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A STUDY OF THE COEXISTENCE OF TWO SPECIES OF DIAPTOMUS  
(COPEPODA:CALANOIDA) IN GULL LAKE, MICHIGAN

By

Donald Lee Mellinger

A DISSERTATION

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## ABSTRACT

### A STUDY OF THE COEXISTENCE OF TWO SPECIES OF DIAPTOMUS (COPEPODA:CALANOIDA) IN GULL LAKE, MICHIGAN

By

Donald Lee Mellinger

The conditions of the coexistence of Diaptomus minutus and D. oregonensis in Gull Lake, Michigan, were examined during the period 1972-1974. The data obtained from vertical series of samples, using a van Dorn sampler, indicated that D. minutus and D. oregonensis occupied the same volume of water, had similar seasonal abundances, and occurred with essentially a 1:1 adult species ratio throughout the course of the study. Metasome length measurements did not appear to lend convincing support to the character displacement hypothesis as proposed by Cole (1961).

By means of the radioisotope in situ grazing method developed by Haney (1970, 1971), filtering rates were calculated for the two species from feeding experiments employing five species of  $^{14}\text{C}$ -labelled green algae. The purpose of these feeding experiments was to explore possible food niche differentiation, based on cell size. The results of experiments using Chlorella sp. and Chlamydomonas

reinhardtii indicated that D. oregonensis females, the largest group, did not collect Chlorella-sized cells (3-8 microns diameter) as effectively as they did the larger sized cells. Both diaptomid species collected Scenedesmus accuminatus (18-26 microns diameter) effectively. These results suggest that, contrary to the Brooks and Dodson (1965) hypothesis of zooplankton food niche differentiation, the area of overlap, in terms of food particle size, is between 8 and 22 microns with the portion of the size spectrum below 8 microns being utilized mainly by the smaller species, D. minutus and the portion above 22 microns being available mainly to the larger species, D. oregonensis.

During the summer stratification period, female daytime filtering rates in the metalimnion were depressed compared to the male rates. This phenomenon may be associated with an alternating pattern of "encounter-feeding" and "filtering-feeding" modes. Summer nighttime filtering rates of migrating individuals were higher than daytime filtering rates.

The general conclusion is that there may be sufficient differences in feeding patterns to account for the coexistence of these two commonly co-occurring species. There was little, or no evidence of space niche or time niche separation in Gull Lake.

To my father and mother, Abram and Mabel Mellinger,  
I dedicate this work.

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Finally, I have warmest appreciation for my wife, Alta, and daughters, Donna and Sharon, who endured the rigors of these years with me.

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## INTRODUCTION

### The Concept of Coexistence

The principle of competitive exclusion has interested biologists for more than seventy years. This principle ("Gause Hypothesis" or "Volterra-Gause Principle") has been verbalized as the proposition, " . . . that species with identical needs and habits cannot survive in the same place if they compete for limited resources--at least if their needs and habits remain identical" (Crombie, 1947). Hutchinson (1965) stated that if two non-interbreeding populations occupying the same ecological niche are sympatric, one will ultimately exclude the other. It has been observed by several authors (Gilbert, et al., 1952; Hardin, 1960; Birch and Ehrlich, 1967) that if two populations are sufficiently distinct morphologically to be recognized as species, they differ to some degree in their genetics, physiology, and ecology as well. So there is an a priori assumption that no two species are ecologically identical. As a consequence, the competitive exclusion principle can neither be proved nor disproved. However, as MacArthur (1968) indicates, the consequences of the principle may

still be valid and well worth examining in some detail. One way of proceeding would be to examine a natural situation and then infer the explanation for the continuing coexistence of closely related species, and a second way could be to simulate a simplified and controlled environment.

MacArthur's (1958) study of a group of warblers living together in the northeastern coniferous forests is an example of the first approach. He found that the five species of warblers actually subdivided trees and each fed mainly in its section on a given tree. The alternative approach of controlled laboratory experimentation is exemplified by Gause (1934), Frank (1952, 1957) and Park (1962). These studies have shown that when two similar species are forced to live together in a simple environment with a single food resource, one species always wins out over the other. By increasing the physical complexity of the experiment, adding bits of macaroni, for example, the outcome of the experiment could be altered. Both approaches emphasize the importance of environmental heterogeneity for the coexistence of two or more similar species.

Environmental heterogeneity may be discussed in terms of "niche". Grinnell (1924) first used the word, "niche," to describe the potential geographical distribution of a species. The limits of the distribution would

be set by physical-climatic barriers rather than limits set by interactions with other organisms. Elton (1927) developed the idea that "niche" can be used to describe the food habits of a species. By this, he referred to the organism's actual or realized place in the environment rather than the potential position as suggested by Grinnell. In an attempt to formalize the notion of niche, Hutchinson (1957) proposed that the niche of an organism may be represented as a hypervolume whose coordinates represent ecological requisites for its existence. Since the concept of niche is quite broad, some ecologists have subdivided it into components, such as the "food niche," "time niche," and "place (space) niche" (Pianka, 1969).

Generally, ecologists have examined two phenomena which may permit coexistence: (1) Habitat selection, whereby two species attain some degree of spatial-temporal separation thus generating differences in their place niche and/or time niche; and (2) resource allocation, when two species use different proportions of two or more resources (e.g. food). Resource allocation is also considered to include the passive situation where the species are differentially selected as a resource by a predator. These two means of coexistence may often operate simultaneously and in an interactive fashion. It is important to emphasize that coexistence per se implies nothing about

competition, although coexistence is often the raison d'être for studies of competitive relationships.

Zooplankton, because of their seemingly identical feeding behavior and habitat utilization have long been considered an enigma in competition theory (Hutchinson, 1961). Coexistence of two zooplankton species frequently may occur if there is a temporary superabundance of food which enables both species to thrive and increase simultaneously (Fryer, 1957; Pejler, 1962; Cole, 1966; Smrcek, 1973), but other factors must be operating to permit the long-term coexistence of two closely related species utilizing the same or similar food resources. As an example, Lane and McNaught (1970) performed a mathematical analysis of the niches of Lake Michigan zooplankton, using the equations of Levins (1968), based on habitat selection and resource allocation in similar species.

Pennak (1957) examined 148 vertical series of samples taken from 27 lakes of Colorado and did not find any single series of samples that contained more than one species of Diaptomus. He concluded that in North America when two limnetic calanoids are found together, it is very seldom that they are both species of Diaptomus but rather it is one Diaptomus and an additional species of Limnocalanus, Epischura, or Senecella. While noting some exceptions to this rule, Pennak suggested that he believed them to be uncommon. On the other hand, Cole (1961)

compiled a list of 34 different combinations of two or more Diaptomus species co-occurring in lakes and ponds. Ten of these combinations involved at least two members of the same subgenus. This list is based on his studies in Arizona and published reports from other parts of the world. Perhaps the most extensive survey of the Diaptomus co-occurrence phenomenon, to date, was carried out in Ontario by Rigler, Langford, and their students. They found that 51% of the 100 lakes studied contained two or more species of Diaptomus (Rigler and Langford, 1967). Turvey (1968) listed the species composition of 226 lakes in Ontario, which included those reported by Rigler and Langford, and found that 38% contained two or more species of Diaptomus. His data show that of 144 headwater lakes, only 21% contained two or more species of Diaptomus. In 82 non-headwater lakes, he found 65% contained two or more species of Diaptomus. These data suggest that some instances of co-occurrence may be the result of continuous immigration.

Vertical and/or temporal separation has been advanced to explain these congeneric co-occurrences in Diaptomus (Carl, 1940; Hutchinson, 1951; Rigler and Langford, 1967; Sandercock, 1967; Tash and Armitage, 1967). It has also often been postulated that related species of zooplankton of differing body size do not occupy the same food niche, presumably due to different efficiencies in

"utilizing" (collecting) different sizes of food particles (Hutchinson, 1951; Fryer, 1954; Brooks and Dodson, 1965; Sprules, 1972). Hammer and Sawchyn (1968), from their study of some Saskatchewan ponds, concluded that a minimum length difference of 0.5 mm was necessary to allow coexistence of two species of Diaptomus. Tash and Armitage (1967) observed that Diaptomus arcticus frequently co-occurred with D. pribilofensis in ponds and lakes of the Cape Thompson area of Alaska. Adult D. arcticus were about twice as large as D. pribilofensis which led the authors to believe that congeneric coexistence depends upon size differences of this magnitude.

In addition to observations that co-occurring congeneric species often display marked size differences, Brown and Wilson (1956) introduced the term, "character displacement" to describe the divergence of metric characters shown when two partly allopatric species of comparable niche requirements become sympatric in part of their range. Hutchinson (1959) reviewed various studies of mammals and birds which appeared to exhibit the phenomenon of character displacement. He concluded that when closely related species co-occur, the ratio of the larger to the small form is roughly 1.3. This ratio, he felt, is indicative of the kind of difference necessary to permit two species to co-occur in different niches but at the same trophic level. Although the ratio was derived from mammal

and bird data, he believed that it had general application to other animal groups, including aquatic insects. Cole (1961) suggested that character displacement may permit closely related species of Diaptomus to partition and consequently share aquatic habitats. He noted that Hutchinson (1951) reported that in the case of the very closely allied Arctodiaptomus wierzejskii (1.4 mm) and A. laticeps (1.3 mm), which generally have complete size variation overlap in lakes where they occur alone, there was a slight length difference (0.1 mm) between the two species when they co-occurred in a lake of the Outer Hebrides, Scotland.

The character displacement hypothesis as applied to diaptomids by Cole suggests that if species A is larger than species B then species A will be larger in lakes where it coexists with species B than it is in lakes where it occurs alone and species B will be smaller in lakes where it coexists with species A than it is in lakes where it occurs alone. The functional consequence of the proposed character displacement phenomenon in diaptomids would be that the increased difference in body lengths enables species A to be more effective in collecting larger food particles from the size spectrum available and species B to be more effective in collecting from the smaller end of the food particle spectrum present in lakes where they coexist. As a consequence, data which would show character

displacement in congeneric coexisting diaptomids could be taken as indirect evidence that body length is indeed correlated with the partitioning of the available food resources into different food niches.

What is meant by the term "coexistence"? Cole (1961) does not differentiate between co-occurrence and coexistence. Pennak (1957) suggests that it is important to consider species dominance when attempting to evaluate coexistence. He suggests that if one species is numerically dominant and 20 or more times as abundant as the other co-occurring species then the situation should not be considered as an example of coexistence but rather the typical situation of a community containing additional species in the "rare" category who function as "seed" nuclei for potential future population cycles. In Hammer and Sawchyn's study (1968) those diaptomid associations which persisted for at least three weeks were considered as examples of true coexistence. In many lakes, this period of time would seem to be too short to preclude situations which are really the overlap of the final phase of one species' life cycle with the beginning phase of another one. Further, one species may be restricted to the hypolimnion while another may occur mainly in the epilimnion and metalimnion. During the summer, Sandercock (1967) found Diaptomus sanguineus to be effectively separated

from D. oregonensis and D. minutus by the discontinuity layer in Clarke Lake, Ontario.

My operational definition of coexistence shall be that two or more species may be considered to be coexisting if they occupy the same volume of water for an extended period of time (months) and are present in relatively similar proportions.

The Co-occurrence of Diaptomus oregonensis  
and D. minutus

Diaptomus oregonensis Lilljeborg 1889 was used by Light (1939) as the type species for the subgenus, Skistodiaptomus. Marsh (1907) suggested that D. oregonensis or its immediate ancestor inhabited the waters south of the ice at the height of the glacial period and as the ice retreated, it gradually moved north. He believed that during this movement it adapted itself only slightly to the changes of the environment.

Diaptomus minutus Lilljeborg 1889 was included in the subgenus, Leptodiaptomus, by Light (1939). He based his classification on the characteristics of the fifth pair of legs of the male. D. minutus has been described from collections made in Greenland, Iceland, Newfoundland (Marsh, 1929) and its range extends west through Maine, New York, Ontario, Michigan, and Wisconsin. Marsh (1907) recognized the specialized features of the fifth legs of both males and females but concluded that its wide

distribution strongly suggested that it is an early form of the tenuicudatus group of the genus Diaptomus.

Marsh (1895) noted that D. minutus was, perhaps, the most common of all the diaptomids in Lake St. Clair and the Great Lakes. He also offered the observation that while D. oregonensis occurred in the Great Lakes, it was not abundant there but was the most common limnetic species in smaller lakes of Michigan. Robertson (1966), however, observed that D. oregonensis seemed to be abundant in the warmer, southerly parts of the Great Lakes but decreased in abundance in the cooler, northerly regions. He found D. minutus to be present in all the Great Lakes but seldom seemed to be present in large numbers. In Lake Erie, D. oregonensis was found to be the most common diaptomid while D. minutus was somewhat less common (Jahoda, 1949; Davis, 1954, 1962). In Parry Sound, Georgian Bay, Carter (1969) observed approximately the same abundance for the two species over an 18-month period. Wells (1960) found significant numbers of both species in Lake Michigan. He found their seasonal abundance to be rather variable from year to year. Langford (1938) reported both species had population peaks during July and August in Lake Nipissing, Ontario.

Turvey (1968) found that D. minutus co-occurred with D. oregonensis in over 33% of the 226 lakes studied in southern Ontario. The two species were identified in

20% of the 45 lakes in the Experimental Lake Area of Northwestern Ontario by Patalas (1971). Hall and Waterman (1967, 1968) found the two species occurred together in three of the eleven Finger Lakes of New York. In selected lakes of the Adirondack region of New York, these authors observed that D. minutus was abundant in most of the 36 lakes and ponds studied while it occurred with D. oregonensis in two of nine large lakes and none of the smaller ones. A survey of 28 lakes in southwestern lower Michigan revealed only three lakes, including Gull Lake, in which both species were present (Shuba and Mellinger, unpublished).

#### Scope of the Study

The work of Rigler and Langford (1967), Turvey (1968), and Robertson (1966) has established the fact that Diaptomus minutus and D. oregonensis co-occur in numerous lakes including the Great Lakes. While a lake is a relatively unstructured environment (Hutchinson, 1961), thermal stratification does offer the potential for place niche differentiation. The initial stage of my study was designed to determine whether these two species of diaptomids co-occurring in Gull Lake, Michigan, actually fit the operational definition of coexistence which I proposed. Do the two species occupy the same volume of water? Do both species migrate into the epilimnion at night during the summer? Is there a seasonal difference between peaks in

species abundances? In short, what biological mechanisms appear to permit the coexistence of these two closely related species?

In order to answer these questions, I took series of vertical samples at two stations with a 8.8 liter van Dorn sampler, including several night series. From these series of samples, I measured metasome (cephalothorax) lengths on four dates for the purpose of examining possible evidence of character displacement as suggested by Cole (1961). Several series of samples were also collected from other lakes in this area in which one of the species was found to be the sole diaptomid present.

The latter stage of my study was devoted to a consideration of filtering rates of the two diaptomid species. These rates were obtained by using the radioisotope in situ method developed by Haney (1970, 1971). One of the outstanding features of this in situ method is that it provided a means of examining the filtering rates of both species simultaneously in each experiment in their natural habitat of the lake. The experimental chamber, therefore, contained the complete spectrum of phytoplankton, zooplankton predators, other zooplankton, and the trace amount of labelled green algae. Five species of green algae were used, ranging from  $36 \mu\text{m}^3$  to  $4300 \mu\text{m}^3$  in volume, in an attempt to identify proposed differences in filtering effectiveness related to cell size. These filtering rates

should provide some insight into the separation of food niches of these two species based on body length as proposed by Hutchinson (1951) and Brooks and Dodson (1965).

## STUDY AREA

Gull Lake (Figure 1) is located in the southwestern corner of lower Michigan, in Kalamazoo and Barry counties, between latitudes  $42^{\circ} 20' - 42^{\circ} 30' \text{ N}$  and longitudes  $85^{\circ} 20' - 85^{\circ} 30' \text{ W}$ . The lake basin was formed by glacial excavation (Wisconsin glacier) of a preexisting valley. The south end of the valley was dammed by a moraine and several large ice blocks in the basin prevented filling by outwash of sediments from the melting glaciers (Martin, 1957). The lake drainage basin is small in comparison with surface area of the lake. The surrounding country is slightly rolling in character and consists largely of calcium-rich glacial drift. Gull Lake covers an area of 822 hectares and has a maximum depth of 33 meters (Taube and Bacon, 1952). The lake is fed by springs and a few small streams. Gull Lake drains into the Kalamazoo River which, in turn, empties into Lake Michigan. The average January air temperature is about  $-3.3^{\circ}\text{C}$  and the average July air temperature is  $22.5^{\circ}\text{C}$ . Mean annual precipitation is 86.3 cm (Senninger, 1963).

Detailed physio-chemical measurements are available from October 1968 to 1974 (Moss, 1972; Lauff, et al., in

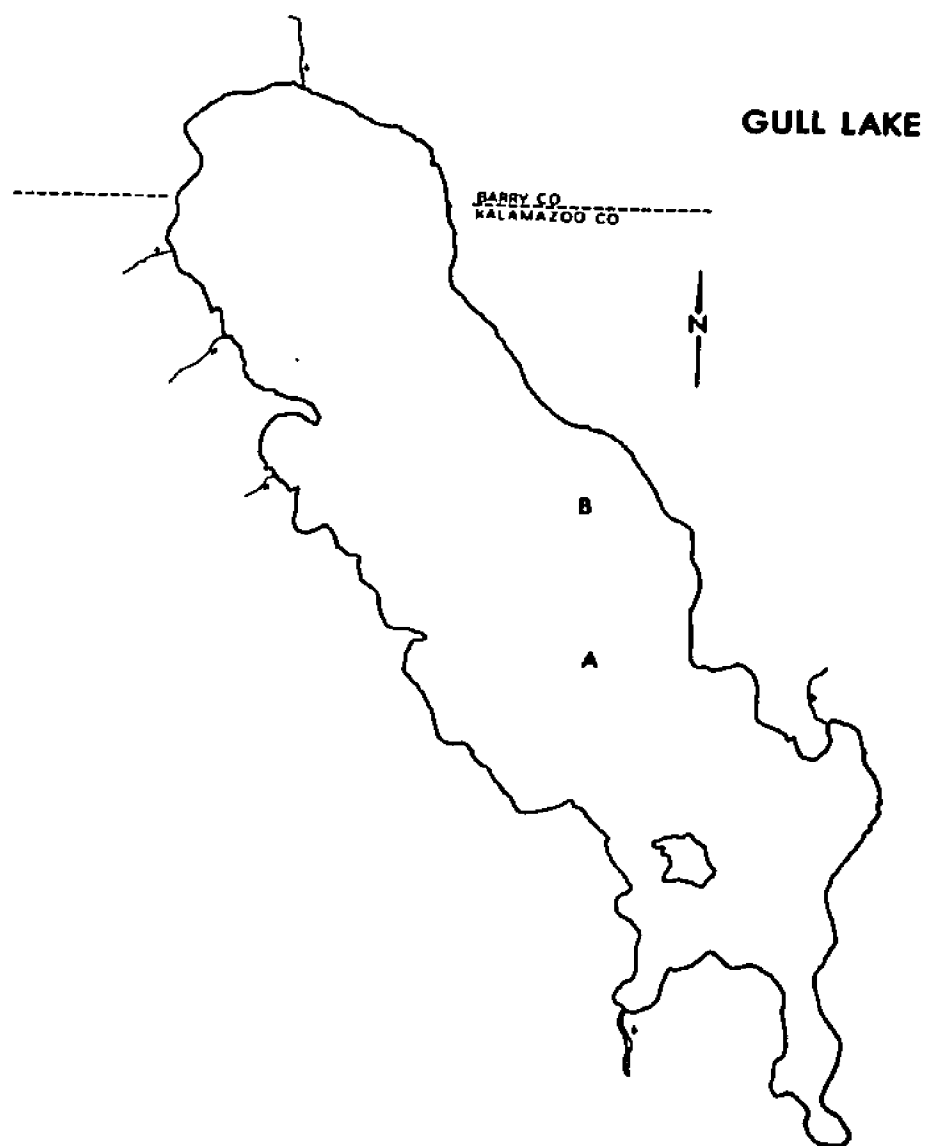


Figure 1. Map of Gull Lake, showing sampling locations.

preparation). Gull Lake is a dimictic deep lake characteristic of temperate continental regions (Hutchinson and Löffler, 1956). Ice covers the lake from early January until mid-March. Overturn occurs in early April and again in late November or early December. The summer epilimnion was about 9 meters deep and the hypolimnion began about 13 m. Surface temperature reached 26°C during late July, 1972. The hypolimnion temperature was 11°C in 1973. During the summer stratification, anoxic water has extended up as far as 15 meters beneath the surface for a brief period prior to turnover (Moss, 1972). The alkalinity of Gull Lake was about 3 m-equiv/l and the pH 8.0.

The phytoplankton of Gull Lake has been intensively investigated by Moss (1972). Spring is characterized by a major growth of diatoms (Fragilaria crotonensis, Asterionella formosa, Cyclotella michiganiana) and Dinobryon. During the summer, green algae predominate. Cryptomonads and chlamydomonad green flagellates (less than 5 µm diameter) appeared in abundance in the thermocline. Blue-green algae (Chroococcus dispersus, Synechococcus sp.) appeared mainly in late summer and autumn. A moderate growth of diatoms also appeared in the autumn.

## MATERIALS AND METHODS

Vertical series of samples were taken at two stations, with an 8.8 liter van Dorn sampler. One station was located at the deepest point (33 meters) of the lake (Figure 1, A) and the other one (16 meters) was approximately 200 meters southwest of the W. K. Kellogg Biological Station boat house (Figure 1, B). Samples were usually taken at depths of 1, 3, 5, 7, 9, 11, 13, 15 m. Occasionally, duplicate sets of samples were taken as well as samples of 17-m and 23-m strata at the deep station. The number of adults/8.8 liter sample ranged from 0 to 227.

The sampler, after being retrieved, was placed vertically into a 12-liter bucket and emptied. The sample was then poured through an overboard drain apparatus in which the zooplankton was collected on 75-micron netting mounted in a piece of 7.6 cm (I.D.) plexiglass tubing. The overboard drain apparatus consisted of a 25.4 cm galvanized funnel mounted against the top portion of a 22.5 x 76 x 2.5 cm piece of wood. The zooplankton-collecting net was supported below the funnel by a 7.6 cm plastic (PVC) elbow, through the wooden support, and emptied into the

lake. This drain apparatus was attached to the transom of the boat with two 15.3 cm clamps.

The zooplankton, on the Nitex net, were then rinsed into a 115 ml bottle and preserved with 4% buffered formalin (Czaika and Robertson, 1968). A Wild M-5 stereodissecting microscope was used for sexing and counting all diaptomids in the sample. Most counting was performed at 25X. For making metasome measurements, a Leitz Ortholux Research Microscope fitted with an ocular micrometer was used. Species identifications were based on the key to freshwater calanoids by Wilson (1959).

The in situ grazing technique used in this study was developed and tested by Haney (1970, 1971). This technique involves lowering a specially constructed (Plexiglas and stainless steel), transparent plankton trap to a particular depth in the lake. When a messenger is dropped to close the trap, a small amount of highly radioactive cells is automatically released from the piston within the trap. After a short experimental feeding period (10 min  $\pm$  30 sec), the trap is retrieved and the zooplankton collected. Later the adult diaptomids were sorted according to species and sex, oxidized, and assayed for radioactivity. Filtering rates can be calculated by knowing the exact radioactivity of the labelled cells released in the trap and the radioactivity acquired by the diaptomids during the feeding period. One of the major advantages of

this technique is that natural conditions are maintained during the experiment by using a large (8.8 liter) transparent grazing chamber (trap) with an extremely short experimental feeding period. Labelled cells are added in quantities so that the food concentration in the lake water is not significantly altered.

Ankistrodesmus falcatus (70-90  $\mu\text{m}$  long) and Chlorella sp. (4  $\mu\text{m}$  diameter) were cultured in 20-liter carboys, using Bristol's solution (Starr, 1964) and soil extract. These cultures were constantly aerated. Chlamydomonas reinhardtii (7-10  $\mu\text{m}$  diameter), Chlamydomonas angulosa (11-15  $\mu\text{m}$  diameter), and Scenedesmus accuminatus (17-26  $\mu\text{m}$  diameter) were cultured in 500 ml Erlenmeyer flasks using Difco algal broth. All cultures were exposed to a 12-hour light, 12-hour dark cycle with "daylight" fluorescent lamps. Cultures were kept at room temperature (19-23°C).

A hemocytometer (AO Spencer Bright-Line) was used to estimate the concentration of cells. The labelling process was started several days before the proposed experimental date. An estimate of the minimum quantity of cells required for each experiment was made and an amount approximately two times as great as this estimate was then withdrawn from the appropriate culture. The algal suspension was then centrifuged for 5 minutes and the culture medium decanted by means of a disposable syringe. The

cells were then resuspended in distilled water and usually 200 microcuries of aqueous  $^{14}\text{C-NaHCO}_3$  was added as radioactive label.

Incubation took place at room temperature with two 60-watt incandescent lamps for illumination. The suspension was stirred by means of an electric magnetic stirrer. The period of incubation was usually 72 hours. At the end of the incubation period, the labelled suspension was centrifuged for 5 minutes, the liquid decanted, and the cells resuspended in distilled water. This process of centrifugation and resuspension was repeated three times to insure complete removal of nonparticulate  $^{14}\text{C}$ . After the last centrifugation, the cells were resuspended in lake water that had been filtered through a Millipore membrane filter (47 mm diameter, 0.45  $\mu\text{m}$  pore size).

An automatic Eppendorf microliter pipette was used to measure and transfer an exact amount of  $^{14}\text{C}$ -labelled algae into the small grazing chamber piston (4 ml capacity). The final concentration of labelled cells in the grazing chamber was  $10^3$  cells/ml for small cells (Chlorella sp., Chlamydomonas reinhardtii) and  $10^2$  cells/ml for the larger cells. This quantity of labelled algae translates to about 5-15% addition to the number of natural cells contained in the grazing chamber. Four pistons were used for an experimental series. These pistons were filled in

the laboratory so as to maximize the accuracy of the quantity of labelled cells placed in each piston.

Two 50-microliter samples of labelled cells were filtered through Millipore membrane filters (0.45  $\mu\text{m}$  pore size) and the filters allowed to dry at room temperature. Two similar samples were taken at the end of the experimental day. These filters were later assayed for radioactivity in 15 ml Fluorally TLA (Beckman)/toluene. The experiments were performed, during the summer, using a 4-meter aluminum boat. A tent was employed for the ice series. A vertical series of samples was usually taken several hours before beginning the feeding experiments for the purpose of identifying the depth at which the adult diaptomid density was the greatest. Feeding experiments were performed on days when the weather was sunny. Daytime feeding experiments were conducted between 1300 and 1700 hours and nighttime ones between 2300 and 0200 hours.

At the beginning of this study, two series of grazing experiments were carried out to determine the appropriate length of time for a diaptomid feeding experiment. Each series covered a range of experimental feeding times (5 to 30 minutes). The experiments were performed at the same depth and according to a randomized scheme to avoid a possible time-related bias. The results of these time-series indicated that a change in the adult diaptomid uptake rate occurred after 15 minutes of feeding.

Therefore, 10-minutes was selected as the length of feeding time for all future diaptomid feeding experiments. Richman (1966) reported that Diaptomus oregonensis adults did not release fecal pellets during the first hour of feeding with an experimental food concentration of 38,000 Chlamydomonas cells/ml.

An individual experiment involved the insertion of a piston, previously filled with labelled cells in the laboratory, into the grazing chamber and lowering the chamber to the appropriate depth. A messenger was immediately dropped to close the chamber and activate the experiment. After 9 minutes, the chamber was quickly raised to the surface and strapped onto the emptying apparatus in the boat. The water from the chamber was then allowed to pass through a 75  $\mu$ m Nitex net and the waste water collected in a 12-liter bucket. Approximately 40 seconds was required to empty the chamber. The Nitex net with the zooplankton was immediately plunged into a container of soda water (Burns and Rigler, 1967). The carbonated soda water killed the zooplankton without causing defecation or regurgitation. After about one minute, the zooplankton were rinsed into a bottle and preserved with 4% buffered formalin. Timing the feeding period began when the chamber doors closed and ended when the chamber was completely empty. A stop watch was used for this timing. The waste water was transferred from the bucket to a 20-liter plastic carboy.

The preserved samples were examined with a Wild stereo-dissecting microscope and by means of Irwin loops, the adult diaptomids were sorted according to species and sex and then transferred onto 7 cm strips of filter paper (Whatman, 41 Smoke Test). The copepodid V stage of D. oregonensis was also collected when present. These strips of filter paper and animals were then folded and pressed into pellets by means of a pellet press. These pellets were then combusted in a Packard Tri-Carb Sample Oxidizer (Model 305). The evolved  $\text{CO}_2$  was collected into ethanolaniline in 15 ml PPO/bis-MSB/toluene (15 g/l, 1 g/l) scintillation mixture. This procedure was used to avoid the problem of self-absorption of the weak beta radiation by the animals. A Beckman LS-150 equipped with Automatic Quench Compensation was used to assay sample radioactivity. This Beckman system automatically compensates for varying quench by measuring the degree of quenching for each sample by the External Standard-Channels Ratio method. Its carbon-14 efficiency is greater than 90%. Each vial was counted for 20 minutes which yielded a two-sigma statistical counting error of 2-7%. Background radiation (Beckman Reference Background, Argon-Toluene) of 40 cpm was subtracted from each sample.

## RESULTS

### Temporal Distribution

The data presented in Figure 2 represent 60 vertical series of samples. The total number of adults collected in each series was divided by the number of samples taken in that series. The means were averaged on a monthly basis. The two species exhibited strikingly similar population trends in Gull Lake during 1972 and 1973. The overwintering adult populations can be seen to have almost disappeared by June. The fall crash of the summer adult populations occurred during October. By November, the adult population of both species had reached a level similar to that of spring and summer. Only D. minutus were found carrying eggs during November and December. Since the data presented here do not provide a clear picture of winter population levels, it is difficult to discern whether these winter adult populations represent single generations or the overlapping of two generations. The trivoltine (three generations/annum) hypothesis would propose that the spring reproduction gave rise to the summer adults (first generation). The early summer reproduction gave rise to the fall adults (second generation). The late

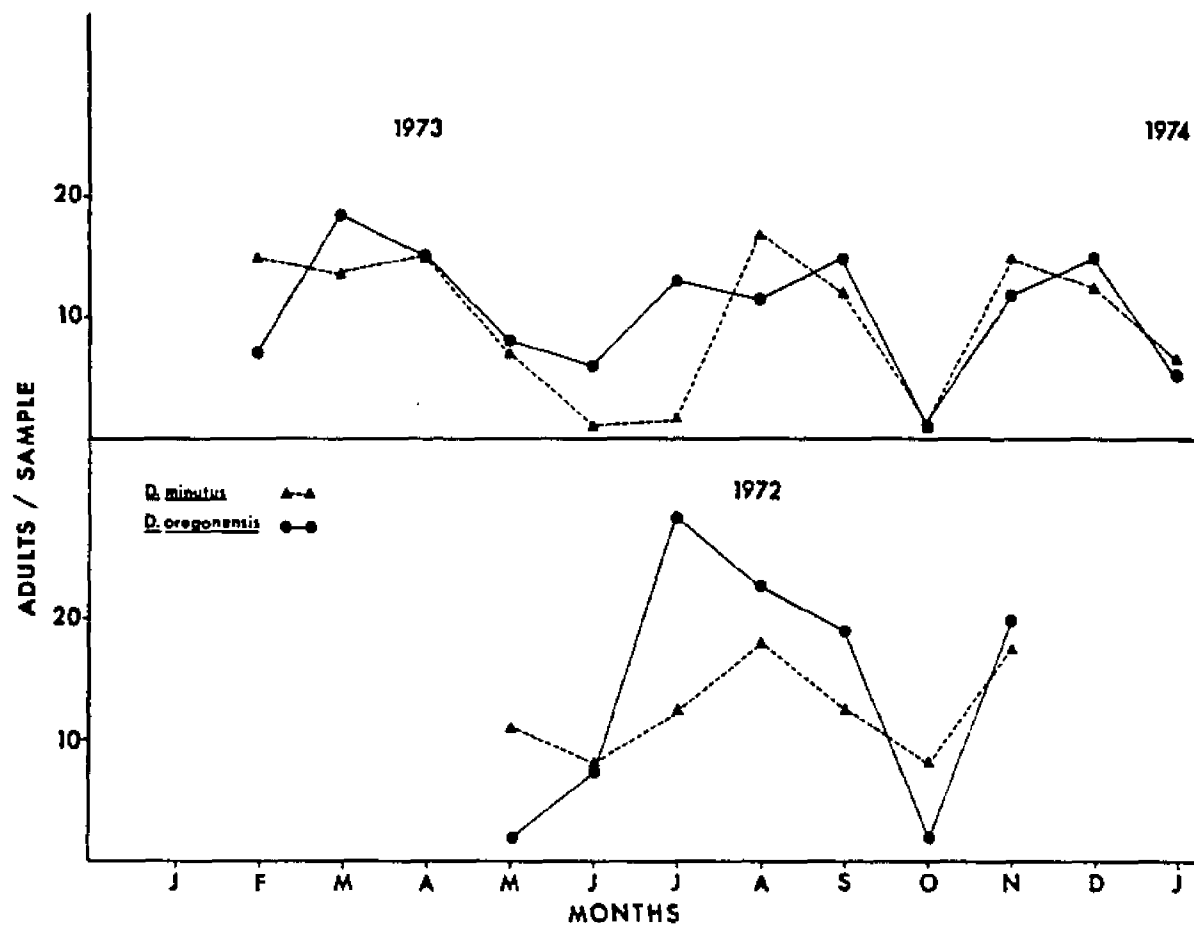


Figure 2. Seasonal distribution of *Diaptomus minutus* and *D. oregonensis* adults in mean numbers/8.8 liter sample. Sample means were averaged on a monthly basis.

summer reproduction developed much more slowly due to the autumn decrease in water temperature. Alternatively, a different type of egg may have been produced during late summer which required a cold stimulus (fall overturn) to trigger the beginning of development (Cooley, 1971). These individuals reached maturity about March and produced the spring pulse of reproduction (third generation).

On the other hand, the bivoltine hypothesis would propose that the winter population levels are the result of the extended summer reproductive period. Development of eggs produced during early summer proceeded rapidly due to higher water temperatures and gave rise to the fall adult peaks. As the water cooled during late summer and fall development was retarded so that there was a continuing input of individuals attaining maturity throughout the period of ice cover. Birge (1898) found that D. oregonensis produced a fall generation only in some years in Lake Mendota and felt that this was correlated to the water temperature of late summer. Lai and Carter (1970) studied the life cycle of D. oregonensis in Sunfish Lake, Ontario, and found three generations/annum during two of three years studied. These authors presume that D. oregonensis produced resting eggs during the year when there was no fall-winter generation. The studies of Comita and Anderson (1959), Hazelwood and Parker (1961), and Sawchyn and Hammer (1968) as well as others indicate clearly that there is a

wide range of responses by diaptomids to the whole complex of environmental conditions. This wide range of developmental time, number of annual generations, etc., is indicative of a large amount of physiological plasticity of species of Diaptomus.

Consequently, in the absence of strong evidence for the trivoltine hypothesis, I propose that it is likely that both species produced two generations/annum, while noting that only D. minutus produced eggs immediately after the fall overturn.

The adult patterns indicated in Figure 2 fail to support the hypothesis that the life cycles of these two species are temporally displaced in Gull Lake. The ratio of D. minutus to D. oregonensis was very nearly 1:1 for both years (Figure 3). D. minutus appeared to mature more slowly after the 1973 spring crash. However, neither species was numerically superior for greater than two months during the study period.

#### Vertical Distribution

For each species, the number at each depth sampled was converted to a percentage of the total number of adults of that species (obtained by summing over depth). The grouping was done from midmonth to midmonth. The percentages of the total numbers of the species for the month at each depth were calculated and graphed (Figure 4).

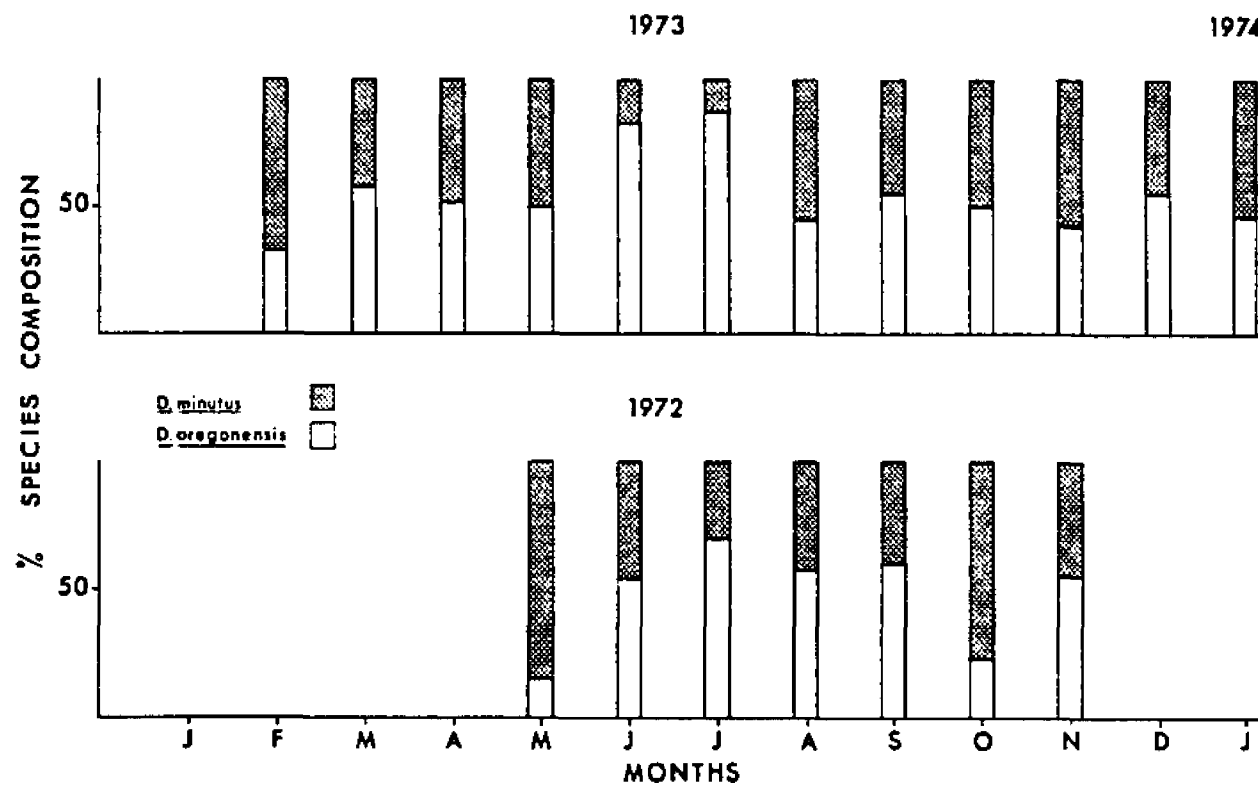


Figure 3. Variation in percentage of adult Diaptomus minutus and D. oregonensis. Samples were grouped on a monthly basis.

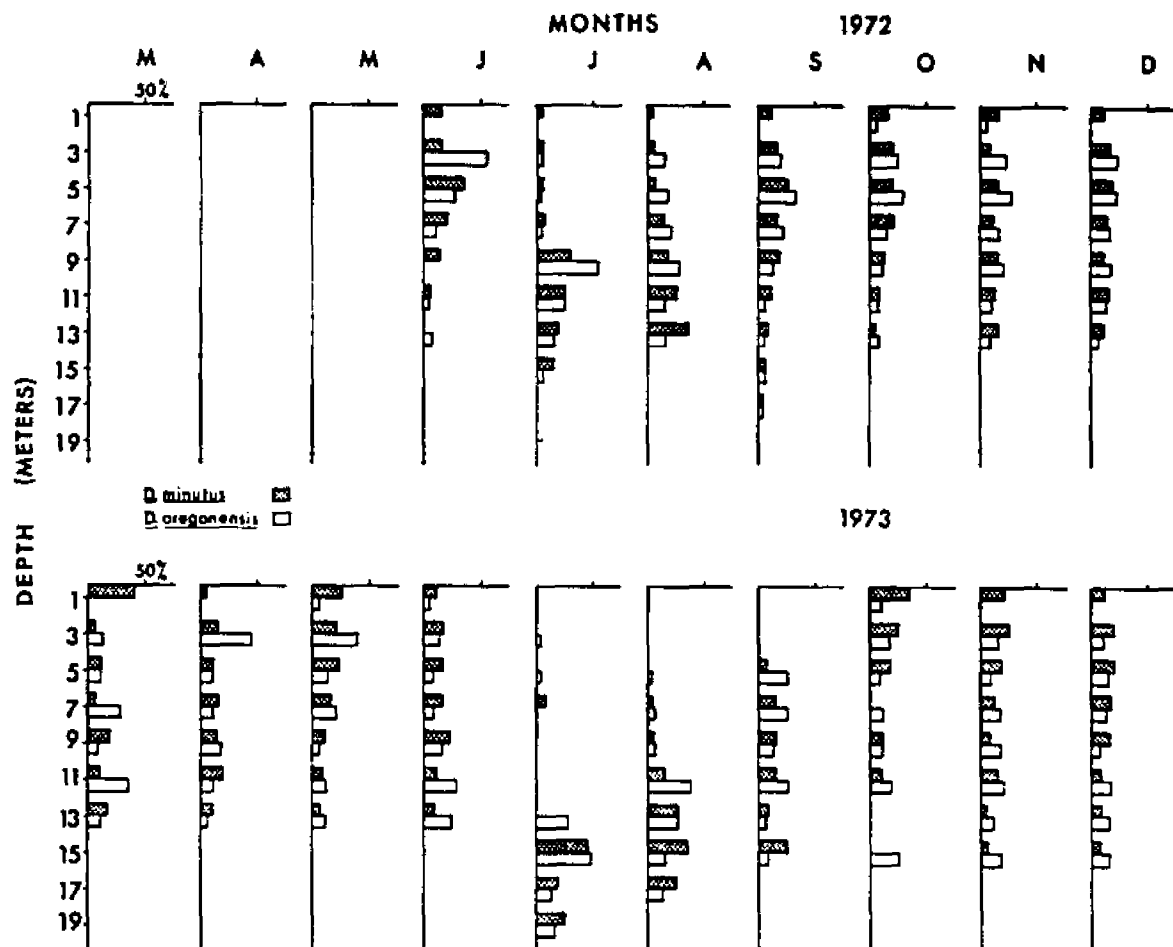


Figure 4. The vertical distribution of adults of Diaptomus minutus and D. oregonensis in Gull Lake.

Both species were rather uniformly distributed throughout the upper 13 meters of water during fall and winter. As the summer stratification intensified, the adults began to concentrate in the metalimnion during afternoon (1200-1700 hours). The depth at which this concentration occurred was obviously deeper in 1973 than in 1972. Transparency data, collected by means of a Secchi disk, showed a significantly higher transparency in 1973 compared to 1972 (Lauff, et al., in preparation). The increased water clarity was 34% for the June 15-July 15 period and 43% for the July 15-August 15 period. This suggests that the diaptomids responded to increased light penetration by moving into deeper water during the summer afternoons since the summer temperature regimes for 1972 and 1973 were quite similar.

The extensive overlap of the vertical distributions of the two species show clearly that they share the same space during the 1200-1800 hours portion of the day. For this reason, no statistics were performed to evaluate the overlap.

Day-night series were done at the near-shore station on two dates during the summer of 1972 (Figure 5). The purpose of these series was to ascertain if the adults of both species migrate into the epilimnion at night. During the day, 5% of the total number of adult D. minutus collected were found in the upper 5 meters while 9% of the

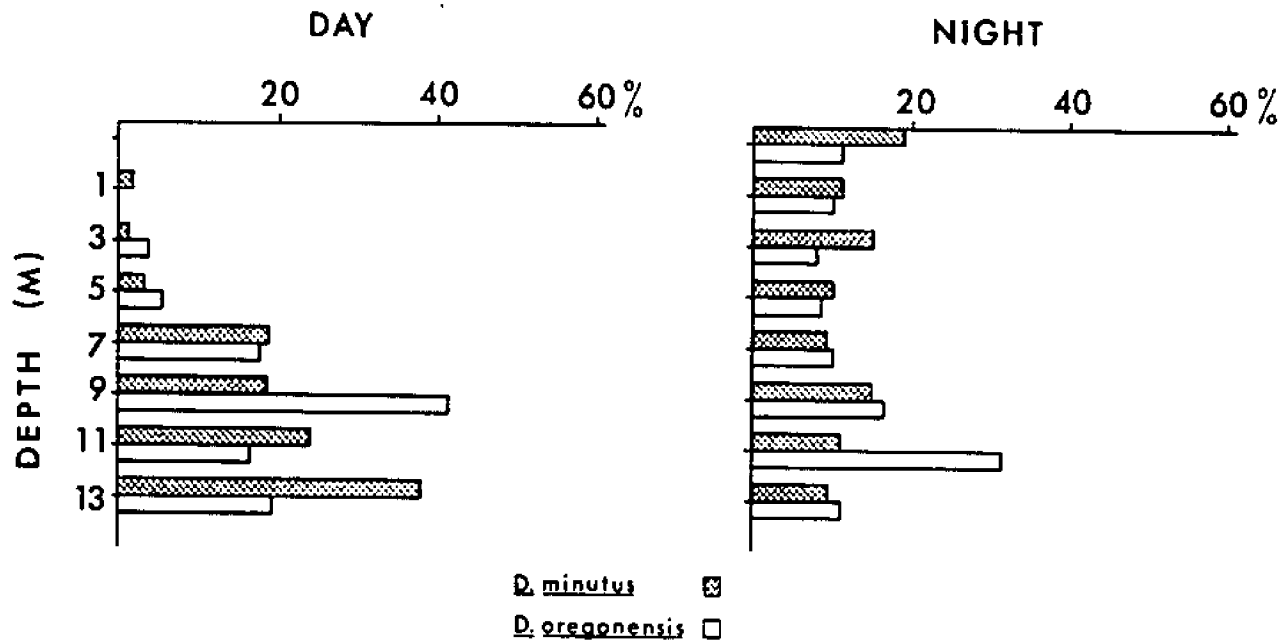


Figure 5. The vertical distribution of adult *Diaptomus minutus* and *D. oregonensis* in two day-night series of July and August, 1972.

D. oregonensis adults were found in this layer. The night samples of the upper 5 meters contained 55% of the adult D. minutus and 37% of the adult D. oregonensis. The summer nighttime behavior of these two diaptomids consisted of a general movement into the epilimnion. The overall effect was to produce a rather uniform distribution throughout the water column at the near-shore station. This distribution was similar to the daytime distribution during the winter.

The total numbers of adults collected at night on both dates were between two and three times as great as the daytime totals. The reason for the increase in numbers of adults collected at night was not obvious. Nevertheless, the species ratio was consistently 1:1 for day and night series. If the nighttime ratios were markedly different from the daytime ones, it would suggest differential horizontal movements by one or both species. This was not indicated by these two day-night series.

#### Size Measurements

The mean  $\pm$  2 SE and the mean  $\pm$  2 SD, presented graphically (after Hubbs and Hubbs, 1953) in Figure 6, indicated no size overlap between the two species. D. oregonensis males were always larger than D. minutus females by factors of 1.29, 1.26, 1.35, 1.27 (February-October). D. oregonensis males were always larger than D. minutus males by factors of 1.41, 1.38, 1.36, 1.35

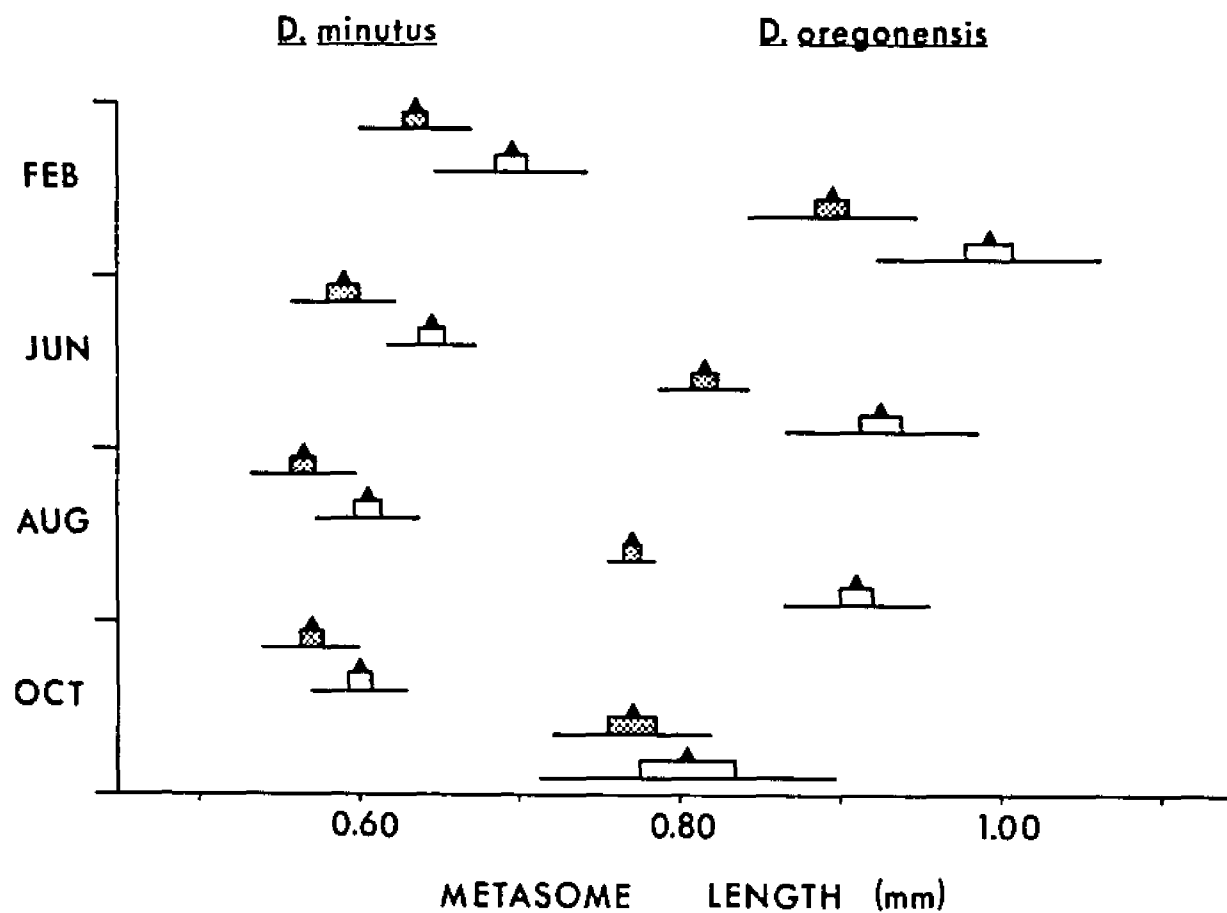


Figure 6. Variation in size of *Diaptomus minutus* and *D. oregonensis* in February, June, August, and October, 1972. (small peak = mean; length of white bar = 4 SE; length of underline = 4 SD)

(February-October). D. oregonensis females were always larger than D. minutus females by factors of 1.43, 1.44, 1.43, 1.32 (February-October).

The males and females of both species were larger in winter than in summer. Males of D. minutus exhibited the least seasonal variation, 12%, while the females of D. oregonensis were 24% larger in winter than in fall, the greatest seasonal variation. These seasonal changes in body length are smaller than those reported by Tomikawa (1972) for Sinodiaptomus volkanoni in small ponds in Hyogo Prefecture, Japan. Turvey (1968) reported seasonal variations of 8-13% in Clarke Lake, Ontario, where D. minutus coexisted with D. oregonensis. In a study of D. ashlandi in Lake Washington, Comita and Anderson (1959) found seasonal variations similar to those in Gull Lake but the summer adults were larger than the winter adults. Deevey (1960) discussed the relative effects of temperature and food on seasonal variation in body length in marine calanoid copepods. While the patterns and degrees of seasonal variation in body length are not uniform in expression, significant seasonal variation in body length would appear to be well documented and consequently, it is essential that any discussion of possible character displacement in diaptomids include consideration of this seasonal variation factor.

The metasome lengths of diaptomids (February collections) of Gull Lake are compared with those of Sherman Lake, in which D. minutus occurred alone, and Big Gilkey Lake and Three Mile Lake, in which D. oregonensis occurred alone (Table 1).

Table 1.--Variation in mean metasome length (mm) of Diaptomus minutus and D. oregonensis in February, 1972. (n>20 for each category)

|                 | <u>D. minutus</u> |        | <u>D. oregonensis</u> |        |
|-----------------|-------------------|--------|-----------------------|--------|
|                 | male              | female | male                  | female |
| Gull Lake       | 0.635             | 0.694  | 0.896                 | 0.992  |
| Sherman Lake    | 0.721             | 0.810  |                       |        |
| Big Gilkey Lake |                   |        | 0.868                 | 0.941  |
| Three Mile Lake |                   |        | 0.938                 | 1.011  |

The D. minutus males and females of Gull Lake were smaller than those of Sherman Lake by 12% and 14% respectively. D. oregonensis males and females of Gull Lake were larger than those of Big Gilkey Lake by 3% and 5% respectively. These differences are significant at the 99% level ( $P < 0.01$ ) as judged by the Student's "t" test. The winter data from these three lakes support the character displacement hypothesis in that D. minutus were smaller when coexisting in Gull Lake with D. oregonensis than when they occurred alone in Sherman Lake and D. oregonensis were larger in Gull Lake where they coexisted with D. minutus.

than when they occurred alone in Big Gilkey Lake. However, when the D. oregonensis of Gull Lake are compared with the D. oregonensis of Three Mile Lake, those occurring alone are equal to or larger than those coexisting with D. minutus.

Turvey (1968) reported mean metasome lengths (summer collections) for D. minutus and D. oregonensis from six headwater lakes where they co-occurred, 25 lakes where D. oregonensis was found alone, and 18 lakes where D. minutus occurred alone. These mean lengths, together with measurements I made of animals collected from several local lakes are presented in Table 2.

Table 2.--Comparison of mean summer metasome lengths (mm) of Diaptomus minutus and D. oregonensis of Gull Lake, Sherman Lake, and Three Mile Lake with those reported by Turvey (1968) from Ontario.

|                   | <u>D. minutus</u> |        | <u>D. oregonensis</u> |        |
|-------------------|-------------------|--------|-----------------------|--------|
|                   | male              | female | male                  | female |
| Gull Lake         | 0.57              | 0.60   | 0.77                  | 0.86   |
| Turvey (6 lakes)  | 0.59              | 0.65   | 0.82                  | 0.89   |
| Sherman Lake      | 0.61              | 0.65   |                       |        |
| Turvey (18 lakes) | 0.60              | 0.66   |                       |        |
| Three Mile Lake   |                   |        | 0.80                  | 0.89   |
| Turvey (25 lakes) |                   |        | 0.79                  | 0.88   |

The diaptomids of Gull Lake are from 3% to 7% smaller than the means from Turvey's study. The Sherman Lake data as well as those from Three Mile Lake correspond closely to the means presented by Turvey. The males of D. minutus of Gull Lake were 6% smaller than the mean length from Turvey's 18 lakes where D. minutus occurred alone and the females were 8% smaller compared to those occurring alone. Although the differences are rather small, the observations conform to the character displacement hypothesis. On the other hand, both sexes of D. oregonensis in Gull Lake are smaller (2-3%) than the Turvey means for this species occurring alone and thus do not support the character displacement hypothesis.

#### Grazing Experiments

The in situ grazing technique of Haney (1970, 1971) was used to obtain all the feeding data of this study. The technique is designed to collect information from which filtering rates of zooplankton can be calculated. The size and type of the algae chosen to be labelled should be appropriate for the animals of experimental interest. If the species of zooplankton to be investigated is known to have a lower limit of filterable particle size of  $100\ \mu\text{m}^3$ , it would be ill-advised to use a labelled cell of  $60\ \mu\text{m}^3$  since this should result in a filtering rate of zero using the in situ grazing technique. It would not be appropriate to conclude that the organisms in question were not

filtering during the experiment but rather that they were unable to handle cells with a volume of  $60 \mu\text{m}^3$ . In the same manner, if a filtering rate of 3 ml/animal/day is obtained when using a type of cell with a volume of  $1000 \mu\text{m}^3$  and a filtering rate of 1 ml/animal/day when using a cell with a volume of  $4000 \mu\text{m}^3$ , the appropriate conclusion would likely be that the organism under study is able to handle the  $1000 \mu\text{m}^3$  cell better than the  $4000 \mu\text{m}^3$  one.

The five species of green algae used during this study are listed in Table 3. Clearly, size is only one of several characteristics of labelled algae which may be important to the test animals in terms of their ability to handle the cells and consequently, to effect the resulting filtering rate (Fryer, 1954; Conover, 1966; Pepita, 1965; McQueen, 1970; Paffenhöfer and Strickland, 1970). Ankistrodesmus falcatus, a solitary cell of acircular or semi-lunate shape (2-3  $\mu\text{m}$  diameter) with apices gradually tapering to fine points, was used for 15 experiments on four dates during July and August, 1973. The filtering rates obtained using Ankistrodesmus falcatus are shown on Figure 7. The nighttime (2300-0200 hours) results show the expected pattern of increasing filtering rates with increasing body lengths (Brooks and Dodson, 1965; Burns, 1969; Burns and Rigler, 1967; McMahon, 1962). The daytime filtering rates, while lower than nighttime rates, also seem to follow this pattern except for the largest size

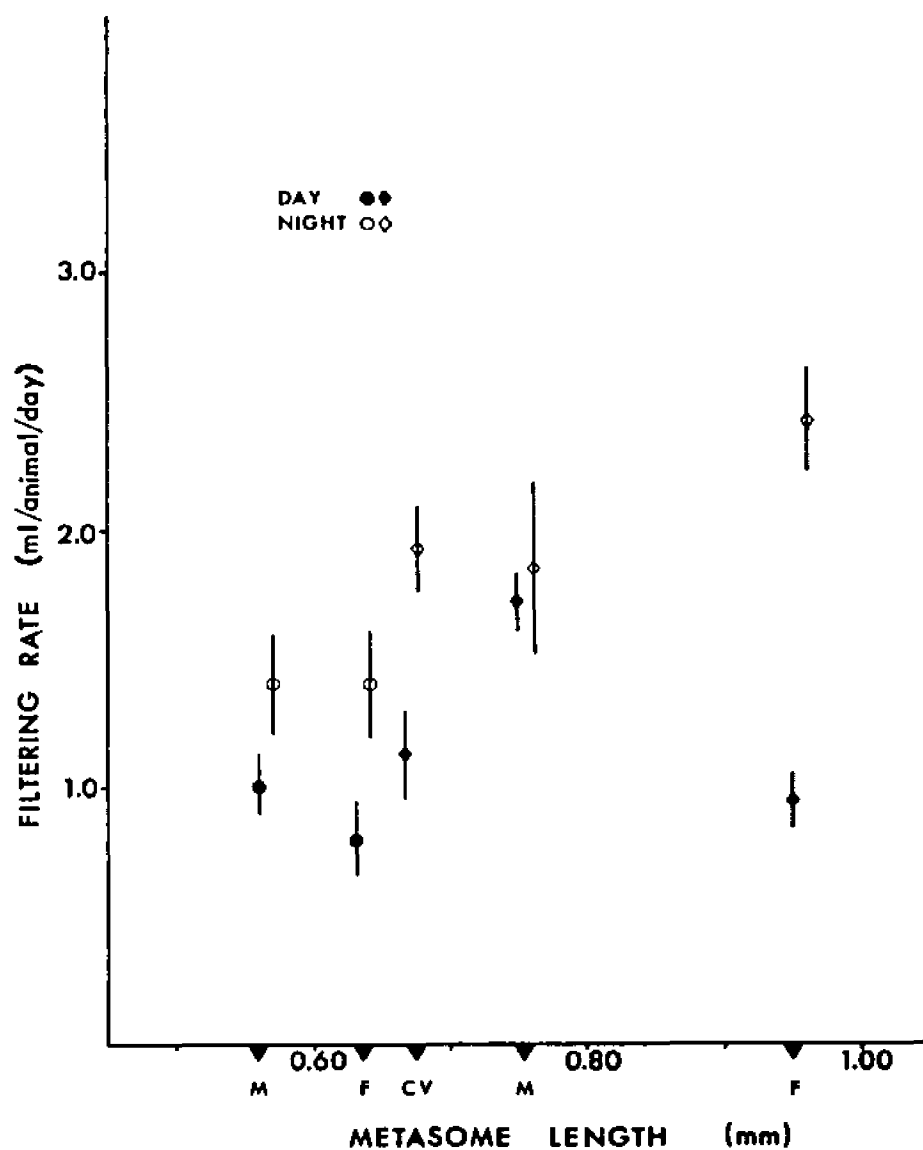


Figure 7. Comparison of the summer daytime and night-time filtering rates of Diaptomus minutus (●) and D. oregonensis (◆), using Ankistrodesmus falcatus (mean  $\pm$  SE).

category, D. oregonensis females. The mean daytime filtering rate for D. oregonensis females was only about 37% of the expected filtering rate, based on a linear regression line fitted to the four smaller size categories by the least squares method. This depression effect was observed in all four experimental series, using Ankistrodesmus falcatus as well as those using Scenedesmus accuminatus (Figure 8) and Chlamydomonas reinhardtii (Figure 9).

Table 3.--Size measurements of the five species of green algae used in the in situ grazing experiments.

| Cell Type                        | Diameter<br>( $\mu\text{m}$ ) | Range of<br>Volumes<br>( $\mu\text{m}^3$ ) | Mean<br>Volume<br>( $\mu\text{m}^3$ ) |
|----------------------------------|-------------------------------|--------------------------------------------|---------------------------------------|
| <u>Chlorella</u> sp.             | 3.6-4.5                       | 25-49                                      | 36.0                                  |
| <u>Chlamydomonas reinhardtii</u> | 7.2-10.8                      | 238-670                                    | 396.3                                 |
| <u>Ankistrodesmus falcatus</u>   | (68.0-90.5)<br>(length)       | 354-466                                    | 418.2                                 |
| <u>Chlamydomonas angulosa</u>    | 10.8-15.4                     | 670-1906                                   | 1307.5                                |
| <u>Scenedesmus accuminatus</u>   | 17.5-26.3                     | 1655-5406                                  | 4329.0                                |

The results obtained using the smallest alga, Chlorella sp. (volume  $36 \mu\text{m}^3$ ) are shown in Figure 10. The smallest size category, D. minutus males, had the highest filtering rates and an apparent trend of decreasing filtering rates with increasing size is evident in the other four categories. Some of this reverse tendency may be explainable in terms of the previously noted daytime

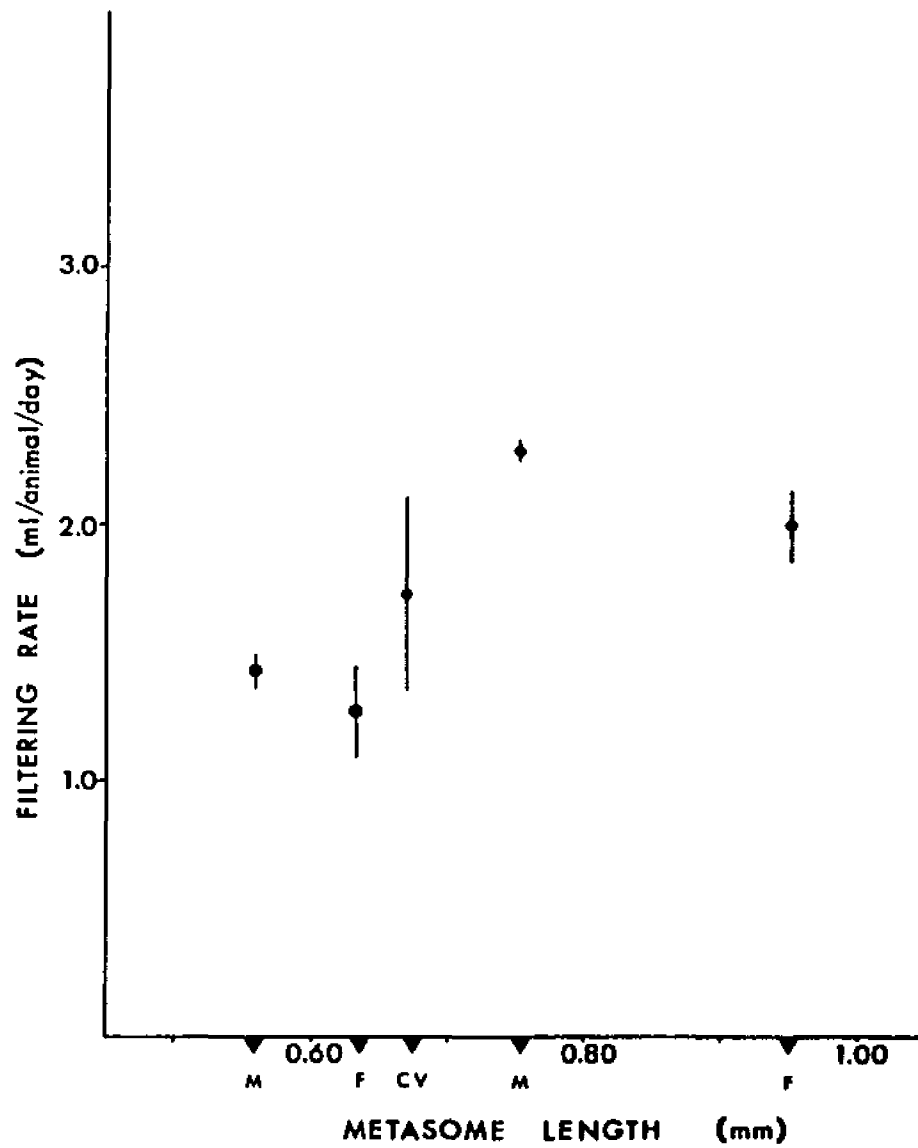


Figure 8. The summer daytime filtering rates of Diaptomus minutus (●) and D. oregonensis (◆), using Scenedesmus accuminatus (mean  $\pm$  SE).

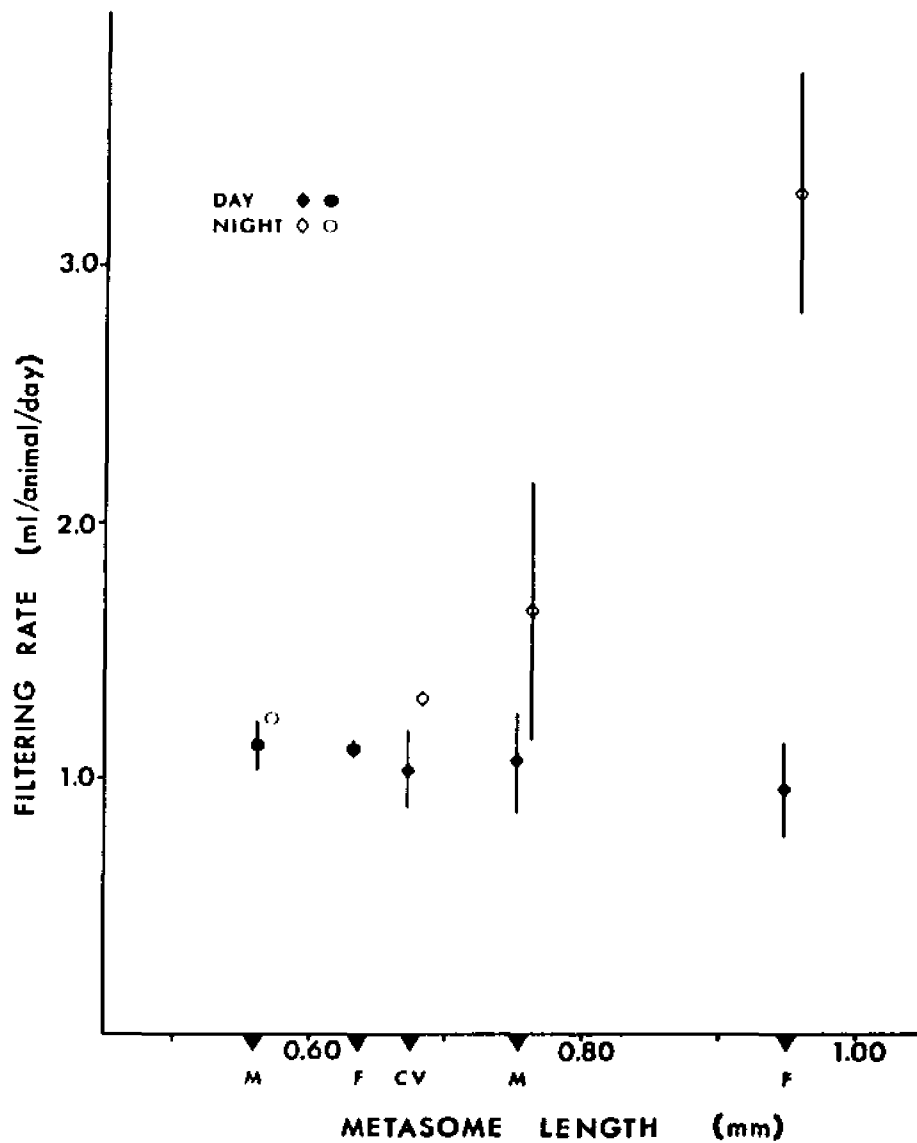


Figure 9. Comparison of the summer daytime and night-time filtering rates of Diaptomus minutus (●) and D. oregonensis (◆), using Chlamydomonas reinhardtii (mean  $\pm$  SE).

filtering rate depression but there is the strong suggestion that D. minutus can handle or capture the Chlorella-sized cells more effectively than can D. oregonensis.

This hypothesis is based on the observation that D. oregonensis females daytime filtering rates were calculated to be 2 ml/animal/day (Figure 8), using Scenedesmus accuminatus (volume  $4300 \mu\text{m}^3$ ) and 0.66 ml/animal/day (Figure 10), using Chlorella sp. (volume  $36 \mu\text{m}^3$ ). Since these experiments were performed during the same time period (July-August) and under similar conditions, it appears that the filtering rates of D. oregonensis females, for the smaller Chlorella sp., are much lower because these animals do not handle or capture Chlorella sp. as effectively as they capture larger cells like Ankistrodesmus and Scenedesmus. The filtering rates of D. oregonensis males (Table 5) also support this hypothesis.

Scenedesmus accuminatus is typically a colony of four cells in a curved series, each cell strongly lunate with sharply pointed apices. The convex walls are adjoined inwardly and the concave faces directed outward (Prescott, 1962). Although some fragmentation of colonies was observed, less than 20% of the labelled cells were single ones. With the exception of the filtering rates calculated for D. minutus males, the highest daytime filtering rates were obtained in experiments using the largest alga, Scenedesmus accuminatus (Table 4 and 5).

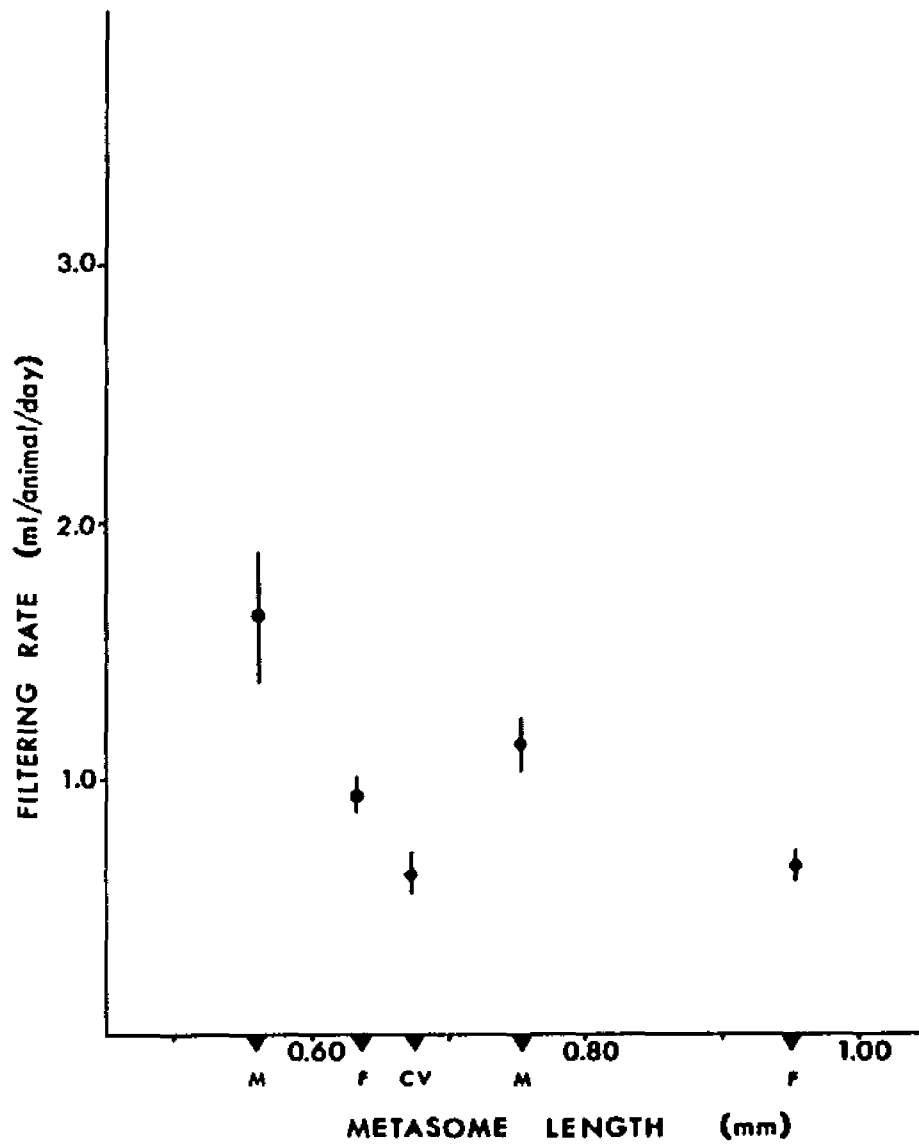


Figure 10. The summer daytime filtering rates of Diaptomus minutus (●) and D. oregonensis (◆), using Chlorella sp. (mean  $\pm$  SE).

Table 4.--Day-night filtering rates of Diaptomus minutus in Gull Lake, Michigan. All data are from summer experiments except where noted. Filtering rates are presented as mean ml/animal/day  $\pm$  SE. Animals were grouped into pellets before combustion to carbon dioxide.

|                                                            | Male            |                         | Female          |                 |
|------------------------------------------------------------|-----------------|-------------------------|-----------------|-----------------|
|                                                            | Day             | Night                   | Day             | Night           |
| <u>Chlorella sp.</u><br>(36 $\mu\text{m}^3$ )              | 1.63 $\pm$ 0.24 |                         | 0.95 $\pm$ 0.07 |                 |
| Dates                                                      | 2               |                         | 3               |                 |
| Pellets                                                    | 7               |                         | 7               |                 |
| Animals                                                    | 85              |                         | 107             |                 |
| <u>Chlamydomonas reinhardtii</u><br>(396 $\mu\text{m}^3$ ) | 1.14 $\pm$ 0.09 | 1.24                    | 1.12 $\pm$ 0.01 |                 |
| Dates                                                      | 1               | 1                       | 1               |                 |
| Pellets                                                    | 2               | 1                       | 2               |                 |
| Animals                                                    | 25              | 15                      | 21              |                 |
| <u>Ankistrodesmus falcatus</u><br>(418 $\mu\text{m}^3$ )   | 1.01 $\pm$ 0.11 | 1.40 $\pm$ 0.20         | 0.80 $\pm$ 0.14 | 1.40 $\pm$ 0.21 |
| Dates                                                      | 2               | 3                       | 2               | 3               |
| Pellets                                                    | 6               | 5                       | 7               | 5               |
| Animals                                                    | 81              | 29                      | 108             | 24              |
| <u>Chlamydomonas angulosa</u><br>(1308 $\mu\text{m}^3$ )   | 0.72(winter)    | 1.46(winter)            | 0.60(winter)    | 0.74(winter)    |
| Dates                                                      | 1               | 1                       | 1               | 1               |
| Pellets                                                    | 1               | 1                       | 1               | 1               |
| Animals                                                    | 13              | 8                       | 6               | 3               |
| <u>Scenedesmus accuminatus</u><br>(4329 $\mu\text{m}^3$ )  | 1.43 $\pm$ 0.07 | 1.07 $\pm$ 0.11(winter) | 1.42 $\pm$ 0.18 | 0.93(winter)    |
| Dates                                                      | 4               | 2                       | 4               | 1               |
| Pellets                                                    | 5               | 3                       | 6               | 1               |
| Animals                                                    | 65              | 26                      | 68              | 8               |

Table 5.--Day-night filtering rates of Diaptomus oregonensis in Gull Lake, Michigan. All data are from summer experiments except where noted. Filtering rates are given as mean ml/animal/day  $\pm$  SE. Animals were grouped into pellets before combustion to carbon dioxide.

|                                                            | Stage V         |                 | Male             |                             | Female          |                             |
|------------------------------------------------------------|-----------------|-----------------|------------------|-----------------------------|-----------------|-----------------------------|
|                                                            | Day             | Night           | Day              | Night                       | Day             | Night                       |
| <u>Chlorella sp.</u><br>(36 $\mu\text{m}^3$ )              | 0.63 $\pm$ 0.07 |                 |                  |                             | 0.66 $\pm$ 0.05 |                             |
| Dates                                                      | 2               |                 |                  |                             | 3               |                             |
| Pellets                                                    | 6               |                 |                  |                             | 12              |                             |
| Animals                                                    | 136             |                 |                  |                             | 234             |                             |
| <u>Chlamydomonas reinhardtii</u><br>(396 $\mu\text{m}^3$ ) | 1.04 $\pm$ 0.15 | 1.32            | 1.08 $\pm$ 0.18  | 1.66 $\pm$ 0.49             | 0.97 $\pm$ 0.17 | 3.31 $\pm$ 0.46             |
| Dates                                                      | 1               | 1               | 1                | 1                           | 1               | 1                           |
| Pellets                                                    | 2               | 1               | 2                | 2                           | 2               | 2                           |
| Animals                                                    | 36              | 23              | 47               | 48                          | 52              | 46                          |
| <u>Ankistrodesmus falcatus</u><br>(418 $\mu\text{m}^3$ )   | 1.13 $\pm$ 0.18 | 1.93 $\pm$ 0.16 | 1.72 $\pm$ 0.11  | 1.85 $\pm$ 0.33             | 0.95 $\pm$ 0.11 | 2.43 $\pm$ 0.19             |
| Dates                                                      | 2               | 3               | 3                | 3                           | 3               | 3                           |
| Pellets                                                    | 4               | 5               | 7                | 5                           | 8               | 5                           |
| Animals                                                    | 94              | 33              | 95               | 40                          | 139             | 26                          |
| <u>Chlamydomonas angulosa</u><br>(1308 $\mu\text{m}^3$ )   |                 |                 | 1.58<br>(winter) | 2.42<br>(winter)            | 1.65            | 2.10                        |
| Dates                                                      |                 |                 | 1                | 1                           | 1               | 1                           |
| Pellets                                                    |                 |                 | 1                | 1                           | 1               | 1                           |
| Animals                                                    |                 |                 | 9                | 4                           | 5               | 1                           |
| <u>Scenedesmus accuminatus</u><br>(4329 $\mu\text{m}^3$ )  | 1.73            |                 | 2.26 $\pm$ 0.29  | 2.30 $\pm$ 0.96<br>(winter) | 2.08 $\pm$ 0.07 | 2.74 $\pm$ 0.47<br>(winter) |
| Dates                                                      | 2               |                 | 3                | 2                           | 3               | 2                           |
| Pellets                                                    | 2               |                 | 4                | 2                           | 4               | 2                           |
| Animals                                                    | 21              |                 | 33               | 8                           | 43              | 9                           |

Chlamydomonas reinhardtii, a spherically-shaped alga (volume  $400 \mu\text{m}^3$ ), was used in the day-night series of August 3, 1973. A characteristic of some of the species of the genus Chlamydomonas is the habit of coming to rest, losing their flagella, and entering a quiescent phase. During this phase, vegetative cell division continues, accompanied by the secretion of mucilage which causes clumping (Prescott, 1962). While constant stirring and the action of centrifugation tended to reduce the clumping effect, the size range of labelled particles was much greater in experiments using cells of the genus, Chlamydomonas, than in those using Ankistrodesmus. In light of this clumping characteristic, the genus, Chlamydomonas, was utilized only sparingly. The results of the summer daytime experiments, using Chlamydomonas reinhardtii (Figure 9), are very similar to those obtained with Chlorella sp. (Figure 10). The nighttime filtering rate of D. oregonensis females appears to be higher than might be expected but since the mean represents only two pellets on one date, it is possible that additional experimentation would show the true mean to be somewhat lower. The number of adult D. minutus captured during the nighttime experiment was sufficient for only one pellet for each sex.

The summer nighttime results using Ankistrodesmus falcatus (Figure 7) show that except for D. oregonensis males, all nighttime filtering rates are higher than

daytime rates. Since there was a water temperature difference of about  $12^{\circ}\text{C}$  between the surface (night experiments,  $25^{\circ}\text{C}$ ) and the metalimnion (day experiments,  $13^{\circ}\text{C}$ ), one might expect an increase in nighttime filtering rates. The fact that neither of the male categories showed a significant day-night difference, as judged by Student's "t" test, does not support this expectation, however. The day-night difference in the D. minutus female and D. oregonensis V copepodid categories are significant at the 95% level ( $P < 0.05$ ) and the difference for D. oregonensis females was highly significant ( $P < 0.001$ ).

The existence of increased summer nighttime filtering rates was not entirely anticipated when this study was proposed. Nauwerck (1959) had actually found higher daytime than nighttime filtering rates for Eudiaptomus graciloides, a Eurasian diaptomid of comparable size to D. minutus and D. oregonensis, in Lake Erken, Sweden. Also, Haney and Hall (1974) could not detect day-night filtering rate differences in D. pallidus, using the in situ grazing method with  $^{32}\text{P}$ -labelled yeast cells.

Singh (1972), however, reported that the tropical calanoid, Rhinediaptomus indicus, in a shallow pond of South India, appeared to feed during the entire 24 hours of the day but showed increased feeding activity during the night hours. He drew this conclusion from his study in which he rated animals captured by placing them into one of

three categories: full gut, 50% full gut, empty gut. Wimpenny (1938) noted that some of his data for the marine calanoid, Paracalanus parvus, suggested a greater assimilation by zooplankton at night, based on the percentage of the gut filled with food. During laboratory experiments to determine the filtering rates of four species of marine planktonic copepods, Gauld (1951) found some evidence to support the hypothesis of Fuller (1937) that marine copepods removed diatoms more rapidly at night. Gauld (1953) attempted to explore this question experimentally as well as with field observations, using Calanus finmarchicus as the test animal. His laboratory observations indicated an absence of any day-night feeding rhythm. This observation was supported by the experiments of Richman and Rogers (1969). However, Gauld's field observations were that where vertical migration occurred, feeding took place mainly at the surface and was restricted to the hours of darkness. In the absence of vertical migration, he found Calanus to be abundant at the surface and feeding continuously throughout the 24-hour period. These evaluations were based on the percentage of the gut containing food.

Two experimental day-night feeding series were conducted during January and February, 1974, when there was an ice cover on Gull Lake. During this period, there was no detectable vertical migration and the water temperature was approximately 2°C throughout the water column.

There was snow on top of the ice but due to melting and wind action, it was rather patchy. The winter day-night experiments were conducted at 9-11 meters depth. The winter depth selection, as well as the summer ones, was based on adult densities observed from a vertical series of samples taken several hours prior to the experiments. Since the adult diaptomid populations were quite dispersed throughout the water column during the winter, it was necessary to pool animals from several experiments in order to obtain a suitable number for radioactivity assay. As a result, the winter data are not as extensive as those of the summer and are more variable. The winter daytime filtering rates (Figure 11), using Scenedesmus accuminatus, are strikingly similar to those obtained during the summer even though the water temperature was only about 15% as warm as it was during summer ( $14^{\circ} \pm 2^{\circ}\text{C}$ ). This observation would appear to be consistent with the trend reported by Kibby (1971) from his study of the effect of temperature on filtering rate of Daphnia rosea after a long term acclimation to low temperature. On the other hand, studies which utilized a short period (less than 48 hours) of temperature acclimation have shown Daphnia to exhibit filtering rate increases of 200% over  $5^{\circ}\text{C}$  (Burns and Rigler, 1967; McMahon, 1965; Nauwerck, 1959).

There were no D. oregonensis V copepodids found during the winter experiments. The depression of the

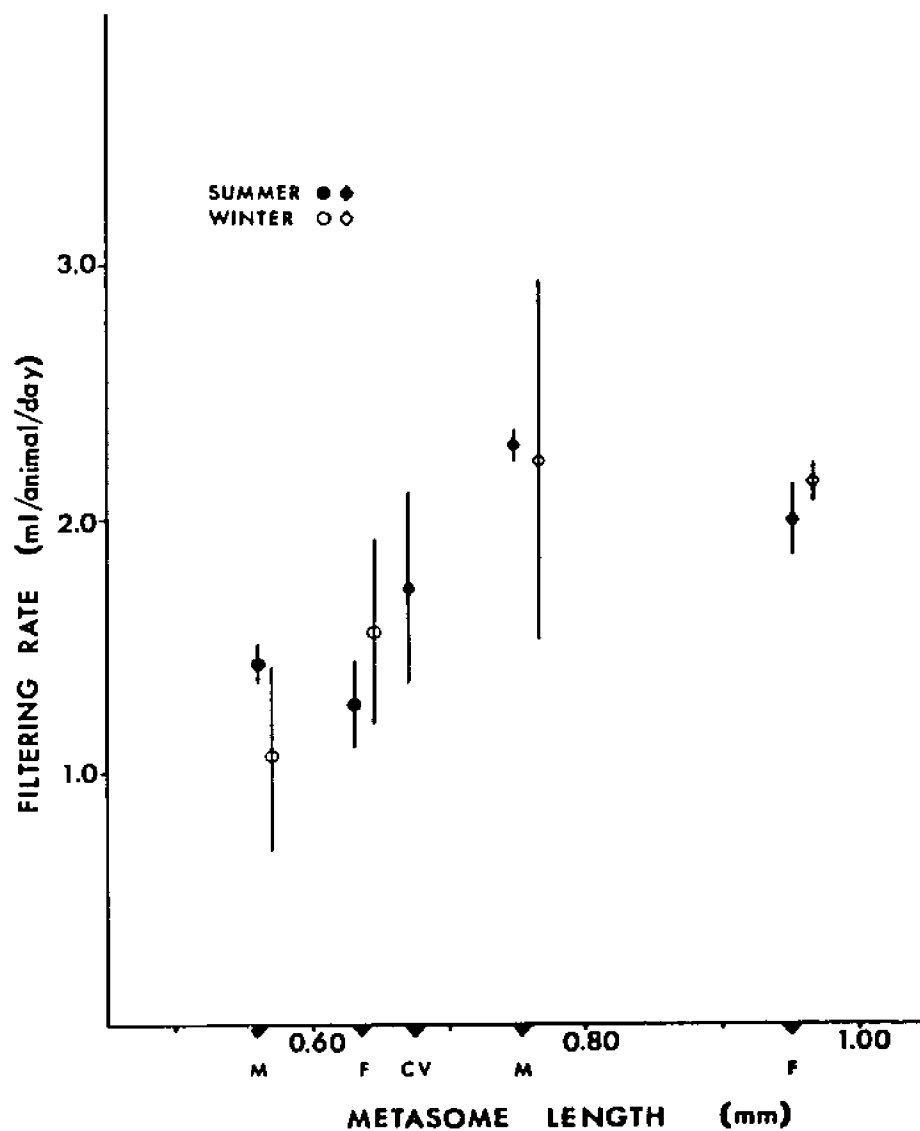


Figure 11. Comparison of winter and summer daytime filtering rates of Diaptomus minutus (●) and D. oregonensis (◆), using Scenedesmus accuminatus (mean  $\pm$  SE).

daytime filtering rates of D. oregonensis females persisted during the winter (Figure 11). The winter day-night differences appear to be less obvious in experiments using Scenedesmus accuminatus (Figure 12). Although the data for Chlamydomonas angulosa (Figure 13) suggest that the trend of higher nighttime rates persisted despite the absence of water temperature difference. Chlamydomonas angulosa, a broadly ovoid cell (volume  $1300 \mu\text{m}^3$ ), was used in the day-night experiments of January 16, 1974, only.

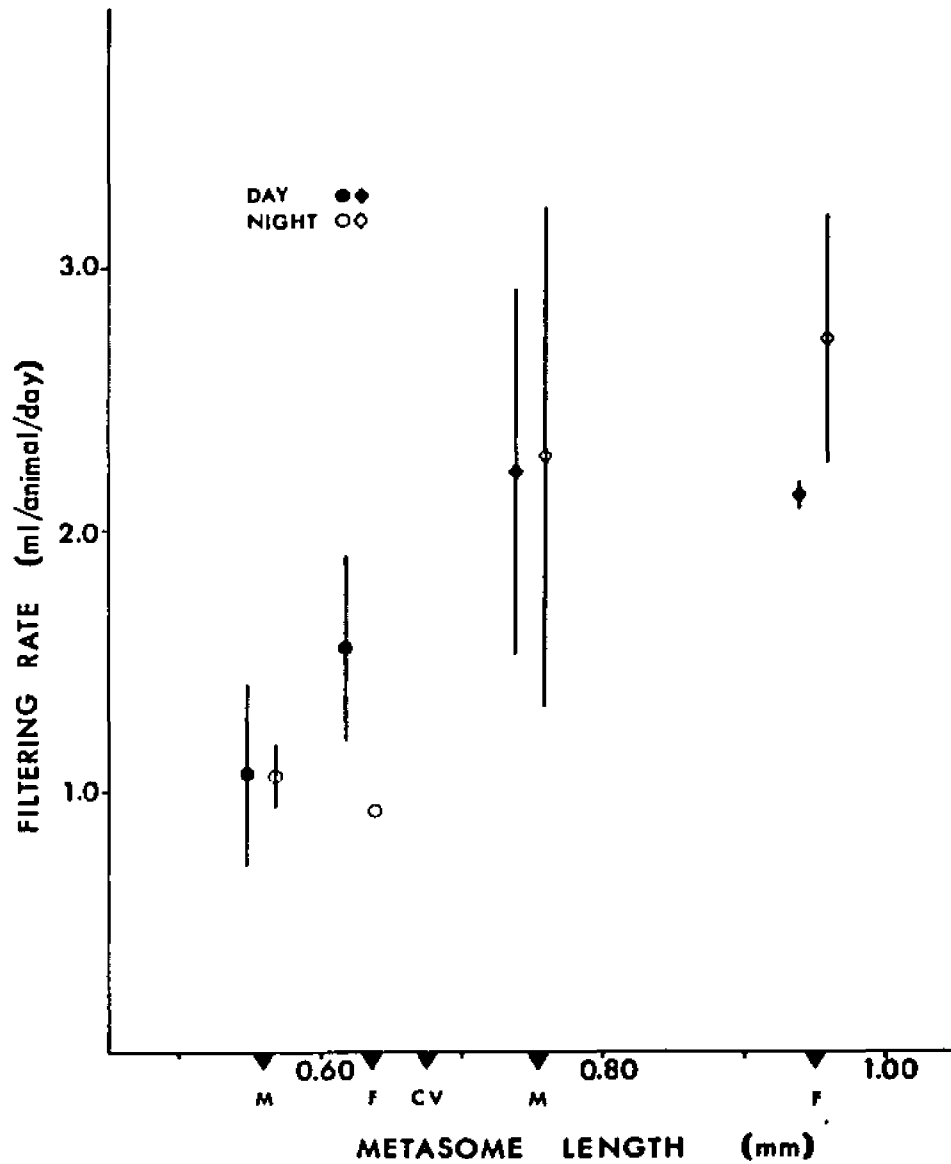


Figure 12. Comparison of winter daytime and night-time filtering rates of *Diaptomus minutus* (●) and *D. oregonensis* (◆), using *Scenedesmus accuminatus* (mean  $\pm$  SE).

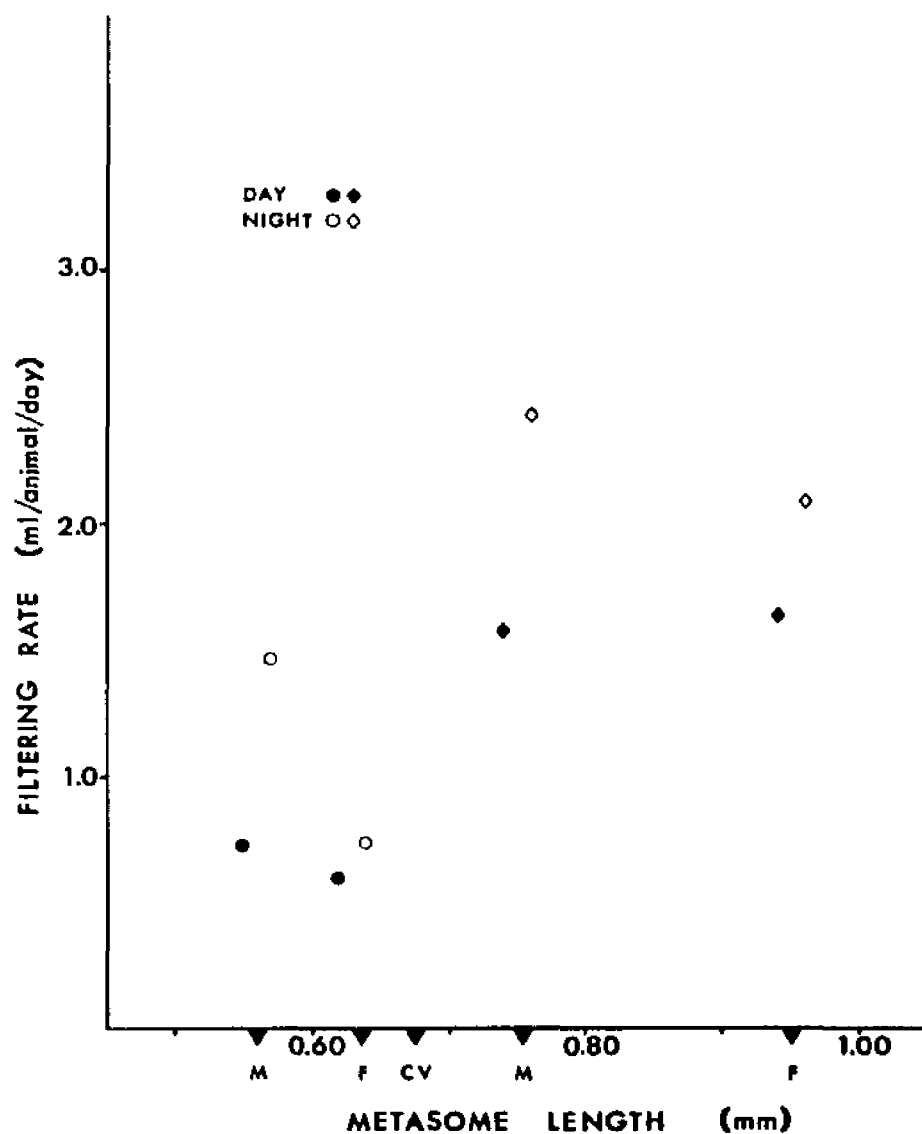


Figure 13. Comparison of winter daytime and nighttime filtering rates of *Diaptomus minutus* (●) and *D. oregonensis* (◆), using *Chlamydomonas angulosa*.

## DISCUSSION

### Habitat Coexistence

The theory of competitive exclusion would seem to predict that in the relatively homogeneous limnetic zone the plankton communities would tend toward a species structure consisting of one species per genus. Hutchinson (1961) discussed the apparent paradox between the prediction of this theory and the actual observations of numerous species of phytoplankton coexisting in the same relatively unstructured limnetic environment. Basically, he postulates that due to the constant changes of the limnetic environment, there is a permanent failure to achieve equilibrium. He also developed the idea that in freshwater, species of phytoplankton may have well-defined benthic littoral niches from which they may invade the limnetic zone.

Pennak (1957) found that the limnetic zooplankton communities which he studied in Colorado conformed to the expectations of the exclusion principle. However, other studies have shown that the co-occurrence of sympatric populations of planktonic copepods of the same trophic

level are not rare (Langford, 1938; Davis, 1954; Wells, 1960; Rigler and Langford, 1967; Hammer and Sawchyn, 1968; Turvey, 1968; Smrchek, 1973). Anderson (1970) has demonstrated that the larger species of the genus Diaptomus are, at least facultative, predators. Consequently, the assumption should not automatically be made that all diaptomids belong to the same trophic level. As an example, Sprules (1972) found D. shoshone co-occurred with D. coloradensis in a shallow pond of Colorado. Although some of the developmental stages of these two species may well belong to the same trophic level, the adult D. shoshone (2.47 mm) are functionally predators while the adult D. coloradensis (1.26 mm) are filter-feeding omnivores.

Since numerous examples of diaptomid coexistence are well-known, it is of interest to determine what factors are related to (or responsible for) this coexistence. The interest in this situation is heightened by the rather limited possibilities for separation of "habitat" (place) niches in the relatively unstructured planktonic environment (Elton, 1946; Pennak, 1957; Hutchinson, 1961). Sandercock (1967) concluded that in Clarke Lake, Ontario, D. minutus successfully coexisted with D. oregonensis by means of at least two mechanisms: size difference and seasonal separation. She found that, while there was considerable overlap of adult numbers, the pattern of change in numbers of D. minutus was significantly different from that of D.

oregonensis in all four years of her study as tested in the analysis of variance. In Clarke Lake, D. minutus had a seasonal maximum in spring while D. oregonensis had its maximum in summer. In contrast, the two species in Gull Lake did not exhibit this separation during the present study. The studies of these two lakes agree that the two species were not separated vertically. Rigler and Langford (1967) found a statistically significant difference of  $2.5 \pm 0.8$  meters between the daytime mean depth for D. minutus and D. oregonensis adults in 19 lakes of southern Ontario. However, Turvey (1968) observed that a frequency distribution of mean depth difference in the Rigler and Langford survey would show that for over 50% of the lakes in question, the difference was a meter or less. In any event, since the epilimnion is defined as a water mass with little or no thermal stratification and with constant mixing (Ruttner, 1963), it would seem to be difficult to ascribe a functional meaning to a difference between mean depths if both means were located in the epilimnion. Certainly, a more careful evaluation of conditions existing 1 or 2 meters apart is necessary before statistical differences can be interpreted biologically.

Recall that only the adults of these two species were considered in this study. With a complex life cycle consisting of 12 post-embryonic life history stages, it is clear that conclusions based on a study restricted to the

adult stage must be held as tentative until more information about the dynamics of at least the last three copepodid stages is obtained. Mullin and Brooks (1970) suggested that the marine calanoids, Rhincalanus and Calanus may achieve niche separation during the naupliar stages rather than as adults. These authors were unable to rear Calanus pacificus nauplii on Ditylum brightwelli but were successful in rearing Rhincalanus nasutus nauplii on this diatom. While separation of food niches of nauplii may occur, the hypothesis has not yet been supported by data. Czaika and Robertson (1968) have developed a key for the identification of the six copepodid stages of the diaptomids of the Great Lakes. They note that there is currently no way to separate the six naupliar stages to species.

Hutchinson (1967), citing the work of Ravera (1954), observed that even though each coexisting diaptomid species may share the same environment (biocoenosis), each species may exhibit a different generation time and/or numbers of generations/annum. So that the regularity of the seasonal ecological variations may enable a univoltine species to coexist with a multivoltine one.

In summary, the present study has not revealed the two species occupying different space niches. In the terms of my operational definition of coexistence, D. minutus and D. oregonensis adults in Gull Lake had

extensively overlapping vertical distributions and adults of both species moved into the epilimnion at night (summer). The third criterion of the definition proposed that both species should be present in relatively similar proportions. Figure 3 shows that this condition is also met.

The population curves (Figure 2) track each other quite closely. A spring and fall die-off of adult populations was observed in 1972 and 1973. While no definitive reason for these events can be given, their occurrence seems to coincide with the formation of the summer thermal stratification and its subsequent breakup in the fall. Although these events may well be synergistic phenomena involving other factors, in addition to water temperature.

To what factor may the controlled amplitude of the intervening periods be attributed? Paine (1966) offered an hypothesis which stated that local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species. He was able to show that the removal of the top carnivore from an intertidal community produced a decrease in species diversity. The absence of predation allowed for a "winner" in the competition for space.

Burbidge (1967) reported that American smelt in Gull Lake consumed copepods mainly during fall and winter. He did not routinely differentiate between cyclopoid and

calanoid copepods but he did observe that diaptomids were included in the smelt diet. During the period of summer stratification, smelt occurred primarily in the hypolimnion during the daytime but moved into the metalimnion at night. Consequently, smelt and adult diaptomids did not appear to share the same space niche during summer. His gut analysis data show that copepods represented less than 1% of the average total volume of food in the gut during summer, 6% during fall and 11% during winter. The role of young smelt and other planktivorous fishes present in Gull Lake is as yet unknown.

Among the zooplankton of Gull Lake, there were four predators present in significant numbers, at least during the summer. They were Mesocyclops edax and Cyclops bicuspidatus thomasi (cyclopoid copepods), Leptodora kindtii (cladoceran), and Epischura lacustris (calanoid copepod). The predation effect of Mesocyclops edax on a population of Diaptomus floridanus has been examined by Confer (1971). He found that the predation by M. edax was highly selective for diaptomids rather than for cladocerans. The maximum estimates of in situ predation rate for two Florida lakes were 1% and 6% of the standing crop of copepodids per day.

In Marion Lake, British Columbia, McQueen (1969) estimated that the Cyclops bicuspidatus thomasi copepodids IV and V and adults could have eaten 30% of the standing crop of D. oregonensis nauplii during the summer of 1967.

Laboratory experiments indicated that C. b. thomasi did not eat many diaptomid copepodids.

Epischura lacustris was present in Gull Lake in low densities during the present study but they have been shown to be predators upon diaptomid nauplii and, to some extent, early copepodids (Main, 1962).

Leptodora kindtii is a fluid feeding predaceous cladoceran which was also found in low density in Gull Lake. A study by Cummins, et al. (1969) suggested that Leptodora, as a predator (6-12 mm long), crops the most readily available prey, usually the most abundant prey zooplankton. In Sanctuary Lake, Pennsylvania, the principal prey zooplanktons included Diaptomus siciloides.

In the process of counting and sorting samples during the present study, I have observed both Mesocyclops edax and Cyclops bicuspidatus thomasi preserved in the act of consuming adult diaptomids as well as copepodids and nauplii. In light of the predation effects reported by Confer and McQueen, it would seem plausible to suggest that cyclopoid predation in Gull Lake may have been a dominant factor in preventing either species from achieving a higher seasonal maximum. This hypothesis states that the cycloid predators would always consume a higher number of the most abundant species of Diaptomus and then "switch" to the other diaptomid if the numbers of the second species began to increase. A rather similar hypothesis was experimentally

explored by Slobodkin (1964). He was able to show that experimental removal (predation by the experimenter, proportional to population densities) of Hydra in two-species laboratory cultures prevented densities from reaching exclusion levels, thus enabling two species to coexist where only one could do so in the absence of predation. This interpretation of predator-controlled competition of Diaptomus remains very tentative due to insufficient quantitative data.

#### Phylogenetic Considerations

As a part of a revision of the North American Species of Diaptomus, Marsh (1907) noted that although the genus occurs world-wide, all the North American species were peculiar to this continent. This suggested that the genus is quite susceptible to the influences of its environment. Marsh acknowledged that it was speculative to comment upon the affinities of the North American species of Diaptomus but he felt that some reasonable observations, nevertheless, could be made. He felt that a phylogenetic scheme could be composed based on consideration of structural relationships and species distribution patterns. He discussed his criteria for primitive structural characteristics though he noted they are of necessity, largely conjecture.

Of interest to the discussion of the results of the present study is the opinion of Marsh that both D.

oregonensis and D. minutus are the primitive form of their respective groups within the phylogeny of the genus, Diaptomus. D. minutus was noted as somewhat of a paradox because the fifth pair of legs of the males show marked reduction that could be considered indicative of high specialization but its wide geographical distribution, noted earlier in this paper, strongly suggests that it represents an early form of its group. Marsh felt the wide geographical distribution should carry more weight than its structural reductions.

D. minutus was identified as a highly variable species, in terms of periods of reproduction and seasonal population dynamics, by Schindler and Novén (1971). These authors were attempting to establish baselines for future fertilization experiments in two shallow lakes of the Experimental Lakes Area, northwestern Ontario. They concluded that the seasonal dynamics of D. minutus in the two lakes studied appeared to bear little relation to either phytoplankton abundance or temperature and thus attempts to identify changes in D. minutus populations due to fertilization would most probably prove futile. This observation of apparent plasticity of reproductive capacity, along with the opinion of Marsh, tend to support the idea that D. minutus functions as a generalist (Pianka, 1974) in zooplankton communities. D. oregonensis also has a rather wide geographical distribution as reported by Marsh

(1929) and thus also qualifies as a generalist. The original identification was made from a collection from Portland, Oregon, but it apparently is not common west of the Rocky Mountains. It has been reported east as far as New Brunswick and the Northwest Territories on the north although it is most common in the Great Lakes region.

### Character Displacement

The term, character displacement, was introduced by Brown and Wilson (1956) to describe the pattern that results when two closely related species have overlapping ranges. When the one species occurs alone, it tends to converge upon or be quite similar to the other species. In contrast, however, in the area where the two species co-occur, the populations are more divergent and easily distinguished. That is to say, they "displace" one another in one or more characters. It should be noted that contrary to the examples of vertebrates cited by Brown and Wilson and Hutchinson (1959), the metasome lengths of D. minutus and D. oregonensis do not overlap in lakes where they occur alone.

Rigler and Langford (1967) performed measurements of body length on animals collected in their survey of 100 lakes in southern Ontario. They compared data from 33 lakes in which D. minutus and D. oregonensis co-occurred with 13 lakes in which D. minutus was found alone and 13 lakes with D. oregonensis alone. There was no difference noted for D. oregonensis and in the case of D. minutus,

rather than divergence, they found a significant convergence! When it occurred with D. oregonensis, it was 8-10% longer than when it occurred alone. Turvey (1968) also was unable to find any evidence of character displacement, in terms of body lengths.

The length measurements presented in this study (Table 1 and 2) indicate that while diaptomids exhibit generally similar measurements, the variation from lake to lake tends to be large enough to obscure evidence of character displacement even if it did occur.

Cole (1966) reported that the cephalothorax length of diaptomids occurring in temporary ponds of Arizona were significantly greater than those of the same species occurring in permanent lakes. Rigler and Langford (1967) noted a population of D. oregonensis in one lake that was unusually small. They were not able to explain this occurrence. Examples such as these tend to reinforce the opinion of Turvey (1968) that while character displacement may indeed take place, controlled experiments will be necessary in order to present convincing evidence of its reality in calanoid copepods.

#### Filtering Rates

In a review of respiration and feeding in copepods, Marshall (1973) noted the assumption that, at least in freshwater, size of body is correlated with size of food and so that small copepods can eat only small food

particles, large copepods can eat both small and large ones (Brooks and Dodson, 1965). The hypothesis that a difference in diaptomid body length represents a difference in food niche is supported by very few data. One supporting case was reported by Fryer (1954). He found that Diaptomus laticeps (1.54-1.65 mm) co-occurred with Diaptomus gracilis (1.14-1.23 mm) in Lake Windermere, England, during the period January through March, 1953. His study of gut contents revealed that D. laticeps fed almost exclusively on the diatom Melosira italica during the time of the study while D. gracilis fed mainly on "tiny spherical green algal cells and fine detritus . . . of vegetable origin" with very few diatoms. He also observed that neither species collected the diatom, Asterionella formosa, although it was abundant during the period of his study.

The results of the experiments in the present study, using Chlorella (volume  $40 \mu\text{m}^3$ ) indicate that the larger diaptomid, D. oregonensis, was unable to collect this small-sized food particle as effectively as did the smaller diaptomid, D. minutus (Figure 10). While no precise estimate of this decreased effectiveness can be calculated, a comparison of the Chlorella data with those of Scenedesmus (Figure 8) suggests that the decrease was on the order of 50%. This observation tends to show that the Brooks and Dodson hypothesis mentioned above is an oversimplification of the true relationship between larger

and smaller diaptomids. In laboratory experiments, McQueen (1970) found that D. oregonensis females and stage V copepodids did not filter small diatoms, volume less than  $125 \mu\text{m}^3$ , in experiments in which they were offered a mixed culture of diatoms, genus Navicula. This size threshold, however, was not as distinctly evident when they were fed natural phytoplankton from Marion Lake, British Columbia. Although Calanus is much larger (3.2-5.4 mm, total length) than Diaptomus, Marshall and Orr (1955a) found a similar decrease in effectiveness, below  $10 \mu\text{m}$  diameter. These results, while hardly conclusive, do tend to support the hypothesis I have proposed, small cells are collected less effectively than larger cells by D. oregonensis (larger diaptomid).

The Brooks and Dodson hypothesis proposed that the upper particle size limit for small herbivorous zooplankton would be approximately  $15 \mu\text{m}$  diameter. Bogatova's study (1965) of Eudiaptmus graciloides (1.0-1.3 mm, overall length) showed selection of algae in the 4 to  $20 \mu\text{m}$  diameter range. Jorgensen (1966) expressed the opinion that particles below 30-50  $\mu\text{m}$  diameter can be filtered by Calanus whereas larger cells are seized raptorially. In a study of zooplankton grazing, Porter (1973) found that gut analysis of D. minutus yielded results which tended to confirm the upper limit of 30-50  $\mu\text{m}$  diameter suggested by Jorgensen. It cannot, of course, be determined by gut

analysis whether the large cells were filtered or seized raptorially but her results indicate that the smaller diaptomid, D. minutus, can collect cells considerably larger than proposed by Brooks and Dodson. In addition, the fact that Ankistrodesmus falcatus was successfully collected by both species in the present study offers evidence that both species can consistently handle larger cells since this species of green algae is usually between 60 and 90  $\mu\text{m}$  long. Gauld (1964) as well as Jorgensen believed that particles larger than 40  $\mu\text{m}$  diameter were excluded from the filter chamber by short setae. These setae might not be effective, however, in preventing Ankistrodesmus falcatus from entering the filter chamber due to its needle-like shape.

In terms of cell volume, Scenedesmus accuminatus was the largest cell ( $4300 \mu\text{m}^3$ ) used during the present study. The filtering rates calculated from experiments using this large cell were the highest obtained for all categories except for D. minutus males. The results seem to indicate that both species are capable of handling larger cells more effectively than smaller ones although there is the hint that D. minutus males may handle cells of the volume of Scenedesmus accuminatus and larger ones somewhat less effectively than smaller ones.

In summary, the range of overlap in particle size collection appears to be between 8  $\mu\text{m}$  (mean diameter of

Chlamydomonas reinhardtii) and 22  $\mu\text{m}$  diameter (mean diameter of Scenedesmus accuminatus). D. minutus exhibited effective collection below that size range and it appears likely that future experiments will demonstrate that D. oregonensis effectively collect cells larger than those in the range of overlap. McQueen (1970) has already shown that D. oregonensis females are capable of collecting cells with a mean cell volume of  $10,000 \mu\text{m}^3$ .

In order to evaluate this size-partitioning hypothesis, it would be helpful to know the nature of the size spectrum of food particles available. The distribution of phytoplankton in Gull Lake during 1973 has been intensively studied by Moss (personal communication). He found 1000 cells/ml at the surface and 300 cells/ml in the metalimnion in the 2-8  $\mu\text{m}$  size category during July and August. This size category included Rhodomonas minuta, green flagellates, and several colonial bacteria.

The principal genera in the 8-22  $\mu\text{m}$  size category were Cyclotella, Peridinium, Cryptomonas, and Oocystis. At the surface, the density was 320 cells/ml and in the metalimnion, 260 cells/ml.

In the 25-50  $\mu\text{m}$  size category, the density was 1260 cells/ml at the surface and 430 cells/ml in the metalimnion. Dinobryon was the major contributor in this size range, however, the presence of a lorica around the protoplast and the tendency to form branching colonies may make this

species unattractive as a diaptomid food item. Even though a quantitative statement describing the 25-50  $\mu\text{m}$  size category is difficult to make because the relative palatability of algal species is unknown, it does appear that a significant number of cells are present in this size category for D. oregonensis to exploit during the period of summer stratification.

Relatively few studies have been conducted to determine the filtering rates of freshwater diaptomids although there is a large literature on the feeding of marine calanoids (see Marshall and Orr, 1955b). Nauwerck (1959) reported filtering rates between 0.3 and 2.8 ml/animal/day for Eudiaptomus graciloides, using an in situ method with  $^{14}\text{C}$ -labelled cells. These results agree quite well with those reported by Malovitskaya and Sorokin (1961) for E. graciloides and E. gracilis (0.7-4.1 ml/animal/day). Richman (1966) studied the effect of phytoplankton concentration on the filtering rates of adult D. oregonensis and reported a range of filtering rates between 0.3 and 2.5 ml/animal/day. From a study of the energy budget of D. siciloides, Comita (1964) obtained filtering rates between 1.0 and 2.0 ml/animal/day. McQueen (1970) conducted feeding experiments, using D. oregonensis females and stage V copepodids as test organisms. Employing a variety of types of cells, he reported that the filtering rates increased with increasing cell volume until a maximum

rate was reached. Beyond this optimum size, the filtering rates decreased with increased cell size. He reported maximum filtering rates of 11.2-12.9 ml/animal/day for natural phytoplankton (mean volume 179-524  $\mu\text{m}^3$ ). The largest size category reported in his natural phytoplankton experiments was 12-15  $\mu\text{m}$  diameter (mean volume, 1150  $\mu\text{m}^3$ ). McQueen obtained a similar pattern in experiments using a mixture of Navicula diatoms instead of natural phytoplankton; however, the maximum filtering rate was 2.1 ml/animal/day for the Navicula mixture compared to 12.9 ml/animal/day for the natural phytoplankton. It is of interest to note that while both rates were calculated by the differential cell count method, the Navicula mixture data was obtained by using a Coulter counter while counts of the natural phytoplankton experiments were obtained using an inverted microscope. While filtering rates over 100 ml/animal/day for marine calanoids have been reported (Marshall and Orr, 1962; Richman and Rogers, 1969), the McQueen study is the only one, to date, reporting rates of over 5 ml/animal/day for freshwater calanoids.

The filtering rates obtained during the present study agree very well with previous studies except for the natural phytoplankton portion of McQueen's work. This seems rather remarkable in light of the variety of experimental techniques used in the studies mentioned above.

The relationship between filtering rate and body size for Daphnia rosea can be described approximately by the Power Law:

$$Y = aX^b,$$

where Y is filtering rate, X is body length, b is the slope of the line, and a is the intercept on the y axis (Burns and Rigler, 1967). These authors calculated a slope of 3.02 for D. rosea over a body length range of 0.64 to 1.60 mm. In a study involving four species of Daphnia, Burns (1969) reported slopes of 2.16 (15°C), 2.80 (20°C), and 2.38 (25°C).

Brooks and Dodson (1965) suggest that the food-collecting surfaces are proportional to the square of the body length. Egloff and Palmer (1971) found that the area of the filtering setae of thoracic limbs 3 and 4 of Daphnia magna and D. rosea indeed supported the Brooks and Dodson hypothesis. These authors noted, however, that when Burns (1969) compared the filtering rates of these two daphnids to their body lengths, the slope values were distinctly greater than predicted by the Brooks and Dodson hypothesis. These studies suggest that the filtering rates of Daphnia increase proportional to numbers between the square and the cube of body length.

Using the least squares fit method, a slope of 2.28 was obtained for daytime experiments employing

Ankistrodesmus falcatus and 2.33 for those using Scenedesmus accuminatus when the D. oregonensis female category was not included. Although the diaptomid daytime filtering rates of this study are lower than those reported for Daphnia, the body length-filtering rate relationship is very similar (excluding D. oregonensis females). The daytime filtering rate depression of D. oregonensis females is very striking. Although perhaps less extreme, the D. minutus females also exhibited daytime filtering rate depression. I have been unable to locate any similar cases of depressed female filtering rates although very few studies have investigated sexual differences in the filtering rates of freshwater diaptomids. Nauwerck (1959) observed similar filtering rates for both males and females of Eudiaptomus graciloides. Investigations of sexual differences in marine calanoids have shown male filtering rate depression. Mullin (1963) reported that the grazing rates of male Calanus helgolandicus, feeding on the diatom, Ditylum, were only between 10% and 33% as great as females of the same species under identical laboratory conditions.

Laboratory feeding experiments by Richman and Rogers (1969) yielded data that suggest that Calanus helgolandicus, feeding on the diatom, Ditylum brightwellii, utilize a combination of passively filtering small cells and actively hunting large ones. Conover (1966, 1968) found that in Calanus hyperboreus "encounter" feeding and

"filter" feeding were separate and mutually exclusive processes. His evidence indicated that the percentage of time spent in one mode varied according to external conditions. "Encounter" feeding was proposed by Cushing (1951) to describe the capture of large cells that come into contact with the feeding appendages. Wilson (1973) also accepted the existence of two feeding modes, nonselective filtering and selective grasping, and hypothesized that there is a constant alternation of modes in the calanoid feeding pattern.

In light of the above hypothesis, one possible explanation of the daytime depressing of the female filtering rates of the present study might be that during the daytime, while residing in the metalimnion, the females switch from a predominately filtering mode of feeding to a mainly "encounter-feeding" mode or to a regime of alternation of these two modes. Since small cells, Chlorella sp. and Chlamydomonas reinhardtii, were collected by the females, although at reduced rates, a constant alternation between a filtering mode of feeding and an "encounter-feeding" mode would seem to offer a more plausible hypothesis than a mainly "encounter-feeding" mode. The hypothesis proposes that while in the "encounter-feeding" mode, small cells cannot be collected since a large cell is being handled by the feeding appendages. During the filtering feeding mode, small cells are collected by the feeding

appendages and large cells are ignored or prevented from entering the filtering chamber by setae as proposed by Gauld (1964). This hypothesis tends to support the proposal that I made earlier in this section that D. oregonensis utilizes cells larger than those found in the range of overlap. This daytime feeding behavior of alternating "encounter-feeding" mode with a "filter-feeding" mode could thus serve as a mechanism of food niche differentiation.

The daytime depression of female filtering rates was evident during the winter as well as the summer (Figure 11). The winter conditions of light were generally similar to those of summer but there was no obvious migration under the ice and the temperature was approximately 10°C less than in summer (metalimnion). Light would seem to be the only constant parameter that could serve as the signal mechanism for this proposed daytime switch in feeding strategy that would be present in summer as well as winter unless there would be an innate day-night filtering rhythm in Diaptomus. This condition, however, doesn't seem likely in light of the experimental work of Richman and Rogers (1969) and the observations of Gauld (1953) which support the idea that there is no innate day-night filtering rhythm in the marine calanoid, Calanus.

The summer nighttime experiments were conducted at a depth of 1 meter. This was in contrast to the daytime experimental depth of 11-15 meters. The summer nighttime

rates (Figures 7, 9) are higher than the summer daytime ones. The day-night difference is most striking in the female and stage V categories. I propose that the difference between the day and night filtering rates of D. oregonensis females, for example, was composed of two components. The first, a daytime filtering rate depression and the second, a nighttime filtering increase. This hypothesis is based on the comparative performances of the other size categories of this study. I believe these comparisons are especially appropriate since all diaptomid size categories participated together in each experiment.

The nighttime increases observed in the present study are directly opposite from those of Nauwerck (1959) who reported higher daytime than nighttime filtering rates for E. graciloides although he did find higher nighttime rates for Daphnia. The winter day-night data (Figure 12) show a muting (or absence) of day-night differences. This could suggest that the increased summer nighttime filtering rates were the result of the large temperature difference between the metalimnion (daytime experiments) and the epilimnion (nighttime experiments) since there was no temperature difference between the day and night experiments under ice cover. Alternatively, the higher nighttime filtering rates may be associated with the day-night migration event.

Much has been written about the significance of vertical migrations of marine crustaceans in particular (Cushing, 1951; Hardy, 1956; Bainbridge, 1961; David, 1961; Wynne-Edwards, 1962; McLaren, 1963; Mauchline and Fisher, 1969; Kerfoot, 1970). Kerfoot (1970) developed a quantitative approach, "pathway analysis," for deriving curves of potential food energy considering the variables of light intensity, productivity, time, and depth. While this approach leads to some interesting ideas, a stated constraint was that the moment the isolumes reach the surface, feeding of individuals within that light range ceased. Consequently, the data of the present study are unsuited for application of the above hypothesis. Kerfoot's contention that light is the dominating stimulus for migration may well be correct.

McLaren (1963) examined the then existing theories about the adaptive values of vertical migration and found them inadequate. He proposed his own theory that an energy bonus may be achieved as a consequence of the more efficient uptake of food at higher temperatures (surface water at night) and the more efficient directing of energy to growth at lower temperatures (metalimnion during daytime). He assumed that migrant zooplankton do not feed constantly and can fill their daily nutritional needs during the time spent in surface water if food is sufficiently rich. However, McLaren (1974) indicates that he now believes that

his earlier explanation of the demographic consequences of vertical migration involved a probably erroneous metabolic model. He offers data to support the proposition that increased fecundity does result from part-time residence in colder water but notes that there are exceptions depending upon the type of life cycle, amount of food present, and naupliar mortality rates.

In a review of the biology of euphausiids, Mauchline and Fisher (1969) make a number of perceptive statements about the importance of vertical migration in light of the complex literature and often contradictory observations and generalizations. These authors offer the opinion that vertical migration probably confers a number of benefits on the organisms rather than one of great significance. They consider it unlikely that a proven general reason for day-night migration of planktonic organisms will be found since they believe it is quite probable that the most important benefits derived by one species (group) will differ from those derived by another species (group). Their conclusion was that the various theories previously offered to explain vertical migration may all be true rather than any one being of paramount importance.

Although the physical parameters are generally similar for migrating organisms in Gull Lake, the strategy of survival or prosperity for Daphnia, which has a short life expectancy, high reproductive capacity via

parthenogenesis, and short developmental time would intuitively seem to be quite different from Chaoborus, which migrates as larvae, then metamorphoses into pupae, and later into flying sexual adults. In a similar way, diaptomids, with only sexual adults, mating rituals, and 12 post-embryonic free living life history stages would seem likely to need yet another strategy. So that it seems reasonable to accept the hypothesis that for the different groups of migrants there will be varying combinations of benefits derived from summer vertical migration even within a single lake.

Additional summer nighttime feeding experiments performed in a vertical series may produce a more definitive picture of nighttime filtering rates and thus support or refute the theory that increased nighttime rates are directly related to temperature. Porter (1973) reported very few diatoms as part of the gut contents of D. minutus while McQueen (1970) found that D. oregonensis females readily filtered diatoms. Further in situ feeding experiments, using diatoms as labelled cells, might show selection based on cell-type that could enhance the food niche differentiation of these two species of Diaptomus.

As noted earlier, Rigler and Langford (1967) reported D. minutus co-occurred with D. oregonensis in 45% of 100 lakes which they studied. D. oregonensis occurred alone in 24 lakes and D. minutus occurred alone in 19

lakes. Clearly, coexistence is quite possible but does not always occur. My study did not produce evidence that would indicate why some lakes have only one diaptomid species present.

It may be suggested that the condition of coexistence of two species of Diaptomus reflects a temporary phase in the eutrophication process of a lake. With the exception of the Great Lakes, very little sampling data is available to use in considering this hypothesis. However, it seems reasonable to infer from the study of Rigler and Langford (1967) that diaptomid coexistence is not a temporary condition since the 100 lakes included in their study ranged from extreme oligotrophy to extreme eutrophy.

MacArthur (1972) pointed out that several competitors can much more easily outcompete and eliminate a species than can a single competitor. This concept of diffuse competition may help to explain the distribution of diaptomids. I have proposed that the range of food particle sizes for D. minutus is 3 to 22  $\mu\text{m}$  diameter and that the range of D. oregonensis overlaps from 8 to 22  $\mu\text{m}$  diameter and extends beyond to larger cells. If these two species of Diaptomus were the only herbivores in the limnetic zone, it could be proposed that while there is a zone of overlap in the food particle size spectrum (8-22  $\mu\text{m}$  diameter), D. minutus has a relative refuge (3-8  $\mu\text{m}$  diameter) below the overlap zone as part of its food niche

while D. oregonensis probably has one above the overlap zone as part of its food niche. However, since the herbivorous zooplankton communities usually consist of varying combinations of rotifers, cladocerans, cyclopoid copepods, and other calanoid copepods, the possibility of one or the other species of Diaptomus being "sandwiched" between several competitors and being unable to survive would seem intuitively quite possible. To date no investigations of diffuse competition have been carried out with the zooplankton.

## SUMMARY AND CONCLUSIONS

Factors related to the coexistence of Diaptomus minutus (0.84-0.93 mm) and Diaptomus oregonensis (1.15-1.34 mm) in Gull Lake, Michigan, were explored during 1972-1974. Conditions requisite for using the term, coexistence, were defined since its usage in the literature has been rather imprecise. The in situ grazing method of Haney (1971), using  $^{14}\text{C}$ -labelled algae, was employed in an effort to determine whether resource allocation was accomplished on the basis of cell size. Advantages of this technique include very short experimental time, naturalness of conditions, high sensitivity, and the ability to include both species together in each experiment. The following conclusions emerged from this study:

1. In Gull Lake, D. oregonensis and D. minutus occupied the same space niche. There was extensive overlap of vertical distributions as well as an absence of pronounced seasonal population maxima. During the summer stratification period, both species migrated into the epilimnion at night.

2. D. oregonensis was shown to filter small cells (3-8  $\mu\text{m}$  diameter) less effectively than did D. minutus. This indicates a partitioning of the size continuum of food particles present.
3. Both species were able to capture large green algae, Ankistrodesmus falcatus (60-90  $\mu\text{m}$  long) and Scenedesmus accuminatus (18-26  $\mu\text{m}$  diameter), effectively. This study did not attempt to explore the possibility of raptorial feeding of large particles by one or both species, which may enhance food niche differences.
4. During the summer stratification period, female daytime filtering rates in the metalimnion were markedly depressed compared to the male rates. This filtering rate depression was most pronounced in D. oregonensis females and may represent an example of an alternating pattern of an "encounter-feeding" mode with a "filter-feeding" mode.
5. Day-night migration was evident during the summer stratification period. The higher nighttime filtering rates were consistent with the higher temperatures experienced by the migrants near the surface at night.
6. Winter daytime filtering rates, under ice cover, were quite similar to those obtained during the summer. This observation appears to support the

trend reported by Kibby (1971) for Daphnia rosea and also to be consistent with the findings of Conover (1956) and Halcrow (1963) regarding the acclimation of respiration rates by marine calanoid copepods to seasonal temperature changes.

7. The general conclusion, although tentative, is that there may be sufficient differences in feeding to account for the coexistence of these commonly co-occurring species. Spatial or seasonal segregation is not involved. Character displacement (size) may possibly be occurring in D. minutus but is not evident in D. oregonensis.
8. The question of their respective distributions; i.e., alone or together, remains unanswered, but it seems clear that taken by themselves coexistence is indeed possible. Diffuse competition from other species (including cladocerans) might account for the absence of one or the other species in a given lake system.

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