ENERGETICS OF VERTICAL MIGRATION IN
CHAOBORUS TRIVITTATUS LARVAE

by

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ABSTRACT

One of the recent theories for the adaptive value of vertical migration (McLaren 1963) states that migrants gain an energetic advantage over non-migrants because by alternating between areas of high and low temperatures they are able to partition energy into growth more efficiently than non-migrants. The energetics of the vertical migration of fourth-instar Chaoborus trivittatus larvae in Eunice Lake, British Columbia were studied to identify and quantify this hypothesized energetic advantage.

Fourth-instar C. trivittatus larvae undergo a regular, synchronous, diel vertical migration which exposes them to a wide range of temperature and prey density. Feeding occurs primarily at night, and near the surface. Although all zooplankton in Eunice Lake are potential prey, Diaptomus kenai constitutes the majority of the biomass in the diet of fourth-instar larvae. In Eunice Lake C. trivittatus larvae grew more slowly than their potential growth rate because of low food availability.

Several energetics parameters including carbon assimilation efficiency, the effect of temperature on respiration rate, and the effects of ration size and temperature on larval growth were measured in the laboratory. Carbon assimilation efficiency of both copepods and cladocerans by C. trivittatus is about 68%. Respiration rate

increases linearly with temperature over the range 5-25°, although there is a suggestion of a plateau in oxygen consumption over the temperature range the larvae are exposed to during their migration. Temperature and ration size interact to determine larval growth rate; fluctuating temperatures limited growth regardless of prey density while at 20° prey density limited the growth rate.

Empirical data from the field and laboratory were incorporated into a generalized computer simulation model of the energetics of a vertically migrating larva. The model was used to examine the effects of various migration patterns, physical parameters, and biological parameters on larval growth.

Analysis of several possible migration strategies showed that, on an energetics basis alone, growth will be maximized by either staying near the surface where there is food, or by vertically migrating with a physiologically determined periodicity based on individual feeding history. The results of laboratory growth experiments and computer simulations agreed with these two alternative strategies. However, C. trivittatus larvae in Eunice Lake do not follow either of these patterns. No alternative hypothesis to explain their migration pattern is attractive, and I conclude that it is a relict of previous selection for this pattern in lakes containing diurnal vertebrate predators.

TABLE OF CONTENTS

	Page
Abstract	i
Table of Contents	iii
List of Figures	vi
List of Tables	viii
Acknowledgements	ix
I. General Introduction	1
II. General Methods	5
Study Area, Sampling, Holding Facilities	5
Controlled Temperature Facilities	6
Carbon-14 Assays	8
Larval Dry Weights and Calorimetry	9
Nomenclature	10
III. Field Studies	12
Introduction	12
Methods	13
Results	15
Temperature	15
Vertical Migration	16
Zooplankton Distribution	18
Feeding	20
Larval Growth in the Field	25
Discussion	27
Summary	33

IV. Energetics Studies	34
Introduction	34
Methods	37
Strike Efficiency, Contact Efficiency, Handling	
Time	37
Friction Coefficient	38
Assimilation	39
Respiration Rates	41
Growth Experiment I	46
Growth Experiment II	47
Results	48
Strike Efficiency, Contact Efficiency, Handling	
Time	48
Energy Cost of Vertical Migration	51
Assimilation Efficiency	53
Respiration	55
Growth Experiment I	59
Growth Experiment II	61
Discussion	65
Summary	77
V. Simulation studies	79
Introduction	79
Theories on the Adaptive Value of Vertical	
Migration	79
The Simulation Model	85
Methods	86

Results	91
Sensitivity	91
The Effect of Food	96
The Effect of Temperature	101
Discussion	104
Summary	119
Literature Cited	121
Appendix I	128
Appendix II	135

LIST OF FIGURES

Figure		Page
1	Diel fluctuating temperature regime for growth experiments I (A) and II (B).	7
2	Schematic diagram of the apparatus used to produce fluctuating temperatures in a water bath.	8
3	Isotherms in Eunice Lake in 1970-1971 and 1971-1972.	16
4	Diel vertical distribution of old fourth-instar <u>C. trivittatus</u> larvae in Eunice Lake.	17
5	Total zooplankton in Eunice Lake in 1972.	19
6	Time of feeding of old fourth-instar <u>C. trivittatus</u> larvae on five dates in 1971-1972.	21
7	Depth of feeding of old fourth-instar <u>C. trivittatus</u> larvae on 20-21 September, 1971.	23
8	The species composition of the diet of fourth-instar <u>C. trivittatus</u> larvae and of zooplankton in Eunice Lake in 1972.	25
9	Growth of <u>Chaoborus</u> larvae in Eunice Lake-- 1971-1973.	26
10	Constant pressure respirometer design.	42
11	Incubation apparatus for micro-Winkler oxygen consumption measurements.	44
12	Strike and contact success of fourth-instar <u>C. trivittatus</u> larvae as a function of prey size.	49
13	Respiration rates of old fourth-instar larvae (1972 year-class) at different temperatures.	56
14	Respiration rates of young fourth-instar larvae (1972 year-class) at different temperatures.	57

15	Larval growth during Growth Experiment I.	60
16	Larval growth during Growth Experiment II.	62
17	Generalized flow diagram of the simulation model.	88
18	The effects of changes in the parameter values of selected parameters on larval growth.	92
19	The effect of migration pattern on larval growth -- natural prey densities.	97
20	The effect of migration pattern and surface prey density on larval growth.	98
21	The effect of migration pattern and prey density profile on larval growth.	100
22	The effect of migration pattern and temperature profile on larval growth.	102

LIST OF TABLES

Table		Page
1	Comparison of feeding by fourth-instar larvae during the day and night.	22
2	Mean and standard error of the time required for fourth-instar larvae to ingest different prey sizes and species, and the analysis of variance table for the differences between sizes and species.	50
3	Experimental measurements of larval sinking velocity and calculated friction coefficients.	53
4	Carbon assimilation efficiencies of fourth-instar <u>C. trivittatus</u> larvae fed on two prey types. The values are means $\pm$ 95% confidence limits.	54
5	Terms of the regression equations: $\ln(R) = \ln(a) + b(\ln(W))$ describing the relationship between oxygen consumption (R) and dry weight (W).	59
6	Results of a two-way analysis of variance with ration and temperature as main effects in Growth Experiment II.	64

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I. GENERAL INTRODUCTION

The vertical migration of planktonic animals is one of the most studied and least understood phenomena in aquatic biology. Biologists have been interested in vertical migration in both marine and fresh waters for at least 250 years. Early understanding of the migration process came from work on marine forms, but freshwater studies are well represented in the vertical migration literature (Hutchinson 1967). As techniques and understanding advanced, there has been a progression from descriptive studies on vertical distribution, to experimental work on the stimuli eliciting and mechanisms controlling the migration, and to experimental and theoretical studies aimed at explaining the adaptive value of this phenomenon (Russell 1927, Mauchline and Fisher 1969).

Vertical migrations occur in almost all groups of plankton and in some fish (Cushing 1951). Light became generally accepted as the stimulus initiating the migration, and light, in conjunction with physiological effects and other environmental factors, has been implicated in the control of the migration. Russell (1927) reviews early work on vertical distribution and control mechanisms.

Cushing (1951) proposed a general scheme for the migration pattern of all vertically migrating zooplankton based on light as the initiating and controlling stimulus. His pattern has four phases: 1) ascent from the day depth, 2)

midnight sinking, 3) dawn rise, 4) sharp descent to the day depth. This pattern, though developed with respect to marine forms, is valid for freshwater forms as well (Hutchinson 1967).

Several theories have been proposed to account for the adaptive value of vertical migration: escape from predators (Manteifel 1959a, b, Pearre 1973), horizontal transport (Hardy and Gunther 1935, Hardy 1956, David 1961), social control of population size (Wynne-Edwards 1962), energy gain (McLaren 1963, Kerfoot 1970), a combination of the above (Hutchinson 1967, Mauchline and Fisher 1969), and demographic effects (McLaren 1974). The merits of these theories are considered in Section V.

McLaren's (1963) hypothesis for the adaptive value of vertical migration is the only proposal to date that considers the energy budget of the migrating animal. He concludes that an "energy boost" accrues to migrants from the more efficient partitioning of energy to growth at low temperatures and that this "energy boost" can be used for growth, fecundity, etc. The object of this study was to examine the energetics of a vertically migrating zooplankter, to see if McLaren's hypothesized "energy boost" could be demonstrated, and to determine the physical and biological factors which affect its magnitude. Chaoborus larvae were chosen as the experimental animal because they are well known vertical migrators, they

are readily collected and easily maintained in the laboratory, and, since they are predators, their food consumption is easily monitored.

The study consisted of three phases. 1) Field studies were done to examine the vertical migration, feeding, and growth of C. trivittatus larvae. 2) Laboratory experiments were carried out to measure the elements of the energy budget equations $C=P+R+F+U$ and $A=P+R$ (C is consumption, P is growth, R is respiration, F is feces, U is excreted material and A is assimilation). 3) A generalized computer simulation model of vertical migration was used in conjunction with the results of field and laboratory studies to examine the effects of various vertical migration strategies, physical parameters, and biological parameters on larval growth.

Larvae of the "phantom midge", Chaoborus, are well known in the fauna of lentic freshwater. They typically spend the daylight hours buried in the mud, emerge at dusk and migrate into the water column to feed, and burrow into the mud again at dawn. Although their migration has fascinated biologists since it was first discovered, most of the literature on this aspect of their biology has been, and is still, descriptive (Juday 1921, Worthington and Ricardo 1936, Wood 1956, Roth 1968, Sikorowa 1973). Some quantitative experimental work has been done on the nature and control of the migration (Berg 1937, Teraguchi and Northcote 1966, LaRow 1968, 1969, 1970,

Chaston 1969). Studies on the ecology of Chaoborus have been particularly concerned with their migration, but some information on their feeding is available (Dodson 1970, Parma 1971, Fedorenko 1973). Studies on Chaoborus physiology have been wide in scope and include the following areas: locomotion (Nachtigall 1965), digestion (Gersch 1952, Montshadsky 1945), respiration (Jonasson 1972, Welch 1968), pupation and emergence (Deonier 1943, Parma 1971, Bradshaw 1973), anaerobiosis (Lindeman 1942, Sikorowa 1968, and Prokesova 1959). A Chaoborus bibliography has been compiled by Roth and Parma (1970) which includes most of the information on this fascinating animal published before 1970.

II. GENERAL METHODS

Study Area, Sampling, Holding Facilities

Experimental work in this study was carried out using fourth-instar larvae of Chaoborus (Shadonophasma) trivittatus (Loew) collected from Eunice Lake, British Columbia. Eunice Lake is a small oligotrophic lake in the University of British Columbia Research Forest near Haney, B. C. The lake lies at an elevation of 480m, has a mean depth of 15.8m, a maximum depth of 42m, and a surface area of 18.2 ha. It is usually ice covered from mid-December to April or May. Details of routine sampling methodology and the general ecology of C. trivittatus in the lake are given elsewhere (Fedorenko and Swift 1972). Special sampling techniques used for specific experiments are described in the pertinent sections. Larvae for experimental use were held in the dark at a constant temperature of 6° in the laboratory. All experiments were run within a few days of when the larvae were captured. Larvae were held with or without food depending on the experiment for which they were to be used; larvae were fed mixed zooplankton from Eunice Lake when necessary.

Controlled Temperature Facilities

Constant temperatures of 5° and $20^{\circ} \pm 1^{\circ}$ were maintained in Percival incubators (Percival, Boone, Iowa). Fluctuating temperatures ($7 - 15^{\circ}$ and $5 - 20^{\circ}$, Fig. 1) were produced in a water bath by alternately cycling cold and hot water. The rate of change was controlled by the degree of mixing of the two water supplies. The water supply system consisted of two 900 liter tanks each containing a submersible pump (Little Giant, model 1-42A) which supplied the water bath. Water return to the tanks was controlled by solenoid valves (Asco No. 7591S, Ascolectric Brantford Ltd., Brantford, Ontario) in each drain line (Fig. 2). The submersible pump and drain valve of each tank were wired to time switches such that the drain valves were open when the pumps were running. Water temperatures were maintained using refrigeration units bucking against room temperature (5° tank) and against a heating coil set above 20° (20° tank). Operation of the two systems was under the control of two time switches (Intermatic, Model T101).

Carbon-14 Assays

All carbon-14 assays were done by liquid scintillation counting (Nuclear Chicago, Isocap/300 or Mark I) with external standard quench correction. Soluble aqueous samples (up to 1 ml) were counted in 10 ml of Bray's scintillation solution (4g PPO, 2g POPOP, 60g naphthalene, 100 ml methanol, 20 ml ethylene

FIGURE 1

Diel fluctuating temperature regime for growth experiments I (A) and II (B). Temperatures are shown for one week in both cases.

FIGURE 2

Schematic diagram of the apparatus used to produce fluctuating temperatures in a water bath. Legend: 1. Inlet hose from 20° tank, 2. Inlet hose from 5° tank, 3. Outlet to 20° tank, 4. Outlet to 5° tank, 5. Heating coil, 6. Submersible pumps, 7, 8, 9. Experimental aquaria.

glycol, made up to 1 liter with 1, 4-Dioxane). Particulate material on filters was combusted or counted in Bray's solution with Cab-O-Sil (finely divided silica) added to form a gel to keep particulate material in suspension. Particulate material was dried and combusted in a tube furnace (Lindberg Hevi-Duty) at 500-600° under a stream of oxygen. Carbon dioxide in the outflow stream was collected in 8 ml of ethanolamine trapping solution (Jeffay and Alvarez 1961) in a Vigreux column. Following combustion and 10 minutes of flushing, the trapping solution was rinsed into a scintillation vial with 10 ml of a toluene scintillation solution (5g PPO, 0.3g POPOP, made up to 1 liter with toluene) and then counted. The efficiency of this combustion procedure has been checked with various amounts of particulate material and known amounts of ^{14}C -glucose, and the recovery was found to be virtually 100%. Raw counts were converted to disintegrations per minute (dpm) and corrected for background before analysis.

Larval Dry Weights and Calorimetry

Larvae were collected using diagonal hauls from 20-0m every two weeks in 1971 and every week in 1972 with a 30cm or 60cm square net. Several samples were taken during the winter of 1971-1972. Samples were sorted and dried at 100° in 1971 and 60° in 1972. The larvae were separated from potential food just after capture and no larvae with freshly caught prey in

their crops were used. Generally 5 or more replicate weights were measured per instar with the number of larvae per replicate varying from 50-100 for the first and second instars to 10 for the fourth instar. All samples were weighed on a Cahn Gram Electrobalance.

Caloric content of young and old fourth-instar larvae was measured in early spring using a Phillipson oxygen microbomb calorimeter (Phillipson 1964) manufactured by Gentry-Weigert Instruments Inc., Aiken, South Carolina. Samples were dried at 60° for three days and stored in a desiccator until used. Five replicates of each sample were combusted. Caloric content was calculated as calories per gram dry weight.

Nomenclature

Because C. trivittatus has a two year life cycle (Fedorenko and Swift 1972) there are two year-classes of fourth-instar larvae present in the lake during part of the summer. I have used the terms "old" and "young" to discriminate between the year classes. Old fourth-instar larvae are those larvae that are in their second summer or winter, and young fourth-instar larvae are those in their first summer or winter. All temperatures referred to are degrees Centigrade. I have used generic names to refer to the various animals discussed after they are first mentioned except for those genera which are represented by more than one

species; these are referred to by their generic and specific names.

III. FIELD STUDIES

Introduction

In order to assess the role of energetics in the adaptive value of vertical migration, it is necessary to know the timing and magnitude of the migration and the temporal characteristics of those biotic and abiotic parameters which affect the energetic budget of the migrator. Preliminary analysis of Chaoborus vertical migration suggested that temperature, through its effect on various temperature dependent rates, and prey density and distribution, through their effect on larval feeding, are the two most important field parameters affecting the energetics of Chaoborus larvae. The field portion of this study was designed to answer four questions. 1) What is the vertical migration pattern of C. trivittatus in Eunice Lake ? 2) What are the physical and biological characteristics of the environment the larvae live in? 3) What are the characteristics of larval feeding? 4) What are the characteristics of the growth of the larvae in the lake? The results of these field studies provide a reference data base for use in the construction of a generalized model of a vertically migrating Chaoborus larva.

Methods

Temperature, plankton vertical distribution, and larval growth were monitored using the methods of Fedorenko and Swift (1972). Temperature and larval growth were measured weekly from May to November. Vertical distribution of larvae and zooplankton was monitored using a Clarke-Bumpus (C-B) plankton net with a No. 20 (0.08mm) nylon net. Samples were taken weekly at noon and midnight using diagonal hauls spaced every 2m from 0-20m. The diagonal hauls were made by slowly raising the C-B sampler 2m while the boat was moving.

Food of the larvae was determined directly by dissecting the crop and enumerating its contents following the method of Swift and Fedorenko (1973). Crops were characterized by the presence or absence of food, and the degree of digestion of the food. Prey items from the crops were designated as "fresh" if they were identifiable as entire, individual zooplankters. This definition excluded animals whose exoskeleton was macerated from the "fresh" category. The rate of digestion varied with temperature and prey type; Bosmina remained "fresh" for about one hour, and D. kenai remained "fresh" for about three hours at summer surface temperatures. These partial digestion times were longer at lower temperatures. Results of these analyses are expressed as the percentage of crops that contained any amount of food and the percentage of crops that contained fresh food.

The time of day that the larvae fed was determined by sampling every three hours over a 24 hour period. This was done on 29 September, 1971, and on 17 July, 8 August, 6 September, and 7 October, 1972. In 1971 horizontal hauls were made at 2m intervals (1-21) with a 30cm square net with the frame fixed to a weighted line. There was probably little contamination from depths not being sampled because the net opening was held vertically when the net was being raised or lowered; the larval distribution based on this method agreed well with that based on C-B samples from the same depths. In 1972 samples for determining time of feeding were collected using vertical hauls with a 1m net.

The 24 hour samples from 1971 were used in conjunction with rates of digestion to directly determine the depth at which feeding takes place.

Results

Temperature

The temperature regime in Eunice Lake was similar during the two years of this study (Fig. 3). In both years a stable thermocline developed at about 4m during the summer months. The sharp decrease in temperature in early July 1972 was due to extremely high rainfall over a period of three days.

Vertical Migration

The migration pattern of C. trivittatus larvae in Eunice Lake generally follows the pattern described by Cushing (1951). The particular form of the depth distribution and migration is instar specific and has been described by Fedorenko and Swift (1972, Fig. 9). The larvae considered in this study are the old fourth-instar larvae. During the summer they spend the day at about 12m, begin to move upward at 1800 hours, reach 3m by 2100 hours, and then sink slowly to the day depth by 0900 hours (Fig. 4). There is little suggestion of a dawn rise. Only about one hour is spent at 3m. This pattern of diel migration is found from May to November. In the winter the larvae are distributed throughout the water column (Fedorenko and Swift 1972).

FIGURE 3

Isotherms in Eunice Lake in 1970-1971 and 1971-1972. Temperatures are in degrees Centigrade.

FIGURE 4

Diel vertical distribution of old fourth-instar C. trivittatus larvae in Eunice Lake. The width of the kite diagrams represents numbers per 100 liters (after Fedorenko and Swift 1972, Fig. 9).

Zooplankton Distribution

Five species, exclusive of Chaoborus, dominate the zooplankton in Eunice Lake on both a number and biomass basis. These are the copepods Diaptomus kenai and D. tyrelli and the cladocerans Daphnia rosea, Holopedium gibberum, and Diaphanosoma brachyurum (Fedorenko and Swift 1972). The zooplankton are distributed throughout the water column (Fig. 5, data from A. Fedorenko) but they are most numerous above 4-6 meters. The prey density in the epilimnion is as high as 600 - 1000 per 100 liters for a short time in June and July but is generally about 400 per 100 liters. The 200 animals per 100 liters isopleth is deeper than 6m only during late September. Throughout the year the density in the hypolimnion is low -- 0-100 animals per 100 liters. There is some diel change in the vertical distribution of some species, but only D. kenai and D. rosea are found below 6m; at night D. kenai spreads over the entire water column as deep as 20m from its day depth of 3m and D. rosea migrates from its day depth of about 9m up to 2m (A. Fedorenko, pers. comm.).

FIGURE 5

Total zooplankton in Eunice Lake in 1972. The lines are zooplankton density isopleths (number per 100 liters). Sampling was done at noon on the dates indicated by arrows. Nauplii, rotifers, and Chaoborus larvae are not included.

Feeding

Only a small proportion of the larval population feeds on a given day (Fig. 6). At most only 40% of the larvae examined had full crops and less than 20% had fresh prey in their crops. There was no significant difference in the number of larvae with full crops during the day (first 4 sampling times in Fig. 6) and night (second 4 sampling times) on any date sampled in 1971 or 1972 (Table 1). In July and October 1972 significantly more larvae had fresh prey in their crops at night than during the day; there was no significant difference on the other dates sampled (Table 1). Larvae with no food in the crop are capable of feeding at any time of the day or night if prey are available. The larvae in freshly caught, concentrated zooplankton samples all catch prey within an hour of the time they are collected.

Data from horizontal tows taken over a 24 hour period in 1971 indicate that old fourth-instar larvae begin feeding about 1800 hours when they are at a depth of 10m and continue to feed during the night (Fig. 7). There is some evidence that feeding occurs during the day, but it is probably an artifact of slow digestion of previously captured prey resulting from low day-depth temperatures.

Fourth-instar C. trivittatus larvae are able to feed on the entire size range of prey in the lake from rotifers (0.1mm) to D. kenai (2.3mm). There are seasonal changes in

FIGURE 6

Time of feeding of old fourth-instar C. trivittatus larvae on five dates in 1971-1972. Percentage full crops (solid circles and squares) and percentage crops containing fresh prey (open circles) are plotted against sampling time. The squares are 1971 data.

PERCENT

Table 1. Comparison of feeding by fourth-instar larvae during the day and night.

Date	d.f.	Full Crops		Crops containing fresh food	
		χ^2	p	χ^2	p
21 Sept. 1971	1	2.37	.1-.25	---	---
17 July 1972	1	0.308	.5-.75	8.26	<.005
8 Aug. 1972	1	0.153	.5-.75	0.35	.5-.75
6 Sept. 1972	1	2.40	.1-.25	3.05	.05-.1
7 Oct. 1972	1	0.65	.25-.5	12.04	<.005

FIGURE 7

Depth of feeding of old fourth-instar C. trivittatus larvae on 20-21 September, 1971. Percentage full crops is plotted against depth at each sampling time. At each depth plotted, $n \geq 20$.

prey species densities, but almost the entire spectrum of prey types is found in the diet throughout the summer (Fig. 8a). Three species -- D. kenai, D. tyrelli, and Holopedium make up most of the zooplankton biomass in the lake (Fig. 8d). Of these three, only D. kenai and D. tyrelli are eaten to any great extent. Holopedium is seldom found in the diet because it is too large to be easily captured. Most of the biomass in the diet of old fourth-instar larvae comes from eating D. kenai. This copepod constituted 30% or more of the biomass of the diet in each month sampled, and as much as 70% (Fig. 8b). Old fourth-instar larvae appear to feed selectively on D. kenai; this species is found in the diet in much higher proportions than in the lake. Bosmina is numerically much more abundant in the lake than in the diet, and D. tyrelli is eaten roughly proportionally to its density.

Larval Growth in the Field

The pattern of growth of C. trivittatus larvae in the field was essentially the same in 1971 and 1972. The eggs hatch in mid-June and the larvae grow for two summers before emerging (Fig. 9, from Fedorenko 1973). At any time during the year, except for a short time before the eggs hatch in the spring, there are two year classes present in the lake. From October to June both year classes are in the fourth instar. In their second year the larvae grow at a faster rate than they do in their first year (Fig. 9); these two growth patterns

FIGURE 8

The species composition of the diet of fourth-instar C. trivittatus larvae and of zooplankton in Eunice Lake in 1972. A. Percentage frequency of occurrence of prey in larval crops. B. Percentage composition by weight of prey in larval crops. C. Percentage frequency of occurrence of some zooplankton in Eunice Lake. D. Percentage composition by weight of some zooplankton in Eunice Lake. Rotifers and Chaoborus are not included in C and D. The species code is as follows: R -- rotifers, B -- Bosmina, P -- Polyphemus, D -- Daphnia, H -- Holopedium, C -- Diaphanosoma and miscellaneous cladocerans, K -- D. Kenai, T -- D. Tyrelli, O -- Chaoborus larvae, X -- unidentified material.

FIGURE 9

Growth of Chaoborus larvae in Eunice Lake--
1971-1973. The points are mean dry weights $\pm$ 95%
confidence limits. The numbers indicate the year
class of the larvae.

were similar in both years of this study. Although the weight at the end of the first and second summer appears relatively constant over the three years studied, the larvae have the potential to grow at a much faster rate. In a 28 day in situ experiment testing growth at high food densities, old larvae reached a higher weight than their counterparts in the lake control (1.58mg as compared to 1.28mg); young larvae grew to the same weight as the old larvae and four times the weight of their counterparts in the lake during the course of the experiment (1.78mg as compared to 0.38mg) (Fedorenko 1973).

Discussion

The most prominent feature of the biology of Chaoborus larvae is their regular, diel vertical migration. The migration pattern in Eunice Lake is similar to that found in most chaoborid populations except that these larvae spend the daylight hours in the deep cold waters of the hypolimnion instead of being buried in the sediment (Fedorenko and Swift 1972). Teraguchi and Northcote (1966) found a similar migration pattern in C. flavicans in Corbett Lake, British Columbia. The descriptive characteristics of the migration, although interesting, are not as important in this study as the physiological consequences resulting from migration through the physical and biological gradients present in the lake (temperature, oxygen concentration, light, and prey density).

The stable thermocline in Eunice Lake is typical of small, deep, temperate lakes in the summer. The presence of the thermocline throughout the summer has a considerable effect on the daily thermal regime of the vertically migrating larvae. Typically, old fourth-instar larvae encounter a wide range of temperature ($5^{\circ} - 20^{\circ}$) during their migration in July and August, and a narrower range in June, September, and October.

The entire water column in Eunice Lake is well oxygenated throughout the year (Fedorenko and Swift 1972). Although low oxygen concentration has been suggested as a regulatory mechanism for vertical migration in C. punctipennis (LaRow 1970), it seems unlikely that oxygen concentration has any effect on vertical migration in Eunice Lake.

Because of light attenuation with increasing depth and the light-dark cycle, light has long been implicated as a controlling factor in the vertical migration of zooplankton. Teraguchi and Northcote (1966) suggested that light intensity was a controlling factor in Chaoborus migrations and LaRow (1969) showed that a critical low light intensity was required to initiate migration. The vertical migration of C. trivittatus in Eunice Lake is probably under photoperiodic control.

In lakes like Eunice Lake which have a low transparency

(Secchi depth 5-6m), most primary production takes place near the surface in the relatively well mixed epilimnion. This layer also supports the highest density of herbivorous zooplankton -- the food of Chaoborus. The distribution of total zooplankton in Eunice Lake clearly demonstrates the sharp gradient in productivity with depth.

One of the explanations commonly given for vertical migration is that zooplankton, whether herbivorous or carnivorous, migrate into the food-rich euphotic zone in order to feed (Hardy 1956, McLaren 1963). The depth at which fourth-instar larvae fed was determined by examining the time and depth where feeding occurred, and by comparing known predator and prey distributions with the actual diet. Although the two ways of examining this question gave somewhat different results, it was clear that most feeding occurred in the epilimnion at night. One of the most surprising findings was that a large proportion of the larval population had no food in their crops at any time. It appears that many larvae do not readily feed either at the relatively high prey densities found in the epilimnion, or at the relatively low prey densities in the hypolimnion.

Estimates of feeding time based on full crop data were found to be less indicative of the actual feeding time than estimates based on the occurrence of fresh prey because of the different digestion times of the various prey types. Thus, no

diel feeding periodicity was indicated by the full crop data, but a feeding peak at night was indicated in July and October by the occurrence of fresh prey in the crops. Analysis of diel feeding periodicity on some prey species taken individually shows a clear feeding peak at night (Fedorenko 1973).

Data on the depth where feeding occurs support the fresh prey occurrence results. Feeding activity, shown by the percentage of full crops at different depths, occurs at night when the larvae are in the epilimnion and are feeding on prey that are restricted to the epilimnion. The apparent feeding during the day (0900-1500) is probably the result of slow digestion of prey captured prior to the sampling time. Prey capture at the day depth is unlikely because of low prey density. The increase in feeding at 1800 hours takes place at the depth and time that the upward migrating larvae overlap with the downward migrating D. kenai.

Knowing the feeding functional response curves of old fourth-instar larvae and the zooplankton depth distribution, one can predict the time that feeding is most likely to occur. For old fourth-instar larvae the feeding functional response curves for D. kenai and D. tyrelli show feeding saturation at prey densities of about 10 and 100 prey per liter respectively (Fedorenko 1973). Since these prey densities do not occur at the day depth of old fourth-instar larvae, one can infer that feeding must occur at night. Analysis of the larval diet shows

this to be the case. The old fourth-instar larvae feed more or less in proportion to prey abundance. On a numerical basis Bosmina and D. tyrelli, the two most abundant prey, are eaten most frequently throughout the summer. They are both found above 5m at all times. On a biomass basis, feeding does not appear to take place entirely at the surface. Diaptomus kenai, the principal prey throughout the summer, is distributed below 5m during the night. Since the larvae overlap spatially with D. kenai throughout the migration period (dusk-dawn), D. kenai may form the principal prey taken below the thermocline. If this is the case, old fourth-instar larvae could be feeding primarily while below the thermocline.

The physiological effects of exposure to the physical and biological gradients discussed above determine larval growth. Fedorenko and Swift (1972) discuss the growth of C. trivittatus larvae and suggest that the two year life cycle seen in this species is due, in part, to low food availability. A field test of this hypothesis has shown that the larvae have the potential to grow very rapidly if provided with large amounts of food (Fedorenko 1973). Both one year old larvae and young of the year larvae grew to their normal pupation weight after only 28 days of high food (Fedorenko 1973). The experiment was terminated in late fall and it wasn't possible to determine whether these "heavy" one year old larvae would pupate if given the appropriate light conditions. While large amounts of food allow the larvae to

grow much faster than in the field, it is interesting to look at the differences in in situ growth among year-classes. The differences in final weight of the three year-classes studied (1969, 1970, 1971) were most probably due to variations in overall food levels. Prey densities were higher in the summer of 1971 than they were in 1972, although the species composition did not change.

Summary

1. Fourth-instar larvae in Eunice Lake undergo a regular diel vertical migration throughout the summer.

2. The migration exposes the larvae to a wide range of temperatures and prey densities.

3. Because of the zooplankton distribution in Eunice Lake, most feeding by old fourth-instar larvae takes place at night near the surface. However, D. kenai may be eaten below the thermocline.

4. The entire spectrum of prey species in Eunice Lake is vulnerable to predation by old fourth-instar larvae. The larvae appear to feed on the various prey species in proportion to their density; D. kenai is the main source of biomass in the diet.

5. Larval growth in Eunice Lake appears to be lower than its potential maximum because of low food availability. Variations in zooplankton density probably account for the differences in growth among year-classes.

IV. ENERGETICS STUDIES

Introduction

The energy budget of an animal is stated (Ricker 1971) by the equations $C=P+R+F+U$ and $A=P+R$ where C is consumption -- the total intake of food during a specified time interval, P is production (growth) -- increase in biomass, R is respiration -- that part of assimilation which is converted to heat or mechanical energy and is used up in life processes, F is egesta -- that part of the total food intake that is not absorbed, U is excreta -- that part of the material absorbed that is passed from the body as urine or through the gills or skin, and A is assimilation (physiologically useful energy) -- the food absorbed less the excreta. All the elements of these equations except C and U were measured individually for old fourth-instar larvae in this study. Consumption (C) data were available (Fedorenko 1973). Excreta (U) was not estimated because it could not be separated from liquid egesta.

Temperature, pressure, and light are the most variable environmental factors encountered by migrating larvae. The pressure change experienced by these larvae is relatively small (1-4 atmospheres), and light has not been shown to have much effect on physiological reaction rates in invertebrates. The effects of these two factors were not examined. Temperature, however, is known to affect physiological

reaction rates, and the larvae were exposed to a wide temperature range (8-20°) during their migration. The effect of temperature on respiration rate was measured directly, since respiration probably represents the major energy loss of the larvae. Consumption and assimilation have been shown to be unaffected by temperature changes (Fedorenko 1973 for C, Lawton 1970 for A). The interaction of temperature and ration size was measured to provide information about consumption (C) and growth (P). The effect of temperature on digestion rate was measured by Fedorenko (1973).

Any consideration of the overall energetics of vertical migration requires an assessment of the metabolic cost of the swimming involved. Most previous studies have assumed, implicitly or explicitly, that this cost is high. Recent studies (Hutchinson 1967, Vlymen 1970) have suggested that this is not the case. Therefore, an attempt was made to assess the swimming cost of old fourth-instar C. trivittatus larvae.

Consumption is the only component of the prey capture process which appears in the energy budget equation. Feeding efficiency, the proportion of attempted captures that are successful, is an important part of any study of feeding. Experiments to quantify this parameter are included in this section.

The integration of all the factors affecting energy gain and loss to an animal is expressed as a change in the weight

of the animal. In an attempt to quantify the effect of prey density and temperature on energy gain and loss, I conducted two growth experiments. The results of these experiments were used to test the generalized model of vertical migration.

The results of the following studies on the parameters of the energy budget equation, on the swimming cost of migration, and on the feeding efficiency were used, in conjunction with field results, as input data for the general model of Chaoborus vertical migration discussed in a later section.

Methods

Strike Efficiency, Contact Efficiency, Handling Time

The strike efficiency, $(\text{captures}) / (\text{strikes} + \text{contacts} + \text{captures}) * 100\%$, and contact efficiency, $(\text{captures}) / (\text{contacts} + \text{captures}) * 100\%$, were measured by watching larvae strike at different prey sizes. The prey were copepods (D. kenai) and cladocerans (D. rosea) varying from 0.6mm to >3.0mm in length. Experiments were carried out at various times of the day with 20-25 larvae in 200-250ml of water at about 10° and incandescent or fluorescent room lighting. All larvae were starved for between one and two days before being used in the experiments. The larvae were exposed to two prey at a time and the number of strikes, contacts, and captures was recorded over a period of 20 minutes to one hour. For the smallest prey the larvae were placed individually into 200ml of water with about 200 prey. A strike was defined as a definite striking movement at a prey in close proximity to the larva; this definition excluded strike-like movements which occurred when no prey were near. A contact was defined as a strike which succeeded in hitting or holding the prey item but was not followed by successful ingestion. A capture was defined as the successful ingestion of a prey item. Captures were scored as contacts also. Confidence limits for the proportion captured for $n > 30$ were calculated from the normal approximation to the binomial distribution (Snedecor and

Cochran 1967) and for $n < 30$ from tabulated values of confidence limits of proportions (Crow 1956).

Handling time was measured, using a stopwatch, from the time contact was made to the time the prey had fully passed the posterior margin of the head capsule. In most cases it was possible to see whether the prey had been ingested head or tail first.

Friction Coefficient

Neither the 14-carbon nor the oxygen method was suitable for directly measuring the metabolic cost of vertical migration. It was necessary, therefore, to approximate this cost with some measureable quantity. I chose the cost of overcoming friction over the distance migrated as an estimate of the cost of vertical migration. A body sinking through the water has an upward force of $VD_wg + fv$ and a downward force of VD_ag where V is the volume, D_w is the density of water, D_a is the density of the body, g is the acceleration due to gravity, v is the velocity of the body, and f is the friction coefficient. At constant velocity, $VD_wg + fv = VD_ag$ and $f = g(VD_a - VD_w)/v$. The friction coefficient was measured experimentally from the sinking rate of fourth-instar C. trivittatus larvae which were artificially weighted by inserting pieces of insect pin the length of the body cavity. The time it took the larva plus pin to sink through 100cm of

water was measured. The pin was entirely within the body cavity and the larva was allowed to sink 20cm before reaching the measured 100cm. Only trials in which the body of the larva containing the pin was in its natural position (horizontal and dorsal side uppermost) were used in the calculation of v . Six different larvae were used to measure v and 6-7 measurements of v were made with each larva before it lost its natural shape and was discarded. The parameters VDa and VDw were measured by weighing the larva containing the pin ($W2$), a known volume of water ($W1$), and the water + larva and pin - displacement ($W3$). Thus $VDa=W2$ and $VDw=(W1+W2)-W3$. The acceleration due to gravity is a constant.

Assimilation

Assimilation efficiency of old fourth-instar C. trivittatus larvae was measured for both a cladoceran (D. rosea) and a copepod (D. kenai). The method essentially followed that of Sorokin (1968).

Labelled algae were prepared by growing cultures of Scenedesmus or Chlamydomonas in 1 liter of Bristol's medium with approximately 42.5 μ C of 14 C-bicarbonate added to it. The labelled algae were centrifuged and resuspended in unchlorinated water. Daphnia were grown on the labelled algae by starting with females carrying embryos that were almost ready to hatch. The newly hatched Daphnia were allowed to grow

on the labelled algae for about one week. Diaptomus were put into the labelled medium as copepodites and allowed to feed for about a week. These procedures produced prey having about 15,000 cpm per individual. Chaoborus larvae were fed a single labelled prey item and immediately placed into unchlorinated water with a pH of about 9.

Ten dishes, each containing five larvae in 200ml of water, were incubated at 15° for 3-5 days. Each day the larvae were transferred to fresh water containing unlabelled food, and the water they had been in was assayed for radioactive carbon in the particulate, CO₂, and dissolved organic fractions. At the end of the experiment the larvae were assayed for 14-carbon. The total amount of labelled carbon ingested was taken as the sum of all the 14-carbon recovered -- particulate, CO₂, dissolved organic, and larval. The assimilation efficiency was taken as: (CO₂-dpm + DOM-dpm + larval-dpm) / total-dpm.

Assimilation efficiency was also measured by comparing the weights of consumed food and undigested material (A=C-F-U). For this experiment I assumed that, on a weight basis, liquid egesta (a portion of F) had a negligible weight relative to solid egesta (the remainder of F) and may be ignored. The formula for assimilation efficiency reduces to $A=C-F/C \times 100\%$. Single D. kenai from a population with a known average dry weight were fed to fourth-instar larvae which were

allowed to egest any undigested material. Five dishes, each containing 10 fed larvae in 200ml of water were held at 15° for 24 hours. The larvae were removed and the water filtered through pre-weighed Ha Millipore filters (pore size 0.45u). The filters were dried at 50° and weighed. The amount assimilated was taken as (weight of egested material) / (weight of one copepod) * 100%.

Respiration Rates

Respiration rates of young and old fourth-instar larvae were measured in the fall of 1972 using constant pressure respirometers. Two respirometers were used: one with a measuring capacity of 5.5ul constructed from a design of Klekowski (1968), and one with a 50ul capacity from Dr. Klekowski's laboratory (Fig. 10). The respirometer chambers were 5ml round bottom flasks connected to the respirometer with ground glass joints. The chambers contained 2-3ml of lake water and one old or two young fourth-instar larvae; carbon dioxide respired by the larvae was absorbed in about 0.1ml of 20% KOH on filter paper. Respiration rates were measured at 5, 10, 15, 20, and 25°; temperatures were maintained within 1° using a water bath.

The larvae were held with food at 6° after being collected. All respiration measurements were done within one week after capture. There was no food in the crops of the

FIGURE 10

Constant pressure respirometer design. A. Detail of the scale tube and adjustment rod. B. Detail of the sidearm and reaction flask. C. View of the entire apparatus. Legend: 1. Mercury level adjustment rod, 2. Mercury, 3. Scale tube, 4. Index mark, 5. Opening from flasks to the atmosphere, 6. Reaction flask, 7. Filter paper for carrying KOH, 8. Control flask, 9. Experimental flask, 10. Plexiglas stand, 11. Water level during operation, (after Klekowski 1968).

larvae used in the experiments. After the larvae were placed in the flasks a one hour equilibration period was allowed before measurements were begun. Incubation time varied according to the temperature but was between three and 30 hours. Measurements were made every 15 minutes during short incubations and every few hours during long ones. After the measurements were completed the larvae were killed in hot water, dried at 50°, and weighed. Oxygen consumption at STP was calculated per individual and per milligram dry weight. Mean respiration rates at each temperature were fitted to the equation

$$\text{Respiration Rate} = aW^b$$

where a is a constant, W is the dry weight of the larvae, and b is the slope of the regression line of $\ln$ respiration rate against $\ln$ dry weight. Respiration rates are given in units of $\mu\text{l mg}^{-1} \text{ hr}^{-1}$ and $\mu\text{l individual}^{-1} \text{ hr}^{-1}$.

Respiration rates of young fourth-instar C. trivittatus larvae were measured at 5, 10, 15, and 20° using a micro-Winkler method for determining oxygen concentration. Incubations were carried out in 50ml flasks with 10ml syringe reservoirs connected to them by needles inserted through rubber stoppers and with Silastic-filled sampling ports in the sides (Fig. 11). The water used in the incubations was saturated with oxygen at 20° and cooled to 6°. The following procedure was used for each experiment. A flask was filled with water and 8-10 larvae were added. A rubber stopper was

FIGURE 11

Incubation apparatus for micro-Winkler oxygen consumption measurements. Legend: 1. 5 ml syringe, 2. Silastic-filled rubber stopper, 3. 50 ml flask, 4. Silastic-filled sampling port.

inserted which displaced water into the syringe. The syringe barrel was filled with water, a needle was inserted through the sampling port and the syringe plunger was pushed into the barrel so that air was excluded and about 3ml of water were displaced out the sampling port. Water removed from the flask through the sampling port during sampling was replaced by water from the syringe reservoir. The flasks were placed at the experimental temperature for two hours before measurements began. Initial and final oxygen concentrations (three replicates each) were measured with a 6-24 hour incubation period depending on the experimental temperature.

The dissolved oxygen determinations were made in the following way. After rinsing the syringe with 0.2ml of water from the flask, a 1.2ml sample was drawn into the syringe and 0.05ml of manganous sulphate and alkaline-iodide-azide solutions were added deep in the sample through the syringe tip. The needle was replaced and 0.2ml of sample was displaced. The needle was stoppered, and the syringe was shaken and stood on end so that the precipitate would settle. One ml of 5% sulphuric acid was pulled into the syringe to liberate the iodine and this was titrated to the starch endpoint with a 100mg per liter solution of sodium thiosulphate standardized each day against 0.0005M biiodate.

After incubation the larvae were dried at 100° and weighed. Oxygen consumption at STP was calculated as the

difference in oxygen concentration between initial and final measurements and converted to $\mu\text{l mg}^{-1} \text{ hour}^{-1}$.

Growth Experiment I

Fourth-instar C. trivittatus larvae were fed excess food from August 17 to October 12, 1971 under three temperature regimes to examine the effect of temperature on growth. Two hundred larvae were held in aquaria at constant 5° and 20°, and fluctuating 8-16° temperature regimes. The fluctuating temperature regime was 8° for 16 hours (0400-2000), 16° for four hours (2200-0200), and was changing for four hours (Fig. 1). This was approximately the temperature change experienced by the larvae migrating in the lake during summer. The larvae at all three temperature regimes were fed mixed Eunice Lake zooplankton (primarily D. kenai, D. tyrelli, and Daphnia) every two days for six weeks; excess food was present at high densities at all times. The 5° and 20° tanks were exposed to a 16:8 light:dark regime in incubators. The fluctuating temperature aquaria were exposed to an approximately 12:12 light:dark regime. More accurate light control was impossible in the facilities available. Larvae were removed for dry weight measurements periodically during the course of the experiment. Growth was taken as the difference between the initial and subsequent dry weights.

Growth Experiment II

Growth experiments were repeated using three temperature regimes and three food levels. The experiments ran from November 3 to November 24, 1971. Two hundred larvae were held in seven liter aquaria at 5°, 20°, and fluctuating 5-20° temperature regimes. The fluctuating temperature regime was 5° for 16 hours (0300-1900), increasing to 20° for three hours (1900-2200), 20° for three hours (2200-0100), and decreasing to 5° for two hours (0100-0300) (Fig. 1). Light was controlled at 16:8 light:dark in the 5° and 20° incubators. The light regime for the fluctuating temperature tanks was uncontrolled but was usually 12:12 light:dark. Food consisted of mixed plankton from Eupice Lake. The three food levels were no prey, 100 prey , and 600 prey aquarium⁻¹ day⁻¹ and corresponded to 0 prey larva⁻¹ day⁻¹, 0.5 prey larva⁻¹ day⁻¹, and 3 prey larva⁻¹ day⁻¹ respectively. The middle prey density approximated the lake prey density. Prey levels were maintained by sampling the remaining prey each day and adding enough plankton to bring prey densities up to the required level. Growth was measured as before.

Results

Strike Efficiency, Contact Efficiency, Handling Time

Strike efficiency and contact efficiency decreased as prey size increased (Fig. 12). The upper size limit for Daphnia was between 2.2 and 2.6mm. The larvae were more likely to avoid or push weakly away from these large Daphnia rather than strike at them. The upper size limit for Diaptomus was probably about the same, but no copepods in this size range were available for testing. The size at which these two prey types became too small to be captured was less than 0.6mm and was below the sizes available for testing.

Strike efficiency was virtually the same on all sizes of both prey types. Contact efficiency was considerably higher on the copepods D. kenai and D. tyrelli than on Daphnia but only when prey size was greater than 1mm.

The time required to ingest a captured prey item increased as prey size increased for both prey species (Table 2). Larvae ingested Diaptomus faster than they ingested Daphnia. The smallest prey tested were ingested faster than could be measured manually -- generally in about two seconds. A two way analysis of variance was used to test the null hypothesis that there was no difference in ingestion time between the two prey species and between the prey sizes within each species. All the data were transformed using the ln

FIGURE 12

Strike and contact success of fourth-instar C. trivittatus larvae as a function of prey size. Data are means $\pm$ 95% confidence limits for strike success (Daphnia-- solid circles and Diaptomus-- open circles) and contact success (Daphnia-- solid squares and Diaptomus-- open squares).

Table 2. Mean and standard error of the time required for fourth-instar larvae to ingest different prey sizes and species, and the analysis of variance table for the differences between sizes and species.

Prey Type	n	Prey Size (mm)	Ingestion Time (sec)	
		mean	mean	SE
<u>Daphnia</u>	28	1.0	24.3	5.6
	24	1.4	74.2	10.8
	21	1.8	210.5	44.1
<u>Diaptomus</u>	16	1.0	5.0	0.2
	22	1.4	11.4	1.1
	35	1.8	103.64	28.0

Analysis of Variance Table

Source	d.f.	SSQ	MS	F	p
Species	1	2.98	2.980	60.92	<0.001
Size	2	4.62	2.310	47.16	<0.001
Species X Size	2	0.11	0.055	1.13	0.326
Error	130	127.50	0.049		

transformation to correct for unequal variances. A significant difference was found in ingestion times between prey species and between sizes within each species (Table 2). There was no significant interaction between size and species on ingestion time.

Energy Cost of Vertical Migration

Chaoborus larvae are able to regulate their density over a considerable range by means of two pairs of air bladders (Damant 1924). When a larva is neutrally buoyant at a particular depth it is at an unstable equilibrium point -- an increase in density will cause it to sink, and a decrease in density will cause it to rise. In addition to the possible density mechanism for changing depth, mentioned above, the larvae can migrate by swimming, i.e. by flexing and extending their bodies rapidly and then gliding. The glide may be in any direction. Whatever mechanism is used to migrate, a larva must at least overcome the force of friction along its migration path.

The energy required for the migration was calculated from the equation $E = (fvs) / (eff)$ where E is the energy required (ergs), f is the friction coefficient for the larva moving perpendicularly to the long axis of its body (gm/sec), v is the velocity of movement (cm/sec), s is the distance travelled (cm), and eff is the metabolic efficiency (the efficiency of

converting the potential energy in food to kinetic energy).

Experimental values for v were similar between trials with the same larva and for different larvae (Table 3). The friction coefficient was between 0.0 and 1.0 gm/sec in all trials.

High values of v (0.33 cm/sec, Teraguchi and Northcote 1966), f (1.0 gm/sec), and s (20m), and a low value of eff (1%) were used in the calculation in order to produce a high estimate of the energetic cost of vertical migration (E). This calculation yields the result: $E = 6.6 \times 10^4$ ergs. Using an oxy-calorific conversion factor of 4.89×10^{-3} cal per ul oxygen, $E = 0.32$ ul oxygen for one half of the daily migration. Using a resting metabolic rate of about 24 ul oxygen per day (1.0 ul oxygen individual⁻¹ hour⁻¹ at 10°, Fig 13) the calculated cost of a complete migration (0.64 ul oxygen) is less than 3% of the daily metabolic rate.

Assimilation Efficiency

The efficiency of carbon assimilation by fourth-instar C. trivittatus larvae is shown for a cladoceran and a copepod (Table 4). Assimilation efficiency was essentially the same for both of these prey types. The low mean assimilation efficiency for the one day experiment is the result of one very low value. There was good agreement between assimilation efficiencies for copepods as measured by the ¹⁴-carbon and the

Table 3. Experimental measurements of larval sinking velocity and calculated friction coefficients.

Trial	Sinking Velocity	Friction Coefficient
	mean $\pm$ 1 S. D.	
1.	8.76 $\pm$ 0.29	0.39
2.	9.35 $\pm$ 0.46	0.42
3.	9.08 $\pm$ 0.37	0.68
4.	8.14 $\pm$ 0.08	0.47
5.	8.41 $\pm$ 0.39	0.53
6.	9.13 $\pm$ 0.52	0.84

Table 4. Carbon assimilation efficiencies of fourth-instar C. trivittatus larvae fed on two prey types. The values are means $\pm$ 95% confidence limits.

Method	Prey Type	
	<u>Daphnia magna</u>	<u>Diaptomus kenai</u>
Radiocarbon		
1 day	56.4 $\pm$ 14.8	---
3 day	67.4 $\pm$ 7.2	76.4 $\pm$ 4.0
Weight		
1 day	---	66.9

percent digested methods.

Respiration

Weight-specific oxygen consumption ($\mu\text{l mg}^{-1} \text{ hr}^{-1}$) and individual oxygen consumption ($\mu\text{l individual}^{-1} \text{ hr}^{-1}$) of old fourth-instar larvae increased linearly with temperature (Fig. 13). There is a suggestion of a plateau in the individual rate over the temperature range 10-15° and in the weight-specific rate over the 15-20° range. These plateaus occur over the temperature range the larvae are exposed to during their diel vertical migration. Weight-specific and individual oxygen consumption rates of young fourth-instar larvae also increased with temperature (Fig. 14) but the micro-Winkler measurements at 5 and 10° were significantly lower than the micro-respirometer measurements (t-test: 5°, $p=.0327$; 10°, $p=.0218$; 15°, $p=.3658$; 20°, $p=.3214$). Both methods showed a sharp increase in weight-specific respiration rate between 10 and 15°. Individual oxygen consumption of the young larvae was lower than that of the old larvae (Figs. 13 and 14). Weight-specific respiration of the young larvae was higher than that of the old larvae at 15, 20, and 25° but was not significantly different between the two types of larvae at 5 and 10° (t-test: 5°, $p=.1839$; 10°, $p=.8307$; 15°, $p=.026$; 20°, $p=.0343$; 25°, $p=.0458$).

The oxygen consumption of both old and young

FIGURE 13

Respiration rates of old fourth-instar larvae (1972 year-class) at different temperatures. The data points are means $\pm$ 95% confidence limits.

FIGURE 14

Respiration rates of young fourth-instar larvae (1972 year-class) at different temperatures. The data points are means $\pm$ 95% confidence limits for measurements with micro-respirometers (solid and open circles) and with the micro-Winkler method (Xs).

fourth-instar larvae was used to determine the effects of size and temperature on respiration rate. The equation

$$R = aW^b$$

(R is oxygen consumption, W is body weight, a and b are constants) defines the relationship between body weight and metabolic rate. A logarithmic plot of R versus W can be fitted with a straight line, the slope of which is the coefficient of respiration (b). A linear regression was calculated for ln oxygen consumption on ln dry weight for 5, 10, 15, 20, and 25°. The terms of these equations are given in Table 5. The slopes of the regression lines relating weight-specific respiration and dry weight are more variable than those relating individual respiration and dry weight. The latter equations for each temperature are used in the simulation model.

Growth Experiment I

The initial experiment was run with three temperature regimes -- constant 5° and 20°, and fluctuating 7-15° -- with an excess food ration. Growth was rapid at 20°, slower at fluctuating temperatures, and slowest at 5° (Fig. 15). At the end of 20 days larvae living at 20° were more than double the weight of larvae of the same year-class living in the lake, larvae living under fluctuating temperatures had grown somewhat more than those in the lake (Fig. 9, C. trivittatus '71, Sept. '71), and larvae at 5° weighed less than the lake

Table 5. Terms of the regression equations:
 $\ln(R) = \ln(a) + b(\ln(W))$ describing the relationship between
 oxygen consumption (R) and dry weight (W).

R= $\mu\text{l mg}^{-1} \text{ hour}^{-1}$ and W= mg				
$^{\circ}\text{C}$	n	$\ln(a)$	b	p of slope being 0.0
5	15	-1.053	-0.3700	0.204
10	16	-0.6577	-0.3127	0.999
15	10	-0.0859	-0.3552	0.014
20	12	0.0128	0.3407	0.046
25	12	0.3919	0.4020	0.019

R= $\mu\text{l individual}^{-1} \text{ hour}^{-1}$ and W= mg				
$^{\circ}\text{C}$	n	$\ln(a)$	b	p of slope being 0.0
5	15	-1.0530	0.6300	0.040
10	16	-0.6639	0.8851	0.003
15	10	-0.0859	0.6447	<0.001
20	12	0.0128	0.6593	0.001
25	12	0.3919	0.5979	0.002

FIGURE 15

Larval growth during Growth Experiment I. The data points are mean larval dry weights $\pm$ 95% confidence limits after 21 and 45 days at the experimental temperatures.

population. By the end of the experiment (46 days) the larvae living at 20° weighed more than the two year old lake larvae and many had pupated. Under fluctuating temperatures growth was twice that of the one year old larvae in the lake, and at 5° growth was equal to that of the one year old larvae in the lake. There was considerable mortality at 20°, and too few larvae survived to allow confidence limits to be placed on the final weight shown.

Growth Experiment II

No Food:

At 5° there was a slow but continuous loss in weight (Fig. 16). At the fluctuating and 20° temperatures there was no loss in weight and perhaps a slight gain in weight over the 21 day experimental period.

High Food:

As in the first growth experiment growth was greater under all three temperature regimes than in the field (Figs. 16 and 9). The greatest growth occurred at 20° where the larvae tripled their initial weight; larvae under fluctuating conditions doubled their weight, and larvae at 5° gained weight slightly. Larvae in the lake did not measurably grow during the experimental period.

FIGURE 16

Larval growth during Growth Experiment II. The data points are mean larval dry weights $\pm$ 95% confidence limits after 13 and 21 days at the experimental conditions.

Low Food:

There was some growth under low food rations but less than under high rations (Fig. 16). Larvae at the 20° and fluctuating temperature regimes grew the same amount, doubling their initial weight during the experiment. At 5° growth was slight.

The amount of growth at 5° and at fluctuating temperatures was the same whether the ration was low or high. At 20° the amount of growth was very different between these two rations. A two way analysis of variance was used to test the null hypothesis that there is no interaction between temperature and ration in their effect on larval growth. The no food ration was not considered in the analysis. The results (Table 6) show that there is a highly significant interaction effect between ration size and temperature on growth.

Table 6. Results of a two-way analysis of variance with ration and temperature as main effects in Growth Experiment II.

Source of Variance	d.f.	Sum of Squares	Mean Square	F	p
Ration	1	.155	.155	19.03	.0002
Temperature	2	1.36	.682	83.47	<.0001
R X T	2	.175	.087	10.70	.0004
Error	27	.221	.008		
Total	32	1.91			

Discussion

The strike and contact efficiencies were, as expected, inversely proportional to prey size over the size range tested; these two efficiencies undoubtedly increase to a peak and then drop rapidly as prey size decreases. The discrete prey size range which can be successfully handled by each instar is determined by the size of the larval head capsule and mouth-parts. Fourth-instar C. trivittatus larvae are larger than most Chaoborus larvae and are able to ingest zooplankton that are quite large (2.2-2.6mm for Daphnia). Dodson (1970) reported a maximum length of 1.7mm for zooplankton eaten by C. nyblaei and C. flavicans. The fact that larvae respond to very large Daphnia (>2.6mm) in a manner very different from their response to more vulnerable prey suggests that the larvae have a sensory system that can assess the size of potential prey rather accurately.

The similar strike efficiency on copepods and cladocerans and higher contact efficiency on copepods suggest that the larvae are not able to discriminate between these prey types before striking, but that once the prey is contacted, copepods are much more easily ingested than cladocerans. The more efficient capture of copepods has been attributed to their swimming motion (Roth 1971). The strike efficiency curve should show the same difference between prey types as does the contact efficiency curve if larvae are able to differentiate

between the two prey types on the basis of their swimming motion. This was not the case. It is more likely that size, shape, and prey behavior after contact are the determinants of successful capture. The different contact success curves for copepods and cladocerans support Roth's suggestion that streamlined, cylindrical copepods are more easily ingested than irregularly shaped cladocerans. The difference in contact success decreases with decreasing prey size and all prey <1.0mm in length are ingested with apparently equal ease. The relative ease of ingestion of these two prey types is reflected in their respective ingestion times. Smaller prey were ingested more easily than large prey and copepods were ingested faster than cladocerans of the same size. Such differences have been observed by others (Roth 1971, Sprules 1970). Swuste et al. (1972) reported a selection mechanism in C. flavicans that operates to accept or reject prey after contact is made. This may be a means of rejecting unpalatable prey of any size.

Every attempt was made in the calculation of the energy cost of vertical migration to produce a maximum estimate of this cost. If this approximation could be shown to be negligible with respect to the daily metabolic cost, and therefore of little consequence to the larva, the cost of migration would not have to be measured directly. The calculated result (<3% of the daily metabolic rate) was low relative to the daily metabolic rate and the actual energy

cost was probably much lower than the calculated value. The metabolic efficiency (eff) was undoubtedly higher than the 1% value used in the calculation; this would lower the calculated energy cost considerably. If these larvae swim upward and downwards actively, the metabolic cost of migration might be higher than that calculated because of energy required for active swimming. However, this increase might be offset somewhat by a lower friction cost due to the larvae moving parallel to the long axis of the body rather than perpendicularly to it. If the migration is accomplished solely by passively rising and sinking, using the air bladders to change larval density, the energy cost might be very low. The actual mechanism is probably a combination of active swimming and density change, and the actual metabolic cost of the migration is probably below the high estimate calculated.

The estimated metabolic cost of overcoming friction agrees well with the results reported by Vlymen (1970) for the energy cost of vertical migration in copepods. He found the cost to be 0.3% of the basal metabolic rate assuming 100% efficiency; because metabolic efficiency is less than 100%, his estimate is probably somewhat low. Hutchinson (1967) concluded on a theoretical basis that less than 0.5% of the organic matter in the body would be oxidized during a 50m migration assuming 1% efficiency. He pointed out that this is of little consequence to a filter feeding organism eating its body weight in food every day. Even though a predator like

Chaoborus eats relatively infrequently, (Fedorenko, 1973), a migration cost of 3% of the daily metabolic cost is probably negligible.

Very close agreement was found between the assimilation efficiencies calculated using two independent methods -- the 14-carbon method and the formula $A=C-F/C$ (symbols as defined on page 34). This agreement indicates that the calculated values are probably good estimates of the actual assimilation efficiencies. The carbon assimilation efficiencies reported here agree well with those reported for other invertebrate predators (Lawton 1970, Monakov 1972); over a wide range of invertebrate groups the assimilation efficiency was generally greater than 60% and often as high as 95%. Schindler (1968) found an increase in assimilation efficiency with temperature in D. magna. Lawton (1970) found no effect of temperature, feeding rate, or diapause on assimilation efficiency in his study of the predaceous damselfly nymph Pyrrhosoma. He did find a significant difference in the efficiency with which different food types were assimilated. It has been suggested that assimilation efficiency increases as caloric content of the food increases (Schindler 1968), but Lawton (1970) found no correlation between assimilation efficiency and either ash content or calorific value in Pyrrhosoma.

In poikilotherms oxygen consumption generally increases directly with temperature (Prosser and Brown 1961). Jonasson

(1972) reported a linear increase in individual oxygen consumption for C. flavicans in response to increasing temperature. Respiration rates of the larvae in his study were higher (0.7-7.8 $\text{ul individual}^{-1} \text{ hour}^{-1}$, at 7-24°) than those of C. trivittatus in the present study (0.4-2.0 $\text{ul individual}^{-1} \text{ hour}^{-1}$, at 5-25° for old fourth-instar larvae and 0.3-0.8 $\text{ul individual}^{-1} \text{ hour}^{-1}$, at 5-25° for young fourth-instar larvae). His larvae were about the same size as young fourth-instar larvae and smaller than old fourth-instar larvae. Both young and old fourth-instar larvae increased their oxygen consumption as temperature increased over the temperatures tested. However, there is a suggestion that the old fourth-instar larvae regulate their oxygen consumption over the 10-15° temperature range. There was no apparent reason for the plateau in individual oxygen consumption to be shifted by 5° from that in weight-specific oxygen consumption. The plateau extends over the middle and upper temperatures that the larvae are exposed to during their diel vertical migration. Regulation of oxygen consumption has been found in other poikilotherms (Moshiri 1969 in the predaceous cladoceran Leptodora, Teal 1959 in a crab (Uca), A. W. Knight, pers. comm., in the shrimp Neomysis). Further study is necessary to conclusively demonstrate a regulatory plateau in the oxygen consumption--temperature curve of old fourth-instar C. trivittatus larvae.

Temperature is the environmental factor which most

affects oxygen consumption, and vertically migrating animals are exposed to wide diel temperature changes. Since up to 90% of assimilated energy may be lost to an animal for maintenance metabolism (Phillipson 1966), any reduction in the magnitude of this energy cost would be advantageous to the animal by making additional energy available for growth or reproduction. Regulators (animals which can maintain an essentially constant rate of oxygen consumption over a wide temperature range) neutralize the effect of rising temperature on oxygen consumption so that their maintenance metabolic cost is relatively constant. It seems strange that this energy saving mechanism is not more widespread considering the number of animal groups which migrate vertically and the time these organisms have had to evolve such adaptations to diel temperature fluctuations. Perhaps the emphasis on acclimatization in many respiration studies has prevented wider exposure of mechanisms of this sort.

Teal and Carey (1967) found that temperature but not pressure affected the respiration rate of vertically migrating, epipelagic copepods that are largely herbivorous. These copepods respired less at the low temperature of their day depth than they did at night. Teal (1971) found, however, that respiration of vertically migrating, predaceous decapods was constant at all times. The depressing effect of decreasing temperature on oxygen consumption was offset by an increase in metabolic rate as pressure increased. Teal postulated that a

constant metabolic rate is required for them to remain effective predators throughout their depth range, by day and by night. Chaoborus larvae are also vertically migrating predators whose metabolic rate decreases as temperature decreases. The effect of pressure on oxygen consumption was not studied either by itself or in conjunction with temperature. The presence of a pressure effect that increases metabolic rate as pressure increases would probably not affect feeding in these larvae since they feed readily at temperatures as low as 4° if prey are available.

The relationship between oxygen consumption and dry weight fits the general pattern of Brody (1945). Individual oxygen consumption was greater for the larger old fourth-instar larvae than for the smaller young fourth-instar larvae, and weight-specific oxygen consumption was greater for the young fourth-instar larvae than for the old fourth-instar larvae. The lack of an increase in weight-specific respiration of young fourth-instar larvae between 5 and 10° may be the result of a temperature threshold in oxygen consumption. Young fourth-instar larvae are found above 10° most of the time and their respiration rate may be at a minimum at this temperature. Thus they wouldn't show a response to a change in temperature from 5 to 10°.

The coefficient of respiration (b) is variable in poikilotherms over phylogenetic and ecological groups

(Hemmingsen 1960, Huebner 1973). The values of b reported here lie between .59 and .89 for individual oxygen consumption and are within the range of values generally reported. The high value at 10° (.89) was the result of a low individual respiration rate for young larvae at that temperature in conjunction with a sharp increase in oxygen consumption between 5 and 10° for old larvae.

Activity in fish has been shown to respond non-linearly to an increase in temperature (Fisher and Sullivan 1958, cited in Fry 1971). This non-linearity may produce an apparent plateau in the oxygen consumption--temperature curve if activity increases and then decreases as temperature is increased (Schmein-Engberding 1953, cited in Fry 1971). The relationship between temperature and activity in Chaoborus remains to be studied. However, in respiration experiments over a wide range of temperatures, the larvae were never observed to move about more than they did in holding tanks. They typically hang motionless in the water column except for occasional sharp striking or swimming movements. Although some effect of activity may be included in the respiration rates reported here, it is not at all clear whether it would bias oxygen consumption upward or downward.

Any analysis of the individual effects of environmental parameters such as temperature and prey density on the elements of the energy budget equation ignores the complex

interaction of such parameters in determining the net energy change in the individual over a given time period. Attempts to examine the effects of these interactions are discussed below.

The first growth experiment showed conclusively that young fourth-instar larvae have the potential to exploit high prey densities and grow at a much faster rate than in the lake. For technical reasons the fluctuating temperature regime in this experiment was not the same as that which the larvae experienced in the lake.

The second growth experiment was designed to measure the interaction of ration size and temperature on the energetic budget of fourth-instar C. trivittatus larvae as represented by the energy budget equation $C=P+R+F+U$ (see p 34). Egesta and excreta (F and U) were not measured during the experiment. Metabolic energy cost (R) was varied by using three temperature regimes, and consumption (C) was varied by changing the prey density. Growth (P) was chosen as the index of the effect of these two parameters because it reflects all the physical and physiological interactions which affect the energy budget.

The maintenance energy cost was to be measured directly in the zero ration treatment. Since no food was provided, C and F were zero and $P+R+U=0$. The weight loss of the larvae during the experimental period would be a minimum estimate of the maintenance metabolic cost for each temperature regime

($-P=R+U$). The use of the zero ration treatment as a measure of R assumed that there was no consumption in this treatment. This assumption was not justified since a slight gain in weight was recorded at 20° and at fluctuating temperatures. Cannibalism occurred at all three temperature regimes, and it probably increased with temperature. Some mortality did occur in each treatment, but it could not be partitioned into "natural mortality" and cannibalism. However, there is evidence that cannibalism could only have been very low. At all three temperatures the larvae in the no food treatment grew much less than those in the low food treatment. If cannibalism had been a significant source of food, the larvae at 20° , at least, should have grown more than they did. The presence of an unknown but probably low amount of cannibalism in this treatment was unfortunate. With no measure of the absolute value of $R+U$, it was impossible to calculate consumption, one of the variables that the experiment was designed to examine. Nevertheless, the conclusions from these results are not affected by the inadequacy of the no food treatment.

The energy budget equation $C=P+R+F+U$ can be used to analyze the conditions necessary for growth. Assuming assimilation efficiency (A) is constant over the temperature range in these experiments, non-assimilated material (F) is constant and can be neglected, and $C=P+R+U$. In order for growth to occur (P positive), C must be greater than $R+U$. If

maintenance cost ($R+U$) is assumed to be constant for all prey densities at a given temperature regime, then growth (P) must be directly proportional to consumption (C). On a physiological basis, temperature-dependent processes such as predator-prey interaction rates, digestion rates, blood sugar utilization rates, etc., increase with temperature. Thus, at high temperatures, food turnover is faster and consumption may potentially be greater. At 20° , growth was greater at a high ration than at a low ration. This was not the case under the 5° and fluctuating temperature regimes where growth was the same at low and high rations. There appear to be two interrelated control mechanisms determining growth in these treatments -- temperature and ration size. Under the 5° and fluctuating temperature regimes temperature was the growth limiting factor. These larvae were feeding at their maximum physiological rate at the low ration; they could not respond to an increase in food by increasing their consumption. At 20° the turnover rate of food and the metabolic cost were higher. At the low ration the larvae fed below their maximum physiological rate, and their growth was less than that at the high ration. At the high ration the larvae were able to increase consumption and this resulted in a greater weight gain. There is thus a clear interaction between the effect of ration size and temperature on growth. Maximum ration size (a function of temperature) apparently increases more rapidly with temperature than does metabolic rate, so that potential

growth rate increases with temperature. The maintenance level of metabolism is reached when consumption equals maintenance costs. When $C < R + U$, weight loss occurs; when $C > R + U$, the amount of growth is determined by the interaction of temperature and prey density on consumption. The amount of weight gained is determined by the balance between the energy gains from higher food turnover rates at the higher temperatures, and energy losses due to the higher metabolic rates associated with these temperatures.

The interaction of food and temperature has important implications for the energetics of vertical migration. Because of digestion rate constraints imposed by the temperature regime they are exposed to, migrating larvae are unable to utilize high prey densities even when exposed to them. Larvae living continuously at high temperatures are able to exploit the differences between increased digestion rate and maintenance cost and can utilize high prey densities to maximize growth. Because of the distribution of prey, non-migrants are usually exposed to higher prey densities than migrants, and this results in faster growth rates. These experiments demonstrate that a strategy of no migration is best for maximizing growth.

Summary

1. Old fourth-instar larvae were relatively inefficient at catching both copepods and cladocerans. Their efficiency of ingesting a prey item after contacting it increased rapidly as prey size decreased to the minimum size tested (0.6mm). The maximum size ingested was 2.6mm for cladocerans and probably about the same for copepods. Copepods of all sizes tested were ingested faster than cladocerans of the same size.

2. The metabolic cost of moving through the distance covered by the diel vertical migration was estimated to be small relative to the daily metabolic cost.

3. The carbon assimilation efficiency for both copepods and cladocerans was about 68%.

4. Respiration rates for both young and old fourth-instar larvae increased linearly with temperature. The suggestion of a plateau over the 10-20° range may indicate some ability to regulate oxygen consumption over part of the temperature range that the larvae are exposed to during their diel vertical migration. The relationship between body size and oxygen consumption was typical; weight-specific oxygen consumption decreased as size increased, and individual oxygen consumption increased as size increased.

5. Larval growth was a function of temperature and prey density. Temperature affects growth through its effect on

several physiological rates; prey density affects growth through its effect on consumption and thus on the ability of the larvae to feed at their maximum potential. It was shown that growth was greater in larvae living at constant high temperature than in those living under a fluctuating temperature regime.

V. SIMULATION STUDIES

Introduction

Theories on the Adaptive Value of Vertical Migration

The various theories advanced to explain the adaptive value of vertical migration have been reviewed by McLaren (1963) and Mauchline and Fisher (1969). They fall into the six categories previously mentioned: escape from predators, horizontal transport, social control of reproductive rate, energetics, a combination of these, and demographic effects.

Potential predators can undoubtedly see their prey at depths well below those to which many zooplankters migrate. Nevertheless, escape from predators is probably a component of the adaptive value of vertical migration and the primary reason for descent by day rather than by night. Vertical migration may aid escape from predation by reducing prey availability to visual predators, and by providing refuges. The reactive field of a fish (the volume within which it can detect a prey item) is determined in part by light intensity and prey behavior. As light intensity decreases the reactive field shrinks. A decrease in prey activity associated with low day-depth temperatures will further decrease the reactive field of visual predators. Vertical migration may also provide a refuge from predators which cannot follow the migration

because of thermoclines, low oxygen zones, or other physical and chemical gradients. However, migration might just as easily expose migrants to a different set of predators at their day depth. Manteifel (1959a,b), Girsal (1959), and Pearre (1973) have suggested that predator avoidance is the main reason for vertical migration.

Several theories have considered the value of vertical migration in utilizing horizontal water transport to effect changes in the horizontal distribution of the migrants. The adaptive value originally proposed for horizontal transport was the avoidance of toxic effects from areas of high phytoplankton density (Hardy and Gunther 1935). Though these toxic effects have been shown to exist, there is no evidence that zooplankton avoid dense phytoplankton patches. Since this theory was advanced, several authors, including Hardy (1956), have suggested that horizontal transport aids in the "colonization" of previously unexploited patches at the surface. In order to arrive at patches which occur randomly in space and time and to remain in them, migrants would have to be able to modify the extent and timing of their migration. The regular nature of most migration patterns suggests that zooplankton are not responding to discrete patches. However, throughout the year surface waters are uniformly more productive than deep water; selection for increased food intake could quite conceivably have produced a migration to the surface. This advantage does not, by itself, explain the

development of the downward movement in a diel vertical migration.

David (1961) suggested that horizontal transport resulting from vertical migration prevents the formation of highly specialized species with little capacity to adapt to changes in the environment. This occurs because the horizontal "mixing" of zooplankton provides additional chances for genetic recombination. Because of their almost complete lack of sexuality, it seems unlikely that horizontal transport would affect recombination in those cladocerans which vertically migrate; this theory certainly doesn't apply to the vertical migration of Chaoborus larvae because they emerge before breeding. There is little evidence that non-migratory marine copepods (Oithona similis group) are more prone to speciation than migratory ones (Calanous finmarchicus group) (McLaren 1963). David's theory assumes that the time scale of mixing necessary for adequate genetic recombination to prevent extreme speciation is shorter than the time scale of physical mixing obtainable without vertical migration. There is no evidence to support this assumption.

Wynne-Edwards (1962) suggested that vertical migration has evolved to produce aggregations of animals near the surface or at other depths in order to carry out epideictic displays. These displays allow the population to assess its numbers and regulate its reproduction rate in order to hold

its density at, or restore it to, the optimum. There is no evidence that zooplankters are able to control their reproduction rate; McLaren (1963) cited considerable evidence that growth and reproduction rates are primarily dependent on food and temperature.

Kerfoot (1970) discussed the adaptive value of orienting to light rather than to pressure in terms of the bioenergetic benefits resulting from these two orientation strategies. He concluded that orientation to light and a nocturnal feeding pattern, rather than orientation to pressure, maximizes exposure to food over the course of a year in temperate latitudes. This is partially a result of night length (feeding time) being longest at the time of year that primary production is lowest. Animals orienting to pressure would be less able to respond to changes in the depth at which peak productivity occurs. Miller et al. (1972) criticised Kerfoot's theory on the grounds that an animal should stay in the most productive region at all times instead of spending the daylight hours in regions of low primary productivity. Neither Kerfoot nor his detractors considered the potential role of temperature in the adaptive value of vertical migration.

McLaren (1963) has proposed another theory for the adaptive value of vertical migration based on energetics. He considers growth and reproduction as functions of temperature alone; feeding is assumed to occur when the animal is at the

surface. His theory is concerned with the potential energetic benefits from an alternation of high and low temperatures as a result of vertical migration. Any energetic benefit resulting from the alternation of high and low temperatures depends on the partitioning of energy to respiration and growth. The proportion of available energy that goes to growth can only increase if respiration rate decreases faster with decreasing temperature than digestion and assimilation rates do. McLaren predicted that the energy gain from alternating temperatures increases as the difference between the high and low temperature increases. Thus, as the temperature differential between the surface and day-depth increases, it becomes more and more advantageous to migrate. Criticisms of McLaren's theory center on his assumptions about feeding and the relationship between temperature and respiration and digestion rates; the theory will be critically examined below (p 107).

Mauchline and Fisher (1969) accepted McLaren's assessment of pre-existing theories but criticised his feeding assumptions. Since migrants ultimately depend on surface productivity, these authors concluded that there are a number of potential benefits derived from vertical migration. The following benefits were included in their analysis: the general pattern of day descent may decrease predation; fortuitous horizontal transport may enable parts of a population to exploit new phytoplankton patches; different light intensity preferences among species may allow the

partitioning of resources. In their view, vertical migration produces the greatest possible utilization of resources.

McLaren (1974) proposed a model of the effect of vertical migration in thermally stratified waters on the rate of increase of a population of marine copepods. The model does not include the metabolic considerations upon which his earlier (McLaren 1963) theory depends. The metabolic model was required to produce a more rapid growth rate, and thus a greater number of eggs, in migrants than in non-migrants in a given time period. McLaren's new theory does not require that migrants grow faster than non-migrants; by including the slower growth rate of migrants in his model, it is not necessary for him to incorporate the metabolic assumptions he needed before. His new model is based on life history strategy theory and requires the following five assumptions: 1) final size is a negative function of temperature; 2) fecundity increases with size; 3) the required reproductive periodicity can be maintained despite prolonged development; 4) age specific mortality is greater on young stages than on old stages; 5) the population is near equilibrium. When these assumptions are satisfied, there will be a particular set of conditions (fecundities, mortality rates, etc.) in which the increased mortality due to prolonged development time is offset by increased fecundity due to larger size, and migrants will produce more eggs than non-migrants. Empirical data on the marine copepod Pseudocalanus minutus support his theory.

McLaren's demographic model may explain the adaptive value of vertical migration for some organisms. However, because it is dependent on a delicate balance among so many parameters, it is not likely to be very widely applicable. It will certainly stimulate interest in the application of life-history strategy theory to the phenomenon of vertical migration.

The Simulation Model

The field and laboratory experiments with C. trivittatus larvae discussed previously (Sections III and IV) were designed to elucidate the effects of temperature on the major energetic processes affecting growth. These relationships were incorporated into a computer simulation model of vertical migration. The simulation model was used to examine the effects of various migration strategies, physical parameters, and biological parameters on larval growth. The simulation experiments were suggested by the results of field and laboratory experiments, and by a consideration of McLaren's predictions.

The following general questions were examined: 1) is there a demonstrable "energy boost" as a result of vertical migration with natural prey distributions? 2) what is the nature of the interaction between prey density and distribution and vertical migration strategy? 3) what migration strategy is "best" for larval growth on an

energetics basis?

Methods

The simulation model was designed to follow the daily energy balance of a vertically migrating larva. The energy gains from feeding and the energy losses due to metabolism were calculated over 20 minute intervals for 30 days. Energy partitioning in the model followed the energy budget equation $C=P+R+F+U$ (Ricker 1971) as modified by Warren and Davis (1967) except where empirical data were missing. Change in weight was the index used to express the net energy change because of the availability of data in mass units. Appendix I contains a detailed description of the model. Graphs of typical input data, flow diagrams of the general model and of the feeding and digestion subroutines, a list of parameter values and their sources, and a list of the FORTRAN variables used in the model and their definitions are included in this appendix. Appendix II contains a listing of the FORTRAN programs used in running the model. All simulations were run on an IBM 1130 computer.

Each simulation begins by setting the position of the larva at 20m and the time equal to zero. The water temperature and prey densities at the depth occupied by the larva are interpolated from temperature and prey density profiles based on empirical data from mid-summer (except when temperature or

prey density are manipulated). The migration pattern is pre-set in graphical form and the position of the larva in subsequent time intervals is determined by interpolation. The general form of the model is shown in Figure 17. After the appropriate depth, temperature, and prey densities have been determined, the energy gain to the larva during the current time interval is calculated. The model enters a feeding phase or a digestion phase depending on the degree of fullness of the crop. If the crop is full the feeding phase is bypassed and only digestion occurs. If the crop is not full, the model enters the feeding phase and then the digestion phase. The model is designed so that once the crop is full the feeding phase is bypassed until a set proportion of the food in the crop has been digested, and the crop has been emptied. This formulation is designed to mimic the digestive process in Chaoborus larvae in which there is a digestive pause after the crop is full followed by the egestion of undigested material from the crop. The model next calculates the energy losses due to respiration and movement. The net energy change is calculated from the energy gained from digestion and energy lost to respiration and movement. The larval weight is then incremented, and the next time interval is begun by the calculation of the new position of the larva.

The feeding phase of the model calculates the number and weight of large and small prey eaten per time interval. The number eaten is stochastically determined from a Poisson

FIGURE 17

Generalized flow diagram of the simulation model.
The diagram represents the sequence of operations
which occurs during one time interval.

distribution. The mean of the distribution varies with prey density according to the Holling disk equation for two prey types:

$$U = (\text{ALPH1} * \text{BFUD}) / (1 + \text{ALPH1} * \text{BFUD} * \text{H1}) + (\text{ALPH2} * \text{SFUD} * \text{H2})$$

for large prey and

$$U = (\text{ALPH2} * \text{SFUD}) / (1 + \text{ALPH1} * \text{BFUD} * \text{H1}) + (\text{ALPH2} * \text{SFUD} * \text{H2})$$

for small prey, where U is the mean of a Poisson distribution, ALPH1 is the "catchability" of large prey, ALPH2 is the "catchability" of small prey, BFUD is the large prey density, SFUD is the small prey density, H1 is the handling time for large prey, and H2 is the handling time for small prey. The stochastic element is introduced to make the feeding phase of the model more closely imitate the natural feeding pattern of Chaoborus larvae. Feeding depends on random encounters with prey items, and the expected number of encounters in one time interval is small. My use of the disk equation is not strictly correct since the random element is the encounter rate (ALPH1*BFUD and ALPH2*SFUD) not the mean capture rate (U). This formulation would permit a larva to eat faster than is physically possible, based on handling time, if a large Poisson number is encountered. However, handling time is short relative to the 20 minute time intervals, and the crop volume has a maximum value. These constraints, and the low probability of getting a high Poisson number, mean that the potential error from my use of the random element in calculating prey capture is very small. The total amount of

food in the crop is updated during the feeding phase. If the total food eaten (large and small) in a time interval would fill the crop to more than its maximum capacity, the amount of food in the crop is set equal to the maximum capacity of the crop and the model bypasses the feeding phase in subsequent time intervals until the crop is emptied. This occurs when the digestible portion of a crop-full of food has been digested. This sequence of crop filling and emptying is based on the observation that larvae do not selectively egest a portion of the crop contents and then feed again. The amount of digestible food in the crop is carried as a separate variable which is increased by a proportion of the total food eaten in each time interval. This proportion (68%) is equal to the assimilation efficiency measured in Section IV.

The digestive phase is entered during every time interval whether or not the model entered the feeding phase in that interval. The amount digested during a time interval is calculated by interpolation from empirical temperature--digestion rate data. The food that is digested is added to a stored food pool that is used in later calculations. The amount of food digested is subtracted from the total food in the crop and from the digestible food. If the amount to be digested is greater than the amount available for digestion, the amount available is digested and both food variables are set to zero. The model will begin to enter the feeding phase again when this occurs.

Respiration and movement are the sources of energy loss considered in the model. Respiratory energy loss is calculated from the equation:

$$R = aW^b$$

The values of a and b are from Section IV. For intermediate temperatures R is interpolated. The energy cost of a migration was estimated in Section IV, and this estimate is added to the respiratory energy loss when the larva is migrating. The total energy loss is used in later calculations.

The net energy change is calculated as the difference between the stored energy and the total energy loss. Stored energy is the digested food minus a constant percentage loss to specific dynamic action. The net energy change is converted to mass units and used to increment the larval weight.

Results

Sensitivity

A number of simulations were done to assess the sensitivity of the model to changes in its parameter values. The results (Fig. 18) show that the effect of parameter changes on larval growth was quite variable. Small changes in handling time (H_1 , H_2) had little effect on larval growth because the formulation of the disk equation is such that they have little effect on the number of prey eaten. As

FIGURE 18

The effects of changes in the parameter values of selected parameters on larval growth. The lines on each graph are the results of simulations using the values associated with the lines as input parameter values for the model.

"catchability" of small prey (ALPH2) was varied the number of small prey eaten varied, but, because of their small size, there was little effect on larval growth. Within the range of reasonable values for the weight of large prey (WBF) and specific dynamic action (SDA), these parameters had a small effect on larval growth. SDA acts only on the amount of food digested, which is low in any time interval. Because there is a maximum weight of food which the crop can hold, any effect of WBF is constrained, and its effect on larval growth is less than it would be if the crop size was unlimited. Changing the proportion of food eaten that could be assimilated (AE) had a relatively large effect on larval growth because this proportion directly affects the energy gain to the larva. The "catchability" of large prey (ALPH1) also has a large effect on growth. It affects the number of large prey captured in the feeding phase of the model. Because of the size of large prey, even small changes in the number eaten have a large effect on growth. The random number initializer (RNI) affects the number of prey eaten by changing the series of random numbers used in the feeding phase of the model. The effect of this stochastic element is to produce a variable pattern of growth and final weight (Fig. 18). The variability introduced by the stochastic element in the model is relatively low compared to the effects of temperature, prey density, and some of the other parameters. For this reason I believe that the qualitative results presented below represent effects of the manipulated

variables rather than variability built into the model.

Predictions from the model depend on several assumptions and functional relationships. Larval migration is assumed to occur every day. There is little evidence that this does not occur in Eunice Lake, but if migration extended over several days it would have a large effect on the energetics of the larvae. Prey vulnerability is assumed to be constant through the day and night. If this were not true, it might have important consequences for the energetics of animals staying at the surface. However, Chaoborus are ambush predators which use vibration receptors to locate their prey so that day-night differences would not be expected on the part of the predator. Zooplankton may be able to see and avoid Chaoborus larvae during the day, but there are no results to test this possibility. In the model I have assumed that once the crop is filled, no more feeding is possible until that amount of food is digested, and the remains egested. If continuous feeding were possible the energy gain to the larva at high densities might be higher than predicted. There is evidence that Chaoborus exhibit a digestive pause, but efforts to quantify it failed. For ease in computation I have assumed that all digested material is assimilated and that the proportion of a prey item that is ultimately digested equals the assimilation efficiency measured for fourth-instar C. trivittatus larvae; this seems to be a reasonable representation of digestion in Chaoborus larvae. The estimated energy cost of migration is

assumed to be constant with respect to temperature. This is probably a negligible source of error because of the small amount of energy involved. The oxy-calorific conversion factor used assumes a constant respiratory quotient. The RQ is probably not constant, but the variability involved is probably low. Some of the parameter values were measured and some are reasonable estimates. Of those discussed above to which the model was sensitive (ALPH1, WBF, and AE), only ALPH1 was not measured directly; it was estimated from laboratory strike experiments.

Experiments were done to characterize and quantify the effects of temperature on metabolism and growth (Section IV). Less emphasis was placed on the relationship between feeding rate and prey density. The feeding part of the model is therefore less rigorous than the metabolism part. Because of the parameter estimates and the form of the feeding part of the model, it is not possible to analyze fine details of energetic cost and benefit. However, using the model, food, temperature, and migration pattern are shown to have a large effect on larval growth. I feel that the model is adequate to demonstrate qualitative differences in the effect of various combinations of food, temperature, and migration pattern on growth. An increase in detail in the feeding part and more accurate parameter estimates would allow a more exact quantification of growth and of the differences between migration strategies, but the results and predictions would

probably be the same.

The Effect of Food

The interaction of food and migration strategy on growth was examined in three ways -- with natural prey densities, with various "surface" prey densities, and with various prey density profiles.

In the first set of simulation experiments the prey density was set at natural summer values for Eunice Lake, and the migration pattern was varied. Growth under these food conditions was greatest if the larva stayed at the surface (Fig. 19) or followed a physiological migration pattern in which downward migration is triggered by a full crop, and upward migration is triggered by an empty crop. Larvae following the natural Eunice Lake migration pattern of 4 hours at the surface and 16 hours at the bottom grew less than larvae which stayed at the top but more than larvae which stayed at the bottom.

The second set of simulation experiments compared staying at the surface and following a physiological pattern to the natural migration pattern, as surface prey densities varied from zero to summer field densities. Prey density was varied from 0 to 300 each of large and small prey per 100 liters at the surface. No food was provided below 7m -- a condition similar to that found in the lake. The results (Fig. 20) again

FIGURE 19

The effect of migration pattern on larval growth -- natural prey densities. The lines are results from simulations with the migration pattern set as labelled.

FIGURE 20

The effect of migration pattern and surface prey density on larval growth. The data points are the final larval weights of single simulations.

show that larvae following the migration pattern found in Eunice Lake grow less than larvae following a physiological migration pattern or staying at the surface. There was little difference between the "stay-at-surface" and physiological patterns because at the prey densities examined the crop seldom fills, and the larvae following the physiological pattern experience the same conditions as those which stay at the surface.

In the third set of simulations with variable food, the food profile was varied to increase the amount of food available at the day depth. The four food profiles had 300 of each prey size at the surface and 50, 150, 200, and 250 of each prey size at the bottom. The four migration patterns used in the previous experiments were tested with each prey profile. The results are qualitative, but they show a gradual shift in the migration pattern which maximizes growth from staying at the surface when food is low at the day depth (Fig. 21 A,B) to staying at the bottom when food is abundant at the day depth (Fig. 21 D). There may be some critical prey density profile which provides maximum growth under the natural Eunice Lake migration pattern, but it is not demonstrated in this set of simulations. With a prey density of 200 at the bottom, the natural migration pattern is best in terms of growth, but the differences in growth between the four migration patterns are within the stochastic variation in the model. As in the previous set of simulations there was little difference

FIGURE 21

The effect of migration pattern and prey density profile on larval growth. The lines are results from simulations with the migration pattern set as labeled (a, b, c, d). The prey distribution is as follows: 300 of each prey size at the surface, and 50 (A), 150 (B), 200 (C), and 250 (D) of each prey size at the bottom.

between the "stay-at-surface" and physiological patterns.

The Effect of Temperature

The effect of temperature on growth was examined by running simulation experiments with natural prey densities, the natural migration pattern, and various temperature profiles. The following temperature profiles were tested: constant 5, 10, 15, and 20°, and profiles with a 1, 2, and 3° difference between surface and bottom temperatures at surface temperatures of 10, 15, and 20° (for example: 10, 9; 10, 9, 8; 10, 9, 8, 7; 15, 14; etc.). The constant 5, 10, 15, and 20° profiles were also tested with the "stay-at-surface" migration pattern. Ten simulations were run with randomly chosen initializers for each temperature profile; the mean growth was plotted against surface temperature. At all the temperature profiles tested, growth was low when the larvae followed the natural migration pattern (Fig. 22). There was little difference between constant temperatures and profiles with 1, 2, and 3° differences between the surface and bottom so these results were pooled. The 5° point is for constant 5° only (the model wasn't set up to handle temperatures below 5°). At all surface temperatures growth was much greater when the larvae stayed at the surface than when they migrated. As the surface temperature increased, growth decreased under both migration patterns.

FIGURE 22

The effect of migration pattern and temperature profile on larval growth. The data points for the surface migration pattern (solid circles) and the natural migration pattern at 5° (open circle) are the mean final weights of 10 simulations. The data points for the natural migration pattern at 10, 15, and 20° (solid circles) are pooled results of the four temperature profiles described in the text.

The results of the simulation experiments agree well with laboratory growth studies. In the laboratory growth experiments the larvae were exposed to constant prey densities and the temperature was varied to match the temperature profile encountered during a migration. In the simulation experiments, however, the larvae were exposed to variable temperature and variable prey density. For this reason the laboratory situation is analagous to only the "surface" simulations and those in which the prey density profile was varied. In both growth experiment II (Fig. 16) and the simulation experiments with variable surface food (Fig. 20), growth was a function of prey density when the larvae were at surface temperatures (no migration). When the prey density profile was varied so that it approached constant prey density throughout the water column (Fig 21, C,D) larval growth was the same or greater for migrating larvae than for non-migrants. This matched the laboratory results for the low food treatment (Fig. 16). The surface prey densities in this set of simulations were too low for the larvae to grow enough to match the laboratory results for the high food treatment; larval growth in the simulation experiments was prey density limited at the surface prey densities.

Discussion

A consideration of the potential strategies of vertical migration suggests three basic migration patterns. They are, in order of increasing complexity: 1) stay in one place, 2) a diel migration pattern of some sort that is synchronous over the whole population, and 3) a pattern that is under the control of the individual animal's physiological state so that the population is migrating asynchronously. The energetic implications of following these patterns are analyzed in terms of their ability to maximize net energy gain to the organism. In considering the energy costs and benefits of these patterns I have assumed that respiration rate varies with temperature, that it decreases faster than digestion and assimilation rates with decreasing temperature, and that the prey vulnerability is constant over time.

The simplest pattern is that of no migration. Many zooplankton groups have representatives which do not migrate (Hutchinson 1967). On an energetics basis there are two cases of non-migration that must be considered -- staying in cold, food-poor, deep water and staying in warm, food-rich, near-surface water. In either case the maintenance metabolic cost will be relatively constant. Staying in deep water where primary and secondary production are low will result in death if consumption is below the level required for maintenance of the organism. At best, growth will be slow because of low food

consumption. The digestion and assimilation rates would have to be greater than the respiration rate for any growth to occur. Staying at the surface presents an entirely different problem. Respiration and digestion rates and prey density are almost universally higher than in deep water. Above the maintenance level of food consumption growth is a function of prey density (Figs. 16 and 20).

Diel vertical migrations are found widely in nature (Cushing 1951, Teraguchi and Northcote 1966, Mauchline and Fisher 1969). Characteristically the migration pattern has a regular periodicity, and most of the population migrates synchronously; the periodicity is usually one that can be modified by exogenous stimuli. An animal migrating with a regular diel migration pattern cannot maximize energy gain in an environment containing sharp biological and physical gradients. No matter what the form of the pattern is, an animal following a diel migration pattern would periodically migrate down out of the food-rich zone with its gut empty, thus decreasing its probability of feeding to nearly zero until it re-ascends on the next migration cycle. This pattern would be particularly bad for predators since they feed more infrequently than herbivores. An adjustable diel migration pattern would be especially advantageous if particular combinations of time and depth are better in some way than others. These "more advantageous" combinations of depth and time are usually assumed to be the result of predation, but,

McLaren (1963) suggests they are energetic in nature.

The most complex migration pattern envisaged is one that is controlled by the physiological state of the animal. Using a control mechanism of this sort, an animal could move up into warm, food-rich water and feed until its gut was full and then move down into cool, water until its gut was empty. Energetically, this pattern is the most attractive because the animal makes the most efficient use of alternation between warm and cold water. An animal using this mechanism to trigger migration is neither left at the surface with a full gut nor left in deep water when its gut is empty. There is no good evidence that this mechanism is very widespread, but it has been suggested recently for chaetognaths (Pearre 1973). A possible reason that this mechanism has seldom been reported is that the population would be migrating asynchronously. Each individual would migrate with its own periodicity and an easily detectable mass migration would seldom occur.

The analysis of the migration patterns presented above is based solely on energetics. The conclusion that a surface pattern or physiologically based pattern is most advantageous is at odds with previous theory (McLaren 1963) on the energetic advantages resulting from vertical migration. It is necessary, therefore, to critically examine McLaren's theory.

The general conclusions of McLaren's (1963) theory on the adaptive value of vertical migration are presented above (page

83). He concluded that the migration pattern most commonly seen in zooplankton (an endogenous rhythmicity capable of being modified by exogenous stimuli) is energetically the most advantageous. This conclusion is at odds with the analysis of the energetics of various migration patterns presented above. The difference between the two analyses of energetic advantage lies in McLaren's assumptions.

The general criticism of McLaren's theory is that it ignores the complex interaction between food consumption and temperature dependent digestion and respiration rates. He makes several assumptions, explicitly or implicitly, which are critical to the proper functioning of his theory on the energetic advantage of alternating between high and low temperatures. These assumptions are the following: 1) "all necessary feeding" can occur at the surface; 2) respiration rate is a monotonically increasing function of temperature; 3) digestion rate is constant or respiration rate must decrease faster with respect to temperature than digestion and assimilation rates do.

McLaren's first assumption is invalid for two reasons. It has been pointed out that not all organisms that migrate feed entirely at the surface. Mauchline and Fisher (1969) found that many euphausiids feed throughout their migration; these authors also question whether grazers are able to filter enough food during the short dark period in the summer to meet

their daily requirements. Several predators have been shown to feed irregularly and to feed both at the surface and in deep water (Teal 1971, Fedorenko 1973, Pearre 1973). The concept of "all necessary feeding" introduced by McLaren is impossible to define. It can refer equally well to a maintenance ration or to a maximum ration.

McLaren's implicit assumption that respiration rate is a monotonically increasing function of temperature has important consequences for the energetic cost associated with moving upward into warm water or downward into cold water. The presence of metabolic adaptations to decrease the effect of high temperature on respiration rate would tend to make it less costly to move up into warm water. Although not widespread, the presence of this type of metabolic "regulation" has been suggested for C. trivittatus (Section IV) and for Neomysis (A. W. Knight, pers. comm.) and reported for the vertically migrating cladoceran, Leptodora (Moshiri 1969). If respiration rate did not decrease as temperature decreased, the potential energy gain from a reduced metabolic rate at low temperature would not be realized. Teal (1971) showed that the respiration rate of predaceous, mesopelagic decapod crustacea did not decrease at the cold temperature of their day depth. This phenomenon might well be widespread in vertically migrating predators, and it could represent a significant energy loss.

Any energetic benefit resulting from the alternation of high and low temperatures depends on the partitioning of energy to respiration and growth. If digestion and assimilation rates are constant with respect to temperature, a decrease in respiration rate at low temperatures will increase the proportion of available energy that goes to growth. Under these conditions the energetic "boost" predicted by McLaren could exist. However, digestion rate varies with temperature (Brett and Higgs 1970, Fedorenko 1973). Under these conditions, for a change in the partitioning of available energy to occur such that more energy is directed into growth at low temperatures, the respiration rate must decrease faster than the digestion rate as temperature decreases. If one accepts this reasoning, the most efficient migration pattern is the physiological one, not the one predicted by McLaren.

From the analysis of the energetics of vertical migration it is clear that the migration strategy maximizing net energy gain is that of staying at the surface or following a physiological rhythm based on the filling and emptying of the gut. Fourth-instar C. trivittatus larvae in Eunice Lake follow neither of these patterns. It is necessary therefore to consider other, non-energetic explanations for their migration pattern.

The diel distribution of these larvae might simply be a reflection of the diel distribution of their prey. This

explanation is unlikely since almost all the zooplankton species eaten by C. trivittatus are found above 5m. Diaptomus kenai, the prey species which makes up most of the biomass of the diet, makes a diel vertical migration which is opposite to that made by fourth-instar larvae.

There is no experimental evidence to support or dispute the hypothesis that disease or parasites might be more abundant if these larvae stayed in warm water. In three years of study no moribund or obviously parasitized larvae were encountered.

It is conceivable that prey vulnerability is not constant. A decrease in prey vulnerability during the day might be expected if zooplankton are better able to detect the presence of a Chaoborus larva during daylight. Since Chaoborus larvae apparently use vibration receptors rather than vision to detect their prey (Horridge and Boulton 1967), and are able to capture prey in complete darkness (Duhr 1955), their ability to detect prey should be constant throughout the day and night. C. trivittatus larvae are able to feed on both copepods and cladocerans in the light with apparent ease, and there is no apparent avoidance response by their prey. A decrease in vulnerability might make it energetically less attractive to stay at the surface during the day if feeding hadn't yet occurred by dawn. The effect of changes in prey vulnerability was examined by adjusting the prey density by a

vulnerability coefficient (BVUL, SVUL) in a few simulations. The results of these simulations showed that prey vulnerability must be 100 times lower during the day than at night to shift the migration strategy maximizing growth from the "stay-at-surface" pattern to the natural pattern. A change in prey vulnerability of this magnitude, however, seems unlikely in this predator-prey system.

Competition between C. trivittatus and C. americanus is unlikely to have produced the migration pattern seen in third and fourth-instar C. trivittatus larvae. Fourth-instar C. americanus larvae stay near the surface at all times, and, based on morphological and diet data, they appear to be restricted to a narrower range of potential prey than are fourth-instar C. trivittatus larvae. Their prey capture apparatus is smaller (head length, mouth gape, antenna length); they are less efficient at capturing large prey items; they feed on a more restricted diet than do fourth-instar C. trivittatus larvae (Fedorenko 1973). C. americanus larvae are also numerically less abundant than C. trivittatus larvae.

The following two theories have been proposed to account for the upward movement of Chaoborus. Neither of them explains why migrants should move down out of their food source. Goldspink and Scott (1971) have suggested that some aspects of the vertical migration of C. flavicans in Lochan Dubh agree

with the epideictic concept of Wynne-Edwards (1962). Third and fourth-instar C. trivittatus larvae in Eunice Lake vertically migrate about 18 months before they pupate and emerge. It seems unlikely that their vertical migration can have any signalling function that would affect fecundity that far in advance. Goldspink and Scott do not consider causes of the downward migration. Hunt (1958) and LaRow (1970) have suggested that low oxygen concentration in the hypolimnion or sediments stimulates the larvae to migrate. Oxygen concentration is high at all depths in Eunice Lake (Fedorenko and Swift 1972) so it seems unlikely that this explanation can account for the upward vertical migration of C. trivittatus larvae. The downward migration is not considered in these studies.

Avoidance of diurnal predators is an attractive hypothesis to explain the occurrence of nocturnal activity patterns. Welch (1968) showed that C. punctipennis larvae which were planktonic at night and benthic during the day were preyed upon very little by fish in a shallow pond. MacDonald (1956) found that chaoborid larvae in Lake Victoria avoided predation by Mormyrus kannume by being planktonic when the fish were feeding on the benthos. Northcote (pers. comm.) suggested that C. flavicans may avoid heavy fish predation in Corbett Lake by spending the day in the anoxic hypolimnion and migrating up to feed at night. Predator avoidance is not so simple as the above discussion suggests. Pope et al. (1973)

found that some Chaoborus species were only found in lakes without fish, some were only found in lakes with fish, and some (including C. trivittatus) occurred in lakes whether fish were present or not. Crepuscular predators are most active at dusk and dawn; these are the times of day that most Chaoborus are migrating (LaRow 1969, Section III). Avoidance of fish predation cannot be considered as a proximal cause of the vertical migration pattern of fourth-instar C. trivittatus larvae in Eunice Lake because there are no fish in the lake. Notonectids are visual predators that are known to be able to capture Chaoborus larvae and are abundant in the lake. They are unable to forage deeper than about 2m and are unable to reach C. trivittatus during the day. The downward migration of C. trivittatus might allow them to escape diurnal predation by notonectids. However, notonectids probably would exert little if any predation pressure on C. trivittatus even if the larvae did not migrate; these larvae never come closer to the surface than about 3-4m, even during the night.

The migration pattern seen in Eunice Lake may be simply the persistence of a migration pattern adapted to some previous selective pressure which is now relaxed or absent. A behavior pattern as complex as a diel migration pattern, whether it be endogenous or exogenous in origin, could be conservative in its evolution in the face of relaxed selection pressure. However, if such a behavior pattern is neither neutral nor advantageous, selection should act to change it.

It appears from laboratory and simulation studies, that it is energetically advantageous for larvae in Eunice Lake to remain at the surface or migrate on a physiological basis; if this is the case, the migration pattern observed in Eunice Lake would not be expected to persist. It is possible that there is an unknown selective force that is acting on C. trivittatus larvae in Eunice Lake that maintains the observed migration pattern, or it may be that there is fast enough exchange between populations in nearby lakes that any population in a lake with no selection pressure favoring diel vertical migration is only recently derived from a parental population in a lake with a high selection pressure for this behavior pattern. Stahl (1966) suggests that one of the reasons for the high frequency of co-occurrence of Chaoborus species in lakes is the chance dispersal of adults to lakes other than the ones they emerged from. This mechanism could provide a continuous source of highly adapted larvae so that the gradual degradation of the highly adapted behavior pattern associated with the removal of selection pressure is not noticeable. It is impossible to study this type of mechanism in a short study. Significantly, Pope et al. (1973) found C. trivittatus in lakes which contained fish and in those which did not; they did not record the migration patterns of these populations. Within a few miles of Eunice Lake in the U. B. C. Research Forest there are several lakes which contain Chaoborus larvae; the species represented include C. flavicans and

C. trivittatus in lakes containing fish and C. trivittatus in lakes without fish.

It is clear from field data (Section III) that fourth-instar C. trivittatus larvae in Eunice Lake are migrating dielly with a migration pattern which shifts with changing day length and is cued by light. Except for the lack of a benthic phase, the migration pattern of C. trivittatus in Eunice Lake is essentially the same as that generally reported for Chaoborus larvae. Since this pattern does not appear to be the most advantageous on an energetics basis, it is necessary to look elsewhere for an explanation of the adaptive value of vertical migration in Chaoborus larvae. Near-surface feeding is sufficient to explain the upward movement. The critical part of the migration which must be explained is the downward movement out of the food-rich surface waters. For Chaoborus larvae in general, the most probable explanation for the downward movement is the avoidance of predation -- especially fish predation -- in the surface waters by day. None of the existing theories, however, convincingly explains the vertical migration of C. trivittatus in Eunice Lake. The explanation which seems most likely for the particular form of the migration of C. trivittatus larvae in Eunice Lake is that its persistence in the face of apparently relaxed selection pressure is due to periodic immigration from populations exposed to strong selection for this behavior pattern.

The young stages of many vertically migrating animals do not migrate, but rather spend the entire day near the surface (McLaren 1963, Teraguchi and Northcote 1966). First and second instar C. trivittatus are no exception (Fedorenko and Swift 1972). These small larvae live about 3m deep from the time they hatch until they reach third instar and begin to migrate. What are the advantages associated with staying at the surface when small? It may be advantageous for young stages to grow as rapidly as possible in order to gain a size refuge from some predators. This would be facilitated by staying in the warm, surface waters where many of the smaller zooplankton species are found. It may be that young animals are less tolerant of food shortages and by staying at the surface where food is more abundant they minimize this risk. Whatever the advantage, we must resolve why they gradually shift to a vertically migrating habit at some point during their development. It may be that commencement of vertical migration is related to size in those species that migrate. As size increases the strategy of migrants may shift from one of maximizing growth with an attendant high metabolic cost when they are young, to one involving slower growth but more efficient partitioning of energy to growth as they get older. The physiological migration pattern would still be best if this were the case. Growth rates of young C. trivittatus larvae are higher than those of third and fourth-instar larvae and the latter larvae appear to spend less time at the surface as they get older.

Vertically migrating carnivores, whether zooplankton or fish, have been largely ignored in considerations of the adaptive value of vertical migration. However, they present some problems when these theories are extended to include them. One such problem, that of the maintenance of a constant metabolic rate throughout the migration (Teal 1971), has been discussed previously (Section IV). Various theories concerning the adaptive value of vertical migration discussed above have been considered for fish (Brett 1971). He concludes that juvenile sockeye salmon in Babine Lake, B.C., behaviourally thermoregulate to maximize energy gain. Unlike McLaren (1963) Brett includes an analysis of the role of food; however, he considers only the case of maximum ration. His conclusions are subject to the same criticisms as McLaren's. Alternation of high and low temperatures can also occur in the horizontal plane. Hyatt (pers. comm.) is studying foraging movements of sockeye salmon which feed in warm shallow water at the edge of Marion Lake and refuge in a cold water spring in the centre of the lake. The temperature regime experienced by these fish during a horizontal migration is similar to that experienced by fish in Babine Lake or by zooplankton during their vertical migrations. The bioenergetic consequences of alternation of high and low temperatures are unclear, but they may play an important part in maintaining these diverse migration patterns.

The analysis of Chaoborus vertical migration in Funice Lake can be viewed as a model for the wider consideration of the adaptive value of vertical migration. McLaren's (1963) provocative theory does not properly establish the relationship between food and temperature and the effect of this interaction on the energetics of vertically migrating animals. Including food in an analysis of vertical migration based solely on energetics leads to the two migration strategies discussed above as the most adaptive -- staying at the surface or following a physiologically mediated migration pattern. Some animals do not migrate at all, and few, if any, have been shown to follow a physiological migration pattern. Most actively migrating zooplankton follow a seasonally adjustable, light mediated diel migration pattern that places them near the surface during the night and deeper during the day. As Mauchline and Fisher (1969) point out, it is unlikely that any single theory can account for the adaptive value of vertical migration. Rather, there are a variety of benefits which vary in importance from group to group. The idea of an energetic advantage derived from the alternation of high and low temperatures is an attractive one, but no adequate theory is presently available that will demonstrate such an advantage. Such a theory would have to take into account temperature dependent respiration and digestion rates, prey distribution, and the possibility of irregular feeding.

Summary

1. A review of early theories on the adaptive value of vertical migration confirms the lack of any single theory that can account for vertical migration. A number of benefits have been suggested for vertical migration in a variety of species.

2. McLaren's (1963) theory on the energetic advantage of alternation of temperature is shown to depend 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. A simulation model of the energetics of vertical migration in Chaoborus larvae confirmed that, on an energetics basis, the two migration patterns cited above are better for larval growth than the migration pattern associated with McLaren's theory.

3. The differences between the existing migration pattern of fourth-instar C. trivittatus larvae and the patterns suggested as the most advantageous on an energetic basis are discussed. With no obvious selective force acting in Eunice Lake to maintain the vertical migration pattern observed, it is concluded that this pattern is probably maintained by slow loss of the migration pattern by the Eunice Lake population and by immigration from populations in other lakes which are subject to selection pressure favoring this migration pattern.

4. With respect to vertical migration in general, it is

concluded that the adaptive value of the migration varies from group to group. One of the potential benefits from migrating is an energy gain due to alternating high and low temperatures. To date there has been no cohesive theory on the energetics of vertical migration that includes a discussion of food availability.

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APPENDIX I

Figure	Page
1. Flow diagrams of subroutines EATIT and DIGST. ..	129
2. Flow diagram of subroutine DOIT.	130
3. Graphs of the input variables for the model. ...	131

Table	Page
1. The meaning of the FORTRAN variables used in the simulation model.	132
2. The meaning, source, and value of the parameters in the simulation model.	134

FIGURE 1

Flow diagrams of subroutines EATIT and DIGST.

SUBROUTINE EATIT

```

BFCTR = YNT (TIME, TM, BVUL)
SFCTR = YNT (TIME, TM, BVUL)
BFUD = BFOOD * BFCTR
SFUD = SFOOD * SFCTR
U = (ALPH1 * BFUD) / (1 + (ALPH1 * BFUD * H1) + (ALPH2 * SFUD * H2))
BFE = POIS (U)
U = (ALPH2 * SFUD) / (1 + (ALPH1 * BFUD * H1) + (ALPH2 * SFUD * H2))
SFE = POIS (U)
WBFE = WBF * BFE
WSFE = WSF * SFE
TFE = WBFE + WSFE
    
```

SUBROUTINE DIGST

FIGURE 2

Flow diagram of subroutine DOIT.

FIGURE 3

Graphs of the input variables for the model.

Table 1. The meaning of the FORTRAN variables used in the simulation model.

Variable	Meaning
A	Coefficient in the respiration rate calculation
AD	Weight of food digested per time interval
BFCTR	Large prey availability coefficient
BFE	Number of large prey eaten per time interval
BFOOD	Large prey density
BFUD	Adjusted large prey density
BFUDE	Input density of large prey
BVUL	Vulnerability coefficient for large prey
DEPTH	Depth
DP	Digestion rate
DT	Depth counter for interpolation
EASS	Weight of food assimilated per time interval
ESTRD	Weight of food stored per time interval
FA	Food available for assimilation
FPIG	Food pool in the gut
IFLG	Flag for switch from feeding cycle to digestive pause
RESP	Total weight cost per time interval
RC	Respiration cost
RRR	Respiration rate
RRRH	Upper interpolation point in the calculation of RRR
RRRL	Lower interpolation point in the calculation of RRR
SC	Swimming cost
SFCTR	Small prey availability coefficient
SFE	Number of small prey eaten per time interval
SFOOD	Small prey density
SFUD	Adjusted small prey density
SFUDE	Input density for small prey
STFE	Cumulative weight of food eaten
SVUL	Vulnerability coefficient for small prey
TEM	Temperature
TEMP	Temperature
TFE	Weight of all prey eaten per time interval
TIM	Time counter for depth interpolation
TIME	Time interval in the simulation
TM	Time counter for the prey vulnerability interpolation
TMTUR	Temperature
U	Mean of the Poisson distribution in EATIT

Variable	Meaning
VC	Crop volume
W	Larval weight
WBFE	Weight of large prey eaten per time interval
WG	Gain in weight per time interval
WSFE	Weight of small prey eaten per time interval
Z	Depth

Table 2. The meaning, source, and value of the parameters in the simulation model.

Parameter	Value	Units	Meaning	Source
ALPH1	0.000128	Number per 100 liters per hour	Capture rate per unit large prey density during searching time	Measured
ALPH2	0.000064	Number per 100 liters per hour	Capture rate per unit small prey density during searching time	Measured
H1	0.1	hours	Handling time for large prey	Section IV
H2	0.30	hours	Handling time for small prey	Section IV
SDA	0.30	---	Specific dynamic action	Hypothetical
SEST	0.0015	mg	Initial weight stored	Hypothetical
SFPG	0.0	mg	Initial food pool in the gut	Hypothetical
VCMAX	0.16	mg	Maximum crop capacity	Measured
WBF	0.08	mg	Weight of large prey	Measured
WF	0.00485	mg per minute	Conversion factor: oxygen consumed to mg	Hargrave (1971)
WSF	0.006	mg	Weight of small prey	Measured
WO	0.15	mg	Initial weight	Hypothetical

APPENDIX II

```

FUNCTION YNT (TX,X,Y)
DIMENSION X(20), Y(20)
I=2
19 IF (X(I)-TX) 20,30,40
20 I=I+1
GO TO 19
30 YNT=Y(I)
GO TO 50
40 YNT=Y(I-1) + ((Y(I)-Y(I-1)) * (TX-X(I-1))) / (X(I)-X(I-1))
50 RETURN
END

```

```

FUNCTION POIS(U)
R=RANDV(0)
XN=0.
XNF=1.
P=0.
E=EXP(-U)
UN=1
5 P=P+UN*E/XNF
IF (P.GE.R) GO TO 10
XN=XN+1.
XNF=XNF*XN
UN=UN*U
GO TO 5
10 POIS=XN
RETURN
END

```

C... THIS SUBROUTINE DRAWS A GRID FOR OUTPUT OF THE
C... SIMULATION RESULTS.

```

SUBROUTINE MOUT
COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1
1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFCOD,SFOOD,B
1FE,SFE,FA,TEMP,TIME,Z(6),TIM(6),TEM(6),BFUDE(11),SFUD
1E(11),RR(6),DP(6),TMTUR(6),A(5),B(5),TMP(5),TM(6),BVU
1L(6),SVUL(6),BFUD,SFUD,BFCTR,SFCTR,NPAR
CALL DATSW (0,JQ)
GO TO (3,4),JQ
3 XSC = 6./XMAX
YSC = 6./YMAX
CALL SCALF (XSC,YSC,0.,0.)
CALL FGRID (0,0.,0.,XMAX/30.,30)
CALL FGRID (1,0.,0.,YMAX,0)

```

```

4      X=0.
      Y=WO
      CALL FPLOT (-2,X,Y)
      IXMAX=XMAX
      DO 40 I=1,IXMAX
      READ (1,I) Y
      IF (Y-YMAX) 30,30,31
31     Y = YMAX
30     IF (Y-YMIN) 33,34,34
33     Y = YMIN
34     X=I
      CALL FPLOT (0,X,Y)
40     CONTINUE
      CALL PENUP
41     RETURN
      END

```

C... THIS SUBROUTINE CONTAINS THE NECESSARY INSTRUCTIONS
 C... FOR MODIFYING THE INPUT PARAMETERS.

```

      SUBROUTINE MMOD
      DIMENSION PAR(40)
      COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1
1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFOOD,SFOOD,B
1FE,SFE,FA,TEMP,TIME,Z(6),TIM(6),TEM(6),BFUDE(11),SFUD
1E(11),RR(6),DP(6),TMTUR(6),A(5),B(5),TMP(5),TM(6),BVU
1L(6),SVUL(6),BFUD,SFUD,BFCTR,SFCTR,NPAR
      EQUIVALENCE (PAR(1),D1)
      M=6

```

C... TO CHANGE A PARAMETER VALUE

```

10     CALL DATSW(1,JQ)
      GO TO (11,20),JQ
11     WRITE (1,12)
12     FORMAT (' ID/NEW VALUE')
      READ (M) ID,X
      PAR(ID)=X
      GO TO 10

```

C... TO CHANGE 'TIM' VALUES

```

20     CALL DATSW(2,JQ)
      GO TO (21,30),JQ
21     WRITE(1,22)
22     FORMAT('NEW TIM VALUES')
      READ(M) (TIM(I),I=1,6)
      GO TO 20

```

C... TO CHANGE 'Z' VALUES

```

30     CALL DATSW(3,JQ)
      GO TO (31,40),JQ
31     WRITE(1,32)
32     FORMAT ('NEW Z VALUES')
      READ (M) (Z(I),I=1,6)
      GO TO 30

```

C... TO CHANGE 'TEM' VALUES

```

40     CALL DATSW(4,JQ)

```

```

        GO TO (41,50),JQ
41      WRITE(1,42)
42      FORMAT('NEW TEM VALUES')
        READ(M) (TEM(I),I=1,20)
        GO TO 40
C...   TO CHANGE 'BFUDE' VALUES
50      CALL DATSW(5,JQ)
        GO TO (51,60),JQ
51      WRITE(1,52)
52      FORMAT('NEW LARGE FUDE VALUES')
        READ(M) (BFUDE(I),I=1,11)
        GO TO 50
C...   TO CHANGE 'SFUDE' VALUES
60      CALL DATSW(6,JQ)
        GO TO (61,70),JQ
61      WRITE(1,62)
62      FORMAT('NEW SMALL FUDE VALUES')
        READ(M) (SFUDE(I),I=1,11)
        GO TO 60
C...   TO CHANGE 'A' VALUES
70      CALL DATSW(7,JQ)
        GO TO (71,100),JQ
71      WRITE(1,72)
72      FORMAT('NEW A VALUES')
        READ(M) (A(I),I=1,5)
        GO TO 70
C...   TO CHANGE 'B' VALUES
100     CALL DATSW(9,JQ)
        GO TO (101,80),JQ
101     WRITE(1,102)
102     FORMAT('NEW B VALUES')
        READ(M) (B(I),I=1,5)
        GO TO 100
80      CALL DATSW(10,JQ)
        GO TO (81,90),JQ
81      WRITE(1,82)
82      FORMAT('NEW DP VALUES')
        READ(M) (DP(I),I=1,6)
        GO TO 90
C...   TO CHANGE 'TM' VALUES
90      CALL DATSW(11,JQ)
        GO TO (91,110),JQ
91      WRITE(1,92)
92      FORMAT('NEW TM VALUES')
        READ(M) (TM(I),I=1,6)
        GO TO 110
C...   TO CHANGE 'BVUL' VALUES
110     CALL DATSW(12,JQ)
        GO TO (111,120),JQ
111     WRITE(1,112)
112     FORMAT('NEW BVUL VALUES')
        READ(M) (BVUL(I),I=1,6)

```

```

      GO TO 120
C...  TO CHANGE 'SVUL' VALUES
120   CALL DATSW(13,JQ)
      GO TO (121,130), JQ
121   WRITE(1,122)
122   FORMAT ('NEW SVUL VALUES')
      READ (M) (SVUL(I), I=1,6)
      GO TO 130
130   RETURN
      END

```

```

C...  THIS SUBROUTINE CALCULATES THE NUMBER OF LARGE AND
C...  SMALL PREY EATEN PER TIME INTERVAL AND CALCULATES THE
C...  VOLUME OF THE CROP AFTER EATING. U IS THE CAPTURE RATE
C...  OF LARGE OR SMALL PREY CALCULATED FROM HOLLING'S
C...  DISK EQUATION FOR TWO PREY TYPES. ALPH1 AND ALPH2 ARE
C...  CAPTURE RATES PER UNIT PREY DENSITY DURING SEARCH
C...  TIME. LFOOD AND SFOOD ARE THE PREY DENSITIES OF LARGE
C...  AND SMALL PREY. H1 AND H2 ARE HANDLING TIMES FOR LARGE
C...  AND SMALL PREY. WBF AND WSF ARE THE WEIGHTS OF LARGE
C...  AND SMALL PREY. POISS IS A FUNCTION WHICH GIVES THE
C...  NUMBERS OF LARGE AND SMALL PREY EATEN USING U AS THE
C...  MEAN OF A POISSON DISTRIBUTION AND A RANDOM NUMBER
C...  GENERATOR.

```

```

      SUBROUTINE EATIT
      COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1
1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFCOD,SFOOD,B
1FE,SFE,FA,TEMP,TIME,Z(6),TIM(6),TEM(6),BFUDE(11),SFUD
1E(11),RR(6),DP(6),TMTUR(6),A(5),B(5),TMP(5),TM(6),BVU
1L(6),SVUL(6),BFUD,SFUD,BFCTR,SFCTR,NPAR
      BFCTR=YNT(TIME, TM, BVUL)
      BFUD=BFOOD*BFCTR
      SFCTR=YNT(TIME, TM, SVUL)
      SFUD=SFOOD*SFCTR
      U=(ALPH1*BFUD)/(1+(ALPH1*BFUD*H1)+(ALPH2*SFUD*H2))
      BFE=POIS(U)
      U=(ALPH2*SFUD)/(1+(ALPH1*BFUD*H1)+(ALPH2*SFUD*H2))
      SFE=POIS(U)
      WBFE=WBF*BFE
      WSFE=WSF*SFE
      TFE=WBFE+WSFE
      IF(TFE.GT.(VCMAX-VC)) TFE=(VCMAX-VC)
      VC=VC+TFE
      FA=FA+(0.68*TFE)
      STFE=STFE+TFE
      RETURN
      END

```

```

C...  THIS SUBROUTINE CALCULATES THE AMOUNT DIGESTED FROM
C...  THE CROP DURING A TIME INTERVAL.
      SUBROUTINE DIGST
      COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1

```

```

1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFOOD,SFOOD,E
1FE,SFE,FA,TEMP,TIME,Z(6),TIM(6),TEM(6),BFUDE(11),SFUD
1E(11),RR(6),DP(6),TMTUR(6),A(5),B(5),TMP(5),TM(6),BVU
1L(6),SVUL(6),BFUD,SFUD,BFCTR,SFCTR,NPAR
  AD=YNT(TEMP,TMTUR,DP)
  IF(AD.GT.FA)AD=FA
  FPIG=AL
  VC=VC-AD
  FA=FA-AD
  RETURN
  END

C... THIS SUBROUTINE DOES THE ACTUAL CALCULATIONS OF ENERGY
C... GAINS AND LOSSES DURING EACH TIME INTERVAL.
  SUBROUTINE DOIT (DF,DT,RTOT,W,ID)
  COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1
1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFOOD,SFOOD,B
1FE,SFE,FA,TEMP,TIME,Z(6),TIM(6),TEM(6),BFUDE(11),SFUD
1E(11),RR(6),DP(6),TMTUR(6),A(5),B(5),TMP(5),TM(6),BVU
1L(6),SVUL(6),BFUD,SFUD,BFCTR,SFCTR,NPAR
C... INITIALIZE
  IFLG=1
  NTEST=3
  W=WO
  FPIG = SFPG
  ESTRC = SEST
  EASS =0.
  FA=0.
  VC=0.
  RTOT=0.
  STFE=0.
C... LOOP AROUND TIME INTERVALS-- 30* 288 FIVE MINUTE INTERVALS
  ITEST=0
  DO 200 K=1,30
  TIME=0.
  DO 105 J=1,72
  DEPTH=YNT(TIME,TIM,Z)
  TEMP = YNT(DEPTH,DT,TEM)
  BFOOD=YNT(DEPTH,DF,BFUDE)
  SFOOD = YNT(DEPTH,DF,SFUDE)
C... IFLG TRIGGERS THE PROGRAM INTO THE FEEDING CYCLE OR
C... DIGESTIVE PAUSE (DIGESTIVE CYCLE ONLY). IT IS
C... DEPENDENT ON THE CROP VOLUME.
  BFE=0.
  SFE=0.
  GO TO (400,510),IFLG
400  CALL EATIT
  IF (VC.GE.VCMAX) IFLG=2
510  CALL DIGST
  IF(FA.GT.0.) GO TO 550
  IFLG=1
  VC=0.

```



```

      FA=0.
C... ENERGY CALCULATIONS: ASSIMILATION, MAINTENANCE,
C... STORAGE, GROWTH, AND RESPIRATION (RRR).
550  L=2
4    IF (TMP (L) -TEMP) 3,2,1
3    L=L+1
      GO TO 4
2    RRR=EXP (A (L) ) *W**B (L)
      GO TC 5
1    RRRL=EXP (A (L-1) ) *W**B (L-1)
      RRRH=EXP (A (L) ) *W**B (L)
      RRR=RRRL+ ( (RRRH-RRRL) * (TEMP-TMP (L-1) ) ) / (TMP (L) -TMP (L-1) )
      GO TC 5
5    RC=RRR/3.
      SC=0.0
      IF (TIME.GE. 24. .AND. TIME.LT. 30.) SC=.045
      IF (TIME.GE. 42. .AND. TIME.LT. 48.) SC=.045
      RESP= (RC+SC) *WF
      ESTRD=FPIG- (SDA*FPIG)
      WG= (ESTRD-RESP)
      W=W+WG
      TIME=TIME+1.
      CALL DATSW (15,JQ)
      GO TC (600,601),JQ
600  WRITE (3,602) TIME,DEPTH,TEMP,BFOOD,SFOOD,BFE,SFE,FPIG,FA,
1RRR, RESP, ESTRD, WG, W
602  FORMAT (1X,F11.0,9 (1X,E10.3))
      WRITE (3,700) L,RRRL,RRRH,RRR,A (L),B (L),TMP (L),TEMP
700  FORMAT (1X,I1,7 (5X,F10.4))
      WRITE (3,1000) VC,IFLG
1000 FORMAT (2X,'***', (F10.6), '***',I2,'***')
601  CONTINUE
      RTOT=RTOT+RESP
      ITEST=ITEST+1
      IF (MOD (ITEST,NTEST) .EQ.0) WRITE (1,ID) W
105  CONTINUE
200  CONTINUE
      RETURN
      END

```

C... THIS IS THE MAINLINE PROGRAM WHERE ALL DATA INPUTS AND
C... OUTPUTS ARE HANDLED.

```

      DIMENSION DT (20), DF (11), PNAME (2), PAR (40)
      COMMON D1,SDA,WO,XMAX,YMAX,YMIN,TF,WF,SFPG,SEST,ALPH1
1,ALPH2,H1,H2,WBF,WSF,VCMAX,STFE,VC,FPIG,BFOOD,SFOOD,B
1FE,SFE,FA,TEMP,TIME,Z (6),TIM (6),TEM (6),BFUDE (11),SFUL
1E (11),RR (6),DP (6),TMTUR (6),A (5),B (5),TMP (5),TM (6),BVU
1L (6),SVUL (6),BFUD,SFUD,BFCTR,SFCTR,NPAR
      EQUIVALENCE (PAR (1),D1)
      DEFINE FILE 1 (730,2,U,ID)
      CALL P1130
      M=6

```

C... READ IN PARAMETERS AND GRAPHS.

```

      READ (2,2) NPAR
2      FORMAT (I2)
      DO 120 I=1,NPAR
      READ (2,104) K, PNAME, PAR(K)
104    FORMAT (I3,7X,2A4,2X,F10.0)
      WRITE(3,112) K, PNAME, PAR(K)
112    FORMAT (3X,I2,1X,2A4,2X,E14.7)
120    CONTINUE
      READ (2,100) (Z(I),I=1,6)
      READ (2,100) (TIM(I),I=1,6)
      READ (2,100) (TEM(I),I=1,20)
      READ (2,100) (DT(I),I=1,20)
      READ (2,100) (BFUDE(I),I=1,11)
      READ (2,100) (SFUDE(I),I=1,11)
      READ (2,100) (DF(I),I=1,11)
      READ (2,100) (TMTUR(I),I=1,6)
      READ (2,100) (DP(I),I=1,6)
      READ (2,100) (A(I),I=1,5)
      READ (2,100) (B(I),I=1,5)
      READ (2,100) (TMP(I),I=1,5)
      READ (2,100) (TM(I),I=1,6)
      READ (2,100) (BVUL(I),I=1,6)
      READ (2,100) (SVUL(I),I=1,6)
100    FORMAT (8F10.0)
      WRITE(3,602) Z
      WRITE(3,602) TIM
      WRITE(3,602) TEM
      WRITE(3,602) DT
      WRITE(3,602) BFUDE
      WRITE(3,602) SFUDE
      WRITE(3,602) DF
      WRITE(3,602) TMTUR
      WRITE(3,602) DP
      WRITE(3,602) A
      WRITE(3,602) B
      WRITE(3,602) TMP
      WRITE(3,602) TM
      WRITE(3,602) BVUL
      WRITE(3,602) SVUL
800    PAUSE
      ID=1
      READ (6,333) C
333    FORMAT (F3.0)
      CALL RANDI(C)
C...TO MODIFY INPUT
      CALL DATSW (8,JQ)
      GO TO (81,90),JQ
81     CALL MMOD
90     CALL DOIT(DF,DT,      RTOT,W,ID)
      WRITE(3,2000) W
2000   FORMAT (1X,'FINAL WEIGHT=',E14.7)

```

```
P=W-WO
RATIO= P/(P+RTOT)
WRITE(3,2001) RTOT,P,RATIO
2001  FORMAT (30X,'RTOT =',E14.7,5X,'P =',E11.4,5X,'RATIO =',
1E14.7)
      WRITE (3,3000)          STFE
3000  FORMAT (          5X,E12.5)
      CALL MOUT
C...TO MAKE ANOTHER RUN
      CALL DATSW(14,JQ)
      GO TO (800,801),JQ
801   CALL EXIT
602   FORMAT (1X,10(1X,F10.4))
      END
```

EXECUTION TERMINATED
T=5.40 DR=8

\$\$SIG