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Regulation of zooplankton vertical migrations by light, food, and fish

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McLean, Elizabeth Susan, Ph.D.

University of New Hampshire, 1988

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REGULATION OF ZOOPLANKTON VERTICAL MIGRATIONS BY LIGHT, FOOD, AND FISH

By

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DISSERTATION

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in

Zoology

December, 1988

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28 November 1988
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To my Family

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ABSTRACT

REGULATION OF ZOOPLANKTON VERTICAL MIGRATIONS BY LIGHT, FOOD, AND FISH

by

Elizabeth S. McLean
University of New Hampshire, December, 1988

The regulation of zooplankton vertical migration has been attributed to the physical environment, and, more recently, to biological factors. This study evaluated the influence of light, food and fish on vertical migration. Laboratory experiments quantified changes in vertical migrations of Daphnia pulex in tall columns in response to short term changes in food concentration and the presence of a fish, under a wide range of natural light conditions.

A stimulus-threshold model predicted the time of the start of migration from a threshold rate of relative light intensity change. Hypotheses that migrations follow isopleths of light intensity, and that velocity of migration is directly correlated to relative rate of light intensity change, were not supported. Concentrations of Chlorella sp. had little influence on the timing, amplitude, or velocity of migration. There was evidence of a sensory response of Daphnia pulex to the short term presence of a fish in the columns. With a fish present, pre-migration population depths were deeper. This response ceased within 24 hours after removing the fish. Juvenile Daphnia pulex started their migrations from shallower depths in the columns, and otherwise migrated similarly to adults.

Field studies of zooplankton vertical migration were conducted on four New Hampshire lakes. The lakes varied in food concentrations, and all contained planktivorous fish. The field results were consistent with an avoidance of ultra-violet radiation by zooplankton. Pre-migration depths were deeper in waters more transparent to visible light. Food stratification was correlated with amplitude and direction of vertical migration, and the direction of migration was apparently influenced by the phytoplankton composition. Although planktivorous fish were present in the lakes, the zooplankton did not take advantage of possible light refugia. Fish density did not significantly affect vertical migrations. Invertebrate predation was not sufficient to explain reverse migrations.

INTRODUCTION

The regulation of zooplankton vertical migrations has often been attributed to physical aspects of the environment, especially light (eg. Clarke 1930; Kikuchi 1937; Schallek 1942; Harris and Wolfe 1955; Ringelberg 1964; Siebeck and Ringelberg 1969), and occasionally pH and dissolved gases (Bayly 1963; LaRow 1970; Meyers 1980; Kring and O'Brien 1981), or temperature (Haney and Buchanan 1980; Calban and Mackerewicz 1982; Gerritsen 1982; Geller 1986). Biological factors, including feeding (Hardy 1956, in Enright 1977), metabolic advantages (Enright 1977; McLaren 1963), reproductive strategies (David 1961; McLaren 1974), and predator avoidance (Zaret and Suffern 1976; Gliwicz 1986), have usually been proposed to act as ultimate factors explaining the selective advantages of migration behaviors. Feeding and predator avoidance are now recognized as proximal factors as well (Haney 1988). Circadian rhythms are thought to underlie migrations (Harris 1963; Enright and Hamner 1967; Ringelberg and Servaas 1971). The principal goal of this study was to evaluate the influence of light, food concentrations, and the presence of a predator, and their interactions, on vertical migration.

Current hypotheses of light control of vertical migration developed from observations that zooplankton avoid the brightly lit surface waters in fresh and salt water (Cuvier 1817 and Bellinghausen 1819 in Bayly 1987; Bogorov 1946). Negative phototropism and positive geotaxis in bright daylight were proposed as the mechanisms controlling avoidance of the surface by zooplankton (Dice 1914 in Cushing 1951;

Esterley 1917). The body orientation of zooplankters in the water column was attributed to chemical cues altering the phototactic reaction of zooplankton. For example, reversals in phototaxis could be induced in the laboratory by pH changes (Baylor and Smith 1957). A geotactic response helps *Daphnia magna* orient vertically (Grosser, *et.al.* 1953). However, experiments with light gradients in horizontally placed tubes indicated that for many zooplankters geotaxis was probably not involved in the light response (Clarke 1930; Schalleck 1943). A preferendum hypothesis for the light control of vertical migrations may be derived from these observations: zooplankton adjust their distribution in order to remain at the depth of a particular light intensity and track an isopleth of light intensity. This results in vertical movements of zooplankton upward in the evening and down in the morning. Few critical studies have provided support for this mechanism (eg. Boden and Kampa 1967; Forward, *et.al.* 1984).

Clarke (1930) proposed an alternative hypothesis: the rate of change in the absolute light intensity stimulated the zooplankton to initiate migration. Laboratory experiments have since shown that *Daphnia magna* respond to a set of instantaneous light changes with a positive phototaxis (Ringelberg 1964); and that their response is to a threshold level of relative change in the light intensity rather than to an absolute magnitude of change (Ringelberg 1964). Ringelberg proposed this stimulus-threshold as a timer or Zeitgeber, initiating upward vertical migrations. Clarke (1930) recognized that changes in light intensity produced the changes in swimming activity and orientation resulting in vertical migrations, while Ringelberg's refinement allowed for the continual adaptation of the eye to changing light intensities. Field studies provide some support for stimulus-threshold control by light for the onset of evening activities. Haney and Hall (1975) showed that for *Daphnia* such a stimulus-threshold model predicted the initiation of evening vertical migrations. In streams, mayfly larvae (*Leptophlebia* and *Ephemerella*) initiate their evening drift activity at a time predictable from the stimulus (Haney, *et.al.* 1983). Vôute, *et.al.* (1974) suggest that pond bats (*Myotis dasyceneme*) begin their evening flight at a threshold of relative decrease in light intensity.

There is evidence that the relative rate of light change may control the migration velocity of zooplankton. The relative rate of change of light intensity shows a positive correlation with swimming velocity for individuals of *Daphnia magna* in experimental tanks (Daan and Ringelberg 1969). In addition, the velocity of migrating populations of *Chaoborus* in the field also correlates positively with the stimulus (Haney, *et.al.* 1987). It is possible that a stimulus-velocity model holds for migrating zooplankton in general.

The position of zooplankton populations in the water column prior to the upward migration may also be regulated by light intensity. Hairston (1976) demonstrated in the laboratory that intensities of ultra-violet B and near blue radiation equal to those at lake surfaces result in cumulative damage to zooplankton. Such damage can cause 50% mortality in 4 - 8 days (Ringelberg, *et.al.* 1984). Hairston (1976) proposed that zooplankton populations would avoid these wavelengths (290-350 nm) by remaining deeper during the day, and would then migrate upward at night.

The evidence for control of vertical migrations by food availability is mostly indirect. In an experimental column, the mean depth of a *Daphnia magna* population rose immediately in response to the addition of concentrated food, even when the food was introduced to the bottom of the column (Haney and Buchanan 1980). In contrast, extremely low food concentrations may be associated with the reduction or near elimination of an evening migration (Huntley and Brooks 1982; Dagg 1985; Johnsen and Jakobsen 1987). Also, starvation conditions may favor zooplankton with the greatest energy reserves (Goulden and Hornig 1980; Dagg 1985) or tolerance for starvation (Borchers and Hutchings 1986). Changes in the composition of a zooplankton community could alter the extent and timing of the migrations observed.

Feeding activity, although not shown to have a direct effect on vertical migration, is known to follow a similar diel pattern (Mackas and Bohrer 1976; Haney and Hall 1975; Starkweather 1975). The location of strata of edible particulates or nutrients may well interact with such feeding cycles to alter the migration (scyphozoan medusae, Hamner and Hauri 1981; *Daphnia* and *Eudiaptomus*, Lampert and Taylor 1985; *Daphnia*, Pijanowska and Dawidowicz 1987). In addition, zooplankton are often associated with maxima of chlorophyll a in the vertical profile of the water column (George 1983; Paffenhoffer 1983; Southward and Barett 1983).

The generalizations that the prey of vertebrate predators elude capture by avoiding encounters, while those susceptible to capture by invertebrates tend to develop means of escaping from capture (Vermeij 1982), appear to apply to zooplankton as well as to other animals. Vertical migrations are believed by some to have evolved as a means of avoiding encounters with visual predators, specifically fish. Zaret and

Suffern (1976) suggested that zooplankton maintain a greater day depth, and so migrate from greater depths, when visual predators are present in the system. Gliwicz (1986) noted that for lakes in the Tatra Mountains there is a positive correlation between the length of time since fish had been introduced and the degree of migration behavior shown by the cyclopoid copepod _Cyclops abbysorum_. The addition of planktivorous fish to a lake has resulted in vertical migration by _Chaoborus_ where none was previously observed (Luecke 1986), and may have resulted in changes in already existing migration patterns for _Daphnia pulex_ (Kitchell and Kitchell 1980). In some cases seasonal differences in the extent of the migrations may be due to variations in predator activity (Stich and Lampert 1981). Because of the relatively short generation time of most zooplankters, it is generally assumed that these seasonal differences are most likely an adaptation to living in systems with fish, rather than a proximal response to their presence.

Zooplankters have been shown capable of responding to the immediate presence of a fish with fleeing actions (Drenner, _et.al._ 1978). Only recently has there been support for the idea that vertical migration might be regulated by a sensory response to predation (Johnson and Jakobsen 1987; Leibold 1988 in Haney 1988; Stirling 1988).

It is unclear how the presence of juveniles influences vertical migrations. Some field observations indicate that juveniles migrate further, while others indicate they migrate lesser distances than adults (Pennak 1944). It has also been observed that juvenile zooplankton migrate for a longer time and more slowly than adults (Hutchinson 1967). Juday (1904) found that copepodites and sometimes juvenile _Daphnia_ would migrate further and arrive at the surface sooner than adult animals. Dini et al. (1987), found only the largest *Daphnia*, greater than 1.4 mm in body length, migrated in their system.

The data collected for this study were used to evaluate three models for control of vertical migrations by light: the preferendum hypothesis, the stimulus-threshold model, and the stimulus-velocity model. The preferendum hypothesis predicts that zooplankton will maintain a day depth corresponding to a particular light intensity, and will follow the isopleth of that light intensity upward in the evening. The stimulus-threshold model predicts that populations will begin to migrate when the relative rate of change of light intensity reaches a certain threshold value. The stimulus-velocity model predicts that migration velocity is continuously regulated by the relative rate of light intensity change.

Food concentrations were intentionally varied during the experiments to assess the relative influence of food concentration on the pre-migration depths, amplitude and timing of evening vertical migrations.

In addition, the study examined whether a visual predator, specifically a fish, can alter the evening vertical migration of zooplankton via short-term sensory responses rather than strictly by genetic selection. The effects of the presence and absence of a fish on the parameters of the migration -- initial depth, amplitude, initiation time, and velocity of the migration -- were evaluated to provide information on how the migration behavior might change in the presence of a visual predator. An experimental chamber and protocol allowed the collection of data on the migration of juveniles of a known range of ages from one set of parents. These data will add to the understanding of how models of vertical migration based on adult behavior may be influenced by the age or size structure of the population.

Laboratory studies of vertical migration in columns (eg. Harris and Wolfe 1955; LaRow 1970; Buchanan 1979; this study) provide detailed information from a controlled environment. Such data allow analyses of how a population will respond to known conditions over short time spans. Collection of equally detailed data is not practical in field studies, even when particular effort is made to gather frequent, limited samples (eg. Enright and Honnegger 1977). This is, in part, because the results are less direct than visual observations. Although field samples differ from those collected in a controlled environment, they enable evaluation of the validity of the lab results for wild populations. They also offer valuable insight about factors which through simplification may have been eliminated from laboratory systems. For this study, a set of field samples were taken from four of New Hampshire lakes to complement and verify the results of laboratory observations. The lakes chosen had a range of food concentrations similar to those used in the laboratory, and all contained populations of planktivorous fish.

METHODS

Laboratory Methods

Experimental Chamber and Columns

An experimental chamber for laboratory observations of vertical migration was designed to simulate the natural light distribution in a lake, and to provide a sufficient depth that vertical distributions and movements of zooplankton populations could be compared to the vertical migrations observed in lakes. The chamber was constructed in the Anadromous Fish and Invertebrate Research Lab (AFAIR Lab) near the Durham Reservoir at the University of New Hampshire, Durham, New Hampshire. The chamber included two clear cast-acrylic columns (4.2 m tall, 8.65 cm inner diameter, and 2 mm wall), each containing 21.5 l of water, and placed in a tent of black plastic, open at the top (Figure 1a). The tent created a light intensity gradient in the columns approximating the depth gradient from 0 - 8 m in local ponds (Figure 2). A white cloth over the top of the tent diffused point sources of light, reducing the light angularity. The vertical columns were located in front of 4.3 m high, south facing windows in the lab, allowing natural lighting and light cycles within the chamber (Figure 1a).

Inside the experimental chamber, a 4-m ladder provided access to the upper reaches of the column (Figure 1b). A black plastic curtain was hung between the columns and the ladder to shield the columns from the observer. A fan at the base of the columns reduced vertical temperature gradients in the air and the columns. Continuous operation of the fan prevented on/off changes in noise, which are felt by zoo-

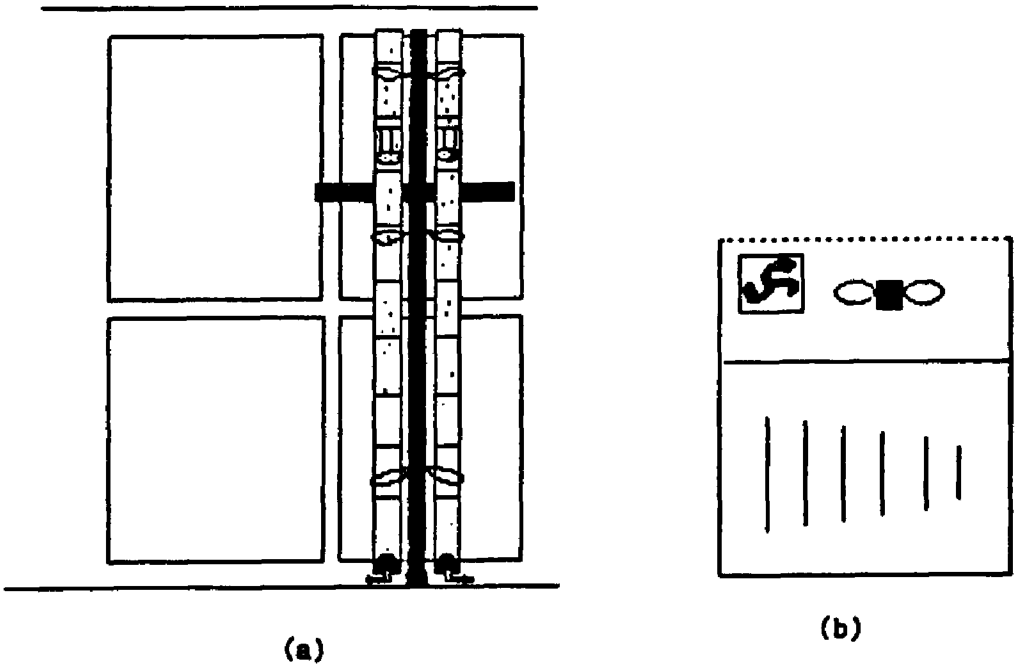


Figure 1. Diagram of the experimental chamber. (a) columns in front of the windows, showing support structure. (b) floor plan with fan beside columns, and a black plastic curtain indicated between the columns and the ladder.

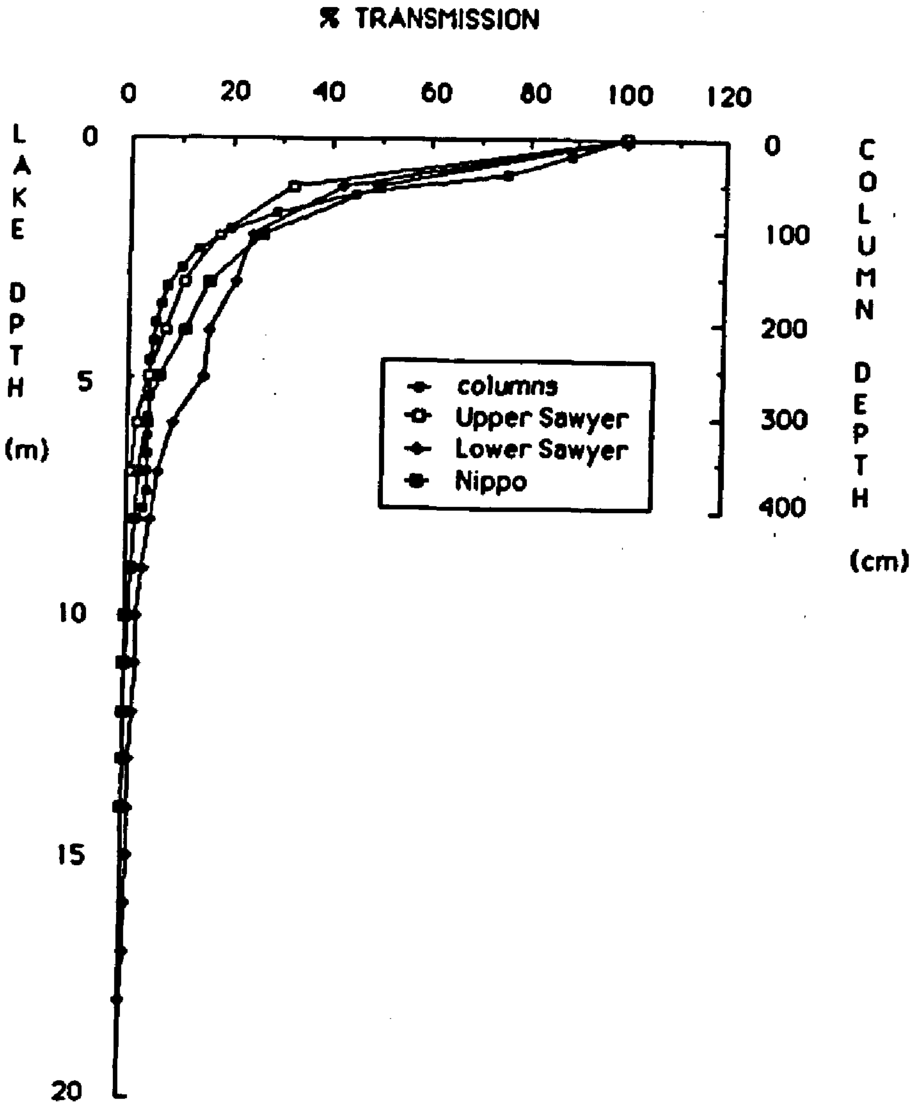


Figure 2. Percent transmission of surface light intensity in the columns inside the experimental chamber, and in three New Hampshire lakes: Upper Sawyer Pond, Lower Sawyer Pond, and Nippo Pond.

plankton as vibrations, and which can disturb their swimming activity (Buchanan and McCartney 1982).

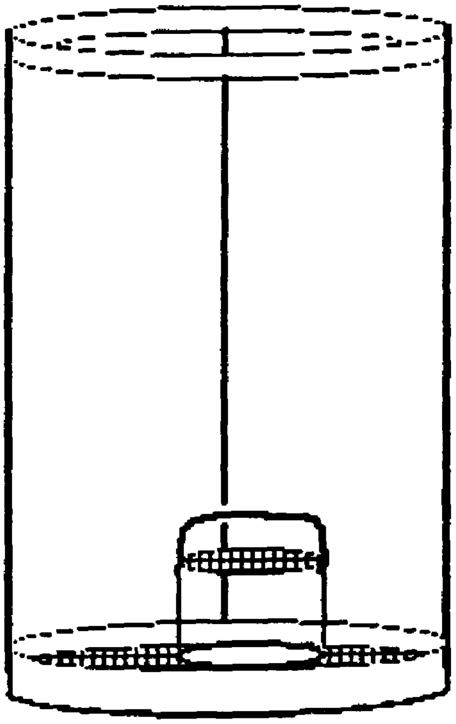
The columns were supported by a 4m wooden post (5 x 10 cm) painted flat black, which in turn was fastened to a black shelf (5 x 15 cm) 2.5 m above the floor. The bottoms of the columns were plugged with rubber stoppers which had glass drain tubes inserted through them. The outer ends of the drain tubes were covered by a length of rubber tubing that was closed with a screw clamp.

Fish introduced into the columns were restricted to the upper portion of the column by a basket made of clear acrylic plastic and 1.8 mm mesh Nitex screening (Figure 3). A central hole in the basket floor, with a removable cap of the same mesh size, allowed access to the water column for drawing out water samples. The baskets hung at 60 cm depth by a clear acrylic sewing thread. Pilot studies showed that 25% or more of the _Daphnia_ in the column could be expected to migrate up to at least that depth. The _Daphnia_ used were generally 1-2 mm in length and never showed any signs of restriction of their movements by the 1.8 mm mesh. Each column contained a basket at all times, although only one column at a time held a fish.

Before starting the study, the distribution of _Daphnia_ in the two columns was observed for 3 evenings to determine whether the two populations behaved similarly. On 23 March, one population was consistently higher in the column. Otherwise, there were no apparent differences between the columns (Figure 4).

Experimental Animals

All of the _Daphnia_ used were the offspring of six individual _Daphnia pulex_ taken from Upper Sawyer Pond (also known as Little Sawyer



sketch of fish basket

Figure 3. Sketch of the basket used for restricting a fish to the upper portion of the columns.

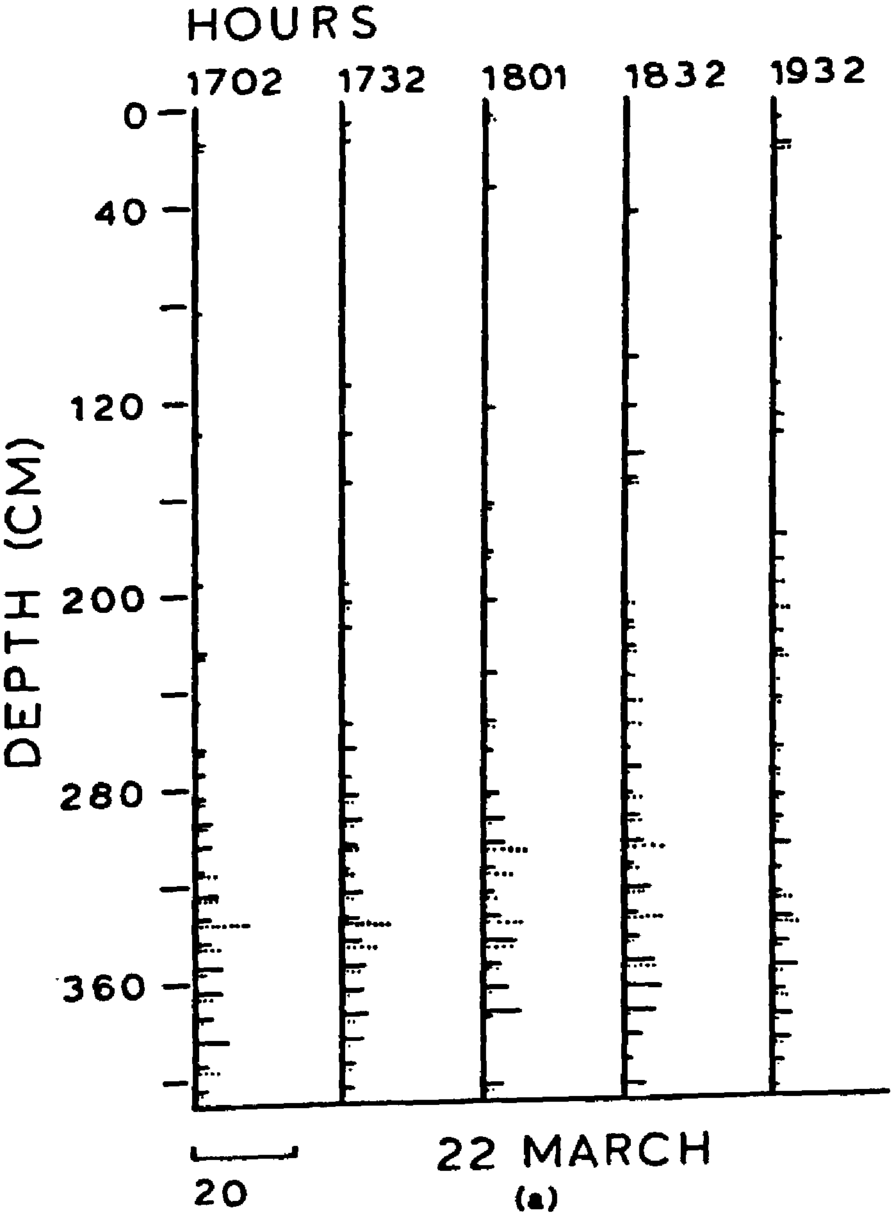


Figure 4. Vertical distribution of *Daphnia pulex* populations in both columns over the course of three evenings. (a) 22 March, (b) 23 March, and (c) 24 March 1985.

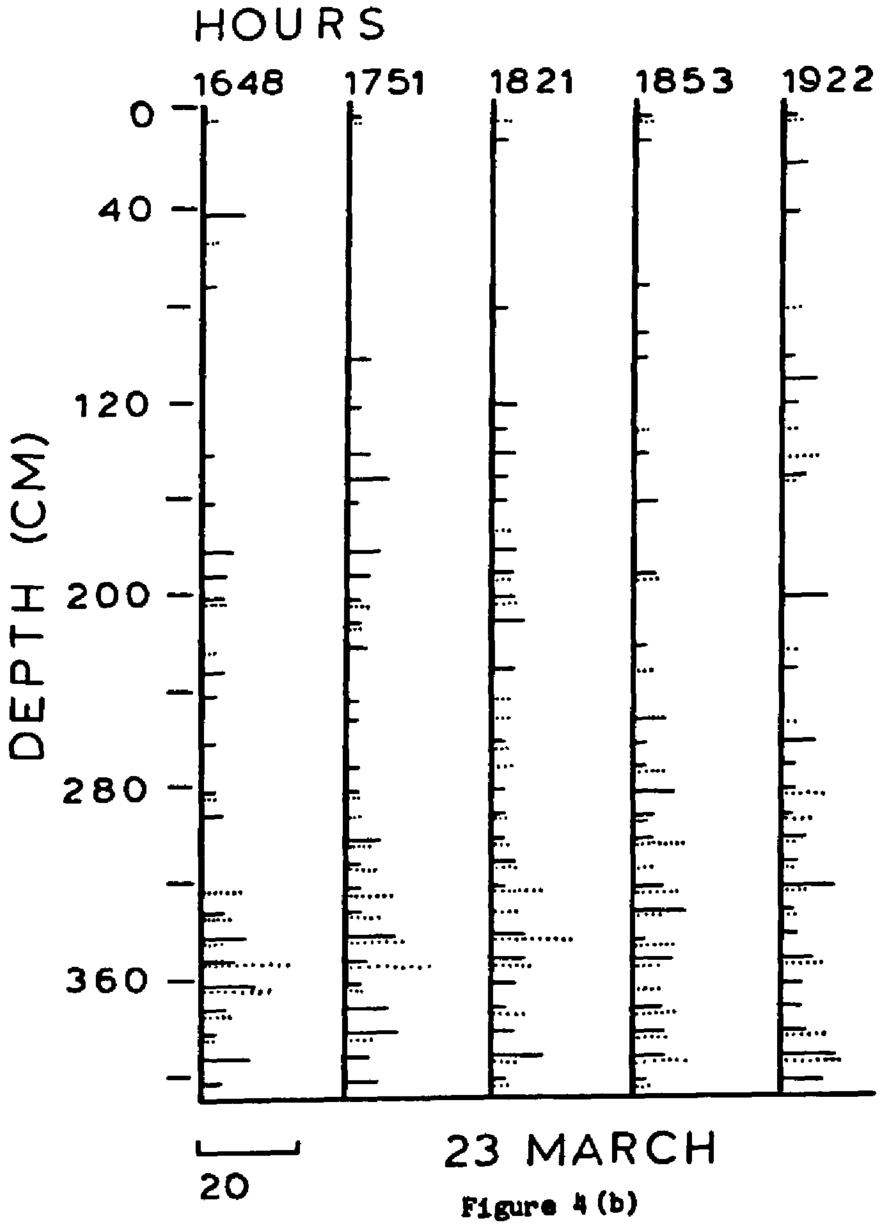

HOURS
1648
1751
1821
1853
1922
0
40
120
200
280
360
DEPTH (CM)
20
23 MARCH

Figure 4 (b)

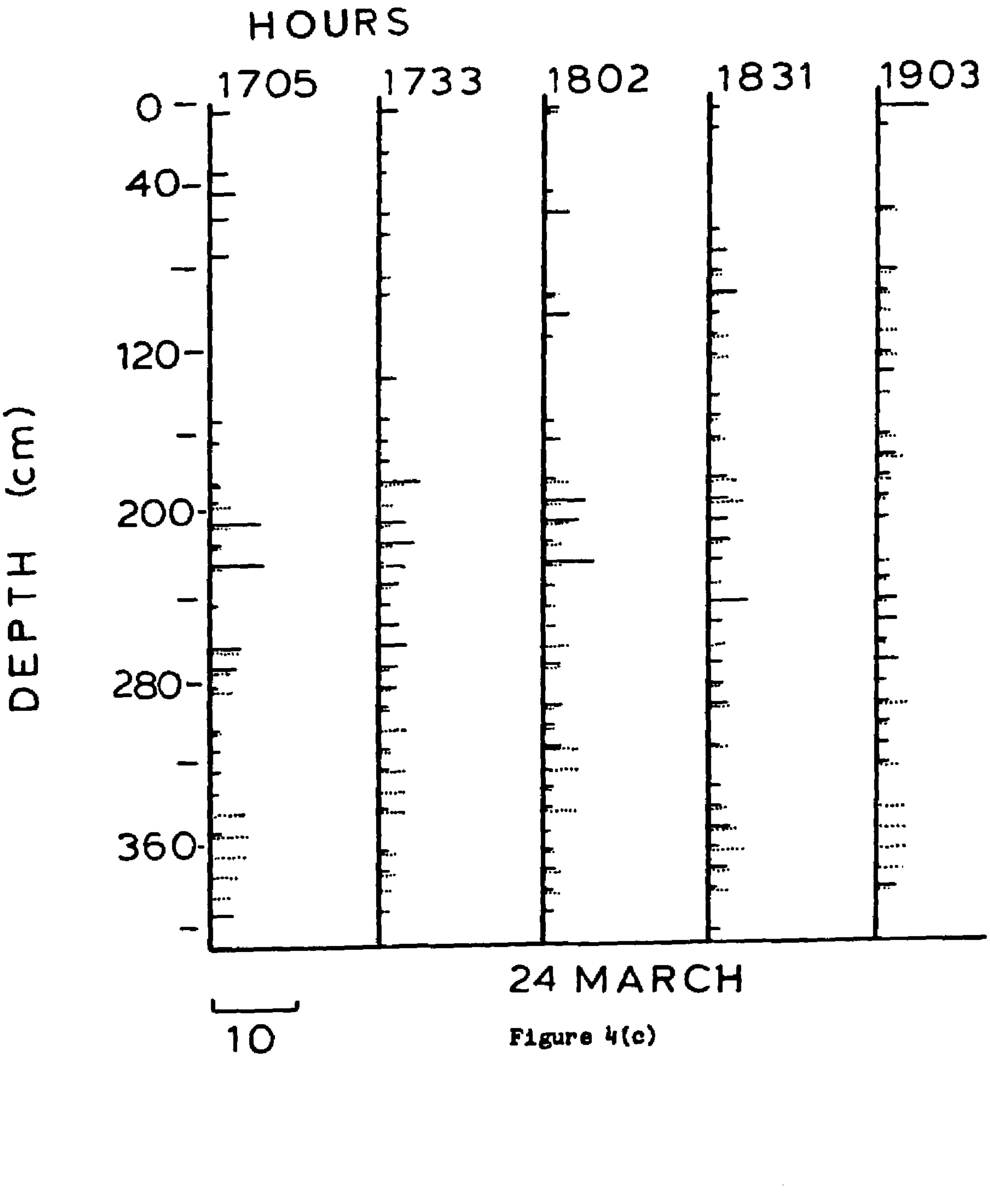

HOURS
1705
1733
1802
1831
1903
0
40
120
200
280
360
DEPTH (cm)
24 MARCH
10

Figure 4(c)

Pond), in Bartlett, New Hampshire, in September of 1984. The animals were identified from Brooks (1957). They were kept in batch cultures in one-gallon jars and fed regularly from a mixed culture of green algae grown in a goldfish tank. Occasionally a blended mixture of yeast, trout chow, and alfalfa was mixed with the fish-tank algae in a 1:10 ratio to provide nutritional variety (Schindler 1971; Porter and Orcutt 1980). The animals were raised in water from the Durham Reservoir, and kept on shelves next to the same windows as the experimental chamber, at light intensities similar to those recorded at the top of the chamber.

Before each experiment, Daphnia carrying embryos in the earlier stages of development (with no sign of limb formation), were separated from the stock cultures and fed ample amounts of Chlorella to keep the water tinted slightly green. After giving birth approximately 2 days later, the adults were sorted again for those greater than 1 mm in body length and carrying early stage embyos, placed in a gallon jar of filtered lake water, and used in the subsequent experiment. The daphnids were sorted at 20 to 30 x magnification by picking out individuals and transferring them with a wide mouth pipette to clean containers. A clear millimeter ruler was fastened to the dissecting scope stage for measuring the daphnids.

These sorting procedures were designed to produce animals known to have the same history of food, light environment, and approximate stage in the molt cycle at the start of each experiment. Since experiments were meant to investigate the behavior of field populations, no attempt was made to increase the genetic homogeneity of the population by working with clones.

As the laboratory culture had been maintained for ten months by July 1985, observations were made to determine whether their behavior was still representative of a wild population. *Daphnia pulex* were brought from Upper Sawyer Pond to compare with the laboratory culture. An equal number of individuals larger than 1 mm in body length were selected from the wild population and the culture, and kept in the lab for two days to allow the wild population time to acclimate to the light conditions in the lab. When introduced to the columns, the wild population maintained a slightly deeper position in the column. Otherwise the two populations moved in the same direction at the same time (Figure 5).

The fish introduced into one column during each experiment was an individual, 2 - 3 cm long, bridled shiner (*Notropis bifrenatus*; identified from Werner 1980). All the fish used in this study were taken from the new Durham Reservoir, and kept in captivity in two ten-gallon aquaria at room temperature in the AFAIR lab, in water from the reservoir. They were fed a regular diet of Tetramin brand fish flakes, occasionally supplemented by excess daphnids from the batch cultures. No fish was used in any two consecutive experiments.

Experimental Procedures

The columns were filled from the top and allowed to stand at least 12 hours before adding the *Daphnia*. This allowed gas bubbles generated by the filling to dissipate. The evening before each experiment, an equal number of *Daphnia* (two to three l^{-1}) was added to each column, permitting them a full 24 hours to acclimate to the light conditions in the columns before observations began.

The fish were acclimated to the ambient temperature and light

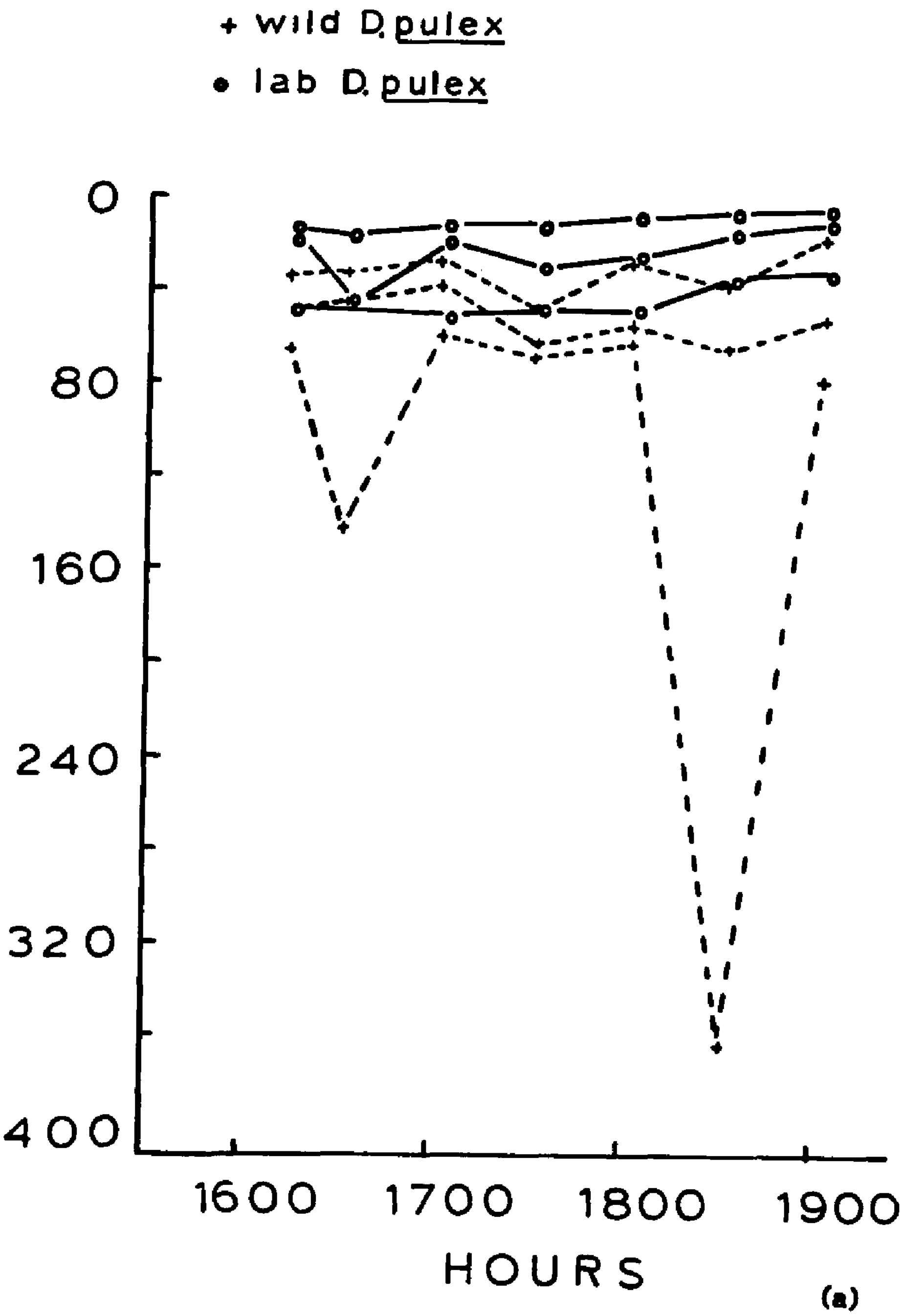


Figure 5. Comparison of the distribution of the *Daphnia pulex* population quartiles over two evenings for a wild and a lab population of *Daphnia pulex*. (a) 9 October, and (b) 10 October 1985.

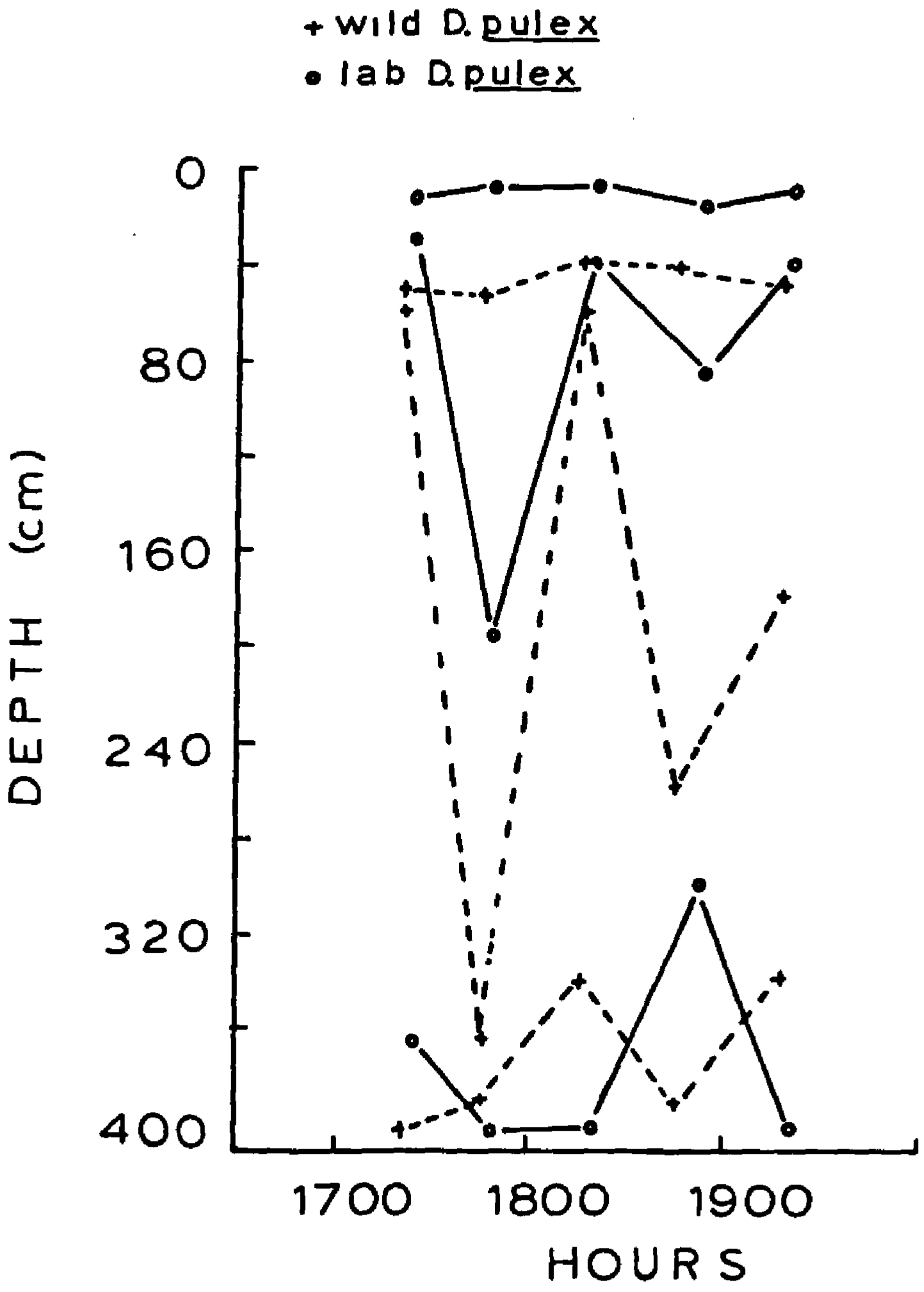

+ wild D. pulex
● lab D. pulex
0
80
160
240
320
400
DEPTH (cm)
1700
1800
1900
HOURS

Figure 5(b)

conditions in the experimental chamber for 12 hours, in a 1000 ml beaker kept on the shelf inside the chamber. The shelf was 140 cm from the top of the columns. The fish was introduced into the column by emptying the beaker into the top of the column. The tops of both columns were covered at all times with a piece of clear-acrylic plastic, in order to contain the fish.

Each experiment ran six to eight days, during which population movements were followed. The columns were filled from a common reservoir of water, and mixed to a predetermined concentration of algae, so that the initial food conditions in the two columns were identical. The food concentrations were then either allowed to decline, or were increased over time by adding more algae.

During the experiment, one of a pair of columns served as a control, while the other column contained a fish. The first two to four evenings neither column contained a predator. A fish was then introduced into one column. After two or three evenings, it was removed, and for the final two evenings, again neither column contained a fish. The first experiment (April 1985) was exceptional in that a fish was present in one of the columns for the first four days, then removed for the final two days. In April, the column receiving the fish was designated arbitrarily before the observations began. For the remaining months, the column receiving the fish was chosen by coin tosses before starting the experiments.

The positions of the daphnids were visually observed each evening with a low intensity red light (wavelength >650 nm; intensity 3.4×10^{-6} wcm^{-2} at 10 cm from the light), held behind the columns to silhouette the animals. The number of Daphnia was counted within each of the 41, 10 cm intervals marked on the face of the columns in black grease pencil. Preliminary observations found that, by moving the light quickly by the *Daphnia*, 30 minutes was the shortest time interval between surveys of the columns which did not cause erratic swimming behavior (such as sinking, somersaulting, or changing direction) in individual animals. Therefore the vertical distributions were noted at approximately 30 minute intervals from one hour before sunset to one hour after dark. The numbers of animals were recorded by counting aloud into a cassette tape recorder. The counts were transferred later to data sheets. Each column required 3 - 6 minutes to survey depending on the population size at the time. The number of juveniles and of adults were recorded separately. The juveniles matured in 4 - 5 days at the temperatures in the columns (15 - 28 °C, Appendix B).

Food Concentration Measurements

Before each set of experiments, water for the columns was taken from the Durham Reservoir, allowed to settle for two to three days to remove silt, and then sieved through a 10 um mesh Nitex screen to remove particulates >10 um. *Chlorella sorokiana*, a single celled alga 3-5 um in diameter, was added to the water to adjust the concentration of edible seston when necessary. The *Chlorella* was centrifuged and resuspended in tap water before being used in the experiments. The *Chlorella* was maintained and grown as uni-algal batch cultures in a modified version of Bristol's E media for *Chlorella* (Appendix A).

At approximately 12-hour intervals during the experiments, water samples were drawn from the columns to measure the weight of edible seston available in the water. The samples were taken by slowly lowering a 4 m length of tygon tubing weighted at the lower end to the bottom of the column. The top was clamped off, and the tubing retrieved with a 125 ml integrated water sample inside. Each sample was pre-filtered through a 0 - 30 um mesh Nitex screen to approximate the size of particulate eaten by Daphnia (Haney 1985). The samples were then forced from a 60 ml plastic syringe through pre-washed and pre-weighed 25 mm glass fiber filters (Gelman GFC, 0.45 um pore size), held in a Swinney-type filter holder (Millepore Corp.). The filters were placed in a darkened dessicator and dried within the next 48 hours at 105±5 ° C for one hour (Haney 1975). A Cahn model G electrobalance was used to weigh the dried filters to the nearest 0.05 mg.

The daily food concentrations ranged from 6.6 to 0.1 mg l^{-1} (Table 1). In the March, April, June, and August experiments, the food concentration was allowed to drop from an initial level, but was supplemented as needed to keep the concentrations in the two columns similar to one another. In the May and November experiments, Chlorella was added daily at 12 hour intervals to raise the food concentration gradually during each series. In all experiments, stratification of alga in the columns was reduced by bubbling the columns with air after adjusting the food concentrations. The food concentrations used represent a range of food concentrations found in oligo- to eutrophic lakes (Haney 1985).

Daily Food Concentrations (mg dry wt l^{-1})

	Column	Day	1	2	3	4	5	6	7	8
March	**A**	**am**	1.9	2.1	2.8	2.8	2.0	0.57	1.1	--
		pm	2.5	3.1	2.2	2.4	---	0.23	0.80	1.0
	B	**am**	--	2.8	1.6	2.5	1.1	0.18	0.75	0.80
		pm	2.6	2.1	1.5	--	--	0.55	0.91	0.99
April	**A**	**am**	3.2	4.0	4.1	3.7	2.0	1.4		
		pm	3.2	--	3.6	--	1.7	1.4		
	B	**am**	3.2	4.1	4.2	2.2	3.2	1.8		
		pm	3.2	--	3.3	2.1	2.6	2.1		
May	**A**	**am**	3.7	3.4	2.8	4.0	4.4	5.0	--	
		pm	2.8	--	4.7	4.0	4.8	4.4	4.9	
	B	**am**	4.2	3.6	3.8	4.9	4.4	4.8	--	
		pm	3.1	--	5.3	4.8	5.7	3.8	4.8	
June	**A**	**am**	6.2	6.2	4.6					
		pm	6.3	4.3	4.0					
	B	**am**	6.5	5.5	4.2					
		pm	--	5.0	3.8					
August	**A**	**am**	0.35	0.24	1.9	0.88	0.17	0.28	0.30	
		pm	0.29	0.21	1.3	--	--	0.36	0.31	
	B	**am**	0.30	0.28	1.9	0.88	0.45	0.53	0.11	
		pm	0.27	0.25	--	0.87	0.48	0.59	0.10	
November	**A**	**am**	--	--	3.3	4.1	--	3.5		
		pm	2.1	3.3	2.5	4.4	4.7	3.2		
	B	**am**	--	--	3.3	3.1	--	3.5		
		pm	2.3	4.5	1.8	5.6	3.4	2.8		

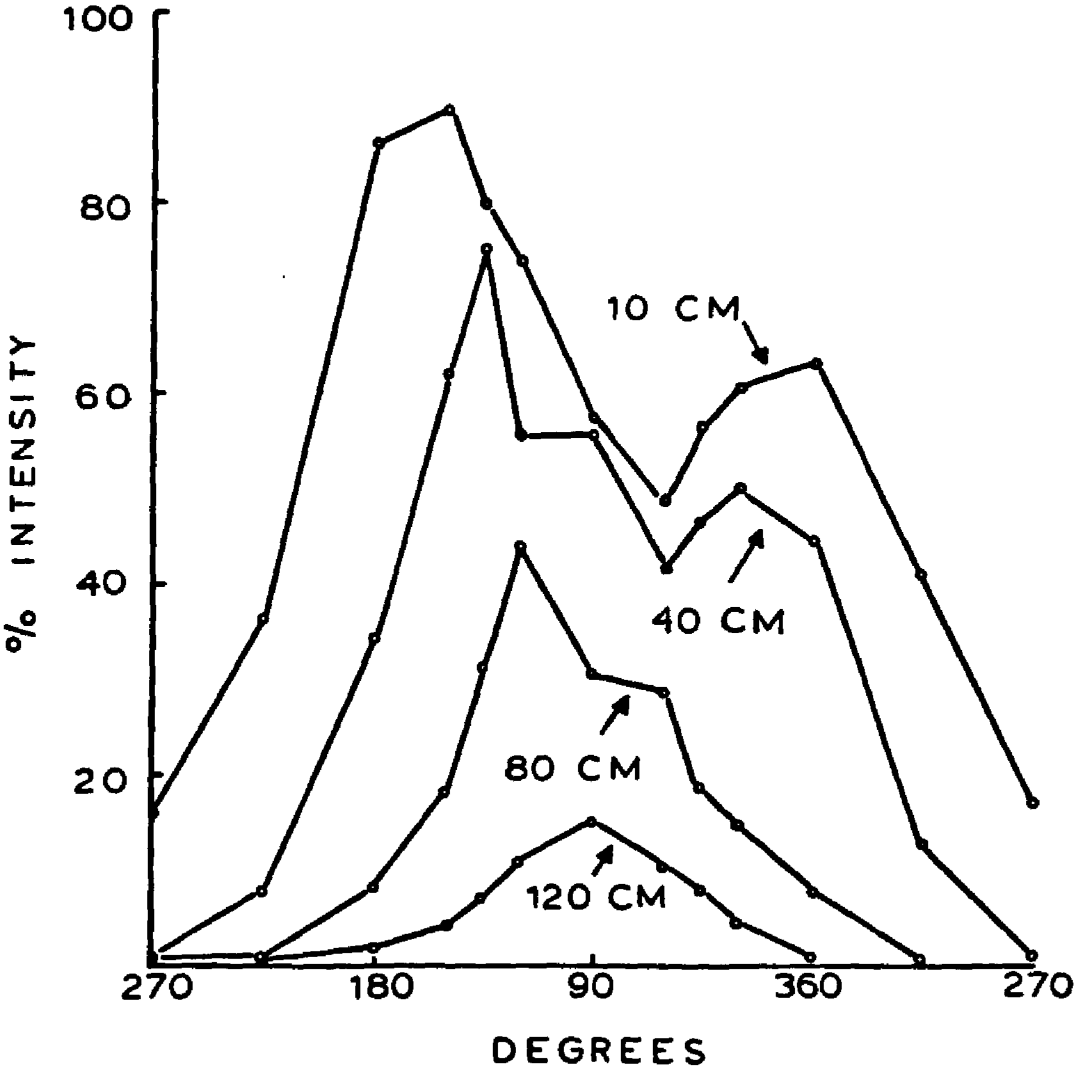
Table 1. Daily food concentrations maintained in the columns (mg dry wt l^{-1}).

Light Measurements

The light intensities in the experimental chamber were measured each evening of the experiments with an International Light Research Radiometer, Models 700 and 500, with an International Light SEA400 series photosensor positioned in one corner of the experimental chamber at the level of a column depth of 20 cm. The light intensity was recorded every 5 to 10 minutes during the evening, allowing calculation of the relative rate of change of the light intensity over these time intervals.

The same light meters and sensor were used to characterize the verical light gradient and the angular light distribution of the experimental chamber. The light in the chamber, and columns, included variations due to cloud cover, wind, sun-angle, angle of the building's roofline, shadows from nearby trees, intensity of moonlight, and snowfall, that also occur in nature. A natural angular light distribution is essential in order to avoid artifactual migrations induced by a positive phototactic response to collimated light (Schallek 1942, 1943). The light gradient was used to determine the light intensities encountered by the zooplankton.

The angular light distribution in the experimental chamber was defined by positioning a photosensor at 14 different angles from the vertical, in a plane parallel to the windows of the building, and measuring the light intensity at each of these positions relative to a reference sensor at 20 cm from the water surface of the columns. All of the measurements were taken in air. The measurements were repeated at eight depths in order to characterize the change in the angular light distribution with depth. Above 80 cm (Figure 6a), there is an



(a)

Figure 6. Angular light distribution within the experimental chamber. (a) between 0 and 120 cm depths. (b) below 120 cm depth. Measurements were taken alongside the column at the water depths marked on the column.

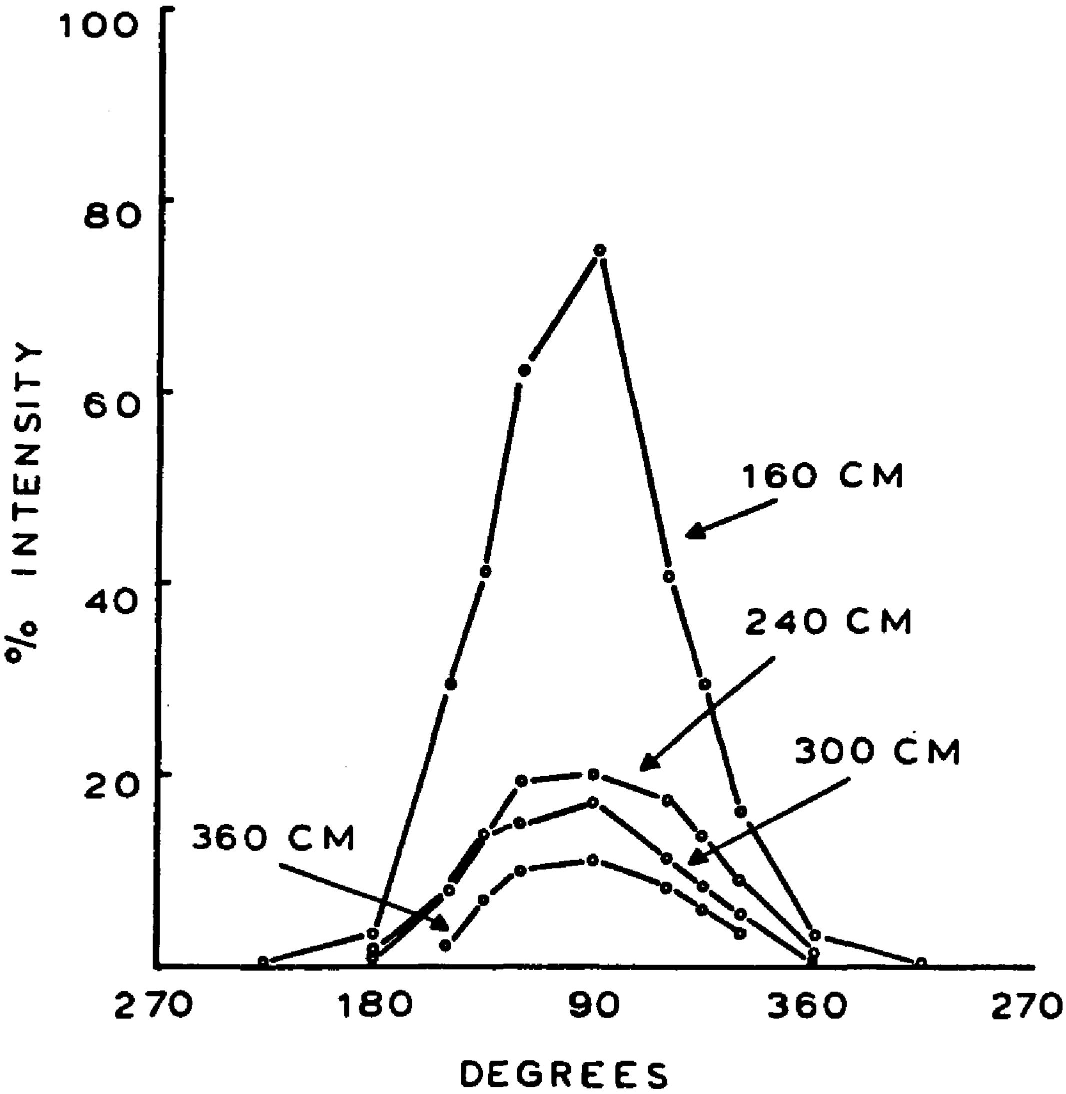

100
80
60
40
20
% INTENSITY
160 CM
240 CM
300 CM
360 CM
270
180
90
360
270
DEGREES

Figure 6 b

asymmetry, especially noticeable at 10 cm, due to a shadow from the roofline of the lab building and a row of trees nearby. From 80 cm downward, the angular light distribution (ALD) becomes increasingly more symmetrical (Figure 6b). In natural systems, the angle of the sun will produce the same effect with a broad but asymmetrical ALD near the surface of the water which becomes increasingly symmetrical with depth (Browne and Axford 1986; Whitney 1941).

Shallower than 80 cm depth in the experimental chamber, the maximal width of the ALD increases steadily until it reaches nearly 180 degrees at the surface. This is typical of the ALD in shallow turbid waters (Timofeeva 1972). The wide ALD in the chamber was due to little horizontal extinction at the top of the chamber, rather than to scattering by turbid water. Decreasing the width of the top of the chamber or increasing the height of the black plastic portion of the chamber walls to achieve a horizontal extinction more typical of clear water would have eliminated the light intensity required to simulate the epilimnetic light intensities of a natural system. As diffuse light does not produce the artifactual positive phototaxis associated with collimated light, I chose not to correct for the small horizontal extinction at the top of the chamber.

The vertical gradient of down-welling light was measured in the water-filled columns for the visible spectrum (400 to 650 nm, peak 450 nm), and for near-blue (405-450 nm, peak 428 nm), and yellow-green (557-590 nm, peak 565nm) wavelengths (Figure 7), using cutoff filters. These wavelengths were chosen to match the spectral sensitivity of the daphnid eye (McNaught 1966). All of the measurements were taken on a bright day between 1300 and 1500 hours. The extinction coefficients

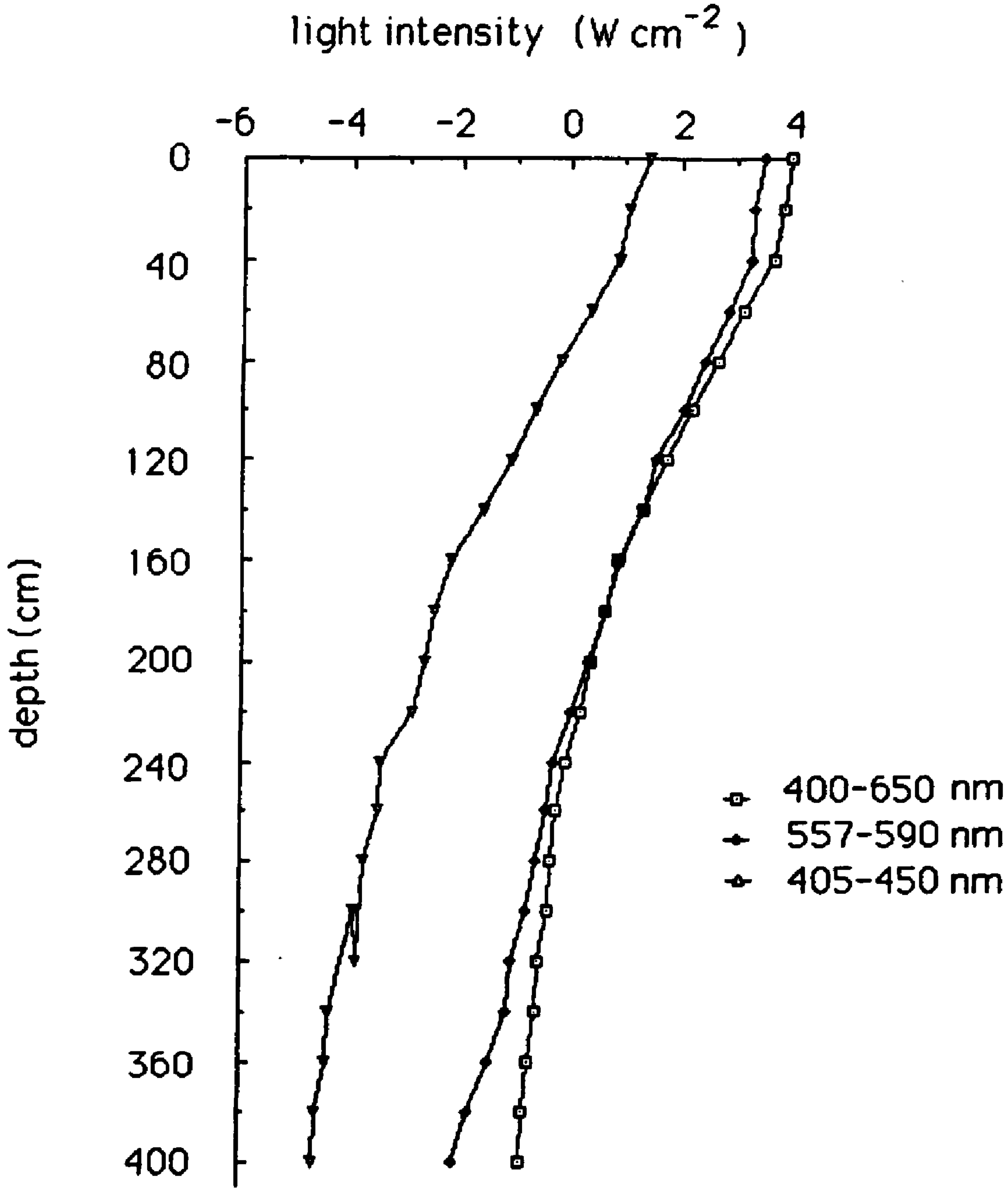


Figure 7. Profiles of light intensity (Wcm^{-2}) at different ranges of wavelength in the columns.

were determined by regressing the natural log of the light intensities against depth in cm. All of the regressions had correlation coefficients greater than 0.95 with $p>>0.001$. Similar extinction coefficients were recorded in natural systems (Figure 2).

The light gradient within the chamber and the clear-acrylic columns was determined by the black plastic walls of the experimental chamber. This allowed the effects of food concentration to be analyzed for a single gradient of light. The latter may influence the velocity of migrations (Ringelberg 1964; Itoh 1970), as the underwater distribution of light is a principal means of orientation for zooplankton (Siebeck and Ringelberg 1969; Stavn 1970; Ringelberg, et.al. 1967).

In natural systems, layers of phytoplankton and particulates commonly form (Baker 1973), each layer with different extinction coefficients (Bowling and Tyler 1986). There are variations in the extinction coefficient with depth in the experimental chamber, related to the internal support structure of the experimental chamber (Figure 6). These variations of the extinction coefficient are similar to that in natural oligotrophic systems (Figure 8).

The absolute light intensity at the depths of the population were estimated from Beer's Law, the light intensity measured over the evening, as shown below, assuming a constant extinction of light with depth:

$$\ln(I_z) = \ln(I_o) - kz$$

where I = light intensity W cm^{-2}
k = the extinction coefficient
z = the depth of the population quartile.

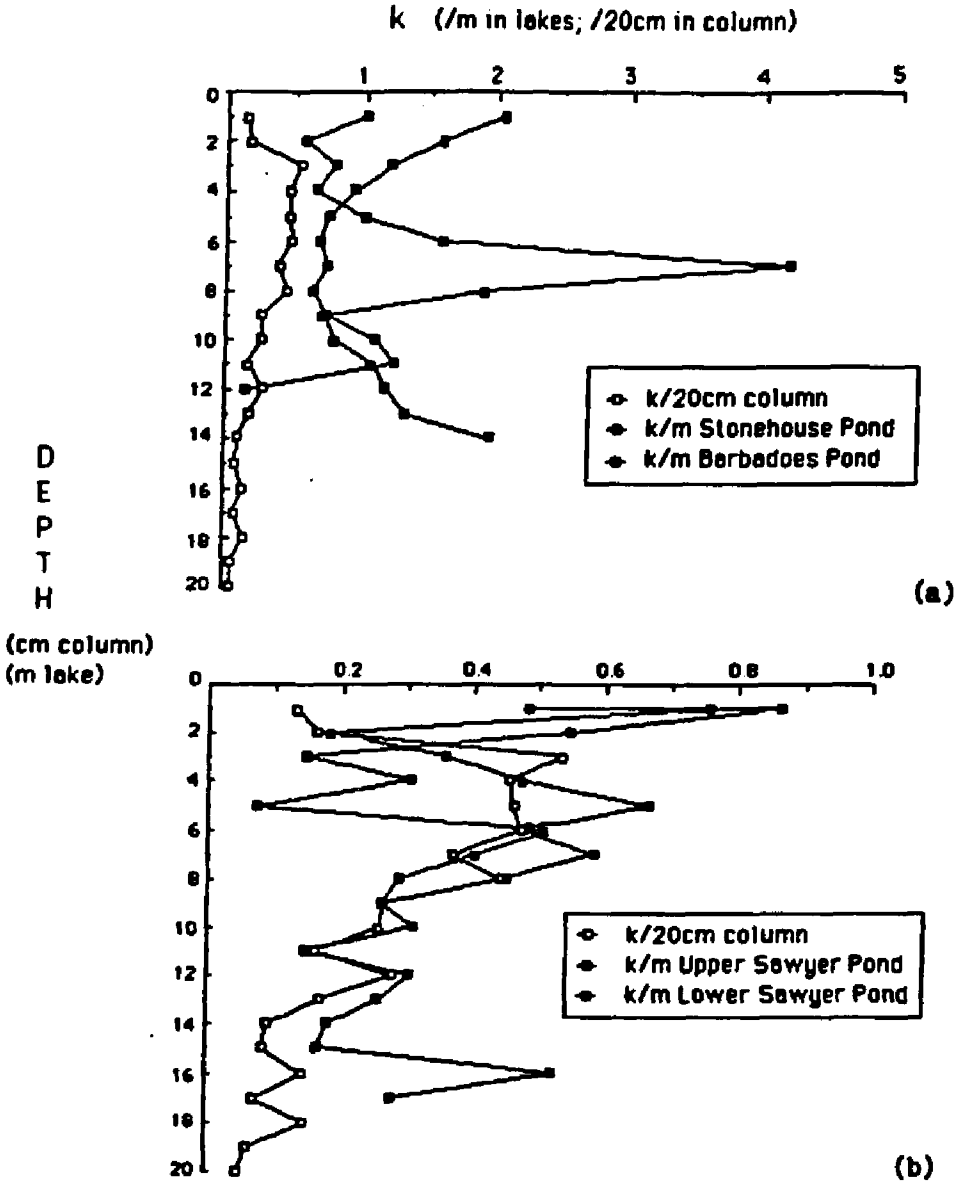


Figure 8. Comparison of the light attenuation in the columns and in (a) Stonehouse and Barbadoes Ponds, and (b) Upper Sawyer and Lower Sawyer Ponds.

The relative rate of change of the light intensity was calculated as below according to Ringelberg (1964):

$$\text{Relative rate of change (or stimulus)} = \frac{\ln(I_t/I_{t_o})}{t}$$

where I = light intensity W cm^{-2}
t_o = time of the recorded I
t = time interval (sec)

The stimulus values represent the midpoint between the two contributing light measurements. Ringelberg's empirical value for a threshold stimulus which produced a positive phototactic response from a *Daphnia magna* population was 17.1 x 10^{-4} sec^{-1}. The time when the stimulus values first exceeded Ringelberg's stimulus threshold value (RST) was estimated to the nearest minute, as a proportion of the interval between the two calculated stimulus times by assuming a linear change in the stimulus values during that time interval.

As an example, the light data for one evening's observations are presented in Figure 9. The stimulus values (equivalent to the slope of the natural log of the light intensity over time) are greatest about 30 minutes after the largest changes in the absolute magnitude of light intensity per unit time have occurred.

A series of light profiles was taken in one of the columns over the course of one evening (25 April 1986) to demonstrate that the confines of the experimental chamber did not alter the relative rate of change of light intensity between depths. Through the time of the most rapid light change, 1945-1950 hours, the relative rate of light change was nearly constant for each depth in a given profile (Figure 10).

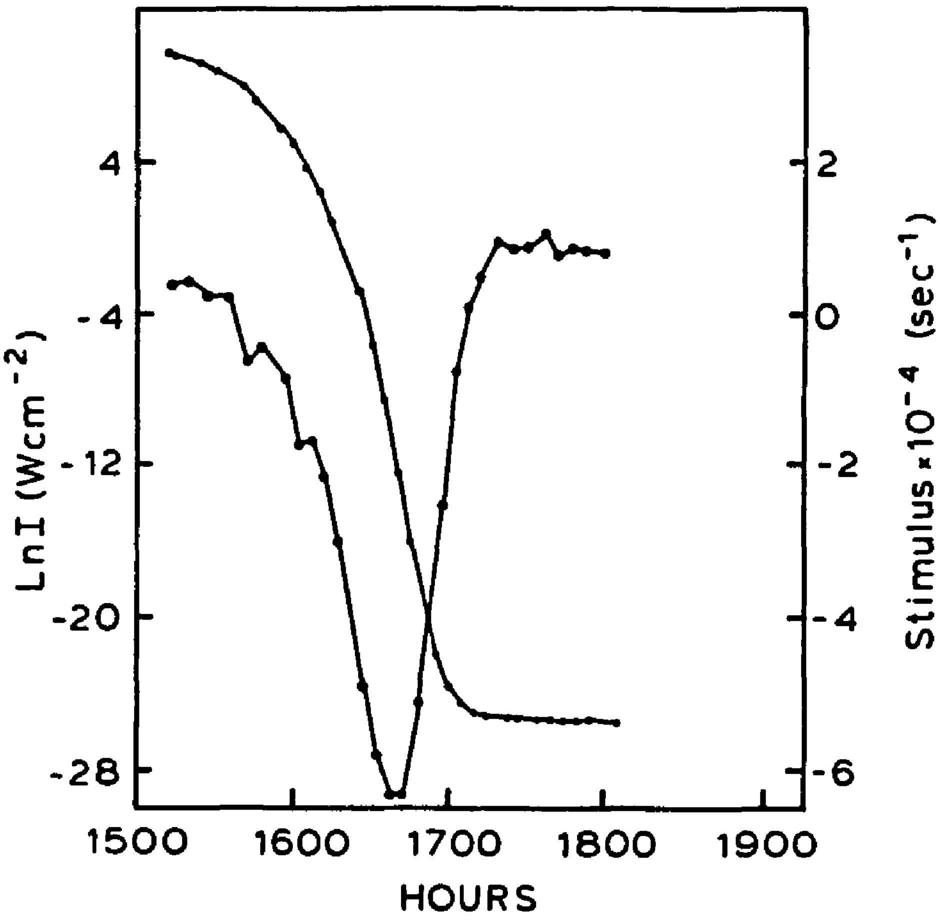


Figure 9. Plot of the light intensity (Wcm^{-2}) and the relative rate of change of light intensity (stimulus) (sec^{-1}) for one evening's observations.

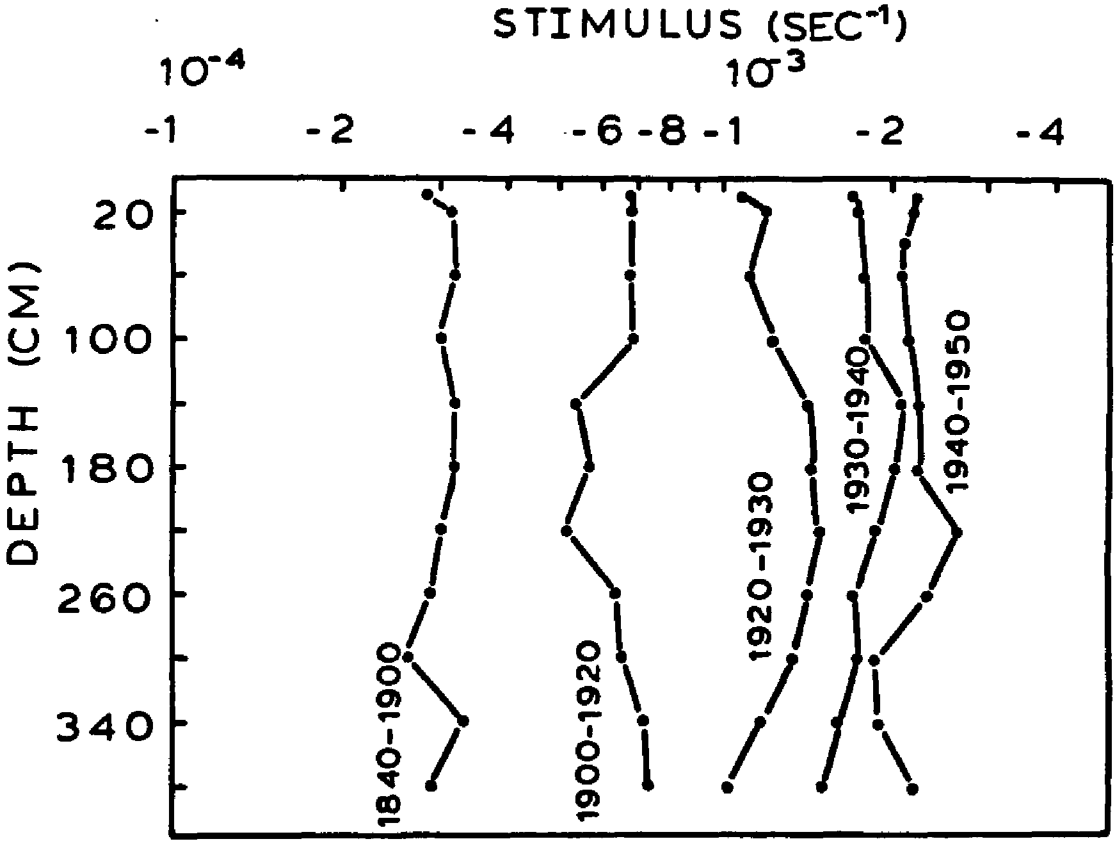


Figure 10. Profiles of the natural log of the relative rate of light change, or stimulus, (sec^{-1}) in the columns for five intervals just before and during the period of most rapid light change.

Temperature Measurements

Temperatures of the water in the columns were monitored during the experiments with a laboratory thermometer suspended at 30 cm in each column by a clear acrylic thread. The columns maintained similar temperature environments. Temperature readings at 30 cm in the columns never differed more than 1°C during each evening (Appendix B). Temperature profiles taken at the end of one evening in the experimental columns and in a third column positioned next to them were nearly identical (Appendix B).

Data Analysis

Frequency histograms of the depth distributions were used to evaluate the timing and extent of the migrations. In natural systems, often a fraction or even the majority of the population may not migrate (eg. Pennak 1944; Haney and Hall 1975). The histograms were used to determine whether there were groups of animals on a given evening which did not move away from the bottom of the columns over the entire course of the evening. For example, on 11 November, 45% of the population in column A and 16% of the population in column B formed small peaks in the histogram, centered at 405 cm (Figure 11). The peaks did not move during the evening's observations. In one-half of the observed migrations, anywhere from 3% - 86% of the population formed such non-migratory peaks. These non-migratory portions of the populations were not included in the analysis. In a pilot study, *Daphnia pulex* appeared to avoid temperatures above 30°C, potentially suppressing the migration amplitude. The data presented were collected only from observations at less than 30°C, thus excluding the last three days of the July experiment.

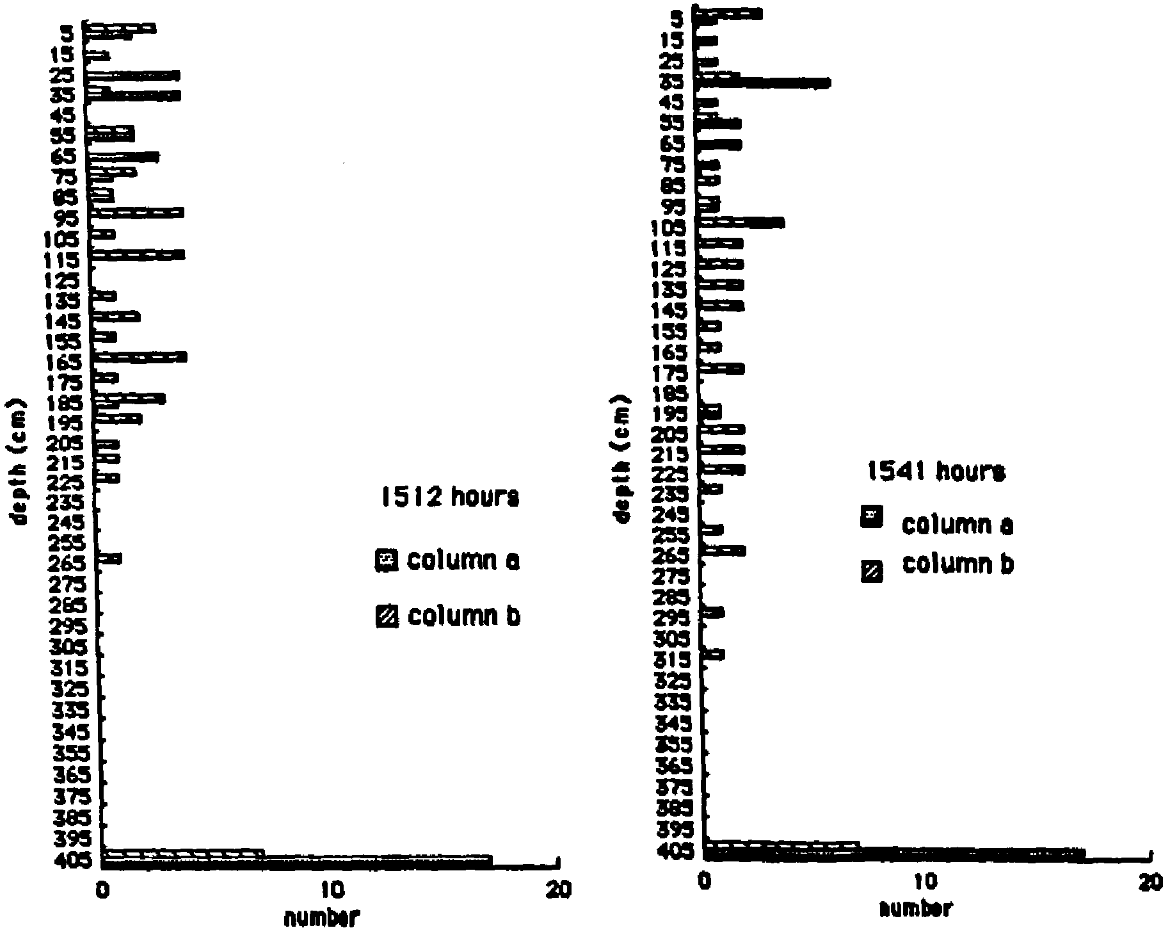


Figure 11. Histograms of the Daphnia pulex population distributions in the columns for one evening's observations.

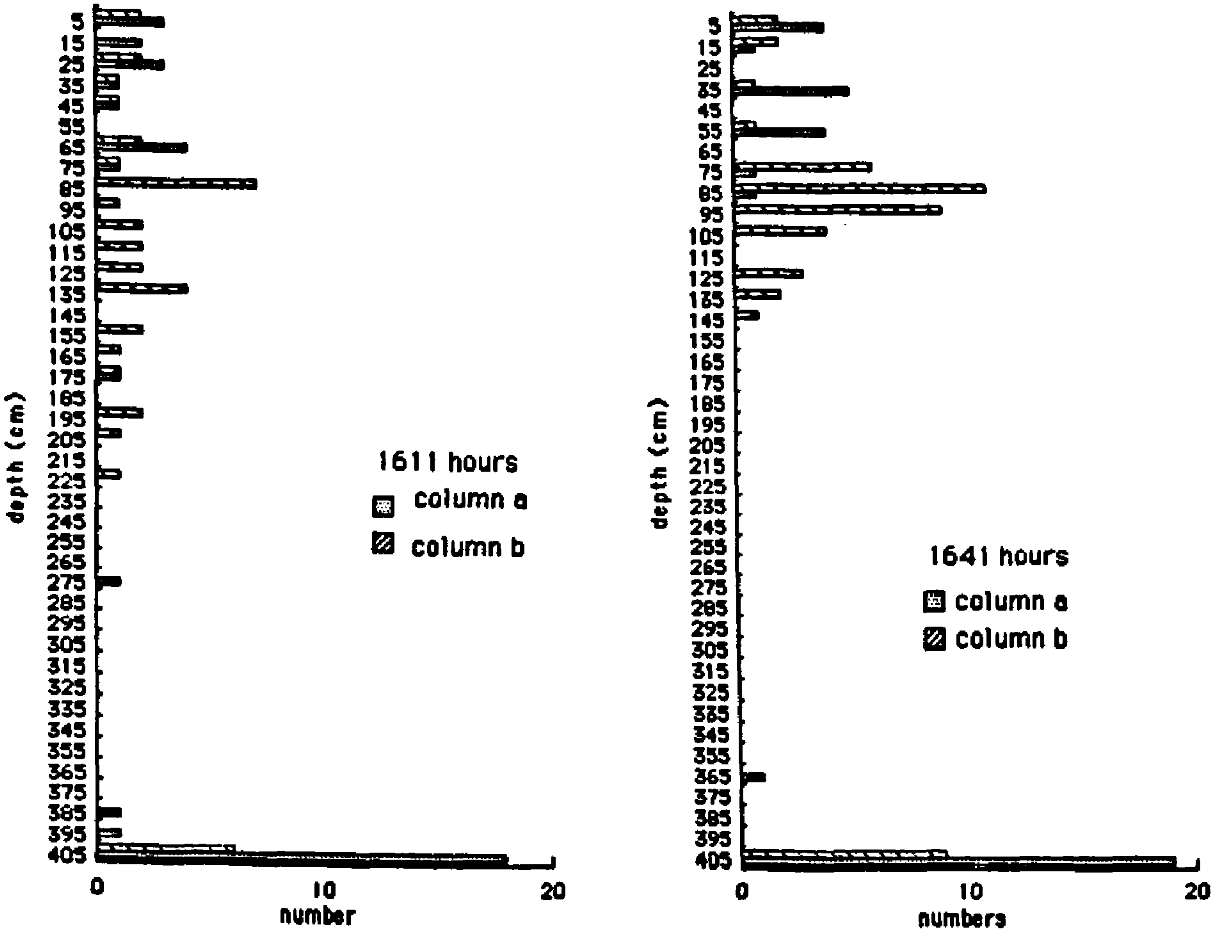


Figure 11 (cont.)

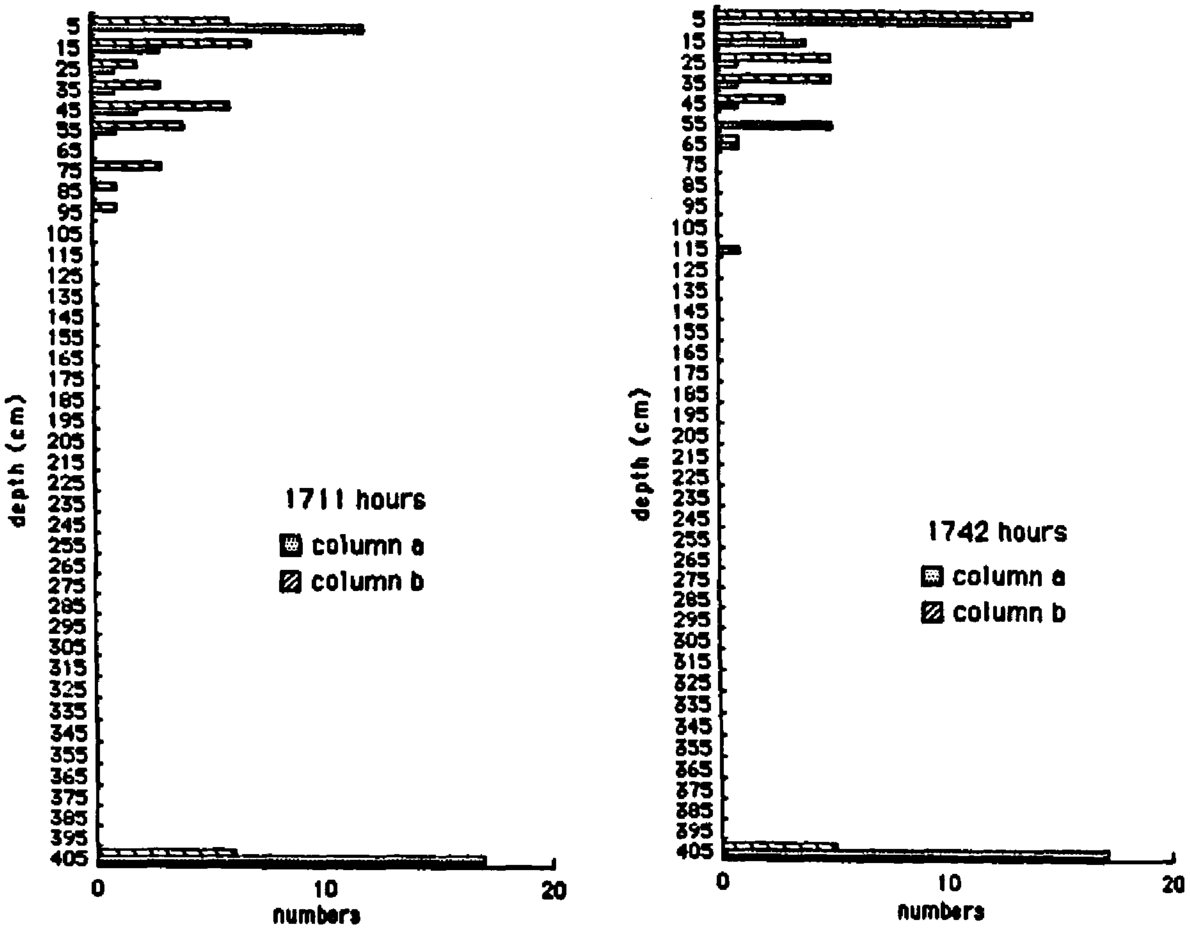


Figure 11 (cont.)

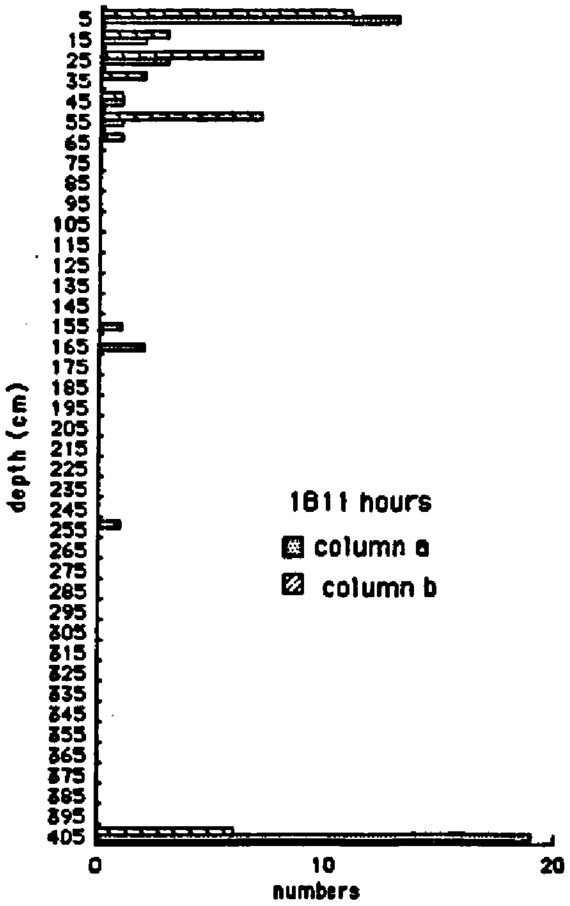


Figure 11 (cont.)

The evening vertical migration is characterized by a steady upward movement of the daphnid population in the evening. Ringelberg (1964) defined a positive phototaxis in his experiments on the phototactic responses of Daphnia, as 50% of the population swimming towards the stimulus (light). Gliwicz and Pijanowska (1988), Geller (1986), and Pennak (1944), used the depth of the population median as the indicator of population movement, while Haney and Hall (1975) chose the weighted mean of the population depth distribution. In order to be able to compare my results with these studies, I have used primarily the movement of the depth of the population median (the 50% quartile depth, or Q50) calculated according to Pennak (1943) to describe and analyze the population movements in the columns. I have also used the depths above which 25% and 75% of the Daphnia were found (the 25% and 75% quartiles, or Q25 and Q75) in the analyses.

The velocity of the population movements was assumed to be linear between profiles and was calculated as the difference between successive quartile values divided by the time in minutes between the observations. As the columns were marked in 10 cm intervals, and observations were taken at approximately 30 min intervals, the resolution of the velocities of the population calculated for the intervals between observations, was 0.3 cm $\min^{-1}$. The migration was defined as consisting of: 1) no downward movement; 2) the longest time of upward movement observed; 3) the maximum upward velocity when two equally long periods of upward movement were observed; 4) no more than one pause during which the population moved less than ± 0.3 cm $\min^{-1}$. The migration was never considered to begin with a pause as defined above. These requirements were imposed to standardize the analyses and to minimize the complexity of the migrations.

For the migrations defined above, the first and last quartile depths were used as the initial and final depths of the migrations respectively. The amplitude of the migration was calculated as the difference between the final and initial migration depths, and ranged from 10 to 400 cm in the experiments.

The time of the evening migration initiation (EMI) was calculated as the midpoint of the first time interval of the migration period. The end of the migration was taken to be the midpoint of the next interval after the observed intervals containing the migration, or as the time of the last observation if the populations still showed some movement at the end of the evening's data collection.

Least squares regression analyses were applied to the results because of the wide and continuous range of values collected for each factor. Absolute light, relative light change, dry weight of edible seston, and the presence of a predator were used as the independent variables, and the dependent variables included population depth prior to migration, and the time of initiation, velocity, and amplitude of the migration. The combined experiments provided at least 31 degrees of freedom, an appropriate number for a multiple regression with three to four variables (Draper and Smith 1981). The laboratory data set contained observations for a total of 72 migrations on 37 different evenings.

For all regression equations, plots of the residuals against the estimated y values, the individual predictors, and the order of the observations, were examined for evidence of homoscedasticity (Draper and Smith 1981). The influence of the presence of a fish in the experimental columns was analysed by assigning two indicator variables (Draper and Smith 1981). For evenings when the fish was present, the values were (1,0), and for evenings after the fish was removed, the values were (0,1). When indicated as necessary by the residual plots, the data were transformed to natural log values to provide the required normality of the error. As the regressions used different numbers of observations, all of the r^2 values reported were adjusted for the degrees of freedom, except for regressions of displacement velocity versus stimulus (which were consistently nonsignificant). The regressions of the measured velocity as a function of stimulus were done with STATWORKS (Cricket Software Inc.). The remaining regressions and all of the ANOVAs were done on the University of New Hampshire VAX mainframe computer (Digital Equipment Corporation) with the Minitab program (Statistics Department, Univ. Pennsylvania). Zar (1984) was used as a general reference for statistics.

Field Methods

Description of the Lake Sites

Upper and Lower Sawyer Ponds are both oligotrophic lakes which drain into the Sawyer River (Bartlett, NH) in the White Mountain National Forest. They are kettle lakes on granitic bedrock with areas of 4.5 and 19 hectares (Newell 1960) respectively (Figures 12 and 13). Upper Sawyer Pond is situated 500 m north of Lower Sawyer Pond and 30 m higher in elevation at 576 m (Newell 1960). It has one inlet at the north end and drains into the lower lake from a single outlet to the south. There is a moderate amount of emergent vegetation along the shore of Upper Sawyer Pond. Salamanders are obvious on the muck bottom (maximum depth 9 m, mean depth 4.3 m; pers. obsv.).

Lower Sawyer Pond is fed by one brook on the southwest shore in addition to the input from Upper Sawyer Pond. A single outlet drains the lake through a swampy area on the northeast shore. The lake has a maximum and mean depth of approximately 30 m and 16 m, respectively (Figure 13).

Stonehouse Pond and Barbadoes Pond lie in the coastal watershed in Barrington and Madbury, New Hampshire, respectively. In contrast to the Sawyer Ponds, these two small kettle lakes (6.1 and 5.7 hectares respectively; Newell 1963), are mesotrophic, and have a maximum depth of approximately 15 m. Stonehouse Pond has an inlet through a marsh along the southwest shore and one outlet to the north (Figure 14). Barbadoes Pond receives some drainage from a wet area at the north end. Otherwise there are no inlets or outlets to this lake (Figure 15).

Plankton Communities

The edible phytoplankton, in September 1986, was dominated in

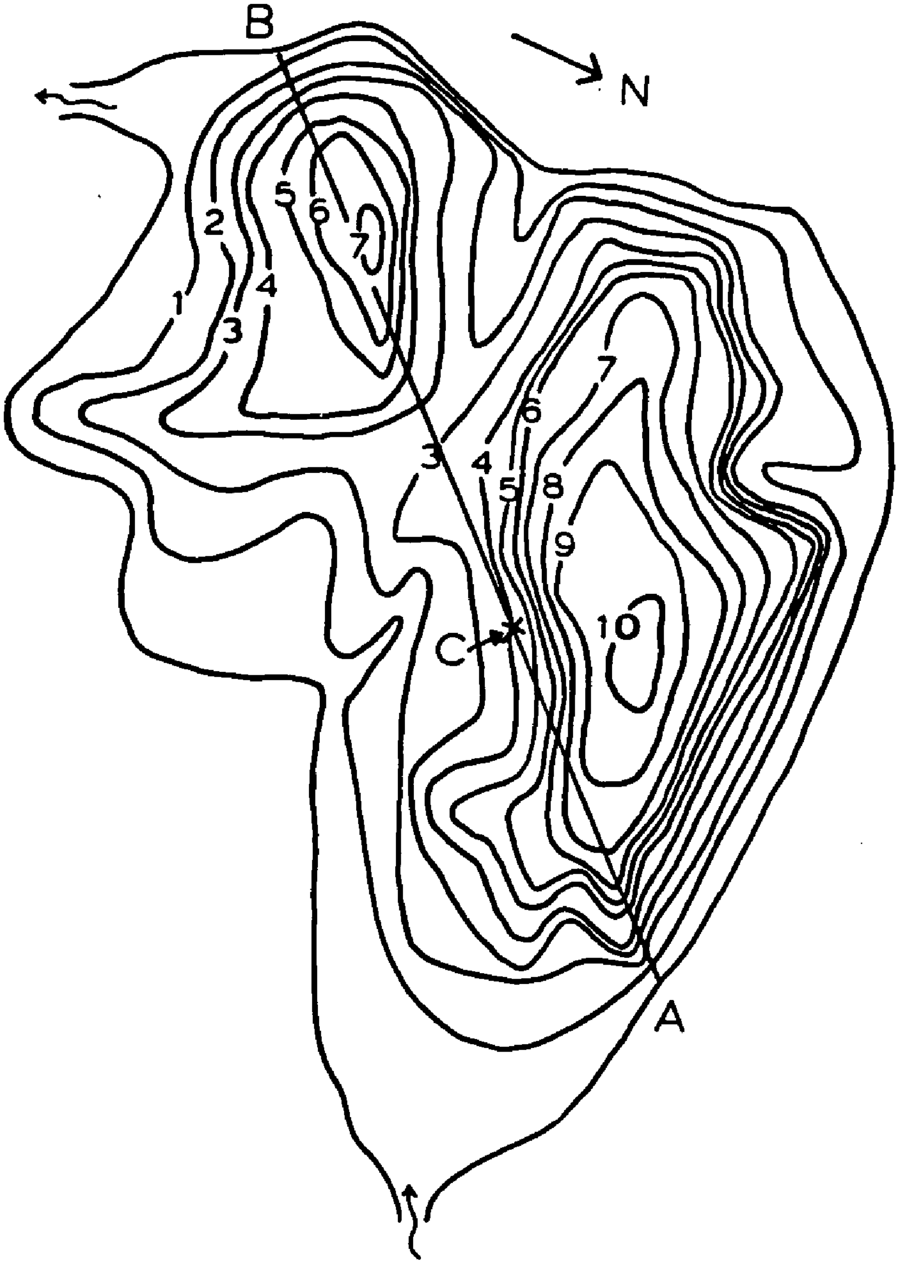


Figure 12. Map of Upper Sawyer Pond.

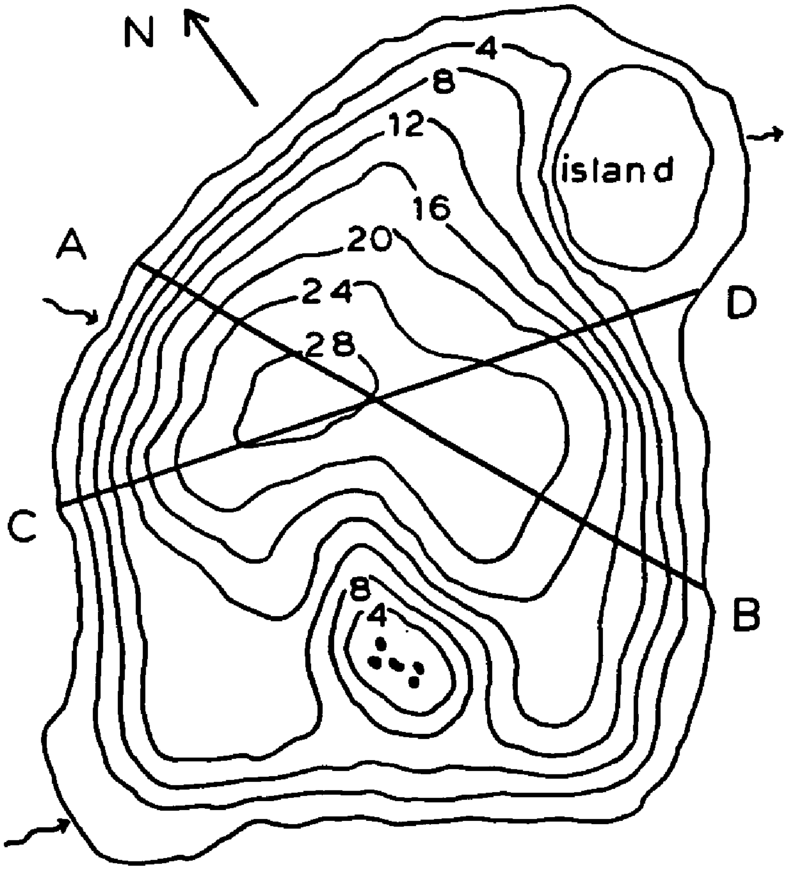


Figure 13. Map of Lower Sawyer Pond.

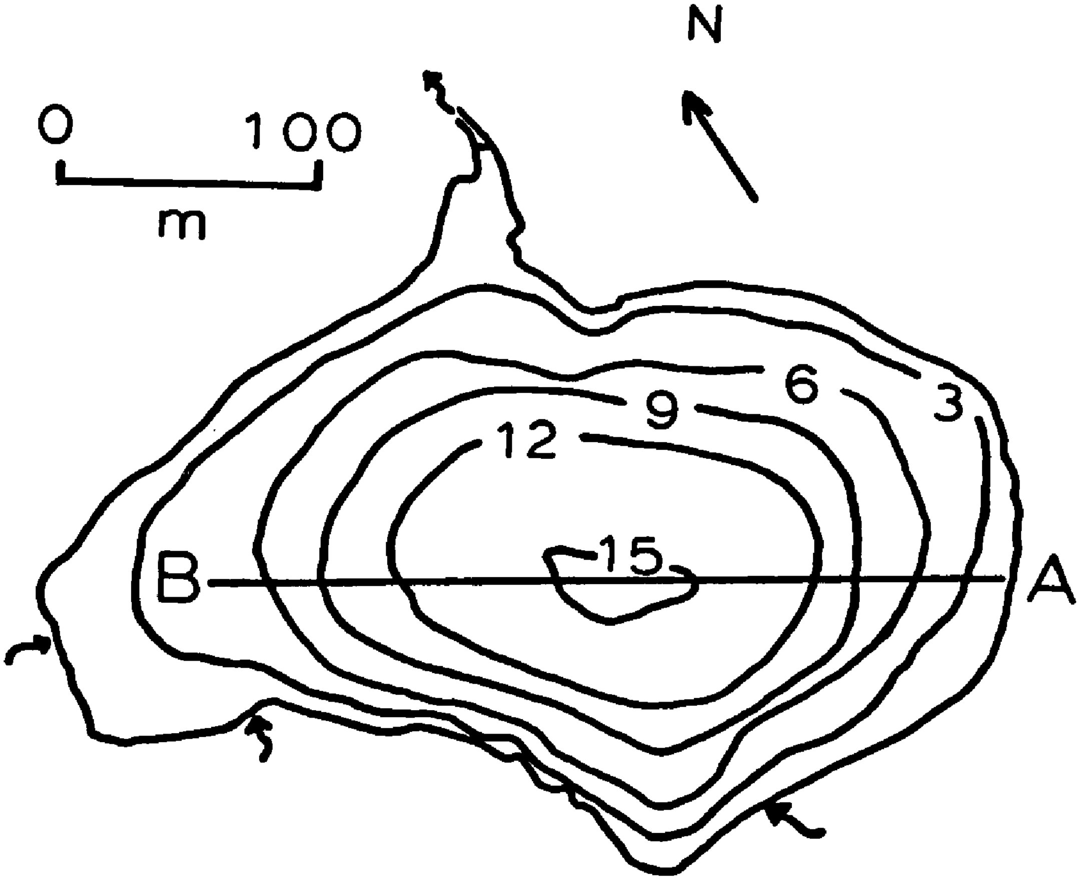


Figure 14. Map of Stonehouse Pond. (Redrawn from Mattson 1979).

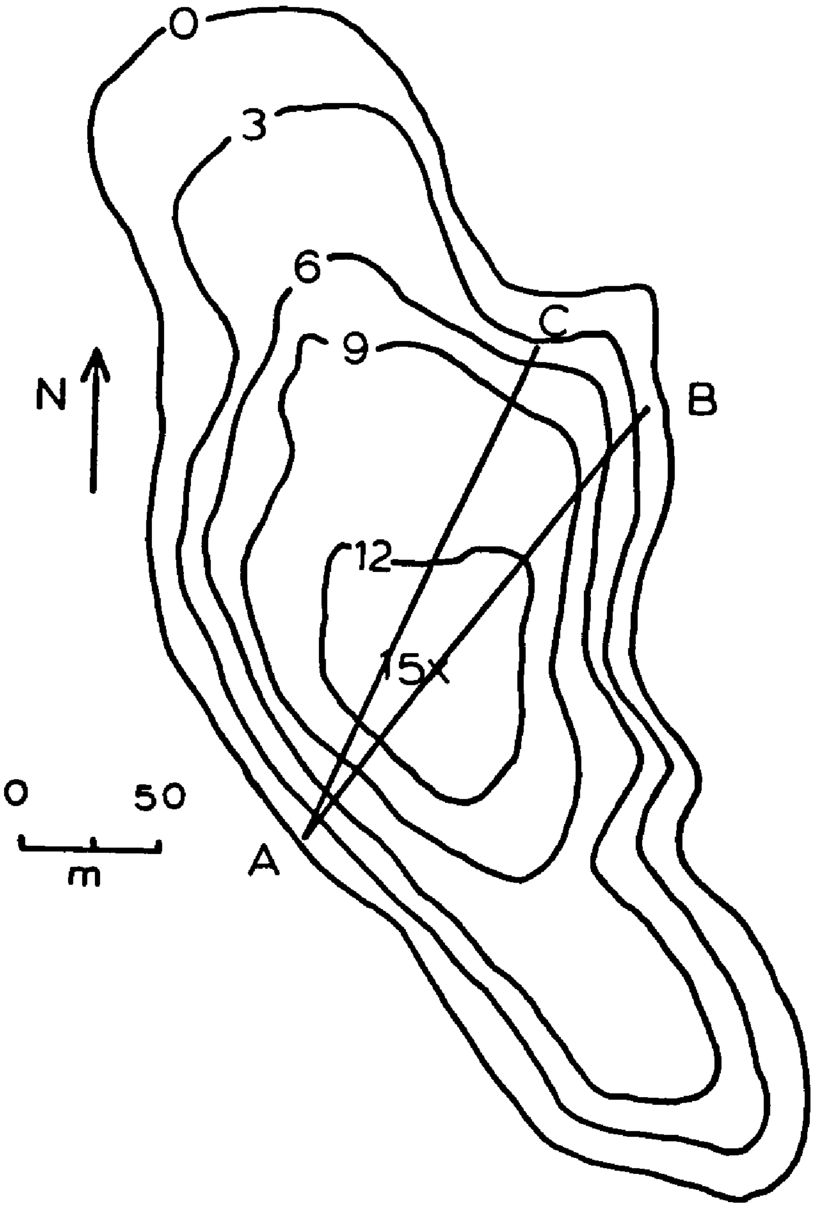


Figure 15. Map of Barbadoes Pond. (Redrawn from Baker, <u>et.al.</u> 1976).

terms of volume by *Euglena* sp. in Upper Sawyer Pond and *Cryptomonas* sp. and *Euglena* sp. in Lower Sawyer. *Gymnodinium* sp. dominated from 2-4 m in Upper Sawyer, and strands of *Anabaena* sp. were caught in zooplankton tows from all depths of the lake (pers. obsv.).

The edible phytoplankton in Barbadoes Pond in September 1986 was dominated by *Cyclotella* sp., *Cryptomonas* sp., and the green sulfur bacterium *Chlorobium* sp. The fall phytoplankton in Stonehouse Pond was dominated in 1969 by *Chlorophycea* sp. and *Chrysophycea* sp. less than 44 um in diameter (Packard, pers. comm.). More recent data are unavailable. All estimates of phytoplankton volume were based on counts from whole water samples.

Diaptomus minutus was the most abundant of the zooplankton in the Sawyer Ponds (pers. obsv.). Upper Sawyer Pond contained *Daphnia catawba*, while Lower Sawyer Pond contained *Daphnia galeata-mendotae* in October and *Daphnia pulex* in September (Table 2). The *Daphnia* populations included both ephippial and parthenogenetic females, and males. Male *Diaphanasoma* were also present in Upper Sawyer Pond. Both lakes contained large populations of the rotifer *Keratella taurocephala*.

Diaptomus spp. was the most abundant zooplankter in the two coastal lakes. In addition, each lake had populations of two *Daphnia* species, D. *catawba* and D. *ambigua* (Table 2). At the time of sampling in 1983, there was a littoral population of *Polyphemus pediculus* in Stonehouse Pond.

Cladocera	**Lake**			
Daphnia galeata mendotae		L		
Daphnia catawba	U		S	B
Daphnia ambigua			S	B
Bosmina sp.	U	L	S	B
Holopedium gibberum	U	L	S	
Diaphanasoma brachyurum	U	L	S	B
Polyphemus pediculus	U	L	**	
Chydoridae	U	L		
Ceriodaphnia sp.	U			
Copepoda				
Diaptomus minutus	U	L		
Diaptomus sp.			S	B
Cyclopoids	U	L	S	B
Rotifera *				
Asplanchna sp.				B
Brachionus sp.	U			B
Conochilus sp.	U	L		B
Euchlanis sp.	U			
Gastropus sp.	U			
Kellicottia sp.	U	L		B
Keratella sp.	U			B
Keratella taurocephala	U	L		
Lecane sp.	U			
Polyarthra sp.		L		
Trichocera sp.	U	L		B
Other				
Chaoborus punctipennis	U		S	B
mites	U			
planarian cocoons	U	L		

Table 2. List of zooplankton identified from the vertical migration profiles of: U = Upper Sawyer Pond, L = Lower Sawyer Pond, S = Stonehouse Pond, and B = Barbadoes Pond. * Rotifera were not identified from the Stonehouse Pond samples. ** None in migration samples, but present in littoral.

Chemical and Physical Measurements

In each lake an initial characterization of the water column was made from temperature and oxygen measurements at 1 m intervals using a combined temperature-oxygen probe (Yellow Springs Instrument Corp.).

The light attenuation in each lake was determined from light profiles taken between 1200 and 1500 hours (Figure 8). At Upper Sawyer Pond light profiles were taken with a Li-Cor Li-185a Quantum Radiometer/Photometer (Lambda Instruments Corp.). A Li-Cor model 1000 data-logger and the above sensor were used to collect light measurements through the time of Ringelberg's stimulus threshold. All other light readings were recorded by hand from an International Light Research Radiometer models 700 (Stonehouse and Barbadoes Ponds), and 500 (Lower Sawyer Pond). Light measurements were taken every 5 to 10 minutes from early evening until approximately 1 hour past sunset. The light measurements made with the Li-Cor instruments were converted to Wcm^{-2} with the conversion factors given in Westlake (1965).

Particulate Dry Weights

Mixed water-samples were taken to determine the dry weight of edible particulate (<30 um) available to the zooplankton. Samples were taken from the epi-, meta-, and hypolimnia of the Sawyer Ponds and Barbadoes Pond using either a 1.75 or 3.0 l Van Dorn bottle, and combined in a clean bucket. An integrated tube-sampler was used to sample the epilimnion of Stonehouse Pond. The samples were thoroughly mixed, pre-filtered through a 30 um mesh Nitex screen, and filtered at once onto 25 mm glass fiber filters (Gelman 0.45 um pore), as described in the laboratory methods.

Plankton Sampling

In each lake, a late afternoon profile and a profile at least one hour after dark were taken with a closing net (30 cm diameter, 150 um mesh) to determine the day-night distributions of the crustacean zooplankton and *Chaoborus* larvae. The intervals used in the profiles were determined on the basis of the depth of the top of the thermocline and the depth of the lake. In Upper Sawyer Pond 1 m intervals were used, while 4 m (from 0 - 12 m) and 6 m (from 12 - 24 m) intervals were used in Lower Sawyer Pond.

In Upper Sawyer Pond, two profiles were taken between the afternoon and night profiles, using Van Dorn bottles (1.75 and 3.0 l samples). In Lower Sawyer Pond, two additional profiles were also taken, with the closing net. These additional samples were used to gain insight into the completeness of the migrations. All of the samples were preserved to a final concentration of 4% sucrose-formalin (Haney and Hall 1973).

The zooplankton samples were subsampled with a Hensen-Stempel pipette for counting under 50x power on a Wild M-5 dissecting microscope. *Daphnia* were identified to species according to Brooks (1957). The rotifers *Keratella taurocephala* and *Gastropus* sp. were identified from Stemberger (1979), and all other zooplankton were identified from Edmondson (1959). Random lots of 30 or more *Daphnia* were chosen with the Hensen-Stempel pipette from each sample, and measured for body length at 24x magnification using an ocular micrometer. When fewer than 30 *Daphnia* were in the sample, all were measured.

Data Analysis

Quartiles were calculated as described in the laboratory methods. Only mature female Cladocera were included in the quartiles presented so that comparisons could be made with the laboratory study, where only female *Daphnia* were used.

The pre-migration depths of the populations were defined as be the depths of the population Q50 in the first profile of samples.

Amplitudes of migration as little as 0.5 m (Juday 1904), or 0.29-0.85 m (McNaught and Hasler 1964), can be found in natural systems. Therefore an upward or downward shift of 0.5 m or more in the depth of the population Q50 was taken as sufficient evidence for a vertical migration. Less than a 0.5 m change in the depth of the population Q50 was scored as a non-migratory behavior.

The sampling intervals used were too broad to allow an evaluation of how closely the evening migration initiation follows the time of Ringelberg's stimulus threshold in these lakes, nor could velocities during the course of the migration be calculated.

In order to examine the hypothesis that zooplankton may migrate to avoid ultra-violet radiation damage, the intensity of ultra-violet B (UV-B) radiation at the pre-migration depths of the lake zooplankton was estimated from attenuation coefficients for UV-B in Smith and Baker (1979) and Ringelberg *et.al.* (1984). The surface intensities of UV-B for fall and summer were estimated from values presented by Damkaer *et.al.* (1980, their Figure 2) for Manchester, Washington.

The stratification of food concentrations in the study lakes was examined as a possible control of vertical migration using Gliwicz and Pijanowska's model. Gliwicz and Pijanowska (1988) defined the tendency to migrate as the ratio of the observed over the expected amplitude of migration. The expected amplitude of migration was defined as the distance from the day depth of the populations to the depth of the highest food concentration in the epilimnion. The model predicts that the tendency to migrate should be positively correlated to the proportion (F) of the food concentration in the epilimnion relative to the concentration below the depth of 1% of the moon surface illumination. The food concentration in the epilimnion was defined as the concentration above the midnight position of the population. Data from Upper Sawyer Pond, Lower Sawyer Pond, and Barbadoes Pond were compared with the predictions of the model.

The regressions used in analysing the field data were done with the STATWORKS program (Cricket Software Inc.). Draper and Smith (1981) was used as a reference for the regression analyses. The r^2 values reported in this section have not been adjusted for the degrees of freedom. The t-tests for comparison of slopes and intercepts of the regression equations were done as presented in Zar (1984).

Sonar analysis

Sonar transects from each lake were used to obtain an estimate of fish densities (Figures 12-15). On Upper Sawyer, Stonehouse, and Barbadoes Ponds, a Lowrance X-15 sonar (200 Kz, 22° angle transducer) was used. On Lower Sawyer Pond a portable Raytheon sonar (200 Kz, 12° angle transducer) was used. A single transect was available for Stonehouse Pond (Figure 15), two replicate transects for Upper Sawyer and Barbadoes Pond (Figures 12 and 14), and two transects in different directions on Lower Sawyer Pond (Figure 13).

The density of fish in each of the lakes was estimated by counting the fish traces seen on the sonar transects. In Upper Sawyer Pond, some traces may have been caused by salamanders, another possible predator of zooplankton. The volume sampled by the sonar transects was calculated as (lake depth) X (radius of transducer signal cone at lake bottom) X (transect length). The radius of the transducer cone is determined by the angle of the transducer signal. The number of fish traces was divided by the volume of water sampled to estimate the lake's fish population density. The fish density was multiplied by 10^4 before being correlated with pre-migration depths, to increase the range of the values.

In Stonehouse and Lower Sawyer Ponds the depth of the thermocline (7 and 8 m respectively) was used to divide the water column into upper and lower strata. In Upper Sawyer Pond the thermocline was at nearly the bottom of the pond (7.5 m), therefore the water column was divided in half, 0-4 m and 4-8 m. In Barbadoes Pond the water column was anaerobic below the 6 m thermocline. Here the upper water was defined as 0-3 m, and the lower water as 3-6 m. Separate estimates of fish density were made for each lake's upper and lower water strata.

RESULTS AND DISCUSSION

Light as the Primary Regulator of Evening Vertical Migrations: Laboratory Tests of the Hypotheses

Responses to Absolute Light Intensity

The preferendum hypothesis. The preferendum hypothesis proposes that absolute light intensity regulates the vertical migration of zooplankton. The hypothesis predicts that changes in the depth of a zooplankton population will correspond to changes in the absolute light intensity during the day, and that the population will track an isopleth of light intensity during the evening migration.

I examined the pre-migration period, defined as the time interval between the two observations taken just prior to the evening migrations. In general, the populations did not rise as quickly as the light was decreasing (examples in Figures 16 and 17). Prior to migration, the light intensity at the depths of the population quartiles, in columns without fish, decreased at least 50% for all but three of the migrations observed, and decreased more than ten-fold for half of these evenings (Table 3). According to the preferendum hypothesis, the populations should rise during this time, at a rate which maintains a constant light intensity at the population depth.

During the evening migrations in columns without fish, the population quartiles moved more slowly than rate of decrease of light intensity. The light intensity at the depths of the population quartiles decreased more than 50% during 85% of the migrations, and more than 90% for over half of the migrations (Table 3). Thus the results from the migration period also fail to support the preferendum

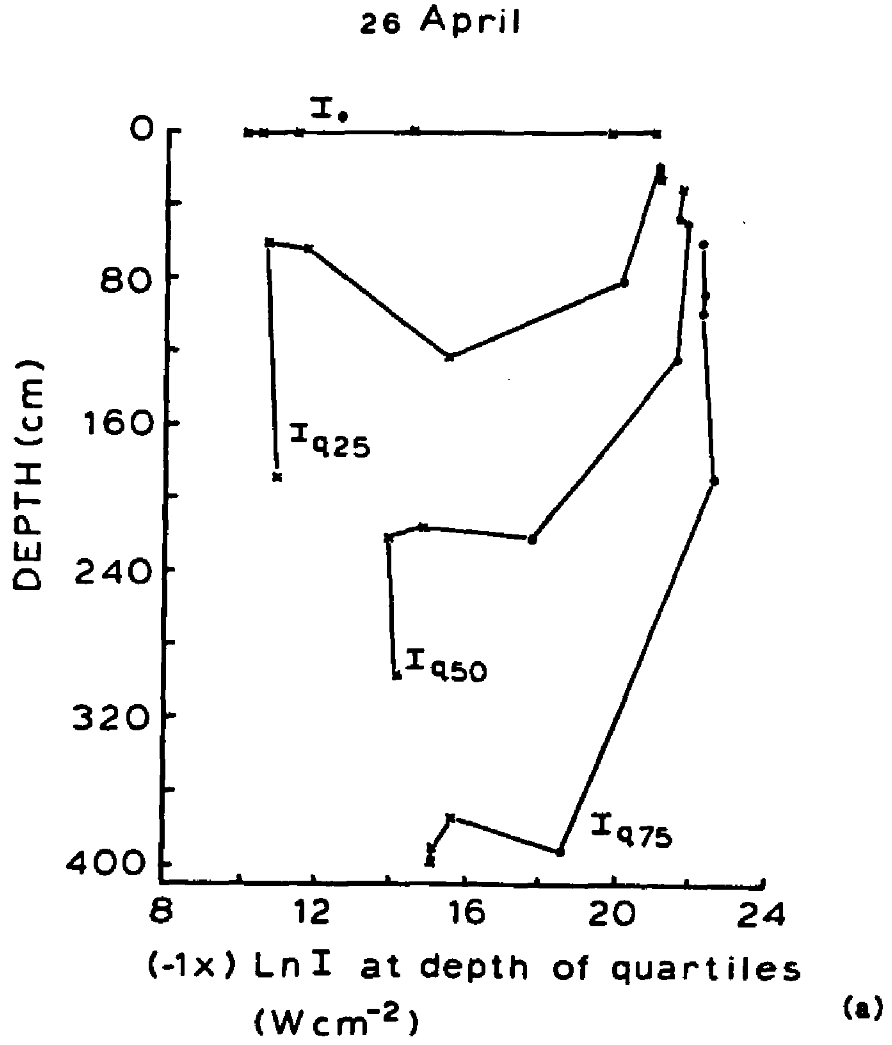
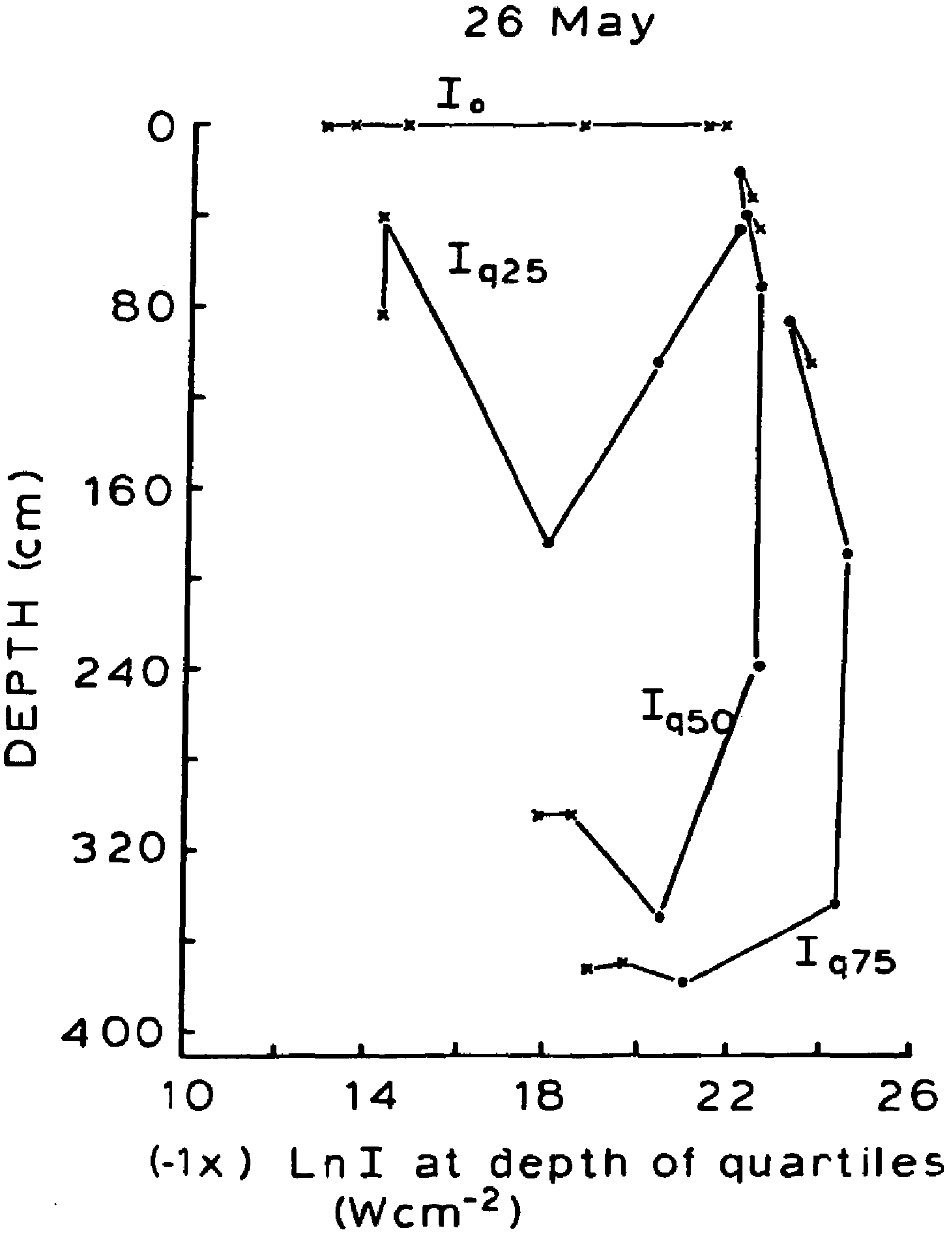


Figure 16. The light intensities (Wcm^{-2}) at the population Q25, Q50, and Q75 depths versus the depths of the population Q25, Q50, and Q75 for one column on the first evening of the experiment. (a) 26 April 1985 (b) 26 May 1985 (c) 8 August 1986. Circles indicate observations during the migration, x's before or after the migration. The surface light intensity I_0 is shown to indicate the light conditions of each evening.



26 May
I_o
I_{q25}
I_{q50}
I_{q75}
0
80
160
240
320
400
DEPTH (cm)
10
14
18
22
26
(-1x) LnI at depth of quartiles
(Wcm^{-2})

Figure 16(b)

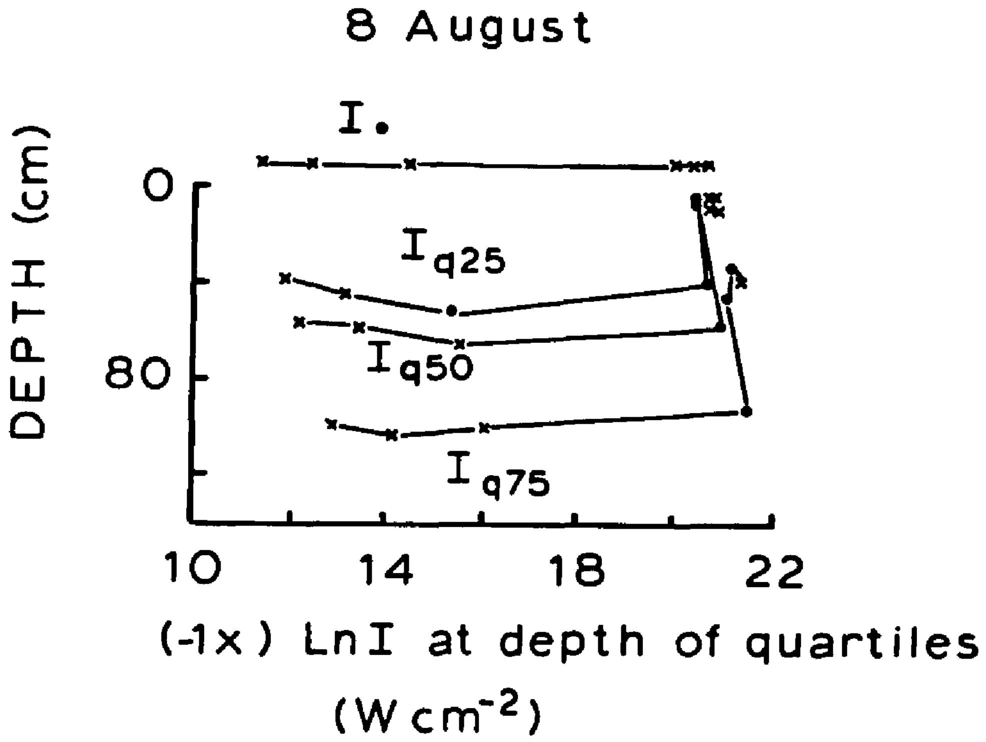

8 August
I.
DEPTH (cm)
0
80
I q25
I q50
I q75
10
14
18
22
(-1x) LnI at depth of quartiles
(W cm-2)

Figure 16 (a)

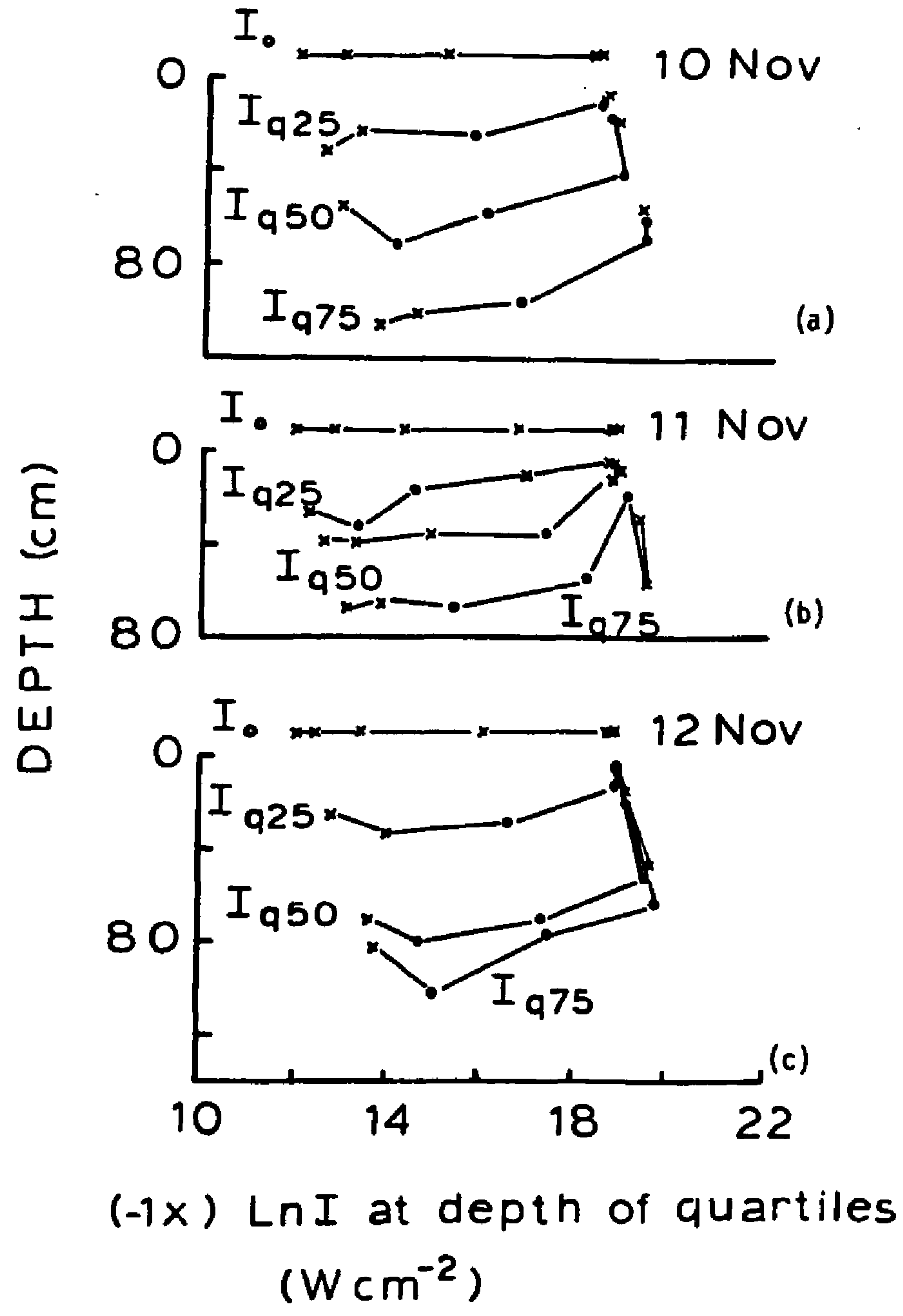


Figure 17. As in Figure 16 for each day of the November observations. (a) 10 November, (b) 11 November, (c) 12 November, (d) 13 November, (e) 14 November, and (f) 15 November 1985.

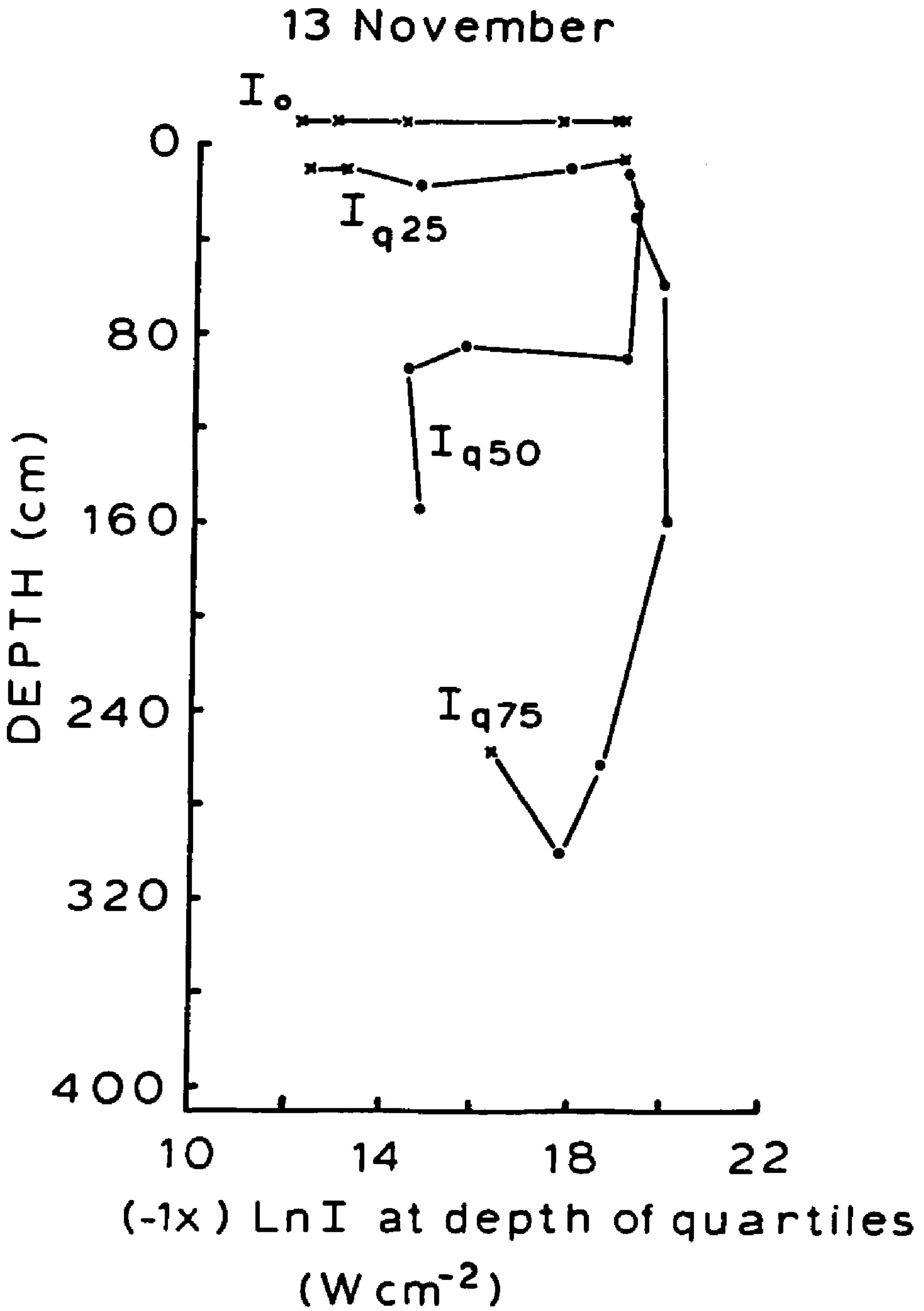

13 November
I_o
0
80
160
240
320
400
I_{q25}
I_{q50}
I_{q75}
DEPTH (cm)
10
14
18
22
(-1x) LnI at depth of quartiles
(W cm^{-2})

Figure 17(d)

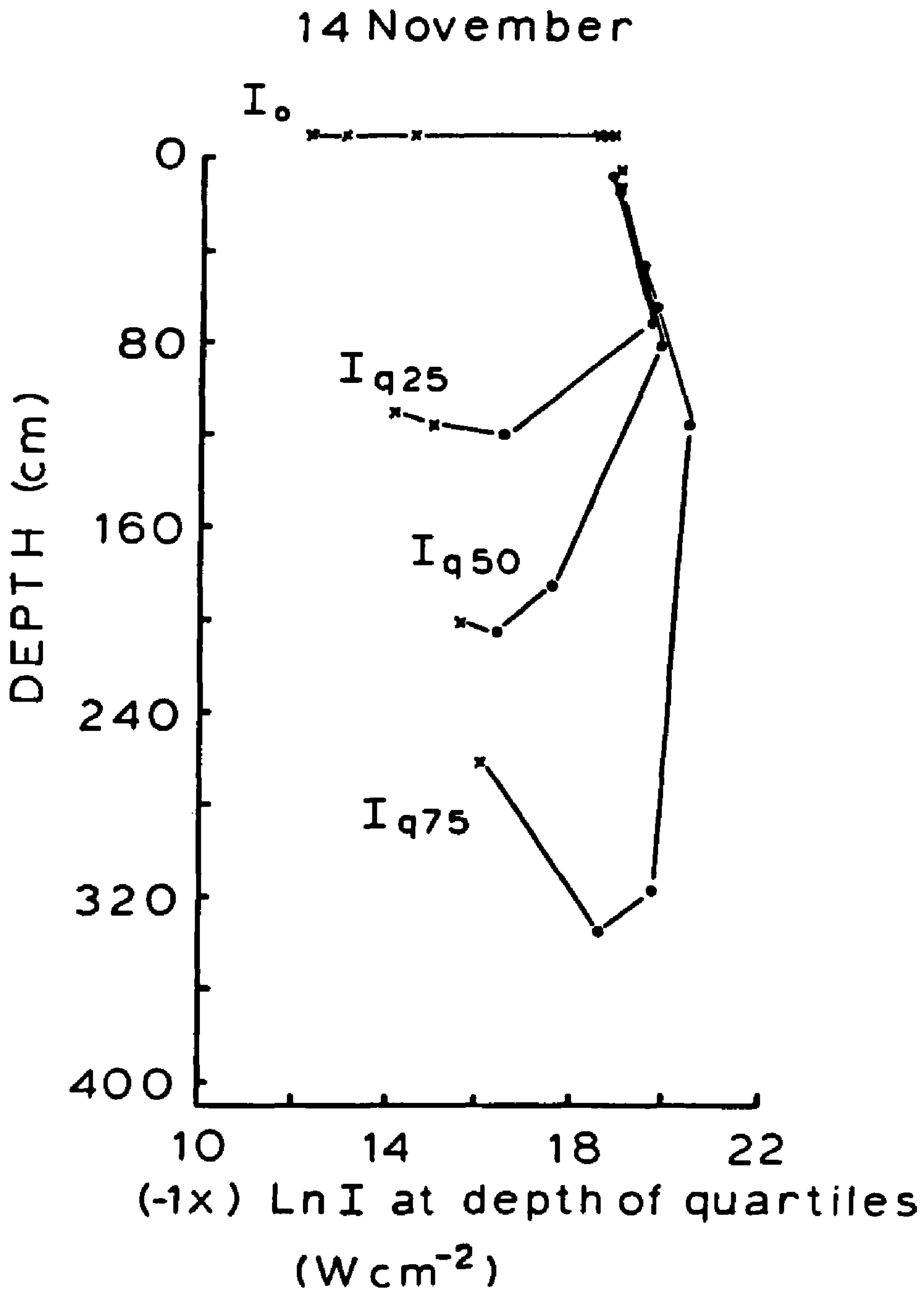

14 November
I_o
I_{q25}
I_{q50}
I_{q75}
DEPTH (cm)
0
80
160
240
320
400
10
14
18
22
(-1x) Ln I at depth of quartiles
(W cm^{-2})

Figure 17(e)

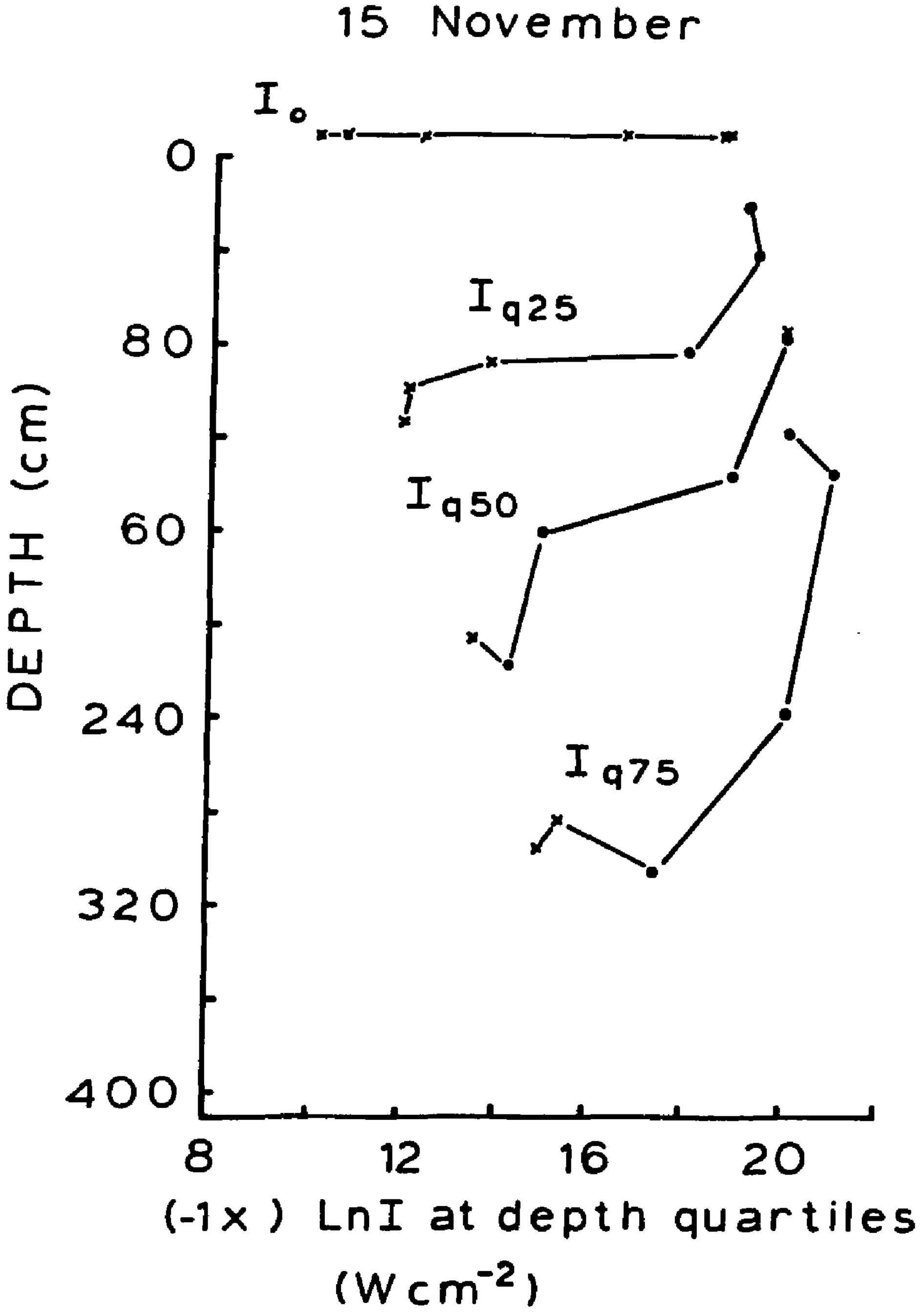

15 November
I_o
I_{q25}
I_{q50}
I_{q75}
DEPTH (cm)
0
80
60
240
320
400
8
12
16
20
(-1x) LnI at depth quartiles
(Wcm^{-2})

Figure 17(f)

hypothesis.

	fish	percent decrease in light intensity				
	treatment	<50%	50-90%	90-99%	99-99.9%	>99.9%
before migration						
Q25	0	3	16	18	7	1
	+	2	6	4	2	0
	-	0	2	2	2	0
Q50	0	3	19	12	8	2
	+	1	10	3	0	0
	-	0	4	2	1	0
Q75	0	4	17	13	6	1
	+	2	4	3	2	0
	-	0	3	1	1	1
during migration						
Q25	0	7	9	15	14	5
	+	2	0	4	4	1
	-	0	0	3	2	1
Q50	0	4	5	17	13	4
	+	1	1	7	2	3
	-	1	0	2	3	2
Q75	0	4	8	14	8	5
	+	1	0	6	5	2
	-	1	1	1	3	3

Table 3. Number of evenings for which the absolute light intensity decreased by the indicated percentage before migration and during migration, (0 before fish, + during fish, - after removal of fish) for each of the quartiles.

Light intensitites at all depths of the water column decrease at the same rate in the evening, and so the isopleths of all light intensities rise at the same rate. Therefore, assuming all of the individuals in a population migrate, the preferendum hypothesis predicts that the entire population distribution should move upward at the same rate as the isopleths of light intensity. However the light intensities decreased by differing percentages for each of the three quartile depths (Figures 16 and 17) during all but one of the migrations observed in this study. This indicates that the individuals at the upper part of the population moved at a different rate than individuals in the lower part.

The incident light intensity determines the depth of any particular isopleth of light intensity from day to day. Thus if the zooplankton return to the depth of one particular light intensity from day to day, we would expect no correlation between the incident light intensity and the light intensity at the depth of the population prior to migration. There was a significant positive correlation between the light intensity at the depths of the population Q50's prior to migration and the surface light intensity ($\ln(I_{Q50}) = 1.22 + 0.903 \ln(I_o)$, $r^2 = 0.459$, 48 df, $p<0.001$). The relationship indicates that the surface light intensity does not influence the pre-migration depth of the populations from day to day. Other factors control the depth of the population when the isopleths of light intensity are rising in the evening.

The effects of food concentration on the responses to absolute light intensity. Among those evenings when the food concentration was greater than 3 mg l^{-1}, the depths of the population Q50's prior to migration were inversely correlated with the light at that Q50 depth (Figure 18, (Q50 pre-migration depth) = $1487 - 38.1 (\ln I_{Q50})$, $r^2 = 0.717$, $p<0.001$). That is, when the light intensity at the pre-migration

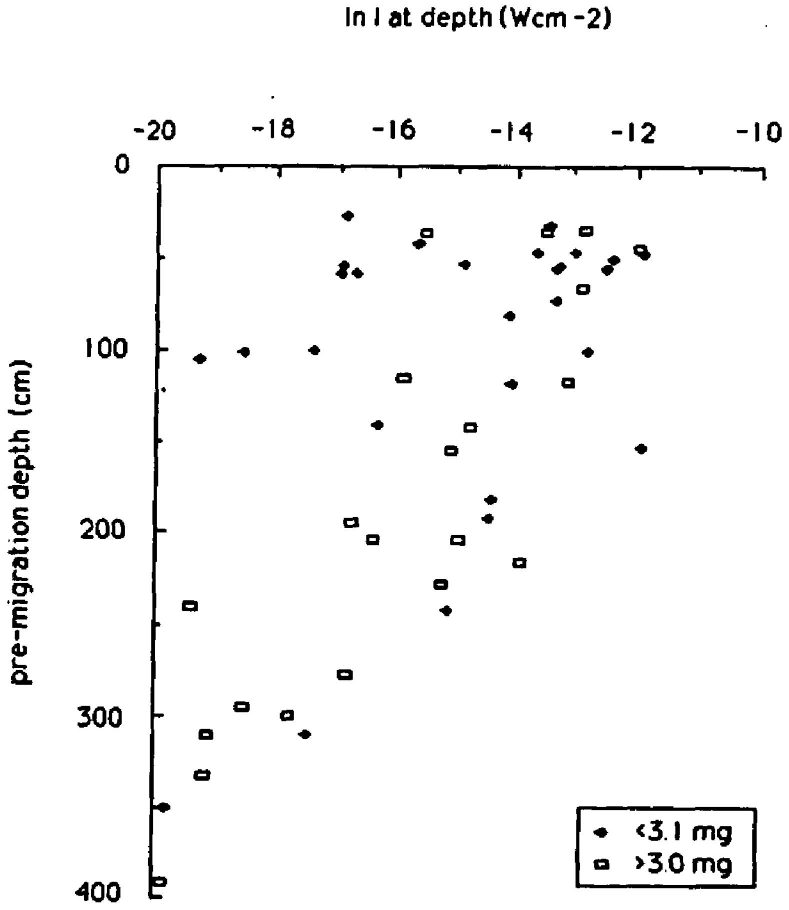


Figure 18. Pre-migration depth of the Daphnia pulex population Q50's (cm) compared with the light intensity (Wcm^{-2}) at those depths, for food concentrations less than or equal to 3 mgl^{-1}, and greater than 3 mgl^{-1}.

depths was low, the populations were deep. At food concentrations less than 3.1 mg l^{-1}, in contrast, there was no correlation; the *Daphnia* did not have deeper pre-migration depths when light intensities were lower (Figure 18).

The effects of a fish on the responses to absolute light intensity. On 12 evenings one column contained a live fish. The relationship between the depth of the Q50's and the light intensity at those depths prior to migration did not change with the introduction of the fish to the columns (Table 3, Figure 19). And on those evenings, the migrations started at light intensities (6.2×10^{-7} to 4.6×10^{-9} Wcm^{-2}) and depths (102 to 402 cm), well within the range for all populations not exposed to fish (Figure 20).

Responses to the Relative Rate of Change of Light

The stimulus-threshold model. According to the stimulus-threshold model, a threshold level of relative light change stimulates the initiation of evening vertical migrations. To test the stimulus-threshold model, I compared the time when the evening migrations observed in my columns began with the time when Ringelberg's stimulus threshold value (RST), 1.71×10^{-3} sec^{-1} (*Daphnia magna*), was first exceeded in the evening (Figure 21). In general the time of RST and the time of EMI were closely correlated, with 77 to 89% of the variability explained by the the time of RST for each of the three quartiles ($p<0.001$, Figure 21). The ranges of EMI for given RST's (Figure 21) indicate that the stimulus-threshold may vary with other factors in the columns.

The effects of food concentration on the stimulus-threshold model. When no fish was present, the time of EMI increased with decreasing

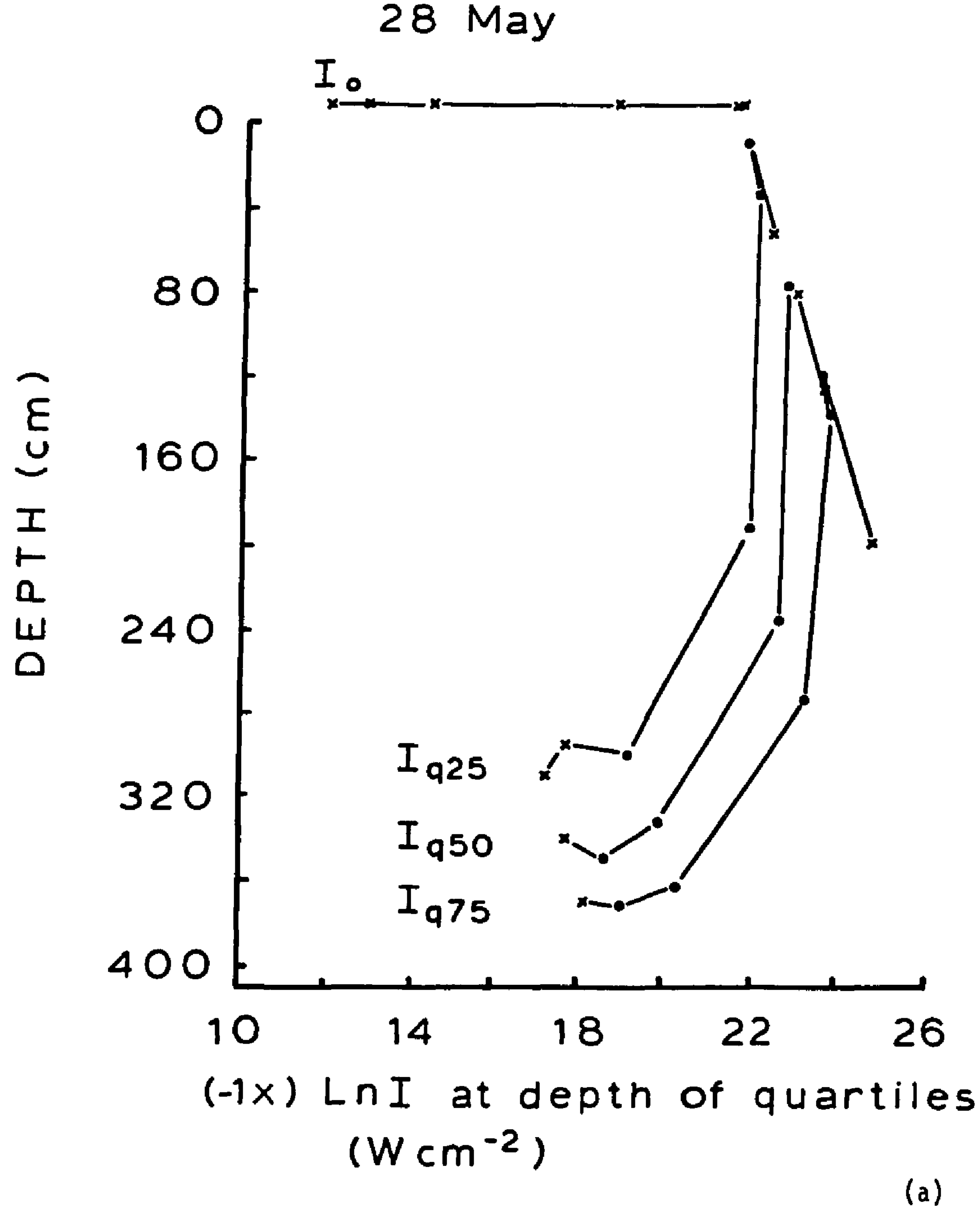
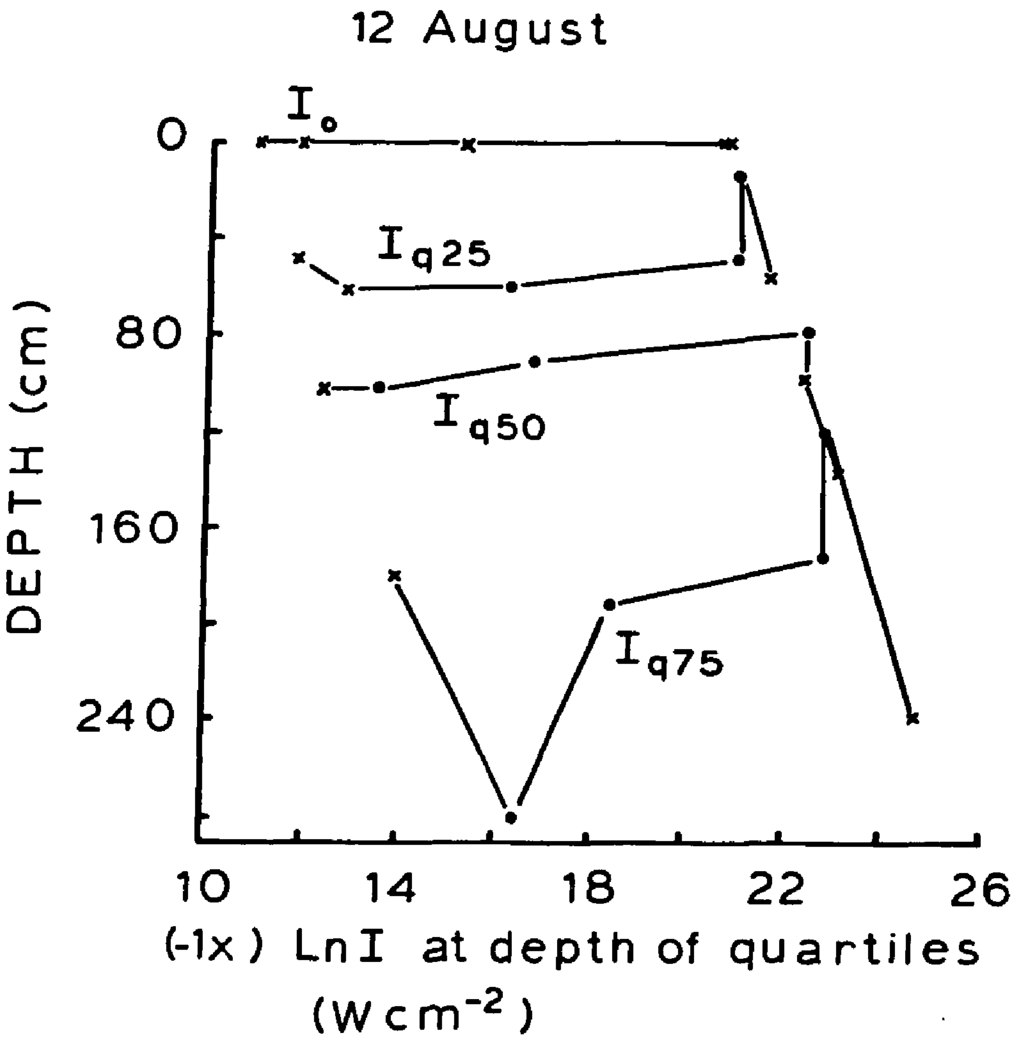


Figure 19. As in Figure 16 for three days when a fish was present in the column. (a) 28 May 1985, (b) 12 August 1986, and (c) 12 November 1985.



12 August
I_o
I_{q25}
I_{q50}
I_{q75}
DEPTH (cm)
0
80
160
240
10
14
18
22
26
(-1x) LnI at depth of quartiles
(W cm^{-2})

Figure 19(b)

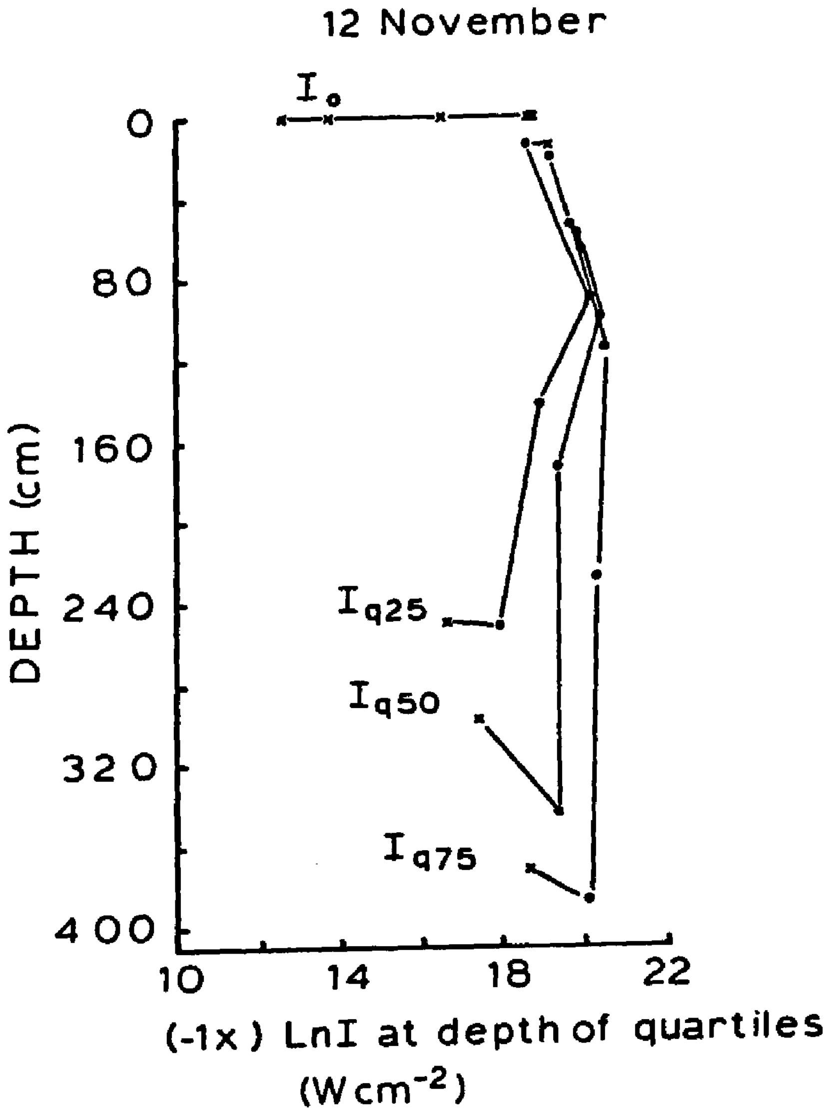

12 November
I_o
0
80
160
240
320
400
DEPTH (cm)
I_{q25}
I_{q50}
I_{q75}
10
14
18
22
(-1x) LnI at depth of quartiles
(Wcm^{-2})

Figure 19(c)

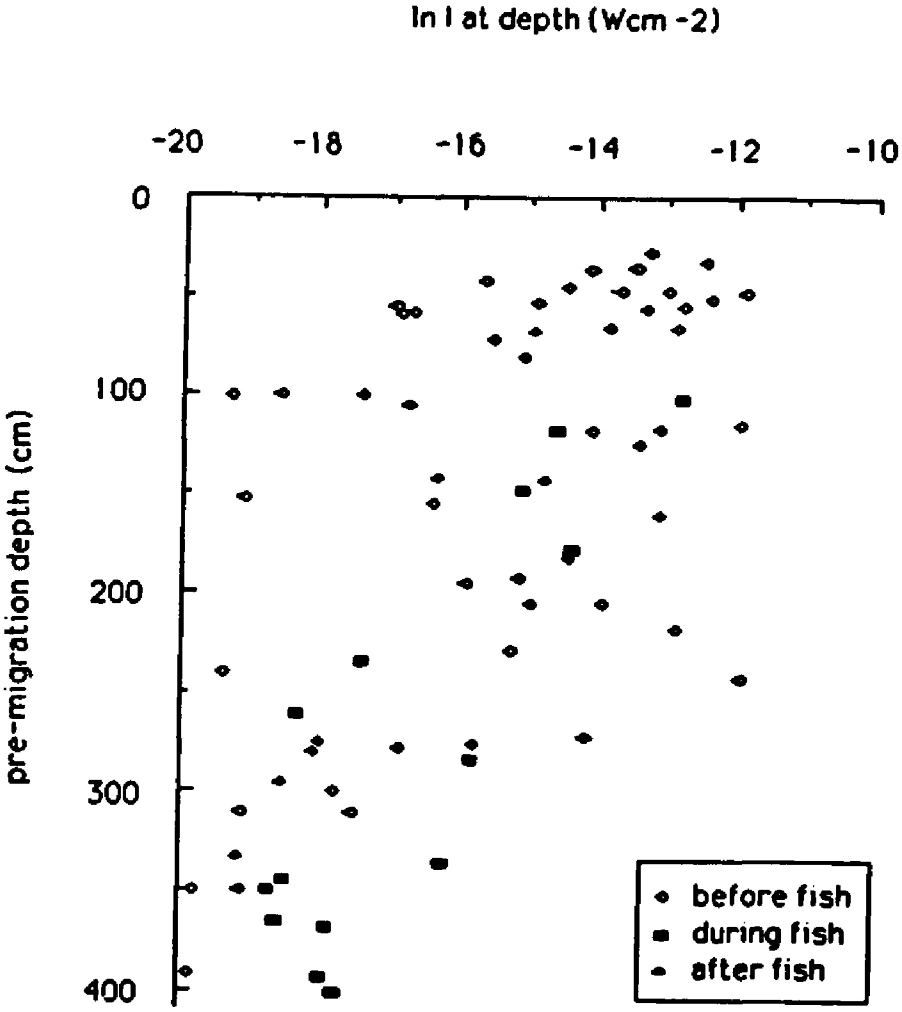


Figure 20. Pre-migration depth of the Daphnia pulex population Q50's (cm) compared with the light intensity (Wcm^{-2}) at those depths for observations taken before, during, and after the presence of a fish in the columns.

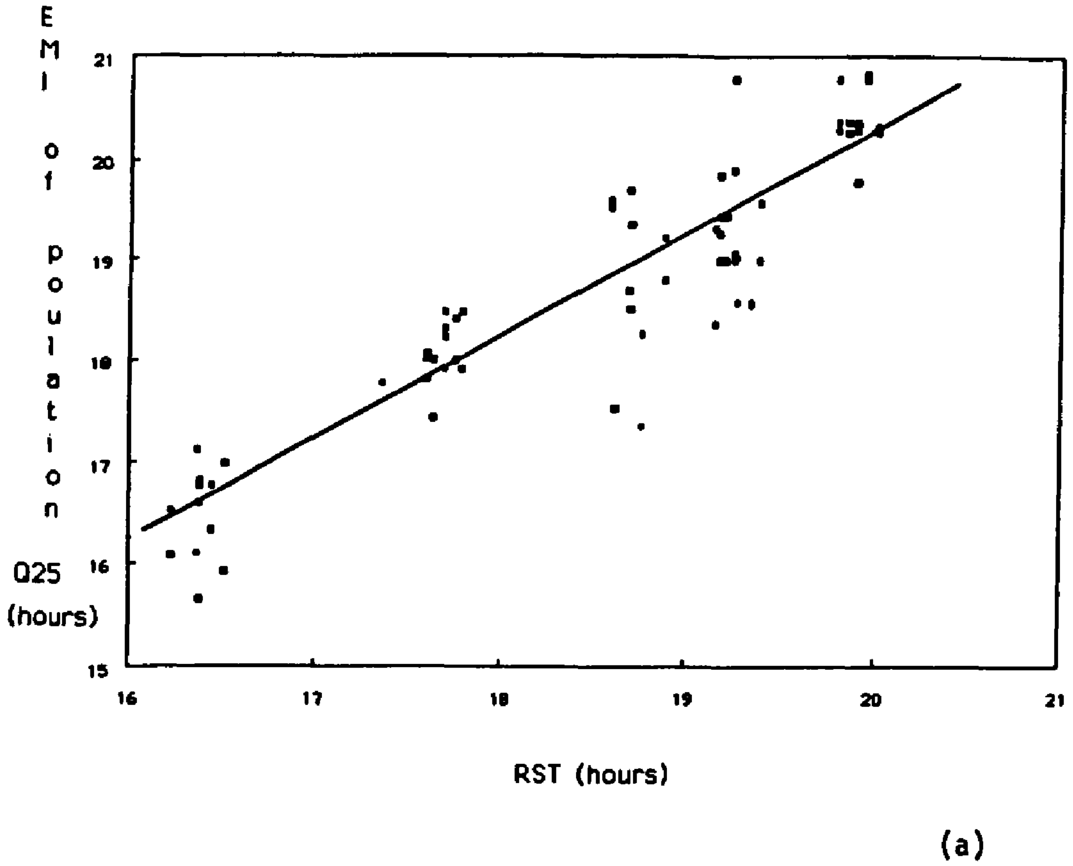


Figure 21. Comparison of the time of evening migration initiation (EMI) to the time of Ringelberg's stimulus threshold (RST) in hours for each of the *Daphnia pulex* population quartiles.
(a) population Q25. $y = 0.74 + 0.975x$, $r^2 = 84.0\%$, $p<0.001$.
(b) population Q50. $y = -1.57 + 1.10x$, $r^2 = 88.0\%$, $p<0.001$.
(c) population Q75. $y = -0.42 + 1.03x$, $r^2 = 77.2\%$, $p<0.001$.

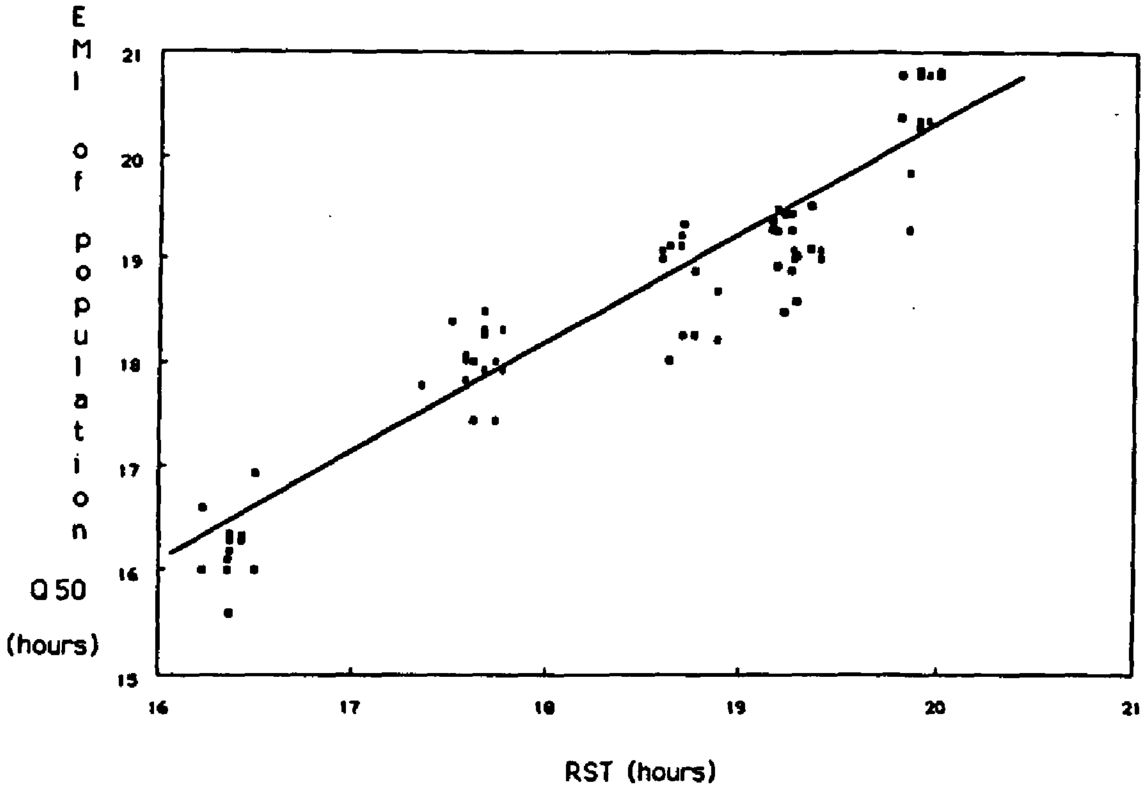

EMI of population Q50 (hours)
21
20
19
18
17
16
15
16
17
18
19
20
21
RST (hours)

Figure 21 (b)

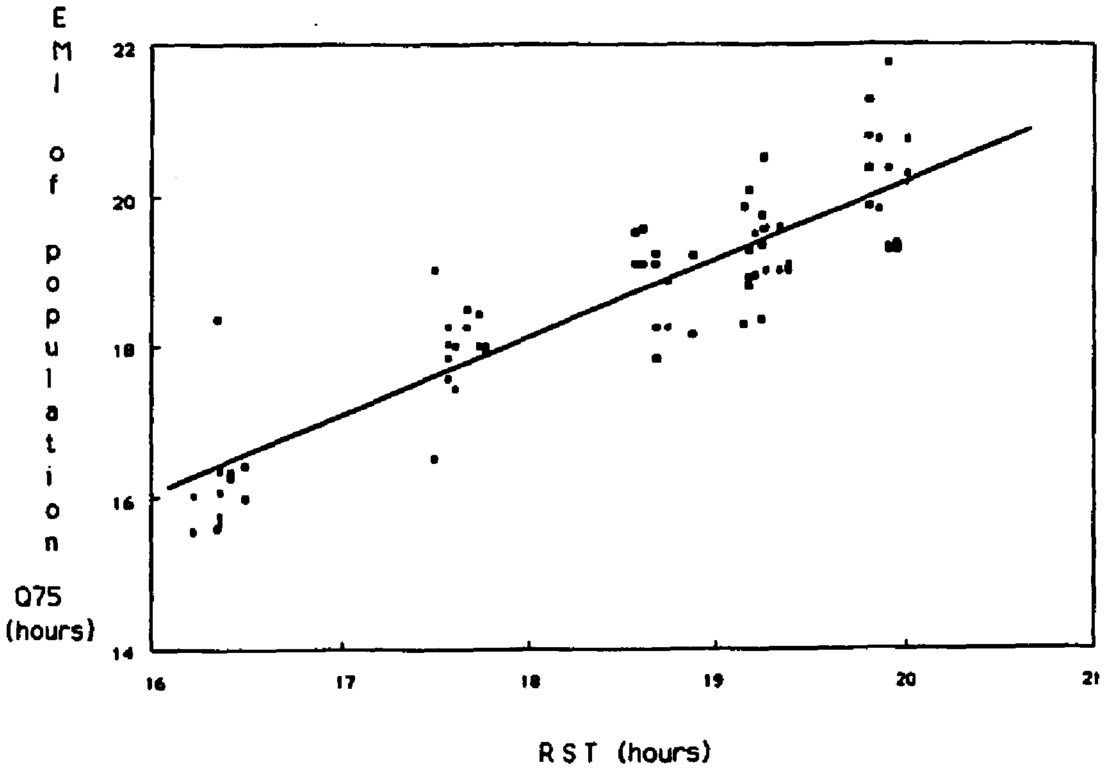

EMI of population Q75 (hours)
22
20
18
16
14
16
17
18
19
20
21
RST (hours)

Figure 21 (c)

food concentration, however the trend was not significant ($F = 0.87$, $p>0.50$).

The effects of a fish on the stimulus-threshold model. The addition to and subsequent removal of a fish from the columns made no significant contributions to the relationship between the times of EMI and RST ($F<1$, Figure 22).

The stimulus-velocity model. The stimulus-velocity model predicts that the velocity of migrating zooplankton has a positive relationship to the relative rate of change of light intensity.

The velocity data for the three quartile depths do not fit the stimulus-velocity model (Figures 23, 24, 25). For example, in May, for all quartiles, and in March for the Q50, there are positive velocities associated with positive stimulus values caused by the sky clearing of clouds and/or by moonlight. The greatest magnitude of stimulus for each month was between -20 and -34×10^{-4} sec^{-1}, and corresponded to velocities which were sometimes close to zero. And high velocities were associated with low stimulus values because the populations often migrated after the light reached night-time intensities (eg. April and May in Figure 23, March, April, and May in Figure 24, and March through July in Figure 25). Apparently the stimulus does not exert a continuous control over the velocity of the migrating populations.

There was evidence of seasonal differences in the range of the velocities between months. In April, May, and July the velocities calculated for the Q50's ranged between 0 and 5.5 to 6.3 cm min^{-1} (Figure 24). During March and August the velocity exceeded 3 cm min^{-1} only once each month. The November data also contained many low velocities, but values ranged up to a maximum of 3.8 cm min^{-1}. When

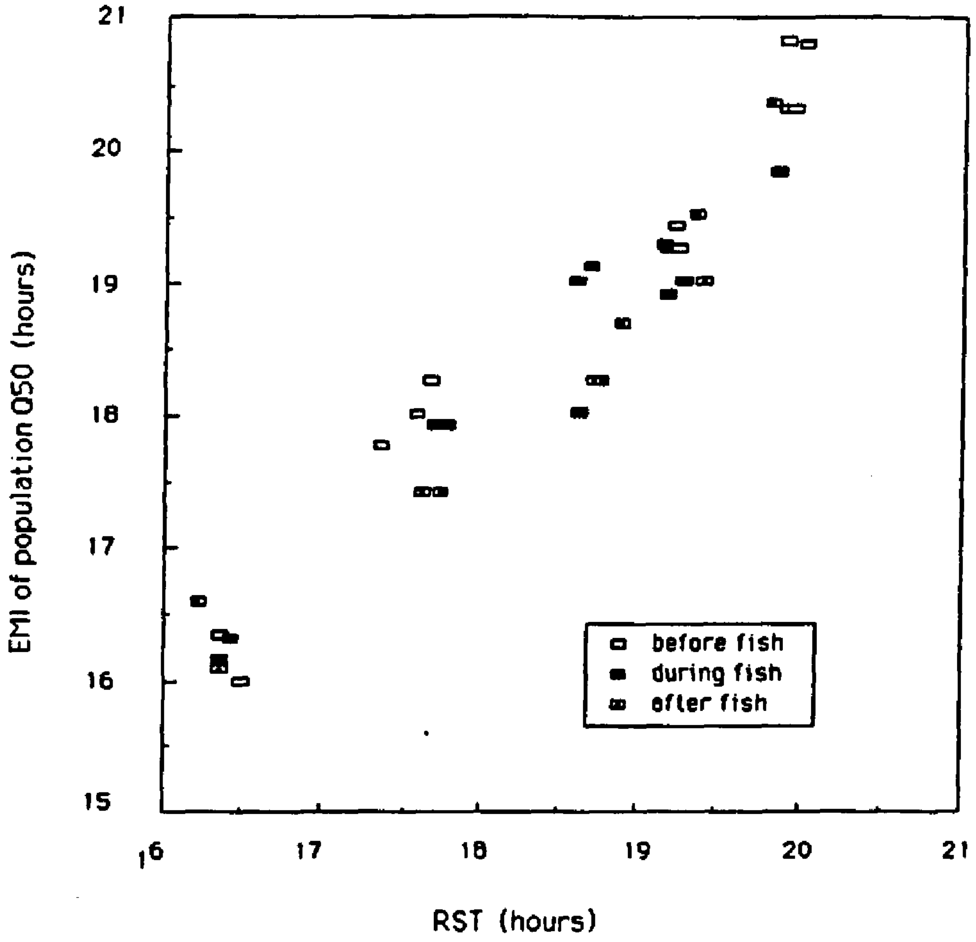


Figure 22. As in Figure 21, for the *Daphnia pulex* population Q50's of those populations exposed to a fish.

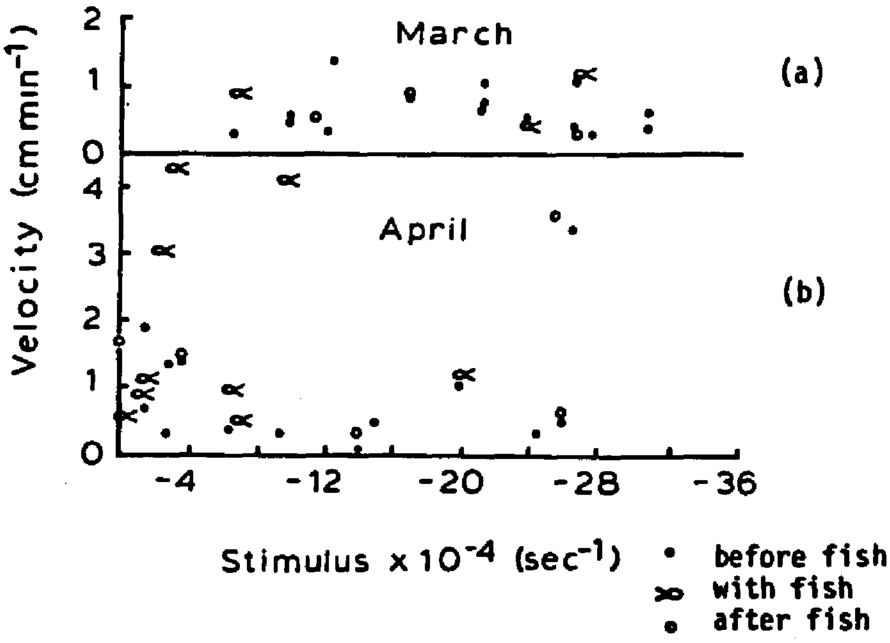


Figure 23. The velocity of the <u>Daphnia pulex</u> population Q25 between intervals of observation (cm min^{-1}) as a function of the relative rate of light change (stimulus) x 10^{-4} (sec^{-1}). (a-f) March, April, May, July, August, and November

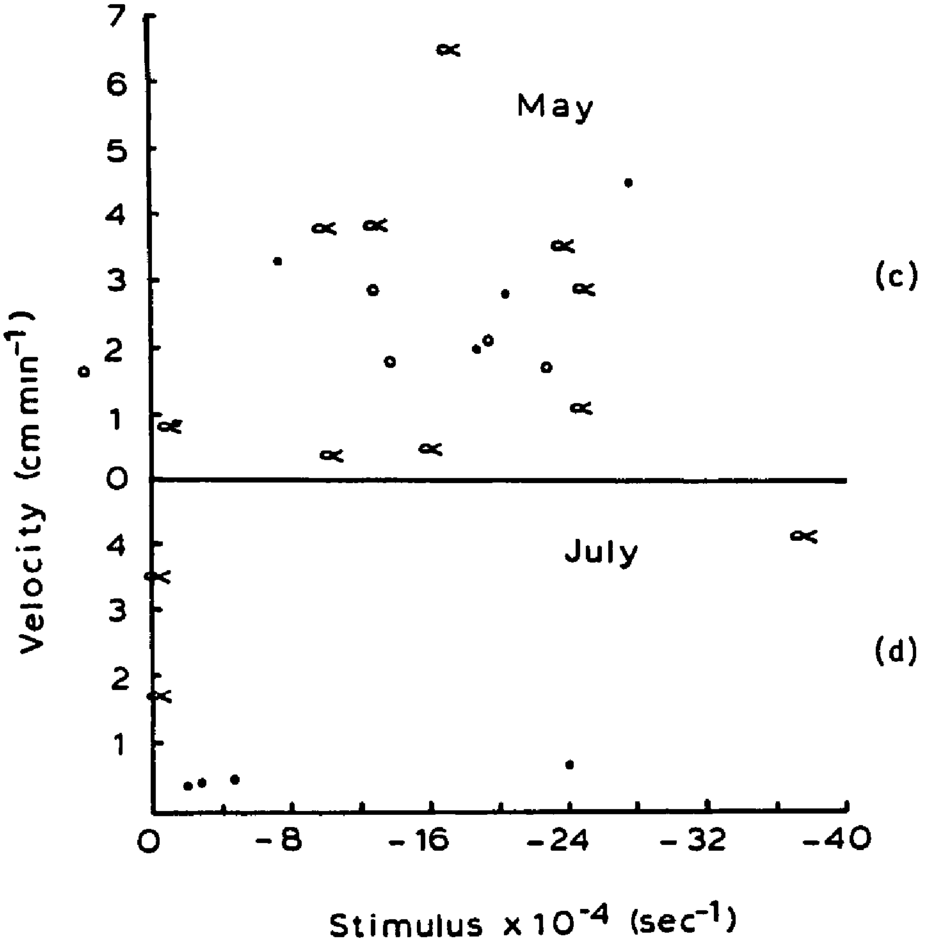


Figure (23) con't.

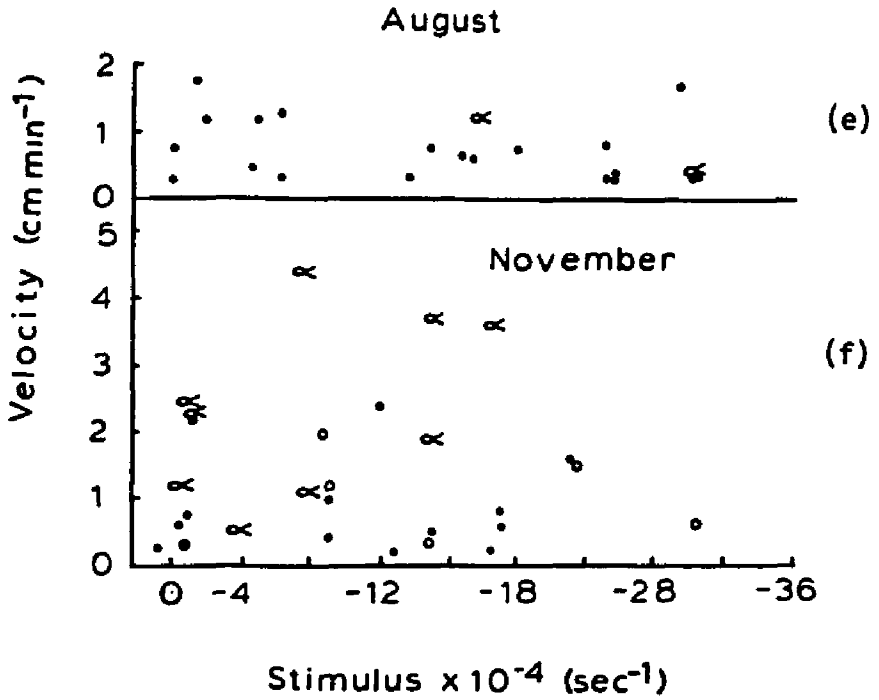


Figure (23) con't.

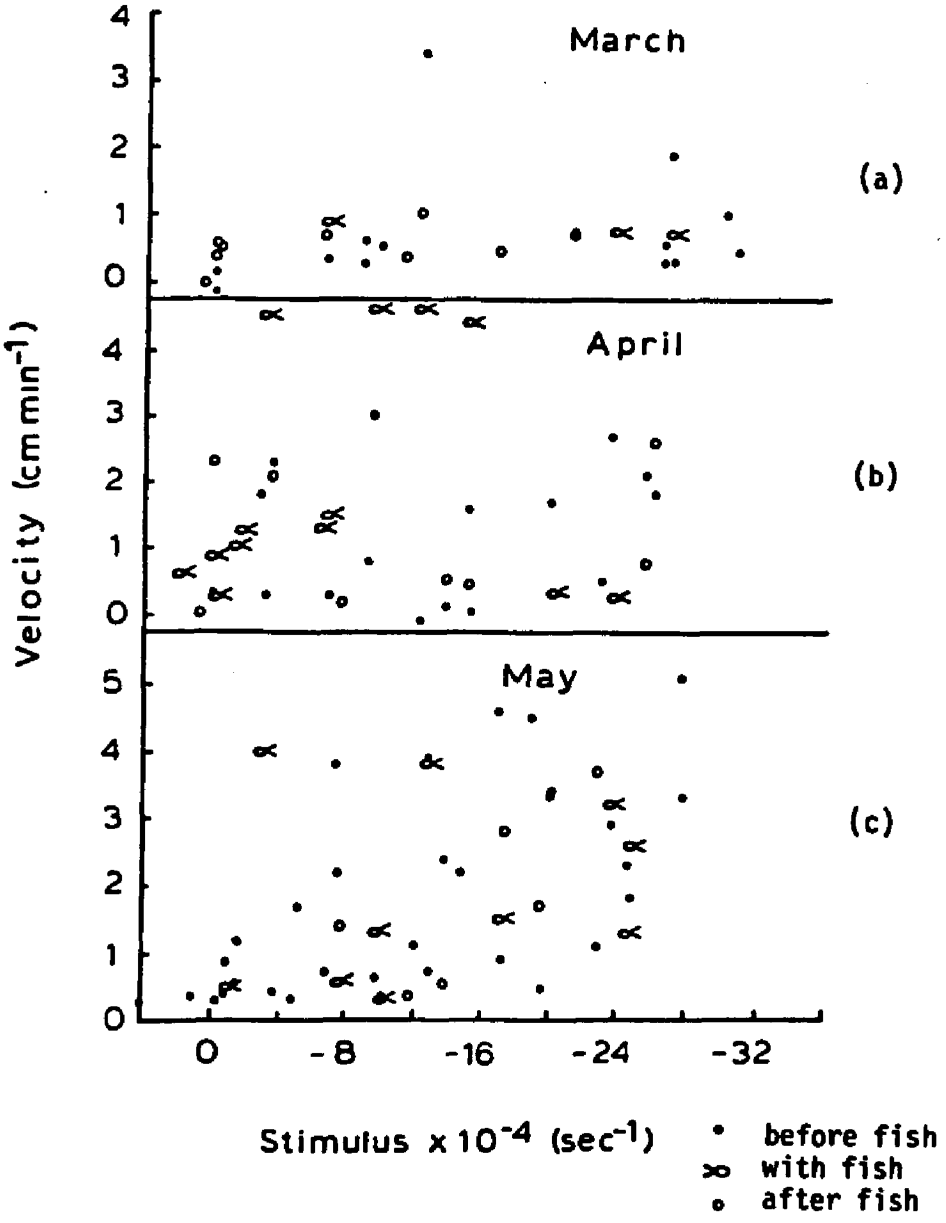


Figure 24. As in Figure 23, for the *Daphnia pulex* population Q50. (a-f) March, April, May, July, August, and November

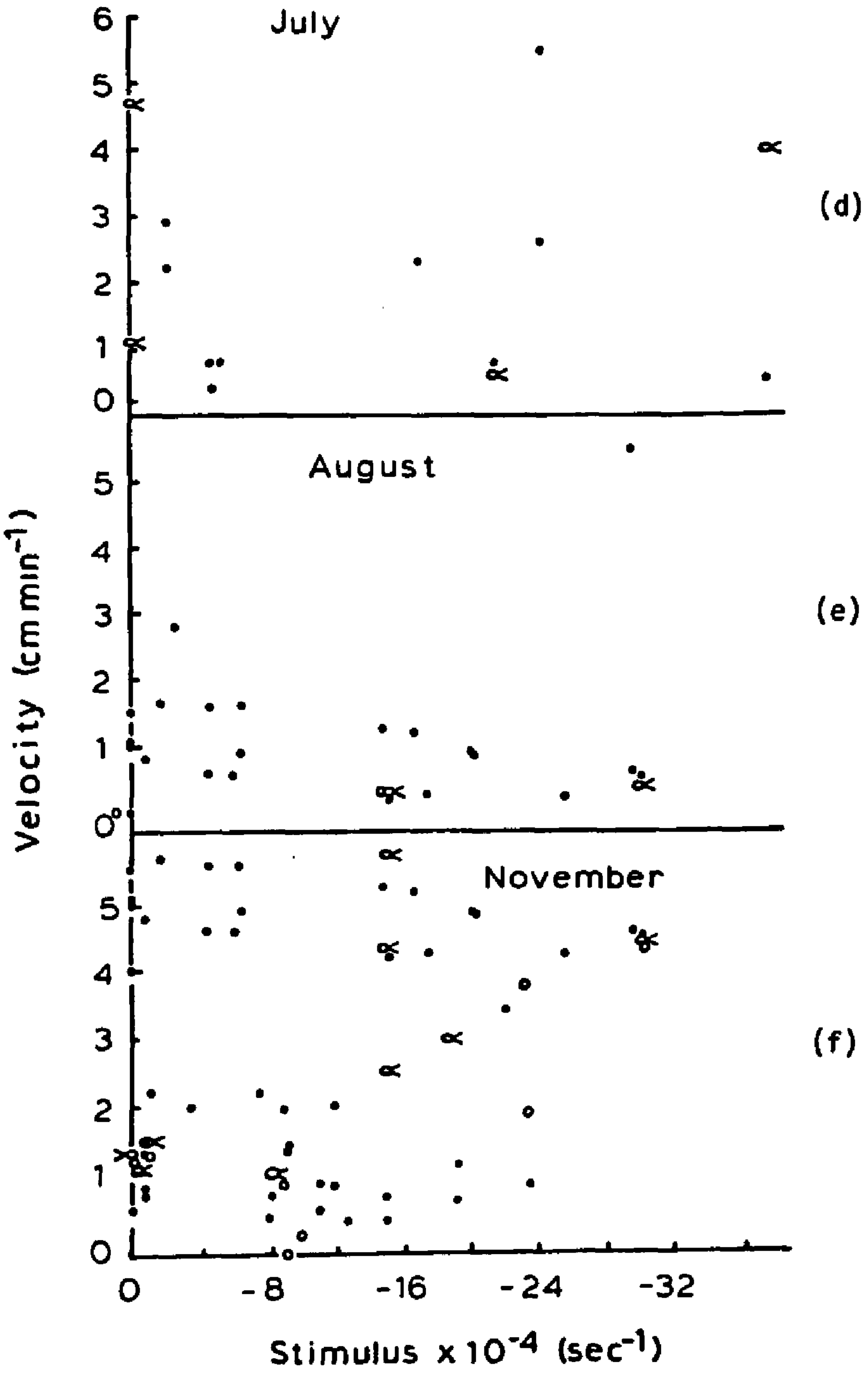


Figure (24) con't.

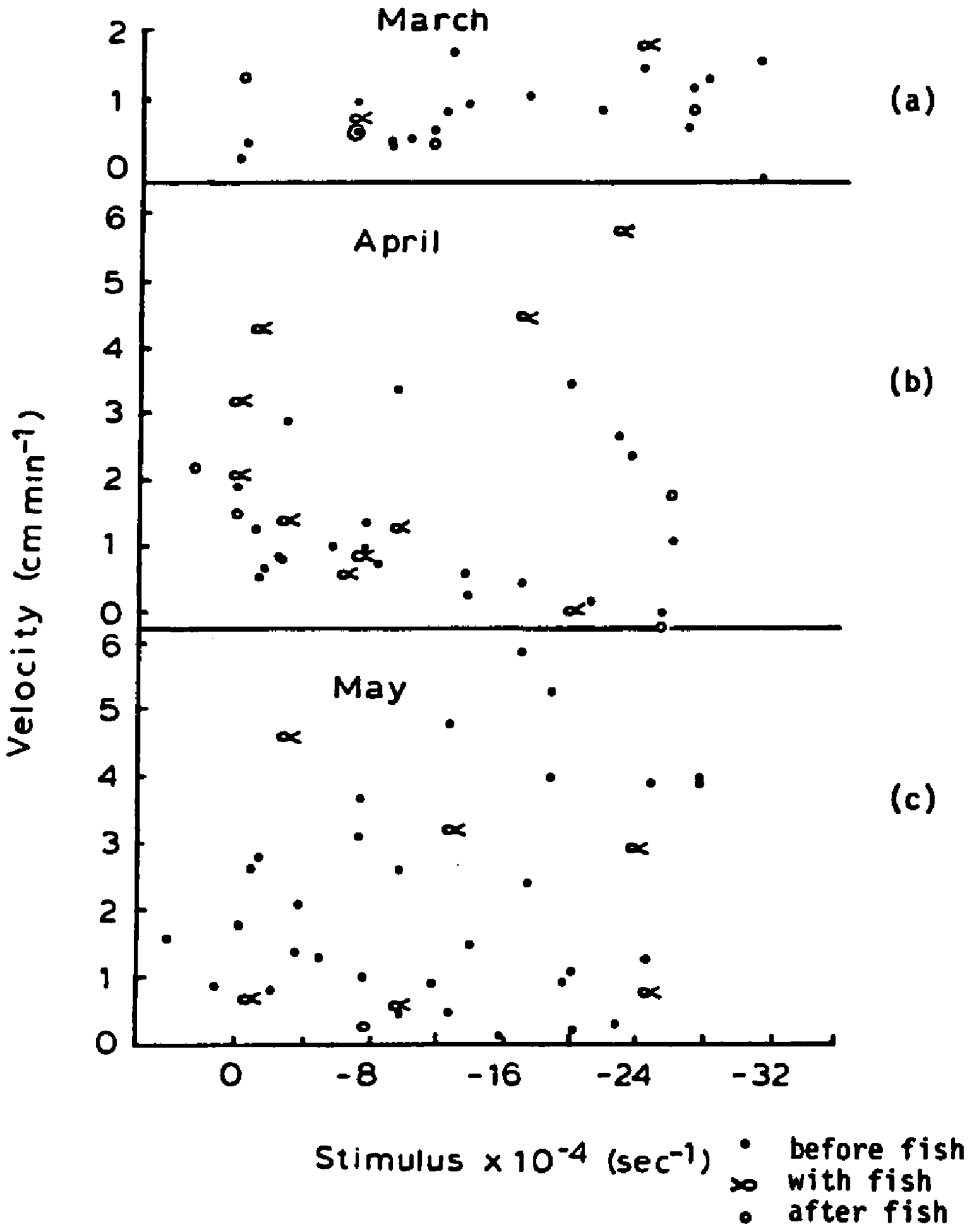


Figure 25. As in Figure 23, for the Daphnia pulex population Q75. (a-f) March, April, May, July, August, and November

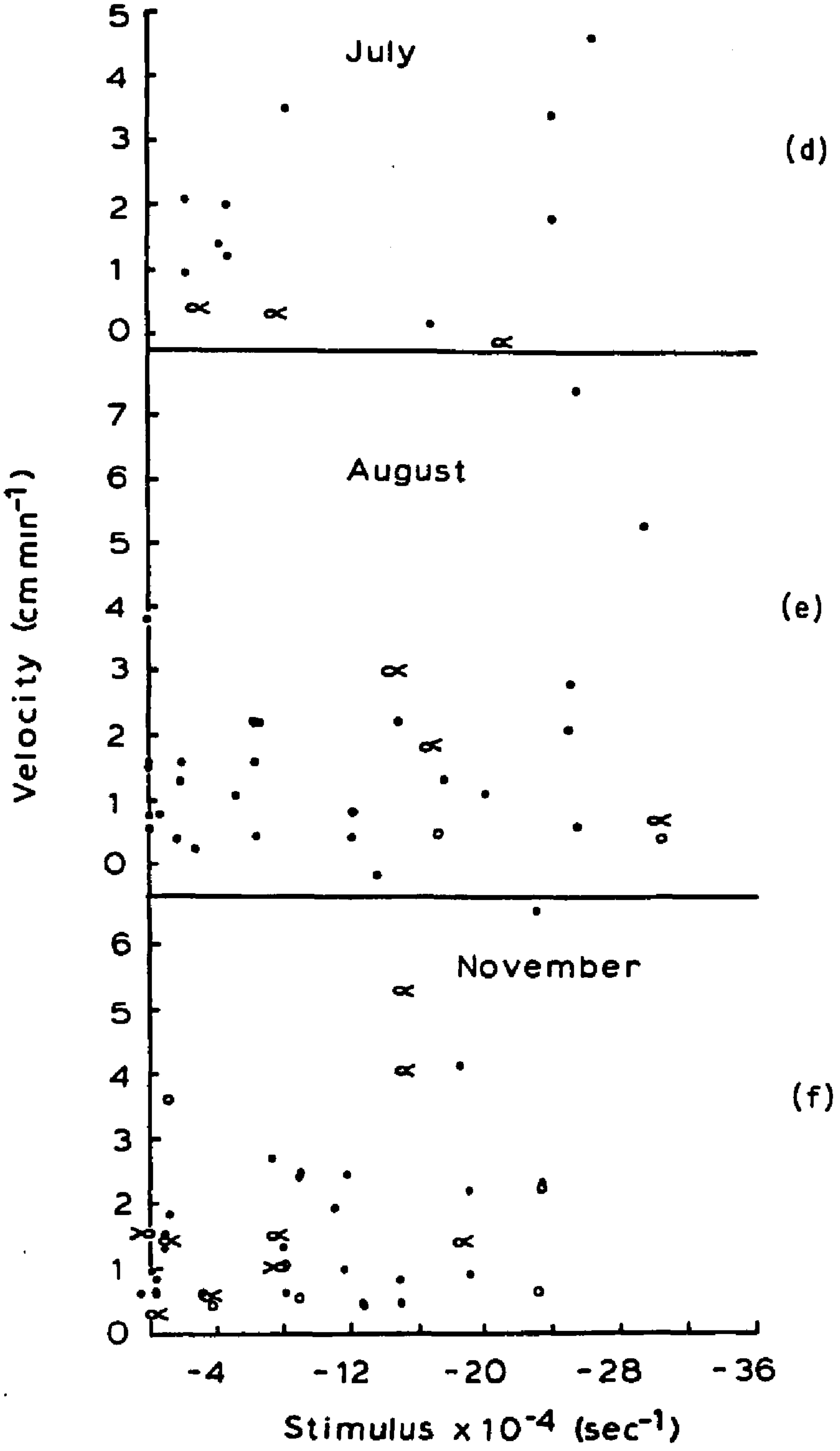


Figure (25) con't.

the mean velocities were tested by ANOVA for differences between months, the test was slightly significant (Table 4).

Although swimming speed has been related to temperature (Gerritsen 1982), mean velocity was not significantly correlated to the mean temperature at 30 cm, either for columns that did not receive a fish, or for columns treated by the addition and removal of a fish ($r^2 < 0.10$).

```
analysis of variance

source        df       ss          ms          f
factor         5      9.656       1.931       2.85      0.10>p>0.05
error         43     29.097       0.677
total         48     38.753

treatment      n      mean       stdev
april          6      1.4821     0.7457
may            9      2.2429     0.9477
june           4      1.6029     1.1495
november       8      1.2692     0.6252
march         11      0.9259     0.9416
august        11      1.1975     0.6005

pooled stdev    0.8226
```

Table 4. Analysis of variance of the mean velocity each evening, with the months of the experiments as treatments, for populations not exposed to a fish.

The effect of food concentration on the stimulus-velocity model. A regression for mean velocity as a function of food concentration for migrations observed for populations not exposed to a fish was not significant (p>0.10, Figure 26).

The effect of a fish on the stimulus-velocity model. The relationship between stimulus and velocity was not significant for

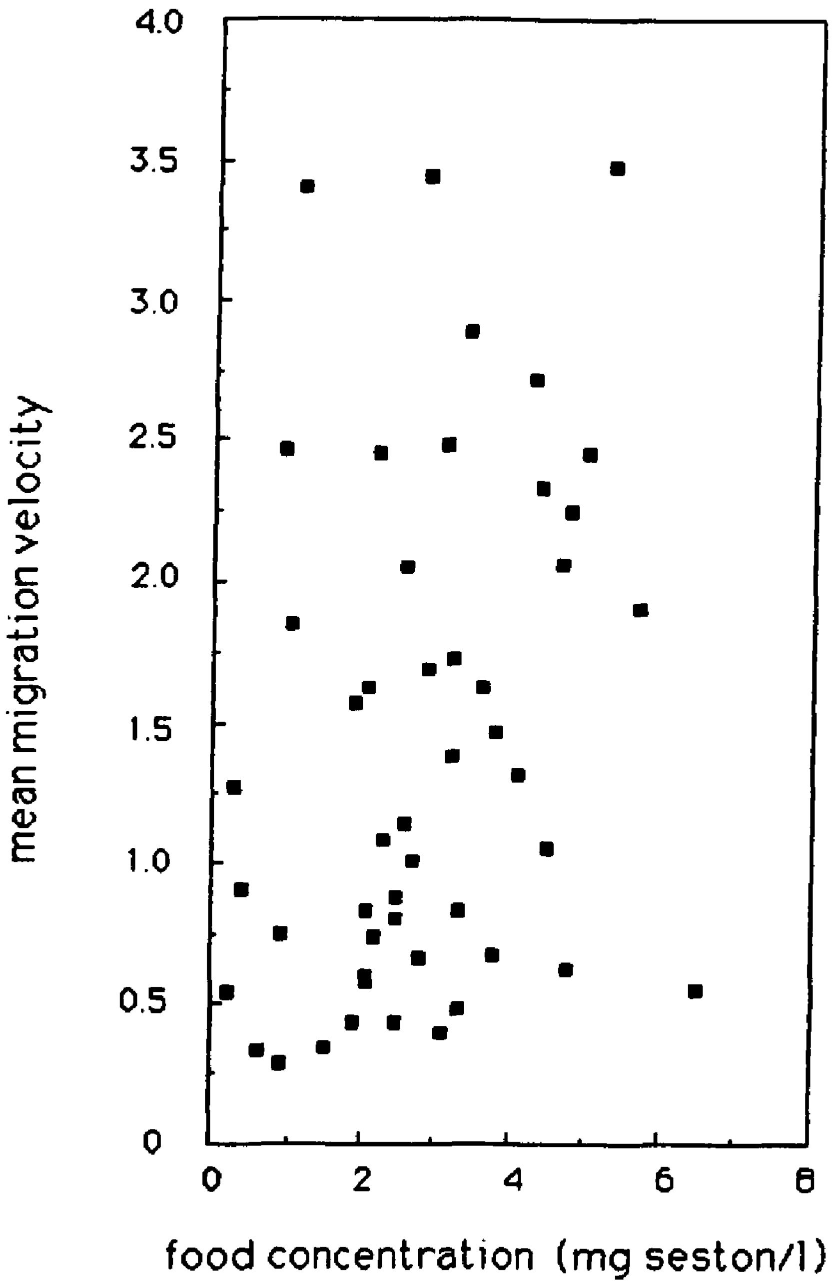


Figure 26. Comparison of the mean migration velocity (cm min^{-1}) of the Daphnia pulex population Q50 with food concentration (mg l^{-1}), for those populations not exposed to a fish.

populations exposed to a fish (Figures 23, 24, 25). The mean velocities of the migrations were also not significantly correlated with the mean stimulus during the migration for populations exposed to the presence of a fish ($p>0.10$).

Influence of Food Concentration and a Fish on Proximal Regulation of Evening Vertical Migrations

The Effect of Food Concentration and a Fish on Amplitude and Pre-Migration Depth

Amplitude. Food concentration had little influence on the amplitude of migration when the populations were not exposed to a fish ($r^2 = 12.7\%$, $p>0.10$). The addition and removal of a fish did not improve the relationship between food concentration and amplitude ($r^2 = 25.4\%$, $p>0.10$).

Population depths prior to migration limit the maximum amplitude of migration in any system. In addition, the pre-migration depths for a population Q75 are deeper than those for the Q50 and Q25. Therefore the relationship between amplitude and pre-migration depth may change with the depth statistic used to represent the population. In this study, amplitude was significantly positively correlated with pre-migration depth for populations not exposed to a fish (Table 5). The choice of population quartiles had no effect on the slopes of the regressions between amplitude and pre-migration depth (Table 5), although the individuals in a population did not move as a cohesive unit.

Pre-migration depth. The pre-migration depths of the lab population Q50 were significantly correlated with food concentration, only when the populations had been exposed to a fish (Table 6; Figure 27). The addition of fish to the columns contributed significantly to this regression (Table 6); however, the subsequent removal of the fish did not. There was no signifcant interaction between food and the presence of a fish (F<1). After fish removal, populations respond similarly to populations not exposed to fish.

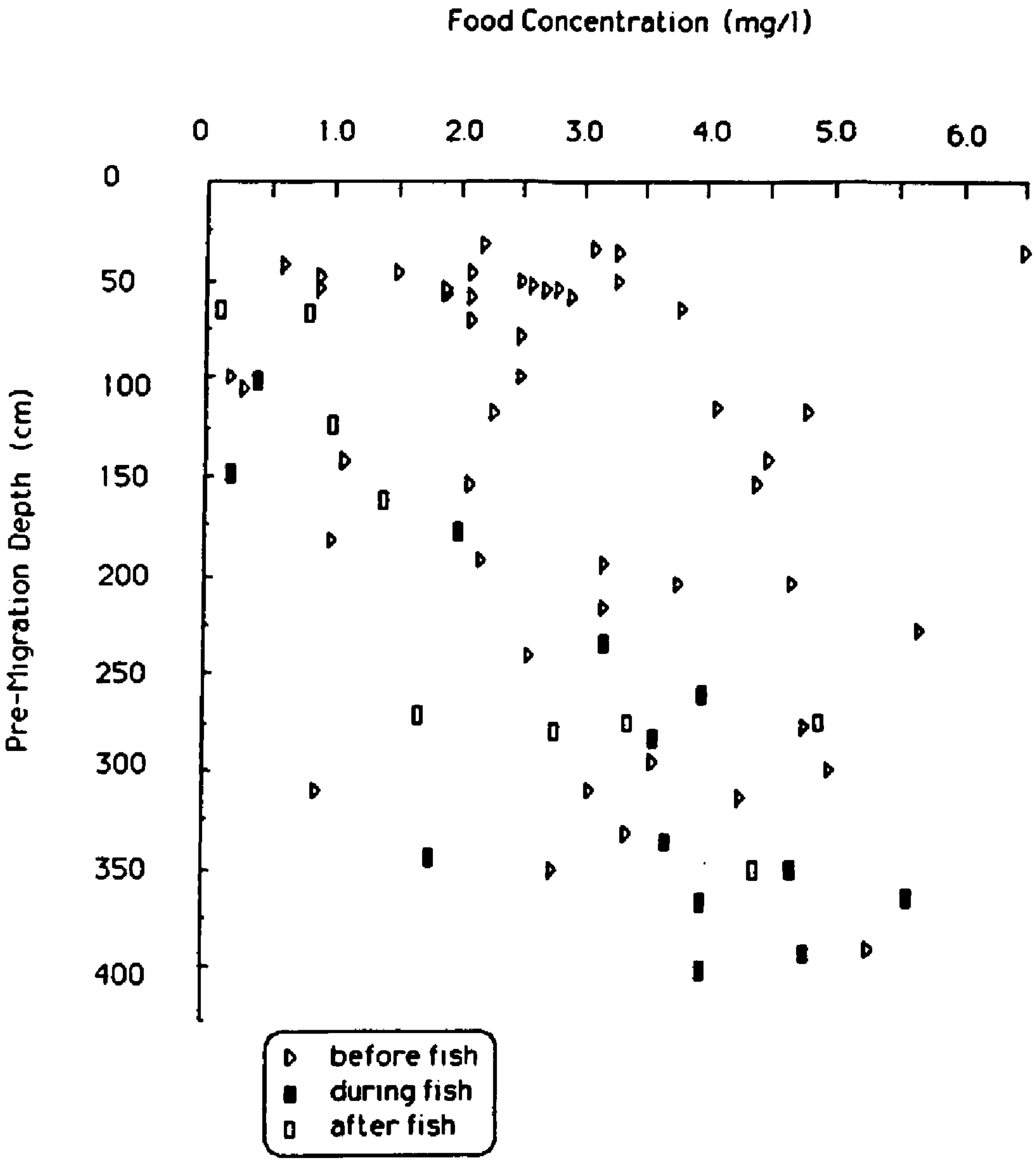


Figure 27. Comparison of the pre-migration depth (cm) of the *Daphnia pulex* population Q50's for differing food concentrations (mgl^{-1}) before, during and after the evenings a fish was present in the column.

regressions

Q25 $\ln(y) = -1.24 + 1.20 \ln(x)$, $r^2 = 0.895$

Q50 $\ln(y) = -1.03 + 1.13 \ln(x)$, $r^2 = 0.815$

Q75 $\ln(y) = -1.47 + 1.17 \ln(x)$, $r^2 = 0.821$

quartiles compared	**slopes of the regressions**	**t**	**df**	**p**
Q25 and Q50	Q25 1.20 Q50 1.13	0.703	91	$0.50>p>0.20$
Q75 and Q50	Q75 1.17 Q50 1.13	0.359	95	$p>0.50$
Q25 and Q75	Q25 1.20 Q75 1.17	0.308	92	$p>0.50$

Table 5. Comparison of the slopes of the regressions between amplitude and pre-migration depths for the three quartiles. y = amplitude (cm), x = pre-migration depth (cm).

In March, April, May, and November, the pre-migration depths of the population Q50 moved downward sharply during the day or evening after the fish had been introduced into the column (Figure 28). On each of the evenings after the fish had been removed, the pre-migration depth rose and on the subsequent evenings the pre-migration depths increased or decreased in the same direction as in the control column (Figure 28). This rebound of the pre-migration depth upon removal of the fish occurred even though the fish had been present through the migrations on the previous evenings, less than 24 hours beforehand. The short response time suggests that the mechanisms regulating the migration of zooplankton populations exposed to a fish include a sensory recognition of the predator's presence.

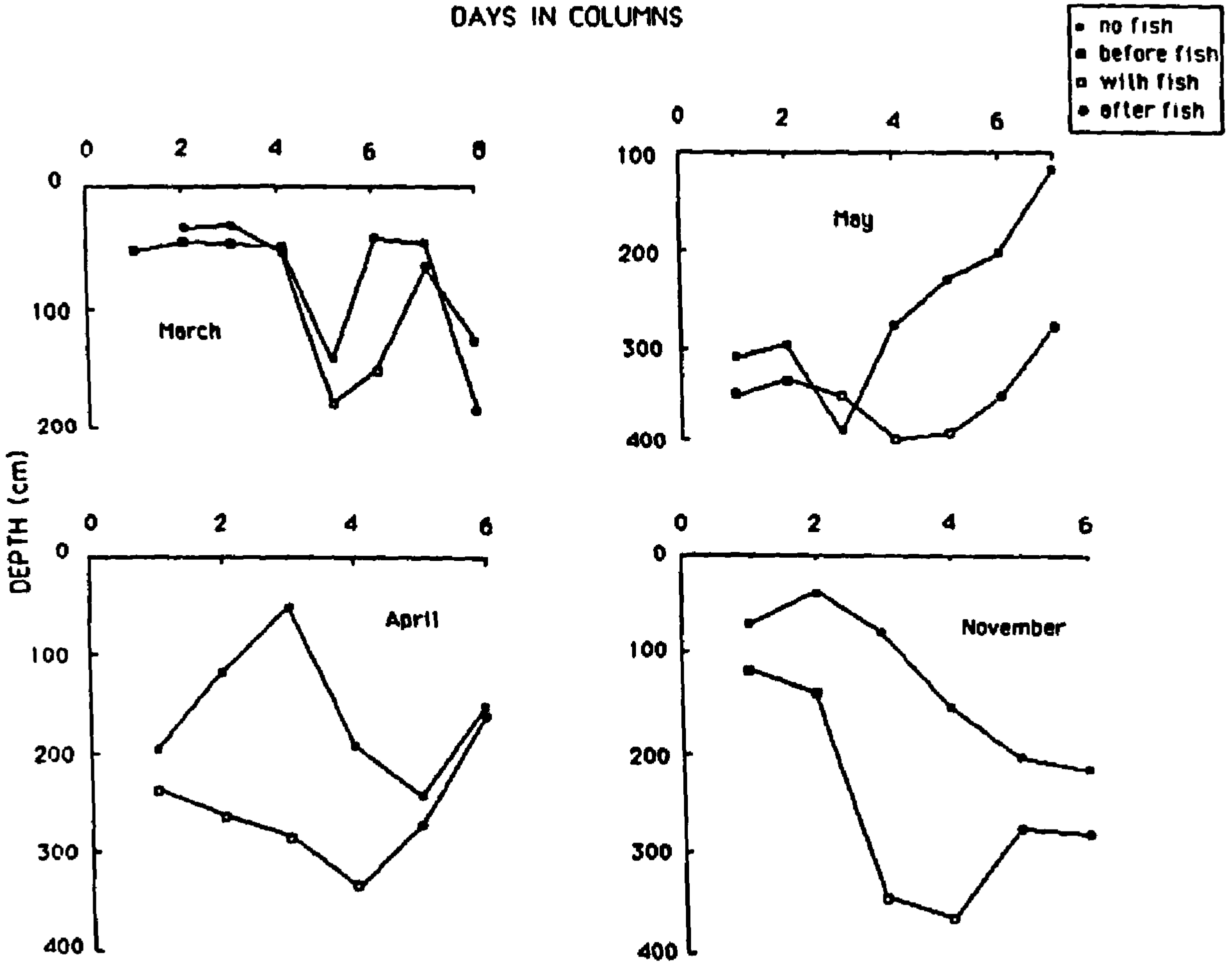


Figure 28. Premigration depths (cm) of the population Q50's for each of the days of the experiments.

regressions

$y_1 = 129 + 8.4\ x + 5.6\ z_1 - 44.3\ z_2 + 39.7\ xz_1 + 45.8\ xz_2,\ r^2 = 45.8\%$

$y_2 = 71.9 + 24.2\ x,\ r^2 = 10.4\%$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	5	263939	52788	6.59	$p<0.001$
error	28	224424	8015		
total	33	488364			

treatment	**df**	**f**	
food conc.	1	19.85	$p<0.001$
with fish	1	6.55	$0.05>p>0.02$
after fish	1	3.19	$0.20>p>0.10$
with fish x food	1	<1	--
after fish x food	1	1.95	$p>0.50$

Table 6. Analysis of variance for the regression between the depth of the population Q50 prior to migration (cm) and food concentration (mg l^{-1}), for populations exposed to a fish (y_1) and for populations not exposed to a fish (y_2). (y = depth of Q50 prior to migration, cm; x = food concentration, mgl^{-1}; z_1 = fish present; z_2 = fish removed).

Daphnia populations not exposed to a fish increased in numbers throughout the experiments, yet there was no significant correlation between either the number of migrating adults or the total number of individuals and the pre-migration depths ($r^2<0.10$, 48 df), indicating that neither crowding nor grazing pressure influenced the pre-migration depths.

For populations exposed to a fish, pre-migration depths were significantly correlated with the total number of adults and juveniles (Tables 7), and with the number of migrating adult _Daphnia_ (Table 8). In both cases the pre-migration depths were shallower as the number of _Daphnia_ increased. Pre-migration depths were also shallower when food concentrations decreased (Table 6), suggesting that increased grazing

regression

$y = 218 - 0.437\ x + 183\ z_1 + 167\ z_2 - 0.201xz_1 - 0.411xz_2,\ r^2 = 47.7\%$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	5	274600	54920	6.95	$p<0.001$
error	27	213330	7901		
total	32	487929			

treatment	**df**	**f**	
total individuals	1	17.74	$p<0.001$
with fish	1	10.74	$0.01>p>0.005$
after fish	1	4.30	$0.10>p>0.05$
inds x with fish	1	<1	--
inds x after fish	1	1.15	--

Table 7. Analysis of variance for the regression between the pre-migration depth of the population Q50 (cm) and the total number of individuals in the columns, for those columns which received a fish. (y = depth of the population Q50 prior to migration; x = mean number of all *Daphnia* counted in the columns each evening; z_1 = fish present; z_2 = fish removed).

regression

$y = -31.8 + 4.91\ x + 384\ z_1 + 376\ z_2 - 6.5\ z_1x - 6.91\ z_2x$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	5	276176	55235	7.29	$p<0.001$
error	28	212187	7578		
total	33	488364			

treatment	**df**	**f**	
number migrating adults	1	10.78	$0.005>p>0.002$
with fish	1	8.82	$0.02>p>0.01$
after fish	1	5.80	$0.05>p>0.02$
no. migrating X with fish	1	<1	--
no. migrating X after fish	1	7.14	$0.05>p>0.02$

Table 8. Analysis of variance for the regression between the pre-migration depth of the population Q50 (cm) and the number of migrating adults in the columns, for those columns which received a fish. (y = depth of Q50 prior to migration; x = mean number of adults migrating each evening; z_1 = fish present; z_2 = fish removed).

pressure may have led to the decreased food concentrations. It is probable that there was also a decline in food quality as *Daphnia* reingest excreted particulates as they filter. The only significant interaction between fish and population densities, was for the regression with numbers of migrating adults when the fish had been removed from the column (Table 8).

These observations are consistent with the proposals of several investigators (Huntley and Brooks 1982, Dagg 1985, Johnsen and Jakobsen 1987) that low food concentrations are associated with shallower premigration depths.

On two-thirds of the evenings with a fish present, at least 25% of the *Daphnia* population migrated into the portion of the column containing the fish (above 60 cm). No predation by the fish was directly observed, since the fish was attracted to the red observation light. However, the decrease in the number of individual daphnids counted in columns with fish (Figure 29 a,c,e,h,j) implied predation. This continued exposure to the fish did not result in a further drop in the pre-migration depths on the following day (Figure 28). Since the *Daphnia* population continued migrating into the portion of the column containing the fish, I propose that the initiation of the migration must show a delay and/or the duration of the migration be extended sufficiently that the *Daphnia* reach the proximity of the fish after dark, for the migration to effectively reduce loss by predation. which the *Daphnia* avoid being eaten by the fish.

The Effect of a Fish on the Timing of Migrations

The avoidance of visual predators could be realized either by delaying the evening migration initiation (EMI), or by increasing the

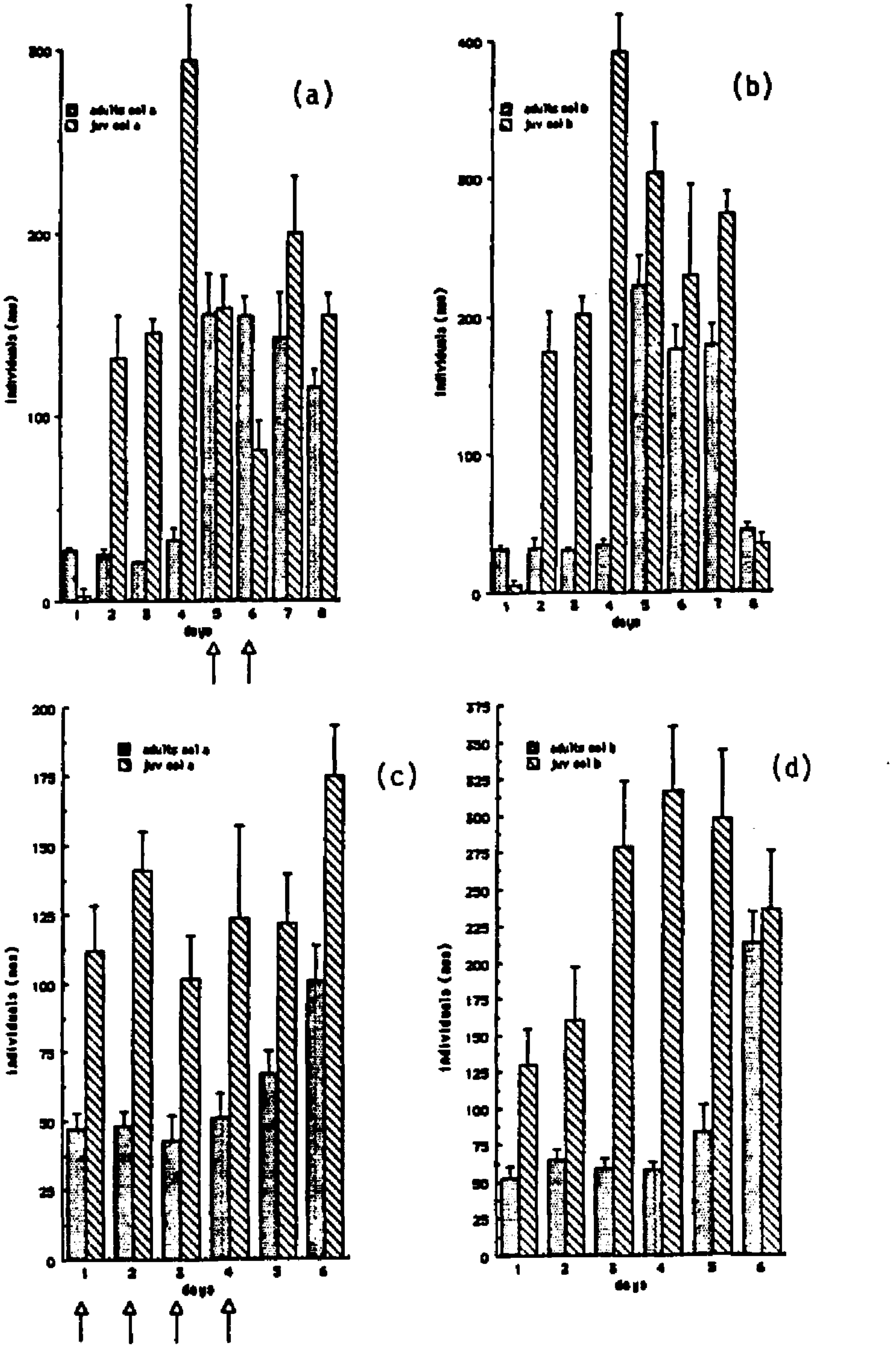


Figure 29. Comparison of the mean numbers, ± one SE, counted in each day's profiles, for juveniles and adults in each column. (a-j) March, April, May, August, and November, columns A and B for each month. Arrows mark days with fish

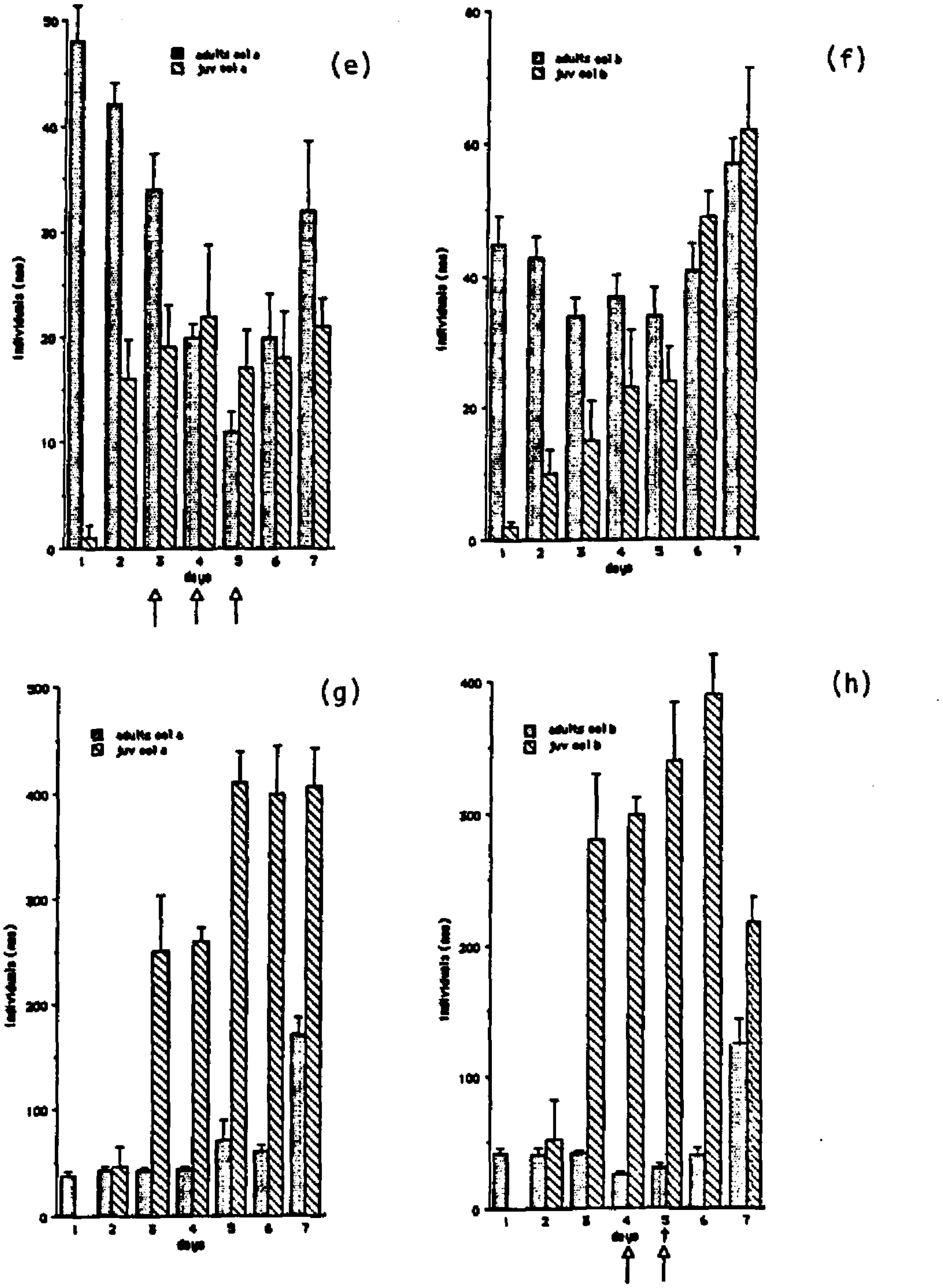

(e)
adults col a
juv col a
individuals (no)
50
40
30
20
10
0
1
2
3
4
5
6
7
days
(f)
adults col b
juv col b
individuals (no)
80
60
40
20
0
1
2
3
4
5
6
7
days
(g)
adults col a
juv col a
individuals (no)
500
400
300
200
100
0
1
2
3
4
5
6
7
days
(h)
adults col b
juv col b
individuals (no)
400
300
200
100
0
1
2
3
4
5
6
7
days

Figure 29 (e-h)

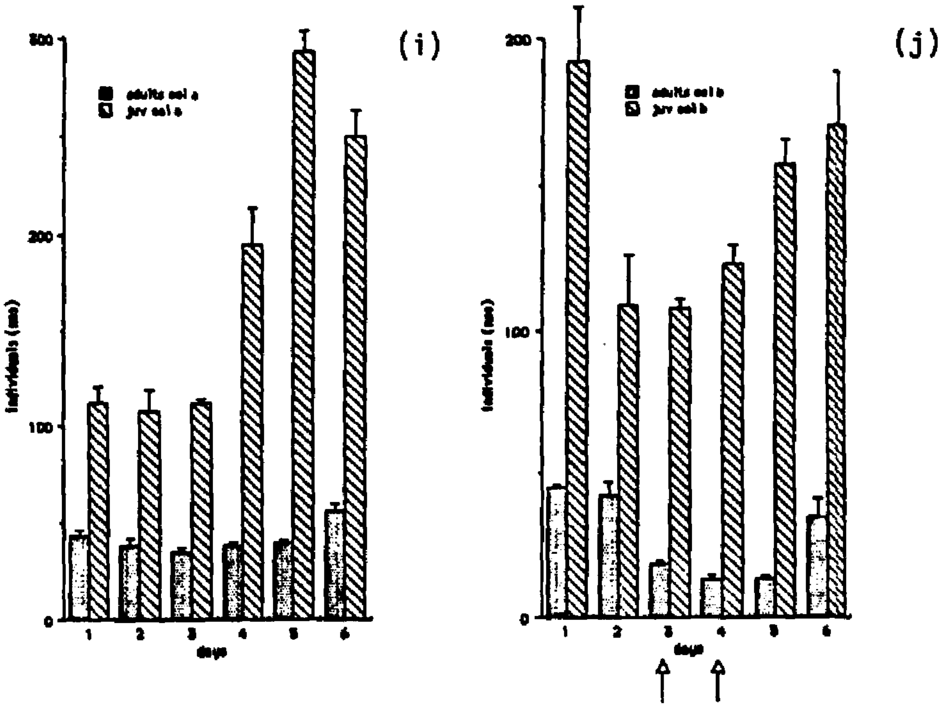

(i)
300
200
100
0
individuals (no)
adults col a
juv col a
1
2
3
4
5
6
days
(j)
200
100
0
individuals (no)
adults col b
juv col b
1
2
3
4
5
6
days

Figure 29 (i-j)

duration of the migration, such that the Daphnia arrive at the surface after dark. Zooplankton which delay their evening migration, should be less subject to visual predation because of the reduced light intensity later in the evening (Confer et.al. 1978). Therefore Daphnia should migrate later on those evenings when they have been exposed to a fish.

The mean difference in the time of EMI from the time of Ringelberg's stimulus-threshold (RST) was, however, not significantly related to the presence of a fish ($F = 3.89$, $p>0.05$).

Without a delay in the EMI, an increase in the duration of the migrations could still have resulted in the Daphnia reaching the proximity of the fish when the light intensity and therefore the visibility was less. There was no significant ($0.50>p>0.20$) trend for the migration to be longer in the presence of a fish, nor once the fish was removed. The Daphnia did not respond to the presence of a fish with significant changes in the duration of the migrations.

Influence of Food Concentration and a Fish on Migration Velocity

Neither the velocity nor the duration of the observed migrations was significantly correlated with the food concentration, with or without the addition of a fish ($r^2 < 8.0\%$). This suggests that although limited food supplies quickly influence the chemical composition of the body (Duncan et.al. 1985), and the feeding rates (Burns and Rigler 1967; Haney 1985) of Daphnia, the food supply does not regulate the velocity of vertical migrations. Nor, as was seen for pre-migration depths, does the presence of a fish interact with food concentrations to regulate migration velocity.

Influence of Recruitment on Pre-Migration Depths

The recruitment of juveniles into the adult population offers an alternative explanation for the rebound in pre-migration depths once the fish was removed from the columns. However, individuals counted as adults had similar histories in their exposure to a fish. Broods of young released early in the experiment were large enough by the fourth or fifth day to be counted as adults, as seen from the numbers of individuals in populations not exposed to a fish (Figure 29 b,d,f,g,i). The fish preyed primarily on the juvenile Daphnia in March, April, August and November, ate both juveniles and adults in May, and primarily adults in March (Figure 29). Juveniles as well as adults were observed to migrate (Figure 30). Thus recruits did not simply replace the original population. The adult Daphnia population showed a reversible avoidance of the fish even though much of the predation fell upon the juveniles.

Amplitude and Pre-migration Depths of Juveniles

There was a significant difference due to juveniles and adults in the intercept of the relationship between amplitude and pre-migration depth of the population Q50's for populations not exposed to a fish, and no significant differences in the slope (Table 9). The juveniles started their migrations from significantly shallower pre-migration depths than the adults (Table 9), but migrated with the same amplitude as the adults at the same pre-migration depths.

Timing of Migrations by Juveniles

Evening migration initiation. The relationship between the time of the evening migration initiation (EMI) and Ringelberg's Stimulus-Threshold (RST) was not significantly different for juveniles as compared to adults, either in slope or intercept (Table 10). The juveniles responded to the stimulus in the same way as the adults.

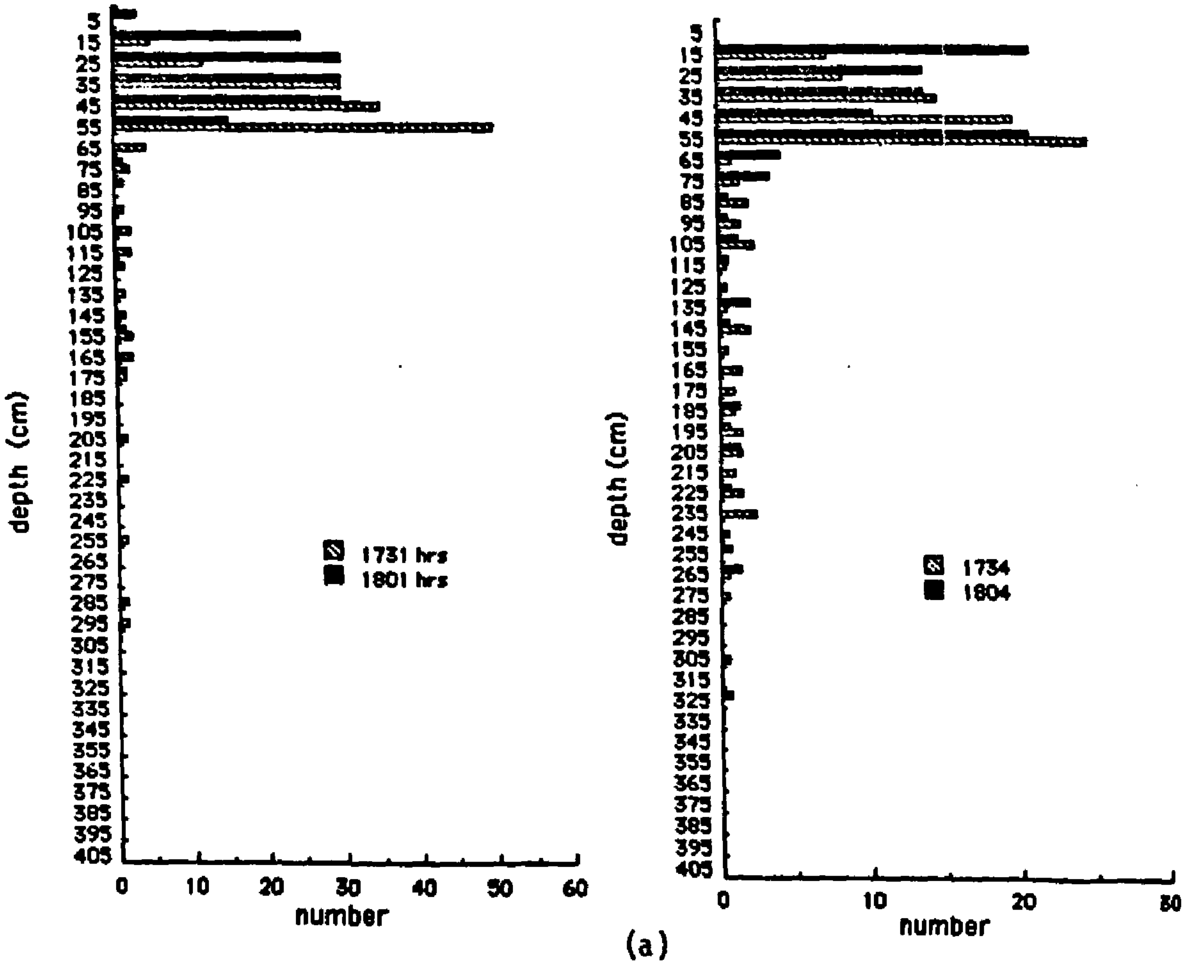


Figure 30. Migration of juvenile *Daphnia pulex* shown in early and late profiles for each column on three evenings. (a) 6 March, (b) 9 August, (c) 11 November.

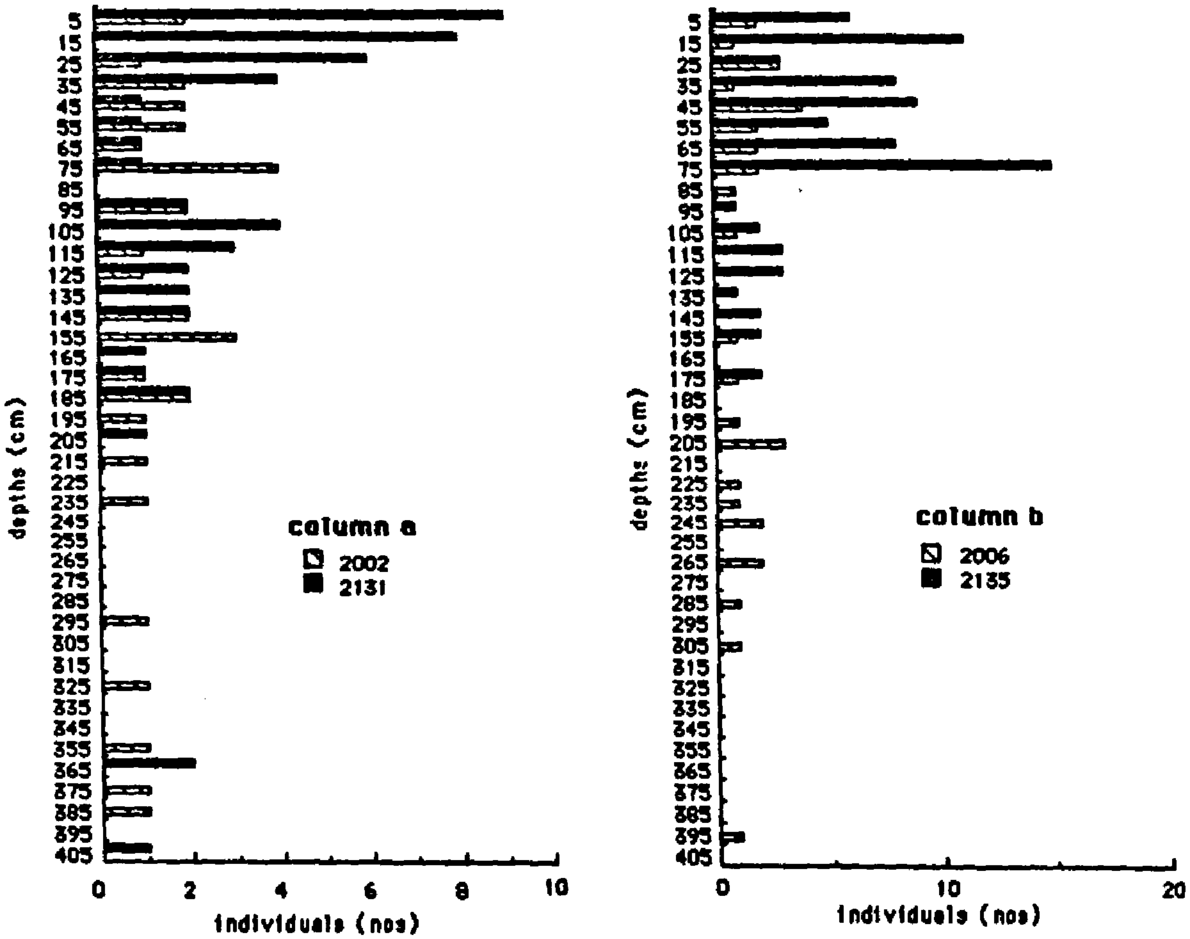


Figure 30(b) 9 August

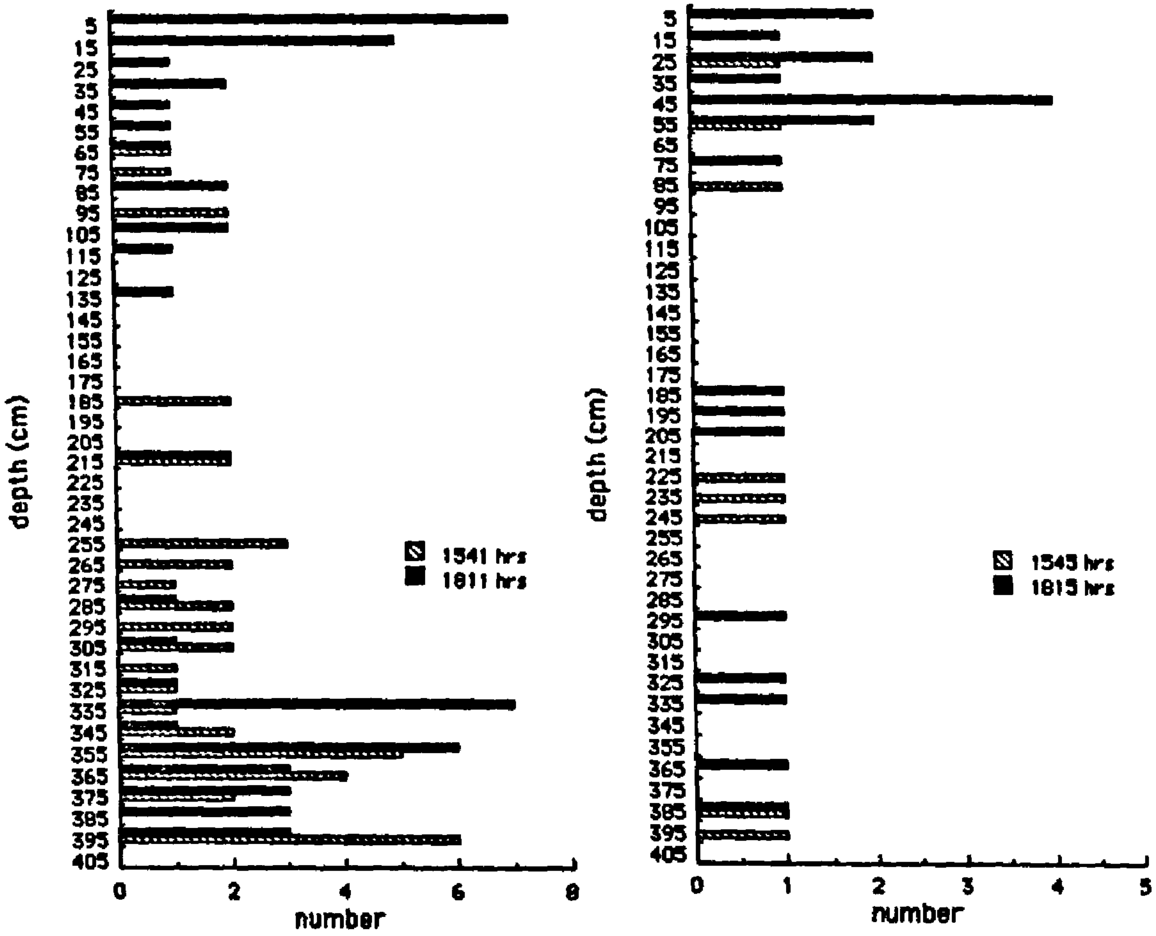


Figure 30(c) 11 November

regression

$\ln(y) = -0.682 + 1.031\ln(x) - 0.350z + 1.06\,xz,\ r^2 = 74.4\%$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	3	51.452	17.151	76.75	$p<0.001$
error	75	16.760	0.223		
total	78	68.212			

treatment	**df**	**f**	
pre-migration depth	1	212.68	$p<0.001$
adults or juveniles	1	10.14	$0.005<p<0.002$
pre-mig. depth x age	1	1.78	$0.50>p>0.20$

Table 9. Analysis of variance for the regression between the amplitude (cm) and the pre-migration depth of the population Q50's (cm) with one indicator (z) for adults or juveniles, assigned -1 and 1 respectively. (y = amplitude of migration for the population Q50; x = pre-migration depth of the population Q50).

regression

$y = -1.26 + 1.07\,x - 0.315\,z + 0.0239\,xz,\ r^2 = 86.2\%$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	3	136.473	45.491	162.78	$p<0.001$
error	76	20.960	0.279		
total	79	157.433			

treatment	**df**	**f**	
time of RST	1	488.02	$p<0.001$
adults or juveniles	1	4.44	$0.10>p>0.05$
time of RST x age	1	<1	--

Table 10. Analysis of variance for the regression between the time of evening migration initiation for the population Q50 (hours) and the time of Ringelberg's stimulus threshold (hours) with one indicator variable (z) for adults or juveniles, assigned -1 and 1 respectively. (y = time of the evening migration initiation, x = time of Ringelberg's stimulus threshold).

Velocity. A paired-t test showed the mean velocity of the juvenile populations during the migrations to be significantly less than the velocity for adult populations ($t = 5.74$, $p<0.001$). The inclusion of juveniles in analysis of a *Daphnia* migration will reduce the estimated values of mean migration velocities for the populations.

Field Studies of Evening Vertical Migrations

Control by Light

Ultra-violet radiation intensity. The penetration of ultra-violet light are hypothesized to control amplitudes of vertical migration by forcing zooplankton to avoid shallower depths during the day (Hairston 1976; Ringelberg, *et.al.* 1984). The field data collected in this study indicate a variable tolerance for ultra-violet radiation as well as a probable avoidance of it. In lakes with 1.9 mg chlorophyll a m^{-3}, lethal doses of UV-B radiation (290-315 nm) (Table 11) should penetrate to about 4.8 m as based on ten hours of daylight (Figure 2 in Ringelberg, *et.al.* 1984). Since the damage sustained from the radiation is cumulative (Damkaer, *et.al.* 1980), the lethal dose is expressed as Wcm^{-2} integrated over time, *i.e.*, $Wscm^{-2}$. The lakes considered in this study have autumnal chlorophyll a concentrations in the range 0.4 to 2.0 mg chlorophyll a m^{-3} (Table 12). In Upper Sawyer Pond more than 50% of the *Holopedium gibberum*, *Diaphanasoma brachyurum*, and *Diaptomus* spp. populations are above 4.8 m (Figure 31). The Lower Sawyer Pond populations were centered within 2 m of this LD50 depth (Figure 32), whereas most of the populations in Stonehouse Pond had pre-migration depths for the population Q50 of 1.5 m or less (Figure 33). And in Barbadoes Pond (Figure 34), where day samples were taken at 1450 hours in bright sun, the population Q50's ranged from 4.86 m (*Diaphanasoma brachyurum*) to 1.00 m (small cyclopoids).

The New Hampshire mountain lakes have lightly colored water, while Stonehouse Pond is stained, and Barbadoes Pond is relatively productive (pers. observ.). In the fall, zooplankton above 2 m depth appear to be in danger of solar damage within a month's time (Table 13). At summer

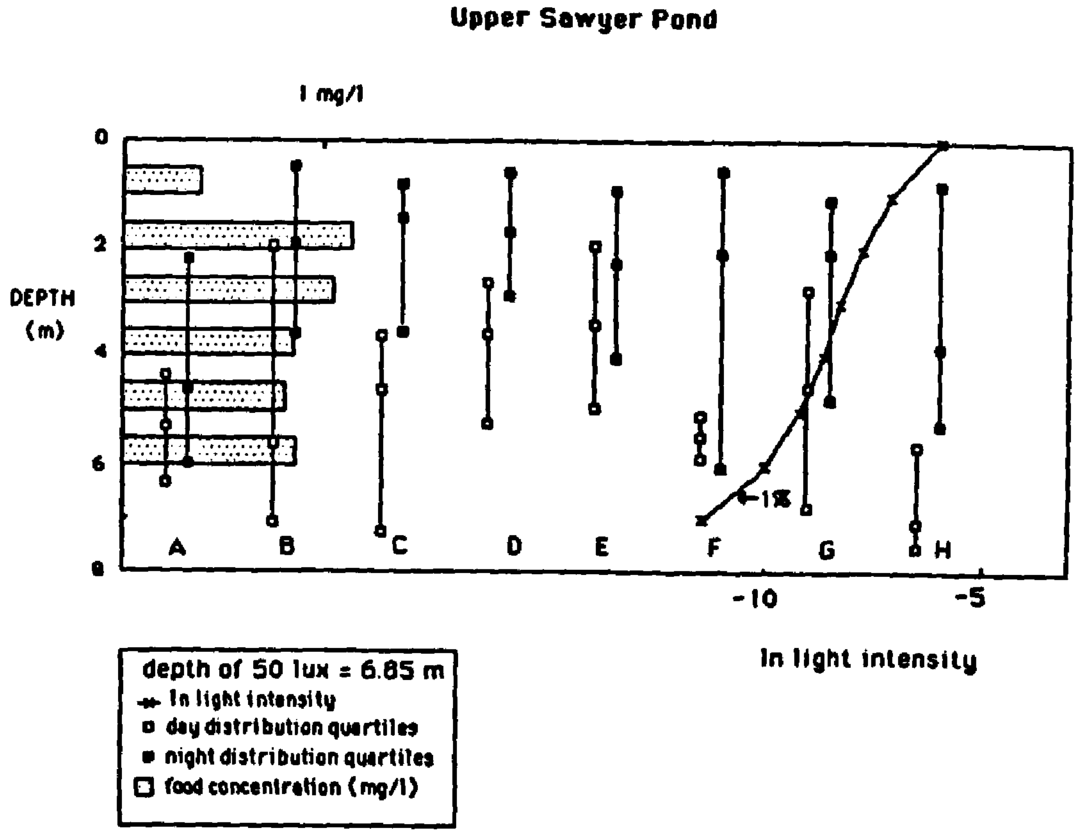


Figure 31. Day and night population quartiles for the zooplankton in Upper Sawyer Pond on 13 Sept 1986 compared with distribution of food concentration (mg dry weight of seston ≤30 um diameter l^{-1}), and the profile of light intensity (Wcm^{-2}) during the day.
A *Daphnia catawba*, B *Bosmina* sp., C *Holopedium gibberum*, D *Diaphanasoma brachyurum*, E *Diaptomus minutus*, F small cyclopoids, G large cyclopoids, and H *Chaoborus punctipennis*.

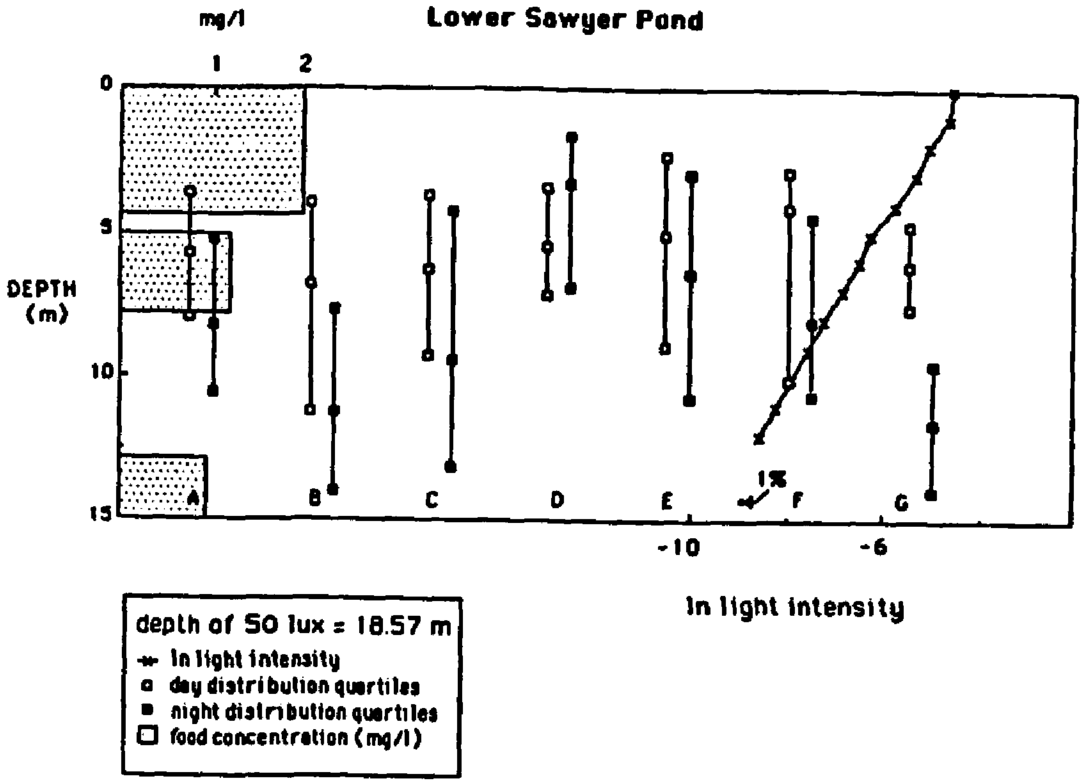


Figure 32. Day and night population quartiles for the zooplankton in Lower Sawyer Pond on 10 October 1986 compared with the distribution of food concentration (mg dry weight of seston ≤ 30 um diameter l^{-1}), and the profile of light (Wcm^{-2}) intensity during the day. A *Daphnia galeata-mendotae*, B *Bosmina* sp., C *Holopedium gibberum*, D *Diaphanasoma brachyurum*, E *Diaptomus minutus*, F small cyclopoids, and G large cyclopoids.

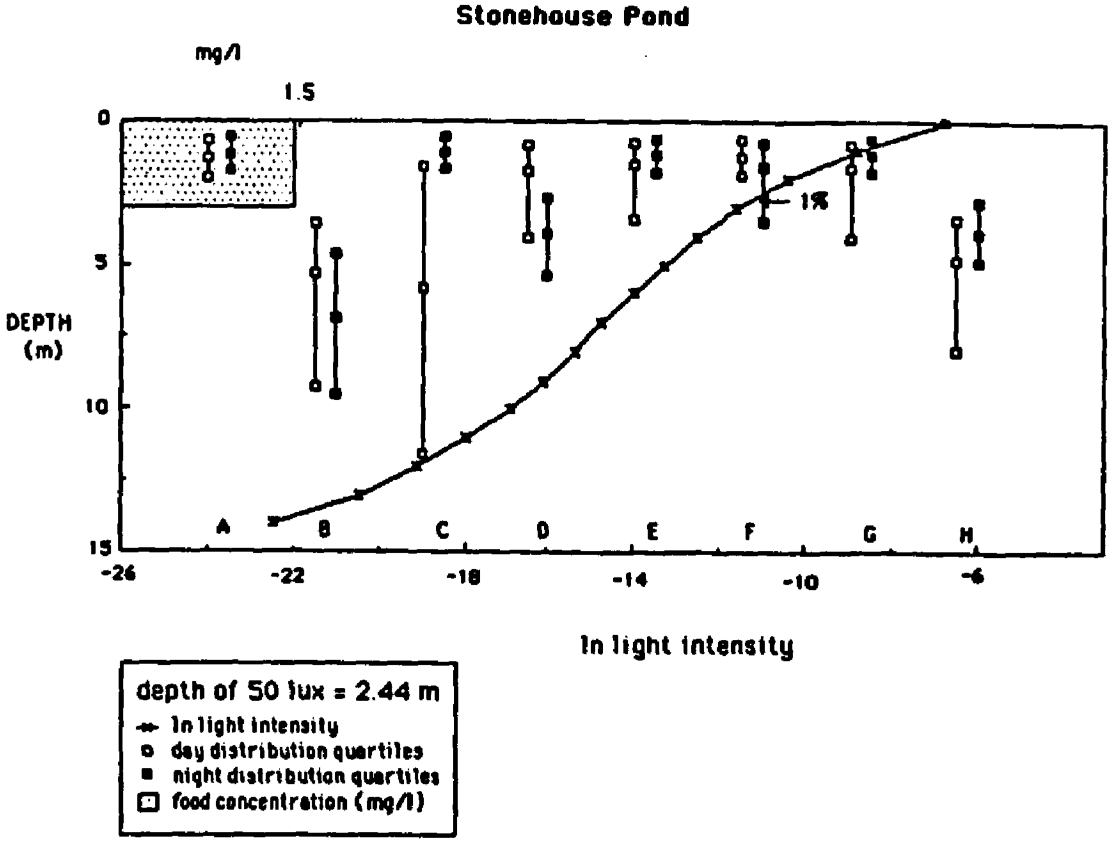


Figure 33. Day and night population quartiles for the zooplankton in Stonehouse Pond on 13 July 1983 compared with the food concentration (mg dry weight of seston $\leq$30 um diameter l^{-1}), and the profile of light intensity during the day (ln Wcm^{-2}). A *Daphnia catawba*, B *Daphnia ambigua*, C *Bosmina* sp., D *Holopedium gibberum*, E *Diaphanasoma brachyurum*, F *Diaptomus* sp., G cyclopoids, H *Chaoborus punctipennis*.

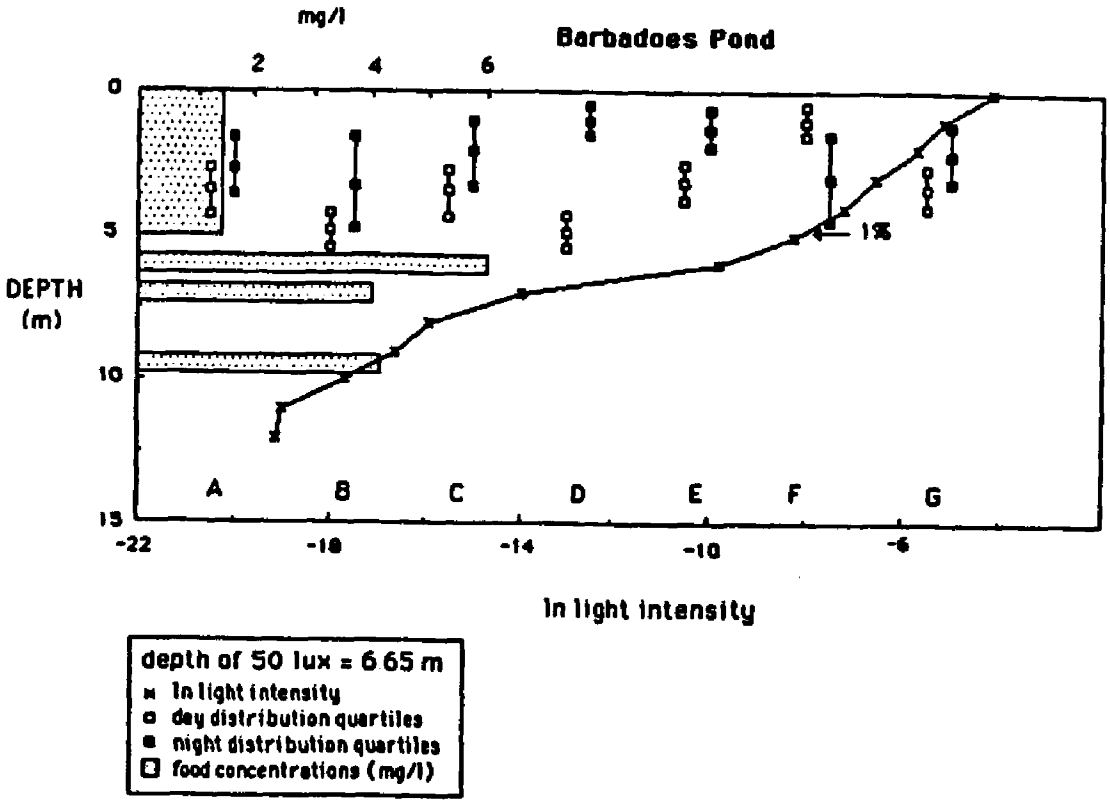


Figure 34. Day and night population quartiles for the zooplankton in Barbadoes Pond on 29 August 1986 compared with the distribution of food concentration (mg dry weight of seston ≤30 um diameter l^{-1}), and the profile of light intensity (Wcm^{-2}) during the day.
A *Daphnia catawba*, B *Daphnia ambigua*, C *Bosmina* sp., D *Diaphanasoma brachyurum*, E *Diaptomus* sp., F small cyclopoids, G large cyclopoids.

zooplankton	Ws cm^{-2}	reference
Daphnia longispina	0.49	Siebeck 1978 LD50 (290-350 nm)
Daphnia pulex	0.77	
clear *Acanthodiaptomus*	0.45	Ringelberg, *et.al.* 1984 LD50 (290-315 nm)
red *Acanthodiaptomus*	0.30	
shrimp larvae	0.36	Damkaer, *et.al.* 1980 minimum effective dose for mortality. (290-315 nm)
crab zoea	0.45	
crab megalops	2.6	
euphausids	0.45	

Table 11. Lethal dosages of UV-B radiation for various zooplankton.

lake	extinction coefficients	fall chlorophyll a epilimnion (mg m^{-3})
Upper Sawyer Pond	-0.679	0.62
Lower Sawyer Pond	-0.342	0.67
Stonehouse Pond	-0.955	---
Barbadoes Pond	-1.429	1.94

Table 12. Fall chlorophyll a concentrations in the Sawyer Ponds and Barbadoes Pond from September, and extinction coefficients for the water column (this study) by regression, $p<0.001$.

surface intensities of ultra-violet radiation, these same populations would suffer a 50% mortality with 8 - 12 days' exposure to UV-B radiation at 0 - 2 m (Table 13). This supports the hypothesis that zooplankton may migrate to avoid damaging radiation (Hairston 1976). In addition the above observations would explain the seasonality sometimes noted in the amplitudes of migration (Stich and Lampert 1981).

Upper Sawyer Pond

	pre-migration depth of Q50 (m)	days to LD50	
		fall	summer
Diaptomus	3.42	32	8
Diaphanasoma	3.59	34	9
lg. cyclopoids	4.56	51	13
Holopedium	4.59	51	13
Daphnia	5.29	68	18
sm. cyclopoids	5.46	72	19
Bosmina	5.60	77	20

Lower Sawyer Pond

	pre-migration depth of Q50 (m)	days to LD50	
		fall	summer
sm. cyclopoids	4.05	41	11
Diaptomus	4.99	60	16
Diaphanasoma	5.41	71	19
Daphnia	5.74	81	21
lg. cyclopoids	6.14	95	25
Holopedium	6.25	99	26
Bosmina	6.77	122	32

Stonehouse Pond

	pre-migration depth of Q50 (m)	days to LD50	
		fall	summer
Diaptomus	1.23	27	7
Daphnia catawba	1.32	29	8
Diaphanasoma	1.48	34	9
cyclopoids	1.65	40	10
Holopedium	1.68	41	11
Chaoborus	4.84	849	222
Daphnia ambigua	5.32	1346	352
Bosmina	5.83	2197	574

Barbadoes Pond

	pre-migration depth of Q50 (m)	days to LD50	
		fall	summer
sm. cyclopoids	1.00	21	6
Diaptomus	3.11	161	42
lg. cyclopoids	3.32	197	52
Daphnia catawba	3.40	213	56
Bosmina	3.41	215	56
Daphnia ambigua	4.82	833	218
Diaphanasoma	4.86	866	226

Table 13. Days to LD50 from ultra-violet radiation damage at the depth of the population Q50 prior to migration. Based on incident ultra-violet radiation for fall and summer in Manchester WA (Damkaer et.al. 1984), k values of 0.40 m^{-1} in the Sawyer Ponds, and 0.96 m^{-1} in Stonehouse and Barbadoes Ponds, and a ten hour day. Siebeck's (1978) value of 0.49 $wscm^{-2}$ LD50 for *Daphnia longispina* was used as an LD50 estimate.

The depths of the population Q50's prior to migration (Table 13) show that the same species are often found in similar positions relative to one another in the water column in all four lakes. This supports the concept of a variable tolerance for ultra-violet wavelengths by the same species found at different depths or in different bodies of water (Siebeck 1981). It is also possible that these populations are capable of photoreactivation, a physiological repair of UV-B damage correlating with exposure to longer wavelengths of radiation (Kalthoff 1975; Siebeck 1978). Those populations found deeper than potentially damaging UV-B intensities may depend more on vertical migrations as a means of avoiding this damage.

Water transparency. The migrations of the zooplankton populations examined showed a significant correlation between pre-migration depth of the population Q50's and the water transparency (Table 14). The zooplankton populations were deeper in more transparent waters.

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regression

$y = 6.05 - 2.298\,x,\ r^2 = 0.293$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	1	23.573	23.573	10.819	$0.01>p>0.001$
error	26	56.651	2.179		
total	27	80.224			

Table 14. Analysis of variance for the regression between pre-migration depths of the population Q50's for all of the migrations observed in the field (Table 11) and the transparency of the lake water (Table 12). (y = pre-migration depth of the population Q50's; x = the water transparency as k m^{-1}).

This suggests that zooplankton avoid high light intensities, and possibly ultra-violet radiation damage, or detection by visual predators.

Control by Food

Low food concentrations are hypothesized to reduce migrations to very small amplitudes (Huntley and Brooks 1982; Dagg 1985; Johnsen and Jakobsen 1987). My field data are not consistent with this hypothesis. The least amplitudes of migration were in Stonehouse Pond where *Daphnia catawba*, *Diaphanasoma brachyurum*, and *Diaptomus* spp. did not migrate, and only *Bosmina* spp. moved further than 2.5 m (Figure 33). Stonehouse Pond had, however, 1.75 times the food concentration found in Upper Sawyer Pond, where all of the populations migrated, and of these, *Bosmina* spp., *Holopedium gibberum*, and small cyclopoids moved further than 2.5 m (Figure 31). The populations in Barbadoes Pond generally migrated a shorter distance than those in Upper Sawyer Pond, and these two lakes were the richest and poorest in seston of edible size to zooplankton grazers, respectively.

Pijanowska and Dawidowicz (1987) proposed that although the food structure of the water column and predation pressure work together to determine whether a population will migrate, a homogeneous food environment precludes migration. Gliwicz and Pijanowska (1988) have suggested a model for testing these hypotheses. The lakes examined in the current study vary in food concentration, and all contain with brook trout. Thus these lakes correspond to the lowland Polish lakes examined by Gliwicz and Pijanowska (1988). Their model assumes that the population pre-migration depth is proportional to the water transparency, as was shown for the New Hampshire lakes (Table 14).

In the Sawyer Ponds and Barbadoes Pond, the tendency to migrate was significantly correlated with the proportion of the difference between epilimnetic and hypolimnetic food concentrations to hypolimnetic food concentration (F) (Table 15).

The Gliwicz-Pijanowska model also predicts that when the ratio of food concentration in the epilimnion to that below the day depth of the populations is less than two, no migration should occur. Although there was some food stratification, this value was less than two for the Sawyer Ponds and Barbadoes Pond. Migrations did take place, however. In Upper Sawyer Pond there was a slight increase in food

	Tendency to Migrate		
	Upper Sawyer	**Lower Sawyer**	**Barbadoes**
zooplankton			
Daphnia galeata-mendotae		-0.63	---
Daphnia ambigua	---	---	0.35
Daphnia catawba	0.19	---	---
Bosmina	0.97	-0.92	-0.54
Holopedium	1.12	-0.73	---
Diaphanasoma	1.05	-0.45	-3.39
Diaptomus	0.69	-0.47	-0.64
F	1.30	0.61	-0.74

regression

$y = -0.64 + 0.86x,\ r^2 = 0.389$

analysis of variance

source	**df**	**ss**	**ms**	**f**	
regression	1	6.805	6.805	7.635	$0.05 > p > 0.02$
error	12	10.695	0.891		
total	13	17.500			

Table 15. Analysis of variance for the regression between the tendency to migrate and the food ratio (F). (y = the tendency to migrate, x = the food ratio (F); see field methods for definitions).

concentration above the pre-migration depths into which most of the populations migrated (Figure 31). In Barbadoes Pond the recorded concentration of edible size particulate was greatest below 6 m (Figure 34), but possibly there was a layer of higher food concentration above the animals into which they moved. Lower Sawyer populations move away from the higher food concentrations above them (Figure 32). The agreement between the results of the model in Polish and New Hampshire lakes, despite less stratified food and the use of seven species in the New Hampshire study, suggests that in nature food concentrations influence migrations more strongly than indicated by the laboratory data.

Phytoplankton Composition

Measurements of seston of edible size by either dry weight (this study) or by carbon analysis (Gliwicz and Pijanowska 1988) do not distinguish between inedible and edible phytoplankton, or between live and decaying cells. Dry weight may provide an approximation of food availability in a lake, but not necessarily its location.

Profiles of chlorophyll a concentration (Table 16) and an examination of the phytoplankton composition in the Sawyer Ponds and in Barbadoes Pond indicate that the phytoplankton composition may influence the direction of the migration. The chlorophyll a maximum in Lower Sawyer Pond in September was found from 8-12 m, the range of the metalimnion in both September and October (Figure 35). In addition, the gelatinous, less edible blue-green alga Aphanocapsa sp. dominated in the top 4 m of the water column, while the highly edible Cryptomonas sp. was dominant from 4-12 m. Thus in Lower Sawyer Pond the downward movements of the zooplankton populations probably took them away from

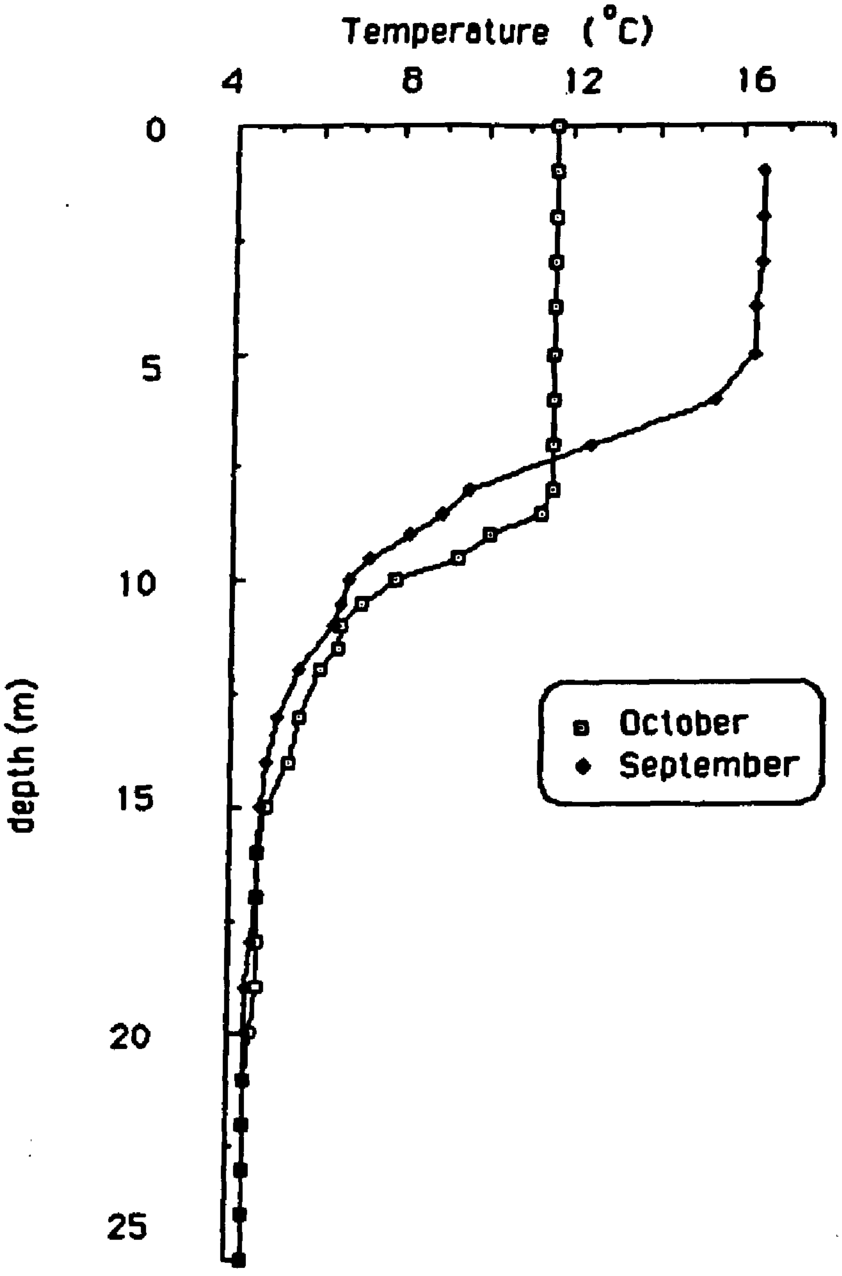


Figure 35. Temperature profiles (°C) from Lower Sawyer Pond on 13 September 1986, and 10 October 1986.

Chlorophyll a profiles

Upper Sawyer		Lower Sawyer		Barbadoes	
depth (m)	Chl a (mg m^{-3})	depth (m)	Chl a (mg m^{-3})	depth (m)	Chl a (mg m^{-3})
0	0.43	0-4	0.41	0.5	1.33
0-2	0.41	4-8	0.93	3.0	2.55
2-4	0.57	8-12	6.59	6	7.00
4-6	1.07	12-16	0.71	9	14.71
		16-20	3.88	12	13.57
		20-24	0.36		
		24-28	3.70		

Table 16. Profiles of chlorophyll a in Upper Sawyer and Lower Sawyer Ponds (September), and Barbadoes Pond (October). (Data from UNH Field Limnology Course, 1986).

an epilimnetic maximum of low quality particulates and into a layer of more edible food (Figure 32, Table 16). The chlorophyll a in Upper Sawyer was homogeneous above 4 m, and was primarily from the edible phytoplankters *Euglena* sp. (0-2 m), and *Gymnodinium* sp. (2-4 m). Therefore, both food concentration and the algal species present favored an upward movement in Upper Sawyer Pond.

In Barbadoes Pond the chlorophyll a rose steadily with depth and became very high in the hypolimnion (Table 16), where the green sulfur bacterium *Chlorobium* sp. dominated from 6-8 m. However, these bacteria were unavailable as food due to low oxygen concentrations (Figure 36). The temperature profile in Barbadoes Pond in 1986 (Figure 36), and a transmisometry profile and a flourescence profile from 1988 (Figure 37) show no distinct layers within the top 5 m. In the fall, 1986, there were distinct layers of algae in the upper 5 m, however, dominated by small highly edible species, *Cyclotella* sp. from 0-2 m, and *Cryptomonas*

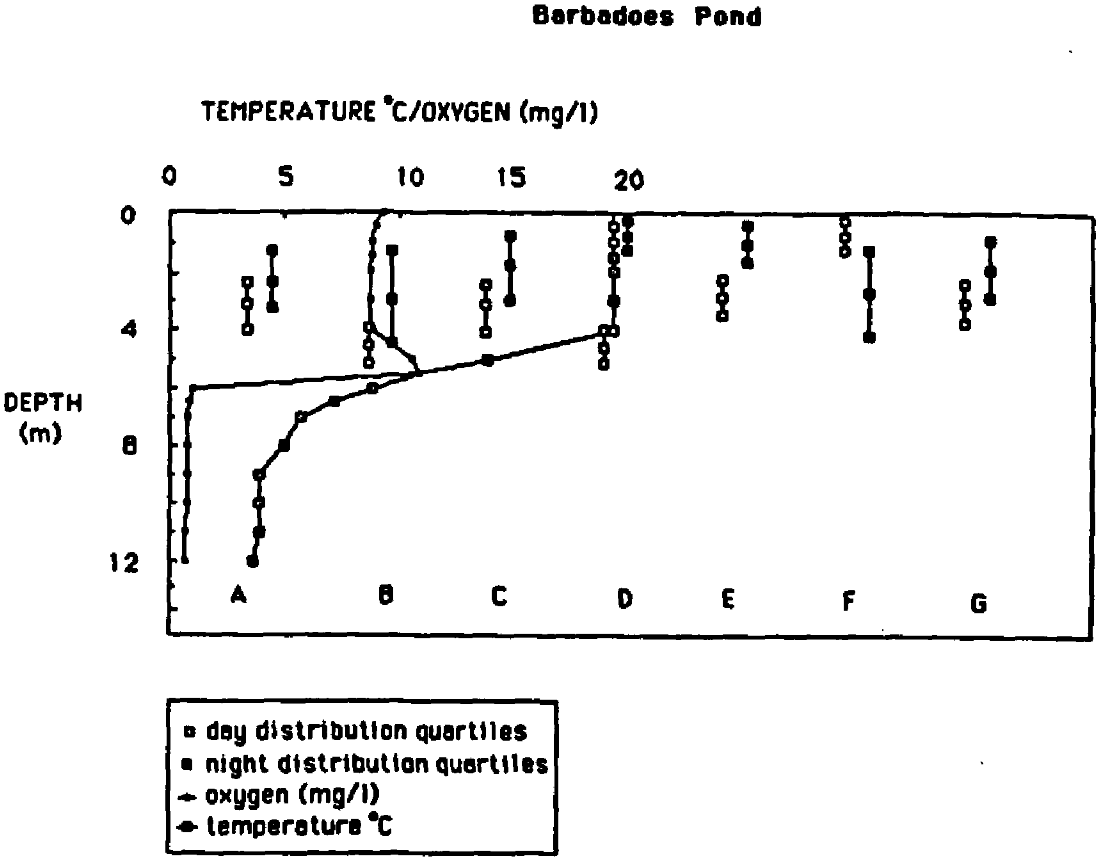
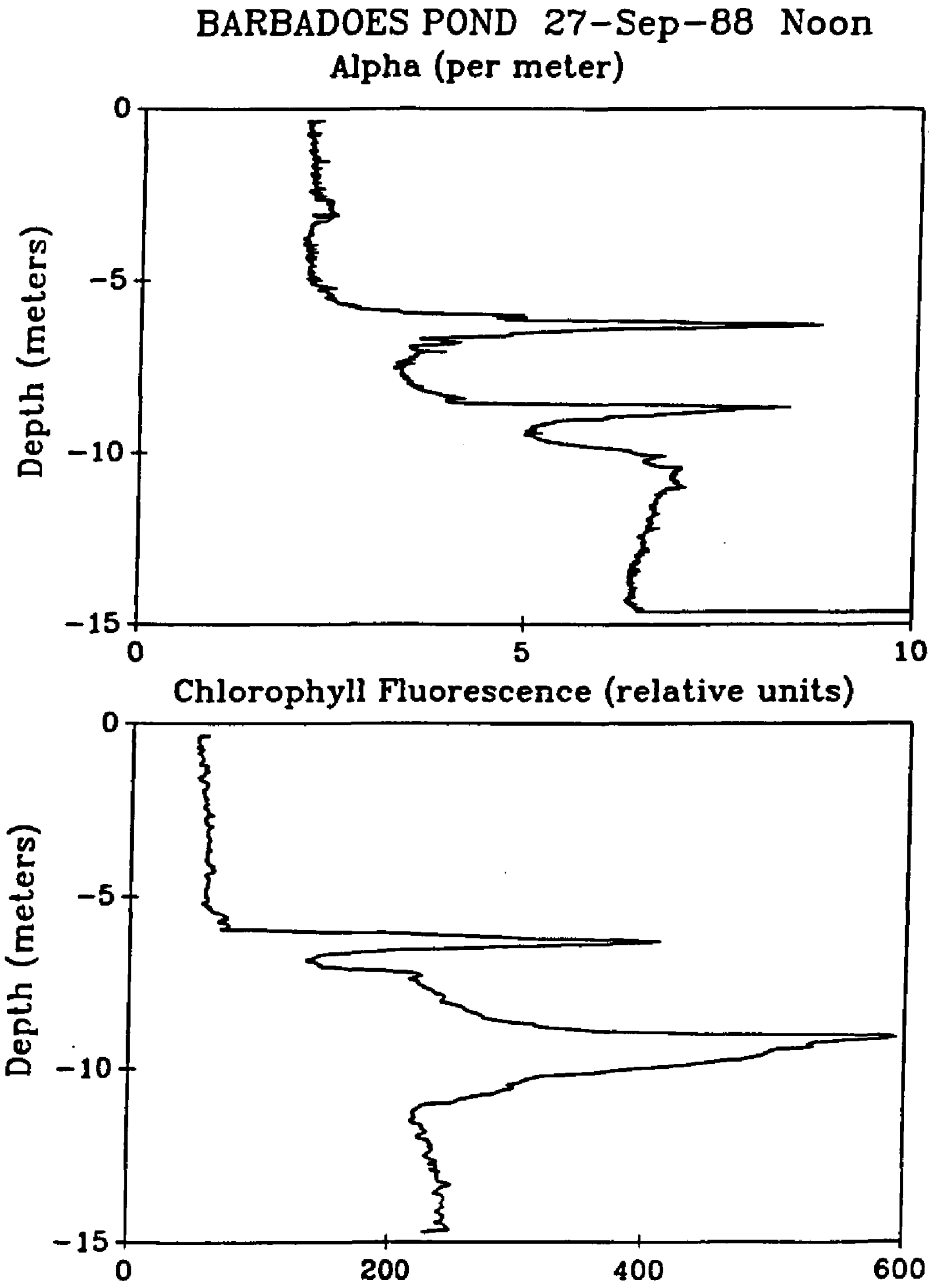


Figure 36. Day and night population quartiles for the zooplankton in Barbadoes Pond on 29 August 1986 compared with the temperature (°C), and oxygen (mgl^{-1}) profiles. Symbols as in Figure 34.


BARBADOES POND 27-Sep-88 Noon

Alpha (per meter)

Chlorophyll Fluorescence (relative units)

Figure 37. Profiles of light absorbance at depth (alpha) and chlorophyll flourescence in Barbadoes Pond. (A.L. Baker, unpub., used with permission).

sp. from 2-4 m. Again the data suggest that the phytoplankton composition rather than food concentration was more important in determining the direction of migration.

Control by Predation

Visual Predators The zooplankton in this study, as found by McNaught and Hasler (1964), did not take advantage of a light refuge from fish during the day in Upper Sawyer, Lower Sawyer, and Stonehouse Ponds. A light refuge was probably not available in Barbadoes Pond as oxygen concentrations were less than 1 mgl^{-1} (Figure 36), well above the lower limit of the photic zone (Figure 34). Confer et.al. (1978) showed that below 50 lux of illumination (about 2.5×10^{-5} W cm^{-2}), the visual acuity of trout preying upon *Daphnia* larger than 1.2 mm in body length begins to diminish. This is the upper size limit of zooplankton in these studies. At 50 lux, then, they should be less vulnerable to visual predation than at greater light intensities. However, of the populations in these lakes, only *Bosmina* sp. and small cyclopoids in Upper Sawyer Pond (Figure 31), and *Daphnia ambigua*, *Bosmina* sp., and cyclopoids in Stonehouse Pond (Figure 33), had pre-migration depths for the population Q50 which were at or below the depth with 50 lux of illumination. Thus this aspect of the field observations does not support the prediction that zooplankton remain deeper in the water column during the day in order to avoid visual predators (Zaret and Suffern 1976). Together, food concentration and phytoplankton composition seem to explain distributions of zooplankton in these lakes better than predation does.

Fish densities estimated from sonar tracings (Table 17) were not significantly correlated with pre-migration depths ($F < 1.8$, $p>0.10$).

This is consistent with the observation that the zooplankton in these lakes did not avoid fish by moving into a light refuge during the day.

		#fish/transect		**estimated density (# m^{-3})(10^4)**	
water column stratum:		**upper**	**lower**	**upper**	**lower**
Sept 1982	**Upper Sawyer**	1.5	8.5	7.09	0.57
Sept 1981	**Lower Sawyer**	12	8	16.5	2.46
Sept 1981	**Lower Sawyer**	13.5	9.5	18.6	2.93
May 1983	**Stonehouse**	17	7	14.6	4.72
Aug 1986	**Barbadoes**	75	26	1050	51.9

Table 17. Estimated density of fish (# m^{-3}) in the upper and lower portions of the water column (see field methods: sonar analysis). Upper Sawyer and Barbadoes numbers estimated are the means of two replicate transects, the remaining counts shown are for one transect.

Tactile Predators. The migrations observed in the field studies were only partly consistent with the suggestion of Ohman, _et.al._ (1983), that invertebrate predation results in reverse migrations. The most abundant invertebrate predators found in the samples from this study were large cyclopoid copepods and _Chaoborus_ larvae. The distributions of the cyclopoids overlapped those of the other zooplankton in all four lakes, indicating that the cyclopoids were either following their prey and so could not be avoided, or that other factors restricted the zooplankton from moving away. The greatest density of large cyclopoids was found in Barbadoes Pond (Table 18), where only the small cyclopoids migrated downward. The cyclopoid density in

Stonehouse Pond was about half as great as in Barbadoes Pond (Table 18). In Stonehouse Pond, Daphnia ambigua and Holopedium gibberum were found at night below the majority of the cyclopoids (Figure 38), and the Daphnia ambigua population was also below most of the Chaoborus population. In Upper Sawyer Pond, the density of cyclopoids was approximately half that found in Barbadoes Pond, and one quarter of that found in Stonehouse Pond (Table 18). There was, however, a population of Chaoborus (Figure 31). Even so, no reverse migrations were observed in Upper Sawyer Pond. In contrast to the other three lakes, there were very few cyclopoids in Lower Sawyer Pond (Table 18), and no Chaoborus observed. Yet, all but one of the zooplankton populations there undertook reverse migrations (Figure 32).

In Upper Sawyer Pond, Lower Sawyer Pond, and Stonehouse Pond, no oxygen deficit restricts the zooplankton to the epilimnion (Figures 39, 40, and 36) The above observations indicate that the presence of invertebrate predators may not be sufficient to elicit reverse migrations in lake zooplankton.

	Upper Sawyer	**Lower Sawyer**	**Stonehouse**	**Barbadoes**
mean density of large cyclopoids ($nos.l^{-1}$)	1.45	0.23	3.04 *	7.08

Table 18. The mean densities of large cyclopoid copepods in the field samples in $nos.l^{-1}$. * includes all cyclopoids.

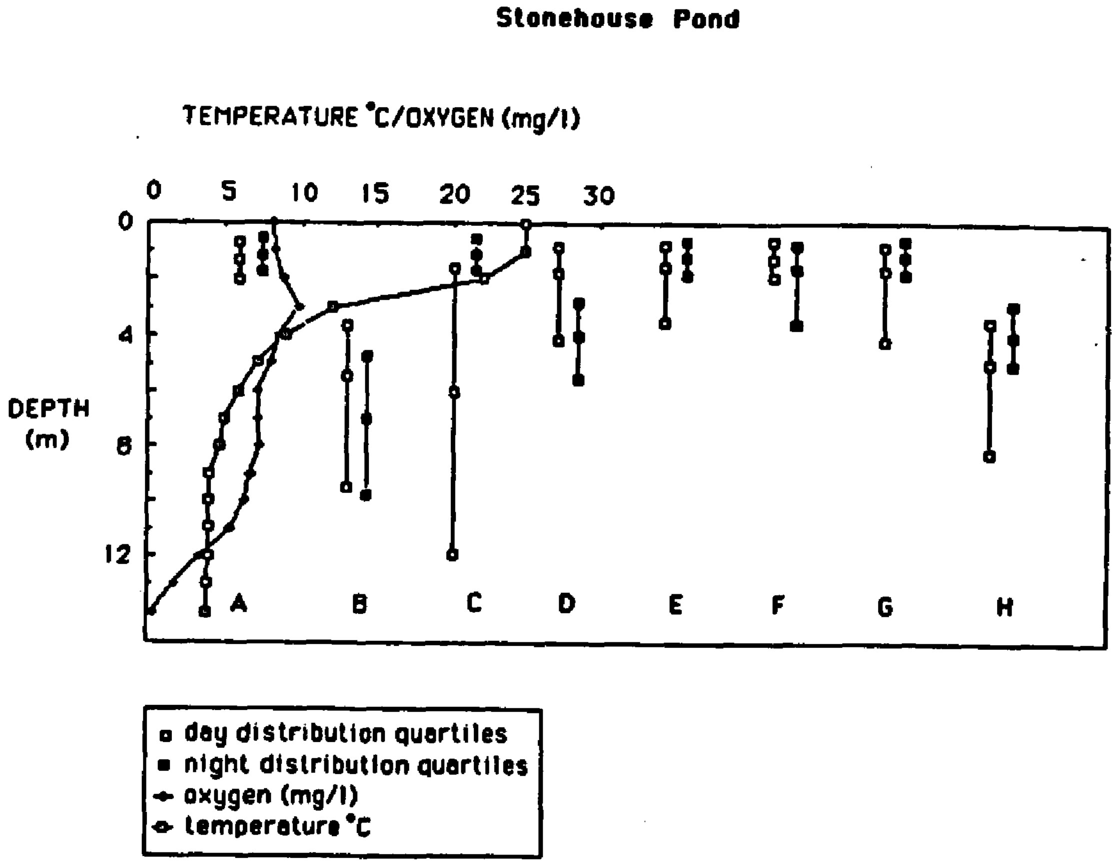


Figure 38. Day and night population quartiles for the zooplankton in Stonehouse Pond on 13 July 1983 compared with the temperature (°C), and oxygen (mgl^{-1}) profiles. Symbols as in Figure 33.

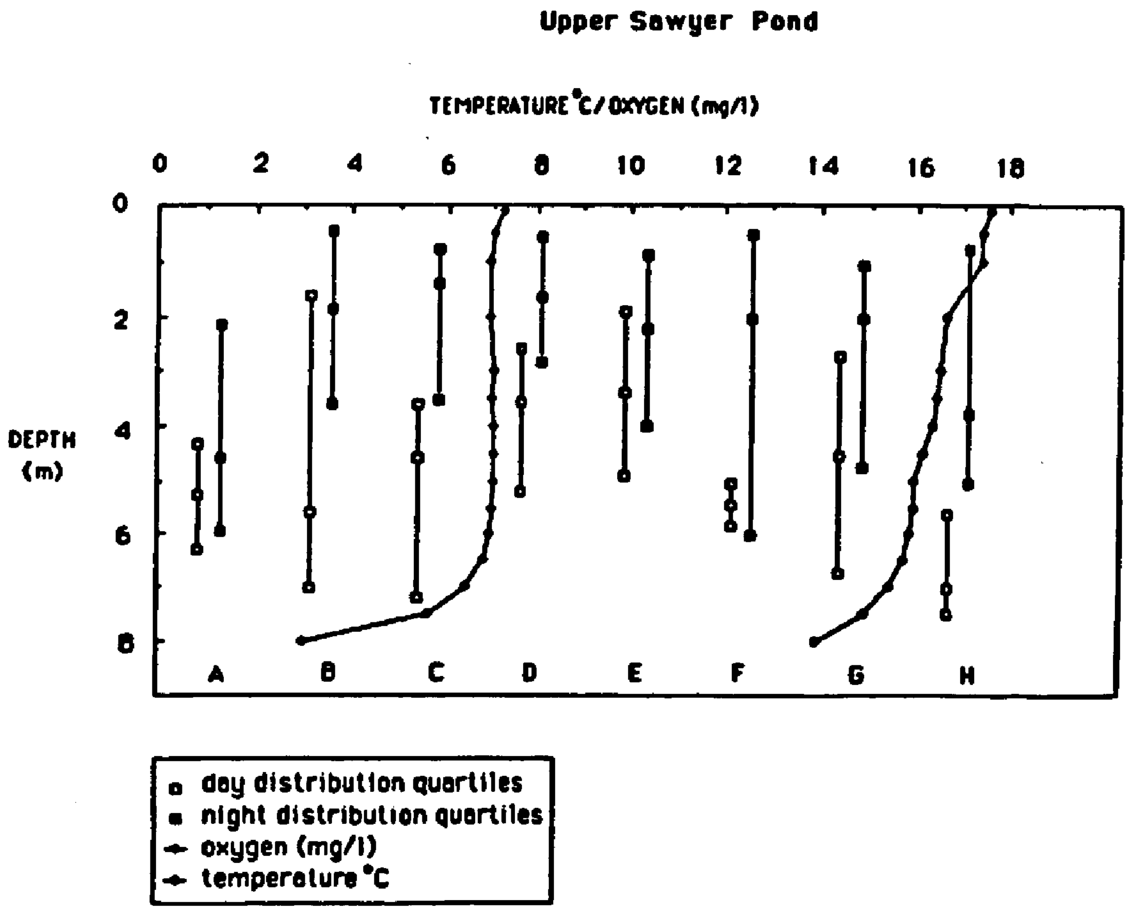


Figure 39. Day and night population quartiles for the zooplankton in Upper Sawyer Pond on 13 September 1986 compared with the temperature (°C), and oxygen (mgl^{-1}) profiles. Symbols as in Figure 31.

Lower Sawyer Pond

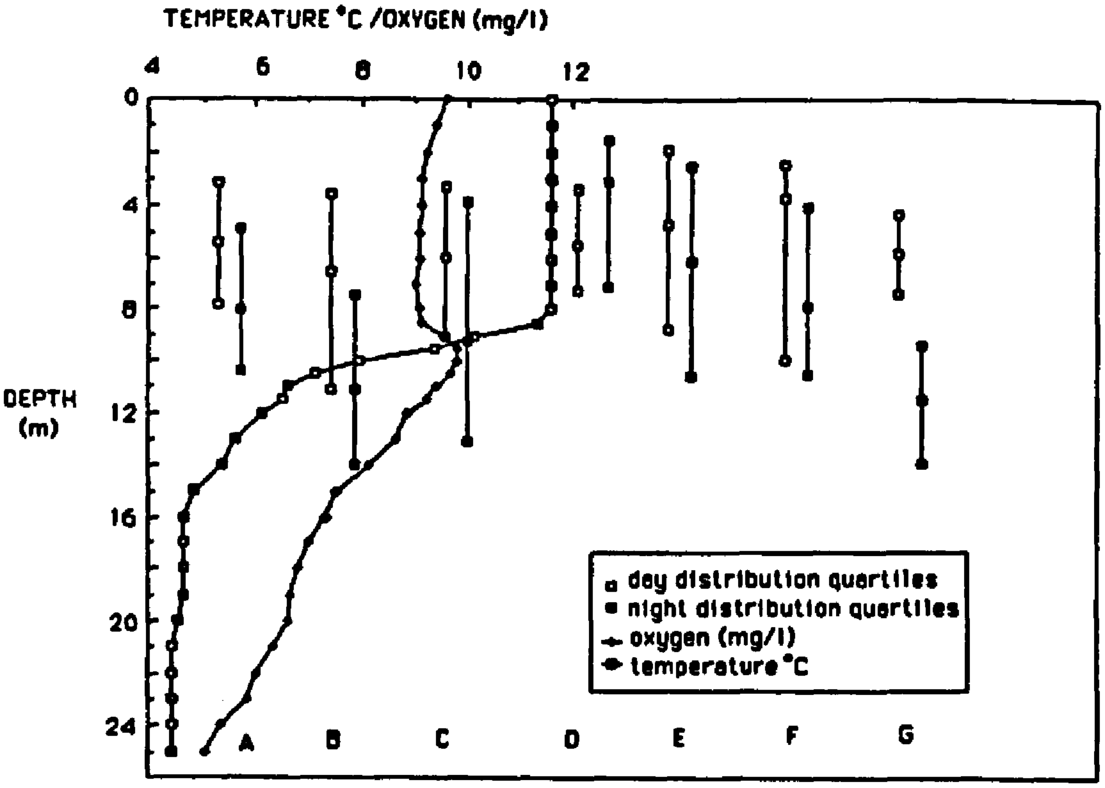


Figure 40. Day and night population quartiles for the zooplankton in Lower Sawyer Pond on 10 October 1986 compared with the temperature (^{o}C), and oxygen (mgl^{-1}) profiles. Symbols as in Figure 32.

The Influence of Temperature

Zooplankton may be found at species specific pre-migration depths associated with narrow ranges of temperature during the summer months (Geller 1986). Temperature may also provide spatial orientation cues to some migrating zooplankton (Moore et.al. 1953). However, there was no noticeable influence of temperature on the direction of migration in this study. *Daphnia* spp. migrated upward in Upper Sawyer Pond at 15.9 to 17.6 °C (Figure 39), and also in the much warmer water of Barbadoes Pond, 19.5 °C (Figure 36). In the epilimnion of Stonehouse Pond, 22 to 25 °C, in Stonehouse Pond, *Daphnia* did not migrate (Figure 38). The epilimnion of Lower Sawyer Pond was cooler than the other lakes at 11.6 °C (Figure 40), while the metalimnion of Stonehouse Pond had a gradient of temperatures from 5 to 22 °C (Figure 38). In these two lakes the *Daphnia* followed reverse migration patterns. A similar variability in migrations was noted for the other Cladocera. The differing responses to warm and cold temperatures might suggest that seasonal variation in the migrations is due as much to related changes in light and phytoplankton production as to temperature.

GENERAL DISCUSSION

Summary of Results

The data collected in the laboratory studies revealed several quantitative relationships. These generalized relationships are summarized in a control model in Figure 41.

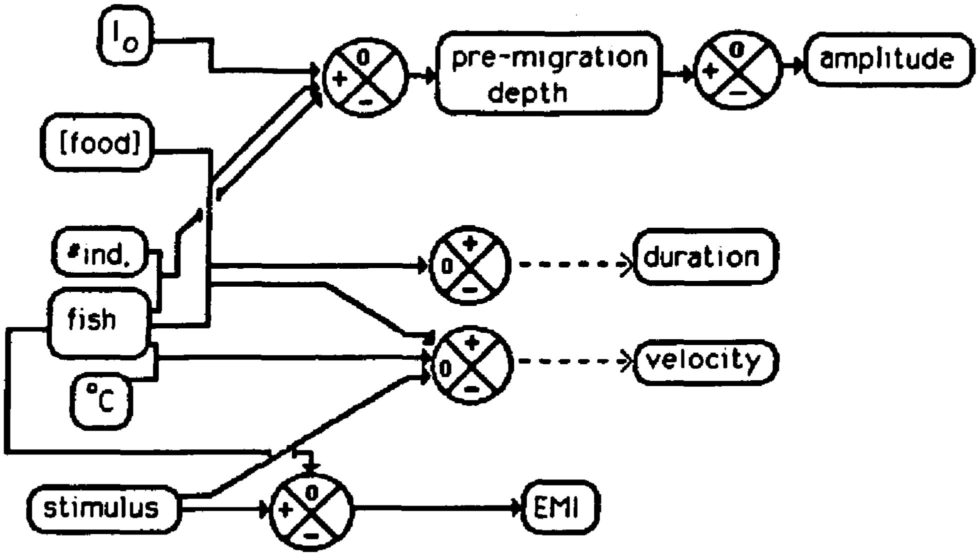
Pre-migration depths were deeper when surface light intensities were greater. Only with a fish present were the *Daphnia* populations deeper when either food concentrations increased or population density decreased (Figure 41).

Amplitudes of migration increased strongly with increasing pre-migration depths, but did not respond to changes in the three regulatory factors considered (light, food concentration, and presence of a fish) (Figure 41).

No significant relationships were found between migration velocity or duration of migration and food concentration, light stimulus, or temperature. The migration velocity was not influenced by the presence of fish.

The timing of the evening migration initiation (EMI) was highly predictable from the time of Ringelberg's stimulus threshold (RST). Neither the presence of a fish, nor differing food concentrations influenced the relationship between EMI and RST.

The results indicate that the relative influences of light, food concentrations, and the presence of a fish are distinct for pre-migration depths, amplitudes of migrations, and timing of migration



Control of evening vertical migration

Figure 41. Summary of the relationships between the controlling factors; light intensity (surface ln I_0, and at population depths ln I_z), light stimulus (sec^{-1}), food concentration (mgl^{-1}), and presence of a fish, and parameters of a migration: the pre-migration depth, amplitude, duration, velocity, and time of the evening migration initiation (EMI).

initiations.

The field results provided additional insight into the regulation of the pre-migration depths. They suggest that UV-B radiation has a seasonal influence on pre-migration depths, with summer intensities resulting in the deepest pre-migration depths. Pre-migration depths were deeper as the transparency of the lakes increased, indicating possible avoidance of light intensities and/or visual predators.

The field results also indicated that low oxygen concentrations restricted zooplankton to the epilimnion. Otherwise neither temperature nor oxygen appeared to influence the migrations. The field studies indicated that phytoplankton distributions may play a determining role in the direction of migration.

In the field studies, the influence of food was generally stronger than the influence of fish. The zooplankton were not deep enough to take advantage of a visual refuge, nor did fish density correlate with pre-migration depths. These observations suggest fish are actively foraging on the zooplankton to influence migrations.

Pre-migration depths

The largest zooplankters should be the most susceptible to visual predation, and thus should be found at greatest depths and should migrate the farthest (Zaret and Suffern 1976). However, the smallest Cladoceran in the New Hampshire lakes, *Bosmina* sp., migrated farthest in all four lakes. *Daphnia ambigua* migrated in Stonehouse and Barbadoes Ponds while the larger *Daphnia catawba* did not migrate and was higher in the water column. The smaller of the two *Daphnia* species in Lake Constance, *D. hyalina*, migrated deepest and farthest (Geller 1986). *Daphnia hyalina* from Lake Constance was shown experimentally to be smaller because of the temperature differences encountered during migration (Stich and Lampert 1984). Possibly Bosmina and Daphnia ambigua are more tolerant of daily fluctuations in temperature than large Cladocera such as Daphnia catawba, and thus able to migrate more often.

The zooplankton in all of the lakes in the present study had pre-migration depths above the depth of 50 lux illumination, which is the light intensity at which trout start to loose visual acuity (Confer et.al. 1978). In contrast, Wright et.al. (1980) reported that the larger zooplankton in Lone Star Lake were found below the depth of 10 lux illumination, the critical level of illumination for prey location by white crappie. Avoidance of visual predators, then, contributes only a portion of the variability seen in pre-migration depths.

The strong positive correlation between pre-migration depths and amplitude in the experimental columns (r^2=80%, $p<0.001$) indicates that the factors controlling pre-migration depths have a substantial influence on the entire migration. Light intensity, food concentration in the presence of a fish, and population density in the presence of a fish, each predicted less than half of the variability of the pre-migration depths (Results and Discussion, p.63, and Tables 6-8). This implies that additional factors contribute to the regulation of the population pre-migration depths. In addition, light, food, fish, and population density may modify the distribution of zooplankton established in the early morning at the end of the dawn descent. The factors regulating dawn descent may also influence pre-migration depth and thus the course of the next evening's migration.

Food Concentration

The contribution of food concentration to the vertical distribution of zooplankton is assigned a different role by different models. Kerfoot (1970) proposed light intensity as a frame of reference for migrating zooplankton. His model emphasizes the food energy potentially available to migrators, assuming a positive correlation between light intensity and daily production of algal cells. Visibility to predators drives the zooplankton down in the day, and food availability stimulates them to swim up in the evening. However, his assumptions that migrating zooplankton cease feeding after dark to allow the algae a respite from grazing, and that they follow isopleths of light intensity (as in the preferendum hypothesis; see Results and Discussion, pp.54-63), have no direct support, and detract strongly from his model.

Both Iwasa (1982) and Gliwicz and Pijanowska (1988) balance the influence of food with that of visual predators. The distribution of zooplankton in the hypothetical lake of Iwasa's computer game is based upon the avoidance of visual predators. The zooplankton remain deep when light intensity is high. Their upward movement takes place when a threshold of light intensity is reached. Food concentrations are assumed to control the light threshold in an inverse relationship. Because decreasing food raises the threshold light intensity, zooplankton can migrate in bright light, even in the presence of a fish. Food overrides the influence of the predators. The result is a preferendum-type control of the migration, where food concentration sets the optimal light intensity that the zooplankton follow. The results of this study rejected the preferendum hypothesis, and so the role of food in setting an optimum light intensity is also rejected.

Gliwicz and Pijanowska (1988) considered two extremes, with either food concentration or predation determining the tendency to migrate, defined as the observed amplitude over the distance between the premigration depth and the depth of highest food concentration in the epilimnion. Although they considered only upward migrations, their model allows the inclusion of reverse migrations by expressing the amplitude of reverse migrations as a negative number. Gliwicz and Pijanowska found a positive correlation between the tendency to migrate and the degree of stratification of food. A positive correlation was found between these two variables for three of the New Hampshire lakes (Table 17), where about half the migrations were reverse migrations. Thus the model appears to predict both the direction and amplitude of migration in New Hampshire lakes.

Gliwicz and Pijanowska predict for their lakes that a ratio of food stratification (see Results and Discussion, p.24) of less than 2 would result in no migration. In New Hampshire lakes, the food stratification ratios were well below 2 (Table 17). The values for these ratios in a given system may depend upon food quality and the food requirements of the zooplankton, which may vary regionally or between different types of lakes. Since migrations take place in oligotrophic New Hampshire lakes with a food stratification value less than 2, perhaps a much higher value than 2 would be necessary to allow migrations in extremely eutrophic lakes. It would be worthwhile to test the proposed relationships of the model between seasons and between sets of lakes.

Food quality was also proposed by Gliwicz and Pijanowska (1988) as a contributor to the tendency to migrate. Food quality appears to be associated with the direction of migration in the Sawyer Ponds and in Barbadoes Pond. As some copepods, including the freshwater Eudiaptomus, can select algal cells from among polystyrene spheres coated with algal extract (DeMott 1988), it is possible that food quality may be a direct regulator of migration as well as an influence on the tendency to migrate.

There is evidence that with a limited food supply zooplankton populations remain closer to the surface in the day and migrate with less amplitude in the evening (Huntley and Brooks 1982; Dagg 1985). Johnsen and Jakobsen (1987) found that as food concentrations in their experimental chambers fell, the pre-migration depths of the zooplankton also rose. Although there were no fish in the enclosures, they interpreted their result as the Daphnia risking exposure to predators rather than going hungry. Their migrations were similar to the migrations in this study in columns with fish present, and to the migrations observed by Dagg (1985) in the field with fish. This study found, however, no significant influence of food in the absence of fish in the columns. This difference in results may be due to the respective origins of the experimental animals. The Daphnia in this lab study had not been exposed to fish for at least 25 generations, whereas Johnsen and Jakobsen's animals were taken directly from a lake with a fish population. Their animals were probably still adapted to the presence of fish, while the animals in this study likely were released from the selective force of fish predation.

Geller (1986) proposed that starvation avoidance was a stronger influence than predator avoidance on Daphnia migrations in Lake

Constance. He postulated that there was a metabolic advantage to descending to a depth of low temperature for the day. However, work with the same populations showed a distinct disadvantage to migrating populations in terms of growth (Stich and Lampert 1984). Geller concentrated on the stability of temperature during the day, while Stich and Lampert emphasized the fluctuation of temperature during the migration cycle. Wright *et.al.* (1980) showed that migration decreased growth rates and reproduction for zooplankton populations. The migration itself is not costly in terms of energy expended in swimming (Vlymen 1970). The results of a simulation model for the growth of *Chaoborus* under different migration patterns (Swift 1975) also predicts that migrating *Chaoborus* do not grow as large as non-migrating individuals. The evidence for a metabolic gain by migrating *Daphnia*, then, is weaker than the evidence for the predator-food balance models discussed above.

Presence of a Predator

Gliwicz and Pijanowska (1988) found a significant correlation between the tendency to migrate and the number of years fish had been present in the ultra-oligotrophic Tatra Mountain lakes. They note that predation intensity and fish density would be more desirable correlates with the tendency to migrate. One possible effect of predation, they suggest, would be to select against the more positively phototactic individuals in a population. This would give the appearance that the population was avoiding high light intensities. Such a selection is not improbable as Dumont *et.al.* (1985) showed that phototactic behavior in *Daphnia* has a strong genetic component. Active predation may influence the selection of phototactic behavior in the populations, which in turn will influence the migration amplitudes and the tendency to migrate.

In this study the influence of a fish on pre-migration depths in columns was reversible, indicating a sensory response to the presence of the fish. A continual presence of the fish, as in lakes, would result in increased pre-migration depths and therefore a relative increase in blue wavelengths of light at the population depth. Since in a population of _Daphnia_, the production of visual pigments can reverse within 45 to 60 days in response to the color of the light environment (McNaught 1971), a sensory response to fish activity could result in a seasonal cycle of photosensitivity. Such a mechanism might operate with or without selection for phototactic traits. The resulting migrations would be consistent with observations of seasonal cycles in the vertical amplitude of migrations (Stich and Lampert 1981).

Timing of Migration

A threshold stimulus of relative light change was confirmed in this work as a Zeitgeber for a circadian pattern of vertical migration. Circadian rhythms of zooplankton vertical migration have been shown to exist both with endogenous control (Harris 1963; Ringelberg and Servaas 1971; Enright and Honnegger 1977), and with exogenous control (Schröder 1962; Enright and Honnegger 1977). The function of light stimulus as a Zeitgeber receives further support from observations that without the stimulus associated with sunset, as in days longer than 20 hours in the arctic (Buchanan and Haney 1980), migration cycles nearly disappear. Muller (1965) also found evidence that under very long LD cycles of 23:1, the mayfly larva _Baetis vernus_ did not show stream-drift behavior.

The actual value of the stimulus threshold may vary depending upon the light intensity to which an individual is adapted (Ringelberg, _et.al._ 1967). At white light intensities of adaptation below 4×10^{-6} Wcm^{-2}, the stimulus necessary to evoke a positive phototaxis in 50% of the observed _Daphnia magna_ rose rapidly. Above that intensity the stimulus required was nearly constant. On dark days, or for deep populations, we should thus expect to find asynchrony among population quartiles in the EMI, as was found in this study.

Enright and Honnegger (1977) proposed that food availability could influence the timing of migrations by shifting the phase of an endogenous activity rhythm entrained on the daily light-dark cycle. Low food concentrations would lead to migrations before sunset. If low food concentrations increased the photosensitivity of the eye, then at a given light intensity of adaptation there would be an earlier migration among populations in lesser food concentrations. The data from this study, however, showed no significant influence for food concentration on the time of EMI or on velocity of migrations. Neither a food mediated shift in the timing of the migrations, nor a light-adaptation which influences the Zeitgeber, explains migrations delayed until after light intensites have ceased changing.

Chaoborus populations induced to migrate by the introduction of trout into the lake did not cease migrating once the trout were removed (Leucke 1986). Leucke interpreted this as evidence that the trout did not provide the proximal cue for the migration. The data from this study showed that the range of EMI times for _Daphnia_ decreased in the presence of a fish, but did not increase once the fish was removed. These observations suggest a genetic control for the timing of the migrations. In contrast, this study indicated that the distribution of the population in space is regulated by sensory responses to food availability, the presence of a fish, and daily changes in climate and food availability.

The complex of relationships controlling pre-migration depths and the strong single correlations for amplitude and timing of the migration (Figure 41) indicate it may be useful to divide the migration into two parts. The day portion would be responsive to short-term changes in temperature, light, food availability, and to sensory perception of the presence of fish. The evening phase including timing and velocity of the migrations would be more directed and largely under control of a genetically established cycle of endogenous activity. A division of vertical migration into kinetic and directional components was suggested by Ringelberg (1981). Such a dual mechanism has also been proposed for the control of stream-drift (Haney et.al. 1983). This proposed model suggests that more intensive study of day-distributions and of responses to biological factors may be a fruitful approach to extending our knowledge of regulatory mechanisms of zooplankton vertical migration.

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APPENDIX A

Bristol's E media for Chlorella
(Dr. Leland Jahnke, University of New Hampshire)

	nutrients		ml H_2O
1.	$NaNO_3$	5 g	
	$CaCl_2.2H_2O$	0.5 g	200 ml
2.	$MgSO_4.7H_2O$	1.5 g	
	NaCl	0.5 g	200 ml
3.	K_2HPO_4	2.0 g	
	KH_2PO_4	3.0 g	200 ml
4.	EDTA (Na)	2.5 g	50 ml
	adjust to pH 6.6 with dilute H_2SO_4		
5.	$Fe(NH_4)_2(SO_4)_2$	0.7 g	100 ml
	adjust to pH 6.6 with 2 drops 10% H_2SO_4		
6.	$ZnSO_4$	0.9 g	
	MoO_3	0.07 g	
	$CuSO_4$	0.08 g (or $CuSO_4.5H_2O$ .25 g)	
	$CoNO_3$	0.05 g	
	$MnCl_2.4H_2O$	0.14 g	100 ml
	adjust to pH 6.6 with 1 drop of 10% H_2SO_4		

Notes

1. Autoclave all stocks with the exception of the $Fe(NH_4)_2(SO_4)_2$, autoclaving the iron will reduce it to an insoluble ferrous precipitate.
2. Stocks numbered 1-3, use 10 ml per 1000 ml distilled water.
3. Stocks numbered 4-6, use 1 ml per 1000 ml distilled water.

Appendix B

Temperature measurements at 30 cm in the columns over the course of each evening's observations.

March		April		May		July	
A	B	A	B	A	B	A	B
Day 1:							
26	26	27	27.75	20	19.5	-	-
24.5	24.5	26	26.75	20	19	-	-
-	-	26	26.75	19.5	19	25.75	-
24	24	25	25.75	19.5	19	25.5	25.5
24	24	24	24.75	19	19	25.5	25
23.5	24	23.5	24.2	19	18.5	25	25
		23	23.25	19	19	25.25	25.25
		22.5	23.25			25.25	25
Day 2:							
22	22	19	19.5	23	23	30	30
22	22	19	19	22	22	29.5	29.5
22	22	18.5	19	22	21.5	29	29
21.5	21.5	18	18	22	21	28.5	28.5
21.5	21.5	18	18	22	21	28	27.5
21.5	21.5	17.5	17.5	21	20	27	26.5
		17	17	21	20	26	26
		-	16			26	25
Day 3:							
23	23	17	17	16	16	28	28
23	23	16.5	16.75	16	15.5	27.5	27.5
22	22	16	16.5	16	15.5	27	27
22	22	16	16	16	15	26.5	26
-	22	15	15.5	16	15.5	26	26
21.5	21.5	15	15	15.5	15	25	25
		14.5	14.75	15.5	15	25	24
		14	14			24	24
		14	14				
Day 4:							
28	28	22.5	22	20.5	20		
26	26.5	21.75	21	20	19.5		
25.5	26	20.5	20.75	19	19		
25	25	20	20	18.5	18.5		
24	24.5	-	19.5	17.75	17.75		
24	24	-	19	17	17		
		-	18	16.5	16		
		-	17				

March		April		May	
Day 5:					
21	21	28	28.25	23.5	23
21	21	27.5	28	23	23
21	21	27	27.25	22.5	22
21	21	26	26	22	21.5
21	21	25	25.25	21	21
21	21	24	24.5	20.5	20
		23.5	24	20	20
				19.5	19.5
Day 6:					
20.5	21	19	19	25	25
21	21	19	19	25	24
21	21	19	19	24	24
21	21	18.25	18.25	24	24
21	21	18	18	23.5	23
21	21	17.5	17.5	23	23
		17	17	23	23
				23	22
Day 7:					
23	23			24	23
22	23			23	22
23	23			23	22
22.5	22.5			22	22
22	22			22	21.5
22	22			21.5	21
				21	20.5
Day 8:					
29	29				
28	28				
27	27				
26	26				
26	26				
25.5	25				

August		November	
Day 1:			
27	27	22	21
27	27	21.5	20.75
27	26.5	21	20.75
26	26	21	20
26	26	20.5	20
26	26	20.5	19.75
25.5	25.5		

August		November		August	
Day 2:				Day 7:	
27	27	18	17.5	27	27
27	27	18	17.75	27	27
27	26.5	18	17.5	26	26
27	26	18	17.5	26	25
26	26	18	17.5	25	25
26	25.5	18	17.5	25	24.5
		18	17.5	24	24
Day 3:					
29	28.5	18	17.5		
29	28	18	17.5		
28	28	18	18		
27	27	18	18		
27	27	18	18		
26	26	17.75	17.5		
26	26				
Day 4:					
28	28	19	18.5		
27.5	27.5	19	18.5		
27	27	19	18.5		
27	27	18.5	19		
26	25	18	19		
25	25	18.5	19		
25	25				
Day 5:					
27	27	18.5	-		
26	26	18	-		
26	26	18.5	-		
25	25	18	-		
25	25	18	-		
24	24	18	-		
24	24				
Day 6:					
26	26	23	-		
26	26	23	-		
25	24.5	23	-		
-	24	22	-		
-	24	21	-		
-	23.5	21	-		
-	23				

Temperature profile in each of three columns at 2025 hours on 12 March 1986

Column Depth (cm)	A	B	C
20	23.0	23.2	23.2
40	23.2	23.2	23.2
60	23.2	23.3	23.2
80	23.2	23.3	23.2
100	23.2	23.2	23.1
120	22.8	23.0	22.8
140	22.5	22.8	22.6
160	22.5	22.5	22.4
180	21.8	22.2	21.8
200	21.6	21.8	21.8
220	21.3	21.5	21.4
240	21.0	21.0	21.0
260	20.5	20.5	20.7
280	20.2	20.3	20.2
300	19.8	20.0	19.8
320	19.6	19.5	19.6
340	19.0	19.0	18.9
360	18.8	18.7	18.5
380	18.2	18.3	18.2
400	17.5	17.8	17.8
410	17.5	17.5	--