

Size divergence and dietary partitioning enhance coexistence of two herbivorous species of *Diaptomus* (Copepoda: Calanoida) in some shallow Quebec lakes

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Received August 23, 1991

Accepted December 11, 1991

CHOW-FRASER, P., and MALY, E. J. 1992. Size divergence and dietary partitioning enhance coexistence of two herbivorous species of *Diaptomus* (Copepoda: Calanoida) in some shallow Quebec lakes. *Can. J. Zool.* **70**: 1016–1028.

We examined the vertical and horizontal distribution patterns of *Diaptomus minutus* Lilljeborg and *Diaptomus oregonensis* Forbes in several shallow Quebec lakes where they occurred allopatrically and sympatrically within a small geographic region. Both species overlapped extensively in their vertical and temporal distributions and were found to be positively associated within and among lakes. Although size displacement could not be detected when body lengths of sympatric and allopatric populations were compared, in lakes where there was a reduction in size overlap between species, the two species coexisted at relatively high densities. This contrasted with situations where convergence in size between species was accompanied by a limited abundance of one or both diaptomids. We conducted stomach-content analyses on the sympatric populations of two of these lakes to determine if diet preference was related to copepod size divergence, and if algae were selected as a function of copepod size. We found that *D. minutus*, the smaller copepod, preferentially ingested a number of small algal particles ($< 10 \mu\text{m}$), whereas *D. oregonensis*, the larger copepod, tended to ingest a greater number of larger particles. Although preference for small algae (*Selenastrum* and small blue-green algae) was negatively correlated with prosome length, preference for larger algal taxa (*Planktosphaerium*, centric diatoms such as *Melosira*, and *Achnanthes*) was positively correlated with diaptomid size. There were, however, differences with respect to the degree of diet overlap between species in the two lakes, which was reflected in a significant negative correlation between dietary and size overlap. These observations are consistent with the hypothesis that reduction in size overlap has resulted in reduced exploitative competition, and that divergence in size and diet may be the mechanism that allows *D. minutus* and *D. oregonensis* to coexist when food becomes limiting.

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Nous avons examiné les répartitions verticale et horizontale de *Diaptomus minutus* Lilljeborg et de *D. oregonensis* Forbes en plusieurs lacs peu profonds du Québec où les deux espèces sont allopatriques ou sympatriques dans les limites d'une région géographique assez restreinte. Les répartitions verticales et temporelles des deux espèces se recoupaient largement et elles étaient en corrélation positive dans un lac ou d'un lac à un autre. Bien que des déplacements des tailles n'aient pu être constatés lors de la comparaison entre des populations sympatriques et des populations allopatriques, les deux espèces cohabitaient à des densités relativement élevées dans les lacs où le chevauchement des tailles était moins grand. Cette situation était inversée lorsque les deux espèces étaient de tailles semblables et il y avait alors réduction de l'abondance de l'une ou des deux diaptomides. Nous avons analysé les contenus stomacaux chez des populations sympatriques de deux de ces lacs, afin de déterminer si les préférences alimentaires sont reliées aux divergences de taille et de découvrir si les algues choisies en nourriture sont fonction de la taille du copépode. Nous avons constaté que *D. minutus*, la plus petite espèce, consommait de préférence un petit nombre de petites particules ($< 10 \mu\text{m}$), alors que *D. oregonensis*, la plus grosse espèce, tendait à consommer un grand nombre de grosses particules. Alors que la préférence pour les petites algues (*Selenastrum* et de petites algues bleues) était en corrélation négative avec la longueur du prosome, la préférence pour les algues de plus grande taille (*Planktosphaerium*, diatomées à symétrie radiale telle *Melosira*, *Achnanthes*) était en corrélation positive avec la taille de la diaptomide. Il y avait cependant des différences dans l'importance du chevauchement de la niche alimentaire entre les deux espèces dans les deux lacs, différence qui se reflétait par une corrélation négative significative entre le régime alimentaire et le chevauchement des tailles. Ces observations s'accordent avec l'hypothèse selon laquelle la réduction du chevauchement des tailles a donné lieu à une réduction de la compétition d'exploitation et selon laquelle aussi la divergence entre les tailles et entre les régimes alimentaires est le facteur qui permet la coexistence de *D. minutus* et de *D. oregonensis* lorsque la nourriture devient un facteur limitant.

[Traduit par la rédaction]

Introduction

The observed distribution pattern of the common planktonic crustacean *Diaptomus* in lakes and ponds of North America has been attributed to two main factors. The first concerns the organisms' dispersal or colonization abilities (Carter et al. 1980; Maly 1984a; Maly and van Leeuwen 1988), which largely determine the geographical distribution of species. The second concerns the species' tolerance of environmental con-

ditions. These conditions include physico-chemical characteristics that determine the extent of overlap in the large-scale distribution of closely related species and (or) biological interactions that regulate their co-occurrence in local distributions. So far as the two herbivorous species *Diaptomus minutus* and *Diaptomus oregonensis* are concerned, the considerable overlap in their geographic ranges is thought to have resulted from shared access to the network of postglacial lakes formed

during Pleistocene deglaciation, and to their mutual tolerance of extremes relating to lake morphometry, water temperature, and water chemistry (Anderson 1974; Roff et al. 1981; Carter et al. 1980, 1983; Maly 1984b). Their co-occurrence in local distributions, however, is thought to be dependent on their ability to reduce temporal, spatial, and size (and presumably diet) overlap (Sandercock 1967; Rigler and Langford 1967; Hofmann 1979; Maly 1984b).

In the Eastern Townships of Quebec, *D. minutus* and *D. oregonensis* have greatly overlapping distributions (Carter et al. 1980). That they co-occur more frequently in these water bodies than any other congeneric species pairs (Maly and van Leeuwen 1988) has generated a great deal of speculation on the evolutionary forces that have led to their coexistence. Based on findings of other diaptomid studies, *D. minutus* and *D. oregonensis* may exhibit temporal (Sandercock 1967; Hammer and Sawchyn 1968), spatial (Rigler and Langford 1967), size (Cole 1961; Maly 1983), or dietary (Maly and Maly 1974; Maly 1976; Bowers 1980) segregation. Although no study has been conducted that specifically evaluates the contribution of each of these factors to the co-occurrence of the two diaptomid species, Maly (1984b) found evidence of size displacement in many of these sympatric populations. In a subsequent study, Chow-Fraser and Maly (1988) proposed and tested the hypothesis that size divergence evolved to minimize interbreeding between co-occurring populations; however, since mate recognition in these diaptomids was independent of copepod size, the size ratio between mating pairs did not have any significant effect on the incidence of interspecific mating. Chow-Fraser and Maly thus concluded that size divergence did not evolve to prevent interbreeding between species that are very similar in body size.

An alternative explanation is that size displacement may have evolved to reduce exploitative competition for food. This hypothesis is based on the assumption that copepod diets vary as a function of body size (Hutchinson 1951) and that there is a negative correlation between diet and size overlap. Although there is no evidence that the latter assumption is valid, there is an expectation of a relationship between body size and the maximum particle size ingested, as has been demonstrated for the marine copepod *Acartia* (Wilson 1973) and two species of *Diaptomus* in Lake Michigan (Bowers 1980). In addition, previous laboratory experiments have demonstrated quite conclusively that copepods are discriminating feeders, capable of selecting algae of specific size, morphology, and nutritional quality (Richman et al. 1980; Fulton 1988; Vanderploeg et al. 1988; De Mott 1990), and this may have some bearing on the ability of copepods to vary their diet as a function of their size.

In this study, we reanalyze data from the 54 lakes and ponds sampled by Maly (1984b). We first examine the spatial and temporal distribution patterns of *D. oregonensis* and *D. minutus* in a subset of these lakes to determine if animals exhibit habitat segregation. We also conducted diet analyses in a subset of these lakes to determine the relationship between copepod size and algal size, and between copepod size and diet overlap. Specifically, we investigate diet differences (i.e., diet breadth) between allopatric and sympatric populations and determine if size overlap is directly related to diet overlap (i.e., whether large copepods show a much greater preference for large particles and small copepods for small particles).

We chose to use in situ stomach content analyses rather than laboratory or feeding experiments to obtain diet information of diaptomids in our lakes. Although qualitative diet analyses

have been carried out for calanoid copepods (Fryer 1954; Maly and Maly 1974; Chow-Fraser and Wong 1985, 1986), they have seldom been used to quantify diet overlap between species. We consider this to be an appropriate approach for examining exploitative competition between field populations of *Diaptomus*, because it provides simultaneous information regarding the food preferences of co-occurring copepods, copepod size, and food size, as well as relative food abundances, all of which are necessary to determine diet overlap and the effect of food availability, animal size, and algal dimensions and quality on the selectivity patterns of diaptomids. By simultaneously examining the relationship between temporal, vertical, and size segregation and copepod diet, we hope to better understand some of the factors that have led to the coexistence of *D. oregonensis* with *D. minutus* in these Quebec lakes.

Methods and materials

Further analysis of the 1979 samples

Between 1978 and 1981, Maly (1984b) sampled 54 shallow lakes and ponds in the Eastern Townships and the foothills of the Laurentian Mountains near Montréal, Quebec. In this study, we reanalyze a small subset that had been sampled in 1979. The data correspond to six lakes in which *D. oregonensis* and *D. minutus* co-occurred, two where only *D. minutus* was found, and one where *D. oregonensis* was found alone. Another calanoid copepod, *Epischura lacustris*, co-occurred with diaptomids in many of these lakes (Table 1); however, its density was usually low (E. J. Maly, unpublished data), which is in agreement with observations made by Rigler and Langford (1967) on 107 lakes in southern Ontario.

During the 1979 survey, quantitative zooplankton samples were collected 3–5 times during the ice-free season (May–November) with a 2- or 4-L van Dorn sampler or a 30-L Schindler–Patalas trap (80- μ m mesh), depending on lake surface area. Because these lakes tend to be well mixed throughout the season and do not stratify, they are relatively homogeneous with respect to ambient temperature and oxygen concentration (Chow-Fraser and Maly 1991). Samples were obtained in duplicate at the surface (usually 0.5 m), mid-depth (ranging from 1.5 to 3.0 m), and bottom (ranging from 2.0 to 10.0 m) of each lake. These were used to provide information regarding the spatial segregation of animals in sympatry and were not used to estimate copepod abundance. On each sampling trip, diagonal net tows were also taken from the deepest part of the lake with a Wisconsin plankton net (80- μ m mesh), and these were used to supplement information on clutch size and prosome length of adults in the respective lakes. All zooplankton samples were preserved in the field with 4% formalin and replaced with 70% ethanol in the laboratory.

Field sampling in 1985 and 1986

In 1985, a subset of the sympatric populations, those in Long, Cromwell, Pin Rouge and Thibault lakes, was sampled approximately triweekly to provide more accurate information regarding the temporal, vertical, and horizontal distribution of copepods and to estimate adult copepod densities. Allopatric populations from Sally and Libby lakes were also sampled during this period. Twelve or 13 samples were taken with 2-L Schindler–Patalas traps at various locations from both the top and bottom portions of each lake for sympatric (6 times from the end of May to the end of August) and allopatric (4 times from the end of May to the end of August) populations. Qualitative samples were also collected by vertical tows on each sampling day at the deepest station in each lake. In 1986, Nick, Trousers, Moulin and Sally lakes were sampled biweekly with Schindler–Patalas traps (10 samples per lake visit) throughout the water column to estimate copepod density. All quantitative and qualitative zooplankton samples were preserved immediately in the field with 4% formalin.

In October 1985, and at roughly monthly intervals from May to September in 1986, zooplankton was collected by horizontal tows

along three or four transects in six of the study lakes, Trousers, Nick, Long, Moulin, Sally, and Libby, for stomach content analyses. On each occasion, triplicate phytoplankton samples were also collected in 8-m lengths of rubber hose in approximately the same vicinity where zooplankton was collected. The contents of these tubes were mixed in a bucket, and aliquots of the mixture were placed in 125-mL bottles. Both zooplankton and phytoplankton were immediately preserved with acid Lugol's iodine solution in the field.

Zooplankton processing

Diatomids in all the quantitative samples were sexed, identified to developmental stage and species, and enumerated with the aid of a dissecting microscope (12× and 25× objectives). Whenever possible, the prosome length of 20 males and females of each species in each sample collected by vertical tow was measured. Depending on availability, the clutch size of 20 females was also recorded. Size measurements were made at 100× magnification (accurate to the nearest 0.01 mm) with the aid of an ocular micrometer.

Only adult animals were processed for stomach contents analysis. Once they had been sexed and their length measured, copepods were isolated with a Pasteur pipette and transferred onto depression slides and rinsed with distilled water several times. Each animal was then transferred onto a clean glass slide and placed in a drop of distilled water. The gut was dissected out with forceps and No. 000 insect mounting pins (affixed with epoxy glue to Pasteur pipettes). Once removed, the gut was placed in a drop of 10% glycerin-water solution, covered with a glass cover slip, and gently squashed with the blunt end of forceps. We circled the outline of the smear with a fine indelible marker; this allowed us to later locate the smear under the light microscope. The preparation was sealed with three coats of nail polish applied to the edge of the coverslip and examined with a phase-contrast microscope (200× or 400× magnification), usually within 24 h. All algal contents (within the area delineated by the marker) were identified to genus (except some colonial forms) and enumerated. We also obtained representative dimensions of each taxon to enable us to estimate cell biovolumes.

In this study, the animals' guts composed almost 75% of the total body length of the animals and consisted of three identifiable segments that we refer to as the fore, mid, and hind guts. The foregut was usually short, the midgut was longer and more slender, and the hind gut was long and easily broken from the rest of the stomach; in this study, we included only preparations containing intact sections of the mid- and fore-guts.

Phytoplankton processing

Duplicate 5-mL aliquots of phytoplankton samples were settled overnight in sedimentation chambers for algal enumeration. All algae were identified and enumerated in three transects at 200× magnification and one transect at 400× magnification; the entire slide was scanned for large dinoflagellate, desmids, filaments, and colonies (longest linear dimension >40 μm). Items that occurred fewer than 10 times in all four transects were counted in a replicate slide, and the average of these two counts was used as a measure of available diet items; otherwise, all items were enumerated from inspection of one slide only. Biomass of phytoplankton was calculated by volumetric approximation to geometric shapes and assuming that the specific gravity is 1.

Index of diet preference and niche overlap

We used Feinsinger et al.'s (1981) "niche breadth" (NB) index to discern differences in the diets of the copepods when they co-occurred. NB is a measure of the degree of similarity between the frequency distribution of diet items used by members of a population and the frequency distribution of diet items available to them. An NB value of 1.0 is the broadest possible niche, which indicates that animals utilize all available diet items; an NB value of 1/n (where n is the number of diet items in the lake) is the narrowest niche, which indicates that the diet consists of one item exclusively. It is calculated as

$$NB = 1 - 0.5 \sum |p_i - a_i|$$

TABLE 1. Summary of physico-chemical characteristics and a species list for the study lakes (taken from Maly 1984b)

Lake	N	Species present	Max. depth (m)	pH
Cromwell	3	DM, DO, EL	7.0	6.4
Long	5	DM, DO, EL	6.5	7.5
Nick ^a	5	DM, DO, EL	7.5	7.7
Pin Rouge	4	DM, DO, EL	12.5	6.7
Trousers	5	DM, DO, EL	5.5	7.4
Thibault	3	DM, DO	5.5	7.2
Libby	5	DM, EL	3.5	7.4
Sally (Knowlton)	5	DM, EL	2.0	7.6
Moulin	4	DO	6.0	7.5

NOTE: DM, *D. minutus*; DO, *D. oregonensis*; EL, *Epischura lacustris*. N is the number of sampling trips taken in 1979.

^aAlthough no *D. minutus* were observed in 1979 and 1980, they were present in samples from 1985.

where p_i is proportion of diet items in stomachs and a_i is proportion of diet items in the lake. To determine the extent of dietary overlap for the two diatomid species in lakes, we used Hurlbert's (1978) "niche overlap" (L) index, a measure of the degree to which the frequency of shared preference for a food item is higher or lower than expected if each species utilized the food in proportion to its abundance in the lake. An L value of zero indicates no sharing, a value of 1 indicates that both are taking items according to their availability, and values from 1 to infinity indicate an increasing degree of sharing. It is calculated as

$$L = n \sum (p_{x_i} - p_{y_i})$$

where p_{x_i} and p_{y_i} are the proportions of diet items used by species x and y , respectively, and n is the number of diet items in the lake. We also used L to determine the extent of overlap in the vertical distributions of sympatric populations. For comparison, we calculated Horn's (1966) overlap index (R_o) because copepod densities in our samples were variable, and sample size has only a minimal effect on the value of Horn's index (Krebs 1989). It is calculated as

$$R_o = [\sum (p_{x_i} - p_{y_i}) \log(p_{x_i} - p_{y_i}) - \sum (p_{x_i} \log p_{x_i}) - \sum (p_{y_i} \log p_{y_i})] / 2 \log 2$$

where p_{x_i} is the proportion of food item i in the diet of species x , and p_{y_i} is the proportion of food item i in the diet of species y ; any base of logarithms may be used. An R_o value of zero means there is no similarity in vertical distribution, whereas a value of 1 means complete overlap in spatial distribution.

We calculated selectivity (α) and electivity indices (ϵ) (Chesson 1978; Chesson 1983) for both species to determine respective food preferences in each lake. They were calculated as

$$\alpha = (p_i/a_i) / \sum p_i/a_i$$

and

$$\epsilon = (n \alpha - 1) / (n - 2) \alpha + 1$$

where n , p_i , and a_i are as indicated for L . α -values reflect how items are selected by the population: a value of 1/n indicates that the item is selected neutrally or opportunistically (ingested according to its availability), whereas a lower or higher value indicates that it is selected against or selected for, respectively. ϵ -values are normalized α -values and range between -1 and +1. An ϵ -value of zero indicates neutral selection of a food, whereas values greater than and less than zero indicate degrees of selection of and selection against the item, respectively. When the food base is constant, α -values are directly comparable; however, when numbers of prey types vary, ϵ -values are more readily compared (Confer and Moore 1987). Since the food

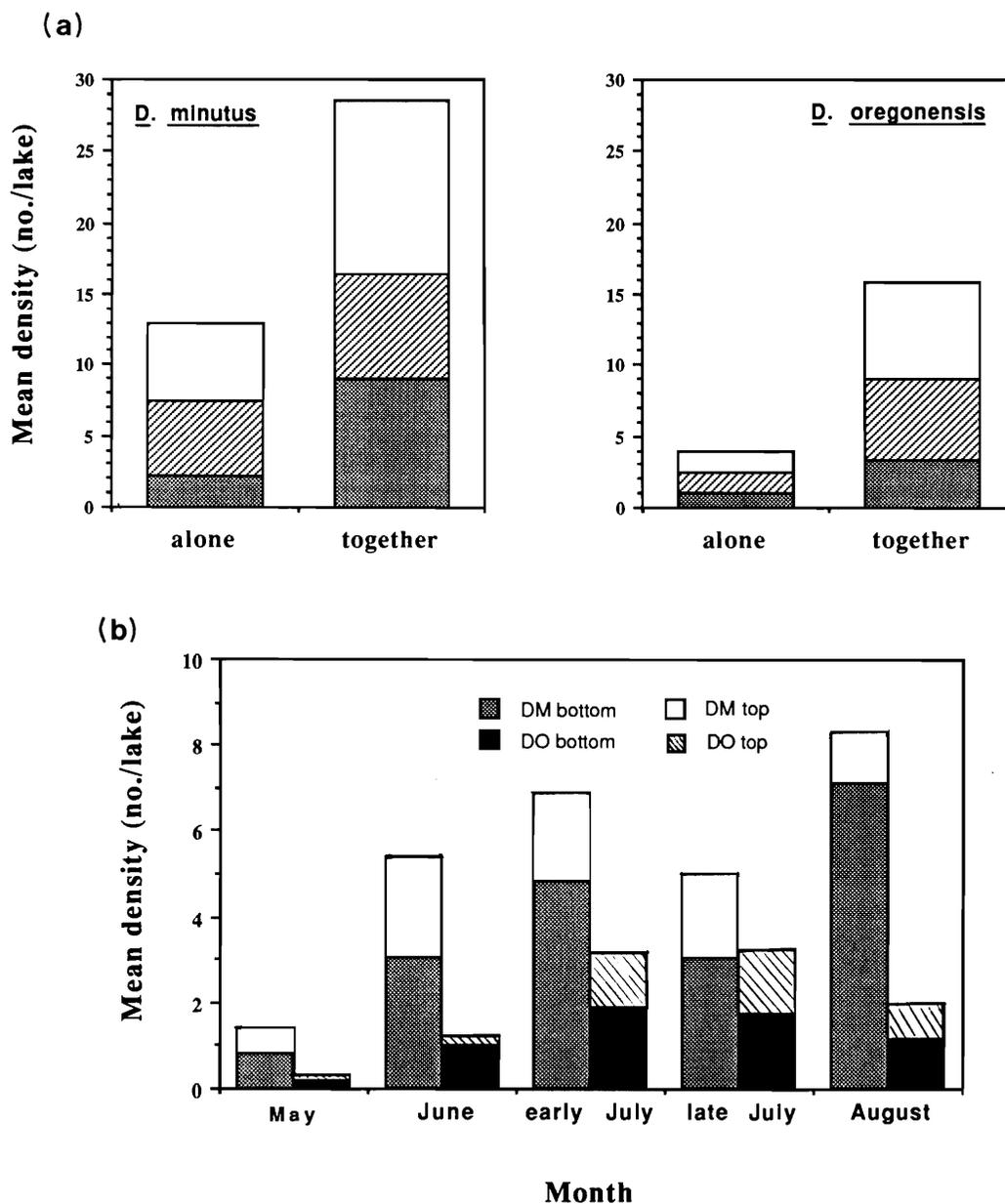


FIG. 1. (a) Vertical distribution of adults and copepodids in the 1979 samples. (b) Comparison of seasonal and vertical distributions of adult diaptomids in the 1985 samples. DM, *D. minutus*; DO, *D. oregonensis*.

base varied among lakes in this study, we used ϵ to compare food preferences among diaptomids.

Because of the large individual variation in stomach contents, with regard to both amount and type of food ingested, we have grouped the stomach data by sex and species for each lake visit; in most cases the number of stomachs ranged from 12 to 15. We used biomass instead of density data to calculate the various indices, since it was found to be the variable of choice in a preliminary analysis and was also recommended by Wallace (1981).

Results and discussion

Spatial and temporal overlap

Between May and November of 1979, 72 Schindler-Patalas traps were collected in the six lakes with sympatric populations, at various depths ranging from just below the surface to a metre above the sediment (Table 1). These water samples represented an extremely heterogeneous data set for determin-

ing the extent of spatial overlap between species. If these diaptomids were spatially segregated, we would expect to find a large percentage of the 72 samples to contain only one species: 7% of the samples contained neither species, 26% contained only one species, and in the remaining samples, both species were found in various proportions throughout the top, middle, and bottom strata (Fig. 1a). The species composition of the samples was significantly dependent on the depth of sampling (3×4 contingency table, $\chi^2 = 13.55$, $P < 0.05$). Both species appeared to congregate near the surface, and this was consistent with the weak positive association between diaptomids as indicated by a test of association (2×2 contingency table; $\chi^2 = 3.96$, $P < 0.05$) and an association coefficient of +0.39 (Cole 1949). In addition, copepod densities were significantly higher in samples where they occurred together than in samples where they occurred alone (one-way ANOVA, $P = 0.0029$). Thus, not only did we fail to find evi-

TABLE 2. Comparison of indices of spatial overlap for samples collected in 1979

	Horn's R_0	Hurlbert's L
Long Lake		
May	0.949	0.948
July	0.774	0.983
August	0.771	0.721
September	0.997	1.448
November	0.978	1.238
Pin Rouge Lake		
July	0.868	2.280
August	0.957	2.490
October	0.987	1.790
November	0.900	1.680
Trousers Lake		
May	0.940	1.758
July	0.942	1.385
August	0.991	1.585
September	0.920	2.550
November	0.874	1.290
Thibault Lake		
July	0.963	1.280
Trap Lake		
June	0.996	1.090
Cromwell Lake		
July	0.859	1.225
August	0.843	2.160
October	0.712	0.949

NOTE: See Methods for equations used to calculate Horn's (1966) and Hurlbert's (1978) indices.

dence of spatial segregation, we found that *D. minutus* and *D. oregonensis* were positively associated in these lakes.

In 1985, a more intensive survey was carried out on four of the six lakes to discern temporal as well as vertical partitioning between diaptomid species. Consistent with the results of the 1979 survey, the distribution of species in these samples was significantly dependent on the depth of sampling; however, copepods appeared to congregate near the bottom instead of in the surface waters (Fig. 1b; three-dimensional contingency table, $\chi^2 = 157.05$, $P < 0.001$). The distribution was also significantly dependent on the time of sampling: copepods occurred together more frequently in the June and July samples than in the May and August samples, and abundances of both species were also higher at these times. Since the top and bottom samples were collected at various locations in each lake, we may have inadvertently minimized any effect of horizontal patchiness on these results. We therefore conducted the following analysis to examine overall spatial overlap, which took into account differences in vertical and horizontal distributions, and was aimed at determining the extent of spatial overlap at any location in the lake.

For each lake surveyed in 1979, we calculated monthly indices of spatial overlap using both Horn's (1966) and Hurlbert's (1978) formulae (Table 2). None of the values for Horn's index was less than 0.75, the majority (12/19) being greater than 0.9. This indicates that the two diaptomid species overlapped a great deal in their spatial distribution in these lakes. Similarly, most of the values we calculated for Hurlbert's index were greater than 1.0, confirming that the overall distribution pattern of the diaptomids involved extensive overlap throughout the summer.

These positive associations between *D. minutus* and *D. orego-*

TABLE 3. Comparison of mean prosome lengths (mm) of copepods in samples collected in 1985 and 1986

	DMM	DMF	DOM	DOF
Sympatric populations				
Trousers Lake	0.63b (0.01)	0.73e (0.01)	0.89i (0.01)	1.02l (0.01)
Nick Lake	0.78c (0.03)	0.86f (0.02)	0.85ih (0.02)	0.92k (0.03)
Long Lake	0.58a (0.01)	0.65d (0.02)	0.82h (0.02)	0.92k (0.02)
Allopatric populations				
Moulin Lake	—	—	0.80h (0.02)	0.92k (0.03)
Sally Lake	0.66b (0.01)	0.73e (0.01)	—	—
<i>P</i>	0.0001	0.0001	0.0036	0.0019

NOTE: *P* is the probability that mean lengths are statistically similar among lakes. Similar letters denote statistical homogeneity ($P > 0.05$) as indicated by Duncan's multiple-range test. Numbers in parentheses are standard errors. DMM, *D. minutus* males; DMF, *D. minutus* females; DOM, *D. oregonensis* males; DOF, *D. oregonensis* females.

nensis (test of association; $\chi^2 = 26.86$, $P < 0.001$ and Cole's association coefficient of +0.214) are consistent with the findings of Sandercock (1967) that maxima for both species occurred during the summer months in Clark Lake, Ontario, and confirm Rigler and Langford's (1967) observation that there was no temporal or spatial partitioning between these species in over 100 lakes in Ontario that they studied.

There was no clear trend of copepod dominance in the six zooplankton communities (Fig. 2). In Cromwell and Nick lakes, *D. oregonensis* was numerically dominant throughout the open-water season; in Long and Thibault lakes, *D. minutus* was dominant; and in Trousers and Pin Rouge lakes, neither species was dominant. The seasonal maxima for *D. minutus* also varied from lake to lake: they occurred in mid-July, late August, and early June in Trousers, Long, and Thibault lake, respectively. The seasonal maxima for allopatric populations of *D. minutus* were also different between Sally and Libby lakes, even though there was little year-to-year variation in the timing of seasonal maxima (Fig. 3).

Size overlap

It is clear from the foregoing discussion that co-occurring populations did not reduce their zone of overlap by partitioning their habitat, either through vertical or temporal segregation. We next examined populations for evidence of size displacement. A testable hypothesis is that body sizes of copepods in sympatry would be significantly different from those in allopatry, since interspecific competition should lead to divergence in copepod size with corresponding changes in diet overlap. Specifically, the smaller bodied species should become smaller while the larger bodied species should become larger. Since pH and temperature can affect the body size of *D. minutus* and *D. oregonensis* independently of any effects of competition (Maly 1984b), we used only data from lakes with pH between 7.3 and 7.8 (pH category in Table 5 of Maly 1984b) that had been sampled at roughly the same time during the season. These lakes included three sets of sympatric populations and three sets of allopatric populations.

We used data collected in 1985 and 1986 to test the size-displacement hypothesis and found no evidence to support it.

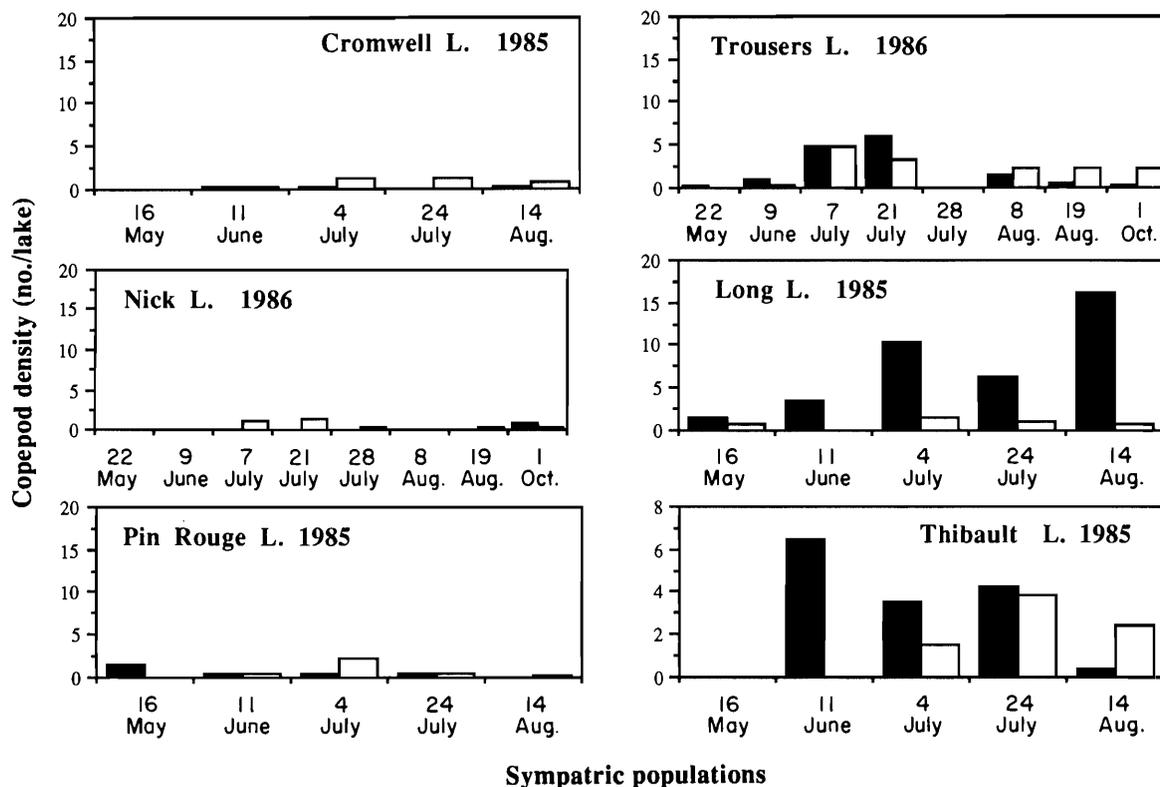


FIG. 2. Distributions of diaptomids in sympatric populations. Data are mean densities of adults collected from 25 and 10 Schindler–Patalas traps in 1985 and 1986, respectively. Solid and open bars represent *D. minutus* and *D. oregonensis*, respectively.

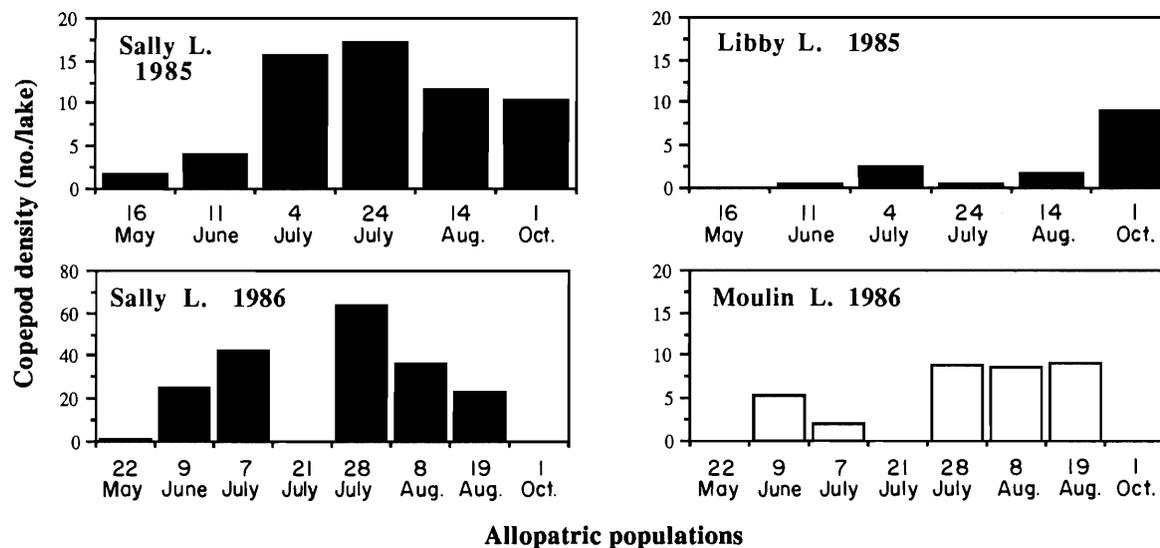


FIG. 3. Distributions of diaptomids in allopatric populations. Data are mean densities of adults collected from 25 and 10 Schindler–Patalas traps collected in 1985 and 1986, respectively. Solid and open bars represent *D. minutus* and *D. oregonensis*, respectively.

Although mean prosome length differed significantly among lakes of origin for both males and females of the two diaptomids (one-way ANOVA, $P < 0.005$ in all cases; Table 3), the differences could not be attributed to the presence or absence of congeneric species. For example, sympatric individuals of *D. minutus*, the smaller bodied species, were expected to be significantly smaller than allopatric individuals; however, of the three sympatric populations in our analysis, only the Long Lake population contained individuals significantly smaller

than those in the allopatric populations. Similarly, only one of the three sympatric populations of *D. oregonensis* contained individuals significantly larger than those in the allopatric population. Thus, copepod body size was generally independent of the species composition in the lake.

These results contradict those of Maly's (1984b) study, in which he showed that individual *D. oregonensis* were generally larger than their allopatric counterparts when this species co-occurred with *D. minutus*, and that individual *D. minutus*

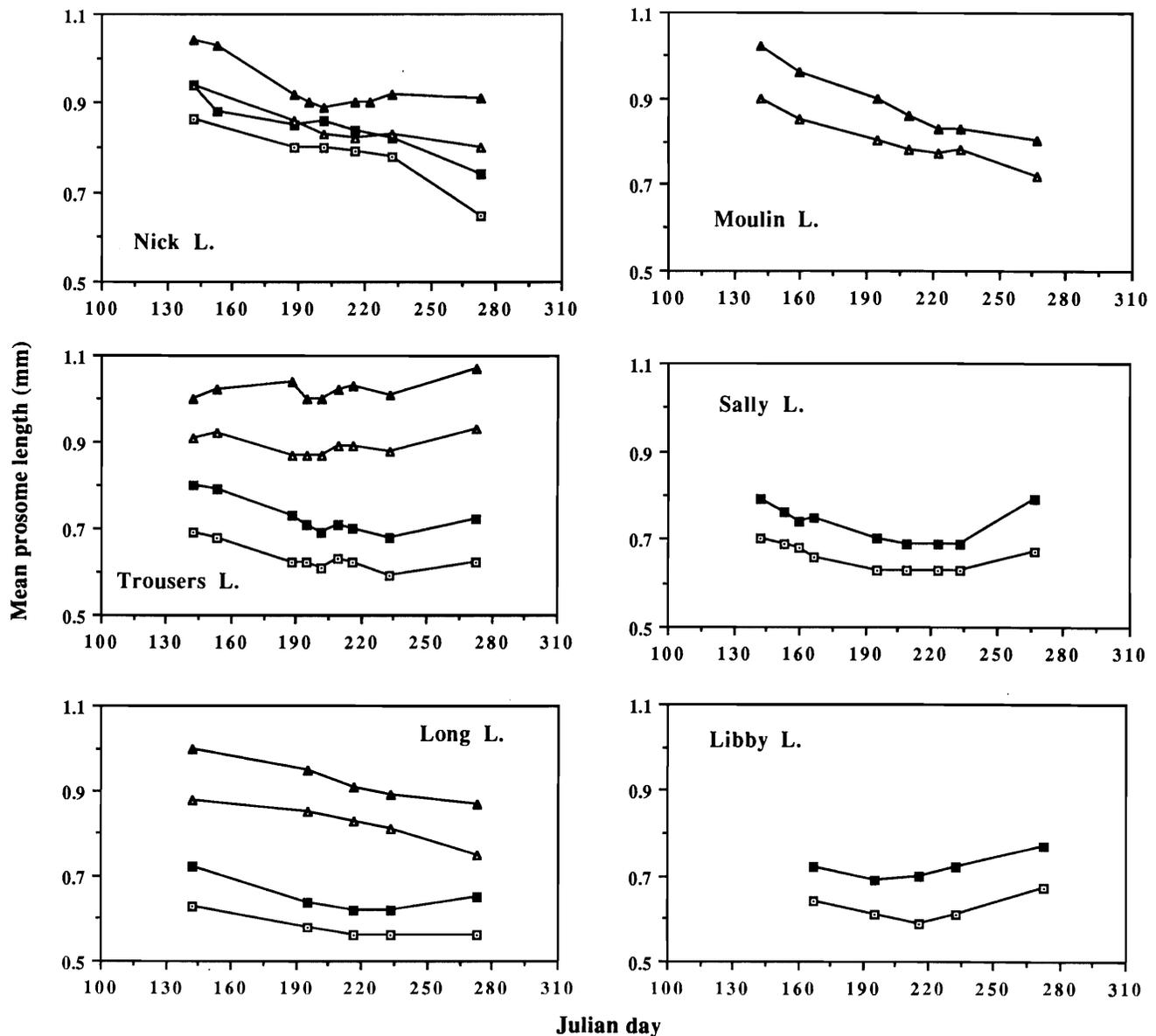


FIG. 4. Seasonal changes in prosome length of adult diaptomids. Data are means of 20 measurements for each species–sex combination. Solid and open triangles represent data for *D. oregonensis* females and males, respectively; solid and open squares represent data for *D. minutus* females and males, respectively.

tended to be smaller than their allopatric counterparts in lakes where *D. oregonensis* was also present. This discrepancy between studies probably reflects differences in sample size, since Maly's comparisons included data from 54 lakes, whereas we have only included 6 lakes. Nevertheless, Rigler and Langford (1967) also failed to find evidence to support the size-displacement hypothesis when they compared differences between allopatric and sympatric populations for their large lake set (in fact, they found a tendency for sizes to converge in sympatry).

A notable problem with this synoptic approach is that copepod size is not only a function of food availability, but may also be influenced by size-selective predation (e.g., Brooks and Dodson 1965) as well as temperature and food availability (Elmore 1983; Williamson and Butler 1987). Therefore, detecting differences in absolute size is not a rigorous enough test to discern the effects of interspecific competition in field data, especially when only a few lakes are involved. A better

approach is to relate the extent of coexistence to relative body size differences in the two populations. The rationale is that divergence in size should lead to coexistence of larger populations, so that a large size ratio should be accompanied by higher densities of both species, whereas a small size ratio should be accompanied by a limited distribution of one or both species.

The relative size of copepods appeared to be an important factor determining the extent of co-occurrence in our lakes (Fig. 4). In Trousers and Long lakes, where both species were common (Fig. 2), there is a divergence in size between males of the larger bodied species, *D. oregonensis* (DOM), and females of the smaller bodied *D. minutus* (DMF). This contrasts with the situation in Nick Lake, where *D. minutus* was rare, and where there was a conspicuous absence of size disparity between species. A comparison of size ratios for the six sympatric populations revealed that the size ratio of DOM to DMF was negatively correlated with the abundance of *D. ore-*

TABLE 4. Mean ratio of DOM and DMF prosome lengths, and mean densities of *D. minutus* (DM) and *D. regonensis* (DO)

	Mean size ratio	Copepod density (no./lake)		
		DM	DO	DM:DO
Long Lake	1.33	9.13	0.85	0.09
Trousers Lake	1.24	2.88	2.62	0.91
Thibault Lake	1.15	2.75	2.59	0.94
Pin Rouge Lake	1.14	0.39	0.87	2.23
Cromwell Lake	1.10	0.22	0.89	4.05
Nick Lake	1.01	0.10	0.77	7.70

NOTE: Means are calculated for data collected between June and August only. For explanation of abbreviations see Table 3.

regonensis relative to that of *D. minutus* ($r = 0.88$, $P < 0.02$; Table 4), suggesting that divergence in size enhances the coexistence of the smaller bodied with the larger bodied species.

Therefore, although size displacement could not be detected when mean lengths of sympatric and allopatric populations were compared, a reduction in size overlap between sympatric populations was accompanied by coexistence of both species at relatively high densities, and this is consistent with the hypothesis that *D. oregonensis* and *D. minutus* have diverged in size as a result of selective pressures to reduce interspecific competition for similar-sized algal particles.

Dietary overlap

If exploitative competitive for food has led to size divergence, then we would expect to find dietary differences between sympatric and allopatric populations. We therefore conducted stomach content analyses to determine differences in diet breadth between allopatric and sympatric populations; however, since these analyses are extremely labour intensive, we concentrated our efforts on only six of the lakes sampled earlier by Maly (1984b). We chose three lakes each in which species occurred sympatrically and allopatrically (Table 5). Unfortunately, our comparison of diet breadth of animals in the six lakes was inconclusive. Values of the three sympatric populations sampled in the October survey did not differ significantly from those of the three allopatric populations (unpaired t -test, $P = 0.25$ and 0.14 for *D. minutus* and *D. oregonensis*, respectively), for although values for both species in Trousers Lake were smaller than those in allopatric lakes, values for the other two sympatric populations were not consistently smaller. Since these results were subject to the same interpretive difficulties as those encountered with the size data (Table 3), we conducted a more detailed analysis to compare diet and size overlap in a reduced lake set.

We chose to study the sympatric populations of Trousers and Nick because these lakes differed in several respects even though they are contiguous basins. A major difference was that size divergence in Trousers Lake was accompanied by coexistence of relatively dense populations of both diaptomid species, whereas size convergence in Nick Lake was accompanied by the establishment of a severely reduced population of *D. minutus* (Figs. 2 and 4). This situation offered us an excellent opportunity to test the relationship between size and dietary overlap. In addition, the mean seasonal phytoplankton biomass of Nick Lake was roughly half that of Trousers Lake (Table 6) and had been dominated by blue-green blooms of *Microcystis* from June to August, whereas that in Trousers

TABLE 5. Comparison of diet breadth of copepods collected and total phytoplankton biomass concentrations in the October samples

	DMM	DMF	DOM	DOF	Biomass concn.
					($\mu\text{g/L}$)
Sympatric populations					
Trousers Lake	0.18	0.23	0.28	0.23	1510
Nick Lake	0.23	0.09	0.50	0.50	1014
Long Lake	0.27	0.53	0.50	0.58	1077
Allopatric populations					
Moulin Lake	—	—	0.32	0.17	1952
Sally Lake	0.43	0.55	—	—	1436
Libby Lake	0.24	0.27	—	—	1979

NOTE: For explanation of abbreviations see Table 3.

Lake had only a small community of colonial blue-green algae (with maximum colonial dimensions $< 30 \mu\text{m}$) throughout the summer. Such differences in algal composition and relative abundances may have had an effect on the degree of dietary overlap in the respective lakes.

We first examined the data for seasonal changes in diet breadth in both lakes. A two-factor analysis of variance revealed differential effects of season and lake origin on diet breadths of *D. minutus* and *D. oregonensis*. Diet breadths of *D. minutus* in the May–August samples were significantly smaller than those for the October sample ($P = 0.0006$; Fig. 5a), indicating that the smaller bodied species in both lakes ($P = 0.94$) maintained a larger selection of diet items in spring and summer than in fall. By contrast, diet breadths of the larger bodied species, *D. oregonensis*, were significantly different between lakes ($P = 0.05$) but were not significantly different among sampling dates ($P = 0.16$; Fig. 5b). *Diaptomus oregonensis* in Trousers Lake tended to select a larger variety of diet items in May and July relative to August and October, whereas *D. oregonensis* in Nick Lake appeared to have a more restricted diet in May and then broadened their food choice from July to October.

Sex and species-specific diet differences within lakes were next quantified in terms of diet overlap. We calculated monthly measures of diet overlap using Hurlbert's (1978) index for each copepod species–sex pair (i.e., DMM–DMF, DMM–DOM, DMM–DOF, DMF–DOM, DMF–DOF, and DOM–DOF). Mean monthly overlap values in both lakes were initially high (Fig. 6a); however, when food became more limiting in late July and early August, copepods in Trousers Lake substantially reduced their dietary overlap, whereas those in Nick Lake continued to exhibit a great deal of overlap. This variation in dietary overlap from month to month within the same lake seemed to be a function of the changing body size ratio between species, since copepods in Trousers Lake diverged in size (Fig. 4), whereas diaptomids in Nick Lake maintained size convergence. The relationship between size and dietary overlap was clearly demonstrated when we plotted log-transformed values of dietary overlap against size ratio and found a significant negative correlation (Fig. 6b; $r = 0.56$, $P = 0.0001$, $n = 56$), indicating that dietary overlap decreased as an inverse function of size overlap.

To further examine how preference for prey items changed as a function of copepod size, we plotted mean seasonal electivity values for each of the diaptomids by sex and species for 24 food categories found in Trousers and Nick lakes (Figs. 7

TABLE 6. Summary statistics of mean seasonal electivity values regressed linearly as a function of mean copepod prosome length (mm) for various algal taxa in Nick and Trousers lakes

Algal taxon	Size (μm)	<i>a</i>	<i>b</i>	<i>r</i>	<i>P</i>
Small <i>Cryptomonas</i>	< 10	+0.10	-1.00	0.57	>0.05
<i>Chlorella</i>	< 10	+0.74	-1.13	0.61	>0.05
<i>Tetraedron</i>	< 10	+0.60	-1.15	0.63	>0.05
<i>Rhodomonas</i>	< 10	+0.46	-1.24	0.63	>0.05
<i>Chlamydomonas</i>	< 10	+1.18	-1.40	0.67	>0.05
<i>Selenastrum</i>	< 10	+1.37	-2.25	0.76	<0.05*
Small blue-green algae	< 10	+0.41	-1.41	0.81	<0.05*
Green filaments	> 10	-0.97	+0.02	0.03	>0.05
Dinoflagellates	> 10	-0.64	-0.12	0.06	>0.05
<i>Gleocapsa</i>	> 10	-0.83	+0.06	0.07	>0.05
<i>Closterium</i>	> 10	-1.04	+0.13	0.10	>0.05
<i>Scenedesmus</i>	> 10	-0.96	+0.18	0.11	>0.05
<i>Cosmarium</i>	> 10	-0.98	+0.49	0.16	>0.05
Large <i>Cryptomonas</i>	> 10	-1.12	+0.87	0.24	>0.05
<i>Oocystis</i>	> 10	+0.89	-0.50	0.25	>0.05
Green and blue-green colonies	> 10	-0.08	-0.23	0.30	>0.05
<i>Asterionella-Tabellaria</i>	> 10	-1.26	+0.82	0.34	>0.05
<i>Dinobryon</i>	> 10	-1.36	+1.19	0.38	>0.05
<i>Arthrodesmus-Staurastrum</i>	> 10	-2.12	+1.84	0.65	>0.05
<i>Cyclotella</i>	> 10	-2.63	+2.90	0.66	>0.05
<i>Achnanthes</i>	> 10	-2.55	+2.56	0.70	>0.05
Centric diatoms	> 10	-1.12	+1.33	0.71	<0.05*
<i>Planktosphaerium</i>	> 10	-1.49	+1.61	0.87	<0.05*

NOTE: Size refers to the longest linear dimension of the respective alga; *a*, *b*, and *r* are the elevation, slope, and correlation coefficient of the regression analysis, respectively. *, significantly different.

and 8, respectively). The largest copepods in either lake were *D. oregonensis* females (DOF), and the smallest were *D. minutus* males (DMM); *D. oregonensis* males (DOM) and *D. minutus* females (DMF) were intermediate between these, even though size divergence was accentuated for animals in Trousers Lake. Food preferences of DMM were sorted in descending order, and data for the other three copepods were plotted in the same algal sequence for easy comparison. In Trousers Lake, preference for the small unicellular algae (Fig. 7, solid bars; longest linear dimension < 10 μm) tended to decrease with increasing copepod size. Though less obvious, this general pattern was repeated in Nick Lake (Fig. 8). By comparison, preference for larger items (Figs. 7 and 8, open bars) tended to increase with copepod size in both lakes.

We further sorted the data by algal taxon and regressed mean seasonal electivity values for each food item against the mean prosome length of copepods in each lake (Table 6). In all cases, preference for small algae (< 10 μm) tended to decrease with diaptomid size; significant negative correlations ($P < 0.05$) were recorded for *Selenastrum* and some small blue-green algae that occurred either singly or in short chains or small colonies. By comparison, significant ($P < 0.05$) positive correlations between preference and diaptomid size were recorded solely for larger algae such as *Planktosphaerium*, a unicellular form with diameters ranging between 11 and 13 μm , *Melosira* with diameters ranging between 10 and 12 μm and filament length exceeding 50 μm , as well as pennate diatoms such as *Achnanthes*, whose length usually exceeded 50 μm (Table 6). Thus, preference for small algae generally decreased with diaptomid size, whereas preference for large algae increased with diaptomid size. The relationship between food preference and copepod size was, however, unclear for

certain algal taxa. For instance, in both Trousers and Nick lakes, copepods showed a strong preference for the green alga *Oocystis*, regardless of copepod size. Other items such as *Closterium*, green filaments (e.g., *Mougeotia*), and green and blue-green colonial forms such as *Scenedesmus* and *Gleocapsa* were strongly selected against, regardless of copepod size. Blue-green colonies (assorted taxa with irregular dimensions) seemed to be ingested more or less opportunistically by all copepods in both lakes, whereas selection of algae such as *Cosmarium*, dinoflagellates (e.g., *Ceratium*), and colonial pennate diatoms (e.g., *Asterionella* and *Tabellaria*) was variable and did not appear to depend on copepod size.

Variations in clutch size

Food availability and prosome length are known to be determinants of clutch size for *D. minutus* and *D. oregonensis* (Chow-Fraser and Maly 1991). Consistent with previously documented studies of other diaptomids (e.g., Maly 1973, 1983; Cooney and Gehrs 1980; Elmore 1983), the clutch size of both species in these lakes varied as a function of prosome length (Fig. 9a). When data were replotted to show changes in clutch size through the season (Fig. 9b), we found that the clutch size of *D. minutus* in Trousers Lake was generally higher than in Sally, Libby, Nick, and Long lakes. Similarly, the clutch size of *D. oregonensis* in Trousers Lake was also higher than for the same species in Nick, Moulin, and Long lakes. We attribute these larger clutch sizes to the much higher algal biomass in Trousers Lake relative to other lakes (Table 7). These observations confirm the findings of Chow-Fraser and Maly (1991) that algal concentration has a significant effect on clutch size of *D. minutus*, independently of prosome length.

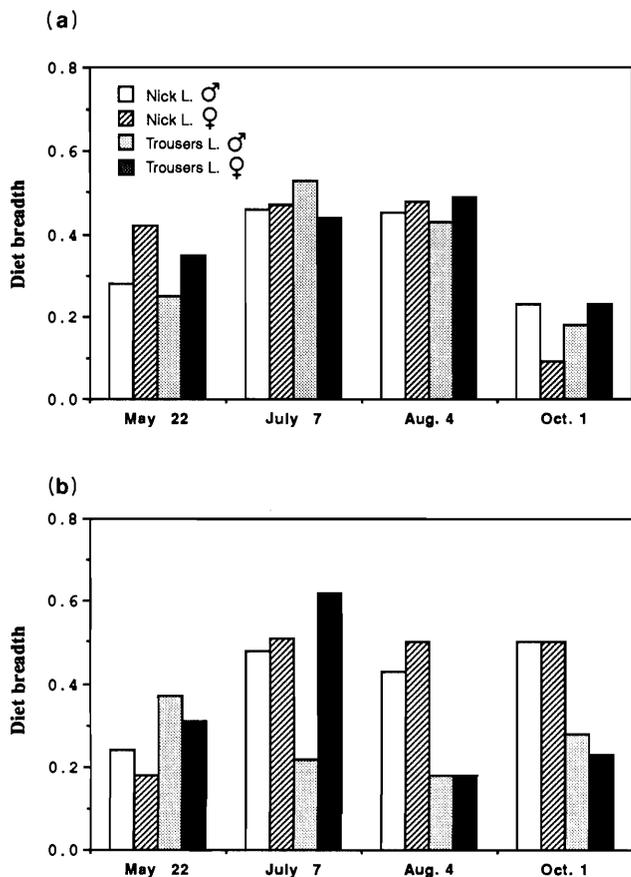


FIG. 5. Comparison of diet breadths for *D. minutus* (a) and *D. oregonensis* (b) in Nick and Trousers lakes. Diet breadth was calculated from pooled stomach contents of 10–15 animals in each case.

General discussion

Analyses of spatial, temporal, and dietary overlap and a comparison of relative body sizes of sympatric and allopatric populations reveal that *D. oregonensis* and *D. minutus* overlapped extensively in their seasonal and vertical distribution in these shallow Quebec lakes, and that dietary overlap was highly correlated with size overlap in sympatric populations. In Trousers Lake, where the two species coexisted at moderate densities (Fig. 2), there was divergence in size and diet (Fig. 6b); by comparison, in Nick Lake which was dominated by *D. oregonensis* alone, there was considerable size and dietary overlap (Figs. 4 and 6a). In both lakes, preference for small unicellular algae tended to decrease with copepod size, whereas preference for larger items tended to increase with copepod size (Figs. 7 and 8). There was also a significant negative correlation between preference for small algae (< 10 μm) and copepod prosome length, and a positive correlation between preference for larger algae and prosome length (Table 6). These observations confirm size-selective feeding on natural algae of other diaptomid species under laboratory conditions (Bowers 1980; Vanderploeg et al. 1988).

That difference in size between *D. oregonensis* males and *D. minutus* females was negatively correlated to the relative abundance of *D. oregonensis* versus *D. minutus* (Table 4) suggests that size divergence enhances coexistence of the two species at moderate densities. The maintenance of both species in any lake probably requires a relatively large food base;

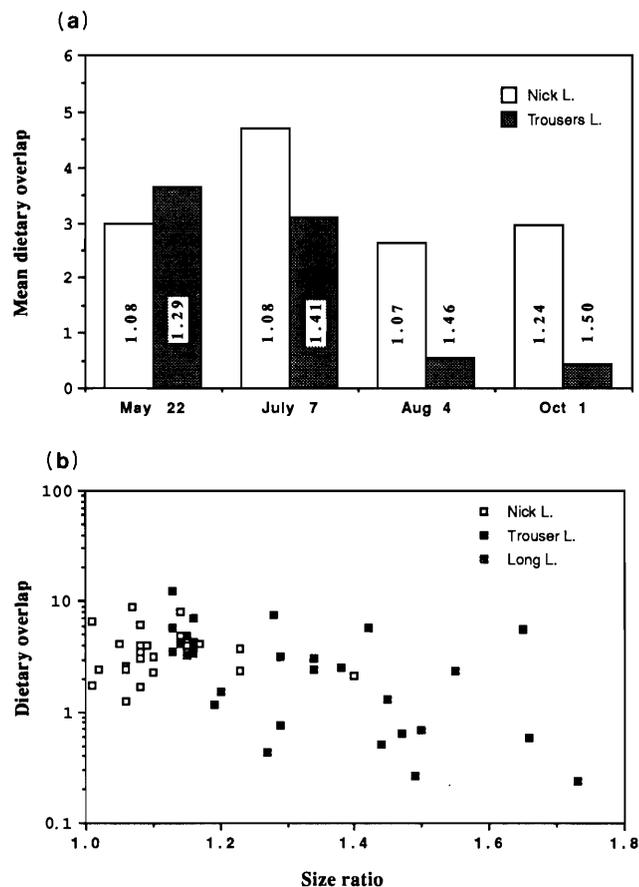


FIG. 6. (a) Seasonal changes in mean interspecific dietary overlap values for Nick and Trousers lakes. (b) Dietary overlap versus size ratio between pairs of copepods, as described in the text.

when food is scarce overall, species do not appear to be able to diverge in size, presumably because both are feeding on the same diet items and thus have similar nutritional intakes. This, in turn, perpetuates their large dietary overlap, which further contributes to the size overlap as well as to lower clutch size (Fig. 9). Thus, the relative abundance of *D. minutus* and *D. oregonensis* in these lakes may be linked directly to food availability and competitive interactions between species within lakes, although we do not discount the importance of size-selective predation in shaping the size structure of these zooplankton communities.

Since the diet breadth of *D. minutus* in Nick and Trousers lakes was similar, despite the greater than twofold difference in algal biomass (Fig. 5a, Table 7), we suggest that this copepod is a more generalized, opportunistic feeder, which takes advantage of all available algae rather than focusing on those of one size, especially in July and August. By contrast, *D. oregonensis* appeared to concentrate on large algae during most of the season, and thus is more of a specialist feeder (Fig. 5b). This difference in feeding strategies may explain why [chlorophyll *a*], which is an estimate of total algal biomass, was a significant determinant of clutch size for *D. minutus*, whereas it was not significantly correlated with the clutch size for *D. oregonensis*, presumably because this species is a more discriminating grazer (Chow-Fraser and Maly 1991).

We will attempt to compare our results with those from

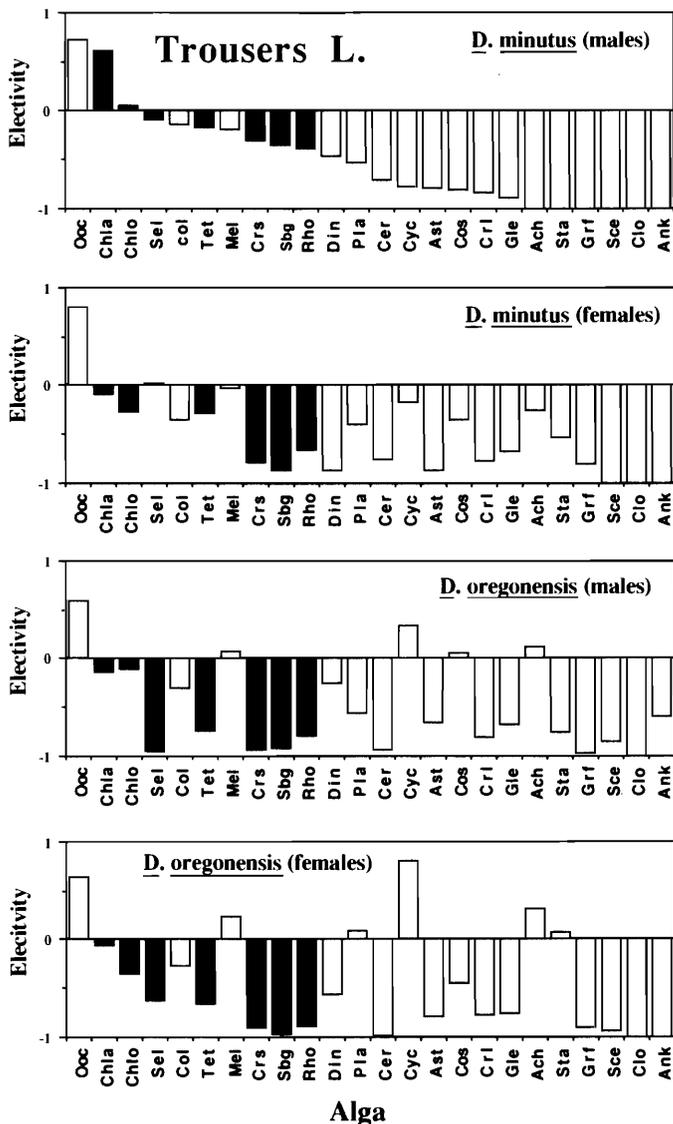


FIG. 7. Mean seasonal electivity values (ϵ) for copepods in Trousters Lake. Solid bars show copepod preference for small algae (longest linear dimension $<10 \mu\text{m}$); open bars show preference for large forms ($>10 \mu\text{m}$; including filamentous and colonial forms). Algae are identified as follows: Ooc, *Oocystis*; Chlo, *Chlorella*; Chla, *Chlamydomonas*; Tet, *Tetraedron*; Pla, *Planktosphaerium*; Col, small colonies of cyanobacteria; Crl, large *Cryptomonas*; Cyc, *Cyclotella*; Rho, *Rhodomonas*; Sel, *Selenastrum*; Mel, *Melosira*; Sta, *Staurastrum* and other large desmids; Ast, *Asterionella*-*Tabellaria*; Sce, *Scenedesmus*; Sbg, small blue-greens (sometimes in chains); Gle, *Gleocapsa*; Ach, *Achnanthes* and other single pennate diatoms; Cos, *Cosmarium*; Din, *Dinobryon*; Ank, *Ankistrodesmus*; Crs, small *Cryptomonas*; Grf, green filaments; Clo, *Closterium*; Cer, *Ceratium* and other dinoflagellates.

laboratory feeding trials, although we recognize that comparisons may be inappropriate, since the animals in our study chose simultaneously from more than 24 different diet items, whereas animals in laboratory studies are usually able to choose from only two algae. For the most part, algal preferences demonstrated in this study are consistent with recent studies on other diaptomid species which indicate that calanoids feed selectively on the basis of size, algal morphology, and nutritional quality (see Vanderploeg 1990). The uniformly high preference for the egg-shaped colonial alga *Oocystis* is

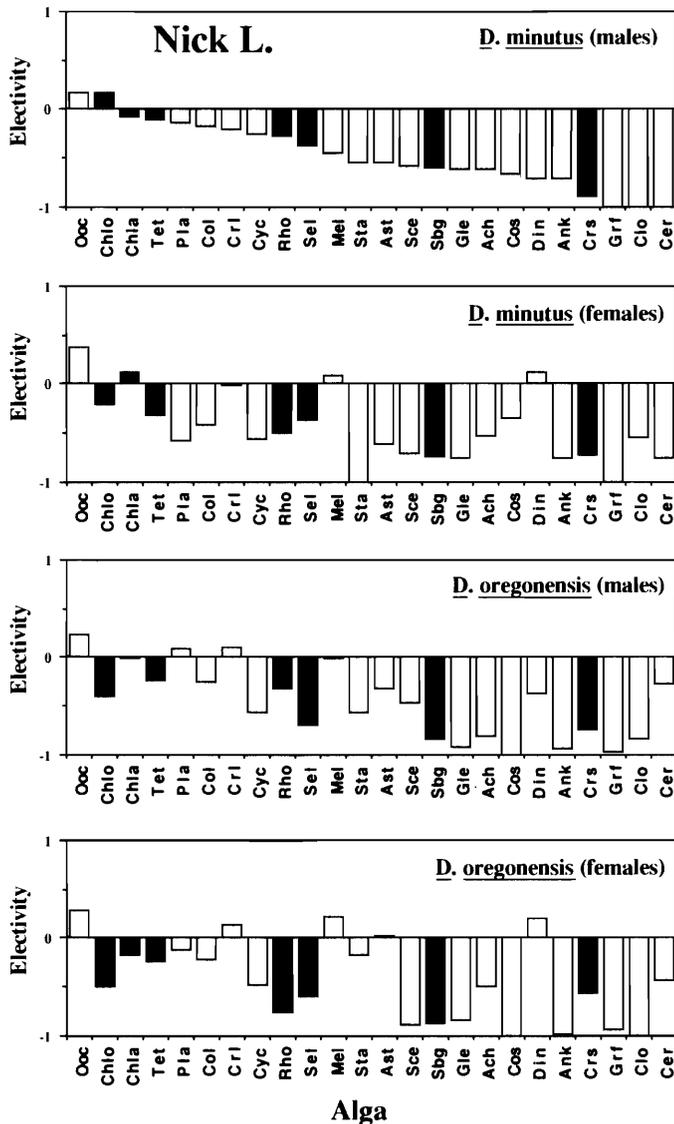


FIG. 8. Mean seasonal electivity values of copepods in Nick Lake. For identification of algae see Fig. 7.

probably due to the fact that it is easily detectable, owing to its size (i.e., large enough to be detected at a distance), and its morphology renders it easy to handle, since it has no spines or protrusions, and requires no special orientation before it is ingested. Flagellates such as *Chlamydomonas* and *Cryptomonas* are also known to be preferred food items of calanoids (e.g., Bogdan and Gilbert 1984; Vanderploeg and Paffenhofer 1985; Williamson et al. 1985), as are large solitary diatoms such as *Cyclotella* and *Achnanthes* (Richman et al. 1980; Chow-Fraser and Wong 1985, 1986; Vanderploeg et al. 1988). The consistent preference of *D. oregonensis* for the filamentous centric diatom *Melosira* (Figs. 7 and 8) is also in agreement with Fulton's (1988) observation that *Diaptomus reighardi* showed an exceptionally high preference for *Melosira granulata* in his laboratory feeding experiments. Vanderploeg et al. (1988) filmed the feeding of individuals of a similar-sized species, *Diaptomus sicilis*, on *Melosira* filaments and found them biting off sections that were $700 \mu\text{m}$ long; presumably *D. oregonensis* also ingests these diatom chains in a similar manner.

By contrast, the stellate diatom *Asterionella* was selected

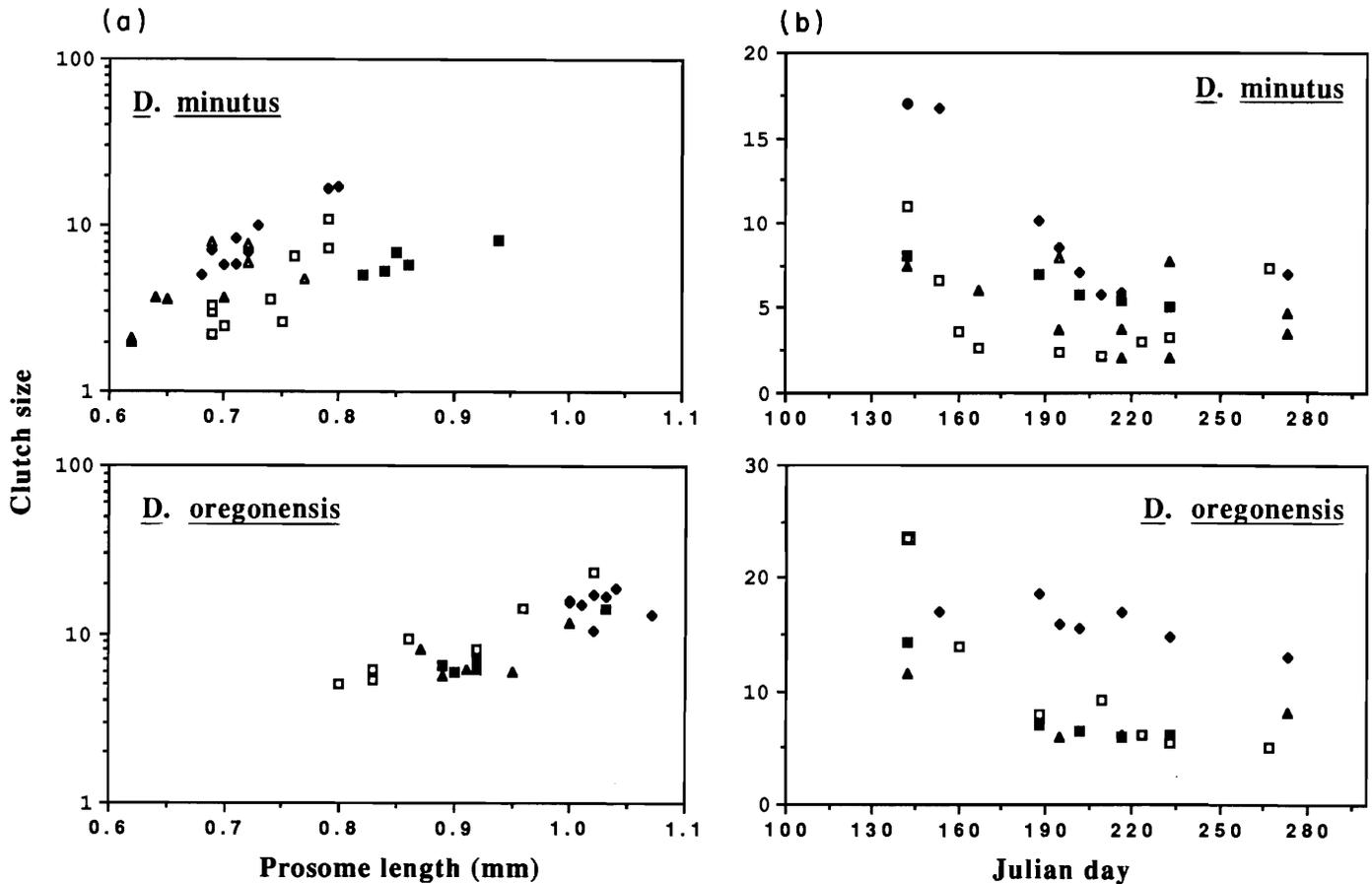


FIG. 9. (a) Mean clutch size versus mean prosome length. (b) Seasonal variation in clutch size of copepods in study lakes. Upper panels: ▲, Long Lake; ◆, Trousers Lake; ■, Nick Lake; □, Sally Lake; △, Libby Lake. Lower panels: □, Moulin Lake; ■, Trousers Lake; ▲, Long Lake; ■, Nick Lake.

TABLE 7. Summary of phytoplankton biomass concentrations in study lakes

	Phytoplankton biomass concn. ($\mu\text{g/L}$)				
	May	June	July	October	Mean
Sally Lake	349	1111	751	1436	912
Libby Lake	—	—	—	1979	—
Moulin Lake	452	1850	790	1952	1261
Long Lake	—	—	—	1077	—
Nick Lake	1098	815	698	1014	906
Trousers Lake	877	3362	1742	1510	1873

against by our diaptomids, and this is consistent with the findings of Vanderploeg et al. (1988), who found that *D. sicilis* avoided *Asterionella formosa* in their laboratory feeding experiments. Our results also support DeMott's (1990) observation that when presented with a choice between *Scenedesmus* and *Chlamydomonas* under laboratory conditions, *Eudiaptomus* always showed a significantly lower preference for *Scenedesmus*. Uniform selection by *D. minutus* and *D. oregonensis* against algae such as *Closterium*, as well as dinoflagellates such as *Ceratium* (Table 6), may reflect the animals' difficulty in orienting these large items for ingestion. That animals did not appear to select against the ensheathed alga *Planktosphaerium*, but essentially ignored *Gleocapsa*, another ensheathed form, is difficult to explain. Even though Vanderploeg (1990) found

that *Eudiaptomus* preferred *Planktosphaerium* to *Chlamydomonas*, it is difficult to make direct comparisons because the diameter of the algae used in his experiments (23 μm) is roughly twice that of the algae in our lakes (11–13 μm), and the animals in our lakes altered their preference for *Planktosphaerium* according to copepod size.

Although there is no experimental evidence that size divergence has led to coexistence of *D. minutus* with *D. oregonensis* in these Quebec lakes and ponds, we have eliminated the possibility that spatial or temporal segregation plays any role in determining their co-occurrence. Moreover, we have demonstrated that dietary overlap is related to size overlap and that copepods appear to select algae as a function of their own body size. These observations therefore lend support to Hutchinson's (1951) hypothesis that diaptomids in general require a minimum size difference in order to coexist, and that size divergence between sympatric populations has evolved to reduce exploitative competition for food of similar size.

Acknowledgements

Laboratory space and equipment for conducting part of the stomach contents analyses were provided by D. O. Trew, Alberta Environment. We also thank N. C. Fraser, Alberta Fish and Wildlife, for providing assistance in manuscript preparation. We acknowledge the technical and field assistance of R. Kirner, J. DeFrenza, S. Plante, and D. Lacroix. Completion of this study would not have been possible without

- encouragement and understanding from Noel, Trevor, and Emmett. Funding was provided by the Natural Sciences and Engineering Research Council of Canada in the form of a Women's Faculty Award to P.C.-F. and an operating grant to E.J.M.
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