LAKE HURON CRUSTACEAN AND ROTIFER ZOOPLANKTON, 1980: FACTORS AFFECTING COMMUNITY STRUCTURE WITH AN EVALUATION OF WATER QUALITY STATUS

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Under contract with:

United States Environmental Protection Agency
Great Lakes National Program Office
Region V
Chicago, Illinois 60605

Grants R005510010, R005510020, and R005510030

Project Officer
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Special Report No. 98
of the
Great Lakes Research Division
Great Lakes and Marine Waters Center
The University of Michigan
2200 Bonisteel Boulevard
Ann Arbor, Michigan 48109

September 1983

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PREVIOUS REPORTS

ON THE STATUS OF LAKE HURON

Rossmann, R., and T. Treese. 1981. Lake Huron bibliography with limited summaries. The University of Michigan, Great Lakes Research Division Special Report No. 88.

Rossmann, R. 1983. Trace metals in Lake Huron waters - 1980 intensive surveillance. The University of Michigan, Great Lakes Research Division Special Report No. 97.

SUMMARY

Zooplankton surveillance cruises were conducted in April, May, June, and July in Lake Huron including the North Channel and Georgian Bay. Eleven (May) to 30 (July) stations were investigated during each cruise. Zooplankton standing stocks were characteristic of those of the more oligotrophic or meso-oligotrophic regions of the Great Lakes. Crustacean standing stocks were low, ranging from a May cruise mean of $14{,}000/m^3$ to a July high of $75{,}604/m^3$. The community was numerically dominated by Cyclops bicuspidatus thomasi, Diaptomus ashlandi, D. minutus, and D. sicilis, while Bosmina longirostris, Daphnia galeata mendotae, D. retrocurva, and Eubosmina coregoni were abundant July species. Species considered indicators of eutrophic waters were rare (Cyclops vernalis, Eurytemora affinis, Mesocyclops edax, Chydorus sphaericus) or not detected (Diaptomus siciloides, Alona spp., Daphnia pulex).

Rotifer standing stocks also were indicative of oligotrophic to meso-oligotrophic conditions, with abundances ranging from $4{,}541/m^3$ in June to $14{,}993/m^3$ in July. A spring assemblage of Notholca squamula and Synchaeta spp. was succeeded by a July assemblage of Conochilus unicornis, Kellicottia longispina, and Keratella cochlearis cochlearis. Species considered indicators of eutrophic waters were rare (Filinia, Ploesoma, Trichocerca) or not detected (Brachionus, Euchalanis).

Crustaceans were the numerically dominant zooplankton in Lake Huron. This dominance was even larger when standing stock was expressed in terms of dry weight. In general, rotifers accounted for less than 1% of the zooplankton biomass. The dominance of the Lake Huron zooplankton community by crustaceans, particularly copepods, is related to life history strategies of these organisms and their apparent capability to withstand periods of stress. For Lake Huron zooplankton, a probable major physiological stress is food limitation. In the oligotrophic waters of Lake Huron, crustaceans, particularly copepods, dominate even in summer months. Adaptive strategies are discussed and their implications applied to the results of various analyses investigating the statistical relationship between physical-chemical factors and zooplankton taxa abundances. In general, rotifer abundances were

more often significantly related to physical-chemical parameters while crustacean abundances were more often intercorrelated with crustacean zooplankton.

Results of statistical analyses (correlation, principal components) provide information on water quality status as estimated from zooplankton population characteristics: such analyses included consideration of the physical-chemical properties of the upper water column at each zooplankton station. In addition, a phytoplankton:zooplankton carbon ratio was used to infer relative grazing pressure. High values (>10) were interpreted as indicating that grazing pressure was low, while grazing pressure was inferred to be intense in areas where the ratio was lower. Furthermore, comparisons of the carbon ratio to chlorophyll concentrations allow for inferences on the relative magnitude of primary productivity. For example, if two areas had similar ratios but different chlorophyll concentrations, it was inferred that the more productive area was the area with the higher chlorophyll concentration. An area characterized by moderate chlorophyll concentrations but a high ratio was inferred to be less productive than an area with similar chlorophyll concentrations but a lower carbon ratio.

Based on such considerations, the nearshore region of southern Lake Huron was the most productive, particularly in the Goderich-Bayfield and Harbor Beach-Lexington areas. Zooplankton standing stocks were high during all cruise months. In addition, chlorophyll concentrations were relatively high despite low phytoplankton:zooplankton carbon ratios. This region was apparently highly productive during all cruise (April to July) months.

A second region of apparently high production was the St. Marys River-North Channel area in July. Chlorophyll concentrations were relatively high despite a low phytoplankton:zooplankton carbon ratio (1.2). It was not determined why this region was apparently high in productivity.

Zooplankton and phytoplankton standing stocks exhibited regional variation over the survey grid. Plankton standing stocks often were low in areas affected by river flow. In April, a high suspended sediment load and flow rates apparently reduced primary and secondary production in the St. Marys

River. River flow also affected qualitative differences in zooplankton composition.

Zooplankton standing stocks were greater in inshore waters than offshore. In April, phytoplankton productivity apparently was higher in the southern basin than in the northern basin. Moderately high plankton standing stocks and productivity in Georgian Bay in April may have been related to basin morphology, run-off, and circulation patterns.

Grazing pressure on the phytoplankton community apparently varied seasonally and spatially. In April, grazing pressure apparently was most intense in Georgian Bay where chlorophyll concentrations were low in the presence of an abundant crustacean community. Conversely, in the nearshore region of southern Lake Huron, chlorophyll concentrations remained high in the presence of a large standing stock of zooplankton. By July, grazing pressure had intensified as zooplankton standing stocks increased and phytoplankton standing stocks decreased. While zooplankton varied markedly in abundance over the surveillance area, chlorophyll concentrations were low with little regional variation. This suggests that, while primary production varied regionally, there was a tight coupling between primary production and grazers so that phytoplankton remained uniformly low over the survey area.

Zooplankton investigations reported here, while not as detailed as the 1980 nutrient and phytoplankton surveillance studies, provide an independent corroboration of the results of these studies. Furthermore, the zooplankton investigations allow a crude estimation of regional and seasonal variations in zooplankton grazing and primary production. Overall, Lake Huron water quality was good in 1980, with zooplankton composition and standing stocks indicative of oligotrophic conditions. Areas of higher trophic status were the nearshore region of southern Lake Huron (all months), the St. Marys River in July, and, on occasion, Harrisville, Cheboygan, and Presque Ile.

ACKNOWLEDGMENTS

Many people assisted in the various stages of this study. The Environmental Protection Agency and the Canada Centre for Inland Waters collected the zooplankton samples. David DeVault, USEPA, Great Lakes National Program Office, was especially helpful. Dr. Richard Stemberger, now at Dartmouth College, provided training in rotifer taxonomy and assisted in quality control. Hillary Egna and Mohammed Omair identified crustaceans and rotifers, respectively. Dan Sell and Loren Flath helped in many of the quantitative aspects including generating data and conducting statistical analyses. Russell Moll provided ready computer access to the physical-chemical data which were essential in interpreting the results of this study. Francis Figg prepared the figures while Marion Luckhardt prepared several of the tables. Loren Flath and Donna Page assisted in the preparation of early drafts of the manuscript while Steve Schneider edited the final revision. Beverly McClellan prepared the final report. Drs. Russell A. Moll, Ronald Rossmann, Claire Schelske, and Eugene Stoermer provided helpful, critical comments on an earlier version of the report. Special thanks are extended to Dr. Rossmann for his support and encouragement during all aspects of this study.

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INTRODUCTION

Lake Huron, with a surface area of 57,340 km^2, is the world's fifth largest lake and the second largest Great Lake. From its Lake Superior inflow (via the St. Marys River), it extends nearly 320 km south to its outflow into Lake Erie (via the St. Clair and Detroit rivers). Lake Michigan also is a source of water to Lake Huron (Powers and Ayers 1960). The drainage basin extends over an area of 59,906 km^2. To the north, it is located in Precambrian bedrock; to the southeast, in Devonian bedrock; and to the west, in Pennsylvanian and Mississippian bedrock. Silurian limestones form Manitoulin Island and the Bruce Peninsula, which separate the main body of Lake Huron from Georgian Bay and the North Channel (Hough 1958). As a result of differences in bedrock composition of the drainage basin, waters in northern Lake Huron are softer and less alkaline than waters in southern Lake Huron. Waters are particularly soft and low in alkalinity in the North Channel where Lake Huron waters are diluted from the outflow from Lake Superior, located almost entirely in a Precambrain drainage basin.

Land usage varies from north to south as a function of climate and geomorphology. In the north, where the climate is harsh and the soils poor, the major land usage (95%) is forestry. This percentage decreases to 27% in the Saginaw Bay drainage basin where rich soils and a mild climate are favorable for agriculture (54%). Extensive (30%) agriculture areas also are located in the southeastern drainage basin. Tributary inputs from agricultural regions and urban areas contain high concentrations of nutrients and salts which affect water quality. While Lake Huron generally is considered oligotrophic, run-off and tributary outflows impart mesotrophic characteristics to regions such as southern Lake Huron and the North Channel, and eutrophic characteristics to areas such as Saginaw Bay (International Joint Commission 1977).

As a result of human activity, particularly over the last few decades, Lake Huron water quality has been altered. This is evident both in changes in major ion concentrations (Beeton 1969) and alterations in fish stocks (Christie 1974). There are few, long-term data documenting changes in plankton composition, abundance, and community structure.

Most Lake Huron zooplankton studies were conducted in the 1970s and described the major region-wide characteristics of crustacean populations. Carter's studies (1969, 1972, Carter and Watson 1977) in Georgian Bay and the North Channel provide valuable information on crustacean zooplankton seasonality and composition. Patalas (1972), Watson (1974), and Watson and Carpenter (1974) provided additional (although less spatially detailed) information on crustacean community struc ure in the main body of Lake Huron. In addition, these authors compared Lake Huron zooplankton populations with those in Lakes Erie, Ontario, and Superior. Gannon et al. (1976) described crustacean community structure in the Straits of Mackinac, a region of dynamic mixing of waters from Lakes Superior, Huron, and Michigan (Powers and Ayers 1960). McNaught (1978) investigated spatial heterogenity and niche differentiation in two species of crustaceans while Swain et al. (1970) discussed the results of plankton recorder studies in Lake Huron. In a later report, McNaught et al. (1980) discussed crustacean grazing and population dynamics in southeastern Lake Huron in 1974 and 1975. Rotifers have been neglected in most investigations, with Stemberger et al.'s (1979) study of Saginaw Bay and southern Lake Huron providing the most complete information on these zooplankton. Less extensive contributions to our understanding of Lake Huron rotifers come from the works of Nauwerck (1978) and Williams (1966). Many of these studies were conducted as part of surveillance programs evaluating Lake Huron water quality.

Zooplankton are a vital component of Great Lakes surveillance studies providing corroborative information on water quality. Individual species are optimally adapted to a specific range of environmental conditions (Makarewicz and Likens 1975). Previous studies have shown that zooplankton community structure varies between the Great Lakes as a function of trophic status and that crustacean abundances are linearly correlated with chlorophyll concentration and phosphorus loading (Patalas 1972). Consequently, regional and temporal differences in zooplankton abundance and composition provide additional evidence of the effects of nutrient loading on water quality. In addition, since phytoplankton are limited to the upper regions of the water column by their light requirements, zooplankton studies can provide additional information on hypolimnetic water quality.

Zooplankton, as grazers, affect phytoplankton standing stocks and composition. Grazing pressure varies seasonally and spatially and is especially intense in summer (Scavia 1979, McNaught et al. 1980, Dagg and Turner 1982). Grazing not only reduces chlorophyll concentrations but results in an increase in phaeophytin concentrations. Phaeophytin may account for over 50% of total chlorophyll pigments in summer and autumn (Glooschenko et al. 1972). Zooplankton selectively consume various size ranges of phytoplankton (Allan 1976) and specific algal types (Porter 1973, Porter and Orcutt 1980, McNaught et al. 1980). Selective grazing may alter phytoplankton community structure with the least palatable species predominating. Zooplankton excretion may provide a major fraction of the daily nitrogen and phosphorus requirements for the phytoplankton community, especially in summer (Scavia 1979, Lehman 1980).

Recently, much effort has been devoted toward developing mathematical models of lake function (Scavia 1979, Di Toro and Matystik 1980, Di Toro and Connolly 1980) and the prediction of effects of reductions in nutrient loading on chlorophyll standing stocks (Thomann et al. 1977). Such models are useful for investigating important processes affecting lake dynamics. Newer models include a zooplankton compartment to describe phytoplankton grazing losses and nutrient regeneration. Zooplankton data are input by trophic characteristic (Di Toro and Matystik 1980, Di Toro and Connolly 1980) and by taxonomic group and size (Scavia 1979). Surveillance studies, by obtaining information on zooplankton community structure, provide new information for refining such models and testing the effects of remedial actions.

The Great Lakes Water Quality Agreement of 1978 calls for the protection and maintainance of biological integrity of the Great Lakes basin ecosystem and for the development of programs to better understand the Great Lakes ecosystem. Thus zooplankton, a vital component of the Great Lakes ecosystem, are an essential part of surveillance studies. Consequently, surveillance studies have and continue to include zooplankton investigations. However, in recent years, there has been a reduction in the research effort directed toward zooplankton studies.

In 1980, the United States Environmental Protection Agency and the Canada Centre for Inland Waters conducted a series of eight intensive surveys to assess Lake Huron water quality. These studies determined the physical-chemical characteristics of Lake Huron water with the primary objectives being the identification of problem areas and the assessment of the effectiveness of remedial actions. Phytoplankton studies also were conducted: these studies determined alga standing stocks and factors affecting phytoplankton community structure.

Zooplankton studies conducted in 1980 were not as intensive as the physical-chemical and phytoplankton studies. Four cruises were conducted (April, May, June, and July) and 11 to 30 stations were sampled during each cruise. This report contains a discussion of the results of these studies.

The objectives of this report are as follows. First, species composition, abundance, and distribution patterns during each cruise are discussed. The presence of certain species and the absence of others provide preliminary information on water quality. Standing stock data provide a crude estimate of secondary production, particularly when compared against other regions of Lake Huron or other Great Lakes.

The second and third objectives of the report are the description, by statistical techniques, of the relationships between the abundance of individual zooplankton taxa and zooplankton community structure and the physical-chemical characteristics of the environment. Phytoplankton data were not available at the time of this report writing and consequently could not be included in the analyses. Statistically significant relationships, while not necessarily indicating causal links, may suggest pathways.

MATERIALS AND METHODS

Collection Methods

Zooplankton samples were collected by the United States Environmental Protection Agency Great Lakes National Program Office and the Canada Centre for Inland Waters in April, May, June, and July 1980 (Fig. 1). A more detailed description of the survey grid, including station depths and

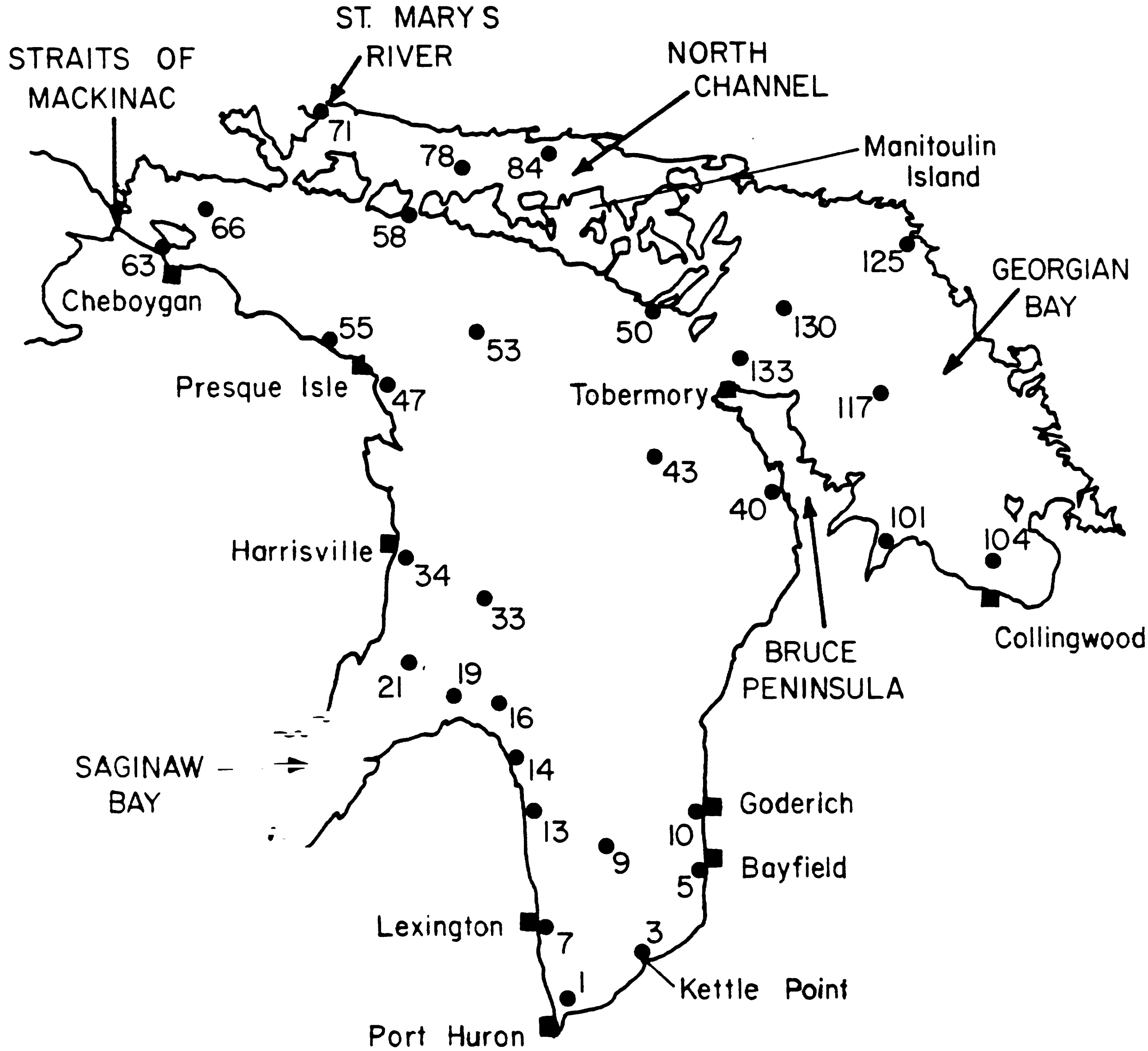


FIG. 1. Location of all stations sampled in April-July 1980.

coordinates, is provided by Moll and Rockwell (in prep). Eleven (May) to 30 (July) stations (Fig. 1) were sampled during each cruise. A 50-cm diameter, #25 mesh (64 µm) net equipped with a flowmeter was used to collect the zooplankton. For stations shallower than 25 m, a single net haul was conducted from approximately 2 m off the lake bottom to the surface. For most stations deeper than 25 m, a haul was taken from 25 m to the surface and a second haul from 2 m off the bottom to the surface.

The flowmeter was calibrated for each cruise by lowering it on a weighted line through a known depth of water and then recording the number of revolutions after the flowmeter was brought back to the surface. This was performed at a number of stations and the relationship between flowmeter reading and station depth analyzed: the relationship was linear. By multiplying station depth by 0.196 m^2 (the mouth area of the 50-cm net ring), the volumetric calibration coefficient for the flowmeter was calculated. This coefficient varied from 26.8 liters/revolution in July to 32.8 liters/revolution in April. For each cruise, the volume of water filtered during each net haul was estimated on the basis of flowmeter reading and calibration coefficient. On occasion, the flowmeter reading for a net haul clearly was inaccurate, with too few or too many revolutions for the station depth. A corrected reading was calculated from the regression model for flowmeter reading versus collection station depth by estimating the appropriate flowmeter reading for the sampling interval.

Living zooplankton in collected samples were relaxed with club soda prior to the addition of a sugar-formalin solution as a preservative (Haney and Hall 1973). Addition of club soda (or tonic water) is essential for the identification of soft-bodied rotifers.

Laboratory Methods

In the laboratory, a two-stage procedure was employed to enumerate and identify zooplankton. For crustacean counts (and the rotifer *Asplanchna* spp.), the original sample was subdivided as many times as necessary in a Folsom plankton splitter to give two subsamples of 250 to 300 organisms each.

All crustaceans and Asplanchna spp. in the two subsamples were enumerated. Cladocerans and copepods were identified to species, immature copepodites to genus, and nauplii combined as a group. Taxonomic keys referred to included Brooks (1957, 1959), Wilson (1959), Wilson and Yeatman (1959), Yeatman (1959), Pennak (1963), and Deevey and Deevey (1971). Primary identifications were made under a compound microscope while most subsequent identifications were made under a stereozoom microscope at 20X to 140X.

For rotifer identifications, the subdivided crustacean sample series was retained. On occasion, the same subsample as the crustacean subsample was examined, although a more concentrated sample usually was examined. The selected subsample was made up to 100 mL and a Stempel pipette used to withdraw several new 1-mL subsamples which were placed in a counting cell for identification and enumeration. Subsamples were enumerated until approximately 200 rotifers were identified. Rotifers were identified at 40X to 400X under a Leitz compound microscope. The major rotifer taxonomic key used was Stemberger (1979).

Quality control was employed at all stages of the sample processing. Approximately 10% of the crustacean and 10% of the rotifer samples from each cruise were enumerated in pairs by the same two research assistants and their species counts and identifications compared. Apart from these samples, one assistant processed all the crustacean samples and a second assistant the rotifer samples. Data were entered on coding sheets and routine computer programs used to calculate summary statistics. Various error-detecting checks were incorporated within each program.

Taxa Correlations With Physical And Chemical Parameters

As a first step in the investigation of the relationship between physical and chemical factors and zooplankton community structure, correlations were calculated between taxa abundances and selected physical and chemical parameters. Correlations were conducted on a cruise-by-cruise basis using the abundance data for the dominant taxa. Parameters used in the analyses were temperature, Secchi disc depth, pH, alkalinity, conductivity, sodium (April

only), chloride (May, June, and July), ammonia, nitrate, soluble reactive silica, chlorophyll, total phosphorus, and total Kjeldahl nitrogen. With the exception of chlorophyll and Secchi disc depth, these data were based on 1-m observations. Chlorophyll values were based on the integrated chlorophyll concentration from 2 m off the lake bottom to the surface or, at deep stations (> 22 m), 20 m to the surface. Thus phytoplankton and zooplankton volumetric estimates were integrated over the same (station depths less than 22 m) or similar depths for the upper 25 m of the water column. Physical-chemical data were collected by the United States Environmental Protection Agency and the Canada Centre for Inland Waters. Descriptions of methodology and a fuller treatment of these data are provided by Moll and Rockwell (in prep).

Analyses were performed using the University of Michigan statistical software package MIDAS (Michigan Interactive Data Analysis System). Since both the physical-chemical data set and the zooplankton data set (upper-water column series) were characterized by some missing values, the MCORR statistical procedure (Fox and Guire 1976) on MIDAS was used. This statistical procedure calculates the product-moment correlation for the specified pairs of variables, the t-statistic, and the attained level of significance. Thus, the procedure uses all pairs of observations to calculate each correlation coefficient and not just pairs for complete cases. Correlations were calculated between specific taxa and the physical-chemical features of their environment. In addition, between-taxa correlations were calculated to investigate the statistical relationships of species co-occurrences.

Principal Component Analysis

Principal component analysis was used to investigate regional differences in zooplankton community structure. Analyses were performed on a cruise-by-cruise basis. Three analyses were performed for each cruise; dominant rotifers, dominant crustaceans, and dominant rotifers and crustaceans. Rotifer and crustacean analyses were conducted separately for two reasons. First, previous Lake Huron investigators have treated each taxonomic group separately. Second, rotifers and crustaceans have different life history

characteristics (see discussion). Separate analyses allowed for the investigation of physical-chemical factors affecting each group of zooplankton. Combined analyses, considering both rotifers and crustaceans, were less useful as a tool in investigating zooplankton community structure with less of the total variance accounted for by the first two principal components. Therefore, only the April results are discussed in this report.

A taxon generally was considered a dominant if it accounted for an average of at least 1% of the rotifer or crustacean standing stock for that cruise. Analyses were restricted to data collected from the upper 25 m of the water column. At a few moderately-deep stations (27 m to 35 m) only one sample was collected from the entire water column and these data were used. For deepwater stations where no upper-water column sample was collected, the station was excluded from the analysis.

Data were log-transformed to decrease the dependence of taxa variances on taxa abundances. Principal component computations were based on the variance-covariance matrix. The analyses were performed using the variance-covariance matrix (rather than the correlation matrix) because all taxa had the same measurement units (Morrison 1976, Pielou 1977). Output included the amount of variance explained by the first three components, the station scores by component, and the taxon loadings by component. Plotting station scores by their first and second principal components (PC1 and PC2) allowed identification of regions in Lake Huron which have similar zooplankton community structure. PC3 generally accounted for a small amount of variance and was not used in further investigation of regional differences in zooplankton community structure.

In order to identify possible environmental parameters affecting regional differences in zooplankton community structure, correlations were calculated between PC1 and PC2 scores and physical-chemical parameters. Essentially this procedure correlates station scores along a principal component axis with limnological characteristics which have high positive or negative correlations with that component (Sprules 1977). For example, stations with high PC1 scores may be characterized by high concentrations of Bosmina longirostris while stations characterized by low PC1 scores may have relatively high

concentrations of Diaptomus sicilis. In addition, station scores may be positively correlated with temperature and chlorophyll. This suggests that differences in zooplankton community structure along the PC1 axis are related to the thermal structure of the water column and phytoplankton standing stocks. It also suggests that B. longirostris and D. sicilis are two especially sensitive indicator species.

Although a component accounted for a major source of total variance, in some analyses no significant correlations were identified. A second set of correlations were calculated based on rotifer or crustacean abundances. These correlations investigated the statistical relationship between station principal component scores and the abundance patterns of the dominant zooplankton in either group (either rotifers or crustaceans) not considered in the original principal component analysis. Such correlations may suggest predator-prey or competitive interactions or some common response to environmental regime.

In order to compare the relationship between zooplankton abundances (#/m^3) and phytoplankton standing stocks (chlorophyll mg/m^3) in various regions of Lake Huron, standing stocks were converted to carbon. For chlorophyll dry weight conversions, a factor of 150 was used (Toyodo et al. 1968). Zooplankton abundances were converted to dry weight using Patalas (1970), Hall et al. (1970), or Hawkins and Evans (1979). A conversion factor of 0.44 (Steele et al. 1972) was used to convert dry weight to carbon. For phytoplankton, the chlorophyll to carbon conversion was 66, a value similar to the value of 60 derived for Lake Michigan phytoplankton (R. Moll, personal communication).

The ratio of phytoplankton:zooplankton carbon was used as a qualitative index of grazing. For example, if phytoplankton carbon concentrations were similar in two regions but zooplankton carbon concentrations were higher in the second region, then it was inferred that grazing pressure was higher in this region. Moreover, it was inferred that primary productivity was higher in the second region because of its similar phytoplankton carbon concentration (as in the first region) despite heavier grazing pressure. While the validity of such a grazing index has not been demonstrated in the literature, the index

does have intuitive appeal. Lorenzen (1967) utilized a similar index based upon the ratio of phaeophytin:chlorophyll and on the ratio of copepod abundance:chlorophyll. There was a positive correlation between the two measures of grazing, suggesting that as copepod abundances increased, there was a concomitant increase in the relative abundance of phaeophytin, a chlorophyll degradation product.

RESULTS AND PRELIMINARY REMARKS

In this section, the general features of zooplankton community structure over the survey grid during the four cruises are presented. This is followed by specific cruise results including taxa distributions, correlations, and principal component analyses. The principal component section includes preliminary discussions of the apparent factors affecting zooplankton community structure during each cruise. A more comprehensive discussion then follows.

General Features Of The Zooplankton Community

A total of 22 species of crustacean zooplankton was collected during the four cruises: four cyclopoid copepods, eight calanoid copepods, one harpacticoid copepod (not identified to species level), and nine cladocerans (Table 1). Thirty-two species (and varieties) of rotifers were identified (Table 2). While the same stations were not sampled on each cruise, taxa cruise means for the upper 25 m of the water column were calculated to summarize seasonal lake-wide community structure.

The April crustacean community was numerically dominated by copepods, with cladocerans accounting for less than 2% of the community. Nauplii, the herbivorous early developmental stage of copepods, were the most abundant crustacean taxon, accounting for approximately 70% of the total population during the April, May, and June cruises. Numerically abundant adult copepods were the herbivorous calanoids *Diaptomus ashlandi*, *D. minutus*, and *D. sicilis*, and the omnivorous cyclopoid *Cyclops bicuspidatus thomasi*. *Senecella*

TABLE 1. Mean density ($\#/m^3$) and percent composition of crustacean taxa, by cruise.

Taxon	Cruise							
	April		May		June		July	
	$\#/m^3$	%comp	$\#/m^3$	%comp	$\#/m^3$	%comp	$\#/m^3$	%comp
Nauplii	11,200	69.4	9,297	66.4	21,317	72.0	21,591	28.6
Cyclops spp. C1–C5	920	5.7	1,121	8.0	2,375	8.0	14,442	19.1
Cyclops bicuspidatus C6	380	2.4	393	2.8	639	2.2	701	0.9
Cyclops vernalis C6	5	0.0	4	0.0	28	0.1	0	0.0
Tropocyclops prasinus mexicanus C1–C5	26	0.0	0	0.0	0	0.0	0	0.0
T. prasinus mexicanus C6	2	0.0	0	0.0	0	0.0	8	0.0
Mesocyclops edax C6	0	0.0	0	0.0	0	0.0	9	0.0
Diaptomus spp. C1–C5	115	0.7	653	4.7	2,514	8.5	15,455	20.4
D. ashlandi C6	2,125	13.2	992	7.1	1,113	3.8	283	0.4
D. minutus C6	623	3.9	540	3.9	251	0.9	660	0.9
D. oregonensis C6	83	0.5	85	0.6	29	0.1	27	0.0
D. sicilis C6	593	3.7	731	5.2	286	1.0	24	0.0
Senecella calanoides C6	2	0.0	0	0.0	0	0.0	0	0.0
S. calanoides C1–C5	0	0.0	0	0.0	0	0.0	0	0.0
Epischura lacustris C1–C5	0	0.0	16	0.1	51	0.2	'25	0.2
E. lacustris C6	0	0.0	0	0.0	0	0.0	6	0.0
Eurytemora affinis C1–C5	7	0.0	11	0.1	23	0.1	48	0.1
E. affinis C6	0	0.0	0	0.0	0	0.0	26	0.0
Limnocalanus macrurus C1–C5	6	0.0	70	0.5	83	0.3	16	0.0
L. macrurus C6	5	0.0	19	0.1	5	0.0	34	0.0
Canthocamptus spp. C6	2	0.0	3	0.0	0	0.0	0	0.0
Bosmina longirostris	20	0.1	51	0.4	695	2.4	16,813	22.2
Ceriodaphnia quadrangula	0	0.0	0	0.0	0	0.0	4	0.0
Chydorus sphaericus	0	0.0	0	0.0	4	0.0	4	0.0
Daphnia spp.	0	0.0	0	0.0	0	0.0	0	0.0
Daphnia galeata	0	0.0	0	0.0	54	0.2	1,605	2.1
D. longiremus	0	0.0	0	0.0	0	0.0	76	0.1
D. retrocurva	1	0.0	0	0.0	0	0.0	1,733	2.3
D. pulex	0	0.0	0	0.0	0	0.0	3	0.0
Eubosmina coregoni	32	0.2	7	0.1	118	0.4	1,194	1.6
Holopedium gibberum	0	0.0	0	0.0	7	0.0	663	0.9
Leptodora kindtii	0	0.0	0	0.0	0	0.0	14	0.0
Polyphemus pediculus	0	0.0	0	0.0	0	0.0	27	0.0
Total crustaceans	16,130		14,000		29,603		75,604	

TABLE 2. Mean density (#/m^3) and percent composition of rotifer taxa, by cruise.

Taxon	April #/m^3	April %comp	May #/m^3	May %comp	June #/m^3	June %comp	July #/m^3	July %comp
Ascomorpha ovalis	0	0.0	0	0.0	0	0.0	4	0.0
Asplanchna herricki	0	0.0	0	0.0	0	0.0	1	0.0
A. priodonta	1	0.0	1	0.0	72	1.5	34	0.2
Collotheca spp.	0	0.0	0	0.0	0	0.0	0	0.0
C. mutabilis	0	0.0	0	0.0	1	0.0	4	0.0
Conochilodes natans	0	0.0	0	0.0	1	0.0	0	0.0
Conochilus unicornis	0	0.0	0	0.0	63	1.3	3,125	20.8
Filinia longiseta	0	0.0	0	0.0	2	0.1	0	0.0
Gastropus stylifer	0	0.0	2	0.1	34	0.7	1,044	7.0
G. hyptopus	0	0.0	0	0.0	29	0.6	0	0.0
Kellicottia longispina	215	3.1	352	7.8	1,228	25.7	2,805	18.7
Keratella cochlearis cochlearis	284	4.1	349	7.7	1,234	25.8	5,561	37.1
K. cochlearis f. tecta	0	0.0	0	0.0	0	0.0	0	0.0
K. cochlearis v. robusta	0	0.0	6	0.2	29	0.6	37	0.3
K. crassa	0	0.0	0	0.0	8	0.2	0	0.0
K. earlinae	0	0.0	1	0.0	18	0.4	19	0.1
K. hiemalis	2	0.0	0	0.0	14	0.3	0	0.0
K. quadrata	10	0.2	48	1.1	151	3.2	87	0.6
Notholca acuminata	0	0.0	0	0.0	0	0.0	0	0.0
N. foliacea	296	4.2	311	6.9	28	0.6	7	0.0
N. laurentiae	369	5.3	299	6.6	61	1.3	0	0.0
N. squamula	4,477	64.1	2,254	49.6	365	7.6	36	0.2
N. squamula (large)	29	0.4	0	0.0	0	0.0	1	0.0
Ploesoma spp.	0	0.0	0	0.0	0	0.0	12	0.1
P. hudsoni	0	0.0	0	0.0	1	0.0	44	0.3
P. truncatum	0	0.0	0	0.0	0	0.0	0	0.0
Polyarthra spp.	10	0.2	0	0.0	0	0.0	0	0.0
P. dolichoptera	20	0.3	7	0.2	196	4.1	238	1.6
P. major	15	0.2	11	0.3	167	3.5	120	0.8
P. remata	0	0.0	1	0.0	68	1.4	392	2.6
P. vulgaris	2	0.0	3	0.1	72	1.5	109	0.7
Synchaeta spp.	1,246	17.8	890	19.6	930	19.4	1,169	7.8
Trichocerca spp.	0	0.0	0	0.0	0	0.0	32	0.2
T. cylindrica	0	0.0	0	0.0	0	0.0	1	0.0
T. multicrinis	0	0.0	0	0.0	0	0.0	99	0.7
Total rotifers	6,986		4,541		4,786		14,993	

calanoides and Limnocalanus macrurus, hypolimnetic, cold-water stenotherms, accounted for a small percentage (<0.5%) of the crustacean population as did Eurytemora affinis, a calanoid copepod which recently invaded the Great Lakes from more brackish environments (Watson 1974).

Among the cladocerans, Bosmina longirostris was the numerical dominant although Eubosmina coregoni, Daphnia galeata mendotae, and D. retrocurva also were abundant. Clad cerans were not a numerically significant component (29.2%) of the crustacean community until July.

Epibenthic genera such as Eucyclops, Paracyclops, Alona, Eurycercus, Ilyocyrptus, and Leydigia were not observed during any of the four cruises. Nor were the planktonic and littoral genera Diaphanosoma, Latona, Macrothrix, and Sida observed.

Total crustacean numbers increased from a mean of $16,166/m^3$ in April to a high of $75,604/m^3$ in July. Lowest mean densities ($13,642/m^3$) were observed in June.

Rotifers generally were less abundant than crustaceans and exhibited less seasonal variability in total numbers, with abundances increasing from an April mean of $6,986/m^3$ to a July high of $14,993/m^3$. Densities were low in comparison to reported concentrations of over $1,000,000/m^3$ in eutrophic areas such as Saginaw Bay (Stemberger et al. 1979). Lowest densities ($<5,000/m^3$) were observed in May and June. The rotifer community shifted from an April assemblage dominated by Notholca squamula and Synchaeta spp. to a July assemblage dominated by Keratella cochlearis cochlearis, Conochilus unicornis, and Kellicottia longispina. Filinia longispina, Trichocerca cylindrica, T. multicrinis, and T. pusilla, species considered indicators of eutrophic conditions, were rare, accounting for less than 1% of the rotifer population during a given cruise. Brachionus and Euchlanis, commonly found in eutrophic regions of the Great Lakes (Watson 1974, Stemberger 1979), were not observed during any cruise.

Rotifers accounted for 13.9% (June) to 30.2% (April) of the zooplankton population by numbers. Thus, in terms of numbers, crustaceans dominated the zooplankton during all four cruise months. The difference in terms of biomass

are even larger. Hawkins and Evans (1979) determined that Lake Michigan zooplankton have mean dry weights ranging from 0.4 μg for nauplii to 45.3 μg for adult female Limnocalanus macrurus, with most taxa ranging in weight from 1 μg to 10 μg. Conversely, Hall et al. (1970) estimated that rotifer dry weights typically range from 0.005 μg to 0.01 μg. Only the relatively large Asplanchna spp. have a weight (0.7 μg) approaching that of the smallest crustaceans (Hawkins and Evans 1979). Thus crustacean zooplankton, which typically have dry weights 100 times greater than that of the rotifers, dominated the Lake Huron zooplankton community in terms of biomass. However, since rotifers can have higher reproductive rates (and turnover times) than crustaceans (Allen 1976), the relative difference in the productivity of the two groups probably was less.

April Cruise

General Features

The April cruise was conducted from April 13 to 26, 1980. Eighteen stations were sampled along a cruise track which began in southern Lake Huron and terminated in Georgian Bay (Fig. 2). No upper water column samples were collected at station 16 (46 m deep) and station 101 (59 m deep). Water temperatures ranged from 1 to 2°C: the lake exhibited inverse thermal stratification. Chlorophyll a values were less than 1.4 mg/m^3 in the North Channel, most of Georgian Bay, and the central portion of the main body of Lake Huron. Highest values (>2.0 mg/m^3) were along the eastern and western shores south of Saginaw Bay and in the Straits of Mackinac. Second highest values (>1.4 mg/m^3) occurred along the northeastern shore of Georgian Bay. Nitrate values were highest (>0.40 mg/L) along the nearshore region of southern Lake Huron in a region of relatively high chlorophyll concentrations. Soluble reactive silica values ranged from 0.2 mg/L to 2.4 mg/L and tended to be higher in the Lake Superior outflow and in regions where chlorophyll concentrations were high (Moll and Rockwell in prep).

Total zooplankton abundances (Fig. 3) ranged from 6,539/m^3 (station 71) to 72,766/m^3 (station 10). Crustaceans were more abundant than rotifers.

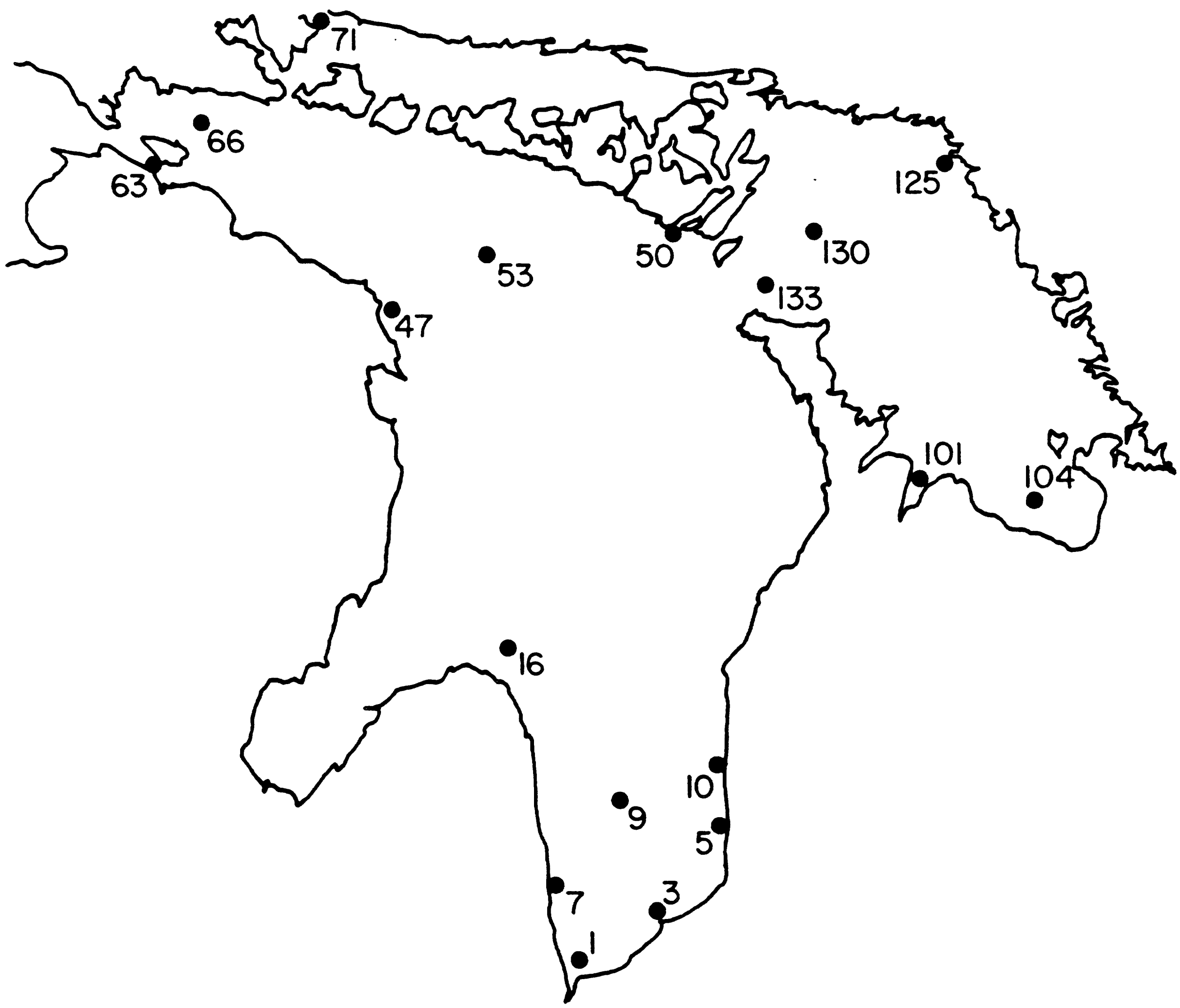


FIG. 2. Location of stations sampled on 13-26 April 1980.

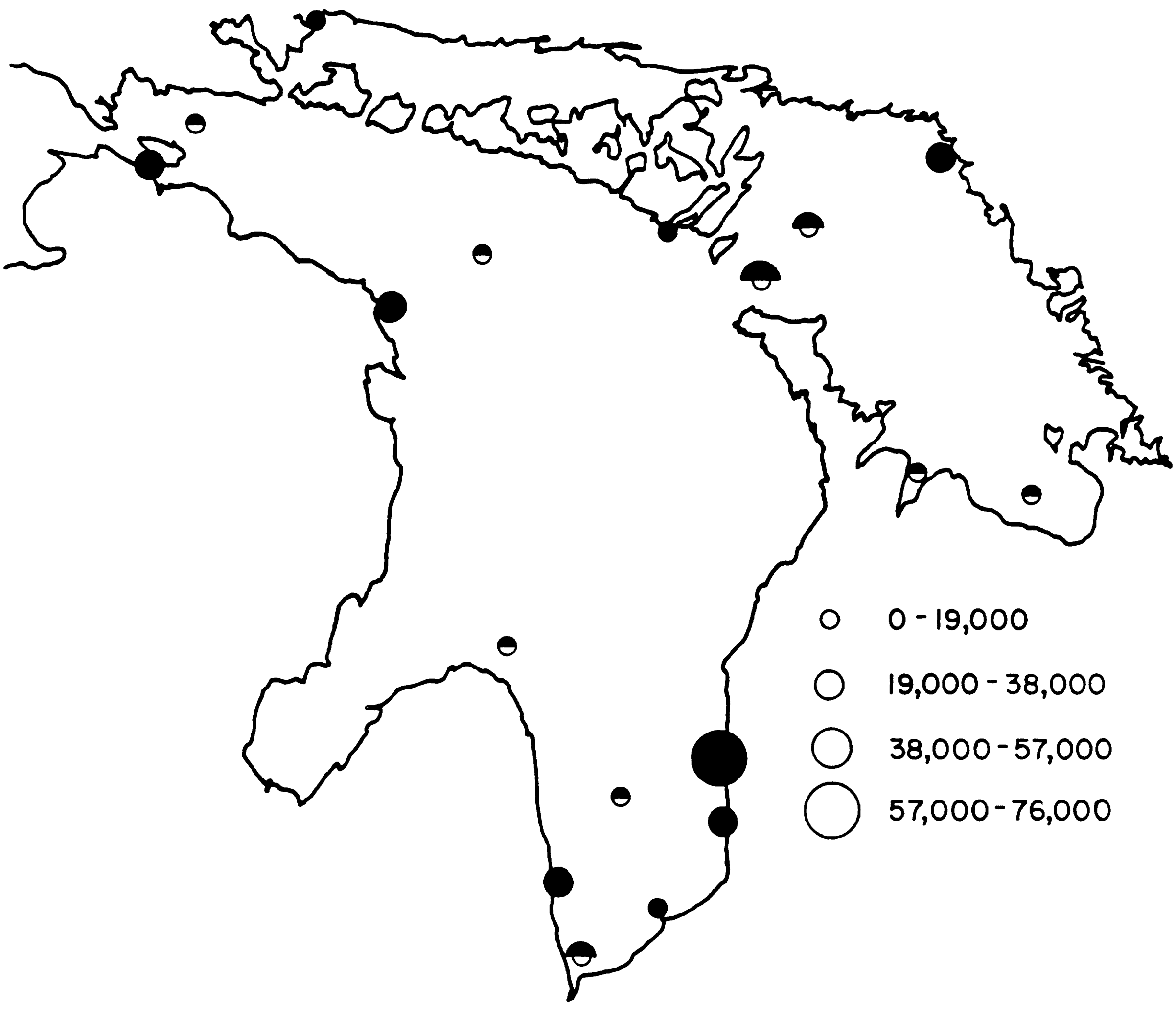


FIG. 3. Distribution (#/m^3) of total zooplankton collected on 13-26 April 1980. Black circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface.

Crustacean zooplankton (Table 1) were dominated by nauplii, the herbivorous early developmental stages of copepods. While nauplii were not identified, they most probably were dominated by the calanoids *Diaptomus ashlandi* and *D. sicilis*, the two most abundant adult copepods. Immature *Diaptomus* spp. copepodites (the developmental stages following the six naupliar stages) were not abundant (Table 1), indicating the April cruise was conducted at an early stage of the calanoid spring reproductive pulse. *Limnocalanus macrurus* was the only other common calanoid. Both immature copepodites and adults were present. The numerically dominant cyclopoid was *Cyclops bicuspidatus thomasi*. This species overwinters in the later copepodid stages, maturing to adulthood in spring (Torke 1975). Immature cyclopoids were more abundant than carnivorous adults, suggesting that overwintering copepodites had not completed their development to adulthood and that *C. bicuspidatus thomasi* exhibited a delayed reproductive pulse relative to that of *Diaptomus* species.

Total crustacean densities (Fig. 4) ranged from $4,556/m^3$ (station 50) to $66,081/m^3$ (station 10). Spatial distribution patterns of the numerically dominant crustaceans were similar (Fig. 4), with most taxa occurring in high abundance at station 10, located on the southeastern side of Lake Huron near Goderich. Nauplii were most abundant offshore of Goderich and at station 133 (offshore of Tobermory in the channel connecting Lake Huron and Georgian Bay). *Diaptomus sicilis* and *D. minutus* adults also were most abundant at these two stations. A secondary high for both species was station 47 offshore of Presque Ile in a region of relatively high chlorophyll concentration (>2.0 mg/L). Immature *Cyclops* spp. copepodites were most abundant offshore of Goderich, with secondary areas of abundance at stations 71 (St. Marys River) and 125 (Georgian Bay), while adult *Cyclops bicuspidatus thomasi* had secondary peaks of abundance at station 133 in Georgian Bay. At deep stations, zooplankton abundances generally were similar in shallow (0-25 m) and deep (>25 m to surface) hauls suggesting that zooplankton were not strongly vertically stratified within the water column.

Total rotifer densities (Fig. 5) ranged from $768/m^3$ (station 9) to slightly more than $14,700/m^3$ (stations 7 and 63). Rotifers were numerically

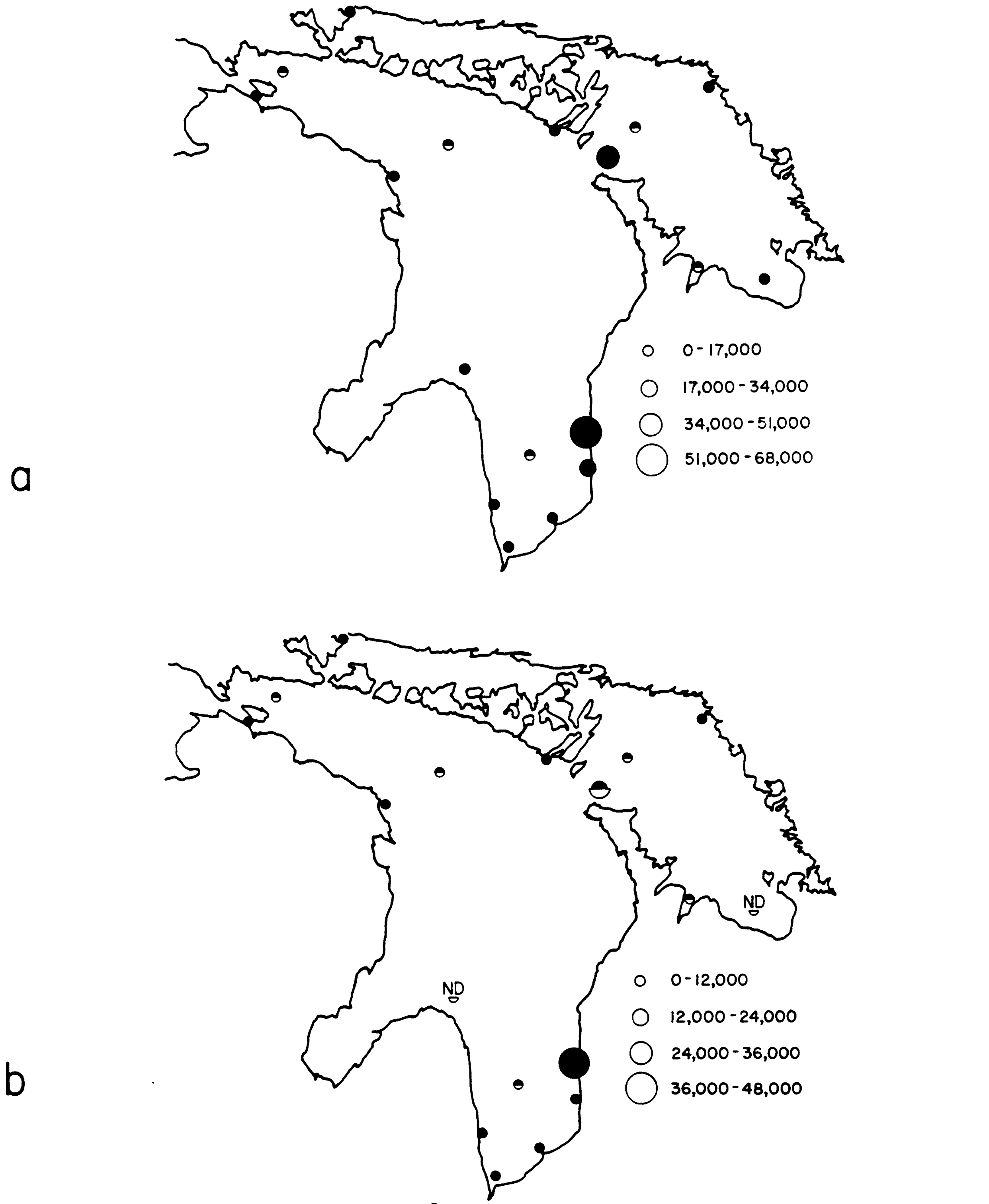
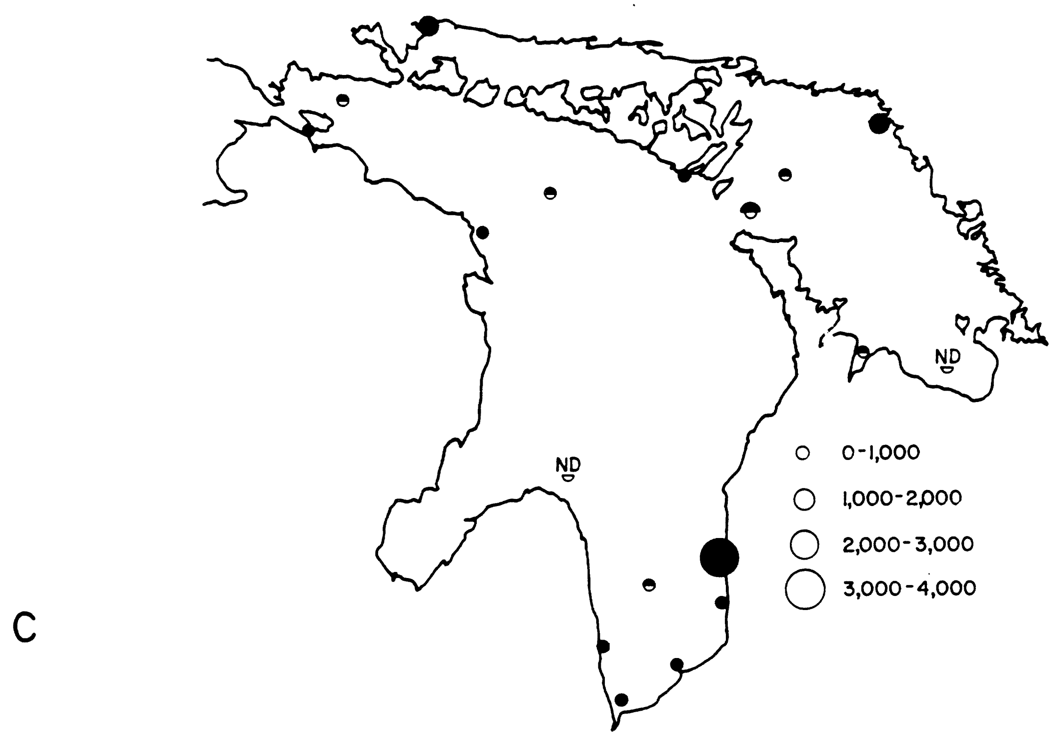


FIG. 4. Spatial distribution (#/m^3) of total crustaceans and major crustacean taxa collected 13-26 April 1980. Mixed circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total crustaceans, b) copepod nauplii,



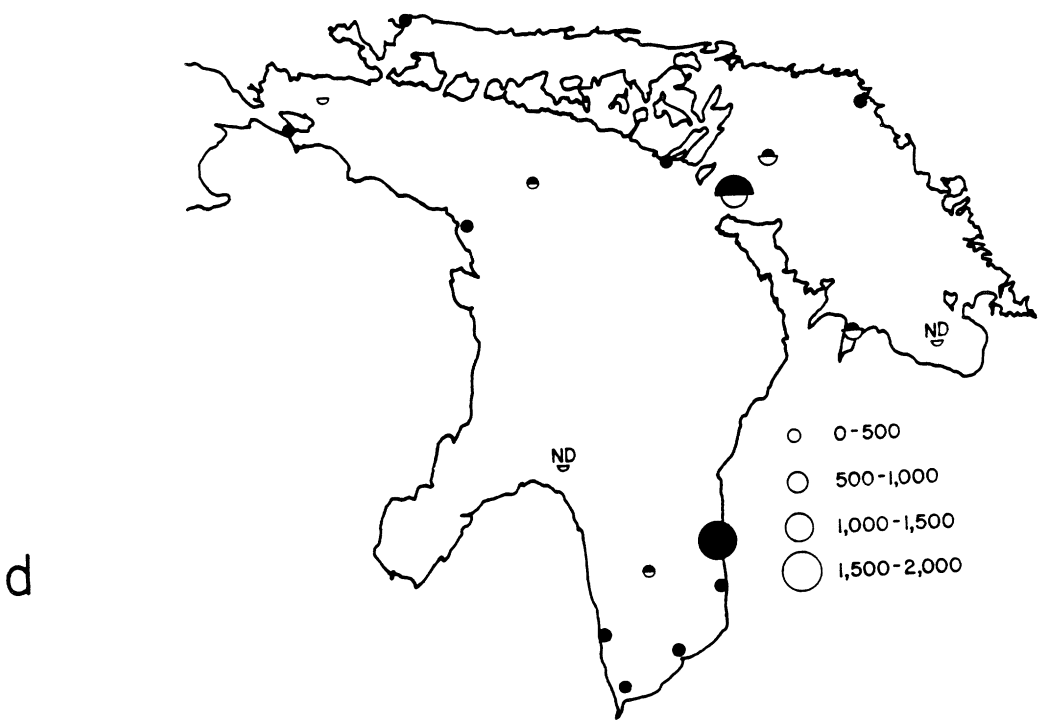
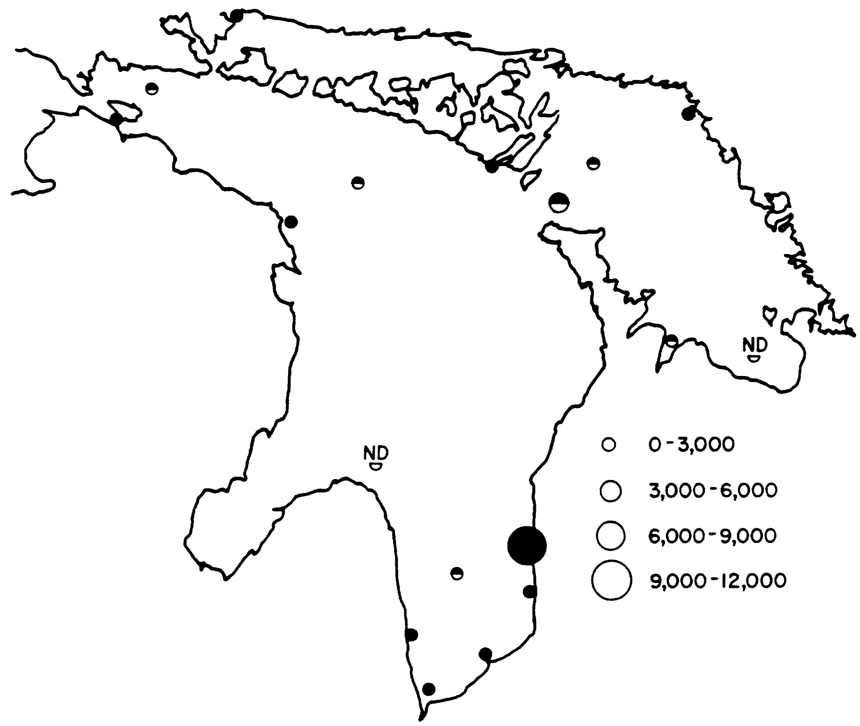


FIG. 4. Continued. c) Cyclops spp. C1–C5, d) Cyclops bicuspidatus thomasi C6,

e



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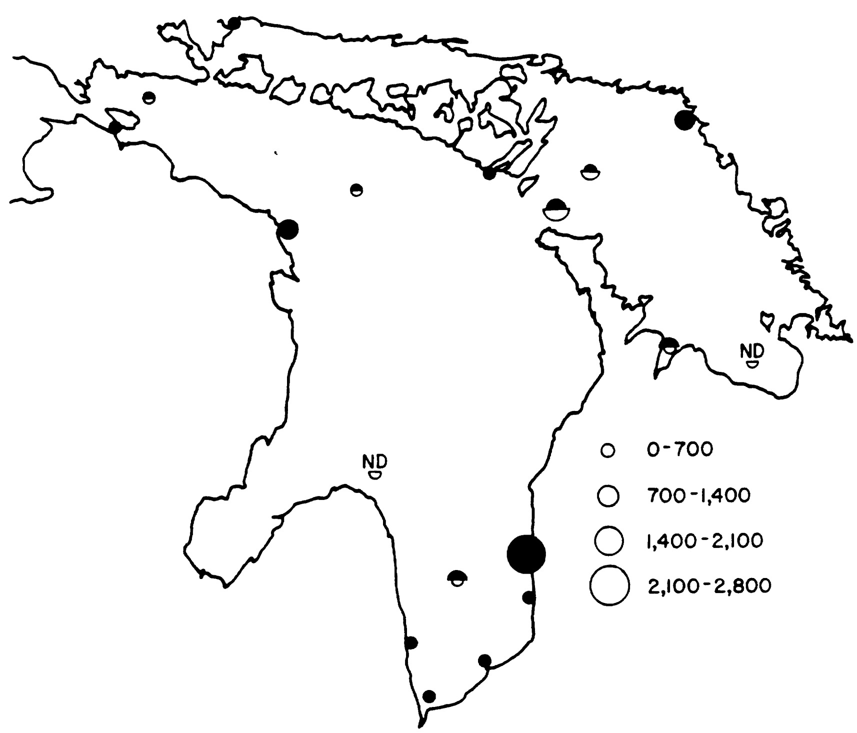
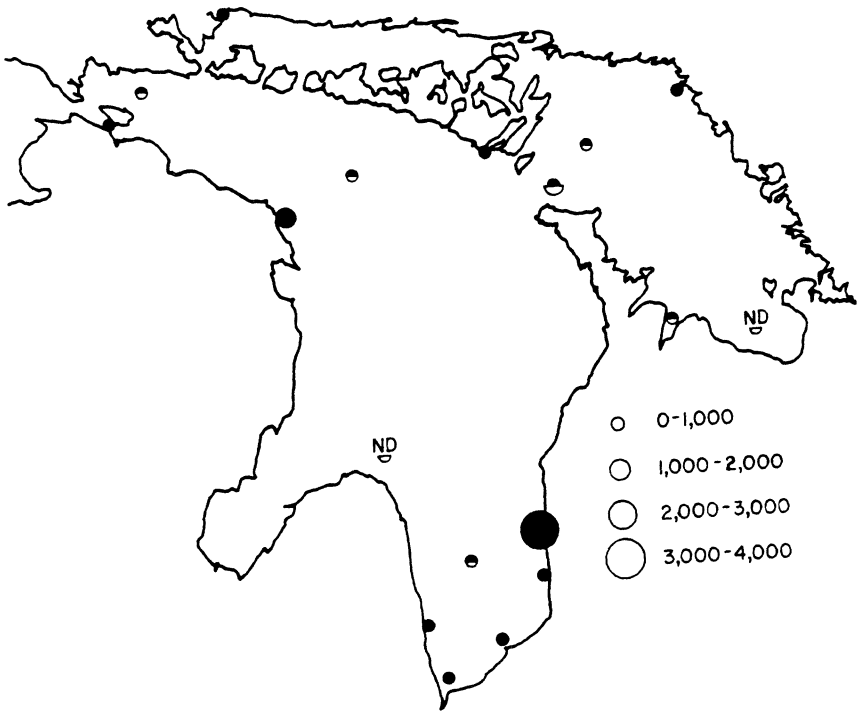


FIG. 4. Continued. e) Diaptomus ashlandi, f) Diaptomus minutus,



g

FIG. 4. Concluded. g) Diaptomus sicilis.

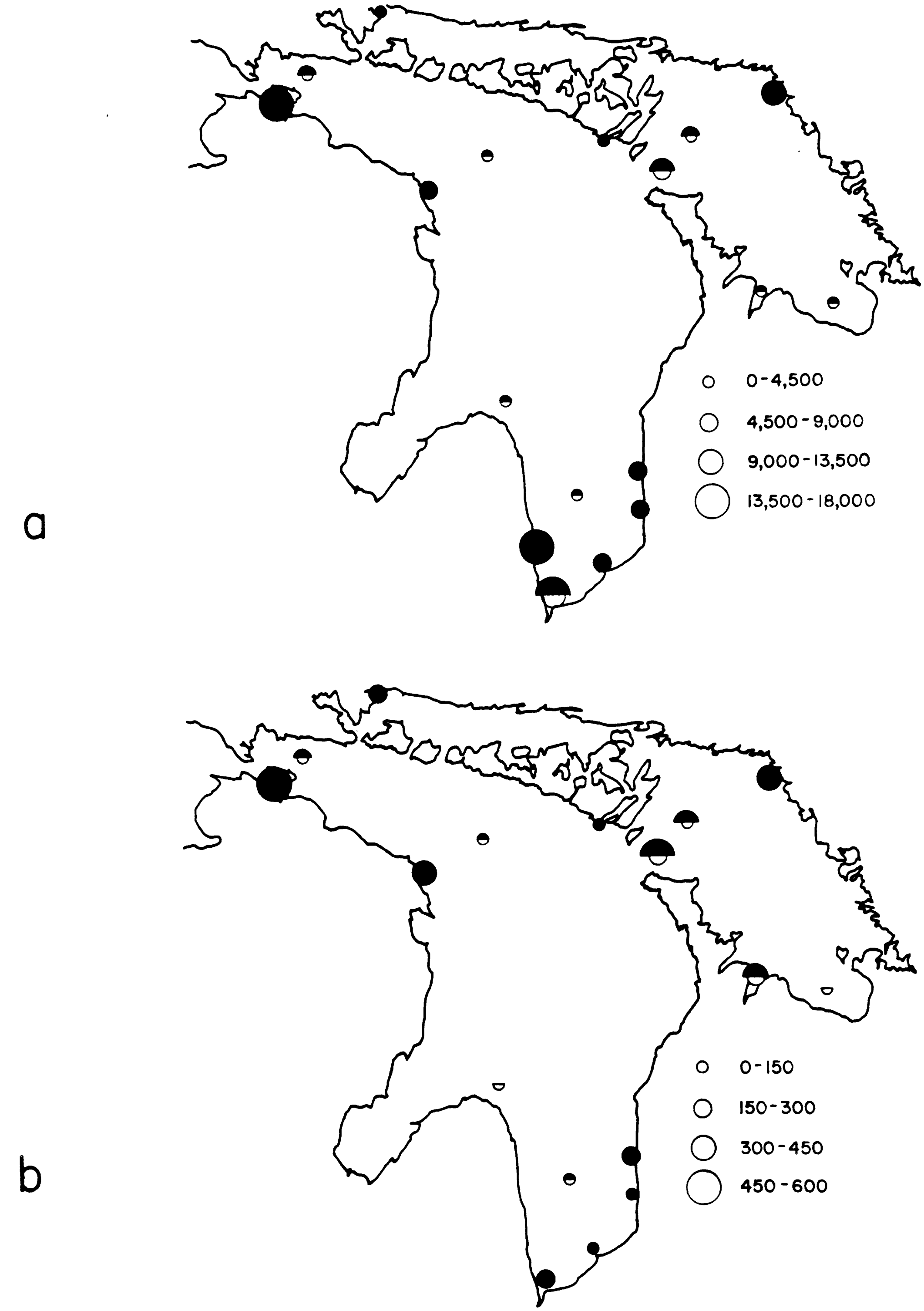
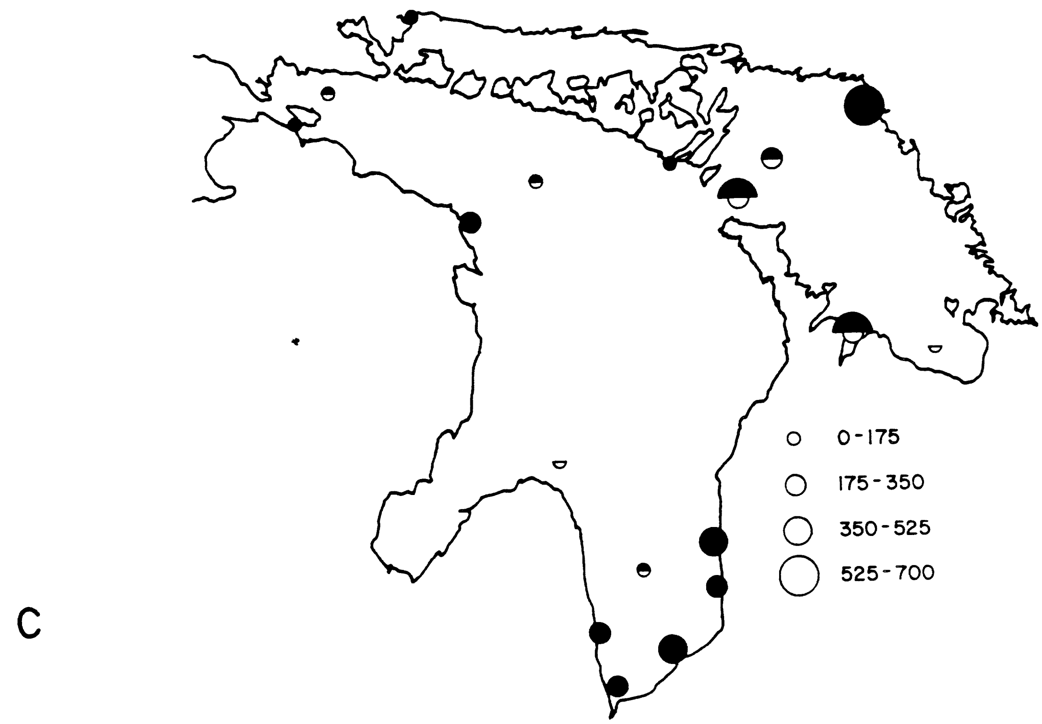


FIG. 5. Spatial distribution (#/m^3) of total rotifers and major rotifer taxa collected on 13-26 April 1980. Black circles represent net haul from 2 m off bottom to surface. Mixed circles (white and black): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total rotifers, b) *kellicottia longispina*,



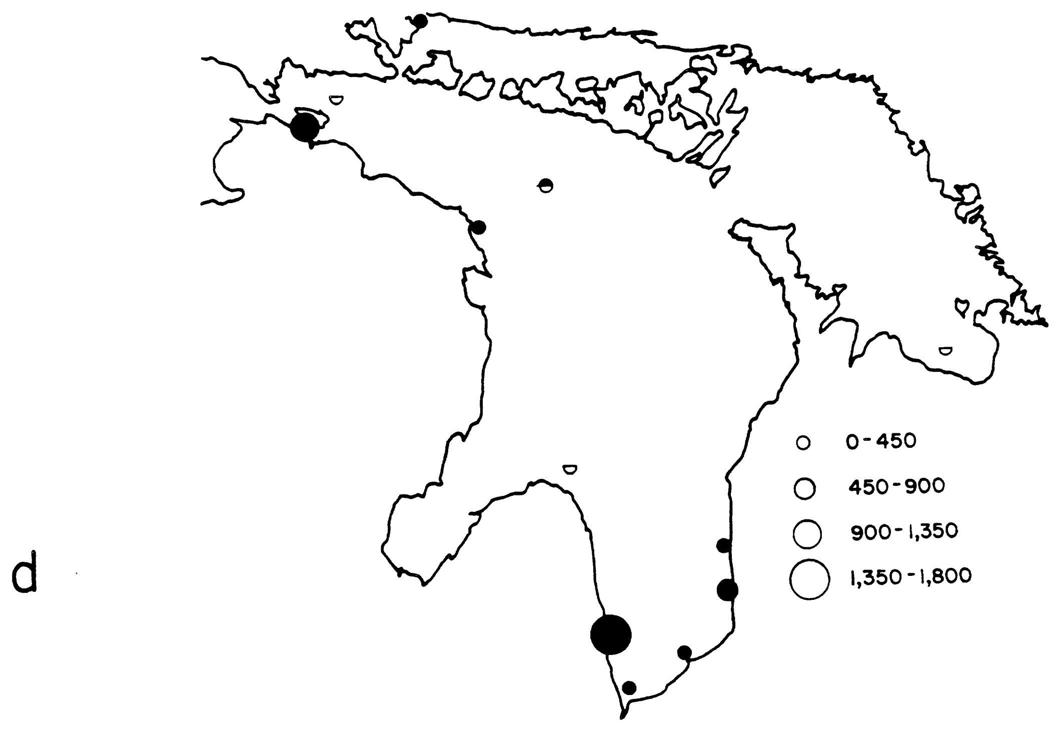
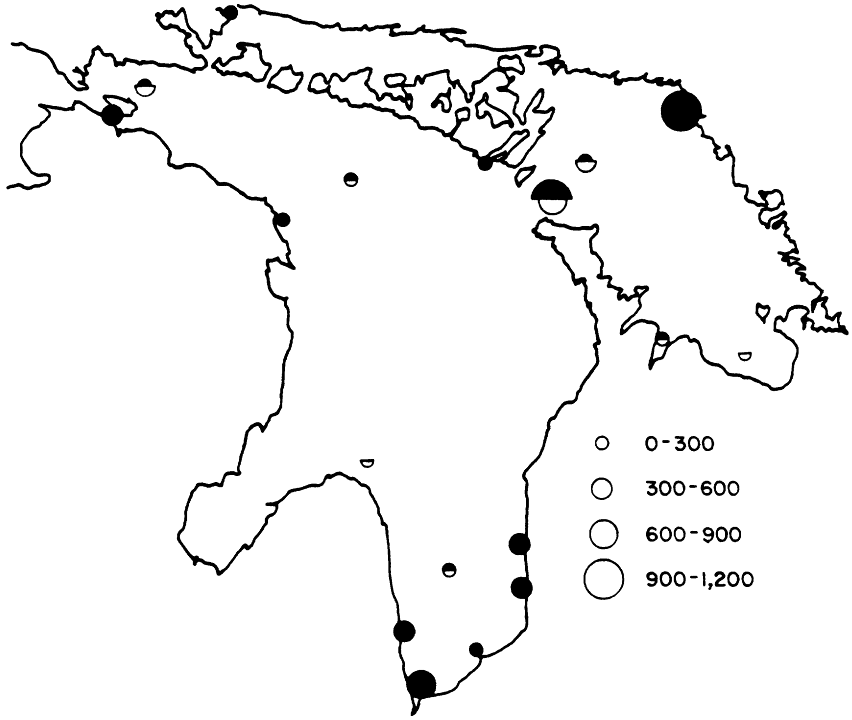


FIG. 5. Continued. c) Keratella cochlearis cochlearis, d) Notholca foliacea,



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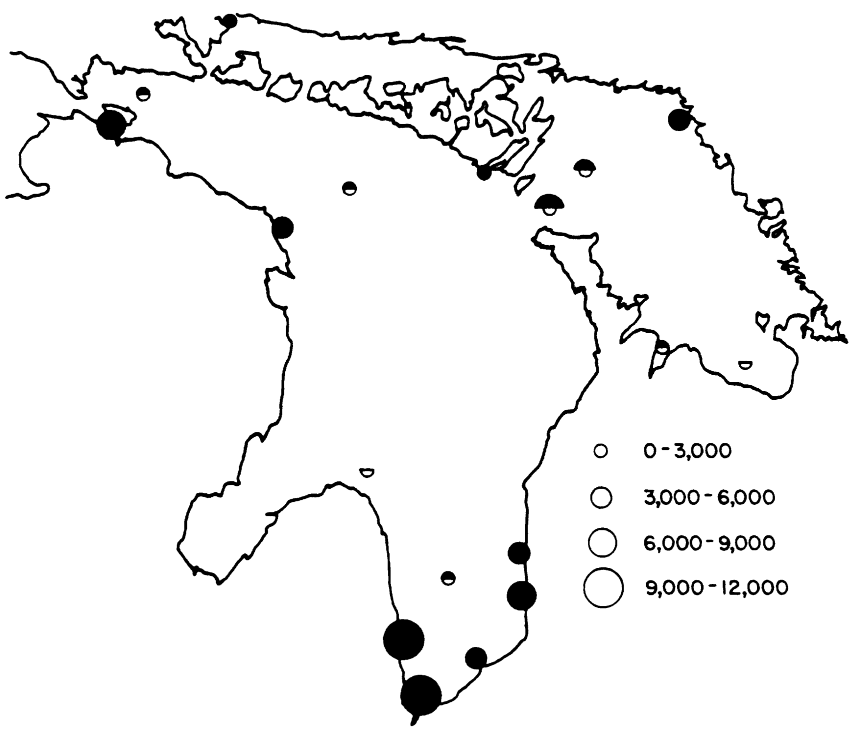
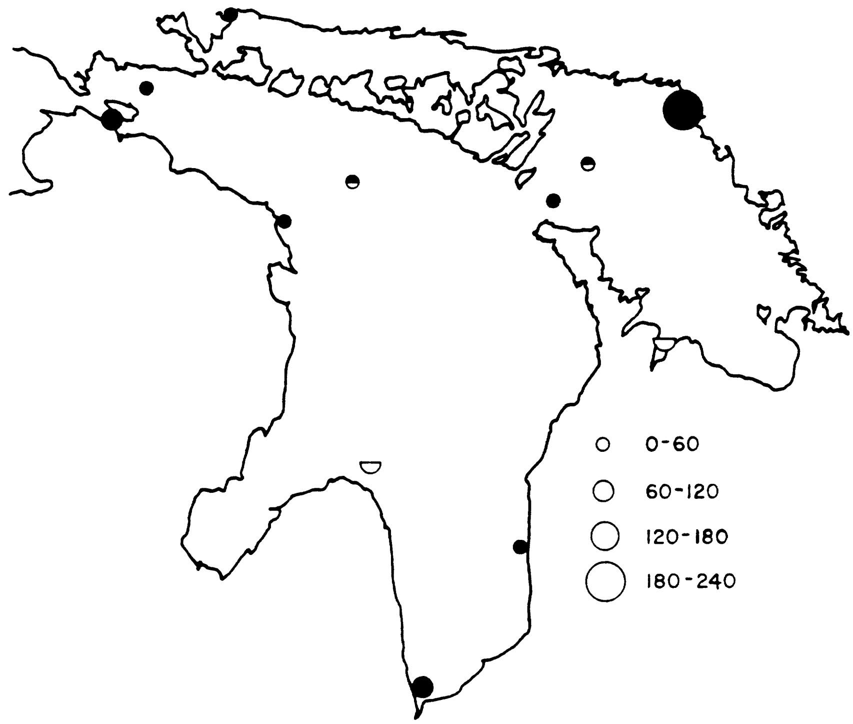


f

FIG. 5. Continued. 3) *Notholca laurentiae*, f) *Notholca squamula*,



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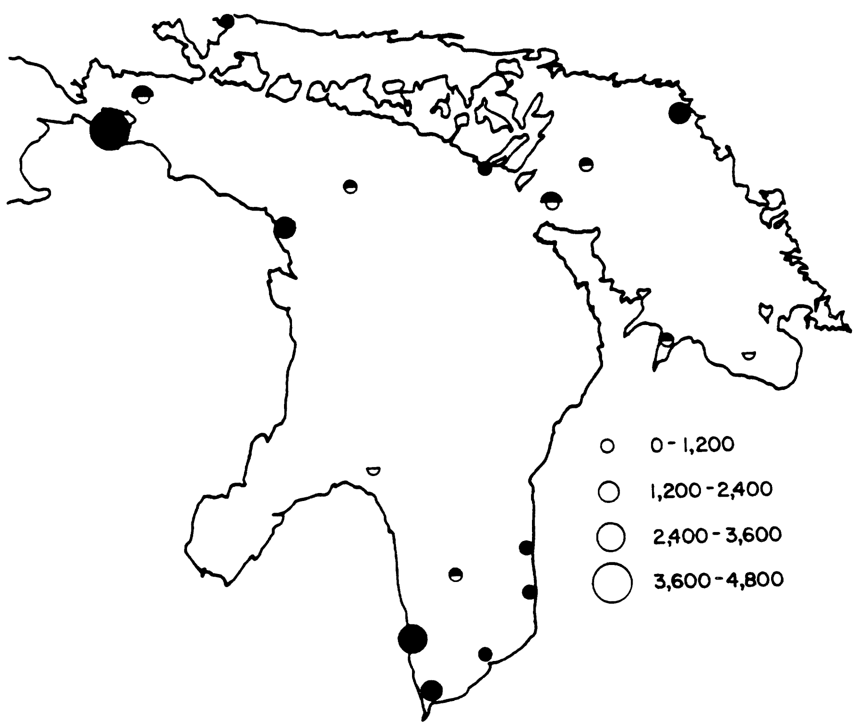


h

FIG. 5. Concluded. g) Polyarthra spp., h) Synchaeta spp.

dominated (Table 2, Fig. 5) by Notholca squamula which occurred in highest abundance in southern Lake Huron and at station 63 near Cheboygan. Synchaeta spp. were the second most abundant rotifer, with population highs in southwestern Lake Huron (station 1 near Port Huron and station 7 near Lexington) and northwestern Lake Huron (stations 47 and 63). N. foliacea occurred in high concentrations offshore of Lexington and in northwestern Lake Huron near Cheboygan, and in low numbers in Georgian Bay, the North Channel, and the deeper regions of Lake Huron. Keratella cochlearis cochlearis, Kellicottia longispina, and N. laurentiae were of lesser numerical dominance. K. cochlearis cochlearis and Notholca laurentiae were most abundant in Georgian Bay while southern Lake Huron was also a region of relatively high concentrations. K. longispina was most abundant in Georgian Bay and northwestern Lake Huron.

Individual Taxa Correlations

Crustacean taxon abundances generally were not significantly ($p>0.05$) correlated with physical-chemical parameters (Table 3). Only nauplii abundances were significantly ($p = 0.03$) correlated with Secchi disc depth.

Unlike crustaceans, whose abundances were not strongly correlated with the physical-chemical characteristics of their environment, such rotifer correlations often were statistically significant (Table 3). Notholca foliacea abundances were positively correlated with chlorophyll with lower correlations for total phosphorus, sodium, and temperature. Notholca squamula abundances were positively correlated with chlorophyll, and negatively correlated with soluble reactive silica, while Kellicottia longispina abundances were negatively correlated with nitrate. Correlations with factors either directly (chlorophyll) or indirectly (nitrate, silica) related to algal standing stocks suggest that rotifer population distributions were strongly affected by primary producers and that rotifers responded rapidly to changes in algal standing stocks. N. foliacea and N. squamula abundances were significantly correlated with temperature. Conductivity, pH, and alkalinity were minor factors correlated with Lake Huron rotifer populations.

TABLE 3. Correlations among physical-chemical parameters and crustacean and rotifer densities (#/m^3) for the April 1980 cruise. * = significant correlation (α = .05).

	T	pH	Alk	Cond	NH_3	NO_3	Sol. S_iO_2	K-N	Sod-ium	Total Phos.	Chloro-phyll	Secchi
Nauplii	-.17	-.01	+.14	+.17	-.24	+.04	-.17	-.13	-.06	-.12	-.08	+.71*
Cyclops immature	-.15	-.32	-.18	-.14	+.09	+.05	+.12	-.03	-.29	+.03	-.14	-.39
Cyclops bicuspidatus	-.07	-.17	+.02	+.05	-.18	-.19	-.22	-.22	-.21	-.19	-.12	-.17
Diaptomus ashlandi	-.21	-.01	+.16	+.18	-.25	+.02	-.14	-.21	-.10	-.15	-.13	-.43
Diaptomus minutus	-.24	-.09	+.08	+.11	-.29	-.28	-.16	-.27	-.11	-.30	-.19	-.16
Diaptomus sicilis	-.20	+.02	+.11	+.10	-.13	-.06	+.06	-.00	-.13	-.04	-.07	-.20
Total crustaceans	-.17	-.04	+.12	+.15	-.22	+.02	-.14	-.15	-.09	-.12	-.09	+.58
Kellicottia longispina	-.16	-.26	-.09	-.13	-.02	-.64	-.09	-.06	-.39	-.33	-.39	-.35
Keratella cochlearis	+.07	-.17	-.02	+.06	-.26	-.06	-.37	-.34	+.01	-.22	-.11	-.02
Notholca foliacea	+.50*	+.49	+.48	+.44	-.19	+.38	-.44	+.11	+.54*	+.61*	+.85*	+.11
Notholca laurentiae	+.28	-.00	+.03	+.08	-.10	-.06	-.16	-.23	-.09	-.06	+.01	-.02
Notholca squamula	+.48*	+.43	+.40	+.43	-.28	+.26	-.50*	-.21	+.35	+.23	+.52*	+.09
Notholca squamula-large	+.09	+.09	-.00	+.04	+.06	-.10	+.08	-.25	-.22	-.21	-.13	-.11
Polyarthra dolichoptera	+.18	-.21	-.14	-.15	-.00	-.42	+.09	+.01	-.20	+.01	-.11	-.25
Synchaeta spp.	+.38	+.40	+.38	+.31	-.23	-.23	-.33	+.00	+.24	+.23	+.44	-.10
Total rotifers	+.49*	+.41	+.40	+.40	-.27	+.11	-.47	-.16	+.32	+.24	+.51*	+.01

Crustacean taxa abundance intercorrelations generally were statistically significant ($p<0.05$). All correlations (Table 4) were positive and high. For example, copepod nauplii abundances were significantly correlated ($r>+0.9$) with the abundances of immature Cyclops spp. copepodites, and adult Cyclops bicuspidatus thomasi, Diaptomus ashlandi, D. minutus, and D. sicilis copepods. This suggests that copepod reproductive activity was in synchrony over the survey area, with regions of dense adult populations also being regions of intense reproductive activity.

While rotifer abundances were intercorrelated (Table 4), correlation coefficients were lower than observed for the crustaceans. This suggests that rotifer population cycles were not as strongly synchronized as crustacean population cycles and/or that rotifer taxa were more uniquely affected by environmental conditions. All statistically significant correlations were positive.

Many rotifer and crustacean taxa abundances were significantly correlated (Table 4). Most statistically significant correlations were positive. However Diaptomus minutus and D. sicilis abundances were negatively correlated with Notholca squamula and N. squamula large form.

Principal Component Analysis: Crustaceans

Six crustacean taxa were used in the April principal component analysis. The first principal component (PC1) accounted for 60.7% of the variance while the second component (PC2) accounted for an additional 24.6% of the variance. PC3 accounted for an additional 8.9% of the variance. PC1 loadings ranged from +0.17 for Diaptomus sicilis to +0.61 for Cyclops bicuspidatus thomasi. PC2 loadings ranged from -0.70 for C. bicuspidatus thomasi to +0.50 for D. minutus.

Plotting the 16 stations by their PC1 and PC2 values did not provide evidence of strong separation between most stations (Fig. 6). The six groupings of stations were separated on the basis of geographic location (especially Groups 2, 3, and 4) and separation on the PC1-PC2 graph. The six regions identified were Goderich (Group 1, station 10), Georgian Bay (Group 2,

TABLE 4. Simple correlations among rotifer and crustacean densities (#/m^3) for the April 1980 cruise. * = significant correlation (α = .05).

	Nauplii	Cyclops immature	Cyclops bicuspidatus	Diaptomus ashlandi	Diaptomus minutus	Diaptomus sicilis	Total crustaceans	Kellicottia longispina	Keratella cochlearis	Notholca foliacea	Notholca laurentiae	Notholca squamula	Notholca squamula-lg.	Polyarthra dolichoptera	Synchaeta spp.	Total rotifers
Nauplii	+1.00															
Cyclops immature	+.90*	+1.00														
Cyclops bicuspidatus	+.87*	+.82*	+1.00													
Diaptomus ashlandi	+.97*	+.91*	+.86*	+1.00												
Diaptomus minutus	+.89*	+.84*	+.85*	+.89*	+1.00											
Diaptomus sicilis	+.85*	+.80*	+.60*	+.87*	+.82*	+1.00										
Total crustaceans	+1.00*	+.92*	+.88*	+.99*	+.91*	+.87*	+1.00									
Kellicottia longispina	+.29	+.21	+.52	+.29	+.41	+.10	+.29	+1.00								
Keratella cochlearis	+.53*	+.51*	+.69*	+.54*	+.59*	+.18	+.54*	+.54*	+1.00							
Notholca foliacea	-.05	-.15	-.12	-.09	-.22	-.06	-.07	-.14	-.17	+1.00						
Notholca laurentiae	+.33	+.32	+.54*	+.33	+.27	.00	+.33	+.44	+.61*	+.15	+1.00					
Notholca squamula	+.10	-.03	+.18	+.07	-.08	-.14	+.08	+.16	+.30	+.67*	+.71*	+1.00				
Notholca squamula-lg.	+.03	+.05	+.05	+.01	-.05	-.01	+.02	+.04	+.01	-.04	+.52*	+.50*	+1.00			
Polyarthra dolichoptera	+.16	+.23	+.28	+.20	+.36	+.16	+.19	+.55*	+.45	+.03	+.55*	+.17	+.02	+1.00		
Synchaeta spp.	-.01	-.15	+.07	-.02	+.03	+.01	-.01	+.44	+.07	+.71*	+.40	+.64*	+.09	+.52*	+1.00	
Total rotifers	+.12	-.02	+.21	+.08	-.01	-.08	+.10	+.30	+.31	+.72*	+.71*	+.97*	+.40	+.35	+.81*	+1.00

a

b

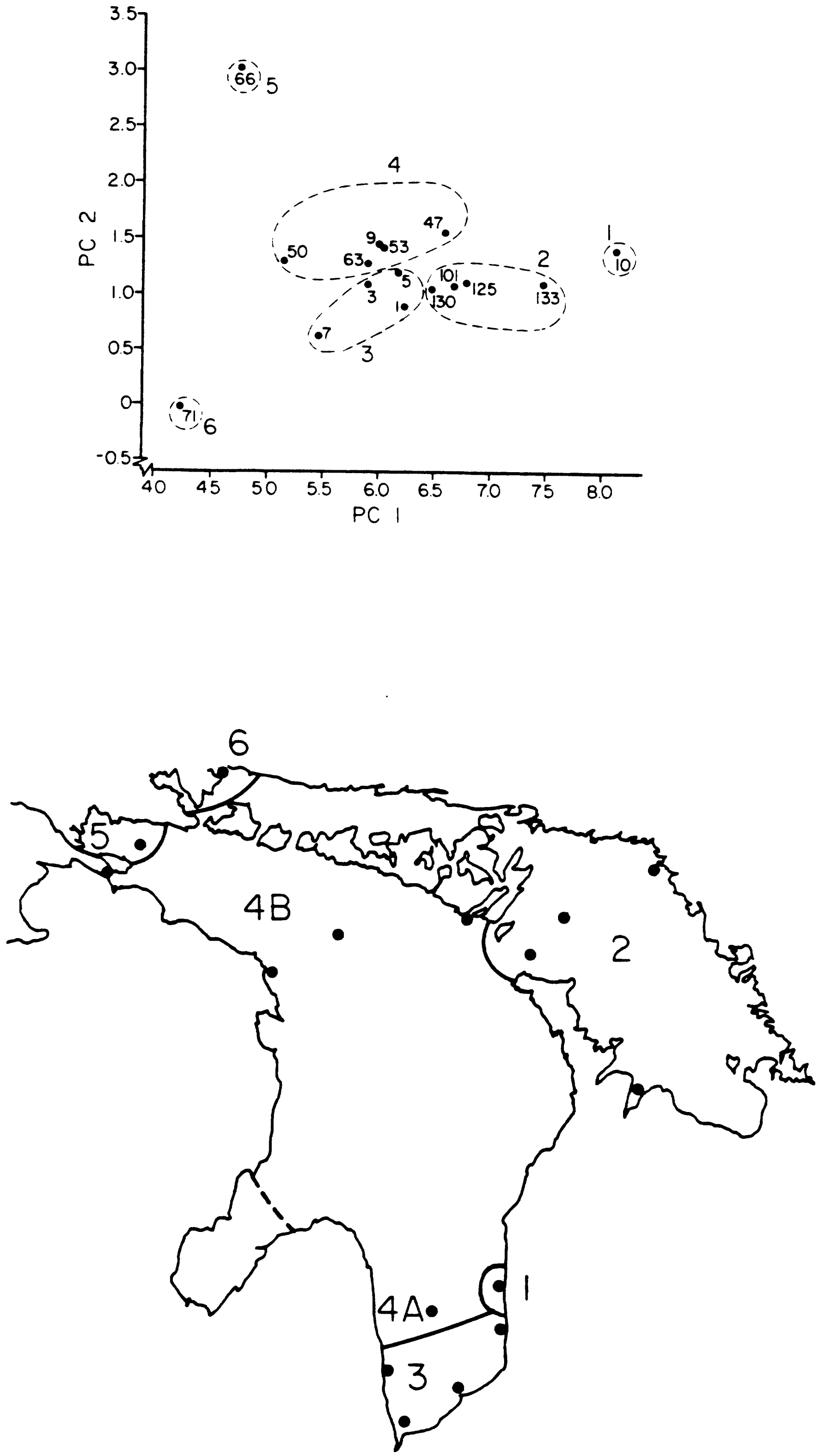


FIG. 6. a) Principal component ordination of stations sampled for crustaceans on 13-26 April 1980. b) Lake map with station groups derived from ordination analysis.

stations 101, 125, 130, and 133), nearshore southern lake Huron (Group 3, stations 1, 3, 5, and 7), Lake Huron (Group 4, stations 9, 47, 50, 53, and 63), the Straits of Mackinac (Group 5, station 66), and the mouth of the St. Marys River (Group 6, station 71).

PC1 station scores were not significantly ($p>0.05$) correlated with the suite of physical-chemical parameters considered. Correlations with the highest attained levels of significance ($r = -0.46$ to -0.49; $p = 0.06$ to 0.08) occurred with ammonia, total Kjeldahl nitrogen, and soluble reactive silica. In contrast, station PC2 scores were significantly ($p<0.04$) correlated with pH ($r = +0.63$), ammonia ($r = -0.58$), and total phosphorus ($r = -0.50$). Station PC1 scores were positively correlated with *Keratella cochlearis cochlearis* ($r = +0.79$; $p<0.01$) with a weaker correlation with *Notholca laurentiae* ($r = +0.48$; $p = 0.06$).

Crustacean regional means (Table 5) ranged from a low of 5,353/m^3 for St. Marys River mouth Group 6 to a high of 65,041/m^3 for Group 1, offshore of Goderich. Population means were higher in Georgian Bay Group 2 (18,728/m^3) than for southern Lake Huron Group 3 (12,108/m^3) and Lake Huron Group 4 (9,403/m^3). Differences in total zooplankton regional means were due primarily to nauplii which accounted for 65.4% to 78.8% (Table 6) of the crustacean population. *Diaptomus minutus*, *D. ashlandi*, and *Cyclops bicuspidatus thomasi* tended to be more abundant in Georgian Bay Group 2 and Goderich Group 1 than Groups 3 to 6 in the main body of the lake and its inflows from Lakes Michigan and Superior. Crustaceans were more abundant at station 66 in the Straits of Mackinac Group 5 than Group 6 in the St. Marys River outflow. Immature *Cyclops* spp. and adult *C. bicuspidatus thomasi* were more abundant in the Lake Superior outflow than in the outflow from Lake Michigan, while *Diaptomus ashlandi*, *D. minutus* and, to a lesser extent, nauplii and *D. sicilis* were more abundant in the Straits of Mackinac than the St. Marys River. While adult *Cyclops bicuspidatus thomasi* were not collected in the upper 25 m of the water column at station 66, they were present in the deep collection (0-66m) at a concentration of 233/m^3. Rotifers accounted for a small fraction of the zooplankton biomass in all six regions.

TABLE 5. Mean densities (#/m^3) of various crustacean taxa and carbon weights (mg carbon/m^3) for the April 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Nauplii	42,537	13,215	9,238	6,749	9,431	3,692
Cyclops C1-C5	3,902	1,098	715	435	195	1,198
Cyclops bicuspidatus C6	1,691	733	200	121	0	62
Diaptomus ashlandi C6	10,797	2,462	1,552	1,229	976	31
Diaptomus minutus C6	2,472	936	191	486	553	6
Diaptomus sicilis C6	3,642	285	213	539	813	364
Total crustaceans	66,081	18,728	12,108	9,559	11,968	5,353
Total rotifers	6,686	7,504	10,695	5,301	4,723	1,068
Crustacean carbon	58.72	11.55	6.84	7.94	9.53	3.73
Rotifer carbon	0.03	0.03	0.05	0.02	0.05	0.01

TABLE 6. Percent composition of crustacean taxa for the April 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Nauplii	65.4	70.6	76.3	70.6	78.8	69.0
Cyclops C1-C5	6.0	5.9	5.9	4.6	1.6	22.4
Cyclops bicuspidatus C6	2.6	3.9	1.7	1.3	0.0	1.2
Diaptomus ashlandi C6	16.6	13.1	12.8	12.9	8.2	0.6
Diaptomus minutus C6	3.8	5.0	1.6	5.1	4.6	0.1
Diaptomus sicilis C6	5.6	1.5	1.8	5.6	6.8	6.8

The relationships between crustacean community structure and the physical-chemical characteristics of each of the six regions are shown in Tables 6 and 7. The St. Marys River mouth Group 6 with low PC1 and PC2 values, had relatively high concentrations of soluble reactive silica (2.4 mg/L), nitrate (0.307 mg/L), total Kjeldahl nitrogen (total organic nitrogen; 0.321 mg/L), and total particulate phosphorus (12.4 μg/L). While Secchi disc depth was low (1.0 m), the 1-m chlorophyll concentration also was low (1.2 mg/m^3), suggesting that most of the turbidity at station 71 was due to detrital matter and mineral particles carried by a rapid and turbulent river flow rather than to phytoplankton. Low chlorophyll concentrations may have affected the low crustacean standing stock (5,333/m^3). The phytoplankton:zooplankton carbon ratio was relatively high (21.2), suggesting that zooplankton did not exert intense grazing pressure on the phytoplankton community in the St. Marys River outflow. Cyclopoid copepods were an important component of this community with many of the animals probably originating in the river.

The Straits of Mackinac Group 5 was influenced by the St. Marys River outflow, as evidenced by its moderately low conductivity (192.0 μmhos/cm^2) in comparison to northern Lake Huron Group 4 (207.4 μmhos/cm^2). Chlorophyll concentrations were higher (1.6 mg/m^3) and soluble reactive silica concentrations lower (1.6 mg/L) than in the St. Marys River outflow. Crustacean standing stocks (11,968/m^3) were greater than in the St. Marys River Group 6 while the phytoplankton:zooplankton carbon ratio was lower (11.0). This lower ratio suggests that zooplankton exhibited a greater grazing pressure on phytoplankton in the Straits of Mackinac than in the St. Marys River outflow. Higher chlorophyll concentrations despite apparently higher grazing pressures suggest that the phytoplankton community was more productive in Group 5 than in Group 6. Compositional differences in the zooplankton community reflect differences in source waters (St. Marys River for Group 6; St. Marys River, the North Channel, and Lake Michigan for Group 5).

Goderich Group 1 had the largest crustacean standing stock and a phytoplankton:zooplankton carbon ratio of 2.5. This southeastern Lake Huron

TABLE 7. Mean values of physical-chemical parameters[1] for the April 1980 cruise (crustaceans).

Parameter	Region 1	2	3	4	5	6
Sample depth (m)	10.0	22.0	11.2	20.4	25.0	31.0
Temperature (°C)	2.1	2.4	2.8	2.1	2.6	2.6
Secchi	-	5.0	7.5	7.6	9.0	1.0
pH	8.0	7.9	8.1	8.1	8.2	7.6
Alkalinity (mg/L)	77.0	67.9	77.7	79.2	74.0	38.0
Conductivity (μmhos/cm)	207.0	183.3	209.7	207.4	192.0	95.0
Nitrate (mg/L x 10^{-2})	32.0	26.5	39.3	27.7	28.8	30.7
Sol. react. silica (mg/L)	1.4	1.3	1.3	1.4	1.6	2.4
Kjeldahl nitrogen (mg/L x 10^{-2})	16.3	16.1	17.0	16.3	20.2	32.1
Total phosphorus (mg/L x 10^{-2})	0.6	0.4	0.8	0.5	0.4	1.2
Chlorophyll (mg/m^3)	2.2	1.2	4.1	1.8	1.6	1.2
Phyto. carbon/zoop. carbon	2.5	6.8	39.3	14.8	11.0	21.2

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

station was characterized by a high standing stock of phytoplankton (2.2 mg chlorophyll/mg^3) which persisted despite apparently intense grazing pressure by a large (65,041/m^3) crustacean population. This suggests that phytoplankton productivity was relatively high in this region. Terrestrial nutrient inputs entering the lake from the Maitland River near Goderich may have stimulated algal productivity.

Georgian Bay Group 2 had lower phytoplankton standing stocks (1.2 mg chlorophyll/m^3) than Group 1. Soluble reactive silica concentrations were moderate (1.3 mg/L) while nitrate concentrations were low (0.265 mg/L). The algal community (including silica-utilizing diatoms) apparently had been productive for some period of time. The crustacean zooplankton standing stock was relatively high (18,728/m^3) while the phytoplankton:zooplankton carbon ratio (6.8) was low. Lower chlorophyll concentrations in Group 2 than Group 1, despite apparently less intense grazing pressure, suggest that the algal community was less productive in Georgian Bay than offshore of Goderich.

Phytoplankton exhibited a north-south gradient in standing stocks. Group 3, in southern Lake Huron, had greater concentrations of chlorophyll (4.1 mg/m^3) and lower concentrations of soluble reactive silica (1.3 mg/L) than Group 4 (1.8 mg/m^3 and 1.4 mg/L respectively) to the north. While crustacean standing stocks were greater to the south (12,108/m^3 versus 9,559/m^3), biomass was higher in Group 4 (7.96 mgC/m^3 versus 6.84 mgC/m^3) due to the greater abundance of <u>Diaptomus sicilis</u>, a relatively heavy copepod. The phytoplankton:zooplankton carbon ratio was higher in Group 3 than Group 4 (34.3 versus 14.8), suggesting relatively less intense zooplankton grazing in the southern nearshore region of Lake Huron than in the main body of the lake. The higher chlorophyll concentration in Group 3 than in Group 4 despite only small differences in zooplankton biomass suggests that southern Lake Huron was characterized by higher primary productivity than northern Lake Huron. Nutrient-rich water from Saginaw Bay and run-off from agricultural areas may have been significant factors affecting phytoplankton productivity in southern Lake Huron.

Principal Component Analysis: Rotifers

Eight rotifer taxa were used in the analysis of the 16-station April data. PC1 accounted for 42.6% of the variance, PC2 for an additional 24.8% of the variance, and PC3 for an additional 15.5% of the variance. PC1 loadings ranged from -0.14 for _Kellicottia longispina_ to +0.95 for _Notholca foliacea_. PC2 loadings ranged from -0.09 for _N. foliacea_ to +0.62 for _Polyarthra dolichoptera_.

Plotting stations by their first and second principal component values provided evidence of six groups of stations (Fig. 7) which differed in rotifer community structure. These regions were a central southern Lake Huron Group 1 consisting of three stations (3, 5, 7), Group 2 consisting of two nearshore stations (1, 10) in southern Lake Huron and two nearshore stations (47, 63) in northwestern Lake Huron, Group 3 consisting of station 71 in the outflow of the St. Marys River and station 53 in central northern Lake Huron, Group 4 consisting of station 9 in a deepwater (54 m) region of southern Lake Huron and station 50 (depth 30 m) south of Manitoulin Island, Group 5 consisting of two stations (101, 130) in Georgian Bay and one station (station 66) in the Straits of Mackinac, and Group 6 consisting of stations 125 and 133 in Georgian Bay. Groups 4, 5, and 6 had low and similar PC1 values and differed primarily in their PC2 values.

PC1 station scores were significantly ($p<0.05$) correlated with chlorophyll ($r = +0.57$), total phosphorus ($r = +0.53$), and nitrate ($r = +0.52$), while PC2 was negatively correlated with nitrate ($r = -0.53$). This suggests that rotifer community structure was affected by factors directly (chlorophyll) or indirectly (nitrate) related to algal productivity. Station PC1 scores also were positively correlated with the abundance of nauplii ($r = +0.54$) and _Diaptomus sicilis_ ($r = +0.52$). PC2 station scores were not significantly correlated with the abundance of the dominant crustacean taxa.

Rotifer group means (Tables 8 and 9) ranged from 1,267/m^3 in the Group 3 Lake Superior outflow to 10,467/m^3 in Group 2 (nearshore southern and northwestern Lake Huron). Rotifers also were abundant (6,443/m^3) in Group 1 in central southern Lake Huron and Group 6 (9,381/m^3) in Georgian Bay. Groups

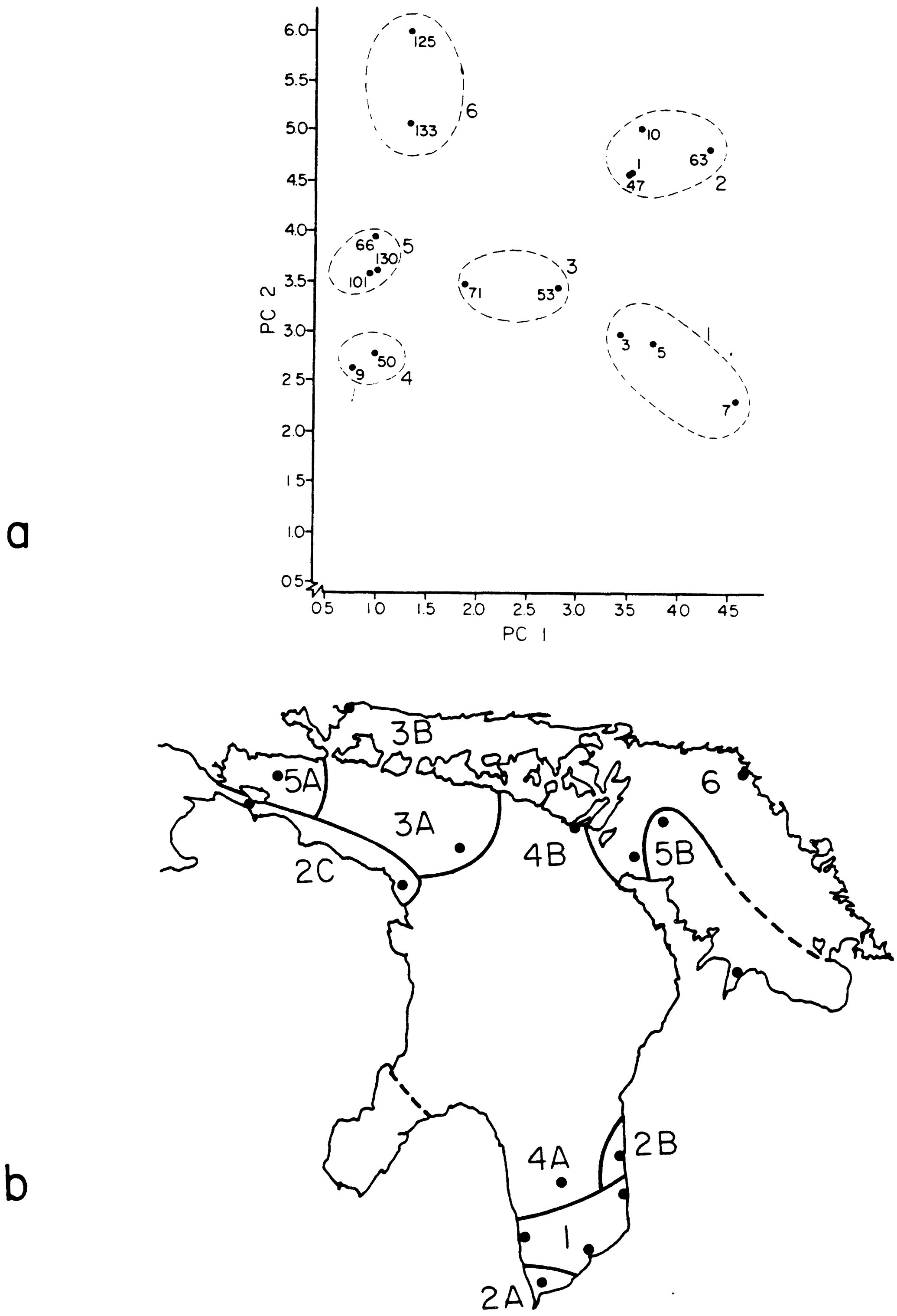


FIG. 7. a) Principal component ordination of stations sampled for rotifers on 13-26 April 1980. b) Lake map with station groups derived from ordination analysis.

TABLE 8. Mean densities ($\#/m^3$) of various rotifer taxa and carbon weights ($mg\ carbon/m^3$) for the April 1980 cruise.

Taxon	Region					
	1	2	3	4	5	6
Kellicottia longispina	30	307	171	23	301	421
Keratella coch. coch.	303	269	76	61	336	646
Notholca foliacea	823	541	58	0	0	0
N. laurentiae	375	508	108	88	148	960
N. squamula	6,966	6,339	676	1,321	3,188	5,915
N. squamula large	0	90	0	3	7	40
P. dolichoptera	0	38	11	0	0	81
Synchaeta spp.	1,204	2,376	167	155	911	1,725
Total rotifers	9,701	10,467	1,267	1,650	4,893	9,788
Total crustaceans	12,289	25,709	9,005	6,187	14,002	23,288
Rotifer carbon	0.04	0.05	0.01	0.01	0.02	0.04
Crustacean carbon	6.64	22.19	6.19	4.64	8.67	16.36

TABLE 9. Percent composition of various rotifer taxa for the April 1980 cruise.

Taxon	Region					
	1	2	3	4	5	6
Kellicottia longispina	0.3	2.9	13.5	1.4	6.2	4.3
Keratella coch. coch.	3.1	2.6	6.0	3.7	6.9	6.6
Notholca foliacea	8.5	5.2	4.5	0.0	0.0	0.0
N. laurentiae	3.9	4.9	8.6	5.3	3.0	9.8
N. squamula	71.8	60.6	53.4	80.1	65.2	60.4
N. squamula large	0.0	0.9	0.0	0.2	0.1	0.4
P. dolichoptera	0.0	0.4	0.8	0.0	0.0	0.8
Synchaeta spp.	12.4	22.7	13.2	9.4	18.6	17.6

1 and 2, with large PC1 values and high rotifer standing stocks, had relatively high concentrations of Notholca foliacea in comparison to Groups 3 to 6 with low PC1 values and low densities of this rotifer species. Groups 2 and 6, with high PC2 values, were characterized by relatively high concentrations of Kellicottia longispina, N. squamula large form, Synchaeta spp., and Polyarthra dolichoptera.

Table 10 shows the relationship between rotifer community structure and the physical-chemical characteristics of the six regions. As in the crustacean analysis, these relationships were dynamic.

Groups 1 and 2 in southern and northwestern Lake Huron were regions of high phytoplankton standing stocks. Chlorophyll concentrations averaged 2.1 to 2.2 mg/m^3 in comparison to means of 1.2 to 1.6 mg/m^3 for regions 3 to 6. Chlorophyll concentration was particularly high (10.0 mg/m^3) at station 7 near Lexington while dissolved silica (0.91 mg/L) concentration was low. Group 1 rotifer standing stocks were large (6,443/m^3) although most of the carbon biomass was associated with crustaceans (6.64 mgC/m^3 versus 0.02 mgC/m^3). The phytoplankton:zooplankton carbon ratio was relatively large (21.8).

Group 2 consisted of two geographic regions; stations 1 and 10 in southern Lake Huron and stations 47 and 63 in the nearshore area of northwestern Lake Huron. Nitrate concentrations were lower (0.288 mg/L) than in Group 1 while chlorophyll concentrations (2.1 mg/L) were similar. Rotifers (10,647/m^3) and, in particular, crustaceans (25,709/m^3) were more abundant than in Group 1. The phytoplankton:zooplankton carbon ratio was low (6.3), suggesting that grazing pressure was relatively intense. Since chlorophyll concentrations were relatively high, primary productivity probably was also relatively high in Group 2 in comparison to other regions of the lake.

Group 6, in Georgian Bay, also had relatively high rotifer standing stocks (9,788/m^3). Soluble reactive silica concentrations were moderate (1.4 mg/L) while nitrate concentrations were low (0.258 mg/L), possibly suggesting that the algal community had been productive for some period of time. Moderately low chlorophyll concentrations (1.4 mg/m^3), particularly in relation to the abundant crustacean (23,288/m^3) and rotifer (9,788/m^3) communities, suggest that grazing pressure contributed to a significant loss

TABLE 10. Mean values of physical-chemical parameters[1] for the April 1980 cruise (rotifers).

Parameter	Region 1	2	3	4	5	6
Sample depth (m)	17.0	11.0	28.0	26.5	25.0	19.0
Temperature (°C)	2.5	2.3	2.4	2.1	2.2	2.9
Secchi	4.0	6.0	5.5	7.0	9.0	5.0
pH	8.1	8.1	7.8	8.1	8.0	7.9
Alkalinity (mg/L)	77.0	79.8	58.3	75.8	71.9	65.0
Conductivity (µmhos/cm)	207.0	209.5	150.0	203.0	191.0	176.0
Nitrate (mg/L x 10^{-2})	40.3	28.5	30.6	27.9	27.8	25.8
Sol. react. silica (mg/L)	1.4	1.4	1.9	1.5	1.3	1.4
Kjeldahl nitrogen (mg/L x 10^{-2})	13.5	16.4	26.4	12.3	17.5	16.1
Total phosphorus (mg/L x 10^{-2})	0.7	0.6	0.8	0.4	0.4	0.5
Chlorophyll (mg/m^3)	2.2	2.1	1.2	1.6	1.2	1.4
Phyto. carbon/zoop. carbon	21.7	6.3	12.8	22.8	9.1	5.6

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

of algal biomass. The phytoplankton:zooplankton carbon ratio was low (5.6). Primary productivity apparently was not as high as in Group 2 where chlorophyll concentrations were approximately 50% greater than in Group 6, but where phytoplankton:zooplankton carbon ratios were similar (i.e., similar grazing pressure).

Group 5 consisted of three stations characterized by moderately high rotifer populations, which were adjacent to areas of greater rotifer standing stocks. Stations 101 and 130 (Group 5A) in Georgian Bay had relatively high concentrations of crustaceans (14,888/m^3) and moderate rotifer densities (5,059/m^3). Silica concentrations (1.19 mg/L) were low, possibly because the algal community had been productive for some time. Conversely station 66 (Group 5B), in the Straits of Mackinac, was characterized by higher silica (1.61 mg/L) and chlorophyll (1.6 mg/m^3 versus 1.05 mg/m^3) concentrations. Rotifer (4,723/m^3) and crustacean (12,293/m^3) populations were similar to those at stations 104 and 130. Moderately high nutrient and chlorophyll concentrations suggest that the phytoplankton spring bloom was not sufficiently advanced to reduce nutrient reserves. Since the phytoplankton:zooplankton carbon ratio for Group 5 was moderate (9.1), zooplankton grazing apparently was relatively more intense than in adjacent Group 3 but less intense than in Group 6.

Rotifer standing stocks were low (1,650/m^3) in Group 4 (stations 9 and 50). Chlorophyll standing stocks were moderate (1.6 mg/m^3) as was soluble reactive silica (1.46 mg/L), indicating that phytoplankton in these deeper areas of Lake Huron had only recently become relatively productive. The phytoplankton:zooplankton carbon ratio was high (22.8), suggesting a time lag between primary and secondary producers in these deeper, offshore waters. This could account for the relatively low rotifer and crustacean biomass despite moderate chlorophyll concentrations.

Group 3, consisting of stations 53 and 71, had the lowest standing stock of rotifers. As discussed previously, station 71 (Region 3B) in the St. Marys River apparently had relatively low primary productivity. Station 53 (Region 3A) was a deep station (93 m) in Lake Huron and an area where vertical mixing of the water column was intense. Chlorophyll concentrations averaged 1.2 mg/

m^3. Rotifer and crustacean standing stocks were low (0.01 mgC/m^3 and 6.19 mgC/m^3 respectively) while the phytoplankton:zooplankton carbon ratio was comparatively high (12.8) in comparison to Groups 5 and 6 with similar chlorophyll concentrations. Thus, the low standing stock of phytoplankton for Group 3 stations does not appear to be strongly related to grazing pressure but more probably was related to the physical characteristics of the water column at .nese cold and deep regions of Lake Huron.

Principal Component Analysis: Combined Rotifer And Crustacean Data

Principal component analyses of the combined rotifer-crustacean data were not as powerful in reducing the multivariate data set to a smaller number of components as analyses utilizing the rotifer-alone of crustacean-alone data. PC1 accounted for 36.5% of the variance versus 50.2% for the crustacean analysis and 42.5% for the rotifer analysis. PC2 accounted for 26.6% of the variance versus 24.8% for the crustacean analysis and 24.8% for the rotifer analysis. PC1 was significantly ($p<0.05$) correlated with nitrate ($r = +0.54$), chlorophyll ($r = +0.56$), and total phosphorous ($r = +0.51$), while PC2 was significantly correlated with total phosphorus ($r = -0.51$). Similar analyses of the May, June, and July data sets confirm the general results of the April analysis. Combined analyses were not as useful in reducing the multivariate data set to a smaller number of components as separate rotifer and crustacean analyses.

May Cruise

General Features

The May cruise (Fig. 8) was conducted from 9 to 12 May 1980. Eleven stations were sampled, with three in southeastern Lake Huron (south of the mouth of Saginaw Bay), one in east-central Lake Huron, four in northern Lake Huron, two in the North Channel, and one in Georgian Bay.

Water temperatures were only slightly warmer than during the April cruise. In the North Channel, northern Georgian Bay, and the inshore region

FIG. 8. Location of stations sampled on 9-12 May 1980.

of the main body of Lake Huron, temperatures exceeded 4°C. Temperatures were less than 2.6°C in the central region of Lake Huron and southwestern Georgian Bay. Surface water temperatures exceeded 2.6°C at all zooplankton stations. Highest chlorophyll concentrations (>2.5 mg/m^3) were along the southeastern shore of Lake Huron and the southeastern shore of Saginaw Bay. Lowest (<1.0 mg/m^3) concentrations were in western Georgian Bay (Moll and Rockwell in prep).

Total zooplankton abundances (Fig. 9) ranged from 9,545/m^3 (station 53) to 30,821/m^3 (station 3). Crustaceans generally were more abundant than rotifers.

Crustacean abundances were similar to those observed a few weeks earlier during the April cruise (Fig. 10) with densities ranging from 6,871/m^3 (station 5) to 26,421/m^3 (station 40). Nauplii (Fig. 10) dominated the crustacean population with the greatest abundance observed at station 78 in the North Channel: lowest abundance was observed at station 125 in Georgian Bay. Adult *Diaptomus* species were the second major group with *D. ashlandi* the numerical dominant, followed by *D. minutus* and *D. sicilis*. Highest densities were observed in the main body of Lake Huron. Immature diaptomids were more abundant than during the April cruise and accounted for a larger fraction of the crustacean population. These immature copepodites were produced from the maturation of the spring pulse of nauplii and occurred in greatest densities at station 1 (near Port Huron) and station 3 (near Kettle Point) in southern Lake Huron. Adult *Cyclops bicuspidatus thomasi* occurred in approximately the same abundance as during the April cruise while immatures were slightly more abundant. Adults were most numerous in Georgian Bay, the North Channel, the Straits of Mackinac, and southeastern Lake Huron. While immatures were not staged, it is probable that they were dominated by the early developmental stages produced by the maturation of the spring naupliar pulse. *Limnocalanus macrurus* occurred in low numbers and was dominated by immature copepodites. Cladocerans were rare, with *Bosmina longirostris* the most abundant taxon followed by *Eubosmina coregoni*. Cladocerans were most abundant in southern Lake Huron.

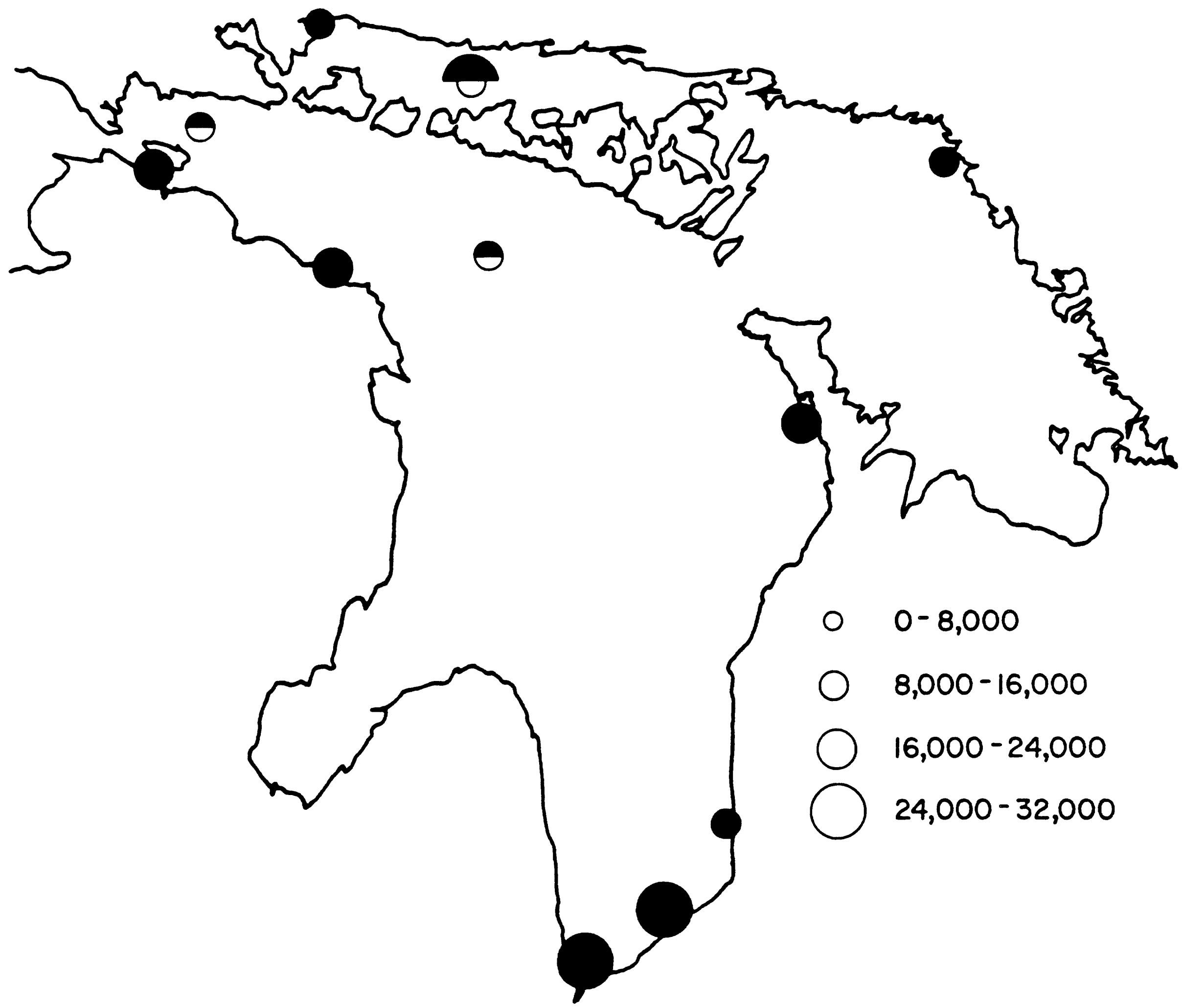
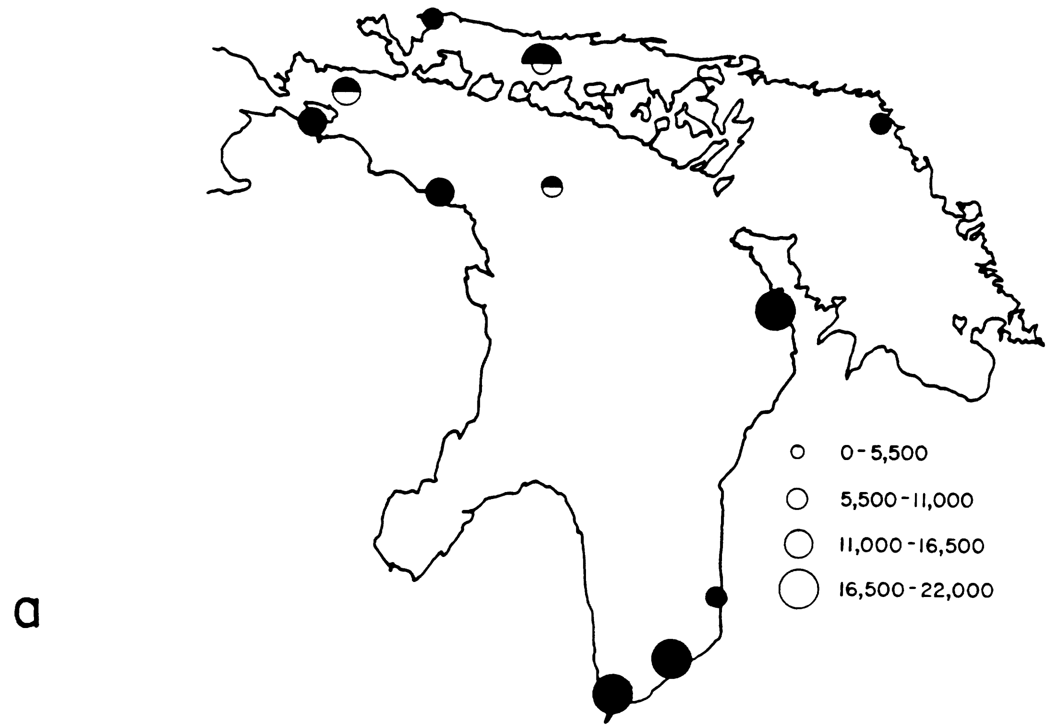


FIG. 9. Distribution (#m/^{3}) of total zooplankton collected on 9-12 May 1980. Black circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface.



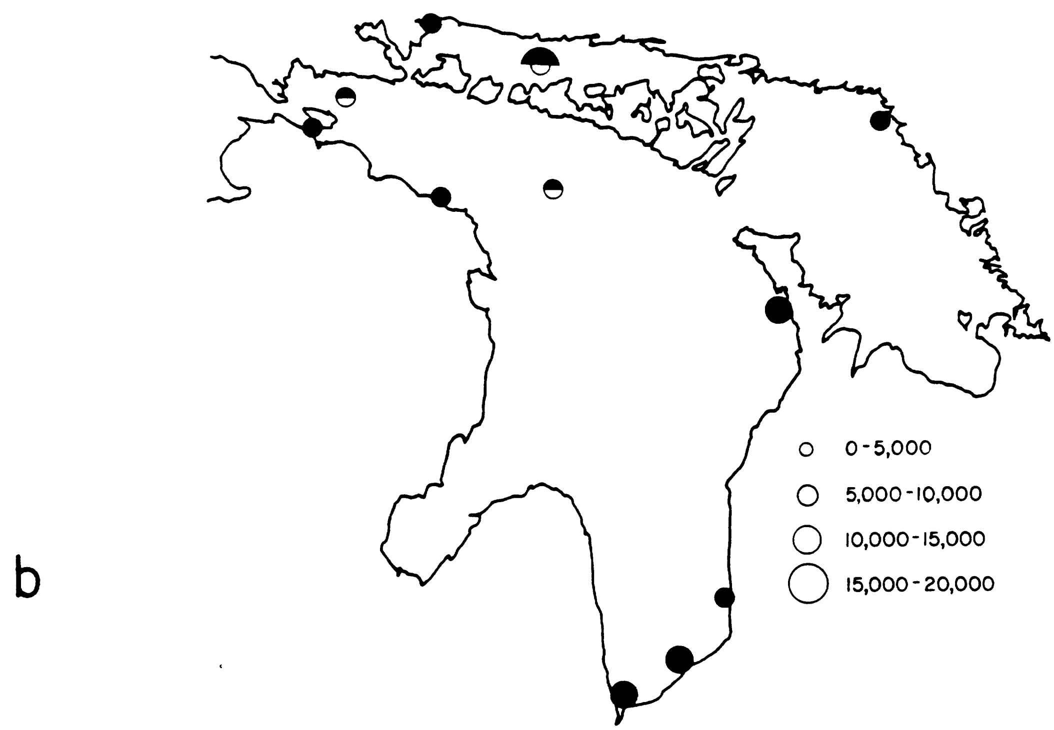


FIG. 10. Spatial distribution (#/m^3) of total crustaceans and major crustacean taxa collected 9-12 May 1980. Mixed circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total crustaceans, b) copepod nauplii,

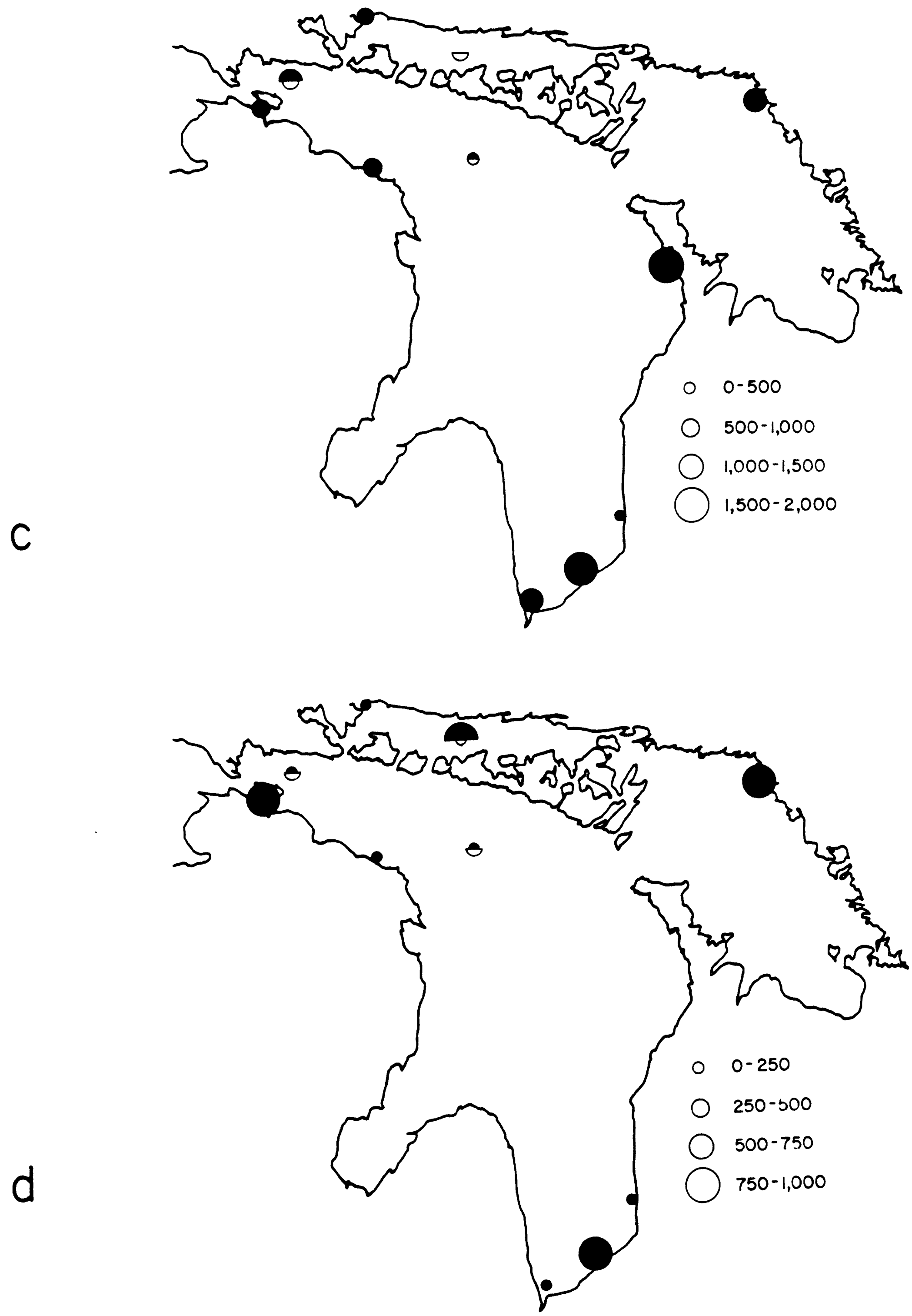
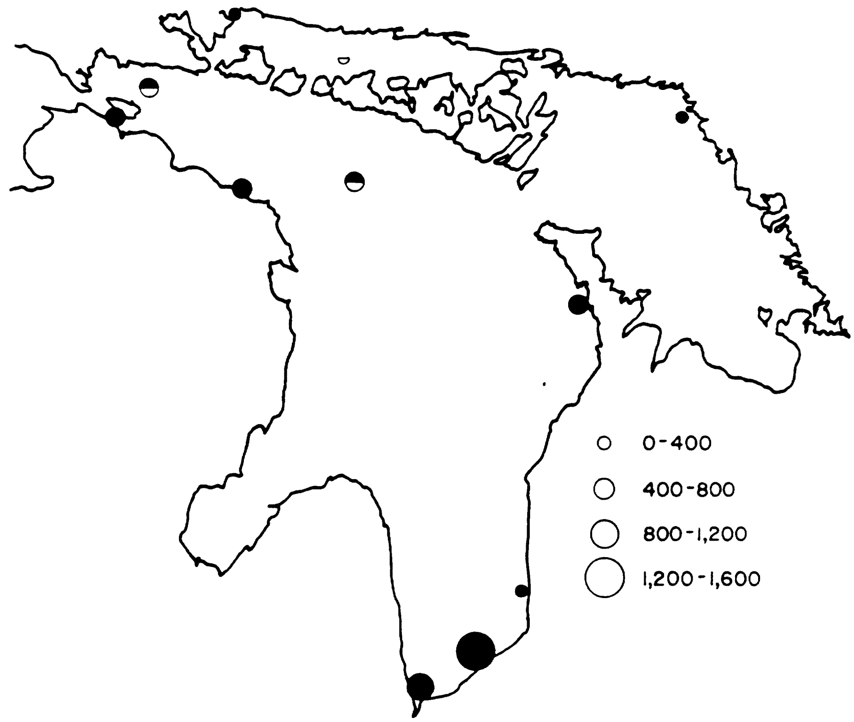


FIG. 10. Continued. c) *Cyclops* spp C1–C5, d) *Cyclops bicuspidatus thomasi*,

e



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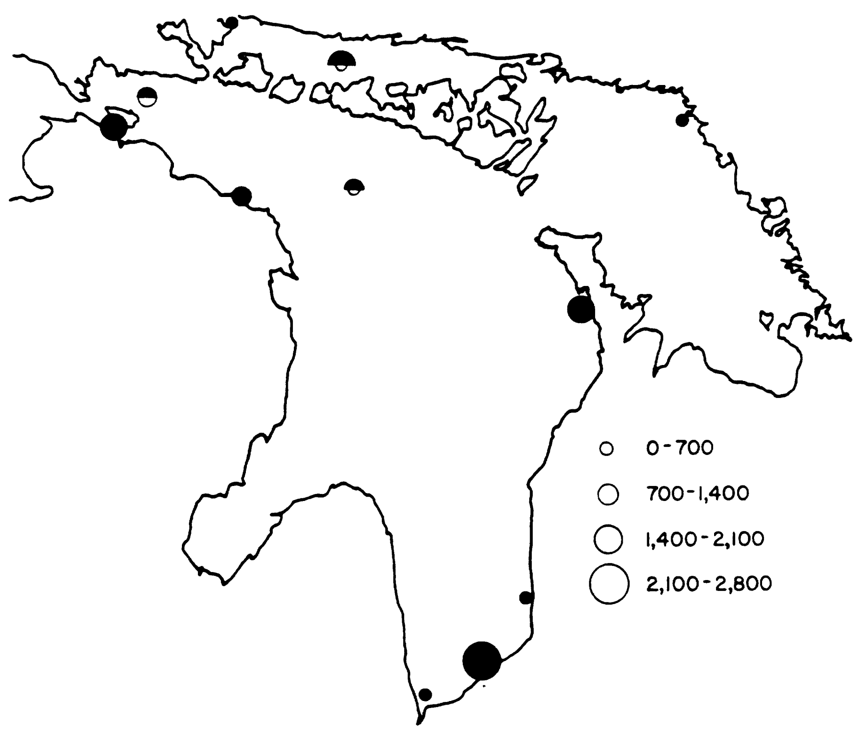


FIG. 10. Continued. e) Diaptomus spp. C1-C5, f) Diaptomus ashlandi,

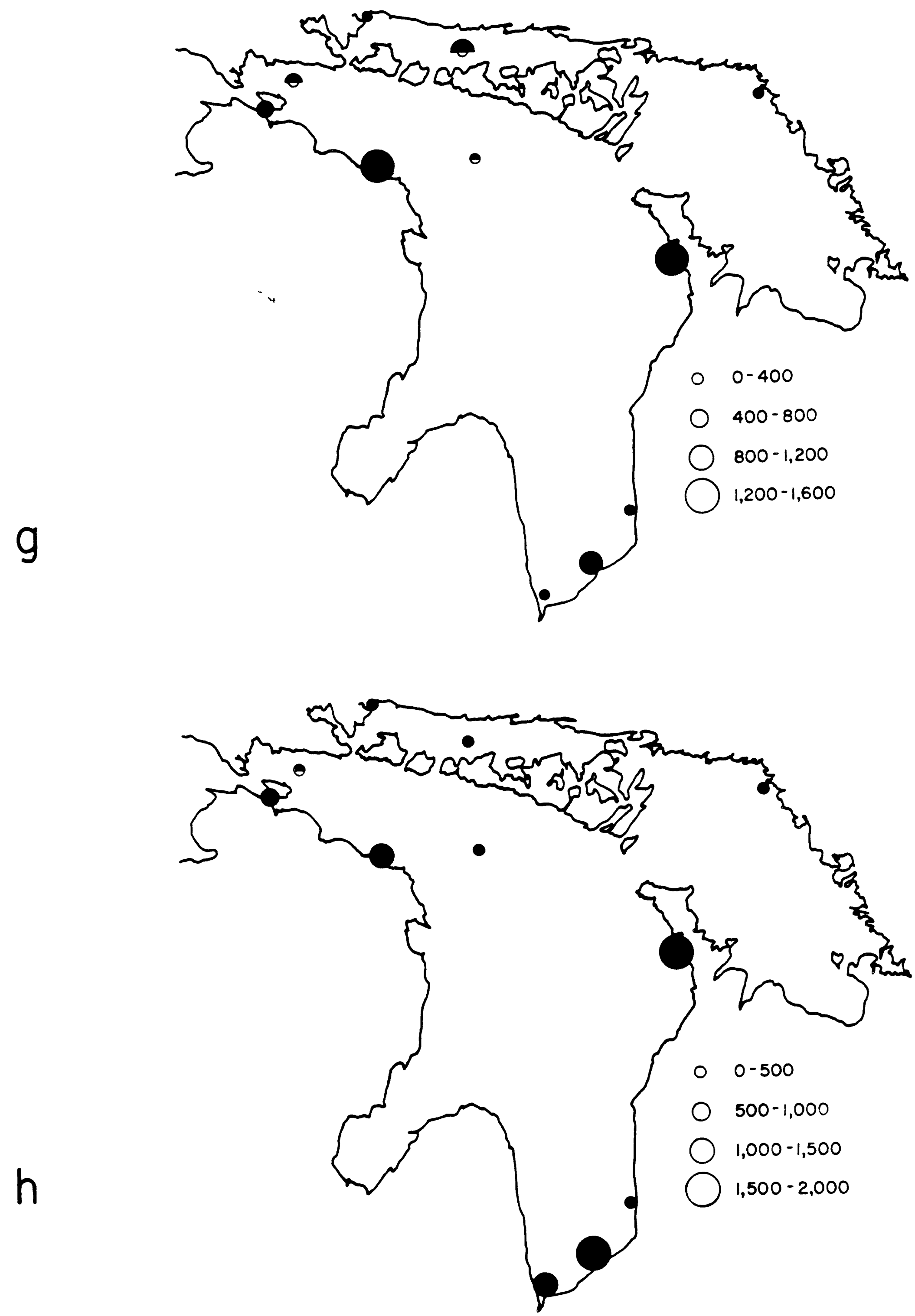


FIG. 10. Concluded. g) Diaptomus minutus, h) Diaptomus sicilis.

Rotifers were slightly less abundant in May than in April with densities ranging from $956/m^3$ (station 53) to $10,415/m^3$ (station 3). Notholca squamula was the numerically dominant (Fig. 11) species, occurring in highest densities in southern Lake Huron (stations 1, 3, and 5) and at station 40 (near Stokes Bay) on the western side of the Bruce Peninsula. Synchaeta spp. was the second most abundant rotifer taxon with highest densities in southeastern Lake Huron (station 3 near Kettle Point and station 5 near Bayfield) and with low populations in Georgian Bay, central Lake Huron, and near Port Huron (station 1) in southwestern Lake Huron. Kellicottia longispina tended to be most abundant in northern Lake Huron, Georgian Bay, and the North Channel with lower abundances in southern Lake Huron. Keratella cochlearis cochlearis attained its highest density at station 125 in Georgian Bay. Notholca foliacea was most abundant in southern Lake Huron and at station 63 (near Cheboygan) in the Straits of Mackinac while N. laurentiae was most abundant in the North Channel. Polyarthra spp. were most abundant at station 3 in southeastern Lake Huron.

Individual Taxa Correlations

For the seven abundant crustacean taxa, correlations were calculated between station abundance and physical-chemical parameters. No correlations were statistically ($p>0.05$) significant with the exception of Diaptomus sicilis with alkalinity (Table 11).

As in the April analysis, rotifer taxon abundances were significantly ($p<0.05$) correlated (Table 11) with physical and chemical factors. Notholca squamula, Polyarthra spp., and Synchaeta spp. abundances were positively correlated with chlorophyll. Synchaeta spp. abundances also were positively correlated with nitrate. Notholca foliacea abundances were positively correlated with pH, conductivity, and alkalinity, and negatively correlated with soluble reactive silica.

All crustacean intercorrelations were positive (Table 12). As in April, many of these correlations were statistically significant ($p<0.05$). For example, nauplii abundances were correlated with immature Cyclops spp. and

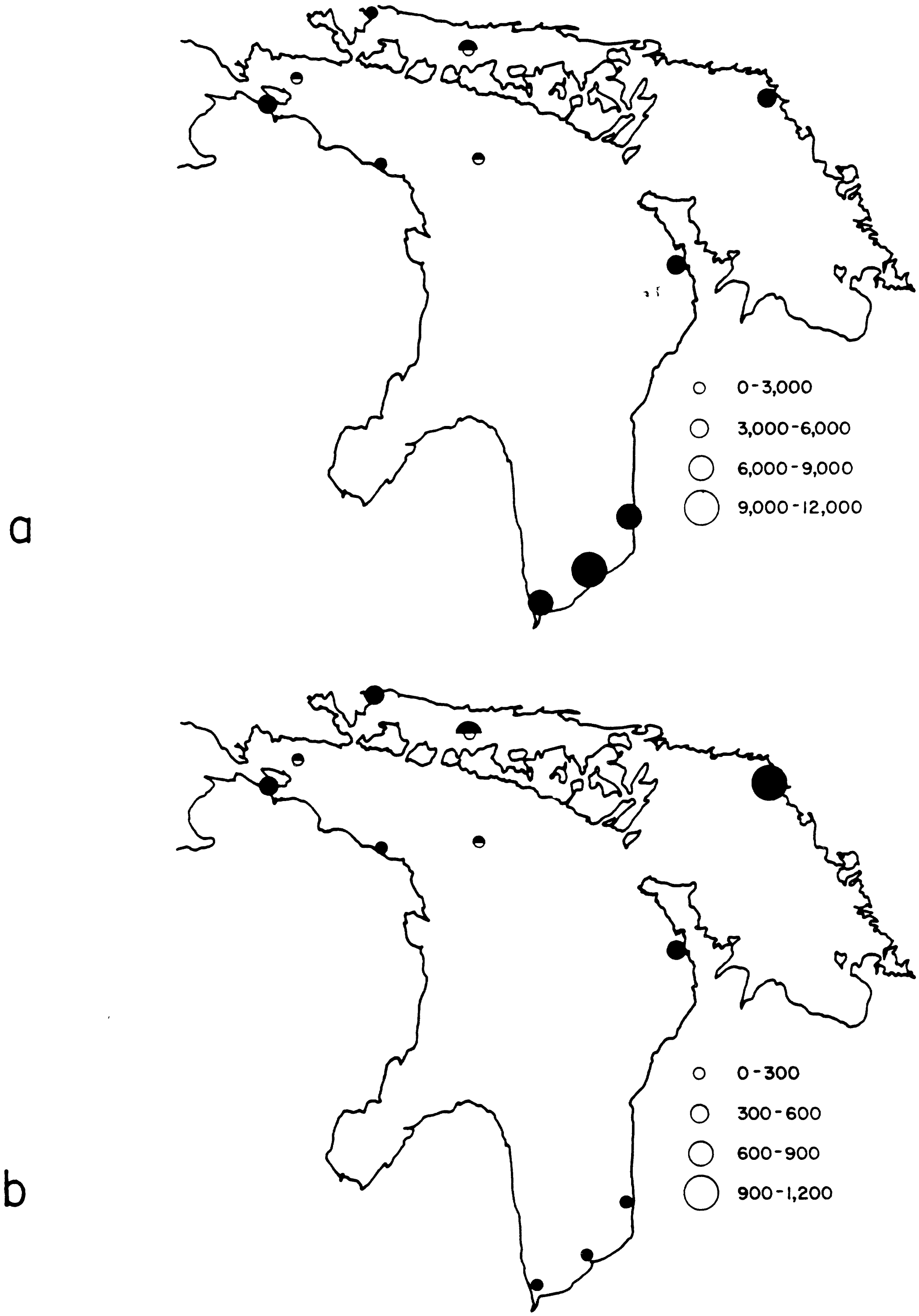


FIG. 11. Spatial distribution ($\#/m^3$) of total rotifers and major rotifer taxa collected on 9-12 May 1980. Black circles represent net haul from 2 m off bottom to surface. Mixed circles (white and black): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total rotifers, b) Kellicottia longispina,

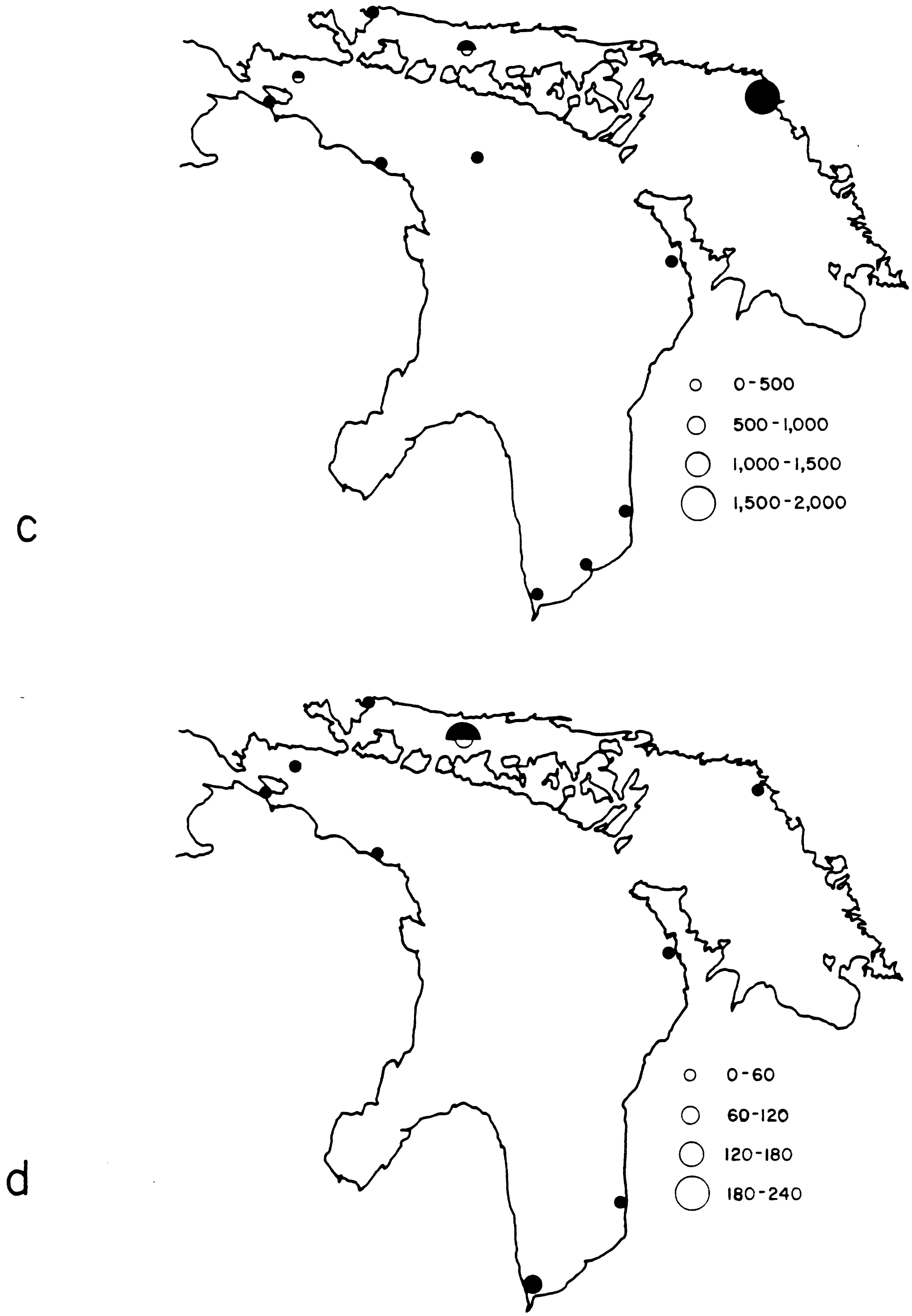
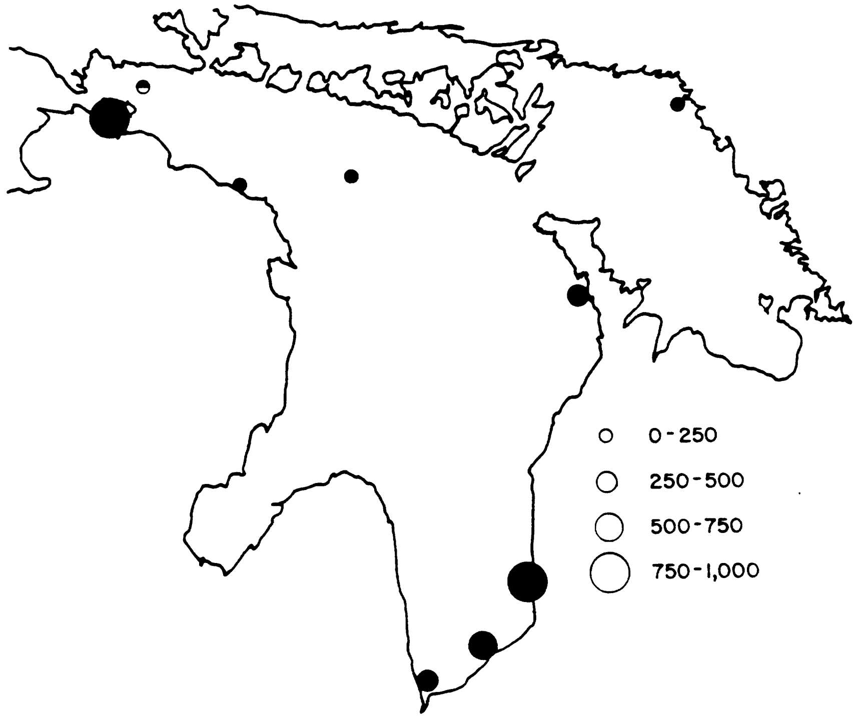


FIG. 11. Continued. c) Keratella cochlearis cochlearis, d) Keratella quadrata,



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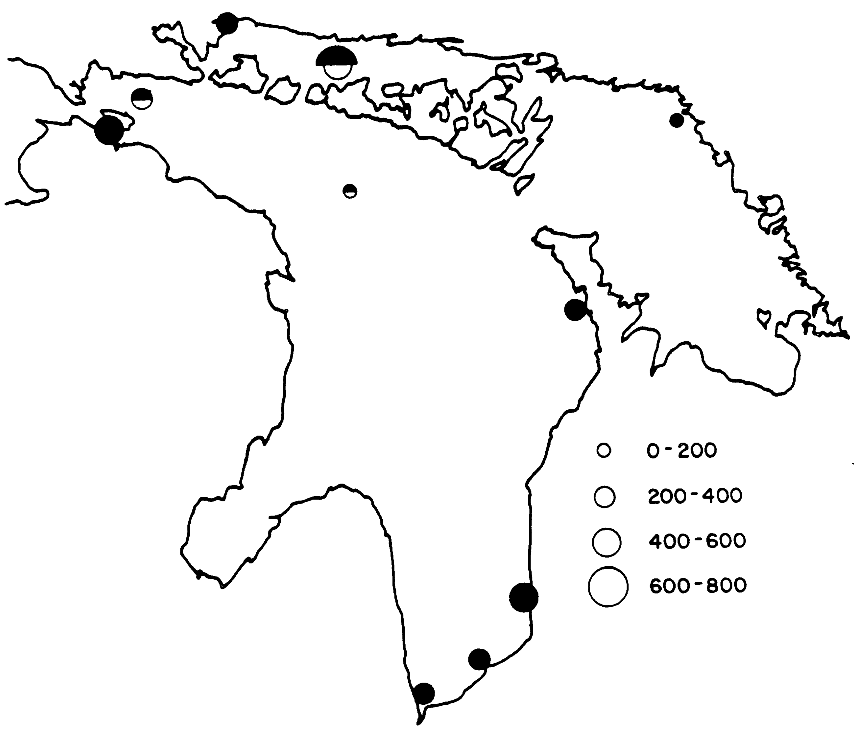

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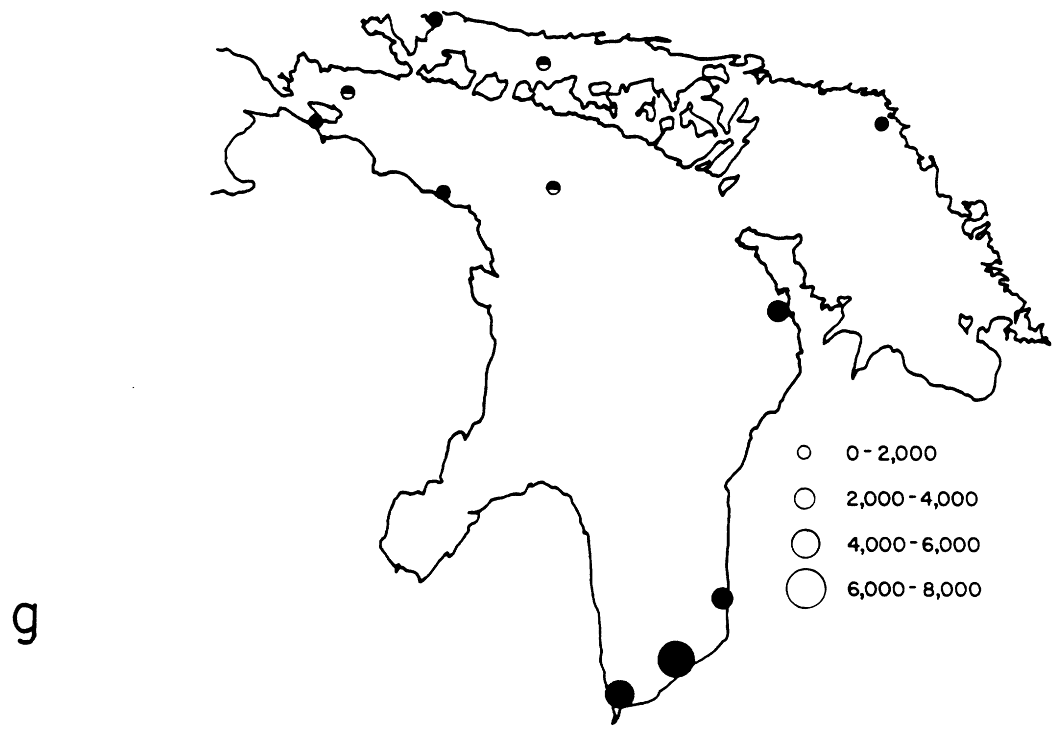
FIG. 11. Continued. e) Notholca foliacea, f) Notholca laurentiae,



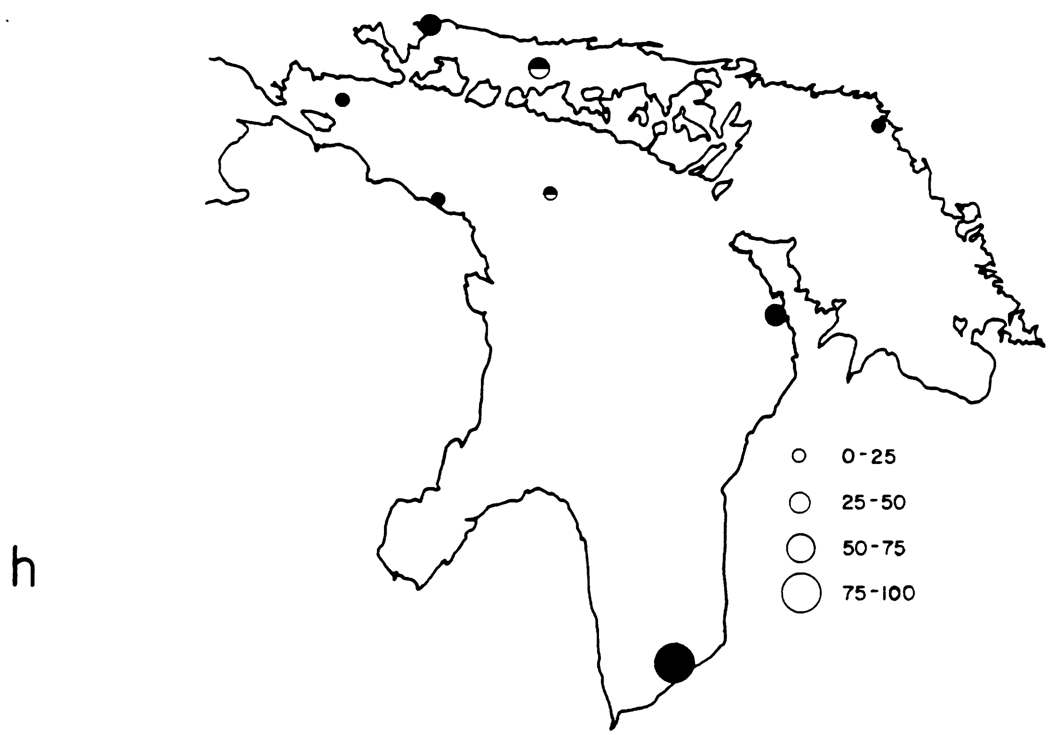


FIG. 11. Continued. g) Notholca squamula, h) Polyarthra spp.,

i

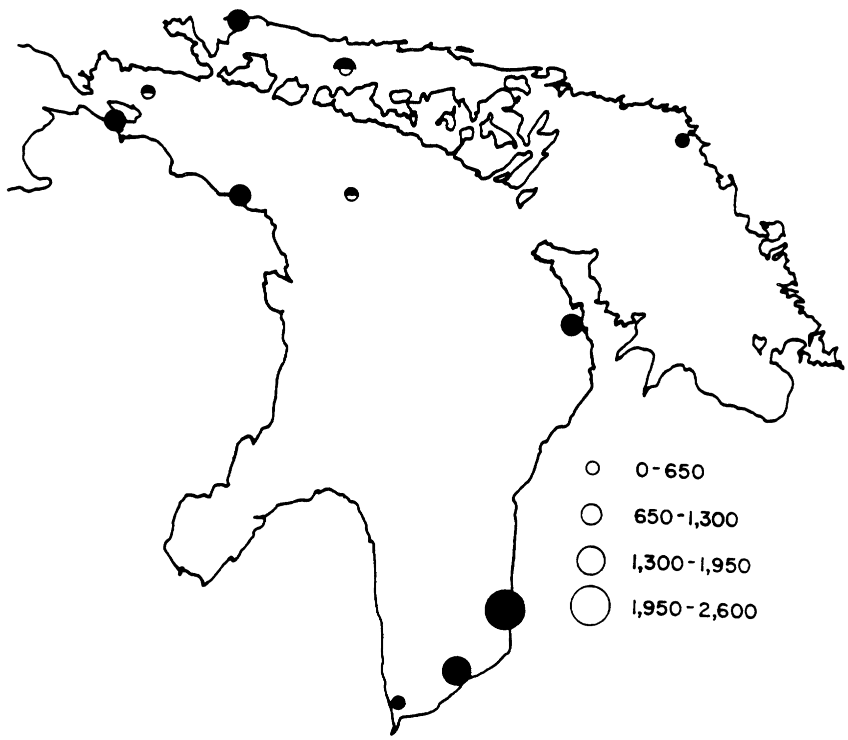


FIG. 11. Concluded. i) Synchaeta spp.

TABLE 11. Simple correlations among physical-chemical parameters and crustacean and rotifer densities (#/m^3) for the May 1980 cruise. * = significant correlation (α = .05).

	T	pH	Alk	Cond	NH_3	NO_3	Sol. SiO_2	K-N	Tot Phos	Chloro-phyll	Chlor-ide
Nauplii	-.05	+.44	+.45	+.37	-.37	-.13	-.31	+.41	-.23	-.11	+.15
Cyclops immature	-.02	+.00	-.02	-.16	-.24	-.46	+.13	+.23	-.11	+.11	-.05
Cyclops bicuspidatus	+.41	+.06	-.04	-.03	-.13	-.42	-.11	+.09	+.26	+.43	+.11
Diaptomus immature	-.02	+.51	+.44	+.40	-.41	-.09	-.40	+.34	-.53	+.58	+.19
Diaptomus ashlandi	-.27	+.26	+.37	+.32	-.43	-.25	-.17	-.39	-.28	+.48	+.24
Diaptomus minutus	-.07	+.35	+.55	+.45	-.41	-.27	-.36	+.22	-.06	+.15	+.21
Diaptomus sicilis	-.01	+.55	+.61*	+.55	-.47	-.21	-.54	+.35	-.28	+.37	+.30
Total crustaceans	-.21	+.28	+.35	+.27	-.42	-.31	-.11	+.09	-.31	+.19	+.12
Kellicottia longispina	+.47	-.41	-.51	-.49	+.18	-.45	+.37	+.29	+.61	-.27	-.27
Keratella cochlearis	+.59	-.34	-.55	-.45	+.09	-.23	+.22	+.45	+.35	-.05	-.04
Keratella quadrata	-.11	-.31	-.26	-.34	+.16	-.09	+.51	-.22	+.24	-.33	-.25
Notholca foliacea	+.26	+.85*	+.71*	+.71*	-.48	+.32	-.80*	-.23	+.13	+.47	+.70*
Notholca laurentiae	+.06	+.20	+.11	+.02	-.03	+.21	+.09	-.36	+.23	+.18	+.04
Notholca squamula	+.10	+.57	+.33	+.33	-.32	+.36	-.37	+.07	-.55	+.81*	+.28
Polyarthra spp.	+.09	+.01	-.05	-.14	+.07	-.10	+.16	-.01	-.21	+.68*	-.26
Synchaeta spp.	+.38	+.60	+.35	+.30	-.04	+.82*	-.39	-.17	-.05	+.75*	+.27
Total rotifers	+.37	+.59	+.27	+.26	-.28	+.43	-.37	+.07	-.29	+.84*	+.32

TABLE 12. Simple correlations among rotifer and crustacean densities (#/m^3) for the May 1980 cruise. * = significant correlation (α = .05).

	Nauplii	Cyclops immature	Cyclops bicuspidatus	Diaptomus immature	Diaptomus ashlandi	Diaptomus minutus	Diaptomus sicilis	Total crustaceans	Kellicottia longispina	Keratella cochlearis	Keratella quadrata	Notholca foliacea	Notholca laurentiae	Notholca squamula	Polyarthra spp.	Synchaeta spp.	Total rotifers
Nauplii	+1.00																
Cyclops immature	+.65*	+1.00															
Cyclops bicuspidatus	+.10	+.56	+1.00														
Diaptomus immature	+.78*	+.53	+.32	+1.00													
Diaptomus ashlandi	+.23	+.54	+.63*	+.53	+1.00												
Diaptomus minutus	+.62*	+.40	+.29	+.63*	+.43	+1.00											
Diaptomus sicilis	+.79*	+.42	+.35	+.90*	+.45	+.84*	+1.00										
Total crustaceans	+.93*	+.81*	+.33*	+.79*	+.52	+.68*	+.78*	+1.00									
Kellicottia longispina	-.01	+.53	+.54	-.27	-.03	-.09	-.22	+.12	+1.00								
Keratella cochlearis	-.22	+.32	+.51	-.30	-.14	-.27	-.32	-.13	+.88*	+1.00							
Keratella quadrata	+.17	+.46	-.05	-.22	+.09	-.23	-.32	+.29	+.51	+.24	+1.00						
Notholca foliacea	+.16	-.11	+.30	+.31	+.37	+.19	+.40	+.17	-.26	-.25	-.26	+1.00					
Notholca laurentiae	+.32	+.53	+.25	+.09	+.40	-.05	-.03	+.47	+.31	+.07	+.73*	+.27	+1.00				
Notholca squamula	+.44	+.29	+.22	+.76*	+.51	+.13	+.49	+.48	-.33	-.24	-.02	+.48	+.35	+1.00			
Polyarthra spp.	+.32	+.57	+.58	+.64*	+.69*	+.46	+.47	+.53	+.04	-.04	+.01	+.02	+.32	+.55	+1.00		
Synchaeta spp.	+.04	-.24	-.02	+.25	+.15	+.06	+.15	+.03	-.42	-.32	-.16	+.60*	+.34	+.61*	+.33	+1.00	
Total rotifers	+.36	+.33	+.38	+.61*	+.49	+.07	+.38	+.44	-.08	+.00	+.09	+.57	+.52	+.93*	+.54	+.70	+1.00

Diaptomus spp., D. minutus, D. sicilis, while immature Diaptomus spp. were correlated with D. sicilis and D. minutus. These positive correlations suggest that, as in April, crustaceans were similarly affected by the characteristics of their environment or that population cycles were in synchrony over the survey grid. For example, areas where nauplii were abundant also were areas where the later developmental stages (immature copepodites) were abundant.

Rotifer abundances generally were not significantly intercorrelated (Table 12). The low number of significant correlations suggests that rotifers were more uniquely affected (than crustaceans) by the physical-chemical characteristics of their environment.

Crustacean-rotifer correlations generally were positive (Table 12), although only two correlations were statistically significant ($p<0.05$). These were Polyarthra spp. with immature Diaptomus spp. and with D. ashlandi.

Principal Component Analysis: Crustaceans

Seven crustacean taxa were used in the analysis of the 11-station May cruise data. PC1 accounted for 72.0% of the variance, PC2 for an additional 17.5%, and PC3 for 3.9% of the variance. Diaptomus sicilis had the highest (+0.73) PC1 loading while nauplii had the lowest (+0.13). Cyclops bicuspidatus thomasi had the highest PC2 loading (+0.73) while Diaptomus sicilis had the lowest (-0.44).

Plotting the eleven stations by their PC1 and PC2 scores (Fig. 12) provided evidence of differences in crustacean community structure over the lake. Group 1 consisted of five nearshore stations (1, 3, 40, 55, and 63) in the main body of Lake Huron and was characterized by high PC1 values and moderate PC2 values. Two stations (53 and 66) in northwestern Lake Huron formed Group 2 with intermediate PC1 and PC2 values. Stations 71 and 78 in the North Channel formed Group 3 while station 125 in Georgian Bay formed Group 4. Station 5, near Bayfield, formed Group 5 with low PC1 and PC2 values.

a

b

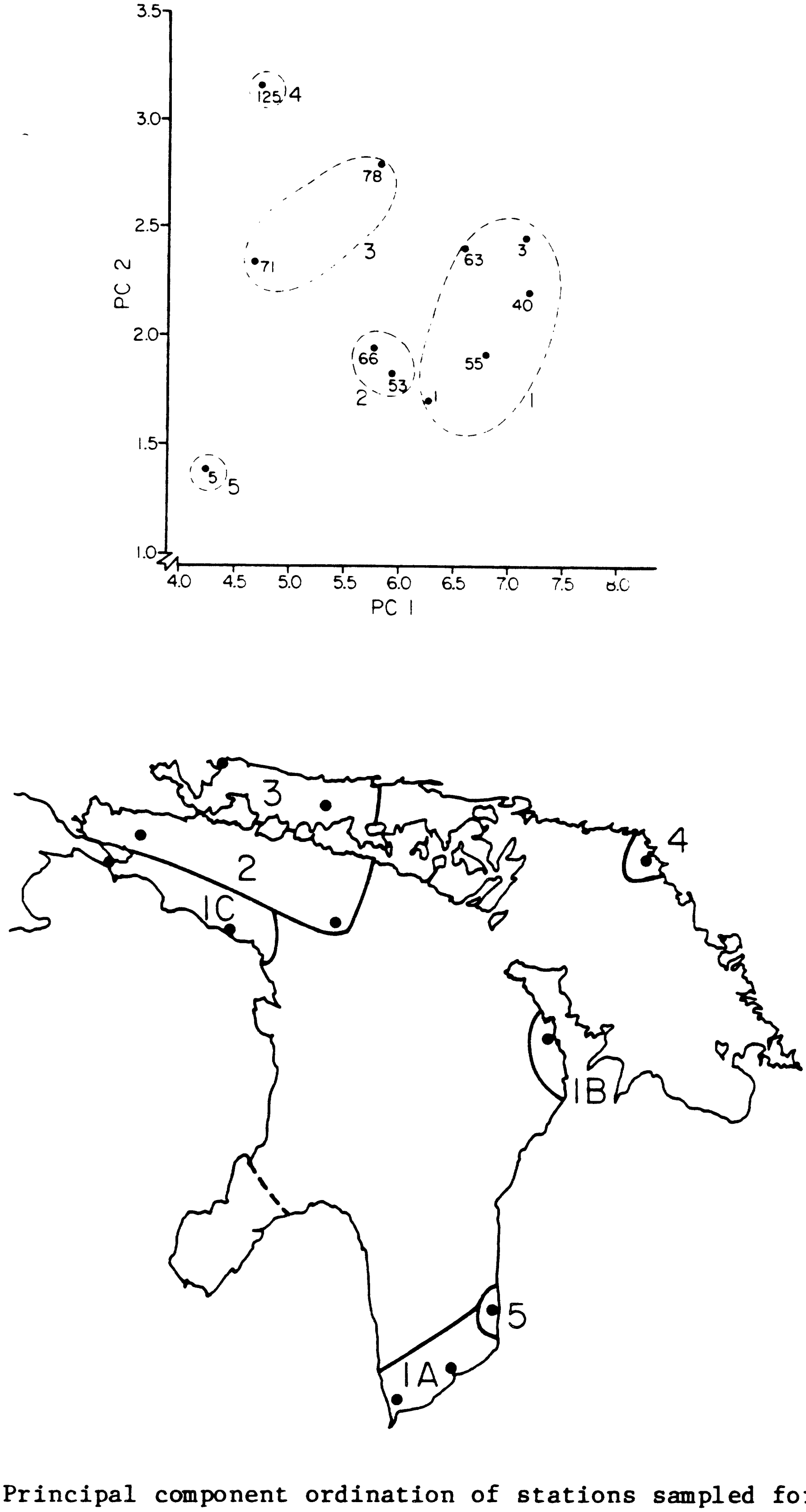


FIG. 12. a) Principal component ordination of stations sampled for crustaceans on 9-12 May 1980. b) Lake map with station groups derived from ordination analysis.

Station scores along the PC1 axis were positively correlated with alkalinity ($r = +0.72$; $p = 0.01$) and conductivity ($r = +0.64$; $p = 0.03$) while PC2 scores were negatively correlated with nitrate ($r = -0.62$; $p = 0.04$). PC1 and PC2 scores were not significantly correlated with the abundance of any rotifer taxa.

Crustacean regional means (Table 13) ranged from 6,762/m^3 (southeastern Lake Huron Group 5) to 18,698/m^3 (Group 1 in the nearshore region of Lake Huron). Groups 1, 2, and 3, with high PC1 values were characterized by relatively large numbers of adult _Diaptomus ashlandi_, _D. minutus_, and _D. sicilis_. Group 5 (near Bayfield) with a low PC2 value was characterized by low numbers and percent composition of immature and adult _Cyclops bicuspidatus thomasi_ (Table 14) and a greater numerical dominance by nauplii.

Table 15 shows the relationship between crustacean community structure and the physical-chemical characteristics of each region. Since very few (11) stations were sampled during the May cruise, only a limited set of interpretations can be derived from the data.

The significant correlation of PC1 station scores with alkalinity and conductivity initially suggests that crustacean community structure was affected by north-south environmental gradients because conductivity and alkalinity generally increase southward. However, as discussed below, factors other than alkalinity and conductivity probably were of greater importance in affecting crustacean community structure.

Group 1 mean sample depth was 15.0 m, indicating that this group of stations was part of the nearshore region of Lake Huron. Conductivity was high (217.2 μmhos/cm^2) at all five stations due to shoreline inputs and, for stations 55 and 66, inflow from Lake Michigan. Soluble reactive silica (1.2 mg/L) concentrations were relatively low while chlorophyll concentrations (3.3 mg/m^3) were high, a value second only to Group 4 in Georgian Bay. Thus, Group 1 appears to have been characterized by relatively high primary productivity which utilized much silica. The crustacean population was abundant (18,698/m^3) while the phytoplankton:zooplankton carbon ratio (12.5) was the lowest for all five regions, suggesting that grazing pressure was most intense at these stations. Despite this apparently high grazing pressure, chlorophyll

TABLE 13. Mean densities (#/m^3) of various crustacean taxa and carbon weights (mg carbon/m^3) for the May 1980 cruise.

Taxon	Region 1	2	3	4	5
Nauplii	12,135	6,959	8,168	5,565	5,785
Cyclops C1-C5	1,339	820	1,272	1,351	109
Cyclops bicuspidatus C6	521	131	327	776	31
Diaptomus C1-C5	993	445	362	268	341
Diaptomus ashlandi C6	1,336	832	883	375	434
Diaptomus minutus C6	926	350	246	94	31
Diaptomus sicilis C6	1,449	320	59	13	31
Total crustaceans	18,698	9,856	11,315	8,442	6,762
Total rotifers	5,750	1,108	3,825	3,631	7,713
Crustacean carbon	17.39	6.34	5.25	3.78	2.52
Rotifer carbon	0.03	0.01	0.02	0.02	0.03

TABLE 14. Percent composition of crustacean taxa for the May 1980 cruise.

Taxon	Region 1	2	3	4	5
Nauplii	64.9	70.6	72.2	65.9	85.6
Cyclops C1-C5	7.2	8.3	11.2	16.0	1.6
Cyclops bicuspidatus C6	2.8	1.3	2.9	9.2	0.5
Diaptomus C1-C5	5.3	4.5	3.2	3.2	5.0
Diaptomus ashlandi C6	7.1	8.4	7.8	4.4	6.4
Diaptomus minutus C6	5.0	3.6	2.2	1.1	0.5
Diaptomus sicilis C6	7.8	3.2	0.5	0.2	0.5

TABLE 15. Mean values of physical-chemical parameters[1] for the May 1980 cruise (crustaceans).

Parameter	Region 1	Region 2	Region 3	Region 4	Region 5
Sample depth (m)	15.0	25.0	25.0	13.0	11.0
Temperature (°C)	6.1	2.7	5.9	10.2	8.1
Secchi	-	-	5.0	6.5	-
pH	8.2	7.9	7.7	7.8	8.3
Alkalinity (mg/L)	84.0	74.5	56.0	48.0	86.0
Conductivity (μmhos/cm)	217.2	200.5	132.0	140.0	230.0
Nitrate (mg/L x 10^{-2})	27.1	28.3	28.6	24.0	58.0
Sol. react. silica (mg/L)	1.2	1.5	2.2	1.7	0.9
Kjeldahl nitrogen (mg/L x 10^{-2})	16.5	15.2	14.5	19.7	15.3
Total phosphorus (mg/L x 10^{-2})	0.6	0.5	0.6	0.6	-
Chlorophyll (mg/m^3)	3.3	1.4	1.8	2.4	4.9
Phyto. carbon/zoop. carbon	12.5	14.6	22.5	41.8	56.2

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

concentrations were high, further suggesting that primary productivity was high.

Group 2 consisted of two stations (53 and 66) located to the east of stations 55 and 63 in Group 1 in the Straits of Mackinac area. Conductivity was low (200.5 μmhos/cm^2) as waters in this region were diluted by the relatively soft waters from Lake Superior. Soluble reactive silica (1.5 mg/L) concentrations were moderately high while chlorophyll concentrations were low (1.4 mg/m^3) indicating a smaller phytoplankton bloom relative to that for stations 55 and 63 in Group 1. The crustacean community was similar to the Group 1 community although copepod standing stocks were lower. Group 2 was located in deeper (mean sample depth 25.0 m) and cooler (2.7°C versus 6.1°C) water than Group 1. Lower phytoplankton standing stocks may be related to the fact that Group 2 is more representative of the offshore region of Lake Huron. The phytoplankton:zooplankton carbon ratio (14.6) also was similar to that of Group 1, suggesting that zooplankton exerted similar grazing pressures on the phytoplankton communities in both regions. Thus, the lower concentration of chlorophyll in Group 2 than in Group 1 suggests that primary productivity also was lower in Group 2 than in Group 1.

Group 3, consisting of stations 71 and 78 in the North Channel, had low conductivity (132.0 μmhos/cm^2) and alkalinity (56.0 mg/L) due to input from Lake Superior. Chlorophyll concentrations were high (1.8 mg/m^3) as was soluble reactive silica (2.2 mg/L) indicating that the Lake Superior input supplemented silica in the North Channel. Crustacean standing stocks were moderately high (11,317/m^3). Nauplii and immature _Cyclops_ spp. copepodites were particularly abundant while _D. sicilis_ concentrations were low. Adult _Cyclops_ spp. accounted for a larger percentage (11.2%) of the crustacean community than in Groups 1, 2, and 5 (1.6% to 8.3%). The increased dominance of cyclopoids in Group 5 may be related to the introduction of these zooplankton into the North Channel through the St. Marys River, as in April. The phytoplankton:zooplankton carbon ratio was 22.5, suggesting that zooplankton exerted less grazing pressure on the algal community than in Groups 1 and 2.

Groups 4 and 5 each consisted of a single station under strong (but different) shoreline influences. This is evidenced by the high conductivity (230.0 μmhos/cm^2) for station 5 (Group 4) and low conductivity (140.0 mhos/cm^2) for station 125 (Group 5). For Bayfield Group 4, nitrate (0.580 mg/L) and chlorophyll (4.9 mg/m^3) concentrations were high while soluble reactive silica concentration was low (0.9 mg/L). The high concentration of chlorophyll and the low concentration of silica indicate that the phytoplankton community was relatively productive, depleting lacustrine silica reserves. Despite the fact that phytoplankton standing stocks were relatively large, crustacean concentrations were low (6,762/m^3), particularly for adult Diaptomus minutus, D. sicilis, and Cyclops bicuspidatus thomasi. Low concentrations of adults could be related to the characteristics of the riverine input from the Bayfield River. The phytoplankton:zooplankton carbon ratio was high (41.8), suggesting that grazing pressure on the phytoplankton community was relatively low. This may, in part, account for the relatively large chlorophyll concentration at this station.

Group 4 also was affected by shoreline inputs. Conductivity and alkalinity were low in comparison to Bayfield Group 4 because this region is located in a Precambrian drainage basin. Nitrate concentration was low (0.240 mg/L) while silica (1.7 mg/L) and chlorophyll concentrations (2.4 mg/m^3) were moderately high. Crustacean standing stock (8,442/m^3) was most similar to Group 2 with the major difference being the high numbers and dominance of Cyclops bicuspidatus thomasi in Group 4. Relatively low concentrations of crustaceans at station 125 despite high chlorophyll concentrations may be related to the characteristics of riverine inputs into Georgian Bay. The phytoplankton:zooplankton carbon ratio was 126.8 suggesting that grazing pressure on the phytoplankton community was very low in this region of the lake. As in Group 4, the relatively high concentration of chlorophyll may, in part, be related to low grazing pressure by the zooplankton community.

Principal Component Analysis: Rotifers

Eight rotifer taxa were used in the principal component of the 11-station May cruise data. PC1 accounted for 41.0% of the variance while PC2

accounted for an additional 25.8% of the variance. As in the April analysis, the first two principal components accounted for less of the total variance in the rotifer analysis than in the crustacean analysis.

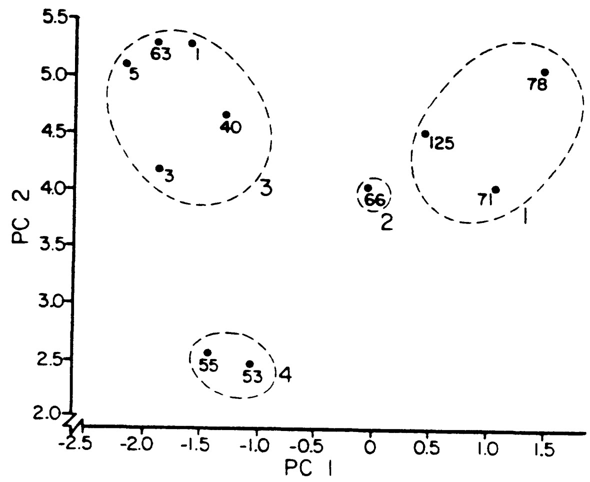
PC1 loadings ranged from -0.86 for *Notholca foliacea* to +0.21 for *Kellicottia longispina*. PC2 loadings ranged from -0.25 for *Polyarthra* spp. to +0.72 for *N. laurentiae*.

Plotting the 11 stations by their first and second principal component scores (Fig. 13) provided evidence of four groups. Group 1, with high PC1 and PC2 values, consisted of stations 71 and 78 in the North Channel and station 125 in Georgian Bay. Stations 1, 3, 5, and 40 in the main body of Lake Huron and station 63 offshore of Cheboygan formed Group 3. This group was characterized by high PC2 values and low PC1 values. Group 4, with low PC2 values, consisted of stations 53 and 55 in northwestern Lake Huron. Station 66, in the Straits of Mackinac, was intermediate to Groups 1 and 4 and was assigned to Group 2.

PC1 was significantly ($p<0.05$) correlated with chloride ($r = -0.82$), pH ($r = -0.86$), alkalinity ($r = -0.83$), conductivity ($r = -0.88$), ammonia ($r = +0.70$), and soluble reactive silica ($r = +0.93$). PC2 was not significantly correlated with any of the physical chemical parameters used in the analysis. PC1 was negatively correlated with the abundance of the hypolimnetic copepod *Diaptomus sicilis*.

Rotifer densities (Tables 16 and 17) ranged from 1,237/m^3 for Group 2 (Straits of Mackinac) to 6,843/m^3 for Group 3 (main body of Lake Huron). *Kellicottia longispina*, *Keratella quadrata*, and *Keratella cochlearis cochlearis* occurred in relatively high densities in Group 1 (Georgian Bay and North Channel) stations in comparison to their abundances in Group 3 and 4 stations. Conversely, *Notholca foliacea*, *Synchaeta* spp., and *N. squamula* occurred in greater densities and dominance in nearshore Group 3 stations. Group 3 differed from Group 4 in its greater abundance of rotifers and, in particular, *Notholca laurentiae*, *N. squamula*, and *Polyarthra* species.

Table 18 shows the physical-chemical characteristics for the four regions identified by the principal component analysis. Group 1, consisting of



a

b

FIG. 13. a) Principal component ordination of stations sampled for rotifers on 9-12 May 1980. b) Lake map with station groups derived from ordination analysis.

TABLE 16. Mean densities ($\#/m^3$) of various rotifer taxa and carbon weights (mg carbon/m^3) for the May 1980 cruise.

Taxon	Region 1	2	3	4
Kellicottia longispina	695	184	264	142
Keratella coch. coch.	873	88	209	42
K. quadrata	109	14	33	9
Notholca foliacea	3	22	630	122
N. laurentiae	390	213	378	8
N. squamula	986	368	3,984	772
Polyarthra spp.	28	7	29	12
Synchaeta spp.	635	338	1,313	492
Total rotifers	3,720	1,237	6,843	1,601
Total crustaceans	12,194	11,238	17,395	11,724
Rotifer carbon	0.01	0.01	0.03	0.01
Crustacean carbon	4.57	5.29	14.86	11.02

TABLE 17. Percent composition of various rotifer taxa for the May 1980 cruise.

Taxon	Region 1	2	3	4
Kellicottia longispina	18.7	14.9	3.9	8.9
Keratella coch. coch.	23.5	7.1	3.1	2.7
K. quadrata	2.9	1.2	0.5	0.6
Notholca foliacea	0.1	1.8	9.2	7.6
N. laurentiae	10.5	17.3	5.5	0.5
N. squamula	26.5	29.8	58.2	48.3
Polyarthra spp.	0.8	0.6	0.4	0.8
Synchaeta spp.	17.1	27.4	19.2	30.7

TABLE 18. Mean values of physical-chemical parameters[1] for the May 1980 cruise (rotifers).

Parameter	Region 1	Region 2	Region 3	Region 4
Sample depth (m)	21.0	25.0	13.0	23.0
Temperature (°C)	7.3	2.6	6.7	4.0
Secchi	5.7	0.0	0.0	0.0
pH	7.7	8.0	8.2	7.9
Alkalinity (mg/L)	53.3	73.0	84.6	79.5
Conductivity (μmhos/cm)	134.6	197.0	221.2	207.0
Nitrate (mg/L x 10^{-2})	27.1	28.3	33.8	26.3
Sol. react. silica (mg/L)	2.0	1.6	1.1	1.4
Kjeldahl nitrogen (mg/L x 10^{-2})	16.3	15.2	16.2	16.0
Total phosphorus (mg/L x 10^{-2})	0.6	0.5	0.5	0.5
Chlorophyll (mg/m^3)	2.0	1.1	4.0	1.6
Phyto. carbon/zoop. carbon	29.4	13.7	17.7	9.6

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

stations 71 and 78 in the North Channel and station 125 in Georgian Bay, was affected by riverine inputs. Conductivity was low (134.6 μmhos/cm^2) while the mean soluble reactive silica concentration (2.0 mg/L) was high. Phytoplankton standing stocks were moderately high (2.0 mg chlorophyll/m^3). The high phytoplankton:zooplankton carbon ratio (29.4) suggests that grazing pressure on the phytoplankton community was relatively low.

Group 3 stations were locate‿ in the nearshore region (mean sample depth 13.0 m) of Lake Huron. Rotifers were abundant (6,843/m^3) as were phytoplankton, with chlorophyll concentrations averaging 4.0 mg/m^3. Soluble reactive silica concentrations were low (1.1 mg/L), indicating utilization by diatoms. The phytoplankton:zooplankton carbon ratio was lower in Group 3 (17.7) than in Group 1. The greater standing stock of chlorophyll in Group 3 despite greater standing stocks of zooplankton than in Group 1 suggest that Group 3 algal productivity was higher than in Group 1.

Group 2 consisted of a single station (66) in the Straits of Mackinac. It was a region affected by outflow from Lake Superior as evidenced by its moderately low conductivity (197.0 μmhos/cm^2). Soluble reactive silica (1.6 mg/L) concentration was moderate and most similar to that observed in Group 1. Chlorophyll concentration (1.1 mg/m^3) also was low. Surface water temperature was only 2.6°C at this 70-m-deep station. Vertical instability of the water column as a result of spring warming may have resulted in much of the phytoplankon community being transported below the compensation depth thus limiting primary productivity. The phytoplankton:zooplankton carbon ratio was moderately high (13.7), suggesting that grazing pressure was not intense in this region. Thus, relatively low phytoplankton standing stocks may have been indicative of low algal productivity.

Group 4 consisted of stations 53 and 55 along the northwestern shore of Lake Huron. These stations apparently were in a mixing region of Lakes Huron and Superior waters, although conductivity (207.0 μmhos/cm^2) was higher than for Group 2. Water temperatures were low (4°C), indicating that the water column was still undergoing vertical mixing with spring heating. Soluble reactive silica concentrations were higher (1.4 mg/L) than in Group 2. Similarly, chlorophyll concentrations were greater (1.6 mg/m^3) despite a

slightly more abundant rotifer and crustacean community and a lower phytoplankton:zooplankton carbon ratio of 9.6. This suggests that algal productivity may have been slightly higher than in Group 2 where chlorophyll standing stocks were lower despite the higher carbon ratio (therefore less grazing). Shallower depths and higher temperatures probably were of importance in affecting greater plankton standing stocks in northwestern Lake Huron Group 4 in comparison to the Straits of Mackinac Group 2.

June Cruise

General Features

The third cruise was conducted between 28 May and 7 June. Thirty stations were sampled (Fig. 14). Surface water temperatures exceeded 9°C in the North Channel, the northern half of Georgian Bay, and along the southern shore of the main body of Lake Huron. Water temperatures were lower (<5°C) in southwestern Georgian Bay and in the offshore region of Lake Huron. Coldest waters (<3°C) were located in central Lake Huron where the thermal bar had not yet disappeared. Chlorophyll concentrations ranged from less than 1.1 mg/m^3 to more than 2.5 mg/m^3, with the highest values occurring in the nearshore region of Lake Huron south of the Bruce Peninsula, the North Channel, and the northern shore of Georgian Bay (Moll and Rockwell in prep).

Total zooplankton abundances (Fig. 15) ranged from 4,725/m^3 (station 63) to 75,886/m^3 (station 34). Crustaceans were more abundant than rotifers.

Fifteen species of crustaceans were observed over the 30-station grid (Fig. 14). Total crustacean abundances (Fig. 16) ranged from 3,825/m^3 (station 63) to 73,432/m^3 (station 34). The crustacean community was dominated by nauplii (Fig. 16) which attained maximum abundances along the southwestern shore of Lake Huron, station 5 near Bayfield in southeastern Lake Huron, and station 104 offshore of Collingwood in southern Georgian Bay. Immature Cyclops spp. were abundant in southwestern Lake Huron and at station 125 in Georgian Bay. Adult C. bicuspidatus thomasi attained highest densities in Georgian Bay, at stations in the vicinity of Saginaw Bay, and at Bayfield in southeastern Lake Huron. Immature Diaptomus spp. were abundant in southern

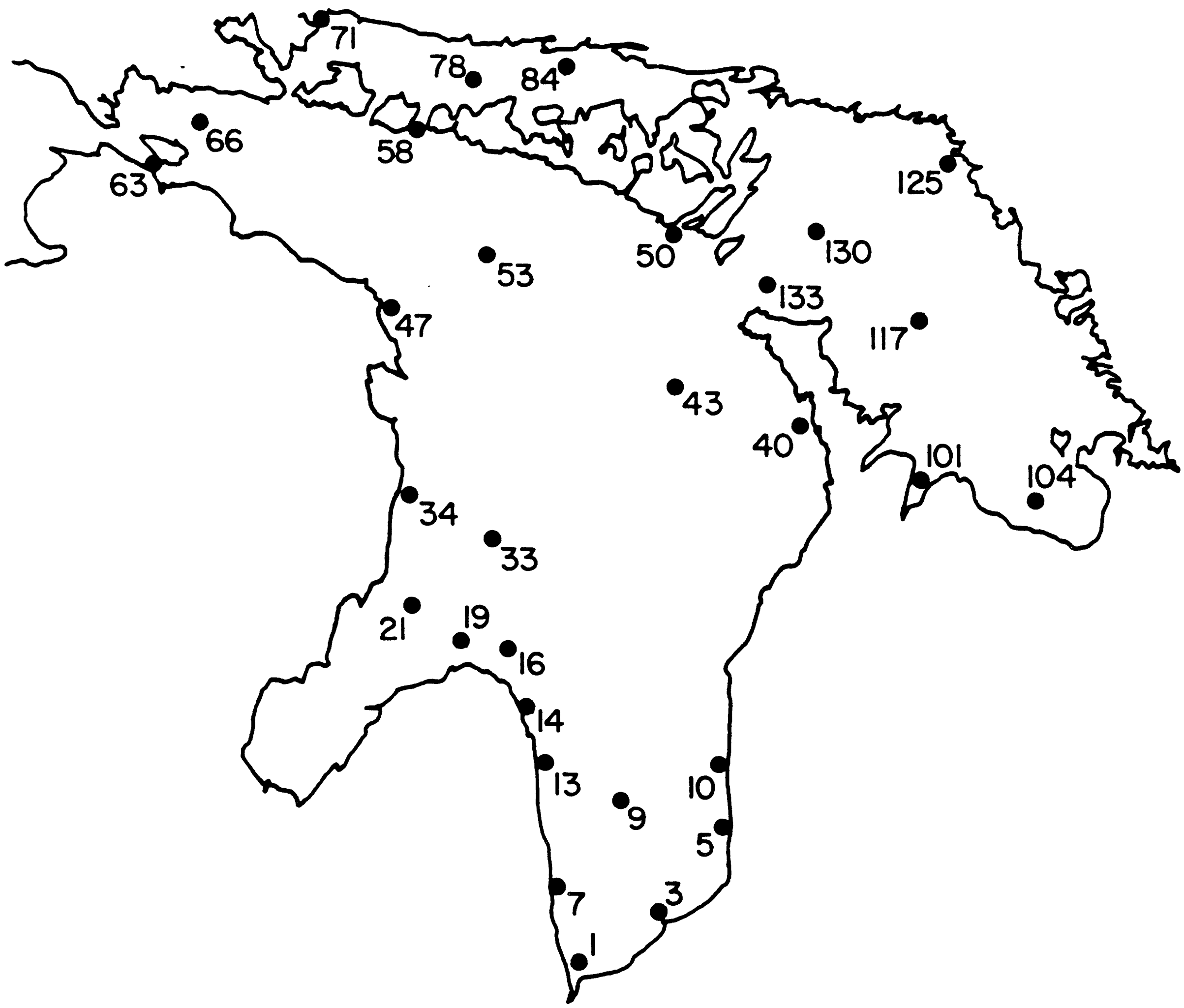


FIG. 14. Location of stations sampled on 28 May-7 June 1980.

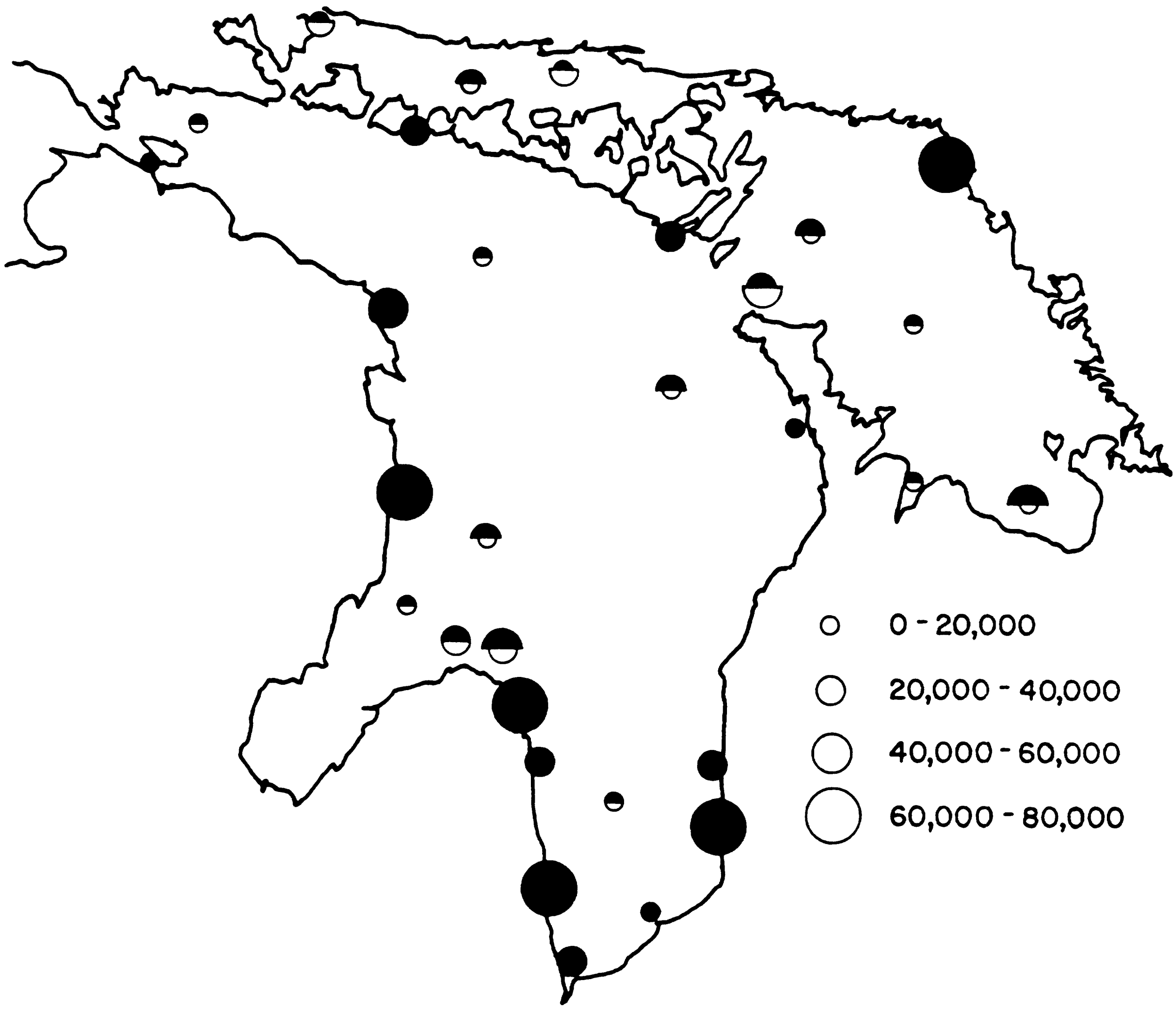


FIG. 15. Distribution (#/m^3) of total zooplankton collected on 28 May-7 June 1980. Black circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface.

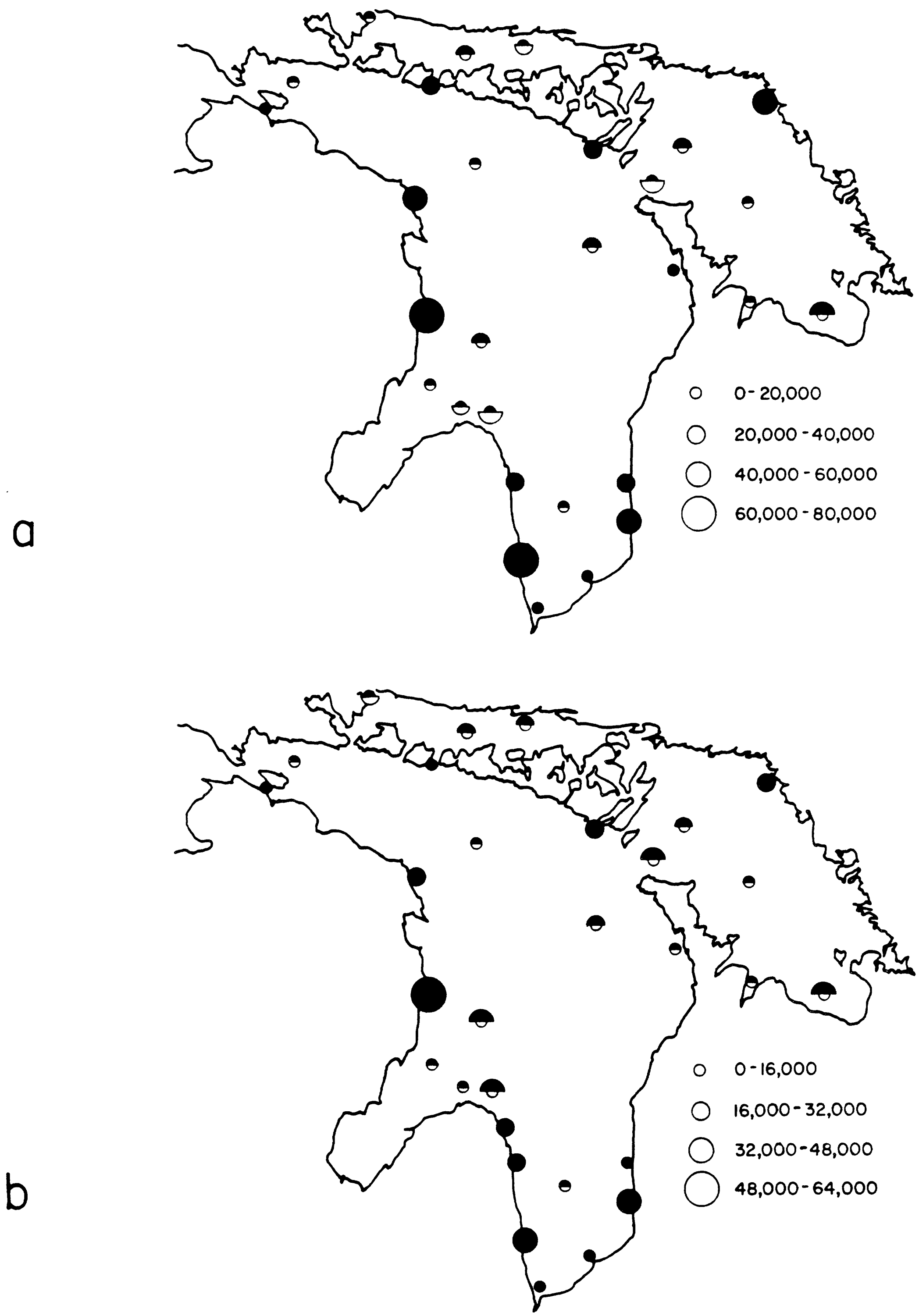
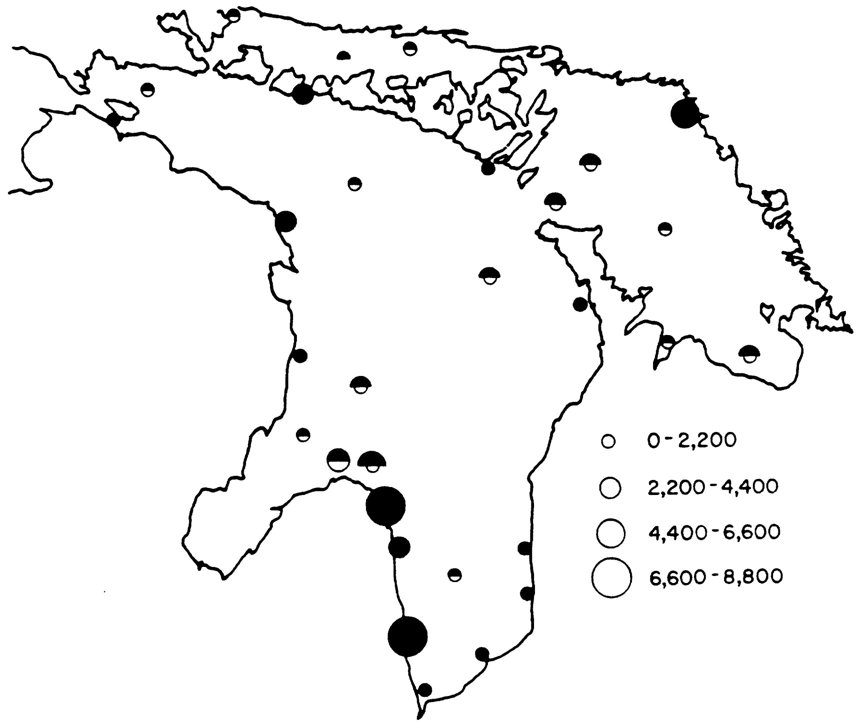


FIG. 16. Spatial distribution (#/m^3) of total crustaceans and major crustacean taxa collected 28 May-7 June 1980. Mixed circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom tc surface. a) Total crustaceans, b) copepod nauplii,



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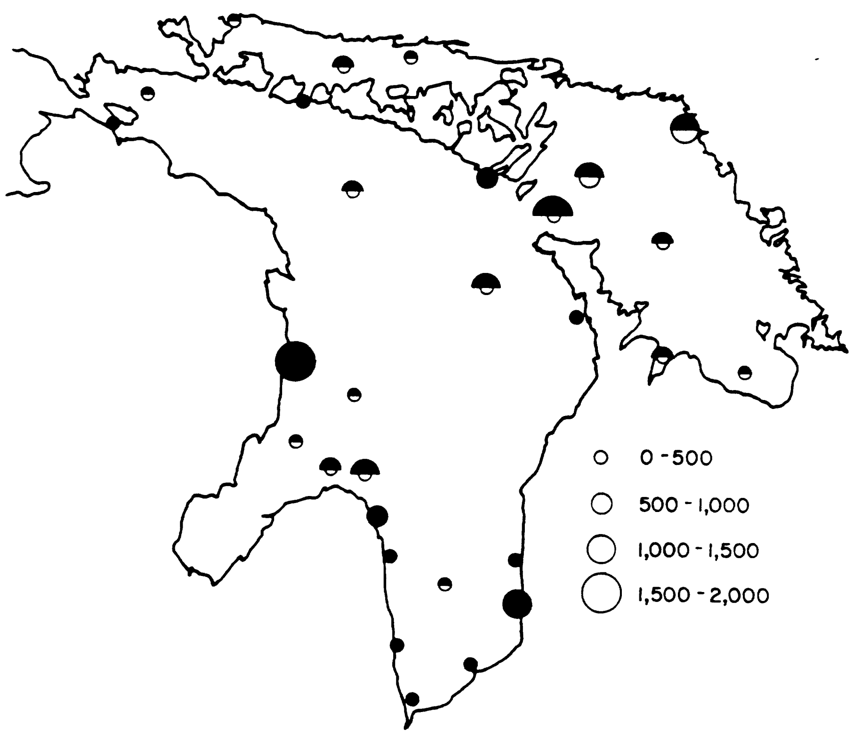
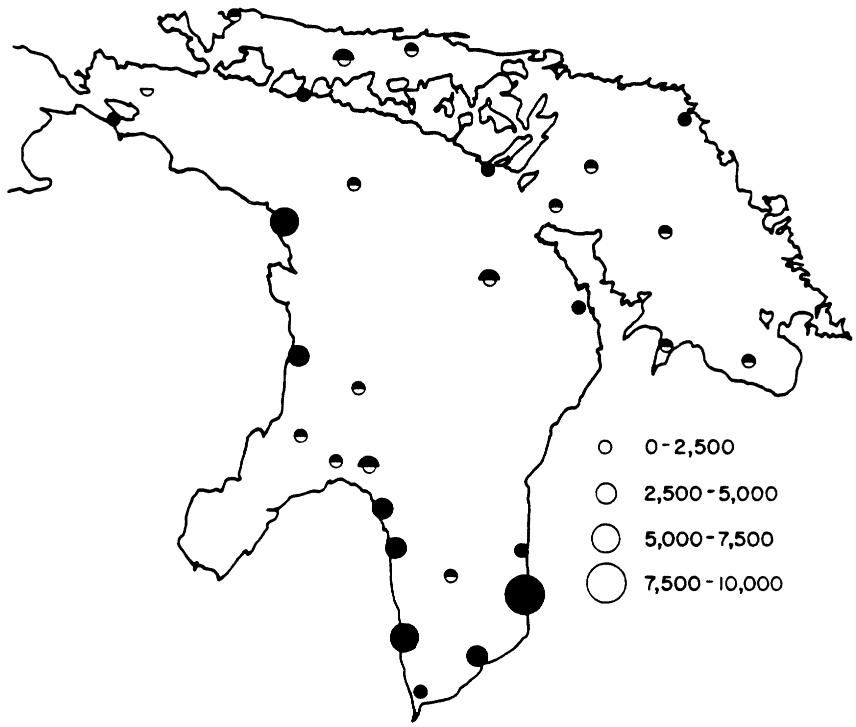


d

FIG. 16. Continued. c) *Cyclops* spp. C1-C5, d) *Cyclops bicuspidatus thomasi*,



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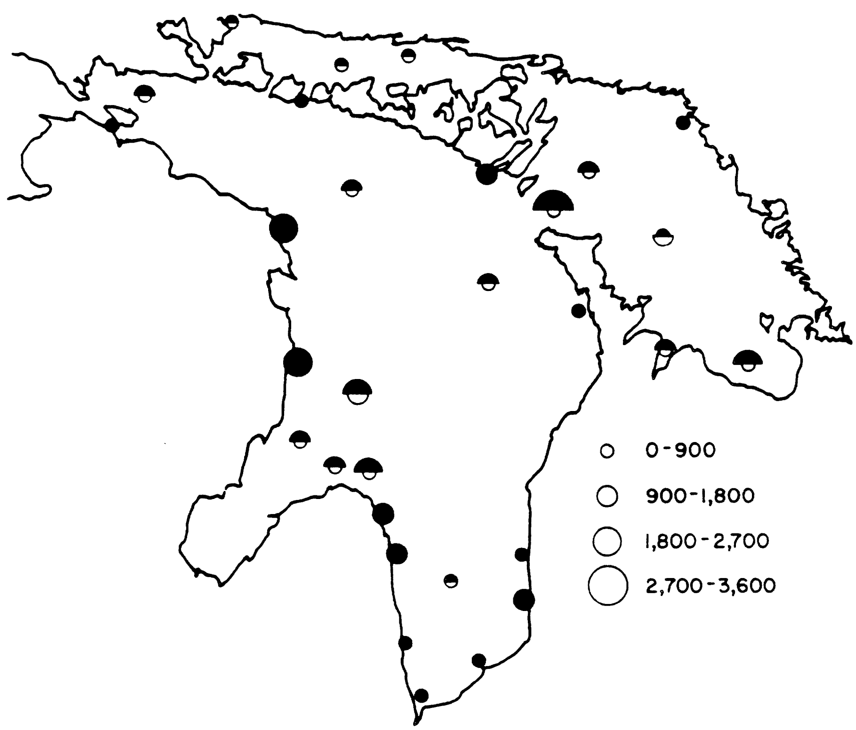

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FIG. 16. Continued. e) <u>Diaptomus</u> spp. C1-C5, f) <u>Diaptomus</u> <u>ashlandi</u>,

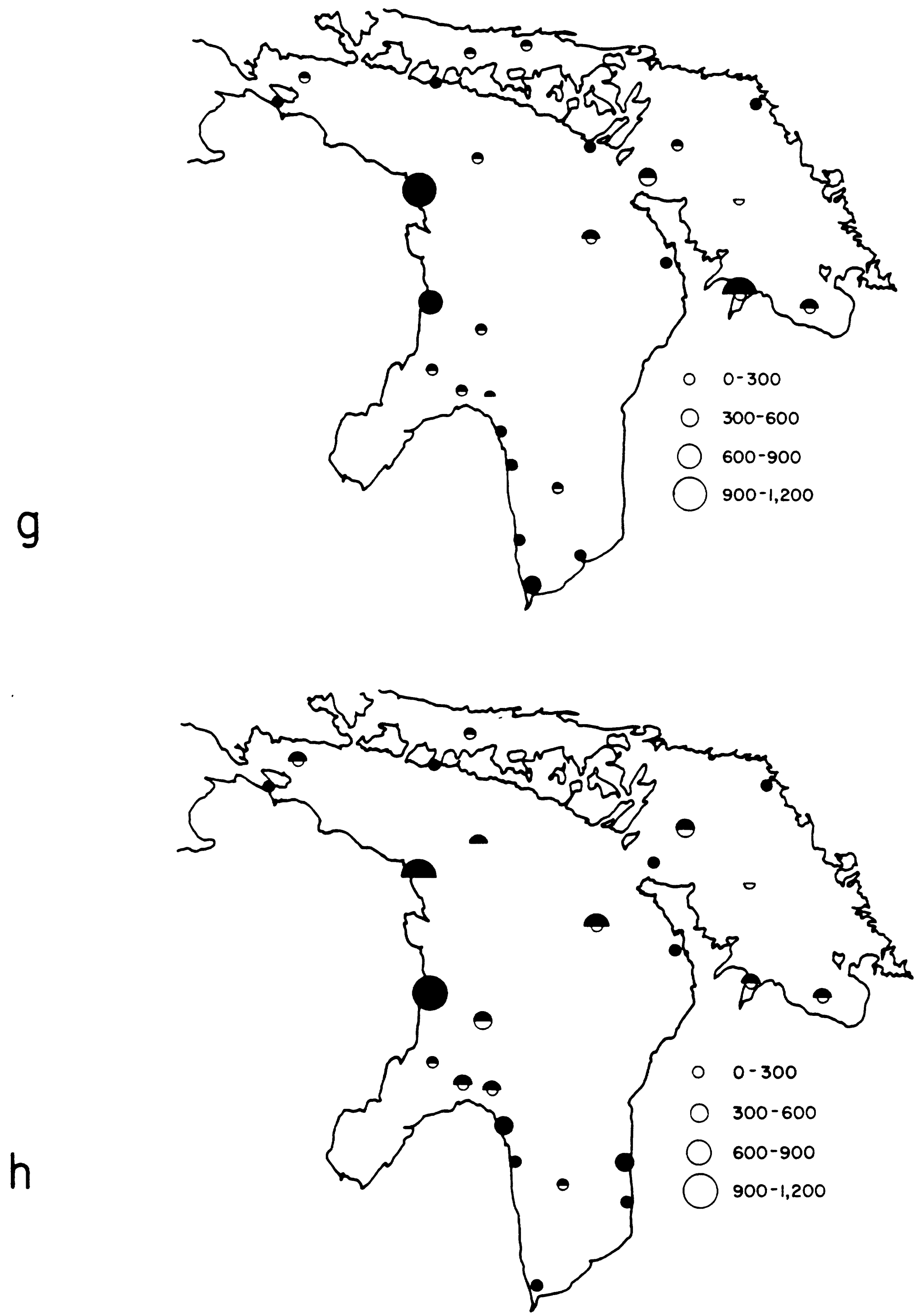


FIG. 16. Continued. g) Diaptomus minutus, h) Diaptomus sicilis,

i

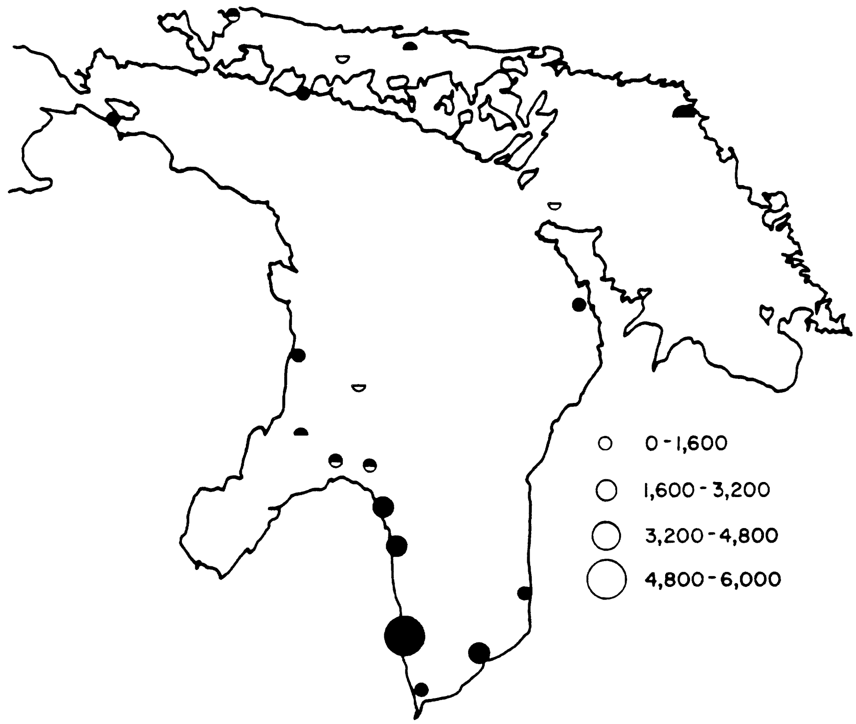


FIG. 16. Concluded. i) Bosmina longirostris.

Lake Huron and along the central western shore. D. ashlandi, D. minutus, and D. sicilis abundances were greatest along the central western shore of Lake Huron with areas of secondary highs in Georgian Bay for D. ashlandi, and D. minutus. Bosmina longirostris, the only abundant cladoceran, occurred in highest densities in southern Lake Huron.

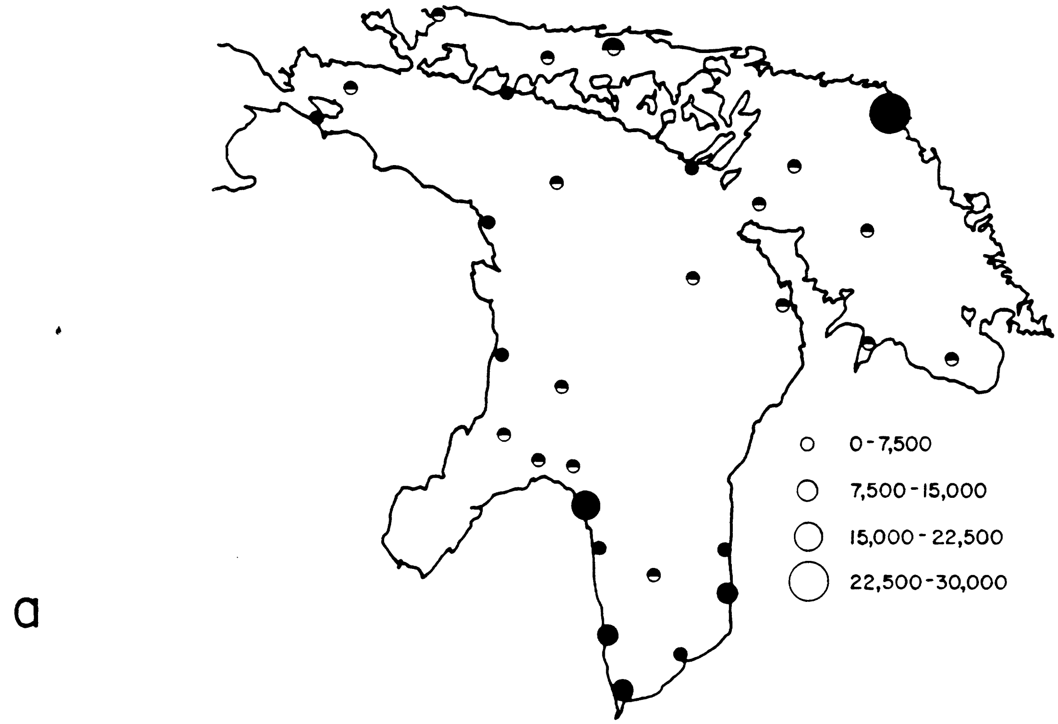
Twenty-two species of rotifers were collected. Rotifer densities (Fig. 17) ranged from $197/m^3$ (station 101) to $26,756/m^3$ (station 125). Keratella cochlearis cochlearis dominated occurring in highest densities (Fig. 17) in southwestern Lake Huron and at station 125 in Georgian Bay. Synchaeta spp. were of secondary dominance, occurring in maximum densities in southeastern Lake Huron. Kellicottia longispina reached highest densities at station 125 in Georgian Bay while Keratella quadrata was most abundant in southwestern Lake Huron. Notholca foliacea generally was more abundant in Lake Huron than in Georgian Bay and the North Channel. N. laurentiae was more abundant in the northern half of the survey grid.

Individual Taxa Correlations

As in previous cruises, crustacean abundances were not strongly correlated (Table 19) with the physical-chemical characteristics of their environment. Statistically significant ($p<0.05$) correlations were observed for Bosmina longirostris with soluble reactive silica; B. longirostris, D. ashlandi, and D. minutus abundances with total phosphorus; and immature Diaptomus spp. copepodite abundances were correlated with chlorophyll.

Crustacean abundances also were significantly ($p<0.05$) correlated (Table 19) with factors not directly related to algal productivity. Immature Diaptomus spp. and D. minutus abundances were significantly and positively correlated with pH, immature Cyclops spp. and B. longirostris with chloride, D. sicilis and D. ashlandi with alkalinity, and C. bicuspidatus thomasi with sodium. D. ashlandi abundances were negatively correlated with temperature while B. longirostris abundances were positively correlated with temperature.

Rotifer abundances were correlated (Table 19) with physical-chemical parameters either directly or indirectly related to algal productivity.



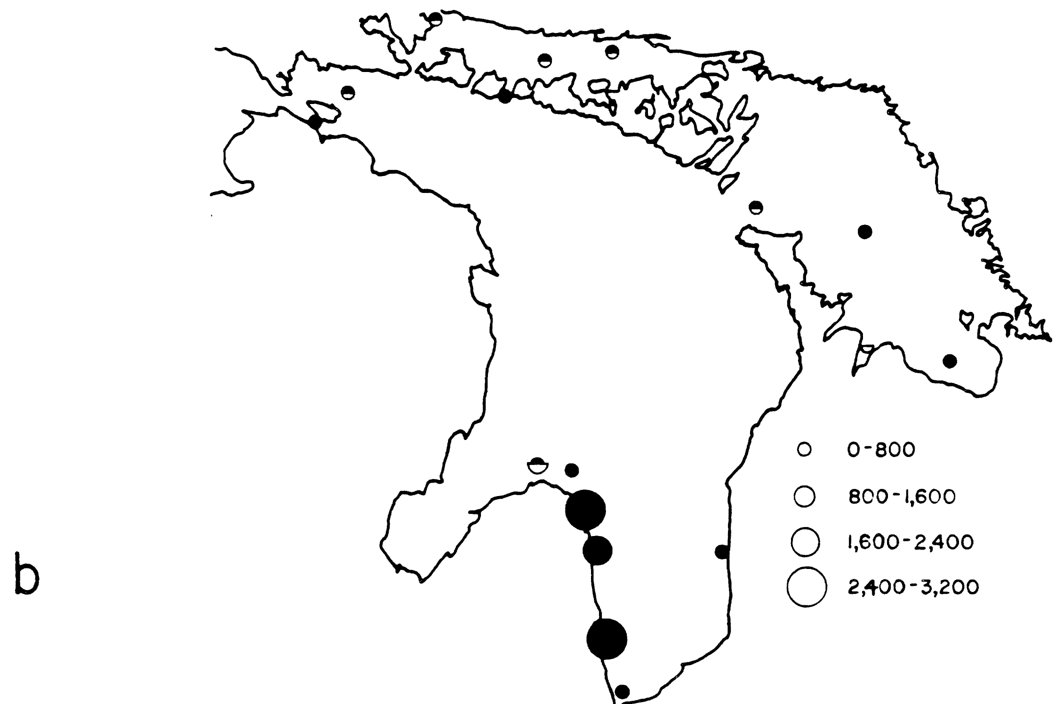
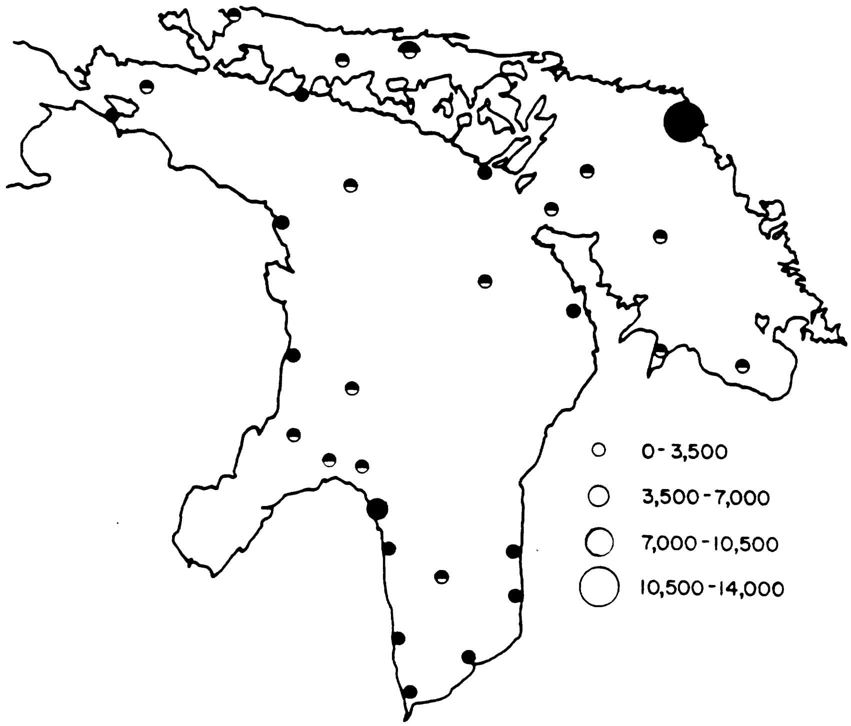


FIG. 17. Spatial distribution ($\#/m^3$) of total rotifers and major rotifer taxa collected on 28 May-7 June 1980. Black circles represent net haul from 2 m off bottom to surface. Mixed circles (white and black): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total rotifers, b) Asplanchna,

c



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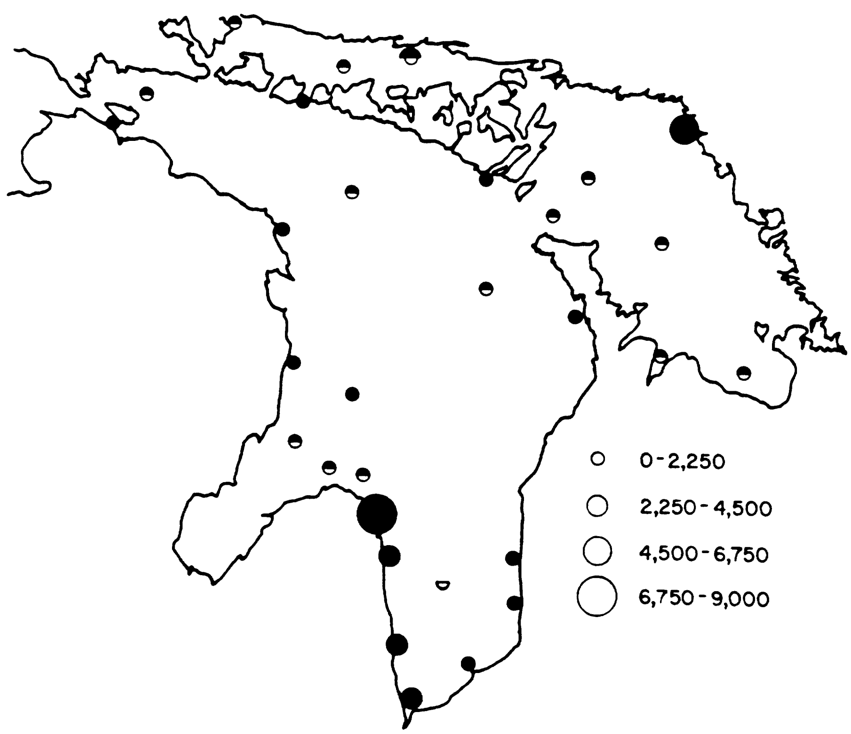
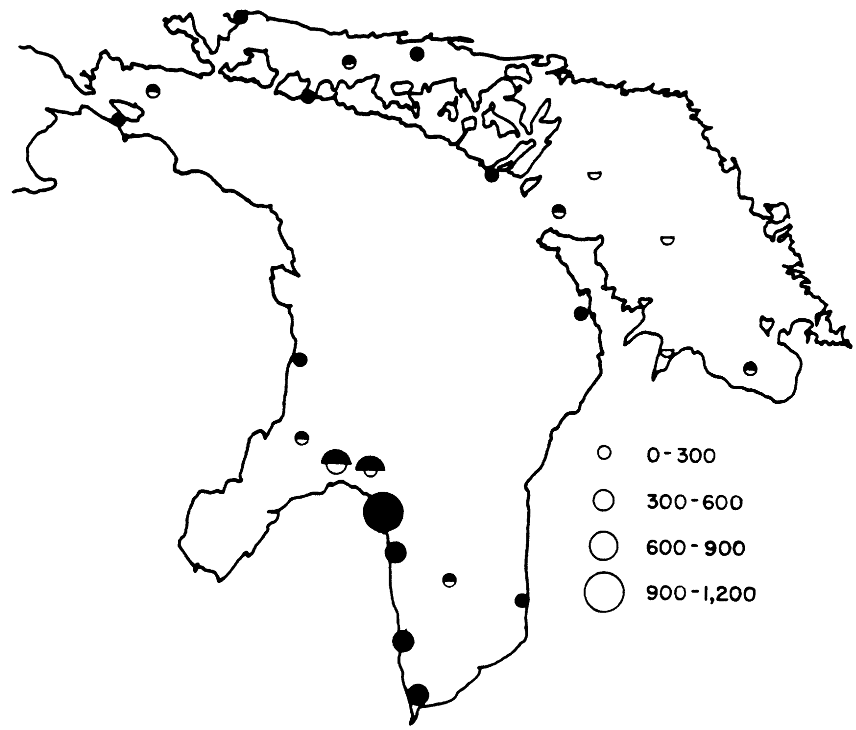


FIG. 17. Continued. c) Kellicottia longispina, d) Keratella cochlearis cochlearis,

e



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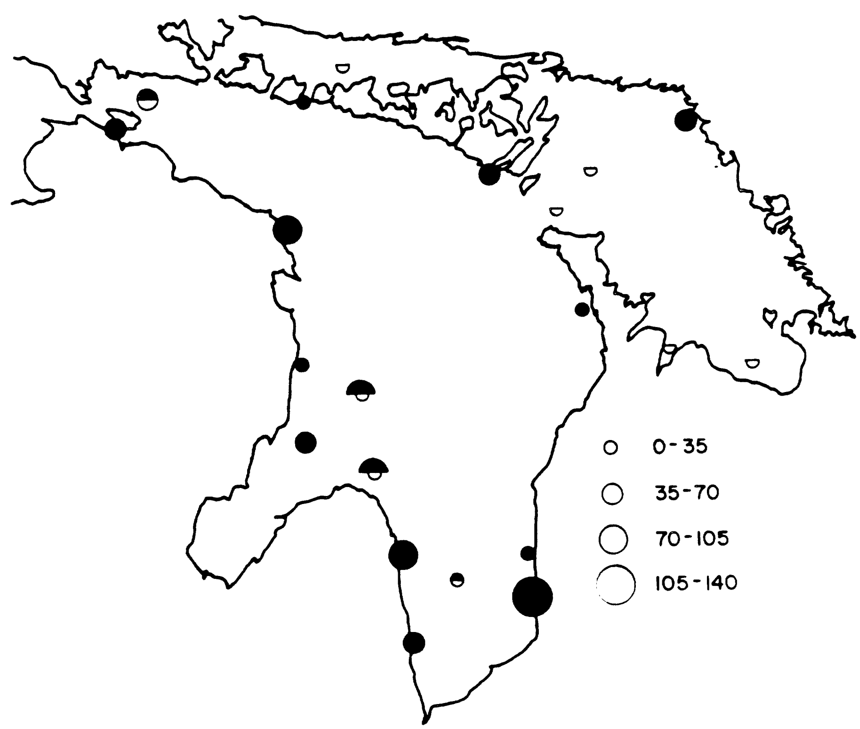
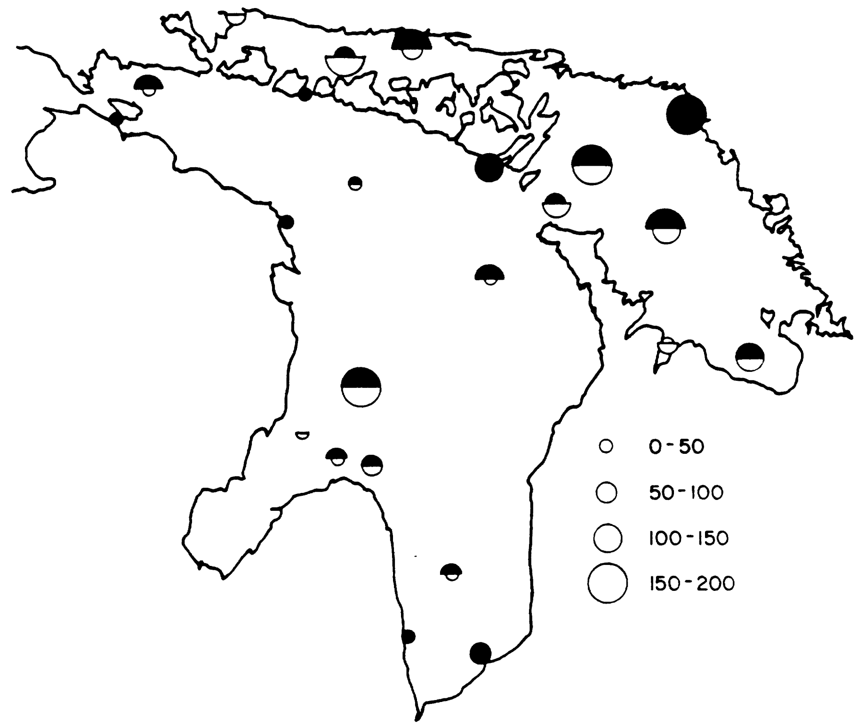


FIG. 17. Continued. e) Keratella quadrata, f) Notholca foliacea,



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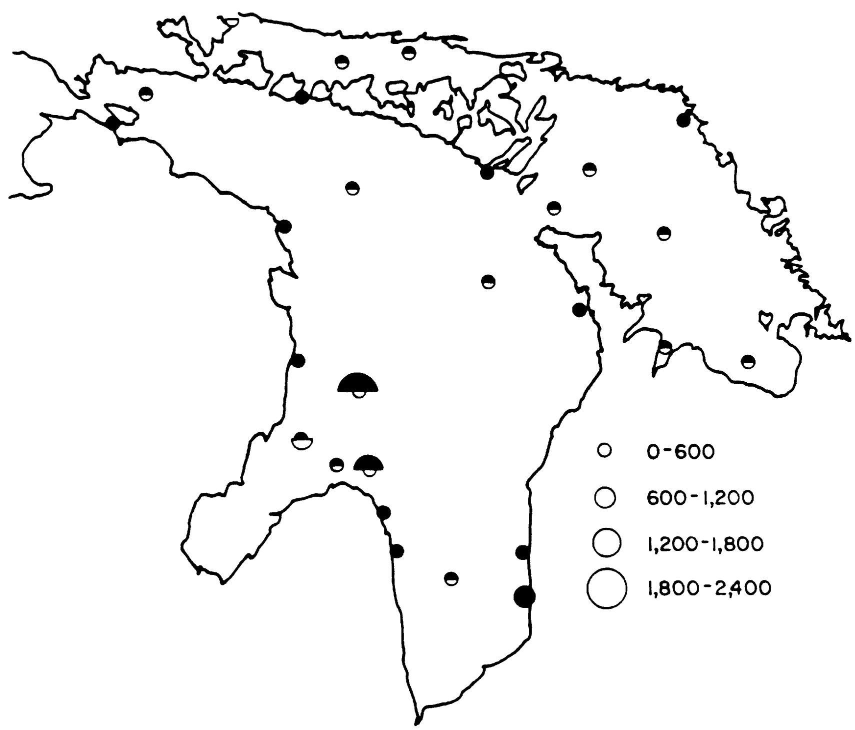

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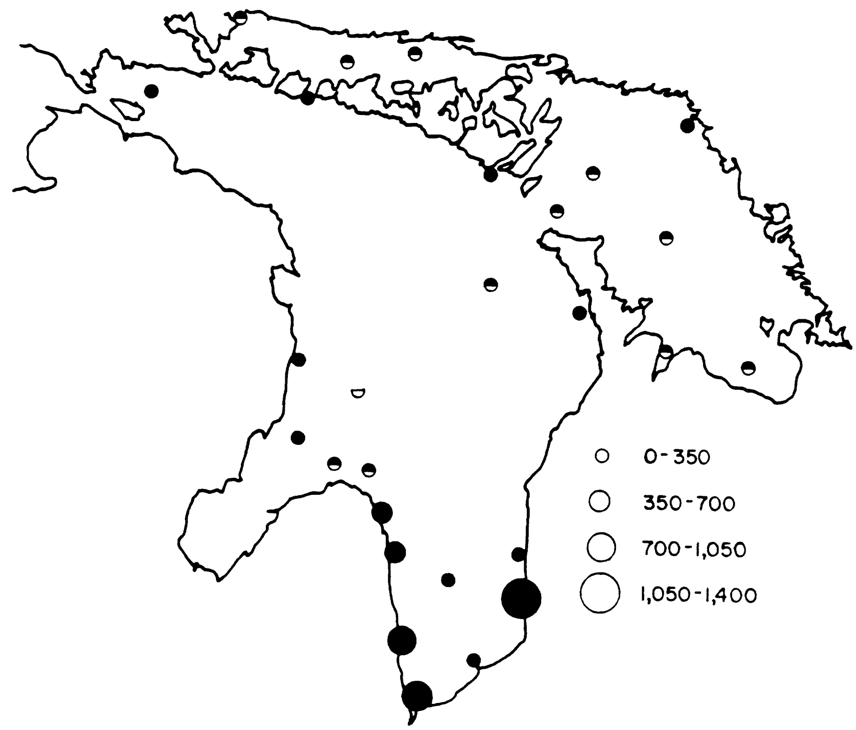
FIG. 17. Continued. g) Notholca laurentiae, h) Notholca squamula,

i



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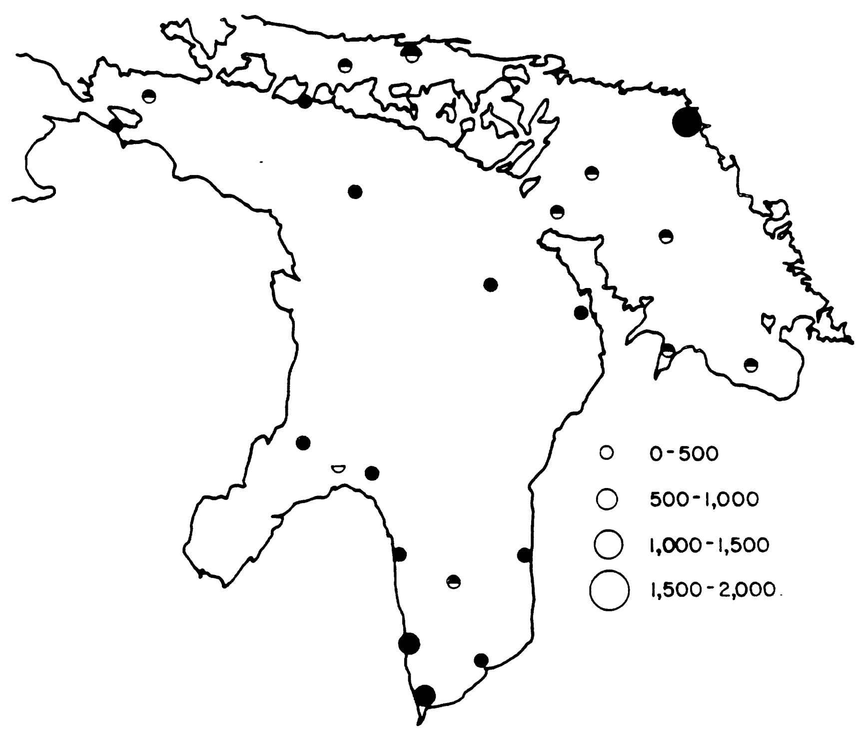


FIG. 17. Continued. i) Polyarthra dolichoptera, j) Polyarthra major,

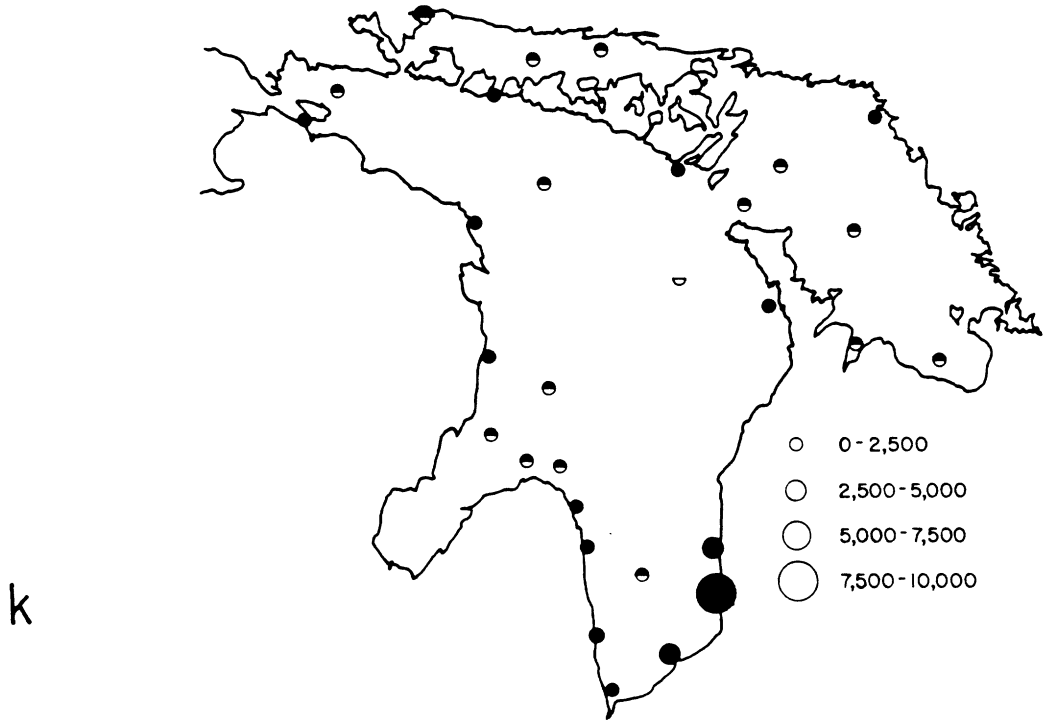


FIG. 17. Concluded. k) Synchaeta spp.

TABLE 19. Simple correlations among physical-chemical parameters and crustacean and rotifer densities (#/m^3) for the June 1980 cruise. * = significant correlation (α = .05).

	T	pH	Alk	Cond	NH_3	NO_3	Sol. SiO_2	K-N	Tot Phos	Chloro-phyll	Secchi	Chloride
Nauplii	+.20	+.10	+.12	+.07	-.07	-.17	-.17	+.03	-.11	-.09	+.26	+.[illegible]
Cyclops immature	+.19	+.13	+.01	+.12	-.22	-.15	-.34	+.04	+.15	-.09	-.25	+.38*
Cyclops bicuspidatus	+.01	+.03	-.04	-.07	-.10	-.22	-.01	-.12	-.15	-.19	+.51*	-.06
Diaptomus immature	+.28	+.45*	+.18	+.20	+.01	+.18	-.35	+.16	+.22	+.57*	-.28	+.32
Diaptomus ashlandi	-.44*	-.06	+.36*	+.23	-.33	-.17	-.12	-.31	-.39*	-.30	+.45	-.04
Diaptomus minutus	-.18	-.42*	-.17	-.04	-.11	-.22	+.04	+.09	-.42*	-.34	+.06	-.21
Diaptomus sicilis	-.35	+.03	+.38*	+.26	-.21	-.16	+.04	-.26	-.30	-.08	+.18	+.08
Bosmina longirostris	+.53*	+.17	+.02	+.10	-.06	+.21	-.43*	+.28	+.48*	+.06	-.30	+.37*
Total crustaceans	+.23	+.17	+.15	+.12	-.11	-.13	-.27	+.05	-.02	-.02	+.17	+.21
Asplanchna spp.	+.34	+.15	+.01	+.17	-.02	-.06	-.39*	+.20	+.33	-.02	-.18	+.42*
Kellicottia longispina	+.44*	-.14	-.45*	-.32	+.00	-.16	-.04	+.08	-.00	-.08	-.42	-.03
Keratella cochlearis	+.49*	-.03	-.29	-.07	+.04	-.11	-.20	+.30	+.23	+.02	-.30	+.27
Keratella crassa	+.32	-.23	-.49*	-.41*	+.02	-.17	+.20	+.01	-.10	+.05	-.30	-.19
Keratella quadrata	+.29	+.29	+.11	+.30	-.03	-.03	-.40*	+.34	+.38*	+.02	-.26	+.52*
Notholca foliacea	-.05	+.42*	+.30	+.28	-.25	-.06	-.13	-.08	-.15	+.48*	-.37	+.25
Notholca laurentiae	-.26	-.46*	-.27	-.31	-.05	-.06	+.24	-.13	-.20	-.22	+.37	-.21
Notholca squamula	-.34	+.23	+.13	+.12	-.19	-.06	-.02	-.20	-.17	+.18	-.13	+.09
Polyarthra dolichoptera	+.48*	+.26	+.03	+.16	+.06	+.20	-.48*	+.56*	+.32	+.44*	-.30	+.33
Polyarthra major	+.43*	-.30	-.36*	-.27	+.01	-.04	-.03	+.33	+.08	-.03	-.24	-.04
Synchaeta spp.	+.37*	+.48*	-.04	+.04	+.08	+.34	-.32	+.19	+.26	+.78*	-.53*	+.08
Total rotifers	+.55*	+.07	-.37*	-.18	+.03	-.03	-.18	+.26	+.18	+.31	-.43	+.13

Notholca foliacea, Polyarthra dolichoptera, and Synchaeta spp. abundances were significantly and positively correlated with chlorophyll while Asplanchna spp., P. dolichoptera, and Keratella quadrata abundances were negatively correlated with soluble reactive silica. P. dolichoptera abundances were significantly correlated with Kjeldahl nitrogen, and K. quadrata with total phosphorus.

Rotifer abundances also were significantly correlated (Table 19) with factors not directly related to phytoplankton productivity. Kellicottia longispina, Keratella cochlearis cochlearis, Polyarthra dolichoptera, P. major, and Synchaeta spp. abundances were positively correlated with temperature. Notholca laurentiae abundance was negatively correlated with pH while Notholca foliacea and Synchaeta spp. abundances were positively correlated with pH. P. major abundance was significantly and positively correlated with alkalinity while correlations were negative for K. longispina and Keratella crassa. Asplanchna spp. and Keratella quadrata abundances were positively correlated with chloride.

All statistically significant ($p<0.05$) crustacean intercorrelations (Table 20) were positive as in April and May. Most significant correlations were associated with nauplii. Rotifer intercorrelations (Table 20) were positive as in April and May. Crustacean abundances were significantly ($p<0.05$) correlated (Table 20) with the abundances of several rotifer taxa. With the exception of Polyarthra remata and Diaptomus ashlandi, these correlations were positive.

Principal Component Analysis: Crustaceans

Eight crustacean taxa were used in the analysis of the 30-station June data. PC1 accounted for 46.0% of the variance while PC2 accounted for an additional 23.6% of the variance. PC1 loadings ranged from -0.36 for Diaptomus sicilis to +0.90 for Bosmina longirostris. PC2 loadings ranged from +0.08 for immature Diaptomus spp. to +0.69 for D. sicilis.

Plotting the 30 stations by their PC1 and PC2 scores provided evidence of six major groupings (Fig. 18) of stations for the survey cruise. Group 1,

TABLE 20. Simple correlations among rotifer and crustacean densities ($\#/m^3$) for the June 1980 cruise. * = significant correlation (α = .05).

	Nauplii	Cyclops immature	Cyclops bicuspidatus	Diaptomus immature	Diaptomus ashlandi	Diaptomus minutus	Diaptomus sicilis	Bosmina longirostris	Total crustaceans	Asplanchna spp.	Kellicottia longispina	Keratella cochlearis	Keratella crassa	Keratella quadrata	Notholca foliacea	Notholca laurentiae	Notholca squamula	Polyarthra dolichoptera	Polyarthra major	Synchaeta spp.	Total rotifers
Nauplii	+1.00																				
Cyclops immature	+.37*	+1.00																			
Cyclops bicuspidatus	+.66*	+.24	+1.00																		
Diaptomus immature	+.54*	+.37*	+.15	+1.00																	
Diaptomus ashlandi	+.57*	+.18	+.59*	+.06	+1.00																
Diaptomus minutus	+.34	-.06	+.16	+.04	+.41	+1.00															
Diaptomus sicilis	+.42*	+.01	+.14	+.21	+.53*	+.62*	+1.00														
Bosmina longirostris	+.28	+.66*	+.03	+.41*	-.28	-.17	-.23	+1.00													
Total crustaceans	+.97*	+.53*	+.62*	+.65*	+.52*	+.29	+.38*	+.43*	+1.00												
Asplanchna spp.	+.16	+.73*	-.07	+.42*	-.09	-.21	-.11	+.65*	+.32	+1.00											
Kellicottia longispina	+.15	+.48*	+.23	+.04	-.23	-.06	-.20	+.43*	+.21	+.19	+1.00										
Keratella cochlearis	+.19	+.78*	+.08	+.24	-.16	-.16	-.20	+.58*	+.31	+.72*	+.74*	+1.00									
Keratella crassa	+.07	+.24	+.20	-.09	-.29	+.01	-.20	+.31	+.09	-.09	+.93*	+.49*	+1.00								
Keratella quadrata	+.14	+.74*	+.08	+.30	+.10	-.18	-.03	+.42*	+.28	+.75*	+.19	+.70*	-.13	+1.00							
Notholca foliacea	+.22	+.13	-.04	+.55*	+.08	+.01	+.16	+.05	+.27	-.04	+.04	-.04	+.02	+.03	+1.00						
Notholca laurentiae	+.09	+.05	+.25	-.28	+.12	-.05	-.20	-.02	+.04	-.25	+.30	+.02	+.45	-.31	-.14	+1.00					
Notholca squamula	+.17	+.19	+.12	+.10	+.40*	-.01	+.05	-.14	+.18	-.15	+.01	-.05	+.01	+.02	+.56*	+.35*	+1.00				
Polyarthra dolichoptera	+.28	+.32	+.02	+.67*	-.26	-.20	-.30	+.53*	+.38*	+.45*	+.20	+.45*	+.08	+.40	+.28	-.24	-.02	+1.00			
Polyarthra major	+.08	+.29	+.08	-.05	-.38*	+.01	-.32	+.51*	+.11	+.03	+.84*	+.53*	+.88*	-.02	-.04	+.33	-.11	+.33	+1.00		
Synchaeta spp.	+.12	-.11	+.03	+.60*	-.28	-.30	-.20	+.10	+.15	+.00	+.11	+.08	+.09	-.01	+.38*	-.24	+.09	+.69*	+.12	+1.00	
Total rotifers	+.25	+.55*	+.18	+.32	-.27	-.19	-.27	+.51*	+.31	+.36*	+.89*	+.83*	+.77*	+.38*	+.18	+.14	+.08	+.56*	+.77*	+.43*	+1.00

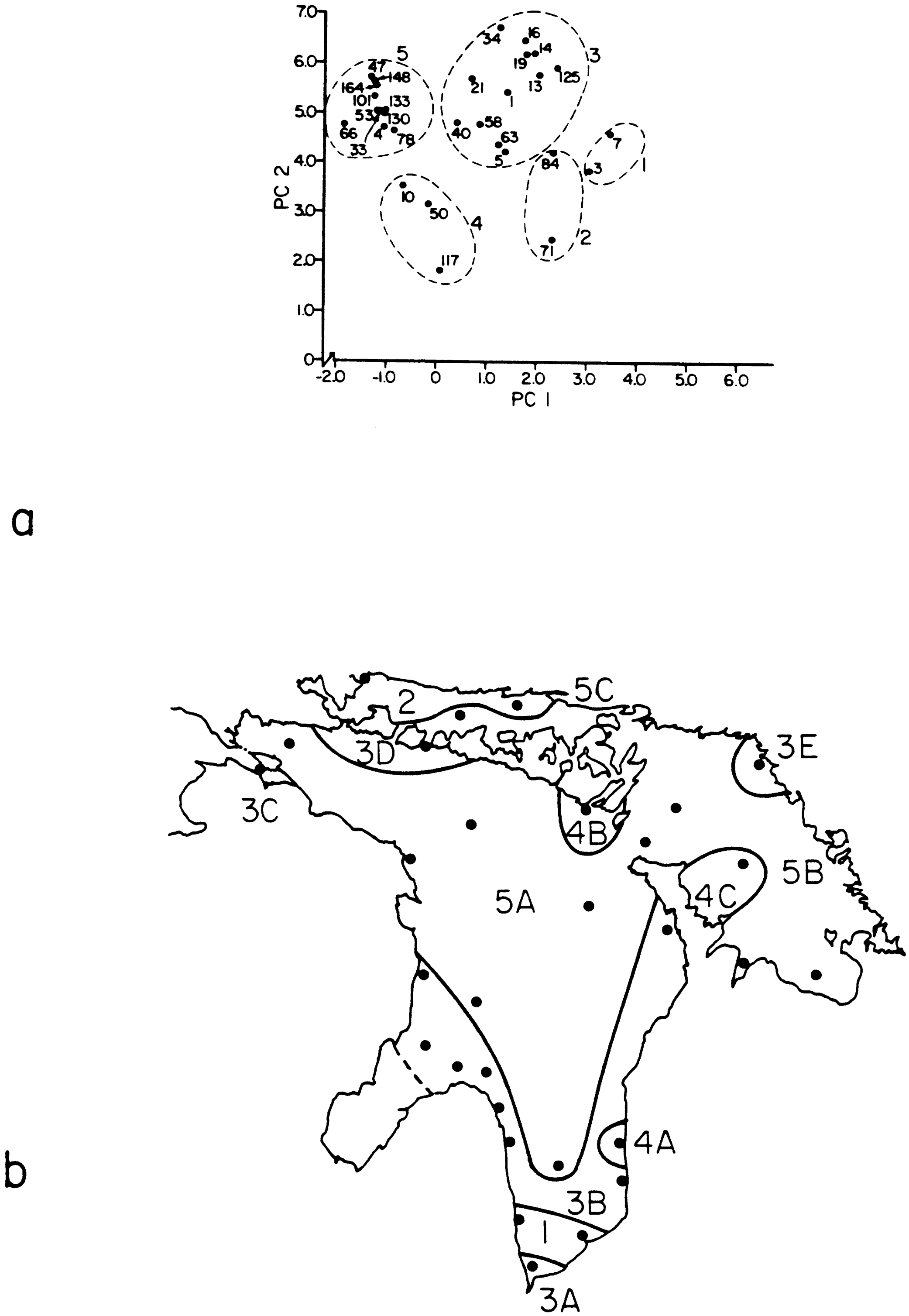


FIG. 18. a) Principal component ordination of stations sampled for crustaceans on 28 May-7 June 1980. b) Lake map with station groups derived from ordination analysis.

with high PC1 and intermediate PC2 scores, consisted of two stations (3 and 7) in southern Lake Huron in the Lexington-Kettle Point area. Group 2, with lower PC1 and PC2 scores, consisted of stations 71 and 84 in the North Channel. Group 3 consisted of 12 stations occupying most of southern Lake Huron and included station 63 near Cheboygan and station 125 in Georgian Bay. Group 4, with lower PC1 and PC2 values, consisted of three isolated stations; station 10 offshore of Goderich, station 50 offshore of South Bay in Manitoulin Island, and station 117 east of the Bruce Peninsula and in Georgian Bay. Group 5 consisted of 11 stations in the offshore waters of Lake Huron, Georgian Bay, and the North Channel. With the exception of station 47 offshore of Presque Ile, station depths exceeded 25 m.

PC1 station scores were significantly ($p<0.05$) correlated with temperature ($r = +0.77$), total phosphorus ($r = +0.59$), and total Kjeldahl nitrogen ($r = +0.37$), while PC2 scores were significantly correlated with chloride ($r = +0.41$). In addition, PC1 scores were significantly correlated with the abundance of several rotifer taxa. Positive correlations were observed with Kellicottia longispina ($r = +0.65$), Keratella cochlearis cochlearis ($r = +0.68$), K. quadrata ($r = +0.43$), Polyarthra dolichoptera ($r = +0.68$), and Synchaeta spp. ($r = +0.60$), while negative correlations were observed for Notholca squamula ($r = -0.48$). PC2 station scores were not significantly correlated with the abundance of any rotifer taxon.

Crustaceans ranged in abundance (Tables 21, 22) from $16,827/m^3$ in Group 2 (North Channel) to $37,882/m^3$ in Group 1 (southern Lake Huron). Groups 1, 2, and 3 with relatively large PC1 values were characterized by relatively large numbers and percent composition of Bosmina longirostris and, to a lesser extent, immature Cyclops spp. and Diaptomus species. Conversely, D. ashlandi and, to a lesser extent, D. sicilis were more abundant and occurred in greater dominance in Groups 4 and 5. Groups 2 and 4, with low PC2 values, had the lowest standing stocks of crustaceans and, in particular nauplii, immature Cyclops spp. and Diaptomus spp., and adult D. minutus. However, nauplii tended to account for a greater percentage of the crustacean population in Groups 2 and 4.

TABLE 21. Mean densities (#/m^3) of various crustacean taxa and carbon weights (mg carbon/m^3) for the June 1980 cruise.

Taxon	Region 1	2	3	4	5
Nauplii	24,159	13,056	22,514	16,797	22,231
Cyclops C1-C5	3,860	1,038	3,050	1,140	1,952
Cyclops bicuspidatus C6	243	303	705	580	718
Diaptomus C1-C5	4,843	1,834	2,940	1,605	1,998
Diaptomus ashlandi C6	231	138	1,038	870	1,601
Diaptomus minutus C6	93	113	194	44	426
Diaptomus sicilis C6	0	0	266	121	457
Bosmina longirostris	4,455	347	939	0	0
Total crustaceans	37,883	16,827	31,646	21,157	29,381
Total rotifers	5,991	7,811	7,786	2,494	1,371
Crustacean carbon	13.79	5.54	13.59	8.29	14.26
Rotifer carbon	0.03	0.03	0.03	0.01	0.01

TABLE 22. Percent composition of crustacean taxa for the June 1980 cruise.

Taxon	Region 1	2	3	4	5
Nauplii	63.8	77.6	71.1	79.4	75.7
Cyclops C1-C5	10.2	6.2	9.6	5.4	6.6
Cyclops bicuspidatus C6	0.6	1.8	2.2	2.7	2.4
Diaptomus C1-C5	12.8	10.9	9.3	7.6	6.8
Diaptomus ashlandi C6	0.6	0.8	3.3	4.1	5.4
Diaptomus minutus C6	0.2	0.7	0.6	0.2	1.4
Diaptomus sicilis C6	0.0	0.0	0.8	0.6	1.6
Bosmina longirostris	11.8	2.1	3.0	0.0	0.0

Table 23 shows the physical-chemical characteristics for the five regions. Temperature and total phosphorus were highest in Group 1 and decreased with increasing group number to reach a low in Group 5. The lowest conductivity was observed for Group 2 in the North Channel.

Group 1 in southern Lake Huron had the highest standing stocks of crustacean zooplankton including Bosmina longirostris. Soluble reactive silica concentrations were low (0.6 mg/L), indicating intense diatom utilization. Nevertheless, nitrate concentrations were high (0.521 mg/L), possibly because terrestrial input supplemented lacustrine sources depleted by the algal community. A large standing stock of phytoplankton (2.1 mg/m^3) supported a large crustacean population and, in particular, Bosmina longirostris. The hypolimnetic Diaptomus sicilis was rare or absent in these shallow, warm waters. The phytoplankton:zooplankton carbon ratio was relatively high (11.5) suggesting moderate grazing pressure.

Group 2, in the outflow from Lake Superior, was similar to Group 1 in some respects. Water temperatures (12.1°C) and phytoplankton standing stocks (2.1 mg chlorophyll/m^3) were moderately high. However, nitrate concentrations were low (0.269 mg/L). The phytoplankton:zooplankton carbon ratio was high (24.9), suggesting that zooplankton exerted relatively less grazing pressure on the phytoplankton community than in Group 1. The low concentration of chlorophyll in the outflow from Lake Superior despite apparently low grazing pressure suggests that algal productivity was low. This was also observed in April and May. Although crustacean standing stocks were low in Group 2 in comparison to chlorophyll concentrations, Bosmina longirostris was abundant as were rotifers. These densities may be related to the relatively high temperatures characteristic of Group 2 stations. The absence or rarity of Diaptomus sicilis may be related to the relatively high temperatures of Group 2 stations, although station depths were sufficiently deep (>25m) for cooler hypolimnetic water to persist and provide a thermal refuge.

Group 3 in the nearshore region of Lake Huron was similar to Group 1 in that chlorophyll concentrations were high (2.1 mg/m^3). However nitrate concentrations were lower (0.282 mg/L) and silica concentrations higher (1.2 mg/L) than in Group 1. Crustacean standing stocks were slightly lower than in

TABLE 23. Mean values of physical-chemical parameters[1] for the June 1980 cruise (crustaceans).

Parameter	Region				
	1	2	3	4	5
Sample depth (m)	10.5	25.0	15.7	20.7	24.7
Temperature (°C)	12.0	12.1	9.4	7.0	5.9
Secchi	-	4.5	6.8	11.0	8.2
pH	8.4	8.3	8.4	8.3	8.2
Alkalinity (mg/L)	83.0	49.5	77.5	75.0	76.4
Conductivity (μmhos/cm)	218.0	128.0	208.8	202.3	195.3
Nitrate (mg/L x 10^{-2})	52.1	26.9	28.2	28.1	28.3
Sol. react. silica (mg/L)	0.6	2.0	1.2	1.2	1.4
Kjeldahl nitrogen (mg/L x 10^{-2})	15.7	12.4	13.1	11.5	11.7
Total phosphorus (mg/L x 10^{-2})	0.6	0.5	0.5	0.4	0.4
Chlorophyll (mg/m^3)	2.4	2.1	2.1	1.8	1.8
Phyto. carbon/zoop. carbon	11.5	24.9	10.2	14.3	8.3

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

Group 1, particularly for the cladoceran *Bosmina longirostris*. Such differences may be related to the cooler waters characteristic of Group 3 stations. The phytoplankton:zooplankton carbon ratio (10.2) was similar to that observed for Group 1. Since chlorophyll concentrations were similar in Groups 1 and 3, this suggests that algal productivity was similar.

Group 4 had moderate soluble reactive silica (1.2 mg/L) and chlorophyll (1.8 mg/m^3) concentrations. Crustacean standing stocks (21,157/m^3) were moderate. The phytoplankton:zooplankton carbon ratio (14.3) was moderately high. Relatively lower water temperatures (7.0°C) for the deeper Group 4 stations (mean sample depth 20.7 m) may account for the absence (or rarity) of the epilimnetic cladoceran *Bosmina longirostris* and for the greater abundance and dominance of adult diaptomids, including the hypolimnetic *D. sicilis*.

Group 5 was located in the deepest regions of Lake Huron, the North Channel, and Georgian Bay. Water temperatures were low (5.9°C) while soluble reactive silica concentrations (1.4 mg/L) were moderately high. Moderate chlorophyll (1.8 mg/m^3) concentrations suggest that the algal community was productive. Crustacean standing stocks were abundant (29,381/m^3), suggesting higher grazing pressure than in Group 3. The phytoplankton:zooplankton carbon ratio (8.3) was low, lending support to this hypothesis. Group 5 stations apparently were more productive than Group 4 stations where chlorophyll concentrations were similar despite the fact that phytoplankton:zooplankton carbon ratios differed substantially between the two groups. Apparently higher algal productivity at Group 4 than at Group 5 stations may be due to a delayed spring algal bloom in these deeper regions of the survey grid. The absence of *Bosmina longirostris* and the greater abundance of adult diaptomids, including *D. sicilis*, probably was related to the lower water temperatures at Group 5 stations.

Principal Component Analysis: Rotifers

The first principal component accounted for 38.8% of the variance while PC2 accounted for an additional 16.6% of the variance. PC1 loadings ranged from -0.21 for *Notholca squamula* to +0.50 for *Asplanchna* species. Taxon PC2

loadings ranged from -0.09 for Notholca squamula to +0.65 for Polyarthra major.

Plotting the 30 stations by their PC1 and PC2 scores provided evidence of regional differences in rotifer community structure (Fig. 19). Group 1, with high PC1 values, consisted of four stations (1, 7, 13, and 14) in the nearshore region south of Saginaw Bay. Group 2 consisted of two stations (16, 17) south of Saginaw Bay, station 10 offshore of Goderich, and three stations (58, 71, and 78) in the North Channel area. Group 3, with low PC2 values, consisted of two isolated stations; station 34 was offshore of Harrisville and north of Saginaw Bay while station 5 was offshore of Bayfield on the southeastern shore of Lake Huron. Group 4 represented a single station (3) offshore of Kettle Point in southeastern Lake Huron, while Group 5 consisted of two stations, one in Georgian Bay (125) and one (84) in the eastern end of the North Channel. Group 6, also with low PC1 values, consisted of eight stations in the main basin of Lake Huron. Group 7 with low PC1 values consisted of seven deepwater stations in Georgian Bay (excluding station 125) and the waters east of Bruce Peninsula.

Station PC1 scores were significantly ($p<0.05$) correlated with temperature ($r = +0.67$), total Kjeldahl nitrogen ($r = +0.54$), and total phosphorus ($r = +0.49$), while PC2 was significantly correlated with pH ($r = -0.54$) and chlorophyll ($r = -0.31$). In addition, PC1 was significantly correlated with the abundance of Bosmina longirostris ($r = +0.68$) while PC2 was significantly correlated with the abundance of Diaptomus sicilis ($r = -0.37$).

Rotifers ranged in abundance (Tables 24 and 25) from lows of 1,064/m^3 (Group 7, Georgian Bay influence) and 1,098/m^3 (Group 6, offshore Lake Huron) to highs of 10,993/m^3 (Group 1, southwestern Lake Huron) to 16,970/m^3 (Group 5, eastern North Channel and western Georgian Bay). Asplanchna spp., Keratella cochlearis cochlearis, K. quadrata, and Polyarthra dolichoptera tended to occur in greater abundance and dominance in Groups 1 and 2 with high PC1 values than in Groups 6 and 7 with low PC1 values. Asplanchna spp., Notholca squamula, and Synchaeta spp. occurred in greater dominance in Groups

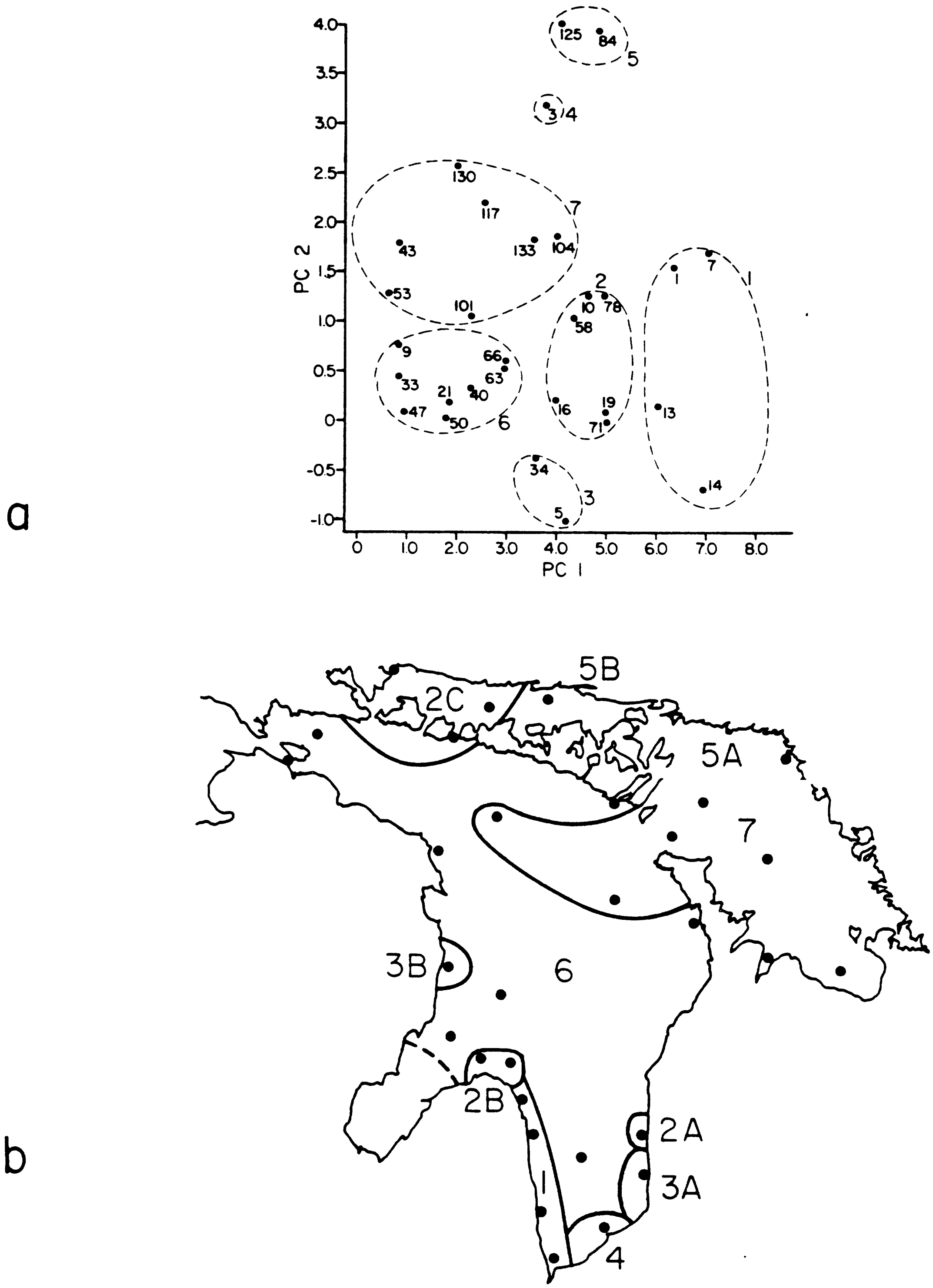


FIG. 19. a) Principal component ordination of stations sampled for rotifers on 28 May-7 June 1980. b) Lake map with station groups derived from ordination analysis.

TABLE 24. Mean densities (#/m^3) of various rotifer taxa and carbon weights (mg carbon/m^3) for the June 1980 cruise.

Taxon	Region						
	1	2	3	4	5	6	7
Asplanchna spp.	1,737	279	0	0	84	5	33
Kellicottia longispina	2,169	968	774	454	8,570	158	265
Keratella coch. coch.	4,141	1,077	359	524	4,609	101	220
K. crassa	0	0	0	0	123	0	0
K. quadrata	643	278	73	0	0	12	7
Notholca foliacea	29	19	73	0	22	52	0
N. laurentiae	9	52	0	70	185	54	102
N. squamula	184	328	483	0	383	559	311
Polyarthra dolichoptera	677	97	720	332	295	6	27
P. major	374	60	0	350	1,289	10	45
Synchaeta spp.	1,013	1,184	4,993	2,517	1,396	138	51
Total rotifers	11,279	4,385	7,476	4,369	16,958	1,098	1,064
Total crustaceans	39,535	26,667	60,628	15,601	32,329	18,823	31,121
Rotifer carbon	0.57	0.11	0.04	0.03	0.12	0.01	0.02
Crustacean carbon	15.59	11.09	23.91	6.42	10.33	9.64	14.16

TABLE 25. Percent composition of various rotifer taxa for the June 1980 cruise.

Taxon	Region						
	1	2	3	4	5	6	7
Asplanchna spp.	15.4	6.5	0.0	0.0	0.5	0.5	3.2
Kellicottia longispina	19.2	22.9	10.4	10.7	50.5	14.4	24.9
Keratella coch. coch.	30.4	25.1	4.8	12.3	27.2	9.2	20.7
K. crassa	0.0	0.0	0.0	0.0	0.7	0.0	0.0
K. quadrata	5.7	6.5	1.0	0.0	0.0	1.1	0.7
Notholca foliacea	0.3	0.5	1.0	0.0	0.1	4.8	0.0
N. laurentiae	0.1	0.8	0.0	1.6	1.1	5.0	9.7
N. squamula	1.6	7.2	6.5	0.0	2.3	50.9	29.2
Polyarthra dolichoptera	6.0	2.3	9.6	7.8	1.7	0.5	2.6
P. major	3.3	0.8	0.0	8.2	7.6	0.9	4.3
Synchaeta spp.	9.0	27.6	66.8	59.3	8.2	12.6	4.8

2 and 3 with low PC2 values while P. major tended to occur in greater abundance in Groups 4 and 5 with high PC2 values.

Table 26 shows the physical-chemical characteristics for the seven groups in Lake Huron identified on the basis of rotifer community structure. For the purposes of simplification, they can be considered as consisting of three basic types of regions, i.e., regions with comparatively low, moderate, or high rotifer standing stocks.

Group 1 had the second highest rotifer standing stocks and was located along the southwestern shore of Lake Huron. Water temperatures were moderately high (10.6°C). Soluble reactive silica concentrations were low (0.8 mg/L), indicating that the diatom community was or had been highly productive. Nitrate concentrations also were low (0.281 mg/L). Chlorophyll concentrations averaged 1.8 mg/m^3 and were low compared to values (2.0 to 3.3 mg/m^3) observed for Groups 2 to 6. Lower values may have been the result of heavy grazing pressure by relatively abundant rotifer (11,279/m^3) and crustacean (39,535/m^3) populations. The phytoplankton:zooplankton carbon ratio was low (7.0), further suggesting that grazing pressure was intense.

Group 5, located along the western side of the North Channel and the eastern side of Georgian Bay, had the greatest rotifer standing stocks (16,598/m^3). This region was affected by inflow from the numerous rivers draining the Canadian Shield and from Lake Superior (via the St. Marys River). Water temperatures were high (11.6°C) probably as a result of shallow station depths (mean sample depth = 19.0 m). Soluble reactive silica concentrations were high (1.8 mg/L) while chlorophyll concentrations (2.0 mg/m^3) were moderately high. The phytoplankton:zooplankton carbon ratio was 30.3 suggesting grazing pressure was moderate. The phytoplankton community apparently was less productive than in Group 1.

Three groups had moderately large rotifer populations. Group 2 consisted of a complex of six stations which were widely separated over the survey grid. However, because rotifer community structure was similar at all six stations, they were placed in a single group. Water temperatures were lower (9.8°C) than in Groups 1 and 5. Chlorophyll concentrations (2.2 mg/m^3) were moderately high as were rotifer standing stocks (4,297/m^3). The

TABLE 26. Mean values of physical-chemical parameters[1] for the June 1980 cruise (rotifers).

Parameter	Region						
	1	2	3	4	5	6	7
Sample depth (m)	11.5	20.2	9.5	12.0	19.0	22.8	25.0
Temperature (°C)	10.6	9.8	10.4	12.1	11.6	6.3	5.6
Secchi	6.5	5.2	9.5	-	5.0	6.7	9.7
pH	8.3	8.5	8.6	8.3	8.2	8.3	8.2
Alkalinity (mg/L)	77.5	68.7	81.5	86.0	55.0	79.8	77.3
Conductivity (μmhos/cm)	215.0	182.3	214.0	226.0	154.5	206.9	197.3
Nitrate (mg/L x 10^{-2})	28.1	29.6	31.6	76.5	24.5	27.3	27.7
Sol. react. silica (mg/L)	0.8	1.5	1.1	0.6	1.8	1.5	1.2
Kjeldahl nitrogen (mg/L x 10^{-2})	16.4	12.1	13.4	16.2	13.0	11.5	11.2
Total phosphorus (mg/L x 10^{-2})	0.5	0.5	0.5	0.7	0.4	0.4	0.4
Chlorophyll (mg/m^3)	1.8	2.2	3.0	3.3	2.1	2.0	1.5
Phyto. carbon/zoop. carbon	7.4	13.0	8.3	33.8	13.3	13.7	7.0

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

phytoplankton:zooplankton carbon ratio was 13.0, suggesting that grazing pressure was less intense than in Group 1 but similar to that observed in Group 5.

Group 3 also consisted of widely separated stations. Water temperatures were slightly higher (10.4°C) than in Group 2. Soluble reactive silica concentrations were lower (1.1 mg/L) while chlorophyll concentrations (3.6 mg/m^3) were slightly higher than in Group 2. The phytoplankton:zooplankton carbon ratio was low (8.3) suggesting that grazing pressure was relatively high for this group. Since chlorophyll concentrations were relatively high, phytoplankton productivity for this group also must have been relatively high. Rotifers were more abundant than in Group 2, possibly as a result of greater primary productivity. Competition with the crustacean community (60,628/m^3) or a lag between primary and rotifer production may account for the fact that the rotifer abundances were not greater in this region of high chlorophyll concentration.

Group 4 consisted of a single station (3) offshore of Kettle Point in southeastern Lake Huron. This station was affected by terrigenous inflows as evidenced from the relatively high conductivity (226.0 μmhos/cm^2) and nitrate concentration (0.765 mg/L) and a low soluble reactive silica concentration (0.6 mg/L). Chlorophyll concentrations were high (3.3 mg/m^3). Grazing pressure apparently was low as suggested by the high phytoplankton:zooplankton carbon ratio (33.8). Both rotifers (4,247/m^3) and crustaceans (15,601/m^3) occurred in relatively low to moderate densities. The reasons for these relatively low densities of zooplankton despite apparently high chlorophyll concentrations is unclear.

Two groups (6, 7) had low standing stocks of rotifers. Both regions were located in the more offshore waters of the survey grid. Water temperatures were low (6.3°C and 5.6°C respectively). Vertical mixing in these deep stations (mean sample depth >22 m) may have limited primary productivity by transporting phytoplankton below the compensation depth.

In Group 6, in the main body of Lake Huron, soluble reactive silica (2.0 mg/L) and nitrate (0.272 mg/L) concentrations were moderately high, suggesting that the algal community had not been highly productive for a long period of

time. Chlorophyll concentration averaged 2.0 mg/m^3. Rotifer standing stocks were lower (1,098/m^3) than in other regions of the lake, possibly because of the effects of lower temperatures on growth rates. The phytoplankton:zooplankton carbon ratio was moderately high (13.7), suggesting that grazing pressure was not intense.

Group 7 was in Georgian Bay and in its outflow waters. Soluble reactive silica concentrations (1.2 mg/L) were lower than in Group 6. Chlorophyll concentrations were the lowest (1.5 mg/m^3) of all seven groups. The phytoplankton:zooplankton carbon ratio was low (7.0) suggesting that grazing pressure was intense, which may account for the relatively low chlorophyll concentration. Groups 1, 3, and 7 all had similar phytoplankton:zooplankton carbon ratios although chlorophyll concentrations were greatest in Group 3. This suggests that the phytoplankton community was most productive in Group 3.

July Cruise

General Features

Thirty stations (Fig. 20) were sampled during the 18 to 29 July cruise. Considerable warming of surface waters occurred between the June and July cruises. Surface water temperatures ranged from less than 15°C in the center of Lake Huron to more than 21°C in eastern Saginaw Bay and southeastern Lake Huron. Soluble reactive silica concentrations were low (0.7 mg/L) in northern Georgian Bay, the Straits of Mackinac, and in the southern nearshore area of Lake Huron. Highest nitrate values (>0.28 mg/L) occurred in southern Lake Huron with low values in the northern inshore region of Georgian Bay and the Straits of Mackinac. Chlorophyll values were lower than during the preceding cruise with highest values (>2.0 mg/m^3) in the outflow from the St. Marys River and central Lake Huron with a secondary high in southeastern Lake Huron (Moll and Rockwell in prep).

Total zooplankton (Fig. 21) ranged in abundance from 24,443/m^3 (station 9) to 253,886/m^3 (station 71). Crustaceans were more abundant than rotifers.

Crustacean zooplankton densities (Table 1) averaged 75,604/m^3, a value twice that of the June cruise and more than five times the May cruise mean

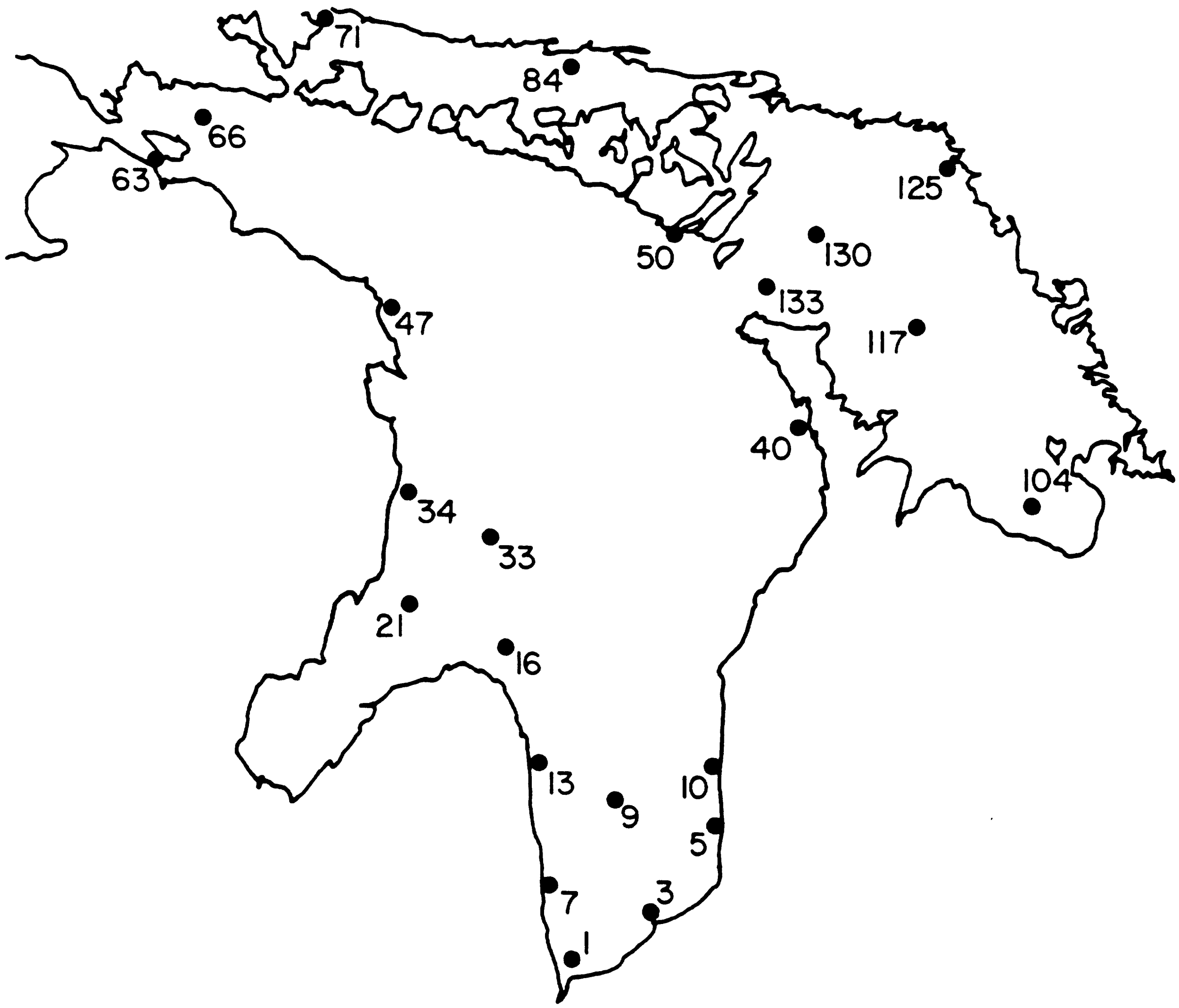


FIG. 20. Location of stations sampled on 18-29 July 1980.

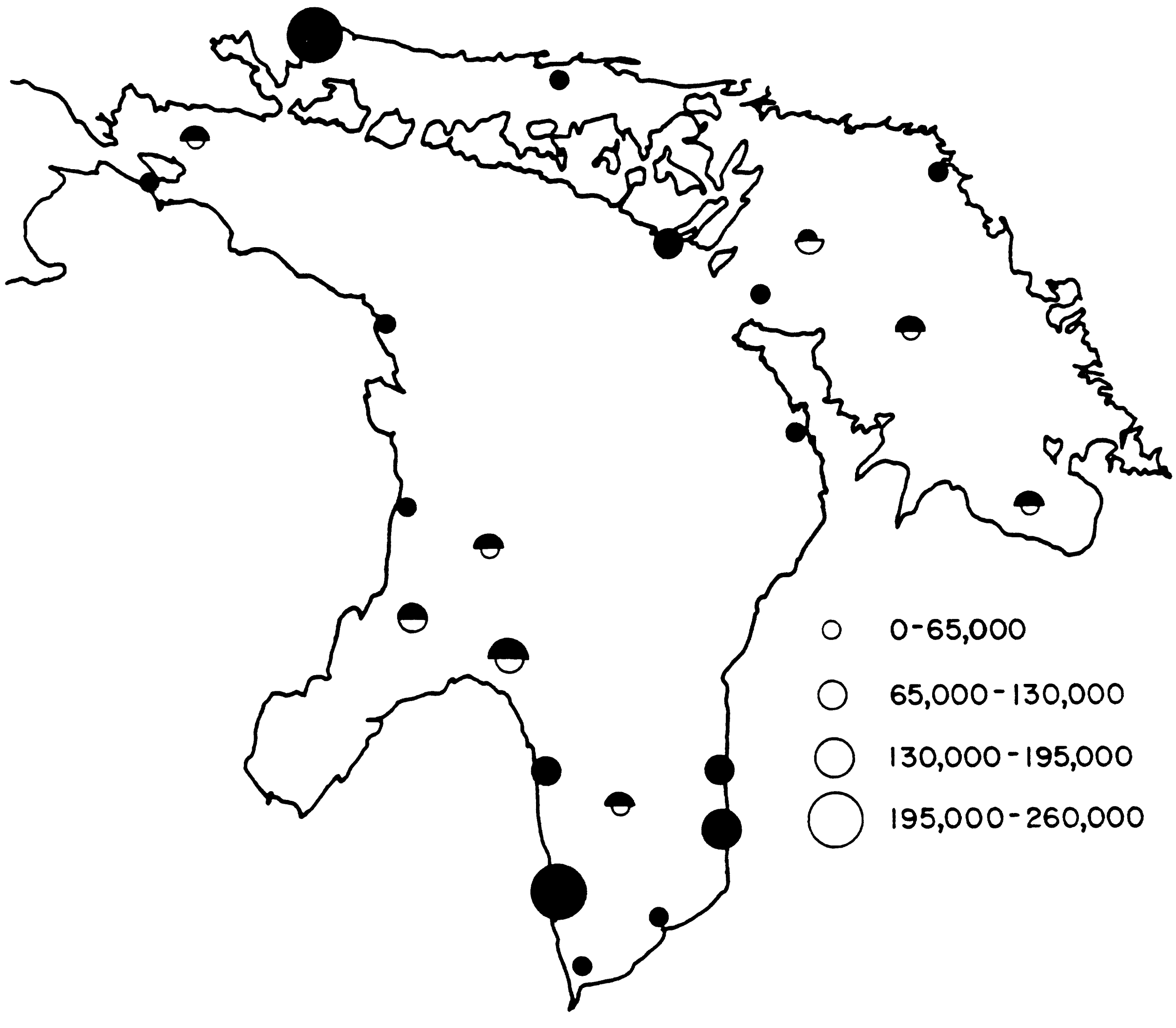
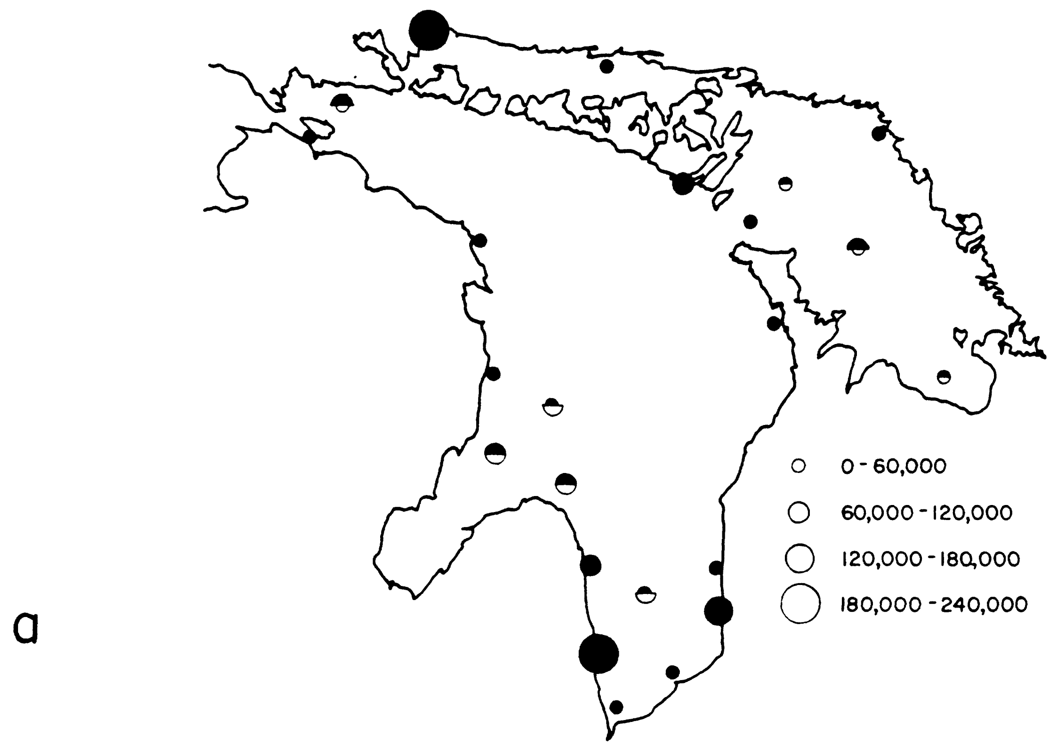


FIG. 21. Distribution (#/m^3) of total zooplankton collected on 18-29 July 1980. Black circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface.

concentration. Densities (Fig. 22) ranged from 21,532/m^3 (station 34) to slightly more than 240,000/m^3 (stations 7 and 71). Nauplii, while approximately as abundant (mean density 21,591/m^3) as during the June cruise, accounted for a smaller percentage of the total crustacean zooplankton. Areas of high concentration (Fig. 22) were the St. Marys River and southeastern Lake Huron. Immature Cyclops spp. copepodites occurred in high concentrations in the St. Marys outflow, southwestern Lake Huron, and outside of the Saginaw Bay region. Immature Diaptomus spp. copepodites also were most abundant in the outflow from the St. Marys River. Both immature Cyclops spp. and Diaptomus spp. copepodites were considerably more abundant (means of 14,442/m^3 and 15,455/m^3 respectively) than during previous cruises. In addition, these immature copepodites accounted for a larger percentage (19.1% and 20.4% respectively) of the crustacean zooplankton.

Cladocerans were more abundant and accounted for a greater percentage of the crustacean zooplankton than during earlier cruises (Table 1). In addition, a greater number of species was observed. Bosmina longirostris was the most abundant cladoceran, with greatest abundance in the outflow from the St. Marys River and in southwestern Lake Huron. Eubosmina coregoni abundances were greatest in southwestern Lake Huron while Daphnia galeata mendotae and D. retrocurva were most abundant in southern Lake Huron.

Rotifer densities (mean 14,993/m^3) were greater (Table 2) than during the preceding cruises (Fig. 23), ranging from 4,036/m^3 (station 125) to 37,341/m^3 (station 34). The numerically dominant species was Keratella cochlearis cochlearis which occurred in highest densities in the vicinity of Saginaw Bay (Fig. 23), station 34 offshore of Harrisville and north of Saginaw Bay, the St. Marys River, and in northern Georgian Bay. Conochilus unicornis also was a major component of the rotifer population, with areas of maximum abundance along the southeastern shore of Lake Huron, southeastern Saginaw Bay, and Georgian Bay. Kellicottia longispina was the third most abundant species, occurring in greatest densities in the outflow from the St. Marys River and station 34 north of Saginaw Bay. Synchaeta spp. and Gastropus stylifer each accounted for an average of more than 5% of the rotifer population. Trichocerca multicrinis, a species considered an indicator of eutrophic



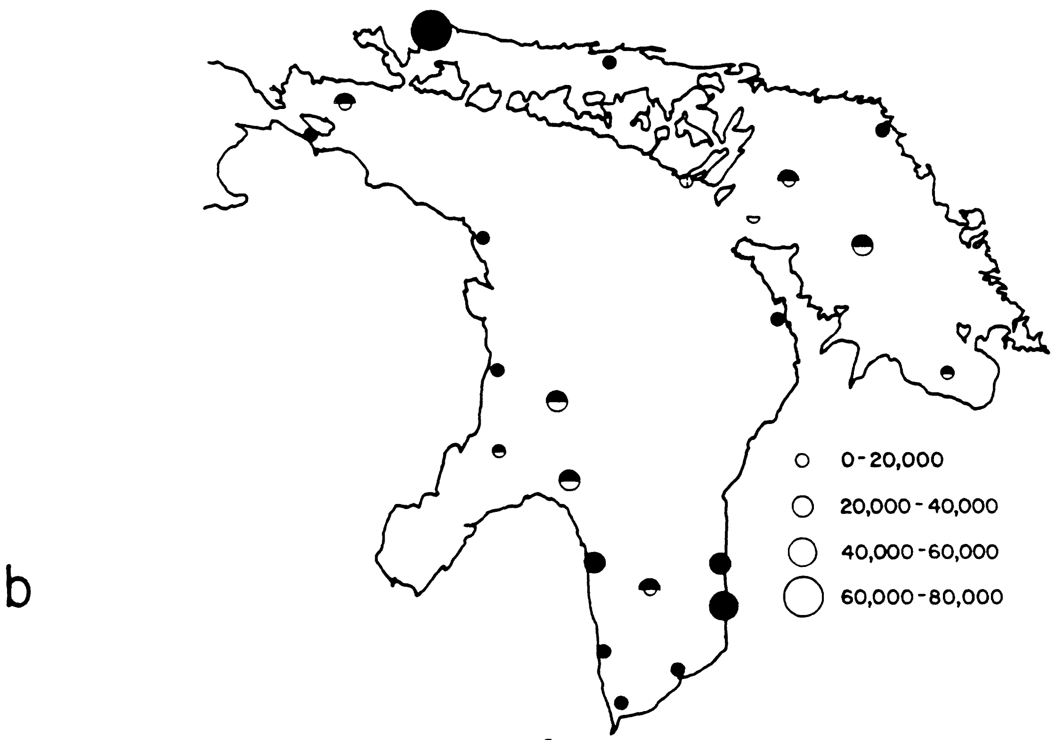
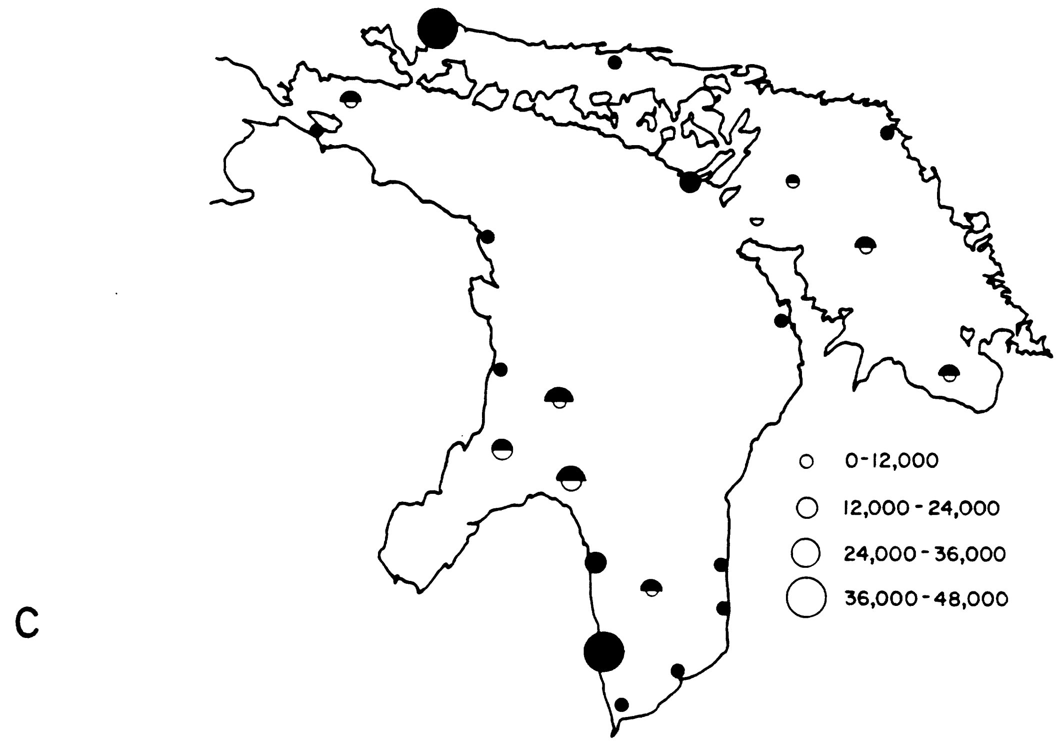


FIG. 22. Spatial distribution (#/m^3) of total crustaceans and major crustacean taxa collected 18-29 July 1980. Mixed circles represent net hauls from 2 m off bottom to surface. Mixed circles (black and white): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total crustaceans, b) copepod nauplii,



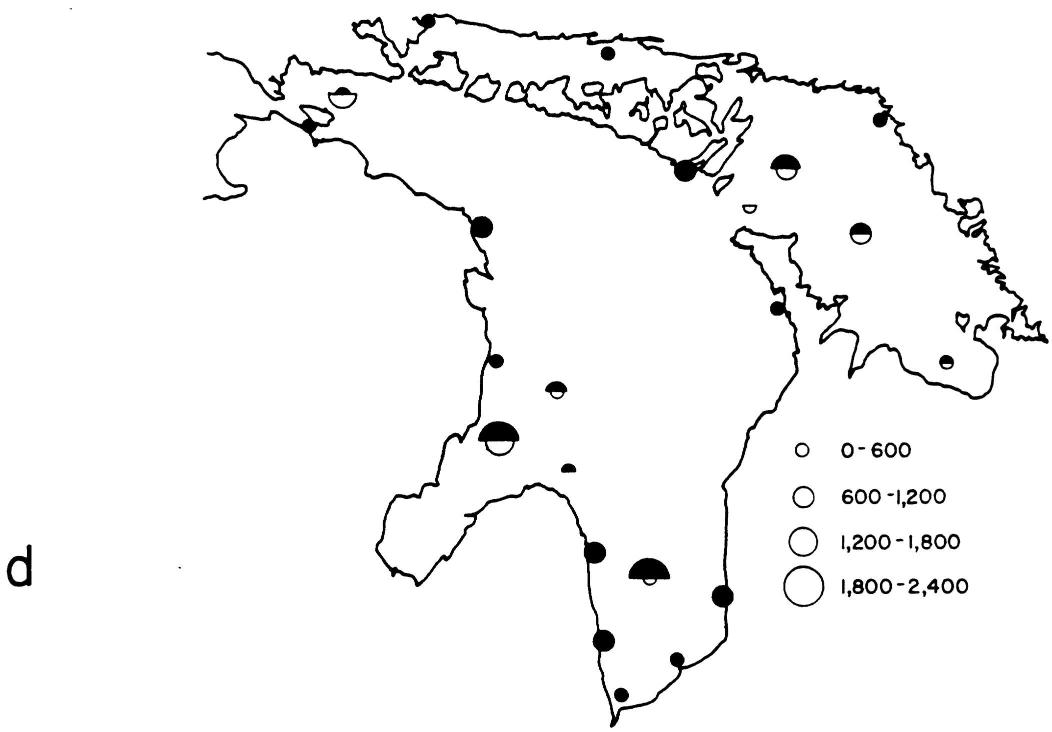
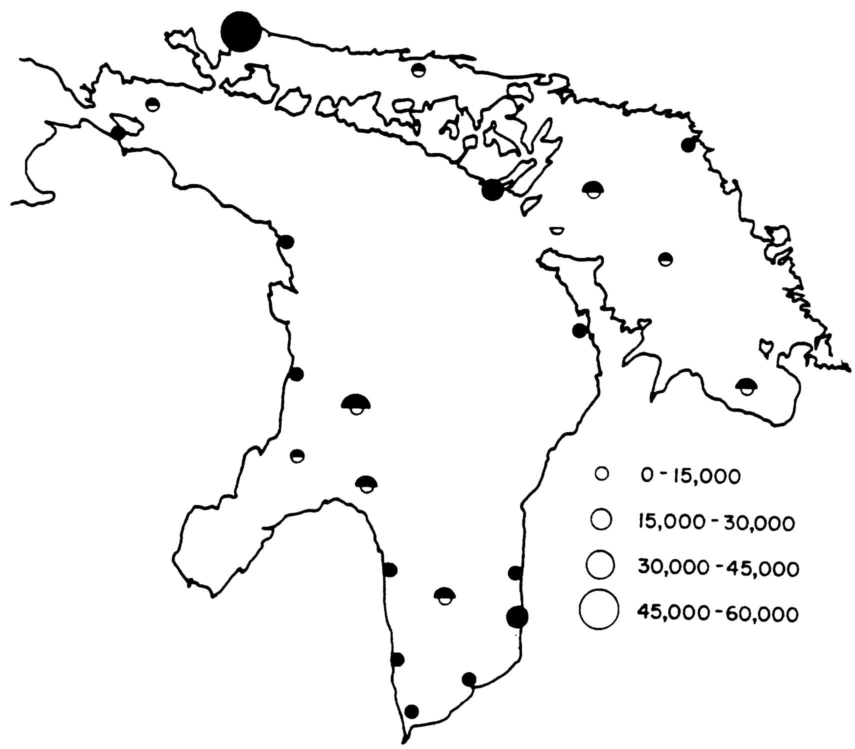


FIG. 22. Continued. c) Cyclops spp. C1–C5, d) Cyclops bicuspidatus thomasi,

e



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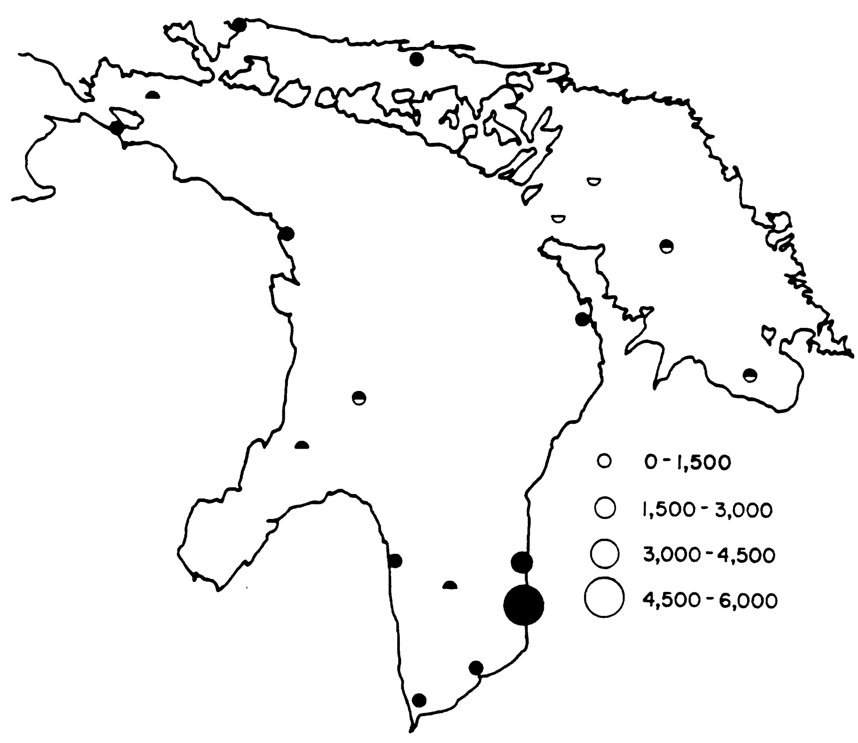

FIG. 22. Continued. e) *Diaptomus* spp. C1–C5, f) *Diaptomus minutus*,

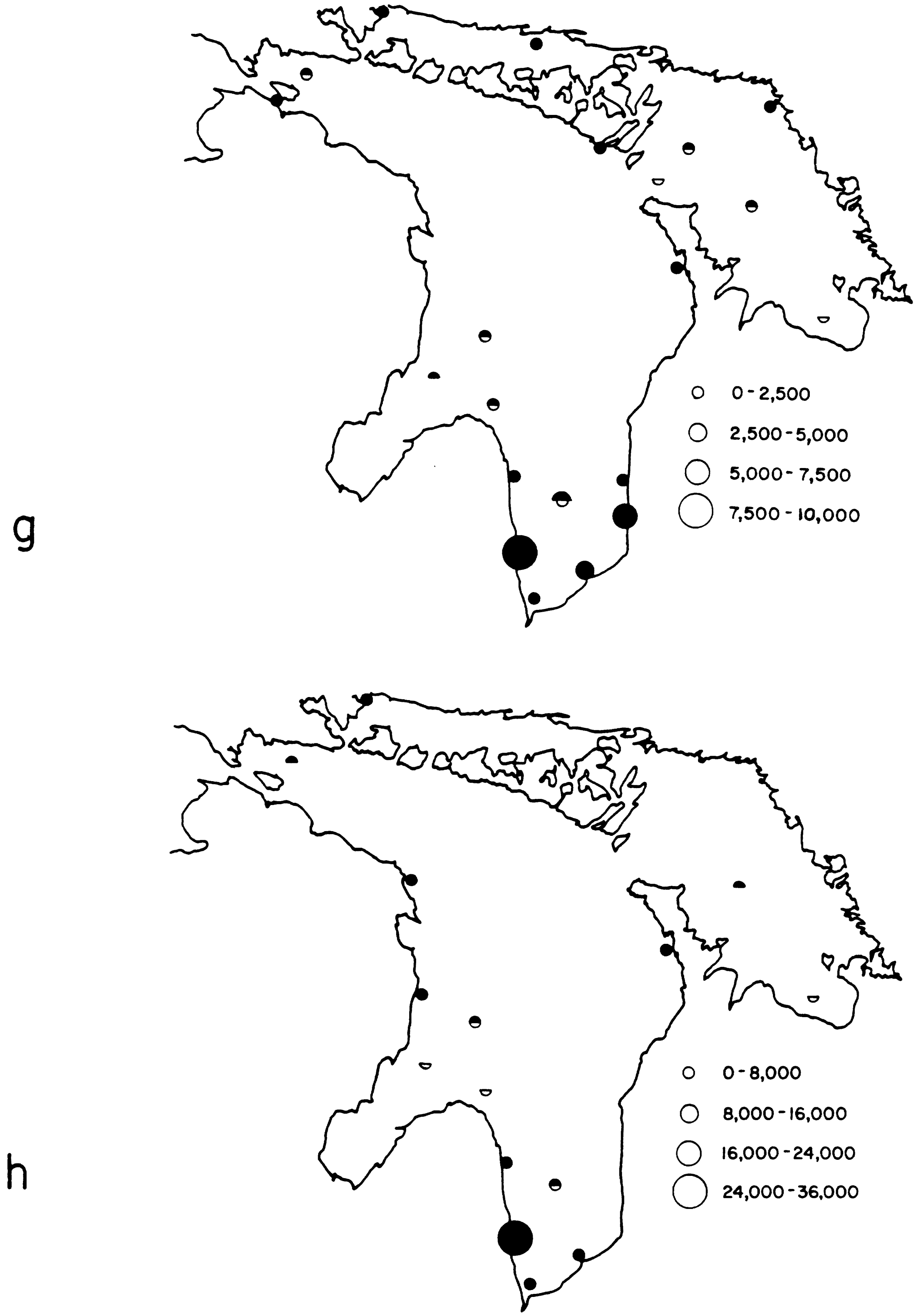

FIG. 22. Continued. g) Daphnia galeata mendotae, h) Daphnia retrocurva,

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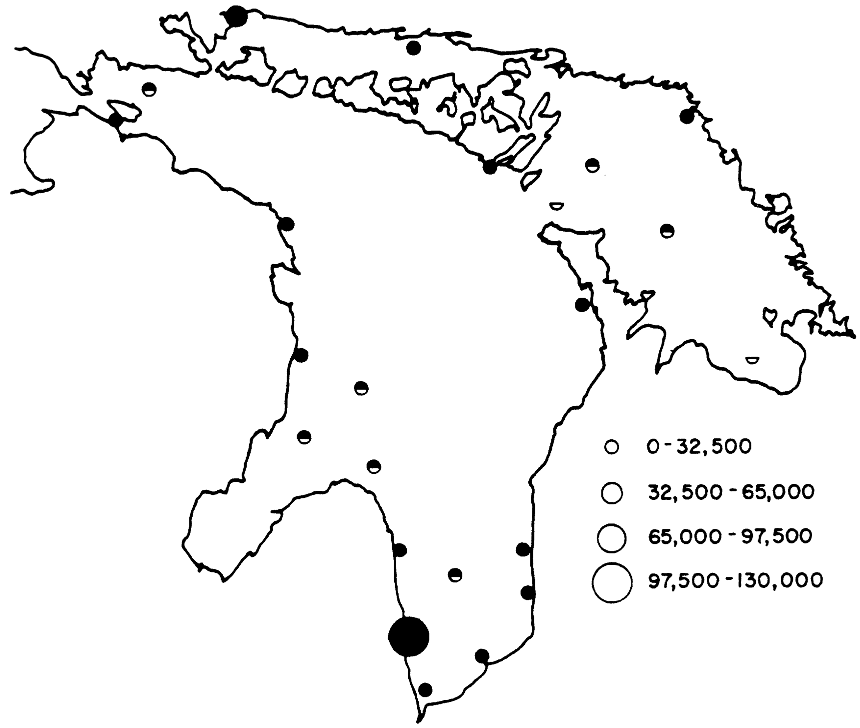

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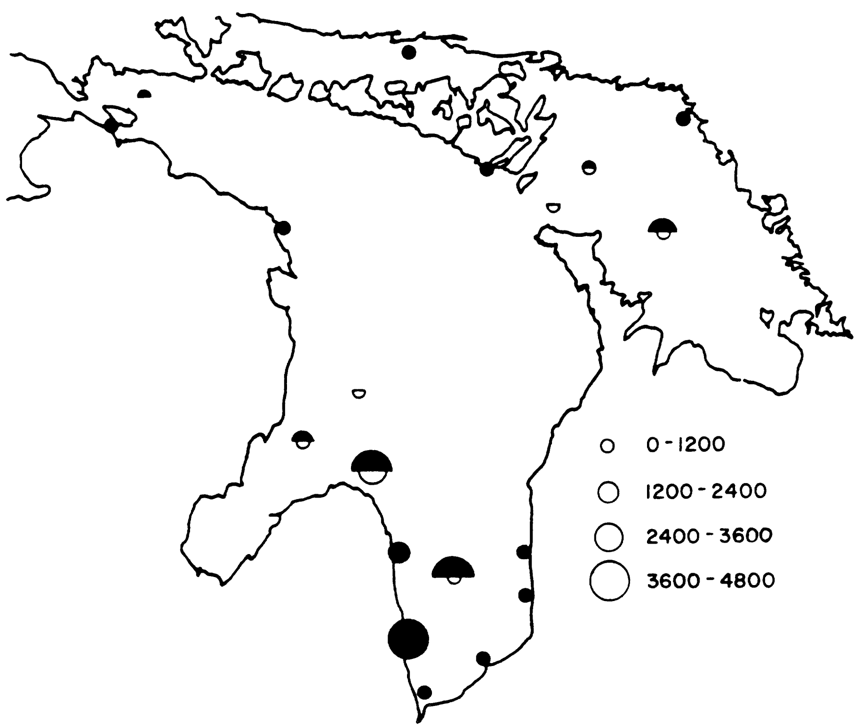

FIG. 22. Continued. i) Bosmina longirostris, j) Eubosmina coregoni,

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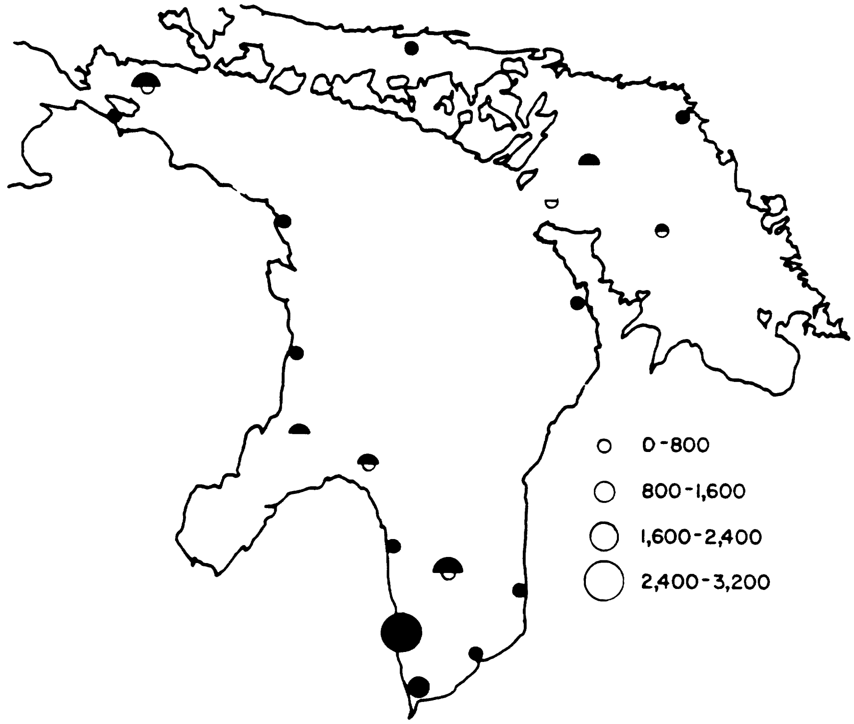

FIG. 22. Concluded. k) Holopedium gibberum.

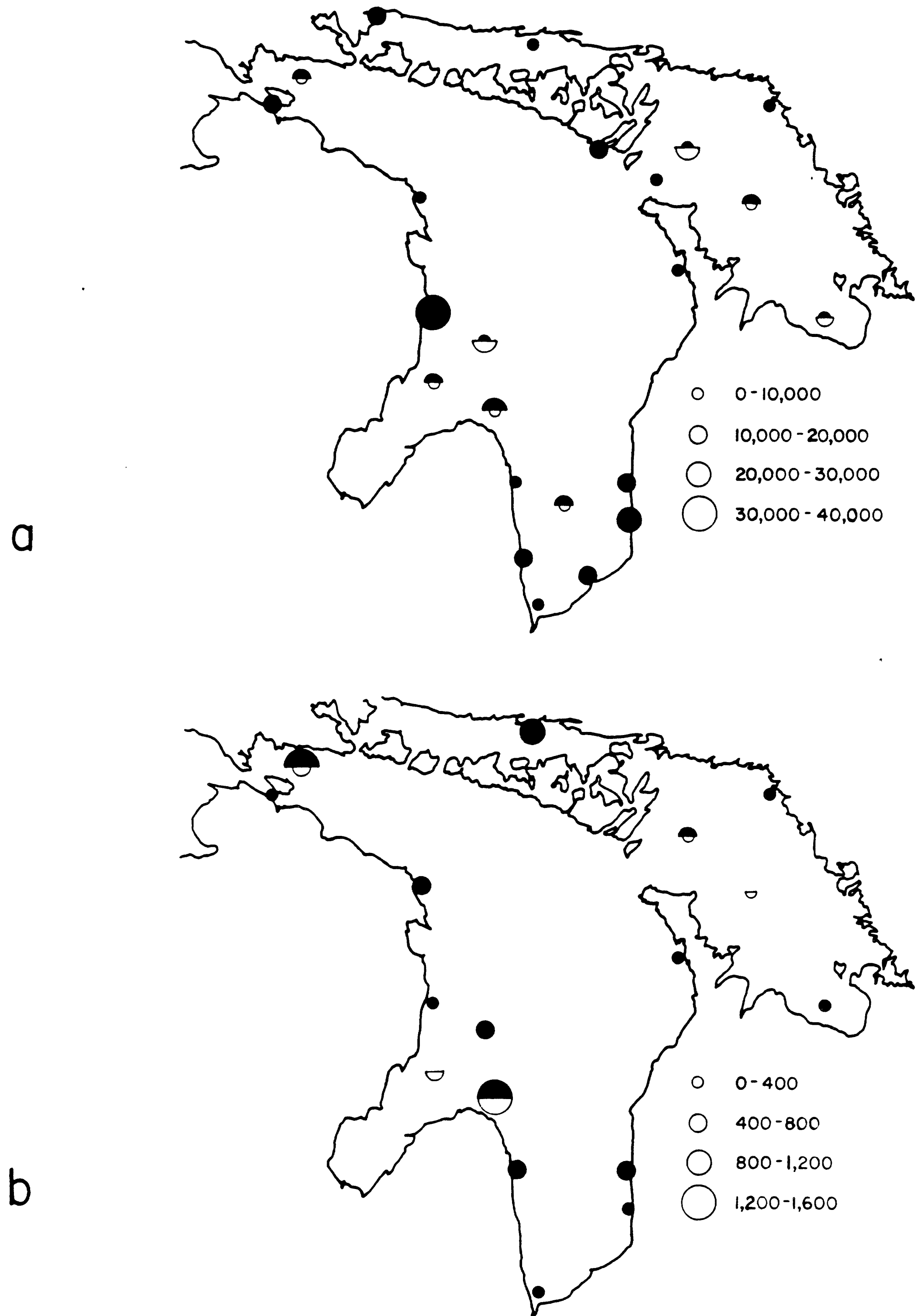

FIG. 23. Spatial distribution (#/m^3) of total rotifers and major rotifer taxa collected on 18-29 July 1980. Black circles represent net haul from 2 m off bottom to surface. Mixed circles (white and black): black part represents net haul from 25 m to surface; white part represents net haul from 2 m off bottom to surface. a) Total rotifers, b) Asplanchna,

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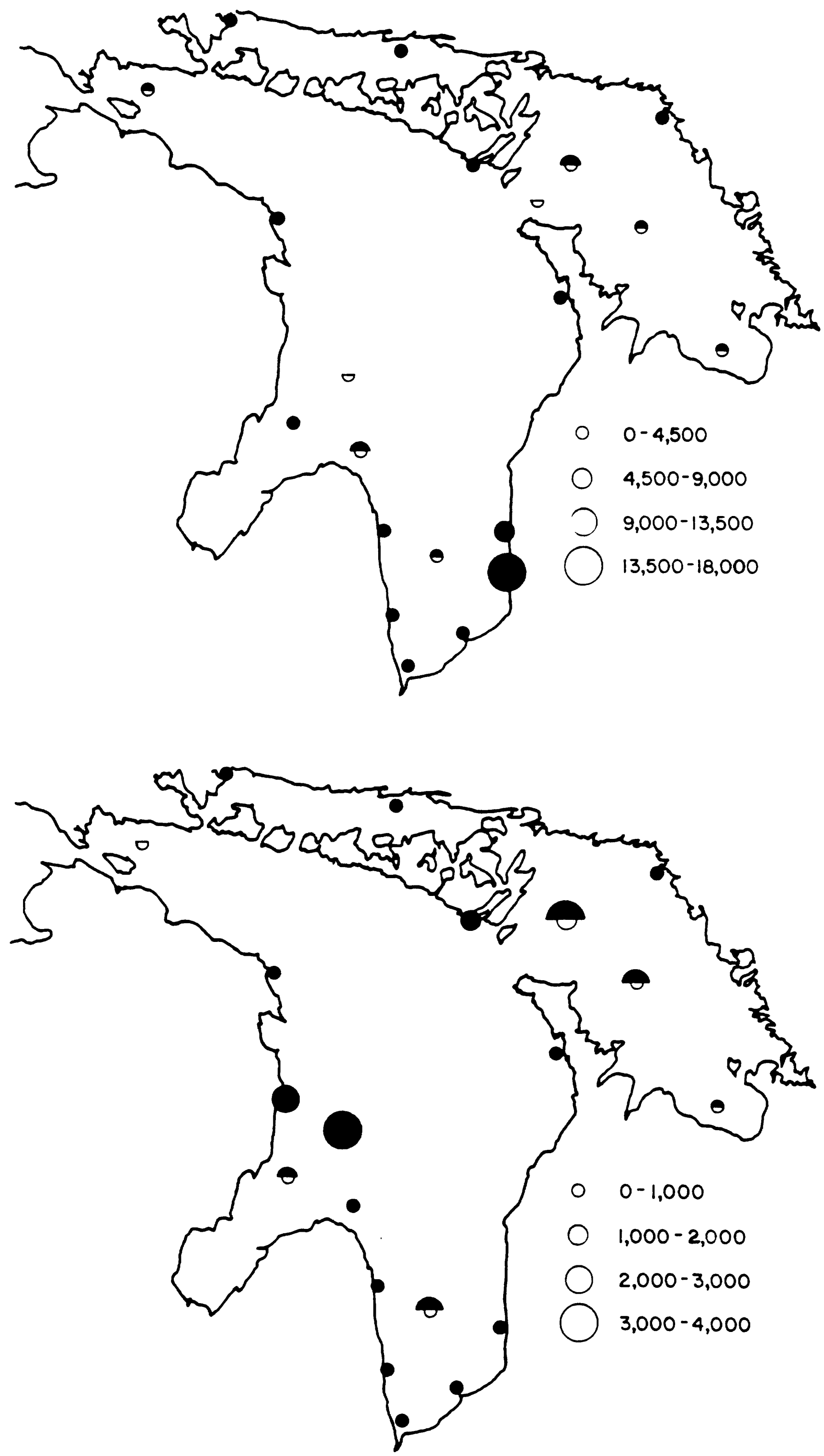
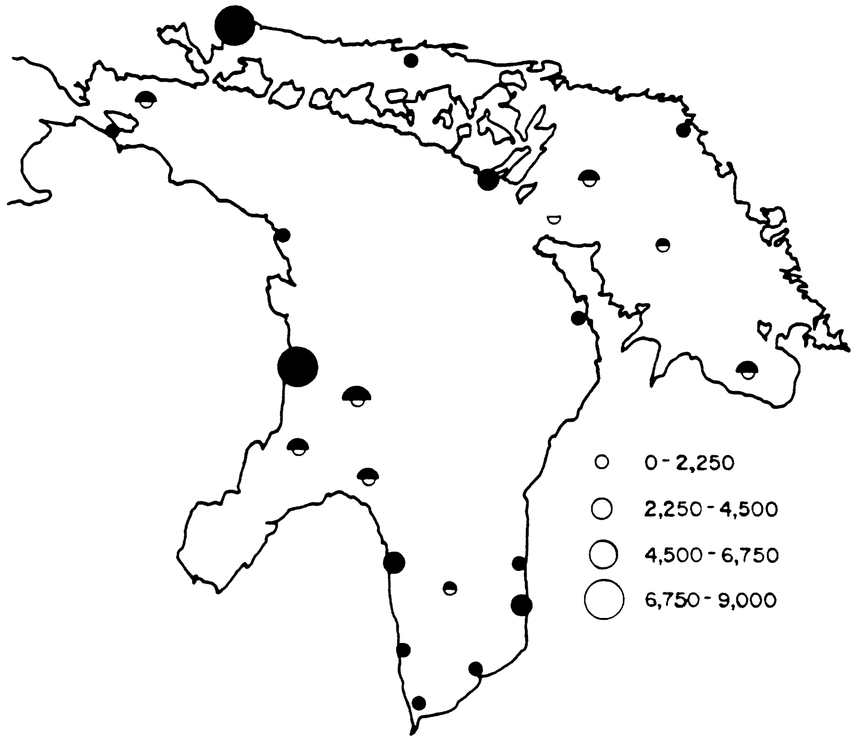


FIG. 23. Continued. c) Conochilus unicornis, d) Gastropus spp.,

e



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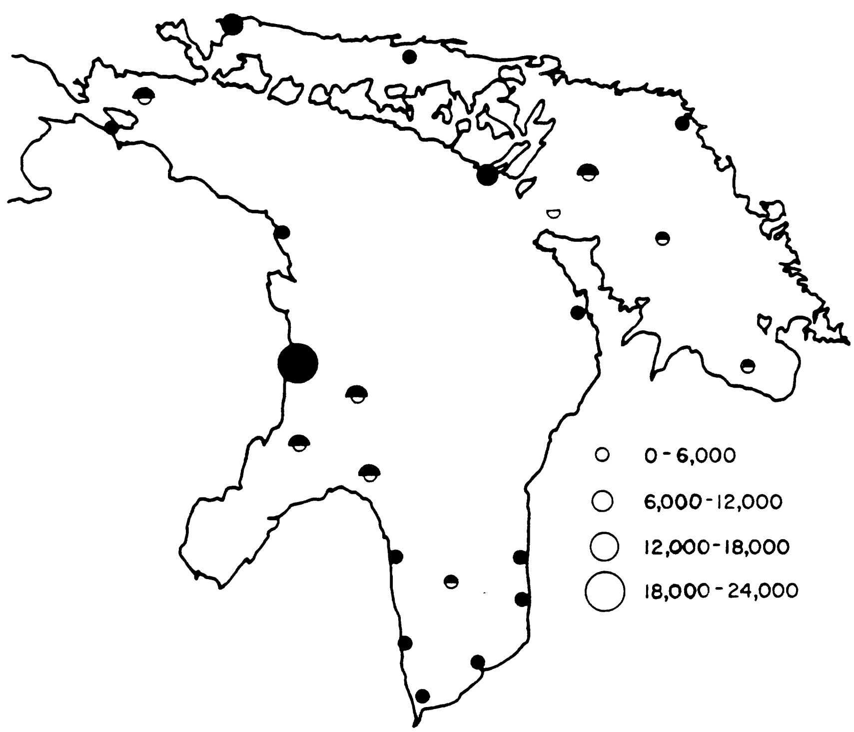
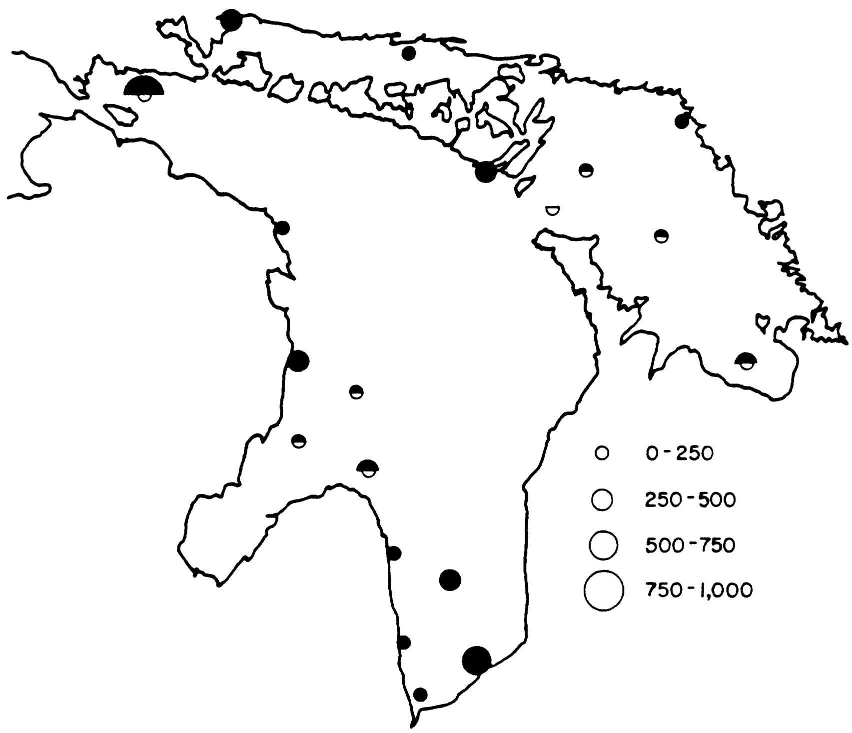


FIG. 23. Continued. e) Kellicottia longispina, f) Keratella cochlearis cochlearis,

g



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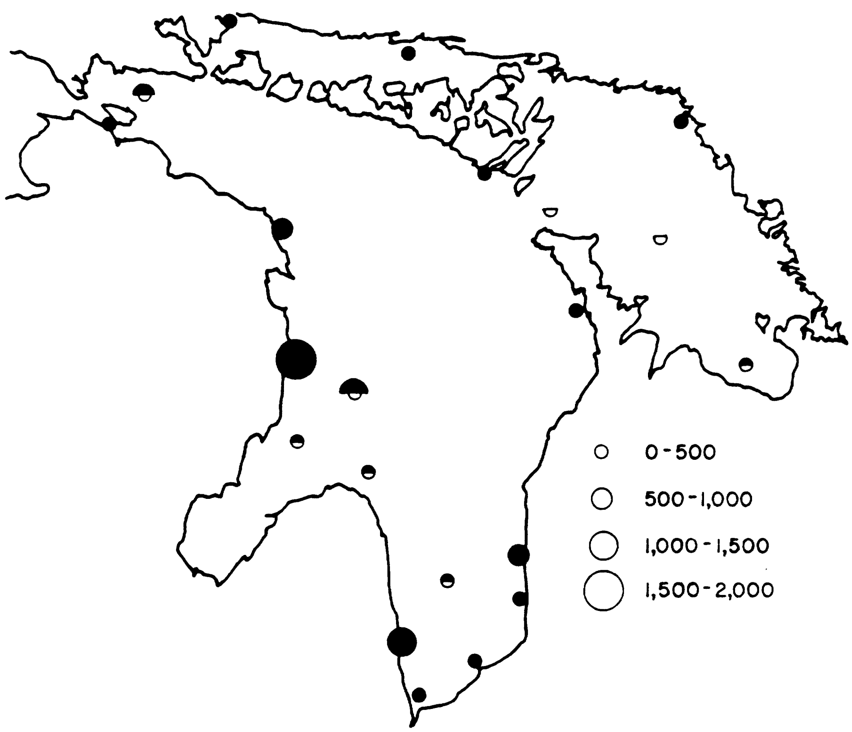
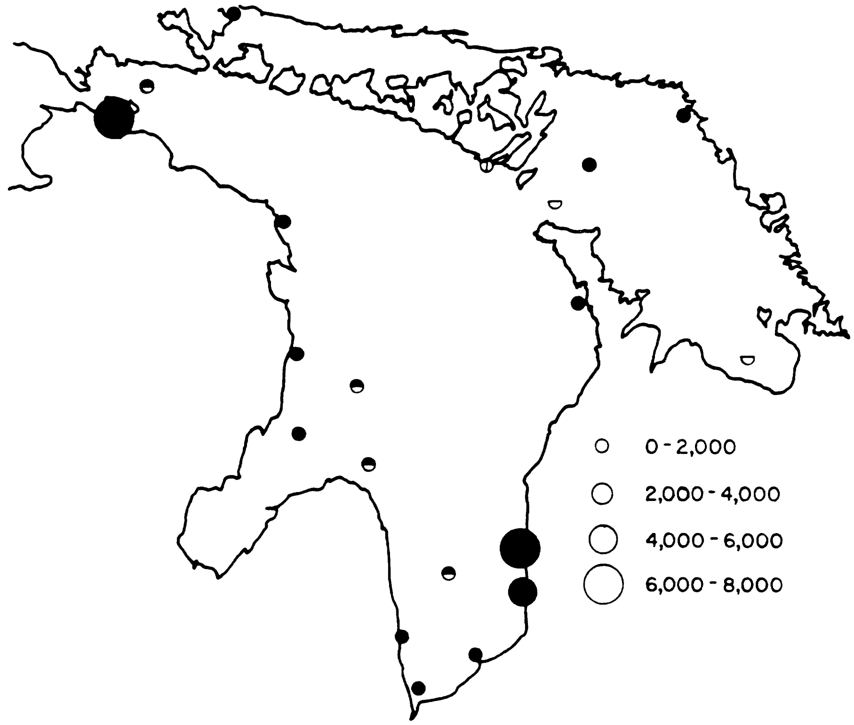


FIG. 23. Continued. (g) Polyarthra dolichoptera, h) Polyarthra remata,



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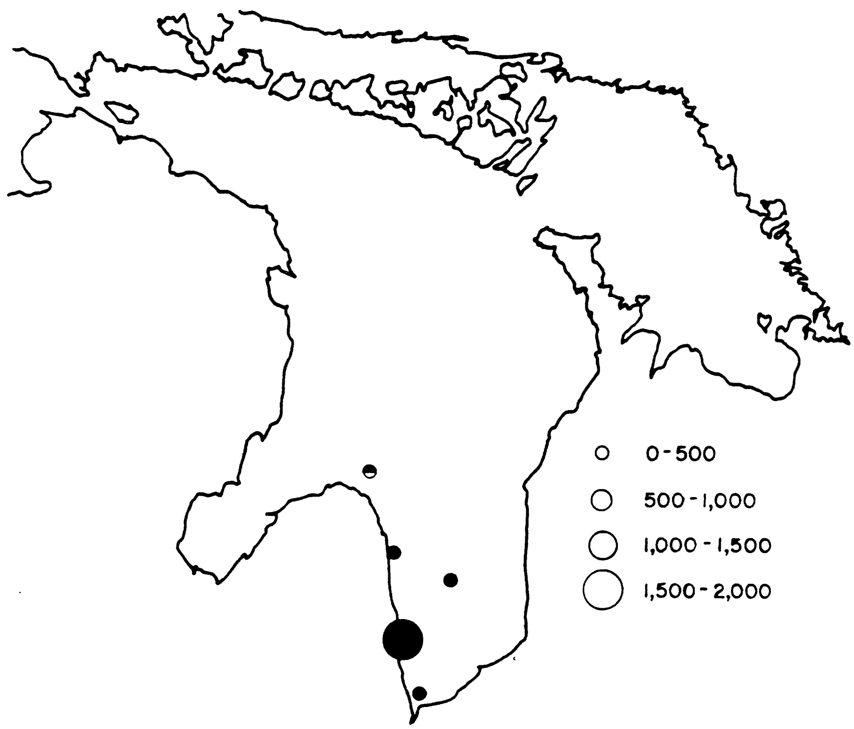

j

FIG. 23. Concluded. i) Synchaeta spp., j) Trichocerca multicrinis.

conditions, occurred at several stations (1, 7, 9, 13, and 16) in southern Lake Huron. A second species, *T. cylindrica*, was observed at stations 47 and 125.

Individual Taxa Correlations

Unlike previous cruises, crustacean abundances were strongly correlated (Table 27) with the physical-chemical environment. Statistically significant ($p<0.05$) variables included nauplii, immature *Cyclops* spp. copepodites, *Bosmina longirostris*, *Daphnia galeata mendotae*, and *D. retrocurva* with total phosphorus; nauplii, immature *Cyclops* spp., and *Diaptomus* spp. with soluble reactive silica; *Bosmina longirostris*, *Daphnia galeata mendotae*, and *D. retrocurva* with total Kjeldahl nitrogen; and *D. galeata mendotae* with nitrate. Correlations not directly related to algal productivity were immature *Cyclops* spp. copepodites with pH, immature *Diaptomus* spp. copepodites with conductivity, and immature *Diaptomus* spp. copepodites and *Eubosmina coregoni* with temperature.

Rotifer abundances (Table 27) were not as strongly correlated with their physical-chemical environment as in preceding months. Soluble reactive silica was significantly correlated with the abundance of *Kellicottia longispina*, total Kjeldahl nitrogen with *Asplanchna* spp. and *Trichocerca multicrinis*, total phosphorus with *T. multicrinis*, and chlorophyll with *Polyarthra dolichoptera*. *Synchaeta* spp. abundances were significantly correlated with pH, alkalinity, and conductivity.

Many crustacean taxon abundances were significantly ($p<0.05$) intercorrelated (Table 28); all statistically significant correlations were positive. As in previous months, nauplii, immature *Cyclops* spp., and immature *Diaptomus* spp. copepodite abundance correlations were statistically significant. Immature *Cyclops* spp. abundances also were significantly correlated with the cladocerans *Bosmina longirostris* and *Daphnia retrocurva*. The abundance of the five cladoceran taxa were significantly correlated, with the exception of *Eubosmina coregoni* with *Bosmina longirostris*. These positive

TABLE 27. Simple correlations among physical-chemical parameters and crustacean and rotifer densities ($\#/m^3$) for the July 1980 cruise. * = significant correlation ($\alpha = .05$).

	T	pH	Alk	Cond	NH_3	NO_3	Sol. S_iO_2	K-N	Tot Phos	Chloro-phyll	Chlor-ide
Nauplii	+.37	-.31	-.31	-.37	-.00	+.20	+.48*	-.01	+.46*	+.32	-.44
Cyclops immature	-.40	-.54*	-.31	-.35	-.03	+.16	+.43*	+.18	+.65*	+.35	-.29
Cyclops bicuspidatus	+.11	+.04	+.05	+.09	-.08	+.14	-.02	+.21	+.12	-.07	+.29
Diaptomus immature	-.42*	-.48*	-.40	-.44*	-.10	+.21	+.55*	-.08	+.38	+.28	-.45
Diaptomus minutus	+.32	+.21	+.08	+.11	+.34	+.41	-.15	+.26	+.05	-.32	+.17
Bosmina longirostris	-.15	-.22	+.05	+.02	+.19	+.04	-.02	+.46*	+.78*	+.06	-.06
Daphnia galeata	+.20	-.12	+.07	+.10	+.38	+.45*	-.13	+.57*	+.43*	-.21	+.12
Daphnia retrocurva	-.00	-.23	+.05	+.05	+.27	+.15	-.11	+.52*	+.60*	-.04	+.08
Eubosmina coregoni	+.44*	+.17	+.24	+.28	+.23	+.39	-.28	+.41*	+.14	-.07	+.38
Holopedium gibberum	+.07	-.04	+.22	+.24	+.24	+.11	-.21	+.36	+.21	-.12	+.26
Total crustaceans	-.31	-.41*	-.19	-.23	+.12	+.19	+.29	+.33	+.78*	+.22	-.27
Asplanchna spp.	+.10	+.26	+.21	+.17	-.31	-.34	+.07	-.46	-.15	-.0[illegible]	-.01
Conochilus unicornis	+.31	+.15	-.01	+.04	+.19	+.40	-.07	+.07	-.16	-.37	+.13
Gastropus stylifer	-.14	-.09	-.09	-.08	-.24	+.06	+.16	-.07	-.31	-.10	+.01
Kellicottia longispina	-.34	-.20	-.15	-.24	-.04	-.11	+.45*	+.06	+.25	+.39	-.31
Keratella cochlearis	-.08	-.05	+.10	+.04	+.09	-.15	+.09	+.16	-.01	+.22	+.08
Polyarthra dolichoptera	-.15	-.18	-.03	-.08	-.14	-.05	+.06	-.16	-.11	+.43*	-.14
Polyarthra remata	-.03	+.19	+.27	+.21	+.26	-.10	-.02	+.26	+.22	-.05	+.16
Synchaeta spp.	+.15	+.68*	+.55*	+.54*	+.09	-.11	-.39	+.11	+.12	-.28	+.34
Trichocerca multicrinis	+.04	-.20	+.09	+.10	+.26	+.13	-.14	+.50*	+.55*	-.10	+.13
Total rotifers	+.01	+.15	+.16	+.12	+.14	+.03	+.08	+.18	+.05	+.01	+.12

TABLE 28. Density (#/m^3) correlations for crustacean and rotifer taxa collected on the July 1980 cruise. * = significant correlation (α = .05).

	Nauplii	Cyclops immature	Cyclops bicuspidatus	Diaptomus immature	Diaptomus minutus	Bosmina longirostris	Daphnia galeata	Daphnia retrocurva	Eubosmina coregoni	Holopedium gibberum	Total crustaceans	Asplanchna spp.	Conochilus unicornis	Gastropus stylifer	Kellicottia longispina	Keratella cochlearis	Polyarthra dolichoptera	Polyarthra remata	Synchaeta spp.	Trichocerca multicrinis	Total rotifers
Nauplii	+1.00																				
Cyclops immature	+.61*	+1.00																			
Cyclops bicuspidatus	+.08	+.24	+1.00																		
Diaptomus immature	+.87*	+.77*	+.18	+1.00																	
Diaptomus minutus	+.33	-.23	+.07	+.16	+1.00																
Bosmina longirostris	+.29	+.59*	+.01	+.17	+.00	+1.00															
Daphnia galeata	+.24	+.38	+.24	+.14	+.38	+.76*	+1.00														
Daphnia retrocurva	-.01	+.48*	+.05	-.05	-.12	+.92*	+.77*	+1.00													
Eubosmina coregoni	+.02	+.24	+.35	-.03	+.03	+.38	+.66*	+.44*	+1.00												
Holopedium gibberum	-.03	+.30	+.35	-.08	-.22	+.57*	+.62*	+.63*	+.66*	+1.00											
Total crustaceans	+.72*	+.86*	+.15	+.68*	+.10	+.82*	+.67*	+.64*	+.32	+.41	+1.00										
Asplanchna spp.	-.01	-.20	-.36	-.15	-.12	-.07	-.22	-.19	-.05	+.09	-.14	+1.00									
Conochilus unicornis	+.27	-.26	+.05	+.13	+.86*	-.05	+.39	-.16	+.15	-.02	+.05	+.18	+1.00								
Gastropus stylifer	-.01	+.19	+.50*	+.18	-.23	-.19	+.03	-.08	+.09	+.14	-.02	-.31	-.10	+1.00							
Kellicottia longispina	+.54*	+.43*	+.02	+.60*	-.01	-.01	-.17	-.21	-.31	-.19	+.32	+.03	-.06	+.28	+1.00						
Keratella cochlearis	-.06	+.20	+.12	+.06	-.31	-.09	-.18	-.07	-.11	+.05	-.03	-.06	-.32	+.44*	+.71*	+1.00					
Polyarthra dolichoptera	+.07	+.18	-.22	+.09	-.27	+.04	-.04	+.02	+.10	+.22	+.09	+.32	-.07	-.12	+.23	+.34	+1.00				
Polyarthra remata	-.18	+.05	-.08	-.18	-.08	+.24	+.09	+.29	-.20	+.06	+.06	-.06	-.24	+.11	+.44*	+.62*	+.04	+1.00			
Synchaeta spp.	+.04	-.37	-.24	-.17	+.55*	+.08	+.08	-.08	-.07	-.23	-.06	+.11	+.37	-.33	-.09	-.32	-.39	+.16	+1.00		
Trichocerca multicrinis	-.05	+.46*	+.03	-.07	-.13	+.91*	+.77*	+.99*	+.49*	+.66*	+.62*	-.11	-.12	-.08	-.23	-.06	+.02	+.27	-.08	+1.00	
Total rotifers	+.27	+.12	+.12	+.27	+.30	-.01	+.09	-.14	-.08	-.03	+.14	+.05	+.32	+.38	+.79*	+.73*	+.16	+.55*	+.17	-.13	+1.00

correlations suggest that cladoceran population cycles over the survey grid were in synchrony and/or had similar responses to environmental variables.

Rotifer taxon abundance intercorrelations (Table 28) were not as frequently statistically significant ($p<0.05$) as in previous cruises: all significant correlations were positive. Many crustacean and rotifer taxon abundances were significantly ($p<0.05$) correlated (Table 28); all correlations were positive. _Trichocerca multicrinis_ abundances were significantly correlated with the abundances of all five cladoceran taxa and with immature _Cyclops_ spp. copepodites.

Principal Component Analysis: Crustaceans

Ten crustacean taxa were used in the July principal component analysis. PC1 accounted for 34.2% of the variance while PC2 accounted for an additional 22.8% of the variance. PC1 loadings ranged from -0.10 for _Diaptomus minutus_ to +0.61 for _Eubosmina coregoni_ while PC2 loadings ranged from -0.33 for _Eubosmina coregoni_ to +0.92 for _Daphnia retrocurva_.

Plotting the 23 stations by their PC1 and PC2 values (Fig. 24) provided evidence of regional differences in zooplankton community structure over the survey area. Station 7 (offshore of Lexington), located in southwestern Lake Huron, was an outlier with high PC1 and PC2 values and was designated as Group 1. Group 2 consisted of four stations (1, 3, 9, 13) in southern Lake Huron, a single station (117) in Georgian Bay, and station 66 in the Straits of Mackinac. Group 3, with intermediate PC1 values and low PC2 values consisted of nine stations in the main body of Lake Huron. This Lake Huron group was bisected by the four (33, 34, 40, 47) Group 4 stations of central Lake Huron. Group 4 stations had PC2 values which were relatively high in comparison to those of Group 3 stations. Station 71 in the St. Marys River outflow and station 104 offshore of Collingwood in southern Georgian Bay were outliers and were designated Groups 5 and 6 respectively.

PC1 was not significantly ($p>0.05$) correlated with any physical-chemical variable with the exception of a weak correlation ($r = +0.38$; $p = 0.08$) with total Kjeldahl nitrogen. PC2 was weakly correlated ($r = +0.36$; $p = 0.10$) with

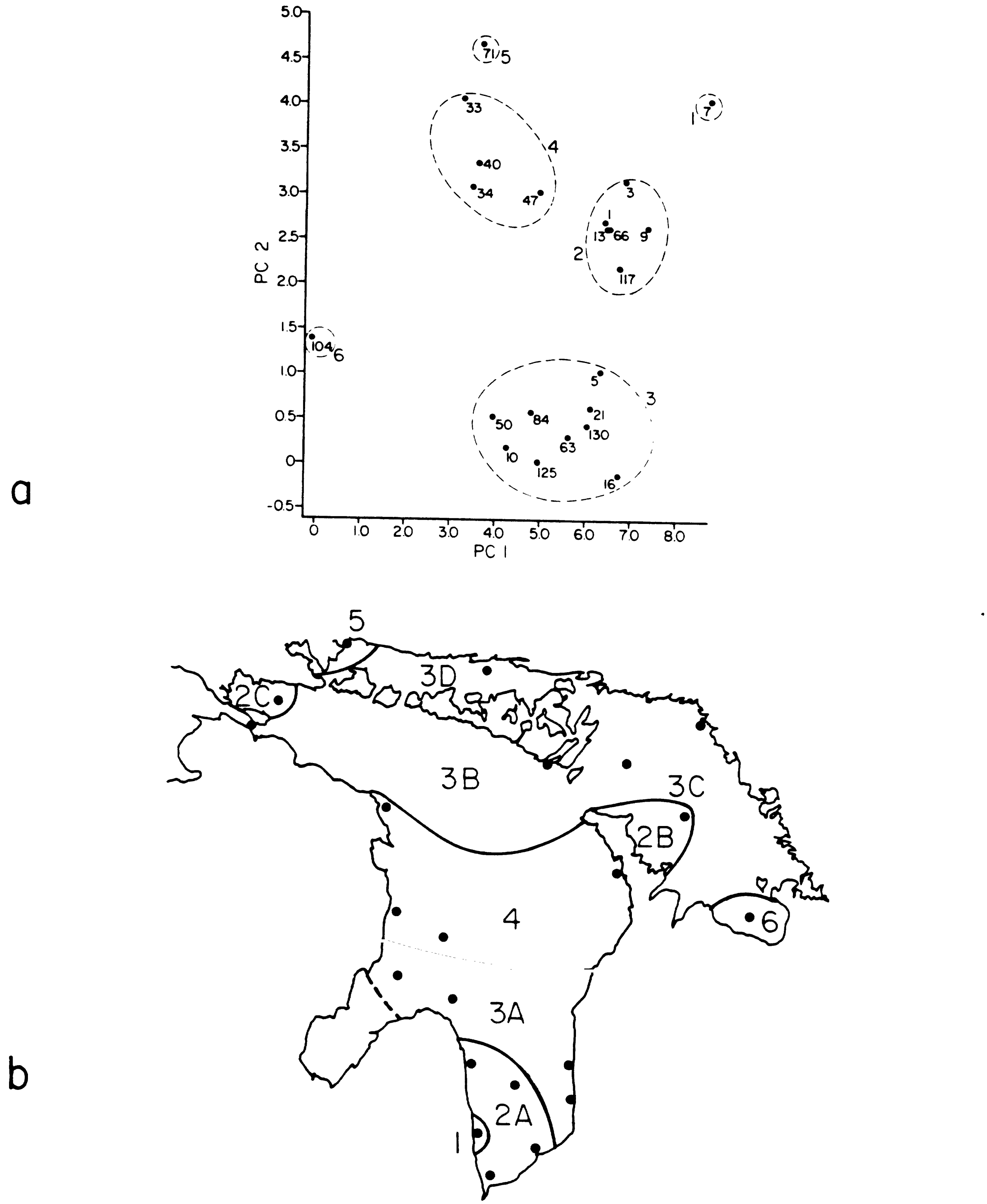

FIG. 24. a) Principal component ordination of stations sampled for crustaceans on 18-29 July 1980. b) Lake map with station groups derived from ordination analysis.

total phosphorus. PC1 station scores were significantly correlated with the abundance of the rotifer Trichocerca multicrinis ($r = +.50$; $p = 0.02$), a species considered an indicator of eutrophic conditions.

Crustacean abundances (Tables 29 and 30) ranged from a low of 43,031/m^3 in Group 4 to highs of 233,839/m^3 in the St. Marys River Group 5 and 241,566/m^3 in southwestern Lake Huron Group 1. Group 1 was numerically dominated by the cladoceran Bosmina longirostris with large numbers of Daphnia galeata mendotae, D. retrocurva, Eubosmina coregoni, and Holopedium gibberum. Among the copepods, immature Cyclops spp. predominated. Group 5, also with large standing stocks of crustaceans, had a different community structure. Nauplii and immature Diaptomus spp. accounted for a larger percentage of the crustaceans than in Group 1 while B. longirostris, D. galeata mendotae, and D. retrocurva were less abundant. Eubosmina coregoni and Holopedium gibberum were absent (or very rare).

Groups 2, 3, and 4 had similar standing stocks of crustaceans and similar community structure. Largest differences were associated with the relative abundance of Diaptomus minutus and cladocerans. Group 6, a single station in Georgian Bay, differed substantially in crustacean community structure from Groups 2, 3, and 4 although standing stocks were similar. Cladocerans were absent (or exceedingly rare) and the community was most strongly dominated by immature Diaptomus spp. copepodites followed by nauplii, and immature Cyclops spp. copepodites. Adult Cyclops bicuspidatus thomasi occurred in relatively low numbers while D. minutus occurred in relatively high numbers in comparison to most of the survey grid.

Table 31 shows the physical-chemical characteristics of the six regions. Alkalinity, pH, conductivity, and chloride showed the expected trend with lowest values in the St. Marys River Group 5 and Georgian Bay Group 6. Temperatures were similar across the survey grid with relatively cool (15.5°C) water found only in the outflow from Lake Superior (Group 5).

In contrast to previous cruises, nitrate and soluble reactive silica exhibited little regional variation. Nitrate values were only slightly higher in Groups 1 and 2 (0.265 mg/L and 0.262 mg/L respectively) than in Group 3 with the lowest nitrate concentration (0.241 mg/L). Soluble reactive silica

TABLE 29. Mean densities (#/m^3) of various crustacean taxa and carbon weights (mg carbon/m^3) for the July 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Nauplii	16,982	23,567	19,109	13,151	77,946	15,920
Cyclops C1-C5	37,360	12,021	10,341	11,428	45,851	16,579
C. bicuspidatus C6	849	792	692	709	382	220
Diaptomus C1-C5	10,189	13,428	13,433	11,629	54,257	24,484
D. minutus C6	0	478	1,129	317	382	988
Bosmina longirostris	128,637	8,556	13,751	4,743	51,582	0
Daphnia galeata	9,340	1,790	1,553	366	1,146	0
D. retrocurva	31,416	501	0	354	2,293	0
Eubosmina coregoni	3,821	2,133	1,127	137	0	0
Holopedium gibberum	2,972	1,134	506	194	0	0
Total crustaceans	241,566	64,373	62,572	43,031	233,839	58,191
Total rotifers	10,163	12,756	15,756	17,961	16,992	12,629
Crustacean carbon	156.08	76.63	34.83	24.54	119.03	36.79
Rotifer carbon	0.04	0.06	0.04	0.08	0.07	0.06

TABLE 30. Percent composition of crustacean taxa for the July 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Nauplii	7.0	36.6	30.5	30.6	33.3	27.4
Cyclops C1-C5	15.5	18.7	16.5	26.6	19.6	28.5
C. bicuspidatus C6	0.4	1.2	1.1	1.6	0.2	0.4
Diaptomus C1-C5	4.2	21.1	21.5	27.0	23.2	42.1
D. minutus C6	0.0	0.7	1.8	0.7	0.2	1.7
Bosmina longirostris	53.3	13.3	22.0	11.0	22.1	0.0
Daphnia galeata	3.9	2.7	2.5	0.9	0.5	0.0
D. retrocurva	13.0	0.8	0.0	0.8	1.0	0.0
Eubosmina coregoni	1.6	3.3	1.8	0.3	0.0	0.0
Holopedium gibberum	1.2	1.8	0.8	0.5	0.0	0.0

TABLE 31. Mean values of physical-chemical parameters[1] for the July 1980 cruise (crustaceans).

Parameter	Region 1	2	3	4	5	6
Sample depth (m)	9.0	20.3	19.2	17.5	25.0	25.0
Temperature (°C)	19.5	20.0	19.5	18.8	15.5	19.7
pH	8.1	8.3	8.3	8.3	8.0	8.1
Alkalinity (mg/L)	80.5	79.5	78.0	77.5	54.0	71.0
Conductivity (μmhos/cm)	209.0	205.3	203.1	199.0	137.0	188.0
Nitrate (mg/L x 10^{-2})	26.5	26.2	23.5	23.9	24.6	24.1
Sol. react. silica (mg/L)	0.7	0.8	0.9	1.0	1.7	0.8
Kjeldahl nitrogen (mg/L x 10^{-2})	24.5	16.7	15.9	14.5	15.7	12.9
Total phosphorus (mg/L x 10^{-2})	0.9	0.4	0.4	0.4	0.9	0.3
Chlorophyll (mg/m^3)	0.9	1.2	1.0	0.9	2.2	0.8
Phyto. carbon/zoop. carbon	0.4	1.0	1.9	2.4	1.2	1.4

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

concentrations were low (<1.0 mg/L) with the exception of Group 5 (1.7 mg/L) in the outflow from Lake Superior: values here were lower than in previous months. Chlorophyll concentrations were high (2.2 mg/m^3) in the St. Marys River (Group 5) and low (0.8 to 1.2 mg/m^3) elsewhere. The phytoplankton:zooplankton carbon ratios were lower (0.4 to 2.4) than in previous months. The lowest value (0.4) was observed for Group 1 (offshore of Lexington in southwestern Lake Huron). The second lowest value (1.2) was observed for Group 6 in the outflow of the St. Marys River. The highest value (2.4) was observed in for Group 4 in central Lake Huron.

These observations suggest the following. First, given the large crustacean standing stocks and low phytoplankton:zooplankton carbon ratios, grazing pressure must have been intense. Since chlorophyll concentrations varied little over the survey grid (with the exception of Group 5), primary productivity must have been higher in some areas than others, i.e., in areas where the phytoplankton:zooplankton carbon ratios were lowest. In addition, since soluble reactive silica exhibited little regional variation (with the exception of Group 5), diatoms probably were a less significant component of daily primary production than in earlier months when silica concentrations were higher. The lack of regional variation in nitrate suggests that resupply and regeneration were balanced by uptake over most of the survey grid, i.e., that steady state conditions prevailed. Given large crustacean standing stocks and the associated heavy grazing pressure, much of the algal productivity was consumed by herbivores. Crustaceans, which accounted for most of the zooplankton biomass, probably were the major grazers. On the basis of phytoplankton:zooplankton carbon ratios and the dominance by cladocerans (particularly Bosmina longirostris), the most productive areas appear to have been southwestern Lake Huron (Group 1) and the St. Marys River (Group 5).

Principal Component Analysis: Rotifers

Nine rotifer taxa were used in the July principal component analysis. The first principal component accounted for 34.5% of the total variance while PC2 accounted for an additional 24.2% of the variance. PC1 loadings ranged

from -0.55 for Synchaeta spp. to +0.51 for Gastropus stylifer, while PC2 loadings ranged from -0.62 for Asplanchna spp. to +0.33 for Polyarthra remata.

Plotting the 23 stations by their PC1 and PC2 scores (Fig. 25) provided evidence of regional differences in rotifer community structure. A large number of groups (6) were identified with a relatively small number (1 to 7) of stations per group. Group 1, with high PC1 values, consisted of two stations (104, 117) in southern Georgian Bay. Group 2 consisted of stations 13 and 16 southwest of Saginaw Bay, station 84 in the North Channel, and station 130 in outer Georgian Bay. Group 3 consisted of stations in southern Lake Huron (3, 7, 9, 21), station 71 in the outflow from Lake Superior, and station 50 east of Manitoulin Island. Group 4 consisted of stations 33 and 34 north of Saginaw Bay while Group 5 consisted of stations in southern (1, 5, 10), eastern (40), and western (47, 66) Lake Huron, and station 125 in Georgian Bay.

Station PC1 scores were significantly correlated ($p<0.05$) with pH ($r = -0.58$), alkalinity ($r = -0.53$), and conductivity ($r = -0.49$). PC2 was not significantly correlated with any of the physical-chemical parameters considered. PC1 station scores were significantly correlated with immature Cyclops spp. copepodites ($r = +0.61$), adult C. bicuspidatus thomasi ($r = +0.49$), and immature Diaptomus spp. copepodites ($r = +0.42$), while PC2 was significantly correlated with Eubosmina coregoni ($r = -0.41$).

Tables 32 and 33 show rotifer community structure in the six regions. Mean abundance ranged from a low of $12,193/m^3$ in northwestern Lake Huron Group 6 to a high of $28,125/m^3$ in Group 4, north of Saginaw Bay. Georgian Bay Group 1 was numerically dominated by Keratella cochlearis cochlearis, Conochilus unicornis, and Gastropus stylifer: Synchaeta spp., Asplanchna spp., and Trichocerca multicrinis were rare or absent. Groups 2 and 3 had larger numbers of Synchaeta spp., T. multicrinis, Kellicottia longispina, and K. cochlearis cochlearis. Group 4, with the largest rotifer standing stocks, was dominated by K. cochlearis cochlearis and K. longispina: T. multicrinis and C. unicornis were rare or absent. Group 5 had rotifer standing stocks similar to Group 3 but large numbers of C. unicornis and Synchaeta spp. while K. cochlearis cochlearis and G. stylifer occurred in lower numbers than in

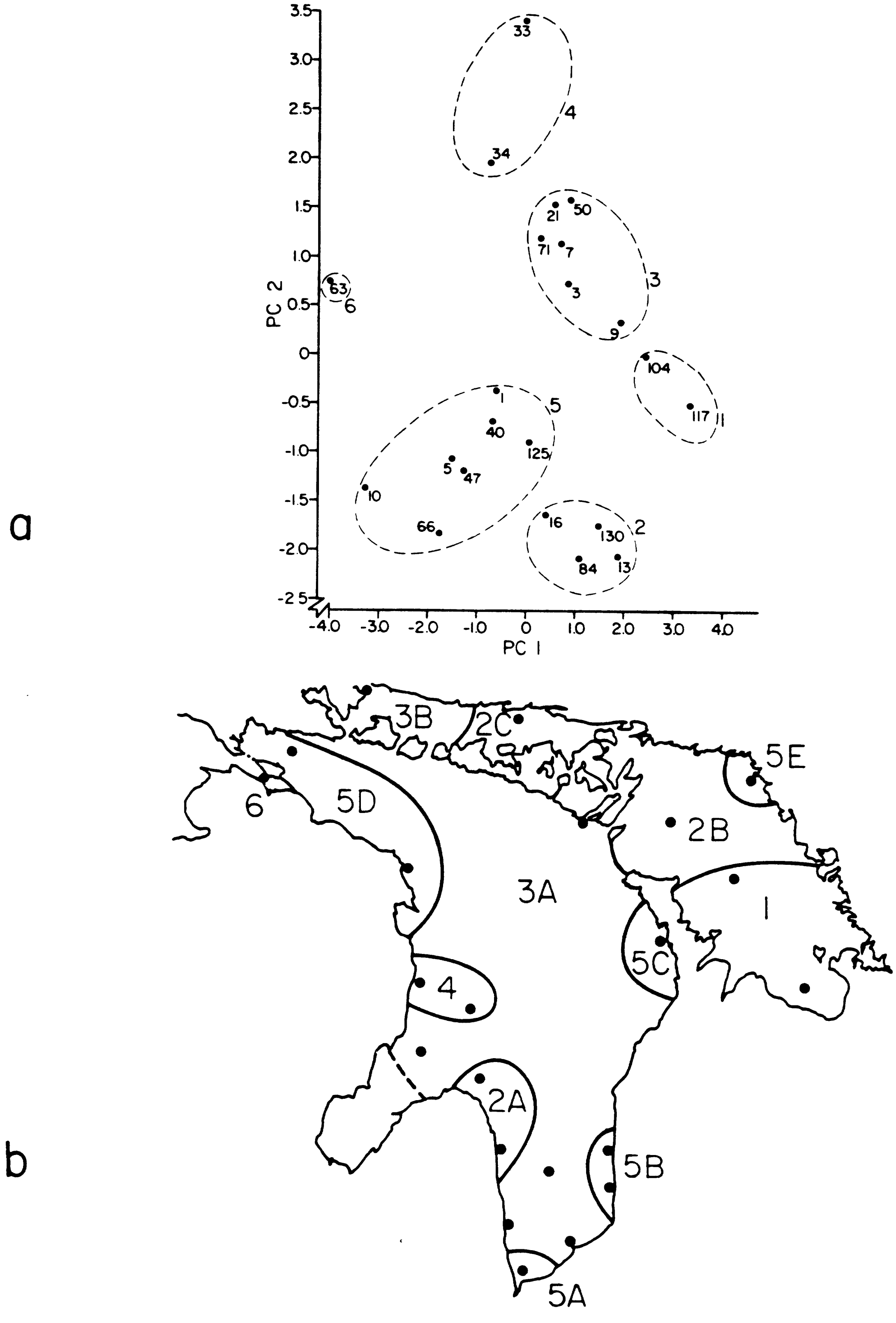

FIG. 25. a) Principal component ordination of stations sampled for rotifers on 18-29 July 1980. b) Lake map with station groups derived from ordination analysis.

TABLE 32. Mean densities (#/m^3) of various rotifer taxa and carbon weights (mg carbon/m^3) for the July 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Asplanchna spp.	0	804	0	119	432	669
Conochilus unicornis	3,281	4,025	1,700	0	5,129	0
Gastropus stylifer	1,848	1,533	1,100	2,747	150	0
Kellicottia longispina	2,171	2,794	2,921	7,079	1,806	1,876
Keratella coch. coch.	5,052	5,151	6,333	15,767	2,866	2,037
Polyarthra dolichoptera	246	222	333	223	201	0
P. remata	46	29	334	1,585	404	429
Synchaeta spp.	0	55	413	603	2,090	7,182
Trichocerca multicrinis	0	61	317	0	4	0
Total rotifers	12,645	14,676	13,453	28,854	13,086	12,193
Total crustaceans	63,352	66,251	122,512	59,721	53,715	41,074
Rotifer carbon	0.08	0.32	0.08	0.30	0.23	0.30
Crustacean carbon	30.17	36.66	71.66	35.55	39.93	18.87

TABLE 33. Percent composition of various rotifer taxa for the July 1980 cruise.

Taxon	Region 1	2	3	4	5	6
Asplanchna spp.	0.0	5.5	0.0	0.4	3.3	5.5
Conochilus unicornis	25.9	27.4	12.6	0.0	39.2	0.0
Gastropus stylifer	14.6	10.4	8.2	9.8	1.1	0.0
Kellicottia longispina	17.2	19.0	21.7	25.2	13.8	15.4
Keratella coch. coch.	40.0	35.1	47.1	56.1	21.9	16.7
Polyarthra dolichoptera	1.9	1.5	2.5	0.8	1.5	0.0
P. remata	0.4	0.2	2.5	5.6	3.1	3.5
Synchaeta spp.	0.0	0.4	3.1	2.1	16.0	58.9
Trichocerca multicrinis	0.0	0.4	2.4	0.0	0.0	0.0

group 3. Group 6, with low rotifer standing stocks, was numerically dominated by *Synchaeta* spp. while *C. unicornis*, *G. stylifer*, *Polyarthra dolichoptera*, and *T. multicrinis* were rare or absent.

Physical-chemical characteristics of the six regions are shown in Table 34. As discussed for the crustacean analyses, there was little variation in nitrate, soluble reactive silica, or chlorophyll over the survey grid. Rotifer standing stocks (numbers/m^3) tended to be highest in regions with high chlorophyll concentrations although biomass did not follow this trend. The phytoplankton:zooplankton carbon ratio was low and varied from 1.3 (Group 3) to 3.2 (Group 6) suggesting that grazing pressure was intense. Group 3 also had the highest chlorophyll concentration, suggesting that algal productivity was highest in this region of the lake. Nitrate and soluble reactive silica concentrations were lowest in Group 6 in the Straits of Mackinac. The relatively high conductivity of these waters suggests that plankton and the associated water mass had its origin in Lake Michigan. Relatively high concentrations of *Trichocerca multicrinis*, considered an indicator of eutrophic conditions, in Group 2 (excluding stations 83 and 130) and in Group 3 may be indicative that the stations in these groups were regions of relatively high nutrient loadings.

DISCUSSION

Zooplankton standing stocks, as quantified during the April, May, June, and July 1980 surveillance cruises, were characteristic of those of the more oligotrophic or oligo-mesotrophic regions of the Great Lakes (Patalas 1972, Watson 1974). Crustacean standing stocks were low, ranging from a May cruise mean of 14,000/m^3 to a July high of 75,604/m^3 (upper 25 m of the water column). Excluding nauplii, these estimates ranged from 4,703/m^3 (May) to 54,013/m^3 (July).

In comparison to the 1980 cruise mean estimates, Watson and Carpenter (1974) estimated that Lake Huron crustacean standing stocks (excluding nauplii) ranged from 2,245/m^3 (June) to 10,835/m^3 (July) for the April to July 1970 period. Lake Ontario crustacean standing stocks for the same period

TABLE 34. Mean values of physical-chemical parameters[1] for the July 1980 cruise (rotifers).

Parameter	Region 1	2	3	4	5	6
Sample depth (m)	25.0	24.5	20.5	17.5	15.1	12.0
Temperature (°C)	20.0	19.7	18.8	19.1	19.4	19.5
pH	8.1	8.2	8.2	8.3	8.3	8.5
Alkalinity (mg/L)	71.0	72.3	75.8	79.5	77.7	106.0
Conductivity (μmhos/cm)	185.0	190.3	196.3	202.5	201.9	263.0
Nitrate (mg/L x 10^{-2})	24.2	24.8	25.9	24.1	24.7	15.1
Sol. react. silica (mg/L)	0.9	1.1	1.0	1.1	0.8	0.3
Kjeldahl nitrogen (mg/L x 10^{-2})	14.3	14.3	18.4	16.4	16.0	13.4
Total phosphorus (mg/L x 10^{-2})	0.3	0.4	0.6	0.4	0.4	0.5
Chlorophyll (mg/m^3)	0.7	1.2	1.4	1.2	0.9	0.9
Phyto. carbon/zoop. carbon	1.5	2.2	1.3	2.2	1.5	3.2

[1] All data, with the exception of sample depth and carbon ratio, were obtained from Moll and Rockwell (in prep.).

ranged from 1,800/m^3 (April) to 27,601/m^3 (July) while Lake Erie standing stocks ranged from 12,489/m^3 (April) to 204,037/m^3 (July). Watson and Wilson (1978) estimated that Lake Superior crustacean (including nauplii) standing stocks ranged from a 1973 November low of 1,350/m^3 to a June high of 3,656/m^3. Thus, 1980 Lake Huron crustacean standing stocks (April to July) were intermediate between those reported for oligotrophic Lake Superior and meso-eutrophic Lake Erie.

For southern Lake Huron, McNaught et al. (1980) estimated the following cruise means for total crustaceans, including nauplii; 2,725/m^3 for April 1975, 79,941/m^3 for May 1975, 47,543/m^3 for May-June 1975, and 115,626/m^3 for July 1974. Nauplii accounted for approximately 51%, 90%, 62%, and 5% respectively of the crustacean zooplankton. Differences between 1970 (Watson and Carpenter 1974), 1974 and 1975 (McNaught et al. 1980), and 1980 Lake Huron crustacean population estimates may be indicative of an increase in crustacean standing stocks between 1970 and 1974 followed by a slight decrease in the latter half of the decade. Alternately, differences may be due to different sampling locations and methodology.

The 1980 Lake Huron crustacean community was numerically dominated by Cyclops bicuspidatus thomasi, Diaptomus ashlandi, D. minutus, and D. sicilis while Bosmina longirostris, Daphnia galeata mendotae, D. retrocurva, and Eubosmina coregoni were important July species. Similar species dominance was reported by Watson and Carpenter (1974). Mesocyclops edax, Eurytemora affinis, Cyclops vernalis, Chydorus sphaericus, and Eurycercus lamellatus, species which are relatively abundant in the more eutrophic regions of the Great Lakes (Patalas 1972), were rare. Diaptomus siciloides, Alona spp., Daphnia parvula, D. pulex, and D. ambigua, species reported from the eutrophic regions of Lakes Erie, Michigan, and St. Clair (Patalas 1972, Watson and Carpenter 1974, Gannon 1972) were not observed. Limnocalanus macrurus and Senecella calanoides, hypolimnetic stenotherms, were observed during the four cruises; low abundances are typical for these deep-living species.

Rotifer standing stocks for the 1980 Lake Huron surveillance cruises also were indicative of oligotrophic conditions. Standing stocks were low, ranging from 4,541/m^3 (June) to 14,993/m^3 (July). In contrast, Nauwerck (1978)

reported 1970 Lake Ontario cruise means as ranging from 10,500/m^3 (April) to 220,800/m^3 (July). Duffy and Liston (1978) reported cruise means of 9,600/m^3 (May 1974) to 364,000/m^3 for central Lake Michigan. These values are similar to those reported by Stemberger (1974) for the open waters of Lake Michigan. However, in the eutrophic waters of Milwaukee Harbor, rotifer densities exceeded 1,500,000/m^3. Similarly, Stemberger et al. (1979) reported considerable variation in rotifer densities in Saginaw Bay. For example, in July 1974, rotifer densities exceeded 4,000,000/m^3 at the mouth of the Saginaw River and declined to less than 100,000/m^3 northeast of Saginaw Bay, a concentration gradient of more than 40. In contrast, the maximum rotifer density observed during the 1980 Lake Huron surveillance cruise was 37,341/m^3 at station 34 (north of Saginaw Bay and near Harrisville) in July.

Rotifer species composition also was typical of oligotrophic waters, with a spring assemblage of Notholca squamula and Synchaeta spp. succeeded by a July assemblage of Conochilus unicornis, Kellicottia longispina, and Keratella cochlearis cochlearis. Nauwerck (1978) observed a similar species assemblage in Lake Ontario. However, he observed that Synchaeta spp. acçounted for a larger fraction of the April and May rotifer population while Polyarthra major was relatively more abundant in July in comparison to the 1980 Lake Huron observations. Stemberger (1974) also observed a greater dominance of the April and May Lake Michigan rotifer community by Synchaeta spp. and the July community by Polyarthra species. Genera considered indicators of eutrophic waters (Patalas 1972, Nauwerck 1978) were rare (Filinia, Ploesoma, and Trichocerca) or not detected (Brachionus and Euchalanis).

Zooplankton standing stocks were dominated by crustaceans. Rotifers accounted for 13.9% (June) to 30.2% (April) of the zooplankton by numbers. The dominance of the zooplankton community by crustaceans is even more apparent when numerical standing stocks are converted to biomass (see the sections discussing regional differences in zooplankton community structure). Crustacean standing stocks ranged from a mean of 2.6 mgC/m^3 (May, Group 5, crustacean analysis) to a mean of 156.1 mgC/m^3 (July, Group 1, crustacean analysis). Conversely, rotifer standing stocks ranged from 0.01 mgC/m^3 (April, Group 3, rotifer analysis) to 1.29 mgC/m^3 (June, Group 1, rotifer

analysis). In general, rotifers accounted for less than one percent of the crustacean biomass.

Copepods, cladocerans, and rotifers have different life history strategies (Allen 1976) which may account for differences in their relative abundances in the oligotrophic, mesotrophic, and eutrophic waters of the Great Lakes. Rotifers have relatively short life cycles with generation times of 5 to 7 days at 10°C and a longevity of about 20 days. Conversely, copepods have generation times of 22 to 24 days and a longevity of about 85 days. Copepods, cladocerans, and rotifers also differ in their reproductive capacity. One such measure of this is "r" or the intrinsic rate of population increase. According to Allen (1976), rotifers are opportunistic animals with a maximum rate of increase (r_{max}) of 0.2 to 1.5 days. Conversely, cladocerans have an r_{max} of 0.2 to 0.6 days while copepods have an r_{max} in the order of 0.1 to 0.4 days. Cladocerans are more opportunistic than copepods (Allen 1976).

Differences in the capacity of rotifers, cladocerans, and copepods to increase in numbers in a relatively short time period has several implications. First, rotifers are more likely to dominate zooplankton populations when conditions become favorable for reproduction and survival. This is because rotifers have the capacity to respond rapidly to improved conditions in their environment. A relatively short generation time allows adults to reproduce and produce progeny which, in a matter of days, are reproductive. Conversely, copepods and cladocerans require longer periods of time before some improvement in the environment manifests itself in changes in crustacean standing stock or composition. Copepods, in particular, must go through several developmental stages before the sexually mature adult stage is reached. Both rotifers and cladocerans reproduce parthenogenetically. This, combined with faster developmental rates, allows animals to respond rapidly to improved environmental conditions. Thus, rotifers and cladocerans are particularly abundant (and dominant) in eutrophic waters, especially during the warmer summer months when developmental times are shorter.

Animals with relatively high rates of population increase such as rotifers and cladocerans can be considered opportunists while animals with slower rates of increase (copepods) are considered generalists (Allen 1976).

In unfavorable conditions, generalists usually dominate. There are several mechanisms accounting for this dominance: one is the physiological ability of the organism to withstand periods of stress. In the case of an oligotrophic water body such as Lake Huron, a major stress is food limitation.

Few researchers have investigated the capability of invertebrates to withstand food limitation. However, Threlkeld (1976) determined that a zooplankter's capacity to withstand food deprivation was linearly (log-log) related to its mean dry weight; larger animals were able to withstand periods of food deprivation for longer periods of time than smaller animals. This suggests that rotifers with a mean size range of 0.2 to 0.6 mm probably are less capable of withstanding long periods of food stress than the larger cladocerans with a size range of 0.3 to 3.0 mm; copepods with a size range of 0.5 to 5.0 mm (Allen 1976) should have the greatest capability to withstand food limitations. Recently, Goulden et al. (1982) determined that the percentage lipid content of new-born cladocerans increased with species body size. They hypothesized that the greater lipid reserves of larger species increased the probability of neonates attaining self-sufficiency in low-food environments. Thus their study supports Threlkeld's determinations.

Rotifers, cladocerans, and copepods have different physiological mechanisms for surviving stress. Rotifers and cladocerans, while reproducing parthenogenetically during favorable conditions, can reproduce sexually during periods of stress. The resulting fertilized egg is a resting egg surrounded by a relatively thick wall of protective material. Such eggs go through a period of dormancy enabling the organism to survive through long periods of desiccation and low temperatures. Conversely, copepods produce resting eggs less commonly although benthic forms (harpacticoids, cyclopoids) may encyst in the copepodite stage to withstand periods of stress (Wetzel 1975).

In the Great Lakes, many rotifers and cladocerans survive winter stress (low temperatures and food availability) by producing resting eggs which probably settle to the sediments. Conversely, most copepods remain in the plankton where they are physiologically active through periods of stress. Mechanisms of withstanding winter stress include storage of lipid reserves, or as in _Cyclops bicuspidatus thomasi_, arrested development in intermediate

copepodite stages (Torke 1975, Evans et al. 1980). Thus, the dominance of the spring Lake Huron zooplankton community by crustaceans probably is related to the capacity of these organisms to survive through the long winter months, a period in which food levels are low. Similarly, the general crustacean dominance during all cruise months may be related, in part, to the greater capability of crustaceans to withstand periods of food limitation in the oligotrophic waters of Lake Huron. Similarly, Allen (1976) related the dominance of copepods in the oceans and the deep, open waters of the Great Lakes to their superior adaptation to nutritionally dilute environments. Conversely, rotifers and cladocerans are rare in the oceans. In the Great Lakes, cladocerans make up a greater fraction of the crustacean zooplankton in shallow and in surface waters where nutrients are more abundant, allowing these rapidly reproducing animals to obtain abundances equal to or greater than the more slowly growing copepods (Allen 1976).

Correlation and principal component analyses reinforce these ideas. In April and May, crustacean abundances were not strongly correlated with any of the physical-chemical parameters analyzed. Conversely, rotifer species such as Kellicottia longispina, Notholca squamula, Synchaeta spp., and Polyarthra spp. abundances were significantly correlated with factors directly (chlorophyll) or indirectly (nitrate, soluble reactive silica) related to algal standing crops and productivity. This suggests that rotifers were able to respond rapidly to increases in algal productivity whereas copepods required a longer response time. However, rotifers accounted for a relatively small percentage of the zooplankton standing stock (biomass).

In June, the cladoceran Bosmina longirostris and immature Diaptomus spp. copepodites abundances were significantly correlated to factors related to algal productivity as were several species of rotifers (Notholca foliacea, Polyarthra dolichoptera, Synchaeta spp., Asplanchna spp., and Keratella quadrata). By July, with warmer water and a more rapid crustacean response to environmental conditions, the abundance of several taxa (nauplii, immature Cyclops spp. and Diaptomus spp. copepodites, Bosmina longirostris, Daphnia galeata mendotae, and D. retrocurva) were significantly correlated with factors directly or indirectly related to algal productivity. Conversely,

rotifer abundances were not as frequently correlated with such factors although significant correlations were observed for *Kellicottia longispina*, *Polyarthra dolichoptera*, and *Trichocerca multicrinis*.

In July, several rotifer and crustacean taxa abundances were significantly correlated with total phosphorus (nauplii, immature *Cyclops* spp., *Bosmina longirostris*, *Daphnia galeata mendotae*, *D. retrocurva*, *Trichocerca multicrinis*) and Kjeldahl nitrogen (*B. longirostris*, *D. galeata mendotae*, *Asplanchna* spp., and *T. multicrinis*). Such correlations may be simply indicative of the fact that particulate phosphorus and nitrogen were most abundant where faunal standing stocks were largest. Alternately, bacteria and organic aggregates were a significant component of this particulate phosphorus and nitrogen. Detritus can account for a major fraction of the particulate matter in lakes (Bloesch et al. 1977). Detritus may have served as an important food base (in addition to phytoplankton) for the zooplankton community, particularly the crustaceans.

Correlation analyses also determined that crustacean abundances were significantly intercorrelated. These correlations were due to the fact that many of the taxa analyzed were different life history stages of a relatively few species. For example, the correlation between nauplii (a significant number of which were diaptomids), immature *Diaptomus* spp. copepodites, and adult *Diaptomus* species (*D. ashlandi*, *D. minutus*, and *D. sicilis*) can be explained on the basis that nauplii tended to be most abundant where adults predominated. However, since these correlations among developmental stages persisted for several weeks, this interpretation is simplistic. Rather the data suggest that certain regions of the surveillance grid were more favorable than others for copepod fecundity, growth, and survival. In addition, it suggests that the various copepodite life history stages were affected similarly by the physical-chemical and biological characteristics of their environment. This is in agreement with the statement that copepods (and to a lesser extent cladocerans) are generalists. Conversely, rotifer abundances were less frequently intercorrelated. This suggests that these organisms were more uniquely affected by the physical-chemical and biological characteristics of their environment.

All statistically significant ($p<0.05$) taxa intercorrelations were positive indicating that, in certain regions of the surveillance grid, conditions were favorable for a number of zooplankton taxa while in other regions, conditions were not as favorable for zooplankton growth and survival. No statistically significant negative correlations were detected. This was unexpected because of known competitive and predator-prey relationships between zooplankton taxa. Given such relationships, some negative correlations were expected. The inability to detect such relationships probably is a function of study design. Stations were widely separated over the survey grid and located in distinct physical-chemical regimes. Differences in these characteristics had a major role in affecting zooplankton community structure. Within each region, predation and competition undoubtedly affected zooplankton community structure but on a finer scale.

The survey grid extended over the 320 km length of Lake Huron, including the North Channel and Georgian Bay. Stations generally were separated by distances of several tens of kilometers. With such spacing, physical-chemical factors probably had a major role in affecting lakewide differences in zooplankton community structure.

Similar zooplankton species occurred throughout the surveillance area during each of the four cruises: most species were observed at all stations. The major differences in zooplankton community structure in the various regions of the lake were in the relative abundances of species and in total standing stocks.

The zooplankton study design did not consist of a sufficient number of stations during each cruise to provide detailed information on the relationship between zooplankton community structure and water quality characteristics. However, the study does allow a number of inferences to be made. Such inferences are based on the abundance (both absolute and relative) of crustaceans and rotifers, and the concentrations of chlorophyll, soluble reactive silica, and nitrate. In addition, the phytoplankton:zooplankton carbon ratio was used to infer the relative magnitude of zooplankton grazing and algal productivity. In general, where the ratio was relatively low (in comparisons to other regions of the lake during the same cruise), grazing

pressure was inferred to be relatively high. If chlorophyll concentrations also were high, then it was inferred that primary productivity was relatively high: this conclusion is necessary for relatively high chlorophyll concentrations to persist despite heavy grazing.

A similar grazing index was used by Lorenzen (1967) who observed a good correlation between zooplankton:chlorophyll ratios and phaeopigment:chlorophyll ratios. As the abundance of zooplankton to chlorophyll concentration increased, the relative concentration of phaeophytin to chlorophyll increased. This suggested that grazing pressure on the phytoplankton community increased with increasing zooplankton abundance and that phaeophytin:chlorophyll ratio could be used as a grazing index. While the empirical value of Lorenzen's grazing index and the index used in this report have not been tested through field and laboratory experiments, both indexes have inituitive appeal. Future research effort should investigate the value of such indexes in surveillance studies.

Based on water chemistry, chlorophyll and zooplankton concentrations, and the grazing index, the most productive area of the survey grid appears to have been the nearshore region of southern Lake Huron. Saginaw Bay was not investigated in this study. Zooplankton standing stocks were consistently large in southern Lake Huron, particularly in the Bayfield-Goderich and Harbor Beach-Lexington areas. Chlorophyll concentrations were relatively high while plankton carbon ratios were low. On occasion, nitrate values also were relatively high (April, Group 1, rotifer analysis; May, Group 5, crustacean analysis; June, Group 1, crustacean analysis; June, Group 4, rotifer analysis). Relatively high nitrate values may be related to outflow of nutrient-rich water from Saginaw Bay along the southwestern shore of Lake Huron or to run-off and river discharge from agricultural areas along the southeastern shoreline (Davis et al. 1980). Proximity to shore and the general shallowness of station depths in this region also may have been significant factors affecting the large algal and zooplankton standing stocks. On occasion, other nearshore regions (Cheboygan, Harrisville, Presque Ile) had large zooplankton standing stocks.

Phytoplankton and zooplankton standing stocks varied between inshore and offshore waters. Standing stocks generally were lower offshore in early spring where intense vertical mixing of the water column probably resulted in phytoplankton being mixed below the compensation depth. Sverdrup (1953), in his classic study on the conditions necessary for the spring blooming of phytoplankton, emphasized the importance of stability of the water column in preventing phytoplankton from being mixed below the compensation depth. The relationship between phytoplankton abundance and thermal stability of the water column was further developed by Pingree (1978). Since fresh water attains its maximum density at 4°C (Wetzel 1975), waters which cool to 1 or 2°C over the winter do not become thermally stable until spring heating raises temperatures to a few degrees above the temperature of maximum density. Thus, part of Lake Huron remained thermally well-mixed until June. As in Lake Ontario (Scavia and Bennett 1980), the spring phytoplankton bloom was delayed in offshore waters, occurring later in the season than in the shallower nearshore waters. This apparently affected inshore-offshore differences in zooplankton standing stocks and, in particular, the lower offshore standing stocks in spring.

In April, phytoplankton productivity apparently was higher in the southern basin than in the northern basin (Group 3 versus Group 4, crustacean analysis). Although zooplankton biomass was similar in both regions, chlorophyll concentrations were more than twice as great in southern Lake Huron. The higher chlorophyll concentrations in southern Lake Huron, despite small differences in zooplankton biomass (and therefore grazing), suggest that phytoplankton populations in southern Lake Huron had higher primary productivity rates than populations to the north. Such apparently higher primary productivity probably was related to higher nutrient levels and regeneration rates in the southern basin and possibly to a longer period of daylight. Water temperatures did not exhibit a strong north-south gradient.

In July, a second region (in addition to the nearshore region of the southern basin) of apparently high primary and secondary productivity was the outflow from the St. Marys River. This was evidenced by the large standing stock of crustaceans, particularly the cladoceran Bosmina longirostris, and

the low phytoplankton:zooplankton carbon ratio (1.2). Chlorophyll concentration was relatively high (2.2 mg/m^3) despite apparently heavy grazing pressure. The reason why primary productivity apparently was high in this region was not determined.

In contrast to July, phytoplankton and zooplankton standing stocks in the St. Marys River and North Channel were low in April. This was a period when the river was characterized by a rapid current flow (due to spring melt) combined with a heavy sediment load. Carter and Watson (1977) also observed that it was not until July that zooplankton became relatively abundant in the North Channel.

River flow may affect plankton populations in a variety of ways. Suspended sediments reduce light penetration, restricting the growth of phytoplankton. In addition, high flow rates can retard the development of plankton blooms. Kierstad and Slobodkin (1953) determined that a plankton population in a finite region can support itself against dilution only if reproductive rates exceed outflow rates. In rivers, loss rates probably are larger than in lentic systems such as lakes where dilution and mixing are less intense. Thus, a river characterized by high flow rates (high dilution) and sediment loads (affecting phytoplankton photosynthetic rates) will contain relatively small phytoplankton blooms. Zooplankton, which have slower growth rates than phytoplankton, will occur in even lower abundances. In addition, plankton may be physically damaged in highly turbulent waters.

In April, low phytoplankton and zooplankton standing stocks in the St. Marys River and North Channel probably were related to the highly turbulent river flow. Standing stocks were higher in the Straits of Mackinac where flow rates and turbidity were reduced. The low standing stocks of zooplankton observed in May in Georgian Bay (Group 4, crustacean analysis) and offshore of Bayfield (Group 5, crustacean analysis) probably were related to dilution effects by river flow.

River flow also resulted in quantitative differences in zooplankton populations. For example, cyclopoid copepods were an important constituent of the crustacean population in the North Channel in April and may have originated primarily from the St. Marys River rather than from Lake Superior.

Kreis et al. (1983) demonstrated that the St. Marys River contains both benthic species (originating from the river) and euplanktonic species originating from Lake Superior: benthic species decreased in relative abundance to total phytoplankton in the North Channel.

In April, Georgian Bay crustacean populations (Group 2, crustacean analysis) were relatively large in comparison to the main body of Lake Huron. Chlorophyll concentrations were moderately high (>1.2 mg/m^3), suggesting that the spring phytoplankton bloom had commenced some time prior to the April cruise and persisted despite heavy grazing (the phytoplankton:zooplankton carbon ratio was 6.8). Relatively large zooplankton standing stocks could be related to run-off from the Canadian Shield (affecting primary productivity), relatively shallow depths (<30 m) over most of the bay, and a counterclockwise circulation (Carter and Watson 1977) which retained zooplankton within the bay. Carter and Watson (1977) also observed that April crustacean zooplankton were most abundant off the tip of the Bruce Peninsula, as was observed in this study. The reason why this region should be an area of relatively high crustacean standing stocks in April is not apparent.

Zooplankton grazing was not measured during this study. However, it is possible to make inferences regarding the dynamics of phytoplankton-zooplankton interactions. Crustaceans dominated the biomass of the zooplankton community and probably were the major grazers on the phytoplankton community.

In April, zooplankton were abundant in the nearshore region of Lake Huron (Groups 1 and 3, crustacean analysis). The high phytoplankton:zooplankton carbon ratio (39.3) for southern Lake Huron Group 3 suggests that a grazing loss were relatively small. The ratio (2.5) was lower for Goderich Group 1, suggesting higher grazing losses. Zooplankton were more abundant in Georgian Bay Group 2 than Group 3 and the phytoplankton:zooplankton carbon ratio (6.8) was lower. This suggests that grazers consumed more of the primary production in Georgian Bay than in southern Lake Huron Group 3.

In July, chlorophyll concentrations were low and homogenously (upper water column integrated measurement) distributed over most of the surveillance grid. Conversely, zooplankton were abundant and exhibited significant spatial

variability. Phytoplankton:zooplankton carbon ratios ranged from 0.4 to 3.2, suggesting that grazing pressure was more intense in July than in earlier survey months. In addition, these ratios suggest that grazing pressure varied over the survey grid. From this it can be inferred that primary production was relatively high in regions where zooplankton were abundant while rates were lower in areas where zooplankton were less abundant. The most productive areas were southeastern Lake Huron and the St Marys River.

McNaught et al. (1980) quantified the importance of crustacean grazing in the southern basin of Lake Huron. According to their calculations, grazing pressure was most intense between late May and early August. In a modeling study of phytoplankton population dynamics in Lake Ontario, Scavia (1979) determined that grazing accounted for most of the algal loss during July with grazing pressure remaining significant until October. Dagg and Turner (1982) determined that copepod grazing on phytoplankton over Georges Bank and the New York Bight varied seasonally, with the greatest uncoupling between primary and secondary producers occurring in spring. Beers and Stewart (1971) estimated that microzooplankton in the upper waters of the eastern tropical Pacific Ocean accounted for 23% to 66% of phytoplankton dry weight. This corresponds to a grazing index of 2.27-6.52, a range of values observed for the July Lake Huron cruise. Furthermore, they estimate that microzooplankton grazed an average of 70% of the daily primary production. This suggests that Lake Huron zooplankton may exert similar grazing pressure on the summer phytoplankton community. Overall, these studies suggest that zooplankton exert heavier grazing pressure on phytoplankton communities in summer than in spring.

RECOMMENDATIONS

Studies of zooplankton composition and abundance are a valuable part of surveillance work. Information on standing stocks and composition provides an independent confirmation of water quality as estimated by studies of nutrient levels and phytoplankton population characteristics. Furthermore, such studies can allow for approximate estimations of the relative variation (seasonal and spatial) in primary production. Since the 1980 surveillance

study did not include direct measures of algal productivity, such estimates are useful in evaluating the quantitative significance of seasonal and spatial variations in algal standing stocks.

The major limitation to this study was the limited number of stations sampled on each cruise. Future studies on Lake Huron (or other Great Lakes) should include investigations of zooplankton. A sufficient number of stations should be sampled in each area of interest to adequately investigate the relationship between zooplankton community structure and water quality. Stations should be consistently sampled between cruises in order to compare seasonal data. Ideally, sample analyses should be scheduled so that maximum use can be made of all appropriate data collected during a surveillance study. For this report, an investigation of phytoplankton-zooplankton relationships would have been especially interesting. The empirical value of grazing indexes should be tested to determine if relative grazing pressure can be estimated through the simple determinations of plant pigment and zooplankton concentrations.

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