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The species diversity of diaptomid copepods in piedmont North Carolina lakes has increased since these lakes were surveyed by McKee and Coker in 1940. This has been due, in large part, to the introduction of the vertebrate predator threadfin shad (*Dorosoma petenense*) and its effect on the only two diaptomid copepods present at that time, *Diaptomus birgei* and *Diaptomus reighardi*. These two copepods were never found together at the time of McKee and Coker's survey, one or the other occupying the entire "*Diaptomus* niche" in any given lake. Ecological maturation of these lakes coupled with predation by *Dorosoma petenense* has enabled other diaptomid copepods such as *D. pallidus* and *D. mississippiensis* to enter these lakes and also has allowed the coexistence of *D. birgei* and *D. reighardi*. Study of seasonal fluctuations in copepod population densities has shown that in shad-inhabited lakes the larger species tend to be dominant during times of low shad predation and the smaller species become dominant when shad activity is high (Beavers and Stavn 1975).

To test the degree of size selectivity of prey by shad, measurements were made of a single species (*D. reighardi*) over a one-year period in two lakes, one lake with and the other lake without shad. Seasonal variation in mean length was found to be similar in the two lakes during winter and early spring; however, from late spring through fall mean length of *D. reighardi* dropped below the yearly average to a greater degree in the shad-inhabited lake. This latter time period corresponded to the time of the year when shad were active in the shad-inhabited lake.

To establish what effect competition has on the size variability of diaptomid copepods, measurements were made of a species (D. pallidus) present in four lakes, each lake differing in the number of other diaptomid copepods present and, hence, in the degree of competition which this species experienced. It was found that variance of body length of this species was very much reduced in situations where a significant degree of competition with other diaptomid copepods existed. This was considered evidence that the size of diaptomid copepods is related to their ability to partition limiting resources and avoid direct competition.

THE EFFECTS OF PREDATION BY THREADFIN SHAD, DOROSOMA PETENENSE, AND COMPETITION ON BODY LENGTH OF DIAPTOMUS IN PIEDMONT NORTH CAROLINA LAKES

by

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APPROVAL PAGE

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TABLE OF CONTENTS

LIST OF TABLES

TABLE

PAGE

LIST OF FIGURES

FIGURE PAGE

INTRODUCTION

As an area ages geologically, assuming conditions of climate and substrate are not so extreme as to prevent habitation, communities of organisms living there tend to become increasingly diverse as plants and animals from other areas invade and colonize. These organisms do not merely coexist alongside one another but interact with each other in a myriad of often complex and, to the extent that we understand them, mathematically predictable ways. Organisms affect the physical environment in which they live as well, altering it so that it becomes better suited to other organisms which then succeed them until a final climax ecosystem is reached consisting of a more or less stable biotic community and physical environment (Odum 1971).

One of the factors which allows this buildup of a large and diverse climax community is predation (Paine 1966). Predation, by reducing the numbers of ecologically dominant species (upon which predation falls heaviest due to their high numbers), allows less efficient competitors to enter the ecosystem and maintain populations. This, in turn, provides additional food niches for other predators and hence encourages predator diversity as well (Dodson 1970). By keeping species in check which would completely dominate the habitat in their absence, predators also contribute to eveness of abundance among prey species.

Another trend in maturing ecosystems is the narrowing of the trophic niche and the microhabitat which each species occupies in the ecosystem in response to competition from an increasing array of similar organisms. This is true even though the community as a whole is becoming more diversified with regard to the number of niches. Niche specialization minimizes competition by reducing the amount of overlap among similar species in their food and space requirements.

Both of these trends tend to reduce inter-specific competition in the ecosystem, predation by maintaining population densities of prey species below that necessary to exclude competitors, and niche specialization by reducing the amount of overlap among similar species in their food and space requirements.

As stated above, moderate predation, by reducing the density of ecological dominants, can be expected to increase species diversity. This has been observed in fresh-water lakes where forage fish such as alewives have been introduced. The larger species of zooplankton, which dominate in the absence of predation, are reduced in numbers and smaller species invade, thus increasing zooplankton diversity (Brooks and Dodson 1965; Wells 1970). However, the introduction of a predator which is highly selective for the ecological dominants may virtually eliminate such dominants which, in turn, are succeeded by other species. Such predation may alter species composition while not significantly increasing species diversity. This is particularly true if the predator population is dense and the habitat is not sufficiently diverse to allow escape by the preferred prey. Such a situation is believed to exist in certain shallow piedmont North Carolina lakes with regard to zooplankton populations and the recently introduced vertebrate predator <u>Dorosoma petenense</u>, commonly called threadfin shad. In the deeper shad-inhabited lakes of piedmont North Carolina such as Lake Hickory and Lake James (depth greater than 25 m) larger zooplankters find refuge in the deep cool water where shad do not normally venture. However, in shallow shad lakes such as Lake Jeanette (depth less than 10 m) large zooplankters such as *D. birgei* cannot find adequate refuge from *Dorosoma petenense* and are present in minimal numbers.

That niche specialization is accompanied by morphological changes or differences has been shown by numerous investigators, for example in studies of the correlation between bill shape and size and the food niche of birds (Johnson 1966; Grant 1972). It has also been demonstrated that morphological variability is often reduced in populations competing with similar species (Van Valen 1965) and that competition can alter body size, biasing the mean up or down (Hutchinson 1951). It seems probable that in some ecosystems, perhaps where the number of species of competitors is not high and the food niche is diversified, there is a selective advantage in maintaining the genetic potential for morphological flexibility which takes advantage of such available food, where food niche and morphology are significantly correlated (Hespenheide 1973). Conversely, it seems probably that in situations of more inter-specific competition it is of greater selective value to maintain a more narrow morphology to avoid food niche overlap (Van Valen 1965). These situations exemplify the young ecosystem with low species diversity and broad niche specialization and the more mature ecosystem with high species diversity and more narrow niche specialization. My study of certain diaptomid copepod populations in piedmont North Carolina lakes has shown that the body length of a species can be quite variable or non-variable, presumably in response to changing levels of competition, which can be affected by the activity of a single vertebrate predator.

In studying copepod populations we are interested in the fact that their morphological changes can reflect the workings of the fundamental biological processes mentioned above. In order to perform such an analysis we also have to take into account other factors which are known to cause variation in the body lengths of copepods and similar planktonic arthropods. In addition to predation and competition, three other factors are known to influence body length in diaptomid copepods. These are: (1) sex - among all species the females are considerably larger than the males (Wilson 1959), (2) temperature - diaptomid copepods tend to become larger in the winter and early spring when water temperatures are cool and to become smaller in the summer when water temperatures rise (Coker and Addlestone 1938). The increased size when water temperatures are cool is due to reduced respiration and more efficient body maintenance, and (3) nutrient richness of the water - diaptomid copepods living in nutrient rich waters tend to be larger than those of more nutrient poor waters. Several investigators have found that clutch size, or the number of eggs carried by egg-bearing females is highly correlated with the trophic status of the habitat, with mean clutch sizes being greater in waters with higher chlorophyll content (Czeczuga 1960; Schacht 1897; Wesenberg-Lund 1904; Comita and Anderson 1959). Clutch size is also significantly and positively correlated with body size (Ravera and Tonolli 1956; Marshall 1949; Davis 1961).

The purposes of this work were to: (1) demonstrate that predation by Dorosoma petenense was size-selective by comparing the seasonal variation in mean length of Diaptomus populations subject to predation with seasonal variation in mean length of populations free of it and (2) show that the degree of competition to which Diaptomus populations were subjected was reflected in the variance of their body lengths.

MATERIALS AND METHODS

Body length measurements were made of diaptomid copepods from zooplankton samples which had been taken from six piedmont North Carolina lakes every six weeks from July 1973 through May 1974 and preserved in 5% formalin solution. The samples were collected with a 24.1 cm diameter Turtox plankton net of 0.210 mm mesh size. Only adults were measured and, where numbers were sufficient, 50 males and 50 females were measured from each collection. In two of the lakes (Lakes Jeanette and Sloan) adults from samples taken at the deepest station in each lake were measured. The deep station in Lake Jeanette fluctuated between 8.5 and 10 m in depth during the sampling period. In Lake Sloan the depth of the deep station ranged between 2.5 and 3 m during this period. In the remaining four lakes (Lakes Taylor, University, Hickory, and James) adults from only one general depth for each of the samples were measured. This depth ranged from 4.5 to 8 m. Body length was measured as the length from the anterior tip of the cephalothorax to the end of the terminal segment excluding terminal setae.

Measurements were initially made using a Wolfe microscope with calibrated ocular and 3,5:1X objective but this was later replaced with an American Optical Lumiscope with 4X objective which enabled the entire specimen to be measured without changing the field. All measurements were made to the nearest .1 ocular unit. With the Wolfe microscope, one ocular unit was equal to .207 mm and with the American Optical Lumiscope, one ocular unit was equal to .323 mm. Samples were withdrawn from vials containing the adults which had been separated from the initial hauls. These were placed in a Sedgewick-Rafter counting cell. Individuals were then lined up and measured in sequence until all specimens or at least 50 males and 50 females had been measured. In cases where more than one species was present in a sample, it was sometimes necessary to remove an individual from the Sedgewick-Rafter cell for staining, dissection, and identification; however, in such cases the animal was measured prior to dissection. The diaptomid copepods were identified according to Wilson (1959). The eggs of egg-bearing females were counted and, when present, sperm sacs were noted as the specimens were measured.

In two of the lakes studied (Lakes Jeanette and Sloan), *Diaptomus reighardi* was the predominant diaptomid copepod present, the only other member of the genus being the larger *D. birgei* which appeared briefly in very small numbers in the deeper Lake Jeanette during the winter. *D. reighardi* was the only species in Lake Sloan. *Dorosoma petenense* was present in Lake Jeanette but absent in Lake Sloan. Adult *D. reighardi* from the collections taken at the deepest stations in both lakes over the entire sampling period were analysed to see if mean body length varied seasonally in a significantly different manner between a shad-inhabited and a shad-free lake.

As previously mentioned, sex, water temperature, and nutrient richness of the water all exert an effect on body length of diaptomid copepods. For this reason they were included in the analysis as independent variables. Analysis of covariance was performed to see if the dependent variable, body length, varied seasonally in a significantly different manner in the two lakes after differences in these factors or covariates were accounted for.

To establish that body length in Lake Jeanette could be predicted in the same manner as in Lake Sloan except during times of shad predation, regression analysis was performed on Lake Sloan and the resulting regression equation applied to both Lakes Jeanette and Sloan. Its accuracy in predicting individual body lengths throughout the sampling year was determined.

In the other four lakes studied, samples were from only one general depth (4.5 - 8 m). The body length of one species present in all of these lakes, Diaptomus pallidus, was measured as described above. In one of these lakes (Taylor Lake) D. pallidus was the only diaptomid copepod present and there were no shad. In another (University Lake), shad were present and there was very light competition with D. reighardi except on one sampling date (July) when competition was severe. In the remaining two lakes (Lakes Hickory and James) shad were present and competition with other diaptomid copepods was severe. The range and standard deviation of body lengths for each sampling date were determined in each of the four lakes to establish the effect of inter-specific competition on variance of body length.

DESCRIPTIONS OF LAKES

Lake Jeanette, Guilford Co., N.C.: 115 ha lake draining through the Haw River into the Cape Fear River; completed in 1941; max. depth 10 m; *Diaptomus reighardi* and *D. birgei* present.

Lake Sloan, Guilford Co., N.C.: 2.4 ha lake draining through Lake Jeanette, the Haw River and into the Cape Fear River; completed in 1933; max. depth 3 m; *Diaptomus reighardi* present.

University Lake, Orange Co., N.C.: 104 ha lake in the Cape Fear drainage; completed in 1932; max. depth 7 m; *Diaptomus pallidus* and *D. reighardi* present.

John R. Taylor Lake, Guilford Co., N.C.: 7.2 ha lake draining through the Haw River into the Cape Fear River; completed in 1951; max. depth 5.5 m; *Diaptomus pallidus* present.

Lake James, Burke and McDowell Cos., N.C.: 2604 ha lake on the Catawba River; completed in 1923; max. depth 28 m; *Diaptomus pallidus* and *D. birgei* present.

Lake Hickory, Alexander, Caldwell and Catawba Cos., N.C.: 1640 ha lake on the Catawba River; completed in 1928; max. depth 31 m; *Diaptomus pallidus*, *D. birgei*, and *D. mississippiensis* present.

RESULTS

Lakes Jeanette and Sloan

Competition: The zooplankton communities of both lakes were dominated by *D. reighardi* with one other diaptomid copepod, *D. birgei*, being briefly present in the winter in negligible numbers in Lake Jeanette. *D. birgei* comprised 2% of the sample taken in February in that lake. Therefore, competition was eliminated as a significant factor in this portion of the analysis.

Sex: Female *D. reighardi* were larger than the males in both lakes. Mean length of females in Lake Jeanette during the sampling period was 1.313±.099 mm while that of males was 1.149±.071 mm. In Lake Sloan females averaged 1.121±.066 mm and males 1.069±.071 mm.

Temperature: Average temperature of the water column from which the specimens came tended to be lower throughout the year in Lake Jeanette due to its greater depth. The only exception to this was in February when average temperature in Lake Sloan was slightly lower due to very cold air temperature. In July, September, and October no specimens were found in Lake Jeanette from the surface to 4 m deep. For this reason, average temperature of the water column was computed as the average from 4 m to the bottom. Temperature data are shown in Figures 1-4 and in Table I.

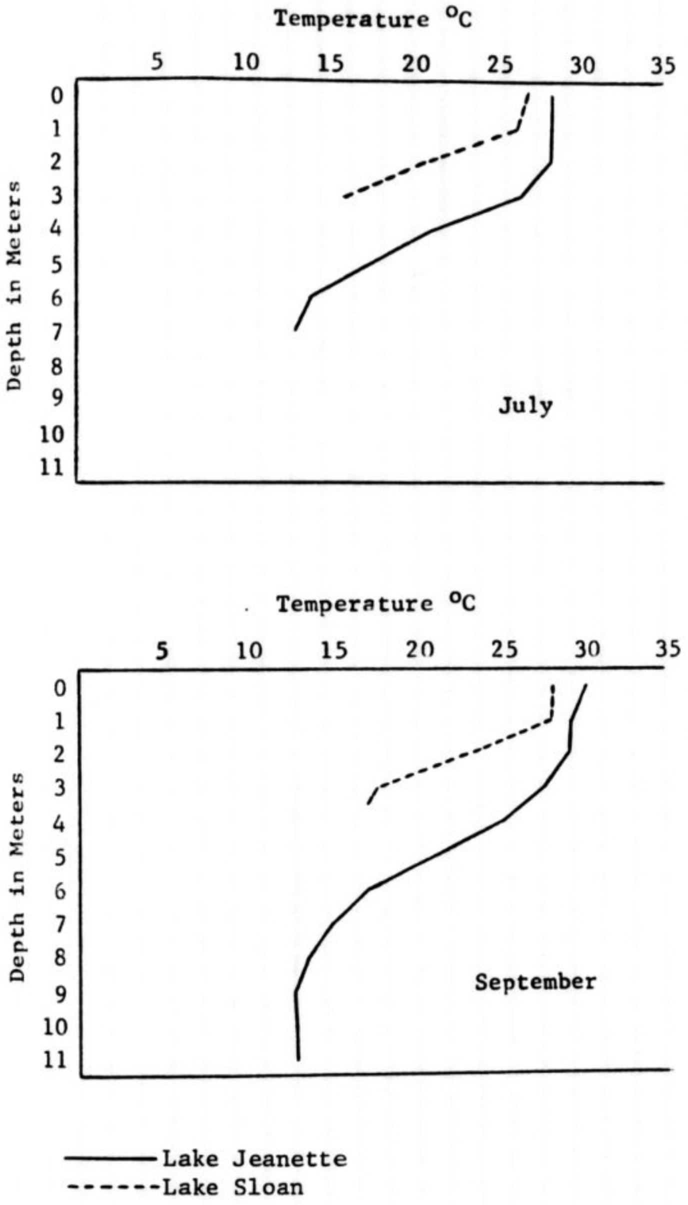

Figure 1. Thermal profiles of collection sites in Lakes Jeanette and Sloan in July and September.

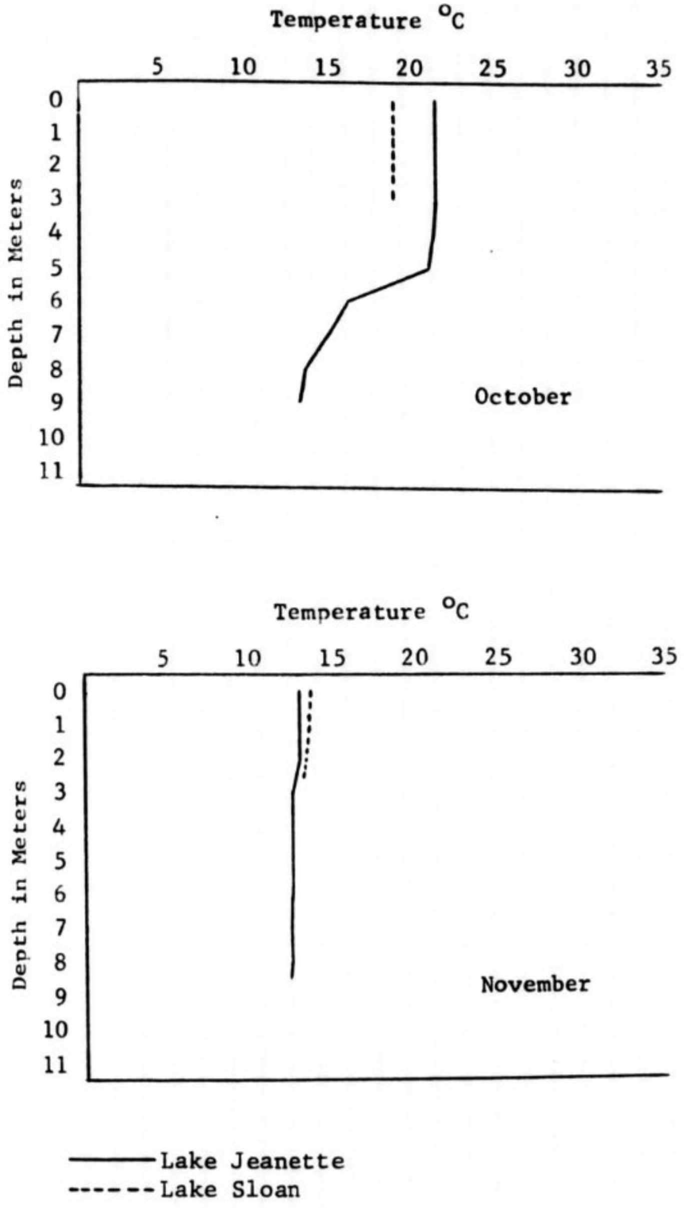

Figure 2. Thermal profiles of collection sites in Lake Jeanette and Sloan in October and November.

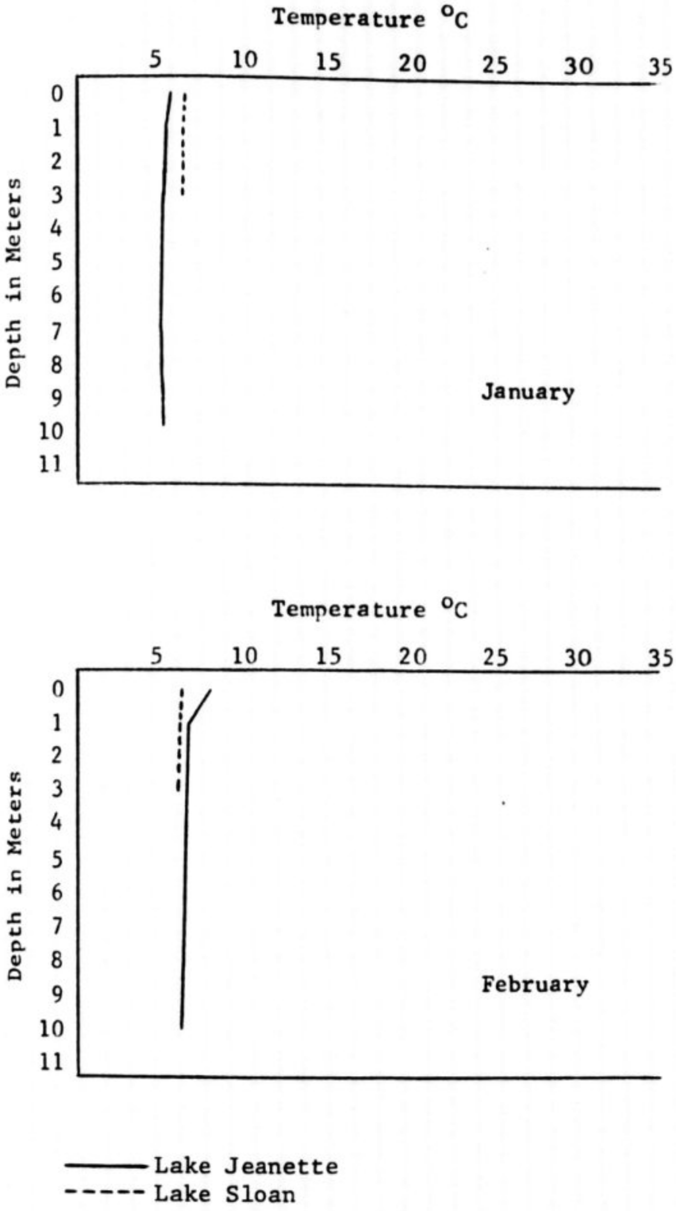

Figure 3. Thermal profiles of collection sites in Lake Jeanette and Sloan in January and February.

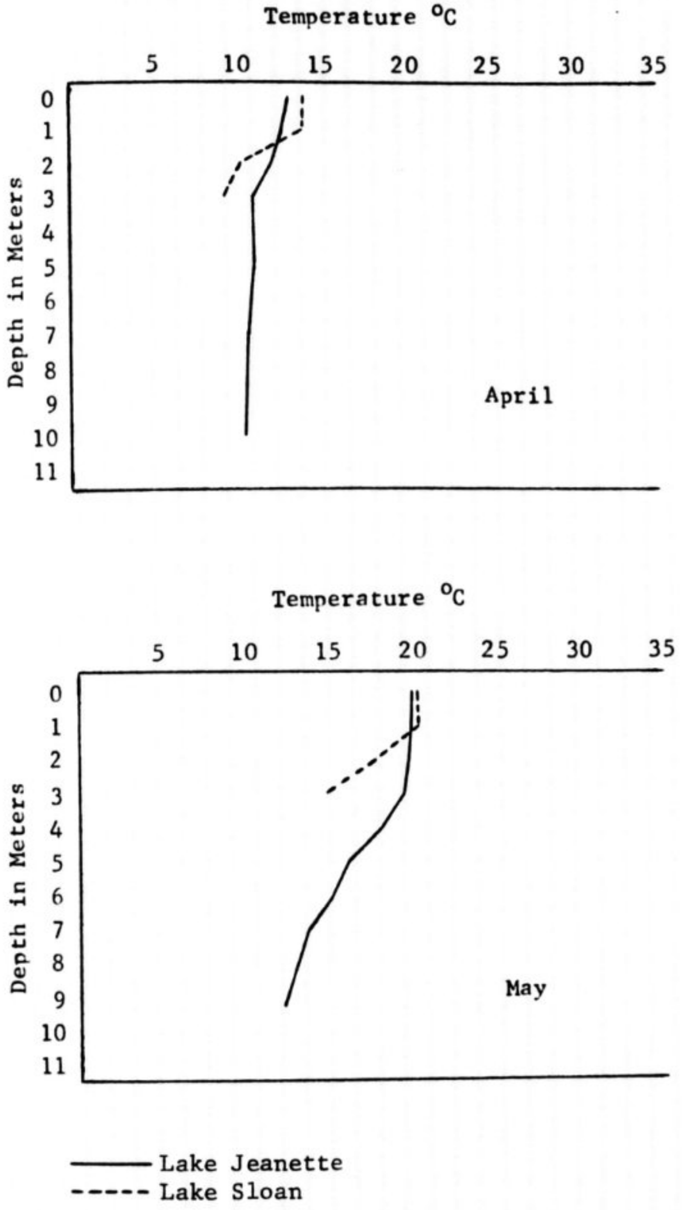

Figure 4. Thermal profiles of collection sites in Lake Jeanette and Sloan in April and May.

TABLE I: Average temperatures (°C) of water columns at collection sites in Lakes Jeanette and Sloan.

Date	Lake Jeanette	Lake Sloan
July	*16.2	22.4
Sept.	*16.3	25.1
Oct.	*16.6	19.1
Nov.	12.6	13.4
Jan.	5.3	6.1
Feb.	6.6	6.1
April	11.0	11.8
May	16.2	18.1

*These temperatures computed as average from 4 m to bottom.

Nutrient Richness: The number of eggs per egg-bearing female, averaged for the sampling period as a measure of nutrient richness, was significantly higher in Lake Jeanette (20.7±9.6) than in Lake Sloan (8.5±3.8). Also, on all individual dates during the sampling period when egg-bearing females were found among those measured, values were higher in Lake Jeanette than in Lake Sloan. However, there were no egg-bearing females found on the September and October dates of 1973 in Lake Jeanette. To ascertain values for these dates 50 individuals were examined from each of these collections in the 1974 Lake Jeanette samples when a larger net was used and more specimens collected. It was felt that using the data from Lake Jeanette for the following year provided the optimal and perhaps most liberal estimates of what egg-counts would be for the September and October dates of 1973. Using 1973 Lake Sloan egg data for these dates would certainly provide the most conservative estimates. The actual values were considered to lie somewhere between. Egg data are shown in Table II.

With these factors it was possible to derive a prediction equation of what body length of D. reighardi should be throughout the sampling year in Lake Sloan. Regression analysis was performed with body length as the dependent variable. Sex, average egg-count per egg-bearing female, and average temperature of the water column from which the specimens came were the independent variables. Males were assigned a numerical value of 1 and females a numerical value of 2. The equation thus derived was:

TABLE II: Egg data for Lakes Jeanette and Sloan.

	Eggs Per Egg-Bearing Female (1973)						Eggs Per Egg-Bearing Female (1974)					
Date	Sloan	SD	N	Jeanette	SD	N	Sloan	SD	N	Jeanette	SD	N
July	8.0	3.2	26	17.0	-	2	8.7	3.9	20	16.0	-	3
Sept.	5.3	3.8	4	-	-	-	-	-	-	10.0	-	2
Oct.	9.7	4.8	10	-	-	-	10.2	4.9	7	22.0	-	1
Nov.	5.0	4.2	2	6.0	-	1	6.5	-	3	5.0	-	1
Jan.	10.7	2.8	6	26.0	-	3						
Feb.	16.0	-	1	25.1	9.8	7						
April	21.7	3.7	23	25.7	8.7	15						
May	13.9	3.5	19	15.1	6.5	41						

$$\text{Predicted Length} = .92797280 + .00499461\ (\text{Eggs/Egg-Bearing Female}) + .15356258\ (\text{Sex}) - .00364468\ (\text{Average Temperature})$$

This equation predicted body length of <u>D. reighardi</u> in Lake Sloan with an R^2 of .7212. R^2 is the proportion of the variance of the dependent variable, length, that is accounted for by the independent or predictor variables of egg-count, sex, and average temperature. This value is obtained by dividing the regression sum of squares by the total corrected sum of squares. The probability that this R^2 was due to chance was $<.0001$. This equation was then applied to both lakes and 95% confidence intervals determined to see if body lengths in Lake Jeanette could also be predicted accurately. It was found that the equation worked quite well for Lake Jeanette from January through April when 94.9% of the individuals measured fell within the 95% confidence intervals. During July through November, however, only 41.2% of the individuals measured fell within the 95% confidence intervals and of the 58.8% falling outside, all were smaller than predicted. In May an intermediate situation existed where almost all of the specimens were within the 95% confidence limits but 97% of the individuals were below predicted mean length. Egg data from 1974 Lake Jeanette samples were used in deriving the predicted lengths for September and October in Lake Jeanette. Thus, the above data were based on what probably were the upper estimates of what body lengths should be in Lake Jeanette on these two dates. When the 1973 Lake Sloan values of eggs per egg-producing female for September and October were substituted into the prediction equation, 93.8% of the individuals collected from January through April fell within the 95% confidence intervals. Only 64.7% of the individuals collected from July through November fell within the 95% confidence intervals. Again, while the 6.2% falling outside the 95% confidence intervals between January and April fell randomly above and below the intervals, the 35.3% falling outside the 95% confidence intervals between July and November were all below the confidence intervals. May again showed an intermediate situation where most individuals were within the 95% confidence intervals but 97% were below predicted length. These data were based on what probably were the most conservative estimates of what body lengths of D. reighardi should be in Lake Jeanette in September and October. Figures 5-10 illustrate how well the predicted lengths fit the actual lengths throughout the sampling period.

The results of the regression analysis and prediction equation show that we can predict what length of D. reighardi will be in Lake Sloan throughout the sampling period based on the three factors of sex, water temperature, and nutrient richness of the water as indicated by egg-counts of egg-bearing females. We can also predict body length of D. reighardi in Lake Jeanette just as well with these three factors except during the period of late spring through fall. Apparently some additional factor is operating in Lake Jeanette at this time of the year but not in Lake Sloan. This deviation from the prediction equation in Lake Jeanette was apparently non-random since all of the lengths fell below predicted values. In order to see if these deviations were an artifact due to small sample size, analysis of covariance was performed to determine if there were real differences between these lakes. Competition was not a significant factor in either of the lakes.

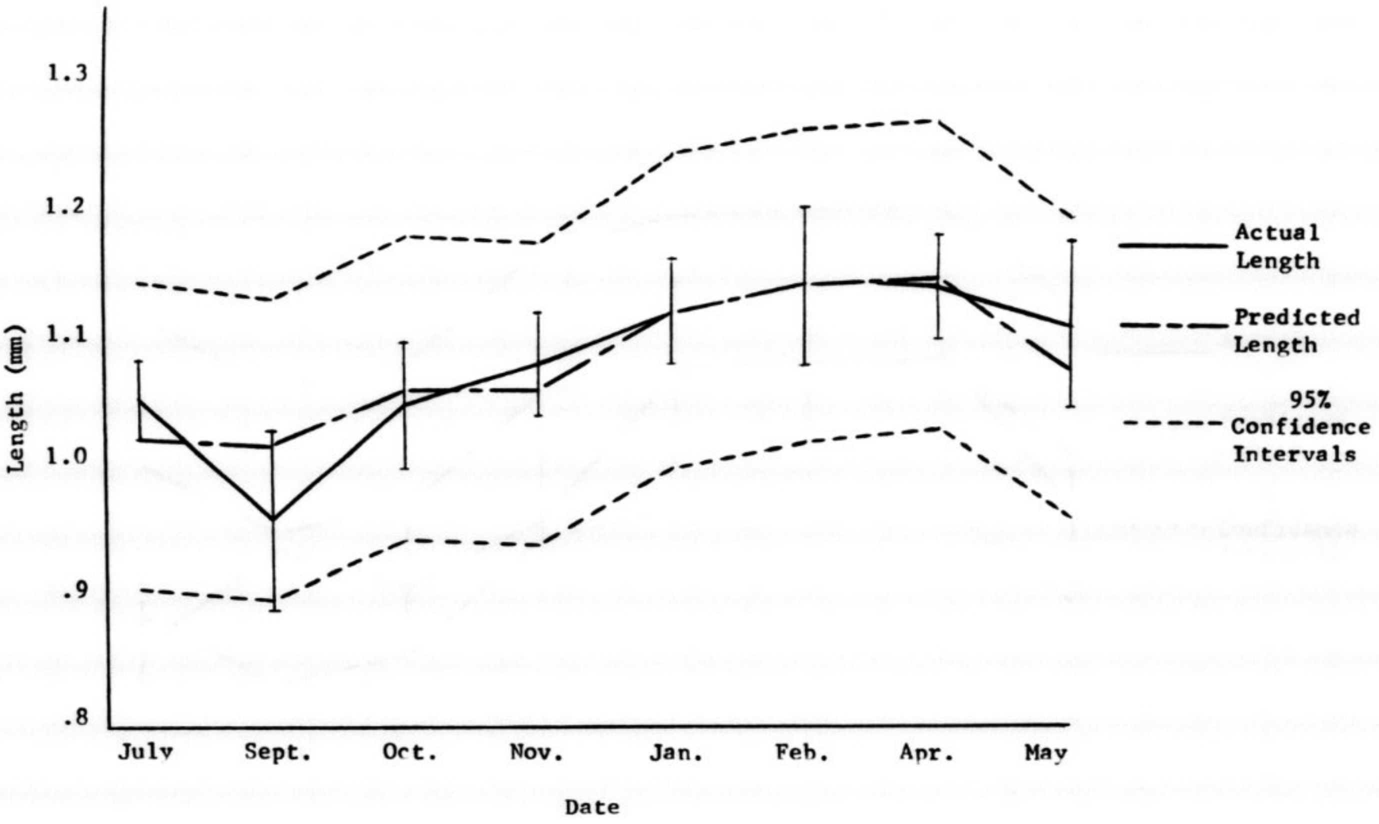

Figure 5. Seasonal variation in mean length of male Diaptomus reighardi in Lake Sloan.

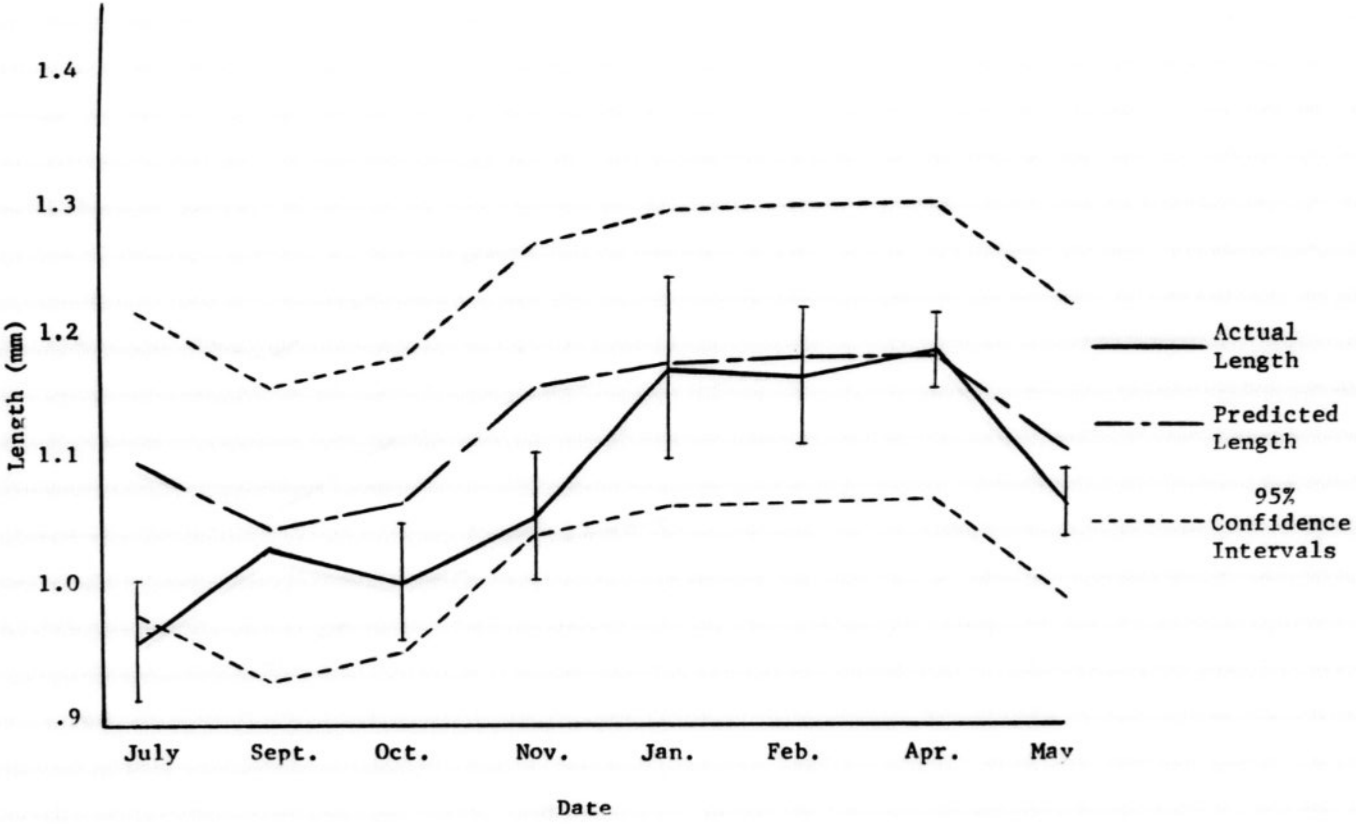

Figure 6. Seasonal variation in mean length of male <u>Diaptomus reighardi</u> in Lake Jeanette (1974 Lake Sloan egg data for September and October dates).

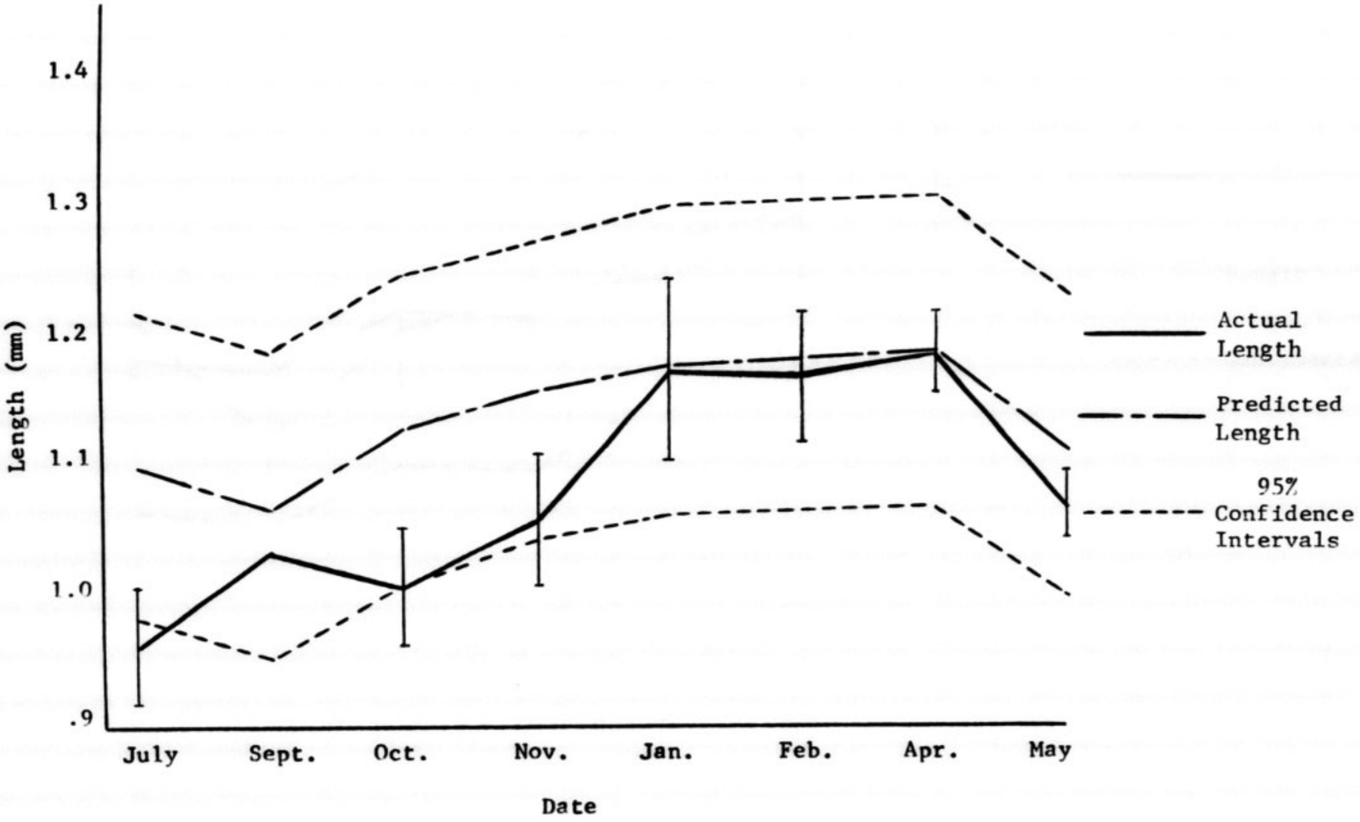

Figure 7. Seasonal variation in mean length of male Diaptomus reighardi in Lake Jeanette (1974 Lake Jeanette egg data for September and October dates).

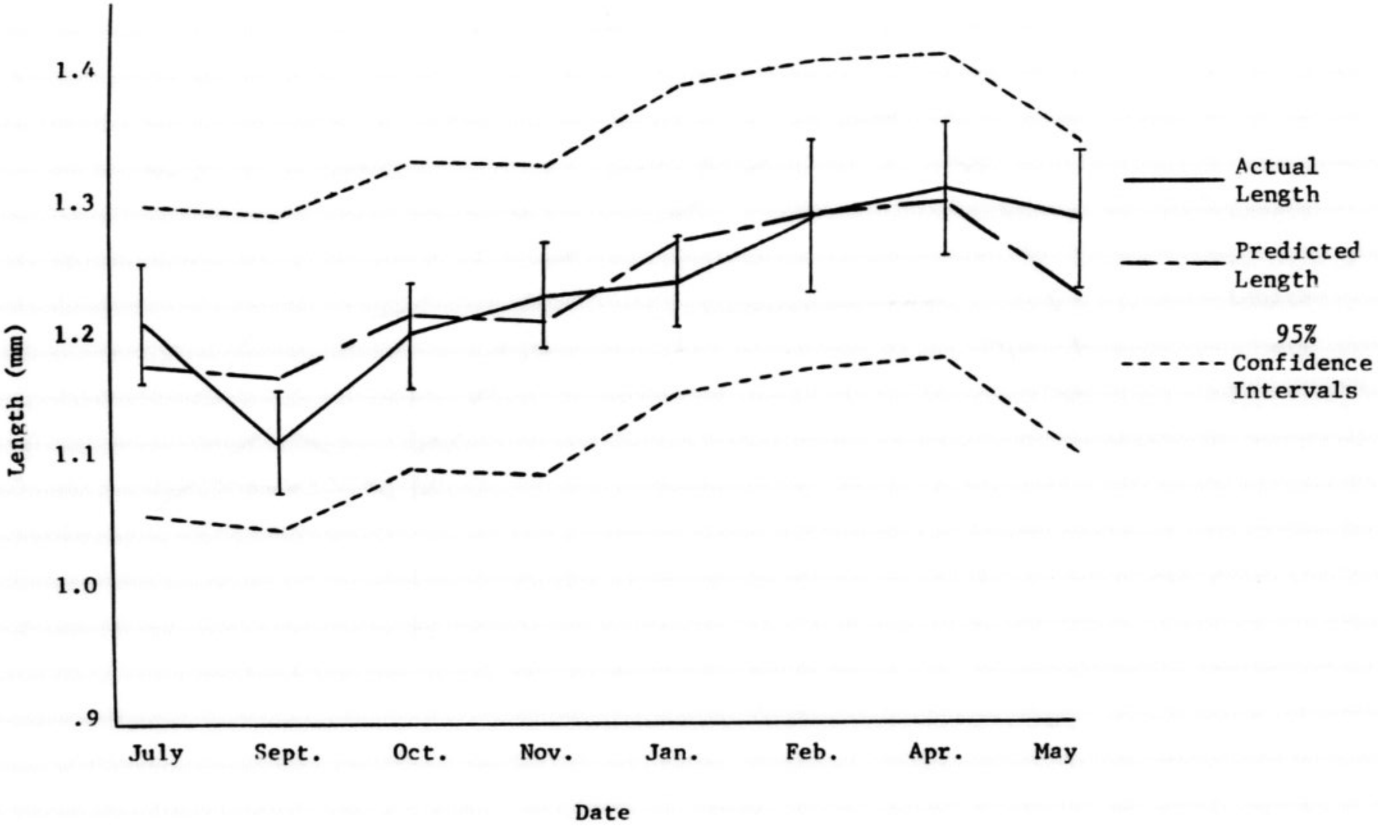

Figure 8. Seasonal variation in mean length of female <u>Diaptomus reighardi</u> in Lake Sloan.

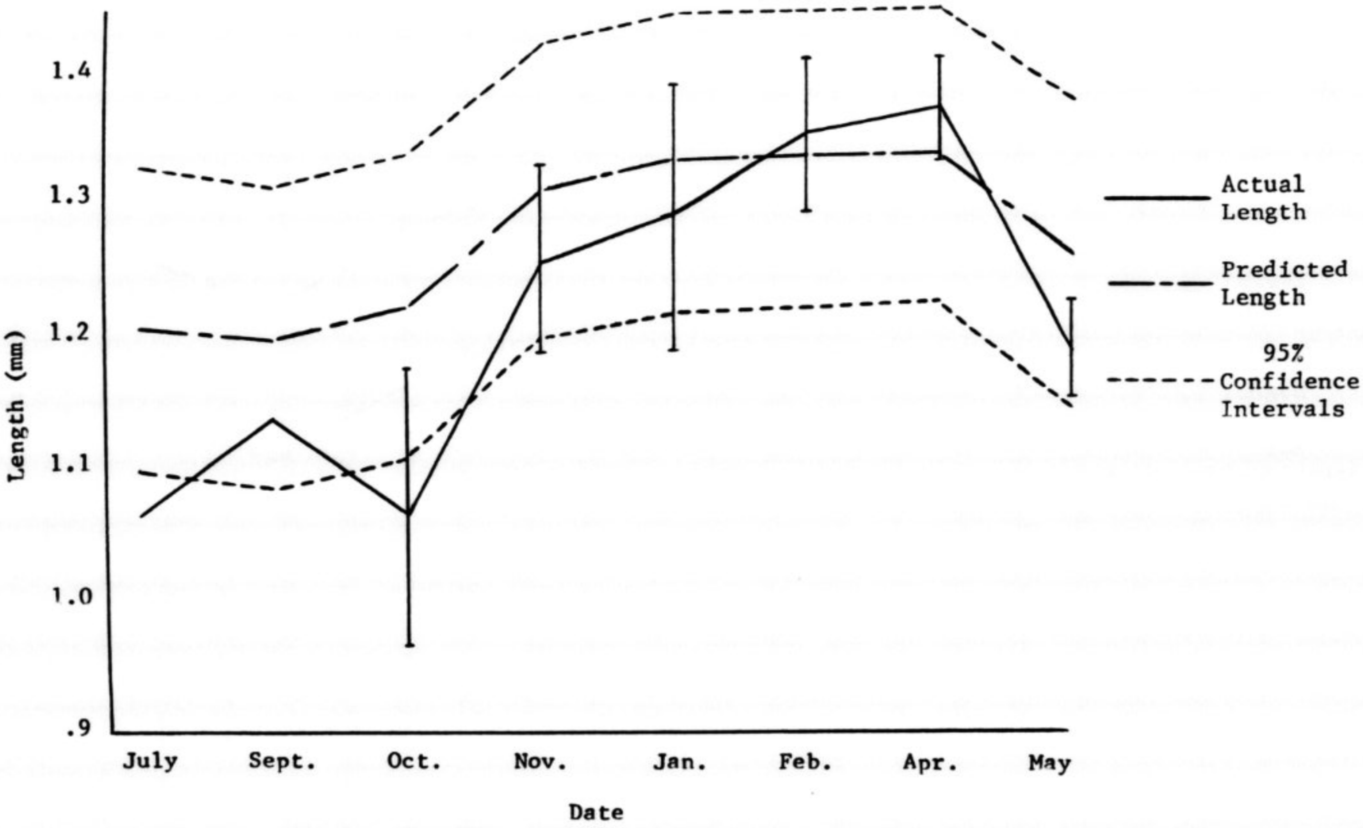

Figure 9. Seasonal variation in mean length of female _Diaptomus reighardi_ in Lake Jeanette (1974 Lake Sloan egg data for September and October dates).

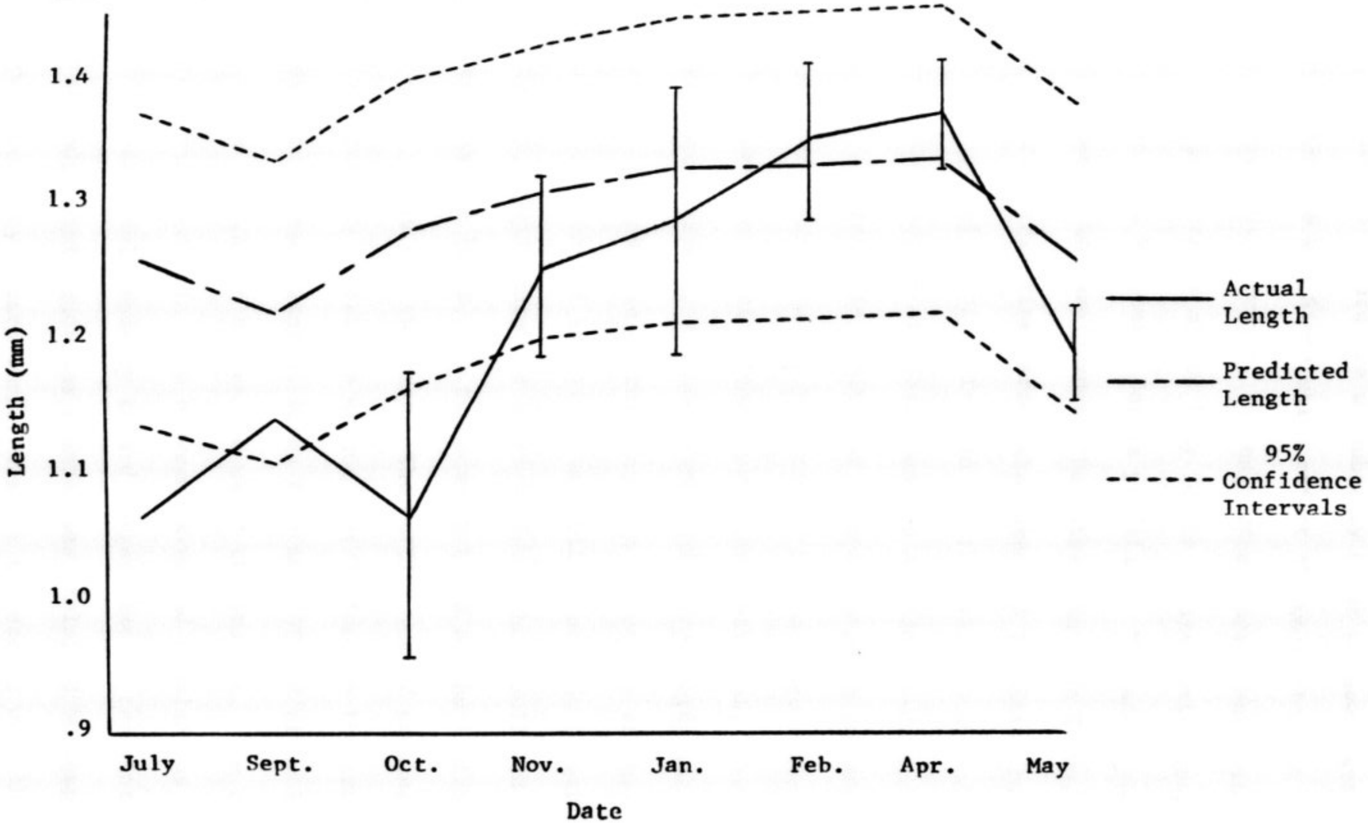

Figure 10. Seasonal variation in mean length of female Diaptomus reighardi in Lake Jeanette (1974 Lake Jeanette egg data for September and October dates).

Predation: There are undoubtedly other unknown factors in Lake Jeanette and Sloan which affect the morphology of diaptomid copepods. However, the only other factor which is known to significantly affect body length of diaptomid copepods and has not been accounted for is predation. Threadfin shad, which are present in Lake Jeanette but absent in Lake Sloan, are active during this time period when seasonal variation in body length of D. reighardi differs in the two lakes, i.e. body lengths in Lake Jeanette are less than the equation predicts.

To analyze this additional factor operating in Lake Jeanette, analysis of covariance was performed. Sex, average water temperature, and eggs per egg-bearing female were the covariates, lake was the independent variable, and body length of D. reighardi was the dependent variable. The purpose of this analysis was to see if there was a significant amount of explained variability of body length not accounted for by sex, temperature, or nutrient level, but explained by a difference between the two lakes. As the summary table of the statistics (Table III) shows, this was the case. The partial sum of squares, which gives each independent variable's unique contribution to the explained variability of body length, shows that most of the variation in body length was explained by sex and water temperature. The obvious and constant difference in size between males and females was explained by sex. The seasonal tendency toward larger size in the winter when the cost of body maintenance was reduced was explained by temperature. The seasonal tendency toward larger size in the spring when the water became more nutrient rich and phytoplankton bloomed was explained by egg count,

TABLE III: Summary table of statistics of analysis of covariance in Lakes Jeanette and Sloan.

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F	R^2
Regression	4	11.30401	2.82600	709.59863	0.0001	0.7030
Error	1201	4.78303	0.00398			
Corrected Total	1205	16.08704				

Source	DF	Partial Sum of Squares	F Value	Prob>F
Covariate				
Sex	1	7.31127	1835.83092	0.0001
Aver. Temp.	1	2.08763	524.19582	0.0001
Egg	1	0.01212	3.04380	0.0813
Lake	1	0.25093	63.00724	0.0001

as an index of nutrient richness; this independent variable, however, showed the least significant correlation with body length (0.0813). It was felt that the remaining variability, explained by a difference in the two lakes, was due, in large part, to size-selective feeding by *Dorosoma petenense* from late spring through fall.

The variance of body length in Lakes Jeanette and Sloan, as indicated by standard deviation and range, did not differ in any discernible pattern between the two lakes. During July the standard deviation was higher in Lake Jeanette than in Lake Sloan for both males and females; range on this date was higher in Lake Sloan for males but higher in Lake Jeanette for females (Table IV). In October both standard deviation and range in Lake Jeanette were lower than in Lake Sloan for males but higher for females. Apparently, while predation reduces mean body length of the population it does not reduce the variability of individual body lengths in the population. The probability that the differences in standard deviation between Lake Sloan and Lake Jeanette were due to chance was <0.0845. The probability that the differences in range between Lake Sloan and Lake Jeanette were due to chance was <0.7787.

TABLE IV: Variability of body length of *Diaptomus reighardi* in Lakes Jeanette and Sloan.

		Male				Female			
Lake	Date	SD	Min. Value	Max. Value	N	SD	Min. Value	Max. Value	N
Jeanette	July	0.047	0.923	1.047	6	0.169	0.964	1.265	3
"	Sept.	-	1.037	1.037	1	-	1.144	1.144	1
"	Oct.	0.047	0.958	1.047	3	0.112	0.943	1.151	3
"	Nov.	0.051	0.977	1.143	8	0.089	1.137	1.368	6
"	Jan.	0.068	0.985	1.391	50	0.098	1.151	1.462	33
"	Feb.	0.051	1.032	1.274	199	0.056	1.213	1.494	139
"	April	0.037	1.071	1.248	109	0.041	1.258	1.472	118
"	May	0.041	0.970	1.202	106	0.045	1.088	1.329	104
Sloan	July	0.031	0.964	1.113	99	0.047	1.037	1.294	106
"	Sept.	0.070	0.870	1.277	47	0.040	1.061	1.235	47
"	Oct.	0.054	0.889	1.203	66	0.042	1.100	1.300	67
"	Nov.	0.043	1.012	1.171	56	0.048	1.125	1.326	59
"	Jan.	0.046	1.025	1.197	54	0.042	1.100	1.320	68
"	Feb.	0.061	1.041	1.261	32	0.072	1.177	1.420	22
"	April	0.035	1.009	1.239	153	0.049	1.093	1.407	157
"	May	0.053	1.016	1.193	22	0.049	1.190	1.391	46

Lakes Taylor, University, Hickory, and James

Competition

The above lakes were chosen because they provided a natural study in determining the effect of inter-specific competition on a single species, *Diaptomus pallidus*, present in all of these lakes. The degree of inter-specific competition which this species experienced from other diaptomid copepods was mild in one lake (University), except on one sampling date, and severe in two others (Lakes Hickory and James). In Taylor Lake *D. pallidus* was the only diaptomid copepod. The results from Lakes Jeanette and Sloan showed that predation did not have a discernible effect on the variability of individual body lengths of *D. reighardi*. The purpose of this portion of the study was to see if the variability of the individual body lengths of *D. pallidus* changed with differing levels of inter-specific competition.

For each sampling date standard deviations were calculated and minimum and maximum values recorded for both males and females (Table V). The percentage of *D. pallidus* in the diaptomid copepod communities in the four lakes varied. In Taylor Lake it was the only diaptomid copepod present throughout the year. In University Lake the only other diaptomid copepod present was *D. reighardi* and only in July did it comprise a significant percentage of the zooplankton community. In Lake James the only other diaptomid copepod present was *D. birgei*. In Lake Hickory *D. pallidus* shared the "*Diaptomus* niche" with two other diaptomid copepod species, *D. birgei* and *D. mississippiensis*. *D. mississippiensis* is the smallest of the diaptomid copepods found in the piedmont lakes studied with a size range of 0.89-1.15 mm in males and 1.03-1.28 mm in females

TABLE V: Variability of body length (measured by standard deviation and range) of *Diaptomus pallidus* in Lakes Taylor, University, Hickory, and James. Presence of other diaptomid copepod species indicated by: B = *D. birgei*, M = *D. mississippiensis*, P = *D. pallidus*, R = *D. reighardi*.

Diaptomid Copepods Present				Lake	Date	Male				Female			
%B	%M	%P	%R			SD	Min. Value	Max. Value	N	SD	Min. Value	Max. Value	N
0	0	100	0	Taylor	July	0.050	0.906	1.103	50	0.054	1.022	1.261	50
0	0	100	0	"	Sept.	0.058	0.908	1.129	50	0.070	1.041	1.303	50
0	0	100	0	"	Oct.	0.068	0.925	1.177	50	0.066	1.067	1.358	50
0	0	100	0	"	Nov.	0.068	0.967	1.229	50	0.066	1.109	1.387	50
0	0	100	0	"	Jan.	0.061	1.022	1.281	50	0.065	1.158	1.442	50
0	0	100	0	"	Feb.	-	-	-	-	-	-	-	-
0	0	100	0	"	April	0.063	1.016	1.265	50	0.074	1.129	1.426	50
0	0	100	0	"	May	0.064	1.009	1.255	50	0.072	1.132	1.407	50
0	0	41	59	University	July	0.017	1.064	1.132	23	0.020	1.229	1.307	24
0	0	100	0	"	Sept.	0.051	0.957	1.164	24	0.055	1.116	1.345	29
0	0	98	2	"	Oct.	0.053	1.012	1.229	50	0.058	1.171	1.420	50
0	0	100	0	"	Nov.	0.061	1.035	1.271	50	0.061	1.200	1.468	50
0	0	100	0	"	Jan.	0.052	1.071	1.300	50	0.060	1.213	1.472	50
0	0	99	1	"	Feb.	0.055	1.129	1.345	50	0.060	1.313	1.569	50
0	0	100	0	"	April	0.052	1.083	1.303	50	0.061	1.258	1.523	50
0	0	99	1	"	May	0.052	1.061	1.268	50	0.054	1.219	1.446	50
2	42	56	0	Hickory	July	0.021	1.028	1.109	24	0.026	1.203	1.300	20
0	52	48	0	"	Sept.	0.023	1.058	1.125	9	0.027	1.242	1.320	8
-	-	-	-	"	Oct.	-	-	-	-	-	-	-	-
-	-	-	-	"	Nov.	-	-	-	-	-	-	-	-
33	6	61	0	"	Jan.	0.020	1.045	1.125	41	0.029	1.171	1.287	46
-	-	-	-	"	Feb.	-	-	-	-	-	-	-	-
-	-	-	-	"	April	-	-	-	-	-	-	-	-
47	3	50	0	"	May	0.021	1.019	1.087	13	0.029	1.148	1.235	10

TABLE V: Continued.

Diaptomid Copepods Present				Lake	Date	Male				Female			
%B	%M	%P	%R			SD	Min. Value	Max. Value	N	SD	Min. Value	Max. Value	N
-	-	-	-	James	July	-	-	-	-	-	-	-	-
-	-	-	-	"	Sept.	-	-	-	-	-	-	-	-
-	-	-	-	"	Oct.	-	-	-	-	-	-	-	-
-	-	-	-	"	Nov.	-	-	-	-	-	-	-	-
14	0	86	0	"	Jan.	0.045	1.048	1.223	51	0.051	1.180	1.381	50
53	0	47	0	"	Feb.	0.028	1.009	1.122	40	0.032	1.148	1.287	43
68	0	32	0	"	April	0.023	0.983	1.067	11	0.026	1.125	1.216	12
73	0	27	0	"	May	0.016	0.977	1.032	11	0.021	1.100	1.164	10

(Beavers 1975). All of these lakes except Taylor Lake contained Dorosoma petenense.

Taylor Lake: In Taylor Lake, where shad are not present and D. pallidus is the only diaptomid copepod present, the standard deviation and range were high throughout the year. Standard deviations remained between 0.050 mm and 0.068 mm for males and between 0.054 mm and 0.073 mm for females (Table V).

University Lake: D. pallidus had a standard deviation and range comparable to Taylor Lake throughout the year except in July when both of these measures of variability dropped precipitously. For the sampling dates other than July the standard deviations remained between 0.051 mm and 0.061 mm for males and 0.054 mm and 0.061 mm for females, but in July the standard deviation dropped down to 0.017 mm for males and 0.020 mm for females (Table V). D. reighardi, the only other diaptomid copepod present, comprised 59% of the diaptomid copepod community in July. On other sampling dates D. reighardi never comprised more than 2% of the diaptomid copepods present.

Lake Hickory: There were sufficient numbers of D. pallidus for analysis in July, September, January, and May. Standard deviation and range of body lengths were lower than either in Taylor Lake or University Lake for these sampling dates except for the July date in University Lake. Standard deviations were between 0.021 mm and 0.023 mm for males and between 0.026 mm and 0.029 mm for females (Table V). The percentage of the diaptomid copepod community which D. pallidus comprised on these dates ranged from

48 to 61%. In July and September D. mississippiensis was present in substantial numbers comprising 42% of the July sample and 52% of the September sample. D. birgei was present in minimal numbers on these dates. In January and May, however, D. mississippiensis had declined in numbers and D. birgei was D. pallidus's most severe competitor, making up 33% of the January sample and 47% of the May sample.

Lake James: There were sufficient numbers of D. pallidus for analysis in January, February, April, and May. Standard deviation and range were considerably lower than in Taylor Lake or University Lake (with the exception of July in University Lake) in February, April, and May. On these dates the standard deviation was never above 0.028 mm for males and 0.032 mm for females. Also, on these dates, D. birgei, the only other diaptomid copepod present, comprised a dominant portion of the diaptomid copepod community, rising from 59% in February to 73% in May (Table V). In January, when D. birgei comprised only 14% of the diaptomid copepod community, standard deviation and range more closely approached that found in Lakes Taylor and University. Standard deviation in January was 0.045 mm for males and 0.051 mm for females.

In Lakes Hickory and James, where there was year-round interspecific competition, mean standard deviations of body length of D. pallidus for all sampling dates were 0.025 mm and 0.030 mm, respectively. Comparing each of these with the mean standard deviations found in both Taylor Lake (0.064 mm) and University Lake (0.051 mm), it was found that they were significantly lower (Table VI). The method of comparison was Scheffe's _post hoc_ test. Also, when the mean standard deviations of Lakes Hickory and James were grouped and compared with the grouped standard deviations of Lakes Taylor and University, again using Scheffe's test, they were found to be significantly lower (Table VI).

In January and May the individual dates in all four lakes could be compared. It was found that in January in Lake Hickory standard deviations of body length of _D. pallidus_ for both males and females were significantly lower than in either Taylor Lake or University Lake (Table VI). _D. birgei_ comprised 37% of the diaptomid copepod community in Lake Hickory in January, while in Lakes Taylor and University _D. pallidus_ was the only diaptomid copepod present (Table V). However, in Lake James in January, where _D. birgei_ comprised only 14% of the diaptomid copepod community, standard deviations of body length of _D. pallidus_ were fairly high for both males (0.045 mm) and females (0.051 mm). Comparing these values with those in Lakes Taylor and University in January, it was found that only the standard deviations of the males in Lake James and Taylor Lake were significantly different from each other (Table VI). In May standard deviations of body length of _D. pallidus_ in both Lake Hickory and Lake James were significantly lower than either in Taylor Lake or University Lake (Table VI). _D. birgei_ made up 47% of the Lake Hickory sample and 73% of the Lake James sample (Table V).

TABLE VI: Scheffe's post hoc comparisons of variance of body length of *D. pallidus* in Lakes Taylor, University, Hickory and James.

Comparisons of standard deviations averaged over the entire sampling period:

Lakes(s)	SD(mm)	N	vs.	Lake(s)	SD(mm)	N	Prob. of Equality of S.D.'s
Hickory	0.025	87		Taylor	0.064	350	.01
Hickory	"	"		University	0.051	347	.01
James	0.030	125		Taylor	0.064	350	.01
James	"	"		University	0.051	347	.01
Hickory and James	0.027	212		Taylor and University	0.057	697	.01

Comparisons of standard deviations for January:

Lake	Sex	SD(mm)	N	vs.	Lake	Sex	SD(mm)	N	Prob. of Equality of S.D.'s
Hickory	M	0.020	41		Taylor	M	0.061	50	.01
"	F	0.029	46		"	F	0.065	50	.01
"	M	0.020	41		University	M	0.052	50	.01
"	F	0.029	46		"	F	0.060	50	.01
James	M	0.045	51		Taylor	M	0.061	50	.05
"	F	0.051	50		"	F	0.065	50	*
"	M	0.045	51		University	M	0.052	50	*
"	F	0.051	50		"	F	0.060	50	*

*These standard deviations were not significantly different at the .05 level. Scheffe's post hoc procedure does not compute the actual level of significance. It gives values which are then judged significant at the .01 level, .05 level, or not significant at these levels according to a table.

TABLE VI: Continued.

Comparisons of standard deviations for May:

Lake	Sex	SD(mm)	N	vs. Lake	Sex	SD(mm)	N	Prob. of Equality of S.D.'s
Hickory	M	0.021	13	Taylor	M	0.064	50	.01
"	F	0.029	10	"	F	0.072	50	.01
"	M	0.021	13	University	M	0.064	50	.01
"	F	0.029	10	"	F	0.072	50	.01
James	M	0.016	11	Taylor	M	0.052	50	.01
"	F	0.021	10	"	F	0.054	50	.01
"	M	0.016	11	University	M	0.052	50	.01
"	F	0.021	10	"	F	0.054	50	.01

DISCUSSION

Several studies have shown that the introduction of piscine planktivores into lakes can cause striking changes in the species composition of the zooplankton community (Brooks and Dodson 1965; Galbraith 1967; Wells 1970; Beavers and Stavn 1975). Usually within a relatively short time after the introduction of such fishes as rainbow trout (Salmo gairdneri), alewives (Alosa pseudoharengus), gizzard shad (Dorosoma cepedianum), and threadfin shad (Dorosoma petenense) the larger species of zooplankton are reduced dramatically in numbers, especially during times of high predator activity. These larger species of zooplankton are usually dominant due to their greater efficiency of feeding and reduced metabolism per unit mass (Brooks and Dodson 1965). This reduction in numbers of large zooplankters allows additional smaller, less efficient zooplankton species to enter and even dominate the habitat. From such studies it has been concluded that these fishes are size-selective in their feeding behavior, selecting, where possible, the largest zooplankters available to them.

Even the introduction of a non-selective predator would be expected to alter, somewhat, species composition of the zooplankton community where there is inequity in species eveness (species eveness refers to how the total numerical abundance of the zooplankton community is distributed among its component species). Random predation would eliminate a higher proportion of the ecological dominant because of its great abundance; this would promote an increase in numbers of less efficient species already present and encourage invasion by additional species. However, in many lakes where shad and alewives have been introduced, species dominance is simply reversed, the less efficient species becoming dominant. If these predators are introduced into shallow waters which lack sufficient spatial diversification for escape by the preferred prey, then the larger species may be permanently removed from the habitat.

In three of the six lakes under investigation in this study zooplankton species composition has changed since they were surveyed in 1938 by McKee and Coker (1940). Lakes James and Hickory contained only one diaptomid copepod (*D. birgei*) and University Lake contained no diaptomid copepods at that time. However, since that survey, the introduction of *Dorosoma petenense* has been accompanied by increased zooplankton species diversity so that all of these lakes now contain at least two species of diaptomid copepods (see Table VII). Lakes Sloan and Taylor lack shad and each contains only one species of diaptomid copepod. Lake Jeanette was not present in 1938.

TABLE VII: Comparisons of diaptomid copepod species composition in piedmont North Carolina lakes in 1938 and 1973. B = *D. birgei*; M = *D. mississippiensis*; P = *D. pallidus*; R = *D. reighardi*.

Lake	1938	1973
Lake Sloan	-	R
Taylor Lake	-	P
University Lake	none	P,R
Lake James	B	B,P
Lake Hickory	B	B,M,P

The analysis of seasonal variation in mean population length of D. reighardi in Lakes Jeanette and Sloan supports the argument that Dorosoma petenense is size-selective in its feeding. Seasonal variation in mean population length of D. reighardi in Lake Jeanette was significantly different from Lake Sloan (Table III and Figures 5-10). The two lakes were similar during the winter and early spring in that body lengths could be predicted well (R^2 of 72%) in both lakes with knowledge of sex, nutrient richness, and water temperature. However, the prediction equation, based on these factors, failed to predict length effectively in Lake Jeanette during late spring through fall. Body lengths during this time period in Lake Jeanette fell below predicted values (Figures 5-10). This time period corresponded to the time of the year when Dorosoma petenense was active in Lake Jeanette.

The feeding habits of the gizzard shad (Dorosoma cepedianum), a species closely related to the threadfin shad, have been more extensively investigated than those of the threadfin shad. Studies such as those of Cramer and Marzolf (1970) and Dendy (1946) have shown that when these fish are young their diet consists largely of zooplankton, particularly larger species; as they mature, their diet gradually consists less of zooplankton and more of phytoplankton and detritus until as adults very few zooplankters are taken. However, threadfin shad are apparently more carnivorous both as young and adults. One study of coexisting populations of Dorosoma cepedianum and Dorosoma petenense, both young and adults, showed that while the phytoplankton and detritus component of gizzard shad stomachs ranged from 23-69%, that of the threadfin shad was always less than 12% (Baker and Schmitz 1967). A similar study by

Haskell (1959), which was limited to adult threadfin shad, showed that during winter months diet consisted mostly of diatoms and unicellular algae while in the spring and summer diet was basically zooplankton, with the greatest bulk being crustaceans and rotifers. Apparently, the extension of carnivorous eating habits of *Dorosoma petenense* well beyond the young-of-the-year stage accounts for both the elimination of *D. birgei* during all but the coldest winter months and the depression of mean population size of *D. reighardi* below predicted length from late spring well into the fall in Lake Jeanette.

There is increased evidence that inter-specific competition reduces the range of an organism to the optimal part of the habitat and that intra-specific competition has the opposite effect, tending to cause the population to spread out into more marginal areas of the habitat (Svardson 1949; Crowell 1962). These effects of inter- and intra-specific competition apply not only to the physical living space occupied by the population but also to the food niche and physical resources utilized by the population. When a species is in competition with another similar species with similar overall requirements it enjoys greater reproductive success and less mortality by utilizing a more unique, specialized portion of the habitat for its needs than if such competition did not exist. Conversely, when such inter-specific competition is not great, natural selection favors a broader utilization of what the habitat has to offer since a larger population can be supported in this manner.

The study of *D. pallidus* in Lakes Taylor, University, James, and Hickory provided a natural demonstration of a single species in differing situations of competition with other diaptomid copepods. These situations ranged from no competition from other diaptomid copepods as found in Taylor Lake to substantial competition from two other diaptomid copepods as found in Lake Hickory.

Van Valen (1965), in a study of phenotypic variation within populations of birds that differed regionally as to width of niche (where niche width meant "the total multidimensional space of limiting resources used by a species or segment of a community"), found that population variations was greater among birds inhabiting the wider niche. Van Valen's comparisons were between island and mainland populations of six species of birds where niches were known to be wider on the islands due to fewer adjacent species. Variation data were based on measurements of bill width. He concluded that there are three extreme ways in which a segment of a community, all individuals of the segment belonging to the same trophic level, can exploit the available supply of limiting resources with gradations in between:

(1) There can be relatively few species, each individual of which is adapted to occupy a relatively broad segment of the resource space. Each individual may occupy this entire segment, or there may be behavioral partitioning of the segment.

(2) There can be relatively few species, but these are relatively variable and different individuals within a species are fitted to, and do, in fact, occupy on the average different narrow niches (or, equivalently, different parts of a broad niche).

(3) There can be a relatively large number of species, each of which is restricted to a relatively narrow segment of the resource space, more or less uniform for each individual.

This classification actually represents a continuum with infinite gradations possible in between, and not all species at a particular trophic level would necessarily or even ordinarily be of the same type in a given habitat. However, they provide points of reference. Intraspecific morphological variation would be expected to be greatest in the type (2) species.

MacArthur (1972) in his concept of "species packing" puts forth the idea that competitive assemblages of species in an area tend to stabilize when their abundances are such that "resource utilization best matches useful production", and that as new species attempt to invade, only those succeed that can improve the matching. This sifting, or rearranging of available species often results in the number of coexisting species and total individuals being maximized. It is possible that in a relatively young habitat such as Taylor Lake other diaptomid copepods which might be able to successfully capture a portion of the "*Diaptomus* niche" and improve this matching of resource utilization to useful production simply have not reached this lake in sufficient numbers to colonize. Lack of significant vertebrate predation makes colonization by other diaptomid copepods more difficult in Taylor Lake.

Variation of body length of *D. pallidus* was high in Taylor Lake the year round, the standard deviation never falling below .050 mm (Table V). Also, the density of the *D. pallidus* population in Taylor Lake was much greater than that of *D. pallidus* populations in any of the other lakes and, in fact, was much greater than the combined diaptomid copepod populations in any of the other lakes. This implies that intra-specific competition was high in Taylor Lake, much more so than in any of the other lakes studied. D. pallidus in University Lake also showed considerable variability in body length year round except in July - the only month when the population density of D. pallidus was sufficiently reduced, possibly due to shad predation, to allow coexistence of D. reighardi. During this month variability was considerably less than half what it was any other month of the year - times when the "Diaptomus niche" was filled virtually by one species. This trend also held true for Lake James and Lake Hickory where two and three diaptomid copepod species, respectively, were present. In each of these lakes measurements from dates when sufficient numbers were present all showed reduced variability in body length compared to Taylor Lake and University Lake (except July).

In Lake Hickory, where D. pallidus encountered significant competition from D. mississippiensis in July and September and significant competition from D. birgei in January and May, all measures of variance were low on these dates; the standard deviation was never above .029 mm and the range was never above .116 mm. In Lakes James, where D. pallidus was in competition with D. birgei, measures of variance were similarly low on all dates with sufficient numbers for analysis except in January when variance was comparatively high. On that date female D. pallidus had a standard deviation of .051 mm and range of .201 mm; male D. pallidus had a standard deviation of .045 mm and range of .175 mm. However, on this date inter-specific competition between diaptomid copepods was the lowest of all dates analysed in Lake James and Lake Hickory; D. birgei comprised only 14% of the sample with D. pallidus making up the remainder. By February D. birgei comprised 53% of the diaptomid copepod community in Lake James and the variability of body length of D. pallidus had become very much reduced. The variance of body length of D. pallidus in January in Lake James closely approached the high year-round variability found in Lakes Taylor and University (except July in University Lake). Scheffe's post hoc comparisons of the length of D. pallidus in the three lakes demonstrated that in January only the males of Lakes Taylor and James were significantly different. It is possible that 14% D. birgei is close to a threshold value for the interaction of D. pallidus and D. birgei in Lake James and that below this threhold variability of body length of D. pallidus is not affected by D. birgei. Additional data would be necessary to establish this argument.

The reduced variability in body length of D. pallidus where it encountered other diaptomid copepod species seems a probable case of a process similar to character displacement, the increased morphological uniformity being one observable manifestation of its reduced niche width in such situations of competition. Presumably, such reduced morphological variation reduced niche overlap and hence competitive interaction, thus increasing ecological compatability.

Different mensural characters have been related to the ecology of organisms. Bill shape and size among birds represents a classic example of how trophic appendages are related to the type and size of prey taken. Jaw length has been correlated with prey size in lizards and among filter feeding fish the distance between gill rakers determines the size of plankton taken.

Overall body size may be closely related to prey size - for instance among parasitic insects which devour whole prey near their own size and among wood-boring and seed-predator beetles. In some cases body weight of birds has been found to be an even better indicator of mean prey size than bill size (Hespenheide 1971). Hutchinson was perhaps the earliest investigator to note size separation in closely related species of zooplankton living in the same habitat and relate these size differences to food partitioning. He observed that in the playa lakes of semi-arid regions the zooplankton often consisted of a single species of Daphnia and two diaptomid copepod species of widely different sizes (Hutchinson, Pickford, and Schuurman 1932; Hutchinson 1937). In a review of the literature on "copepodology", Hutchinson (1951) noted that several other investigators had found similar size separations among copepods living in the same habitat, among them Mann (1940), Carl (1940), and Harding (1942). One example cited in Hutchinson's review was a study of two closely allied copepods, Arctodiaptomus wierzejskii (Richard) and A. laticeps (Sars), which differ only in the most minute characters of certain segments of the antennule. Considering the two species as a whole, their range of size overlaps completely. However, on the rare occasions when they are found co-existing, they are separable by small size differences (Gurney 1933). However, Hutchinson (1951) does not state that variance of body length in the two species was found to be reduced with co-existence as was the case with D. pallidus but simply that the body lengths were biased to new means.

Among calanoid copepods, which feed largely by filtration, the antennae are used as a screw to produce a water current from which food particles are filtered by the feeding apparatus, the maxillae (Storch and Pfisterer 1925; Lowndes 1935). It has been found by several investigators that such filtration is not always purely automatic but that particles of certain sizes can be selected for while others are rejected by the copepod simply adjusting the distance separating the maxillae (Lowndes 1935; Mullin 1963; Brooks and Dodson 1965). Brooks and Dodson (1965) further found that the size of the maxillae varies directly with body length. Thus a larger species would be capable of taking large particles unavailable to a smaller species. This strongly suggests that, among diaptomid copepods in situations of competition, the phytoplankton food source is somewhat divided up, the size range of the phytoplankton taken by the feeding apparatus being correlated with the overall size of the animal.

In conclusion, there appear to be at least three factors affecting the morphology of diaptomid copepods in piedmont North Carolina lakes in addition to sex, nutrient richness of the water, and temperature. These factors are size-selective predation by vertebrate planktivores such as *Dorosoma petenense*, inter-specific competition, and intra-specific competition. As the results of the study of *D. reighardi* in Lakes Jeanette and Sloan demonstrated, when there is not significant competition from other diaptomid copepods and population density is such that intra-specific compeition is not severe, then size-selective predation will reduce mean size of the population from late spring through fall. However, the population will recover when predator activity falls off during the winter so that in a more productive and cooler lake such as Lake Jeanette, mean population body length may equal and even exceed a non-shad lake such as Lake Sloan. In fact, the mean population body length for the entire year may be greater in the shad-inhabited lake.

The study of D. pallidus in Lakes Taylor, University, James, and Hickory showed that size variability was invariably reduced when this species encountered substantial competition from other diaptomid copepods. While inter-specific competition always tended to reduce variability in size, high intra-specific competition, as demonstrated by the densely populated Taylor Lake, increased size variability.

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