u> (<u>Corethra</u>). Zool. Jb., Abt. Allg. Zool. Physiol. 67: 337-364.
- Sikordwa, A. 1968. The behaviour of <u>Chaoborus</u> Licht. larvae under favourable oxygen conditions. Ekol. Pol. Ser. A. 16: 185-192.

Sikorowa, A. 1973. Morphology, biology, and ecology of species belonging to the genus <u>Chaobarus</u> Lichtenstein (Diptera, Chaoboridae) occurring in Poland [in Polish, English summary]. Zesz. Nauk. Akad. Roln.-Tech.

Olsztynie, Ochr. Wod Rybactwo Srodladowe. 1: 1-121. Skierska, B. 1969. Larvae Chaoborinae (Diptera, Culicidae)

occurring in small water reservoirs. Bull. Inst.

Mar. Med. Gdansk. 20: 101-108.

Sladecek, V. 1952. Les larves du genre <u>Chaoborus (Corethra</u>) dans les eaux de la Boheme. Cas. Nar. Mus., Odd. Prir. 121: 94-102. Slobodkin, L. B., and S. Richman. 1961. Calories/gm in species of animals. Nature 191: 299.

- Snell, J. B., and W. E. Hazeltine. 1963. The use of insecticide to determine the life history of an aquatic gnat <u>Chaoborus astictopus</u>. Ann. Entomol. Soc. Amer. 56: 816-818.
- Staddon, B. W. 1962. The larval excretory system of <u>Chaoborus</u> <u>crystallinus</u> (De Geer) (Diptera: Culicidae). Proc. R. ent. Soc. Lond., A. 37: 99-103.
- Stahl, J. B. 1966. The ecology of <u>Chaoborus</u> in Myers Lake, Indiana. Limnol. Oceanogr. 11: 177-183.
- Stahl, J. B. 1966. Coexistence in <u>Chaoborus</u> and its ecological significance. Invest. Indiana Lakes Streams. 7: 99-113.
- Stone, A. 1956. Corrections in the taxonomy and nomenclature
   of mosquitoes (Diptera, Culicidae). Proc. Ent.
   Soc. Wash. 58: 333-344.
- Swift, M. C. 1974. Energetics of vertical migration in <u>Chaoborus trivittatus</u> larvae. Ph.D. Thesis, Univ. of British Columbia. 142p.
- Swuste, H. F. J., R. Cremer and S. Parma. 1973. Selective predation by larvae of <u>Chaoborus flavicans</u> (Diptera, Chaoboridae). Verh. Internat. Verein. Limnol. 18: 1559-1563.
- Teraguchi, M., and T. G. Northcote. 1966. Vertical distribution and migration of <u>Chaoborus flavicans</u> larvae in Corbett Lake, British Columbia. Limnol. Oceanogr. 11: 164-176.

- Tubb, R. A., and T. C. Dorris. 1965. Herbivorous insect populations in oil refinery effluent holding pond series. Limnol. Oceanogr. 10: 121-134.
- Twinn, C. R. 1931. Observations on some aquatic animal and plant enemies of mosquitoes. Can. Entomol. 63: 51-61.
- Valle, K. J. 1936. Fortgefuhrte Bodenund Tiefentierokobogische - Untersuchungen in einigen sudostfinnischen Seen. Archum Soc. Zool. Bot. Fenn. "Vanamo". 4: 1-45.
- Verbeke, J. 1957. Chaoboridae (Diptera, Nematocera)
  stades immatures et adults. Result. Sci. Explor.
  Hydrobiol. Lacs Kuri, Edouard, Albert (1952-54).
  3: 183-201.
- Ward, F. J., and G. G. C. Robinson. 1974. A review of research on the limnology of West Blue Lake, Manitoba. J. Fish. Res. Board Can. 31: 977-1005.
- Wesenberg-Lund, C. 1914. Bidrag til nogle myggeslaegters, saerlig <u>Mochlonyx</u> og <u>Corethra</u>'s Biologi. Minderskrift i Anledning af Hundredaaret for Japetus Steenstrups Fodsel, no. 34. 25p.
- Wesenberg-Lund, C. 1943. Biologie der Susswasserinsekten. Berlin: Springer Verlag. 682p.
- Wong, B. 1972. Growth, feeding and distribution of yellow perch fry, <u>Perca fluviatilis flavescens</u> (Mitchill), during their first summer in West Blue Lake. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 45p.

Wong, B., and F. J.Ward. 1972. Size selection of Daphnia

pulicaria by yellow perch (<u>Perca flavescens</u>) fry in West Blue Lake, Manitoba. J.Fish. Res. Board Can. 29: 1761-1764.

Wynne-Edwards, V.C. 1962. Animal dispersal in relation to social behaviour. Oliver and Boyd, Edinburgh. 653p.

# APPENDIX A. Rearing Tanks

Two metal containers set into a wooden frame covered with fly screen were used as rearing tanks to study adult emergence, mating and egg-laying (fig. Al). The tanks were located outdoors.

133

15 to 20 gallons of lake water placed in each container were oxygenated with an air pump. Fourth instar larvae and their natural prey were caught with a plankton net and were placed in the tanks. Larvae were allowed to metamorphose and emerge. After egg deposition, adults were collected with an aspirator inserted through the fly screen.

134 Rearing tanks. 1 - screen cover, 2 - air pump, 3 - table, 4 - rearing tank. Fig. Al.



### APPENDIX B. Feeding Chambers

A transparent polyvinyl chloride (PVC) plastic feeding chamber (fig.Bl) was used in <u>in situ</u> incubation experiments to study larval feeding.

Chamber volume was 15 liters. PVC parts were glued together with epoxy cement. Two inch square ventilation openings covered with 73u mesh were cut out of two sides. A section of PVC pipe was fitted into the chamber's bottom. A conical net and collection bucket were fastened to the pipe with a hose clamp. A small opening in the top was plugged with a rubber stopper.

Galvanized "O" rings fastened to the chamber's sides accomodated a rope cradle (fig.B2). A depth-calibrated rope attached to the rope cradle suspended the feeding chamber from a surface float ( fig.B3 ).

Fig. Bl.

Transparent PVC feeding chamber. 1 - rubber plug, 2 - hole, 3 - feeding chamber, 4 - "0" ring for rope cradle, 5 - screencovered opening, 6 - PVC pipe, 7 - hose clamp, 8 - fine mesh conical net, 9 - collection bucket.



Fig. B2. Rope cradle. This cradle is fitted through "0" rings on the sides of the feeding chamber. 1 - "0" ring, 2 - pipe, 3 - "0" ring, 4 - plastic rope, 5 - galvanized disc.



Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope; 3 - rope oradle, 4 - feeding chamber.								Teses.
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope; 3 - rope cradle, 4 - feeding chamber.			· · ·					
Fig. B3. Freeding chamber suspended in the water. 1 - float, 2 - depth-callbrated rope, 3 - rope cradle, 4 - feeding chamber.	138							
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.					·			
Fig. D3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.			· · ·		•			
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope oradle, 4 - feeding chamber.				· · ·				
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.					·			
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.			•	- - -	•			
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.				• • • •				
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.		· ·					••	•
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.		•		н	• • • • • •	· ·		
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.							•	
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.								
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.			•		<b>1</b> .		• • •	
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.				·				
Fig. B3. Feeding chamber suspended in the water. 1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.								
1 - float, 2 - depth-calibrated rope, 3 - rope cradle, 4 - feeding chamber.	Fig.	B3, Feed	ling chamber	suspended in	the water	. *	,	: : :
3 ~ Tope Gradle, 4 ~ feeding chamber.	<b></b>	1 -	float, 2 -	depth-calibrat	ted rope,		•	
		3 -	rope cradie	, 4 - feeding	chamber.			: . *
			•		•		•	21 1
						. ••	•	
						•		
		- 				· · ·		
			· . · · ·					
	v						•	
					· ·			
				· · · · · · · · · · · ·			• •	:
	1				· · · ·	•		
			· · ·		•			•
								1
							•	
					· · · ·			
						•••		
					· · · · ·			•
				· .			•	• •



## APPENDIX C. Trial Feeding Experiment

An experiment to determine the density of <u>C</u>. <u>flavicans</u> larvae needed to produce optimum feeding rates in the 10 1. and 15 1. feeding chambers was performed on June 2, 1975. This experiment also provided an estimate of relative efficiencies of the two types of feeding chambers.

A Wisconsin plankton net (mesh size 73 u) was used to take 20 vertical tows from the bottom to the top of the lake at Station 5. Tow contents were filtered through a 1050 u filter to remove <u>C</u>. <u>flavicans</u> larvae and large <u>D</u>. <u>pulicaria</u>. The filtrate was diluted to 6.875 liters. The diluted filtrate was stirred and divided into eleven 375 ml. aliquots and eleven 250 ml. aliquots. Three 375 ml. aliquots and three 250 ml. aliquots were kept as control samples. One 375 ml. aliquot was poured into each 15 l. chamber.

Varying numbers of fourth instar <u>Chaoborus</u> larvae (table C1) that had been starved for 24 hours were placed in each chamber. Chambers were suspended at 5 m. depth from a float and were incubated for 24 hours.

At the end of the incubation period, midge larvae and remaining food were removed from feeding chambers. In the laboratory, experimental larvae were removed from test samples. Test and control samples were dried at 105°C Table CI. Numbers and densities (no. liter<sup>-1</sup>) of larvae used in trial feeding experiment.

Feeding	Chamber number							
volume	I `	2	3	4	5	6	7	8
15 1.	5(.34)	10(6.7)	15(1)	20(1.34)	25(1.7)	30(2)	35(2.3)	40(2.66)
10 1.	5(.5)	10(1)	15(1.5)	) 20(2)	25(2.5)	30(3)	35(3.5)	40(4)

for 2 days. Dried samples were weighed on a Sartorius balance.

Results (table C2, fig. Cl) indicate that a predator density of about 1.5 to 2 larvae liter  $^{-1}$  produces optimum feeding in the chambers.

A one-way analysis of variance testing the hypothesis that chamber type does not affect feeding of <u>C</u>. <u>flavicans</u> larvae yielded an insignificant F value of 0.012 (P = .05, d.f. = 1, 14).

Feeding		Chamber number							
volume	I.	2	3	4	5	6	7	8	
15 1.	.011	.023	.015	.024	.031	.027	.028	.019	
IO 1.	.015	.019	.027	.026	.021	.019	.020	.015	

Table C2. Amounts of food (mg. larva<sup>-1</sup>) eaten in feeding chambers.

Fig.Cl. Effect of predator density on ingestion in 10 1. and 15 1. feeding chambers.



a series and a series of the series of th The series of the series of

## APPENDIX D.

Benthic Densities of Chaoborus larvae, 1974.

Date	Station	Mean number of <u>Chaoborus</u> per core	deviation	Number $m.^{-2}$
May 20	1	8	3.37	4081.68
· - · ·	5	10.25	3.59	5229.65
May 27	1	6.25	3.77	3188.81
	5	7.75	4.11	3954.13
June 3	1	8.5	2.08	4336.79
	5	7.25	3.40	3699.02
June 10	) 1	3.50	2.38	1785.74
	5	4.25	2.75	2168.39
June 17	1	1.00	0.82	510.2
	5	1.75	1.26	892.87
June 24	1	0.5	0.58	255.1
	5	1.0	0.82	510.2
July 1	1	0		
~ 1 0	5	0		
July 8	1	0		
	5	U		
July 15		0		
Teo 1	5	. 0 .		
July 22		0		
T.1. 20	5 , 1	0 5	0 5 9	255 1
July St	/ <u>1</u>	0.5	0.00	382 65
λμα 5	1	0.75	0.96	382.65
Auy. J	. <u>т</u> . Б	1 0	0.82	510.2
Aira 12	) 1	1 25	0.96	637.75
Huy. 12	· <u> </u>	1.00	0.82	510.2
Oct. 16	; 1	13.00	4,97	6632.6
	, <u>-</u> с	11 75	3 30	5997 85

Table Dl. Benthic densities<sup>+</sup> of <u>Chaoborus</u> larvae during 1974.

+ One core = 19.6 cm<sup>2</sup>. To extrapolate to no.  $m^{-2}$ , densities were multiplied by  $(\frac{1000 \text{ cm}^2}{19.6 \text{ cm}^2})$  510.2.
APPENDIX E.

Depth-weighted Peaks of Vertical Migration of <u>C. flavicans</u>, <u>D. pulicaria</u> and <u>C. bicuspidatus</u>.

Table El. Depth-weighted vertical migration peaks of <u>C</u>. <u>flavicans</u>.

ite	Time	animals		animals x dep	th peak	( meters)
ne 5, 1974	10a.m.	17		189	11.	12
	2p.m.	26		327	12.	58
	6p.m.	28	,	309	11.0	)4
	10p.m.	31		270	8.	71
· · · · · · · · · · · · · · · · · · ·	2a.m.	34		240	7.(	06
	6a.m.	39	•	393	10.0	8
ly 6, 1974	10a.m.	144		1176	8	17
-	2p.m.	101.		885	8.1	76
	6p.m.	115		846	7.3	36
	10p.m.	110		651	5.9	)2
	2ā.m. '	119		630	5.2	29
	6a.m.	92		624	6.	78
ly 21, 1974	10a.m.	152		1290	8.4	19
	2p.m.	131	· .	1131	8.6	53
	6p.m.	116		891	7.6	58
	10p.m.	84		561	6.6	58
	2a.m.	89		474	5.3	33
	6a.m.	94	•	687	7.;	31
gust 7, 1974	10a.m.	83	·	882	10.6	33
	2p.m.	81		918	11.3	33
. ,	6p.m.	85		885	10.4	1
	10p.m.	105		1095	10.4	3
	2a.m.	109		828	7.6	50
	6a.m.	76		825	10.8	36

9	Time	animals	animals x depth	peak (meters)
28, 1974	10a.m.	531	2606	4.91m
. : ·	2p.m.	1055	9158	6.68
	6p.m.	688	5326	7.74
· .	10p.m.	1190	13257	11.14
	2a.m.	1494	18184	12.17
	6a.m.	1187	10815	9.11
				· ·
11, 1974	10a.m.	941	9787	10.40
•	2p.m.	1408	14692	10.43
	6p.m.	1499	15592	10.40
• •	10p.m.	1423	15844	11.13
• • • • • • • • • • • • • • • • • • •	2a.m.	2476	25352	10.24
	6a.m.	2876	29406	10.22
9, 1974	10a.m.	557	9326	16.74
	2p.m.	999	16275	16.29
	6p.m.	783	10582	13.51
	l0p.m.	812	7673	9.45
	2a.m.	1596	9009	5.64
	6a.m.	1442	22664	15.72
st 16. 1974	10a.m.	585	6992	11.95
	2p.m.	617	4919	7.97
	6p.m.	433	3707	8.56
• .	10p.m.	830	4314	5.20
	2a.m.	1305	7544	5.78
	6a.m.	728	4573	6.28

Table E2. Depth-weighted vertical migration peaks of D. pulicaria.

Depth-weighted vertical migration peaks of C. Eic Table E3.

# C. bicuspidatus.

ate Time animals animals x depth peak(meters	;)
uly 21, 1974 l0a.m. 1110 15838 14.27	
2p.m. 1018 14622 14.36	
6p.m. 910 12900 14.18	
10p.m. 883 14317 16.21	•
2a.m. 1376 14782 10.74	
6a.m. 929 12914 13.90	

#### APPENDIX F.

Emergence and Sex Ratio of <u>C</u>. <u>flavicans</u> Adults.

Table Fl. Numbers of male and female C. flavicans caught

in emergence traps on station 1.

Date		1 d': \$	Tra 2 0": 9	p number 3 0 <sup>7</sup> : 9	<u>4</u> o": <del>2</del>	5 ơ': ♀	mean no. of adults	standard deviation
June	25	0	0:	0	0	0	0	0
	26	0	0	0	0:1	0	0.2	.45
	27	1:1	0	0:1	0	0	0.6	. 89
•.	28	1:1	1:0	0	1:0	1:0	1.0	.71
	29	2:0	1:0	0	1:1	1:2	1.6	1.14
	30	1:3	0:2	1:0	0:2	2:1	2.4	1.14
July	1	2:2	1:2	1:1	3:1	2:3	3.6	1.14
	2	4:3	2:4	2:1	1:2	3:5	5.4	2.30
	3	4:5	3:4	1:2	2:2	4:2	5.8	2.39
	4	4:3	4:1	2:2	4:2	7:4	6.6	2.70
•	5	5 <b>:</b> 7	5:2	3:2	3 <b>:</b> 3 <sup>:</sup>	4:5	7.8	2.77
	6	6:2	2:2	2:1	2:4	6:4	6.4	2.61
•	7	2:3	2:1	1:1	1:3	4:2	4.0	1.58
	8	2:1	1:0	0	1:0	1:1	1.4	1.14
· .	9	0:3	<u>l;1</u>	0:1	0	0	1.2	1.30
Mean of ac	no. dults	4.53	2.80	1.73	2.67	4.27		

Total	number	of	adults	=	240
Total	number	of	males	=	126
Total	number	of	females	=	114
f:d se	ex ratio	) =	$\frac{114}{126} = .9$	904	17

APPENDIX G. Numbers of <u>C</u>. <u>flavicans</u> and Amphipods Caught

in Submerged Traps at Station 1.

Table Gl. Numbers of <u>C</u>. <u>flavicans</u> and amphipods caught in submerged traps at station 1. P - pupa, IV - old instar IV, N - new instars I and II, A - amphipods.

Date	Depth (meters)	1.	2	3	4	5
June 28, 1974	5	2P, 6A	4A	2P. 5A	1P. 2A	32
	10	4P, 6IV	2P, 2IV	3P. 5IV	1P. 1TV	7P 3 TV
	15	l IV	4IV	, 1 1 IV	,	2TV
	20	no trap	l IV			no trap
July 5, 1974	5	1P, 18N, 5A	7N, 2A	12N,4A	9N, 3A	11N, 4A
	10	4N	2N, 2IV	6N, 2IV	5N	4N
	15	l IV	· · · ·		3IV	
	20	no trap			l IV	no trap
July 12, 1974	5	3A	2N, 3A	4A	3A	lN, 3A
	10	4N	1 IV,8N	7N	2IV,5N	3N
	15	l IV	2 IV,1N	3N	2N	
	20	no trap				no trap
	· · · ·					
July 19, 19/4	5	lA	3A	5A	4A	2A
	10		5N	5N	ЗŅ	
	15		2N	ln		
	20	no trap				no trap

Dry Weights of <u>C</u>. <u>flavicans</u> Larvae and Pupae.

Number Number of Mean individual Standard ΔW ate of lots animals/lot dry weight (mg) deviation (mg) ay 20/74 10 20 .6032 .021 ay 27 10 20 .6888 .006 .0856 une 3 larvae 10 20 .7162 .014 .0274 pupae 10 10 .8162 .062 une 10 larvae 10 20 .7765 .019 .0603 pupae 10 10 .8948 .072 .0786 une 17 larvae 10 20 .7772· .019 .0007 pupae 10 10 .8155 .0074 .0793 une 24 larvae 10 .79,46 20 .031 .0164 pupae 10 10 .8204 .0106 .0049 uly l 10 100 .00191 .000736 X=.0243 S.D.=.053 uly 8 10 100 .0291 .000943 .02719 uly 15 10 100 .0425 .00103 .0134 uly 22 10 100 .0647 .0188 .0222 uly 30 10 100 . .0924 .025 .0277 ug. 5 10 50 .1030 .0106 .152 ug. 12 10 50 .1489 .004 .0459 ug. 19 10 50 .1563 .022 .0074 ug. 26 10 50 .1683 .057 .0120 ept. 15 10 50 .2122 .086 .0439 ct. 16 10 10 .2934 .114 .0812 ay 14/75 10 20 .6286 .0415 .3352 ay 21 10 20 .6377 .025 .0091 ay 28 10 20 .6996 .013 .0619 une 4 10 20 .7262 .019 .0266 une ll larvae 10 20 .7940 .089 .0678 pupae 10 10 .8920 .077 une 18 larvae 10 20 .8692 .097 .0752 pupae ' 10 10 .9049 .112 .0129 une 25 larvae 10 20 .9354 .086 .0662 10 pupae 10 .9015 .068 .0034  $\overline{X}$ =.03175 S.D.=.027

able H1. Mean dry weights of <u>C</u>. <u>flavicans</u> larvae and pupae.

### APPENDIX I. Instar-specific Growth Data.

				· · · · · · · · · · · · · · · · · · ·			·	
nstar ype	Del <b>Date</b>	Time (days	Sample ) size	No. of samples	Mean dry weight (mg)	S.D.		
I	July 1, 1975 July 4 July 8 July 12 July 15 July 19 July 22 July 26 July 30	0 3 7 11 14 18 21 25 29	100 100 100 50 50 50 25 20		.0019 .0023 .0055 .0097 .0124 .0153 .0168 .0182 .0193			
<b>TT</b>	July 8, 1975 July 12 July 15 July 19 July 22 July 26 July 30 August 2 August 5 August 9 August 12	0 4 7 11 14 18 22 25 28 32 35	20 50 75 100 100 . 100 50 50 50 25 15		.0036 .0047 .0087 .0136 .0188 .0273 .0348 .0408 .0408 .0462 .0481 .0493			
<b>II</b>	July 12, 1975 July 15 July 19 July 22 July 26 July 30 August 2 August 5 August 9 August 12	0 3 7 10 14 18 21 24 28 31	15 20 25 50 50 50 50 50 50 50 50		.0019 .0123 .0179 .0228 .0363 .0556 .0744 .1025 .1287 .1543			
IV (19	974-75 generat August 26, 19 Sept. 16 Oct. 16	ion) 74 0 21 51	50 50 10	10 10 10	.1683 .2121 .2934	.057 .086 .114	7 5 1	
	May 14, 1975 May 21 May 28 June 4 June 11 June 18 June 25	261 268 275 282 289 296 303	20 20 20 20 20 20 20 20 20	10 10 10 10 10 10 10	.6286 .6377 .6996 .7262 .7940 .8692 .9354	.041 .025 .013 .019 .089 .097 .086	-5 ; ; ; ;	

able Il. Instar-specific dry weights.

No. of Date Time Sample Mean dry Instar samples weight(mg) S.D. (days) size уре IV (1973-74 generation) May 20, 1974 0 10 20 .6032 .021 May 27 7 20 10 .6888 .006 14 20 10 .014 June 3 .7162 June 10 21 20 10 .7765 .019 June 17 28 20 10 .7772 .019 June 24 35 20 10 .7946 .031

'able Il. Instar-specific dry weights. (cont'd)











Calorific Content of C. flavicans Larvae and Pupae. APPENDIX J.

Kilocalories per gram (dry weight) of C. flavicans larvae and pupae. Table Jl.

•

Date	Instar type		2	3	san 4	nple numb∈ 5	e r	7	ω	6	10	
May 14, 1975	IV pupae	5.6558 6.6864	4.9436 5.8223	5.6821 5.7382	6.4663 5.8474	5.6377 5.3802	5.7263 5.4894	5.9463 5.1248	5.8623 5.3042	5.6376 5.0884	5.6860 5.5903	
May 21, 1975	IV pupae	5.6056 5.8374	5.5863 5.7984	6.2892 5.8408	5.7622 5.2125	6.8304 5.5924	5.2238 5.8336	5.5489 5.4323	5.5426 6.2394	5.1422 5.0389	5.7532 5.8474	
May 28, 1975	IV pupae	5.8768 6.0154	5.4108 5.1949	5.7862 5.4611	5.9128 5.7819	6.2140 5.8604	5.7942 5.3886	5.7863 5.3746	5.6576 6.2932	5.1847 5.5102	5.4278 5.3892	
June 4, 1975	I V pupae	5.9915 5.8164	6.0206 5.7923	5.7113 5.7648	6.3121 6.0289	5.9499 5.6624	5.8292 5.7648	6.5255 5.8296	6.5771 5.4693	6.1734 5.5804	6.0077 6.0327	
June 11, 1975	IV pupae	5.7211 5.3778	5.8488 5.1025	5.4388 4.8182	6.0741 4.7820	6.3592 <b>5.</b> 2042	5.9342 5.7259	7.3642 5.2246	6.1849 5.1514	6.2907 4.9033	5.6263 5.9560	
June 18, 1975	IV pupae	5.4551 5.5995	5.9141 6.0849	6.1478 6.2878	6.6710 5.7061	6.2124 5.6380	5.5021 5.8590	5.1658 6.4904	5.5189 5.6805	6.6866 5.7821	6.7991 6.8189	
June 25, 1975	IV pupae	5.5508 6.1391	5.7434 7.0781	5.4852 5.9748	6.9658 7.0436	<b>6</b> .4073 7.1203	6.3947 6.1356	6.1606 6.5588	6.6903 5.6807	5.8453 5.4138	7.0358 5.3452	
July 1-12, 1975	I	7.3832	7.5277	6.2453			· · ·		•			
July 15-22, 1975	<b>}1</b>	5.8746	5.8336	5.6357					· ·	-		
July 22-30, 1975	<b>⊢</b> 4	5.7734	5.8032	5.8794							•	
July 12-22, 1975	1-4 1-4	5.8860	6.2241	5.9980			-	•	•			
July 26-Aug.2,19	75 II	5.6881	5.7643	5.8434		•						
Aug. 5-12, 1975	II	6.0347	5.9874	5.9081				•			· ·	
July 15-22, 1975	II	5.6354	6.2009	5.8392								

153

		•	
	10		
ਰ    ਰ		,	
cont	6		
ednd	ω	· ·	
and		•	
arvae	7		
		· .	
a V1 C	9	· ·	
	lber		
01	e nur		
i gn t.)	s amp I		
. Ме	4	·. ·	
ש ה- ב	e M	.193	
her in the			· .
	2	. 823	•
		4 6	
2	<b>r</b>	5.734	
	e e		
Tuc + an -	typ	975 I I	:
		2, 1! 75	
		-Aug. 2, 19	
-    a		Ty 26 g.5-1	
		Ju Au	

A one-way analysis of variance with instar types as treatments yielded an F value of 1.15. Critical F (P = .05, d.f. = 4, 162) is 2.43. Thus there are no differences in kcal. per unit weight among larval instars and pupae.

Mean caloric content of any larval instar or pupae is 5.8638 kcal. gm.<sup>-1</sup> (S.D. = 0.5019).

#### APPENDIX K.

Carbon Content of <u>C</u>. <u>flavicans</u>.

# Table Kl. Mean carbon content (ug.C) of <u>C</u>. <u>flavicans</u>

larvae and pupae.

Instar		· · · · · · · · · · · · · · · · · · ·	Sample n	.0.			Sample
уре	Date	1	2	3	X	S.D.	size
I	July 1, 1975 July 8 July 15 July 22 July 30	1.335 3.79 8.23 10.85 11.25	1.485 3.99 7.735 11.93 10.64	1.605 3.44 8.345 8.96 10.93	1.475 3.74 8.103 10.58 10.94	.135 .278 .324 1.503 .305	20 20 20 10 10
	July 8, 1975 July 15 July 22 July 30 Aug. 5 Aug. 12	$2.605 \\ 5.69 \\ 11.43 \\ 21.54 \\ 25.42 \\ 24.25$	2.235 5.13 12.26 20.87 26.61 25.18	2.82 5.765 10.84 21.21 24.97 23.79	2.553 5.528 11.51 21.207 25.667 24.407	.296 .347 .713 .335 .847 .708	20 20 10 10 10 10
<b>I</b>	July 15, 1975 July 22 July 30 Aug. 5 Aug. 12	7.68 14.37 36.68 63.9 93.2	8.24 15.12 35.56 68.3 79.7	7.93 13.63 37.24 58.7 88.4	7.95 14.37 36.49 63.63 87.1	.281 .745 .855 4.806 6.843	10 10 5 1 1
V	May 14, 1975 May 21 May 28 June 4 June 11 June 18 June 25	309.7 330.4 273.3 405.1 437.8 254.2 384.7	394.9 381.1 382.9 324.4 344.1 339.1 296.5	269.6 486.2 358.1 264.0 367.2 375.6 274.3	324.73 399.23 338.1 331.17 383.03 322.97 318.5	63.988 79.467 57.472 70.793 48.815 62.287 58.40	1 1 1 1 1
ıpae	June 11, 1975 June 18 June 25	321.6 340.8 403.4	336.9 387.0 426.0	303.7 264.3 372.3	320.733 330.7 400.567	16.617 61.98 26.962	1 1 1

star pe	Date	Individual dry weight (mg.)	Mean individual 	g) ugCmg. <sup>-1</sup> dry wt. <sup>+</sup>	
I	July 1, 1975 July 8 July 15 July 22 July 30	.0019 .0055 .0124 .0168 .0193	1.475 3.74 8.103 10.58 10.94	$776.32$ $680.00$ $653.47$ $629.76$ $566.84$ $\overline{X} = 661.278$ S.D.=76.743	
I	July 8, 1975 July 15 July 22 July 30 Aug. 5 Aug. 12	.0036 .0087 .0188 .0348 .0462 .0493	2.553 5.528 11.51 21.207. 25.667 24.407	$709.17$ $635.40$ $612.23$ $609.40$ $555.56$ $495.07$ $\overline{X} = 602.805$ S.D.= 72.591	
I	July 15, 1975 July 22 July 30 Aug. 5 Aug. 12	.0123 .0228 .0556 .1025 .1543	7.95 14.37 36.49 63.63 87.1	$646.34 630.26 656.29 620.78 564.48 \overline{X} = 623.63S.D.= 35.823$	
]	May 14, 1975 May 21 May 28 June 4 June 11 June 18 June 25	.6286 .6377 .6996 .7262 .7940 .8692 .9354	324.73 399.23 338.1 331.17 383.03 332.97 318.5	$516.59$ $626.05$ $483.28$ $456.03$ $482.41$ $371.57$ $340.50$ $\overline{X} = 468.061$	
bae	June 11, 1975 June 18 June 25	.8920 .9049 .9015	320.733 330.700 400.567	5.D.= 94.411 359.57 365.45 444.33 $\overline{X} = 389.783$ 5.D.= 47.33	

Table K2. Carbon content per unit dry weight of C. flavicans.

ne way ANOVA testing to see if differences exist between carbon content unit dry weight of different instars and pupae yielded F = 10.612 tical F (4 21 d.f., P 0.05) = 2.84. Differences do exist between boncontent per unit dry weight of different instars and pupae. 549.1114ug. C per unit dry weight, S.E. = 51.465.

157

.

Dry weights of larval instars and pupae were converted to carbon content by multiplying the dry weight of a given life history stage by the mean carbon content per unit dry weight of that life history stage.

Allen curve production in terms of carbon was obtained by multiplying the dry weight production value by 549.1114 ug.  $C mg.^{-1}$  (dry weight).

APPENDIX L. Hatching Success of <u>C</u>. <u>flavicans</u> Eggs.

Table Ll. Numbers of eggs and numbers of hatched eggs of

 $\underline{C}$ . <u>flavicans</u>.

Sample Number	Number of eggs	Number of hatched eggs	% hatched		· · ·
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25	249 175 247 263 231 264 186 193 248 239 278 181 193 170 209 218 280 218 280 218 199 182 234 248 199 182 234 248 191 175	$\begin{array}{c} 244\\ 164\\ 242\\ 255\\ 229\\ 251\\ 182\\ 189\\ 246\\ 232\\ 272\\ 177\\ 187\\ 168\\ 205\\ 207\\ 274\\ 216\\ 195\\ 180\\ 232\\ 243\\ 185\\ 172\\ 172\\ 172\\ 172\\ 172\\ 172\\ 172\\ 172$	98 94 98 97 99 95 98 98 99 97 98 99 97 98 97 99 98 95 98 95 98 95 98 99 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 98 97 99 97 98 98 97 98 99 98 97 98 98 97 98 98 97 98 98 97 98 98 97 98 98 97 98 98 98 97 98 99 98 99 98 99 98 99 98 99 98 99 99		
26 27 28 29 30 31 32 33	192 194 223 219 243 169 212 208 227	178 186 221 215 241 164 208 202 225	96 99 98 99 97 97 98 97 98	· · · · ·	
X S.D.x S.E.x	216.606 32.23 5.61	211.73 31.89 5.55	97.73 1.257 .2188		• • •

APPENDIX M. C. flavicans Respiration Data

Table Ml. O2 uptake (ul. O2 hour<sup>-1</sup>animal<sup>-1</sup>) of <u>C. flavicans</u>

Life History Sample Temperature (°C) stage Number 5 10 25 15 20 instar II .0984 1 .1181 .1299 .1889 .2125 2 .1181 .1259 .1299 .1614 .2322 3 .1102 .1259 .1141 .1535 .2479 4 .1220 .1181 .1299 .1417 .2400 5 .1141 .1141 .1181 .1889 .2283 6 .1181 .1299 .1259 .1388 .2361 7 .1220 .1102 .1378 .1574 .2440 8 .1063 .1220 .1220 .1535 .2479 9 .1417 .1259 .1417 .1732 .2400 10\* .0276 .0315 .0354 .0315 .0276 X .1168 .1216 .1273 .1673 .2366 S.D. .012 .007 .009 .020 .011 instar III 1 .3857 .4211 .4407 .5470 .7988 2 .3975 .4132 .4329 .5509 .8185 3 .3739 .4171 .4357 .5509 .8303 4 .4014 .4211 .4368 .5981 .8264 5 .3778 .4171 .4357 .5903 .8342 6 .4132 .4053 .4289 .6021 .8499 7 .3935 .4211 .4289 .5903 .8224 8 .3975 .4211 .4357 .5863 .8382 9 .4132 .5981 .3975 .4329 .8499 10\* .0276 .0433 .0354 .0394 .0315 X .3922 .4176 .4343 .5793 .8299 S.D. .011 .004 .004 .023 .016 instar IV 1 2.479 2.636 2.479 3.384 6.060 2 2.400 2.558 2.912 3.581 5.509 3 5.116 2.440 2.873 2.676 3.423 2.282 2.440 2.755 3.738 4.329 4 5 2.243 2.676 2.715 3.660 5.037 6 2.204 2.518 2.794 3.699 5.194 7 2.794 2.951 3.778 4.879 2.479 3.502 5.706 8 2.204 2.715 2.597 5.784 9 2.164 2.400 2.833 3.384 10\* .079 .079 .079 .079 .079 x 2.322 2.623 2.746 3.572 5.290 .531 S.D. .128 .159 .150 .155

larvae and pupae at various temperatures.

Table M	11. O <sub>2</sub> upt	ake (ul. C	2 <sup>hour<sup>-1</sup>a</sup>	nimal <sup>,1</sup> )	of <u>C</u> . <u>f</u>	lavican	3	
	larva	e and pupa	e at var	ious tem	perature	es. (co	nt'd)	, · ·
Life History	Sample		Te	emperatur	ce (°C)	25		
stage	Number	<u> </u>	<u></u>	10	20	25	· · · · · · · · · · · · · · · · · · ·	
oupae	1	2.597	3.030	7.083	8.106	9.287		
	2 3	2.322 2.715	3.187 3.266	7.398 7.122	8.382 8.224	8.972 8.342	•	
	4	2.361	3.502	5.627 7.240	8.303 8.421	9.090		•
	6	2.282	3.345	7.870	8.460	9.405		
	8	2.636 2.518	3.227 2.991	7.437	8.499 7.831	9.483		
	9 10*	2.361	2.991	7.319	8.618	8.185	·	
· · ·		$\overline{X}$ $\overline{2.475}$	3.183	7.149	8.316	9.116		
	S.	D153	.1/3	•010	.231	. 222	,	· .

Control sample

k

Table M2. 0, uptake per unit dry weight of C. flavicans larvae

······				
Life history stage	temperature (°C)	mean O <sub>2</sub> uptakė́ (ul.O2 hour <sup>-1</sup> animal <sup>-1</sup> )	individual dry weight (mg)	O2 uptake per unit <sup>+</sup> dry weight (ul. O <sub>2</sub> hour <sup>-1</sup> mg <sup>-1</sup> )
instar II	5 10 15 20 25	.1168 .1216 .1273 .1673 .2366	.0330	3.539 3.685 3.858 5.070 7.170
instar III	5 10 15 20 25	.3922 .4176 .4343 .5793 .8299	.1183	3.315 3.530 3.671 4.897 7.015
instar IV	5 10 15 20 25	2.322 2.623 2.746 3.572 5.290	.7262	3.197 3.612 3.781 4.919 7.284
pupae	5 10 15 20 25	2.475 3.183 7.149 8.316 9.116	.8920	2.775 3.568 8.015 9.323 10.220

and pupae at various temperatures.

\* Two way ANOVA testing Ho: $d_1 = d_2 = \ldots = d_1 = 0$  yielded F = 55.356. Critical F (3, 12 d.f., P 0.05)<sup>2</sup> = 3.49. Differences exist between O<sub>2</sub> uptake rates of various instars and pupae. + Two way ANOVA testing Ho:  $d_1 = d_2 = \ldots = d_1 = 0$ , yielded F = 4.386. Critical F (3, 12 d.f., P 0.05) = 3.49. Differences exist between O<sub>2</sub> uptake rate per unit dry weight of various instars and pupae.

# APPENDIX N. Allen Curve Production

Table N. Population densities and weights used to calculate

Allen curve production.

Date	mean density (no. m <sup>-2</sup> )	mean individual dry weight (mg.)
July 8, 1974	7850.456	.0291
July 15	6107.436	.0425
July 22	5781.16	.0647
July 30	5119.5	.0924
August 5	5252.3	.0130
August 12	5158.6	.1489
August 19	3876.57	.1563
August 26	3266.6	.1683
September 16	2451.0	.2122
October 16	2148.97	.2934
May 14, 1975	1806.55	.6286
May 21	1262.496	.6377
May 28	1330.09	.6996
June 4	1331.436	.7262
June 11 larvae	1053.646	.7940
pupae	367.813	. 8920
June 18 larvae	65.546	.8692
pupae	108.513	.9049
June 25 larvae	77.71	.9354
pupae	33.69	.9015

No significant differences in caloric content exist between various larval instars and pupae (appendix J). Therefore the Allen curve production in caloric terms is 1982.551 mg. m<sup>-2</sup> yr.<sup>-1</sup> x .0058638 kcal. mg<sup>-1</sup> = 11.6253 kcal. m<sup>-2</sup>yr.<sup>-1</sup>.

Mean carbon content per unit weight of any larval instar pupa is 549.1114 ugC.mg<sup>-1</sup>. The Allen curve production in terms of carbon content is 1982.551 mg.  $m^{-2}yr^{-1}$ x 549.1114 ugC.mg.<sup>-1</sup> = 1088641.355 ug.Cm.<sup>-2</sup>yr.<sup>-1</sup>.

The first point on the Allen curve was calculated according to the IBP handbook no. 17 (Edmonson and Rigler 1972) as follows:

> Mean density of larvae on June 11, 1975 = 1053.646Mean density of pupae on June 11, 1975 = 367.813= 1421.459 (1)

Sex ratio = .9047:1.000  $\widehat{\P}: o^{7}$  (Appendix F) fecundity = 216.606 eggs female<sup>-1</sup> (Appendix L) hatching success = 97.73% (Appendix L) number of  $\widehat{\P}$  in (1) = 1421.459 x  $\frac{.9047}{2}$  = 642.9969 total number of eggs laid = 642.9969 x 216.606 - 139277.0036 total number of first instar larvae hatching from eggs = 97.73% x 139277.0036 = 136115.4156 production from time of egg-laying (about July, 1974) to July 8, 1974 is 2094.70343 mg. (dry weight) m.<sup>-2</sup>.week<sup>-1.</sup>

APPENDIX O. Feeding Experiment Results

The four categories of food sizes used in the food type and size preference experiments were: 73-243u, 243-500u, 500-783 u, 783-1050 u. Rotifers and nauplii were predominant in the first size category, copepods in the second, small <u>Daphnia</u> in the third and large <u>Daphnia</u> in the fourth.

30 larvae per chamber were used in experiments on the first three instars. 20 larvae per chamber were used in the last experiment.

The number of prey ingested per predator per day was calculated as follows:

(mean control value - mean test value) x 15 liters ÷ number of <u>Chaoborus</u> larvae.

Table Ol. Results of food type and size preference experiments.

nstar type	Sample type	Sample no.		· · · · · · · · · · · · · · · · · · ·	no. of pre	y per liter	· ·	
			73 - rotifers	243 u nauplii	243-500u copepods	500-783u small <u>Daphnia</u>	783-1050u large Daph	nia
I	control	1 2 X	$\frac{41}{32}$	38 $43$ $40.5$	33 <u>45</u> 39	20 <u>14</u> 17	$\frac{12}{17}$	
	test	$\begin{array}{c}1\\2\\\overline{x}\end{array}$	19 <u>15</u> 17	33 $28$ $30.5$	35 $48$ $41.5$	11 24 17.5	$\frac{11}{15}$	
	no. e per 1	eaten Larva	9.75	5			.75	
	% of prey per ]	total eaten .arva	6.6	3.4			•5	
							•	a star a star

				· · · · · · · · · · · · · · · · · · ·		······
nstar type	Sample Sampl type no.	.e	·····	no. of pre	ey per liter	<u> </u>
II	control 1 2 $\overline{X}$	33 26 29.5	$\begin{array}{r} 42\\ 35\\ \overline{38.5} \end{array}$	29 <u>38</u> 33.5	18 12 15	11 15 13
	test $1$ 2 $\overline{X}$ .	$\frac{10}{6}$	16 22 19	32 $21$ $26.5$	$ \begin{array}{r}13\\20\\16.5\end{array} $	10 <u>16</u> 13
	no. eaten per larva	10.75	9.75	3.5	 	
	% of total prey eaten per larva	8.3	7.5	2.7 ,	. <b></b> ·	
II	$\begin{array}{c} \text{control}  1 \\ 2 \\ \overline{X} \end{array}$	31 $24$ $27.5$	46 <u>34</u> 40	43 <u>28</u> 35.5	$\frac{16}{11}$ 13.5	$\frac{12}{7}$
	test 1 2 $\overline{X}$	$\frac{17}{11}$	27 $20$ $23.5$	19     26     22.5	$\frac{15}{\frac{8}{11.5}}$	12 <u>8</u> 10
	no. eaten per larva	6.75	8.25	6.5	1	
	% of total prey eaten per larva	5.4	6.5	5.2	• 8	0
IV	control 1 2 $\overline{X}$	$\begin{array}{r} 46\\ \underline{31}\\ \overline{38.5} \end{array}$	34 $47$ $40.5$	39 31 35	$\begin{array}{r} 24\\ \underline{15}\\ 19.5 \end{array}$	18 12 15
	test 1 2 $\overline{X}$	34 27 30.5	32 26 29	26 <u>19</u> <u>22.5</u>	19 $12$ $15.5$	$\begin{array}{r}10\\15\\12.5\end{array}$
	no. eaten per larva	6.0	8.625	9.375	3.0	1.875
	% of total prey eaten per larva	4.0	5.8	6.3	2.0	1.3
- : - :						

able O1. Results of food type and size preference experiments.(cont'd)

166

Table O2.	Ingestion	rates of	first	instar	<u>C</u> .	flavicans
	larvae at	differer	t temp	eratures	s ai	nd food

concentrations.

Temperature (°C)       Initial food concentration (mg.Cl <sup>-1</sup> )       Ingestion rate (mg. C larva <sup>-1</sup> dry weight of l dry weight of l (mg)       Inge per dry weight of l mg <sup>-1</sup> Epilimnion ly 3       19.0       0.746       .00038       .0022         19.0       1.003       .00049       .00088         19.0       1.375       .0078       .00088         -y 8       19.3       0.761       .00091       .0055         19.3       2.283       .00331	estion rate unit weight larva (mg.C ] .1727 .2227 .3545 .8545
Epilimnion         .y 3       19.0       0.746       .00038       .0022         19.0       1.003       .00049       .0078         19.0       1.375       .0078       .00088         .y 8       19.3       0.761       .00091       .0055         19.3       1.522       .00191       .0055         19.3       2.283       .00331	.1727 .2227 .3545 .8545
Lpriminion         .y 3       19.0       0.746       .00038       .0022         19.0       1.003       .00049       .0078         19.0       1.375       .0078         19.0       1.577       .00088         .y 8       19.3       0.761       .00091       .0055         19.3       1.522       .00191       .0055         19.3       2.283       .00331	.1727 .2227 .3545 .8545
.y       3       19.0       0.746       .00038       .0022         19.0       1.003       .00049         19.0       1.375       .0078         19.0       1.577       .00088         .y       8       19.3       0.761       .00091       .0055         19.3       1.522       .00191       .0055       .00331	.1727 .2227 .3545 .8545
19.0       1.003       .00049         19.0       1.375       .0078         19.0       1.577       .00088         .y       8       19.3       0.761       .00091       .0055         19.3       1.522       .00191       .0055       .00331	2227 3545 8545
19.0       1.575       .0078         19.0       1.577       .00088         .y 8       19.3       0.761       .00091       .0055         19.3       1.522       .00191       .0055         19.3       2.283       .00331	. 3545
y 8       19.3       0.761       .00091       .0055         19.3       1.522       .00191         19.3       2.283       .00331	6040
y 8 19.3 0.761 .00091 .0055 19.3 1.522 .00191 19.3 2.283 .00331	
19.3     1.522     .00191       19.3     2.283     .00331	1655
19.3 2.283 .00331	3473
	6018
19.3 2.764 .00292	5309
y 10 19.4 1.872 .00264 .0076 .	,3474
<u>19.4</u> 2.815 .00368	4842
19.4 $2.975$ $.00421$	. 5539
±2.4 3.598 .00526	6921
$v_{12}$ 19.6 4.038 00525 0007	5/12
19.6 4.583 .00622	5412 6412
19.6 5.248 .00630	6495
19.6 6.007 .00642	6619
Hypolimnion	
y = 5  0.1  0.746  .00022  .0022  .0022	1000
0.1 $1.003$ $.00044$	2000
6 1 1.575 .00073	3318
······································	4000
y 8 6.2 0.761 .00067 .0055	1218
6.2 1.522 .00187	3400
6.2 2.283 .00328	5964
6.2 2.764 .00346	6291
	. '
y 10 6.3 1.872 .00231 .0076 .	3039
6.3 2.815 .00377 ·	4961
6.3 2.975 .00357 ·	4697
b.3 3.598 .00446 ·	5868
v 12 6.4 4.038 00506	5216
6.4 4.583 00566	5035
6.4 5.248 00578	5055
6.4 6.007 .00580	5979
•••••••••••••••••••••••••••••••••••••••	515

167

Table 03. Ingestion rates of second instar <u>C</u>. <u>flavicans</u>

larvae at different temperatures and food

concentrations.

te	Temperature (°C)	Initial food concentration (mg. CL <sup>-1</sup> )	Ingestion rate (mg. C larva <sup>-1</sup> day <sup>-1</sup> )	Mean individual dry weight (mg)	Ingestion per unit of larva mg <sup>-1</sup> )	rate weight (mg.C
Epi Ly 14	limnion 19.1 19.1 19.1 19.1 19.1	0.594 0.897 1.283 1.645	.0014 .0019 .0024 .0056	.0074	.1892 .2568 .3243 .7568	
Ly 16	19.2 19.2 19.2 19.2 19.2	0.833 1.576 2.198 2.904	.0023 .0042 .0062 .0068	.0099	.2323 .4242 .6263 .6869	
y 20	19.3 19.3 19.3 19.3	1.134 2.067 2.781 3.925	.0051 .0069 .0087 .0098	.0153	.3333 .4510 .5686 .6405	· · · · · · · · · · · · · · · · · · ·
y 24	19.5 19.5 19.5 19.5	1.843 3.819 5.324 6.849	.0087 .0116 .0129 .0131	.0231	.3766 .5022 .5584 .5671	· ·
Нуро. у 14	limnion 6.4 6.4 6.4 6.4 6.4	0.594 0.897 1.283 1.645	.00098 .0018 .0021 .0047	.0074	.1324 .2432 .2838 .6351	
y 16	6.4 6.4 6.4 6.4	0.833 1.576 2.198 2.904	.0021 .0038 .0057 .0059	.0099	.2121 .3838 .5758 .5960	
y 20	7.1 7.1 7.1 7.1	1.134 2.067 2.781 3.925	.0046 .0063 .0079 .0089	.0153	.3007 .4118 .5163 .5817	
y 24	7.2 7.2 7.2 7.2 7.2	1.843 3.819 5.324 6.849	.0083 .0110 .0118 .0120	.0231	.3593 .4762 .5108 .5195	

	Table 04. In	gestion rates o	f third ins	tar <u>C</u> . <u>flav</u>	icans
	La co	rvae at differe ncentrations.	nt temperat	ures and fo	od
	Temperature (°C)	Initial food concentration (mg.CL1)	Ingestion rate (mg. C larva <sup>-1</sup> day <sup>-1</sup> )	Mean individual dry weight (mg)	Ingestion rate per unit weight of larva (mg.C mg <sup>-1</sup> )
Epili 28	mnion 19.4 19.4 19.4 19.4 19.4	0.639 1.102 1.662 2.314	.0073 .0103 .0136 .0327	.0460	.1587 .2239 .2957 .7109
30	19.0 19.0 19.0 19.0 19.0	1.054 2.138 3.125 3.987	.0119 .0232 .0344 .0370	.0556	.2140 .4173 .6187 .6655
st l	18.2 18.2 18.2 18.2 18.2	1.498 3.210 4.625 6.147	.0217 .0281 .0350 .0414	.0681	.3186 .4126 .5140 .6079
st 3	18.1 18.1 18.1 18.1	1.526 3.752 5.854 7.415	.0315 .0417 .0448 .0468	.0838	.3759 .4976 .5346 .5584
Iypol 28	imnion 7.1 7.1 7.1 7.1 7.1	0.639 1.102 1.661 2.314	.0058 .0096 .0116 .0281	.0460	.1261 .2087 .2522 .6107
30	7.0 7.0 7.0 7.0	1.054 2.138 3.125 3.987	.0108 .0201 .0292 .0305	.0556	.1942 .3615 .5252 .5486
t 1	7.0 7.0 7.0 7.0	1.498 3.210 4.625 6.147	.0208 .0265 .0337 .0396	.0681	.3054 .3891 .4949 .5815
st 3	7.0 7.0 7.0 7.0 7.0	1.526 3.752 5.854 7.415	.0255 .0394 .0417 .0423	.0838	.3043 .4702 .4976 .5048

....

169

	lar con	vae at different	temperature	s and food		
.e	Temperature (°C)	Initial food concentration (mg. C liter <sup>-1</sup> )	Ingestion rate (mg C larva <sup>-1</sup> day <sup>-1</sup> )	Mean individual dry weight (mg)	Ingestion rate per unit weight (mg. C mg <sup>-1</sup> )	
Epil:	imnion		•			
just 6	17.8 17.8 17.8 17.8 17.8	.0.576 1.123 1.620 1.956	.0134 .0182 .0199 .0367	.0883	.1518 .2061 .2254 .4156	
just 9	17.1 17.1 17.1 17.1	0.934 2.047 2.835 3.746	.0193 .0335 .0456 .0420	.1046	.1845 .3203 .4359 .4015	
just 12	2 16.8 16.8 16.8 16.8	1.326 2.513 3.738 4.689	.0232 .0359 .0453 .0523	.1294	.1793 .2274 .3501 .4042	
ust l	4 16.3 16.3 16.3 16.3	1.573 3.591 5.316 6.983	.0234 .0332 .0452 .0616	.1557	.1503 .2132 .2903 .3956	
Нуро.	limnion					
just 6	6.9 6.9 6.9 6.9	0.576 1.123 1.620 1.956	.0151 .0213 .0314 .0340	.0883	.1710 .2412 .3556 .3851	
just 9	6.8 6.8 6.8 6.8	0.934 2.047 2.835 3.746	.0152 .0283 .0391 .0399	.1046	.1453 .2706 .3738 .3815	
just 1:	2 6.8 6.8 6.8 6.8 6.8	1.326 2.513 3.738 4.689	.0201 .0254 .0286 .0442	.1294	.1553 .1963 .2210 .3416	
just l	4 6.7 6.7 6.7 6.7	1.573 3.591 5.316 6.983	.0205 .0288 .0367 .0485	.1557	.1317 .1850 .2357 .3115	

# APPENDIX P. AUTHORS OF SPECIES

Table P . Authors of some species listed in the text.

Species	Author
Chaoborus flavicans	(Meigen)
<u>C</u> . <u>crystallinus</u>	(De Geer)
C. punctipennis	(Say)
<u>C. trivittatus</u>	(Loew)
C. americanus	(Joh.)
C. astictopus	Dyar and Shannon
<u>C. nyblaei</u>	(Zett.)
<u>C. obscuripes</u>	(V.D. Wulp)
<u>C. pallidus</u>	(Fabr.)
Leydigia sp.	Leydig
Daphnia pulicaria	Leydig
Diaptomus tyrelli	Рорре
Cyclops fimbriatus	(Fischer)
Cyclops bicuspidatus	Thomasi
Keratella quadrata	(Muller)
Keratella cochlearis	(Gosse)
<u>Hyallela</u> azteca	(Saussure)

171 · ·