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John Korstad
*University of Michigan-Ann Arbor*



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# NUTRIENT REGENERATION BY ZOOPLANKTON IN SOUTHERN LAKE HURON

**John Korstad**[1]
*Division of Biological Sciences*
*Natural Science Building*
*The University of Michigan*
*Ann Arbor, Michigan 48109*

*ABSTRACT. Rates of nutrient regeneration by zooplankton (μmol/mg dry wt/hr) in southern Lake Huron from April to August 1975 ranged from undetectable to 2.6 for total phosphorus (TP), undetectable to 0.8 for total soluble phosphorus (TSP), undetectable to 0.12 for soluble reactive phosphorus (SRP), undetectable to 0.97 for ammonia ($NH_3$), undetectable to 3.8 for nitrate plus nitrite ($NO_3 + NO_2$), and undetectable to 2.9 for silica ($SiO_2$). Two diel experiments were conducted. Times of highest rates of regeneration varied for the different nutrients on these dates. Using the average concentration of zooplankton in the surface waters during this study, the calculated average concentration of nutrients regenerated by zooplankton was 0.012 μmol P/L/hr for TP, 0.0046 μmol P/L/hr for TSP, 0.0016 μmol P/L/hr for SRP, 0.0146 μmol N/L/hr for $NH_3$, 0.043 μmol N/L/hr for $NO_3 + NO_2$, and 0.058 μmol Si/L/hr for $SiO_2$. The contribution of nutrient regeneration by zooplankton to the turnover time of the various nutrients in the surface waters was calculated to be 212 hr for TP, 239 hr for TSP, 69 hr for SRP, 62 hr for $NH_3$, 505 hr for $NO_3 + NO_2$, and 531 hr for $SiO_2$. Although the turnover time for most of these nutrients is fairly slow, the nutrient pools for SRP and $NH_3$ are replenished in less than 70 hr by nutrient regeneration. Zooplankton therefore appear to play a significant role in the cycling of SRP and $NH_3$ in southern Lake Huron.*

*ADDITIONAL INDEX WORDS: Water chemistry, nutrient cycling, phosphorus, nitrogen, silica.*

## INTRODUCTION

The concentration of each nutrient in a body of water is dependent not only on the rate of supply, rate of uptake, and loss rate from the body of water, but also on the rate at which each nutrient is recycled between available and unavailable pools within the water body. In those lakes and regions of the ocean where the rates of supply and loss are fairly low, processes that recycle nutrients take on added significance.

Nutrient regeneration can be defined as the release of soluble organic or inorganic plant nutrients by or from organisms or their remains (Johannes 1968). In aquatic ecosystems, three mechanisms operate to return these nutrients to the nutrient pool: 1) direct release by plants, 2) excretion by zooplankton, and 3) enzymatic hydrolysis of organic compounds excreted by organisms or produced by autolysis or decomposition of dead plankton (Rigler 1973). This paper considers the contribution of living zooplankton to the cycling of nutrients. Mechanisms of zooplankton regeneration include release of nutrients from food material broken up by the mandibles, egestion (voided undigested material), and excretion (dissolved metabolic waste material).

Nearly all of the soluble phosphorus excreted by zooplankton is in the form of orthophosphate (Peters and Lean 1973). Butler *et al.* (1969) estimated that 71 to 87 percent of the phosphorus released is in the form of soluble reactive phosphorus (SRP). Most of the nitrogen released is in the form of ammonia (about 75%: Corner and Newell 1967, Jawed 1969), with the rest as urea, amino acids, or other organic compounds.

Previous studies indicate that zooplankton recycle from 0.001 to 0.921 μmol P/mg dry wt/hr as SRP and from 0.001 to 0.522 μmol N/mg dry wt/hr as $NH_3$ (Rigler 1961; Whittaker 1961; Barlow and Bishop 1965; Hargrave and Geen 1968; LaRow 1971; Peters and Rigler 1973; Ganf and Blazka 1974; LaRow *et al.* 1975; Peters 1975; Ferrante 1976; Gophen 1976; Jacobsen and Comita 1976;

[1]Present address: Department of Natural Science; Oral Roberts University; 7777 S. Lewis; Tulsa, Oklahoma 74171.

Lehman 1978, 1980a, b). (Table 2-1 with converted data is available in Korstad 1980 or by request.) These released nutrients supply 3 to 171 percent of the total daily nitrogen and phosphorus requirements of the phytoplankton (Hargrave and Geen 1968; Peters and Rigler 1973; Ganf and Blazka 1974; LaRow and McNaught 1978; Lehman 1978, 1980a, b), depending on nutrient concentrations, phytoplankton standing crop, physiological status of the phytoplankton, and other factors. The extreme range of regeneration rates appears to reflect more than differences caused by different environments, animals, or methodology, and may include gross contaminations or miscalculations (Rigler 1961, Whittaker 1961, Barlow and Bishop 1965, Peters and Rigler 1973, Ferrante 1976).

Much controversy still prevails in this field of research. There is a quandary in nutrient regeneration measurements because zooplankton must be feeding to exhibit true egestion and excretion, but phytoplankton if present can immediately take up the released nutrients (Takahashi and Ikeda 1975). Some workers have tried to overcome these problems by crowding zooplankton or doing the experiments in the dark. However, Mullin *et al.* (1975) have cautioned that use of crowded, unsorted animals results in higher than normal regeneration rates because of loss of nutrients from damaged zooplankton. Also, Ketchum (1939), Eppley and Coatsworth (1968), and Ganf and Viner (1973) have reported that phytoplankton can take up nutrients even in the dark.

No previous investigations of nutrient regeneration by zooplankton have been done in any of the Laurentian Great Lakes. This study demonstrates the importance of zooplankton to the cycling of nutrients in one of these lakes by presenting field measurements of zooplankton nutrient regeneration rates in southern Lake Huron from April to August 1975. Some of the questions investigated include:

1) What are the ranges in regeneration rates of different nutrients by zooplankton in southern Lake Huron?
2) Are the regeneration rates of these nutrients uniform at all sampling stations (e.g., nearshore vs offshore, Saginaw Bay vs open lake, etc.)?
3) Are there diel differences in nutrient regeneration rates at one sampling location?

## MATERIALS AND METHODS

Nutrient regeneration was measured on shipboard on the research vessel *Roger R. Simons* at various

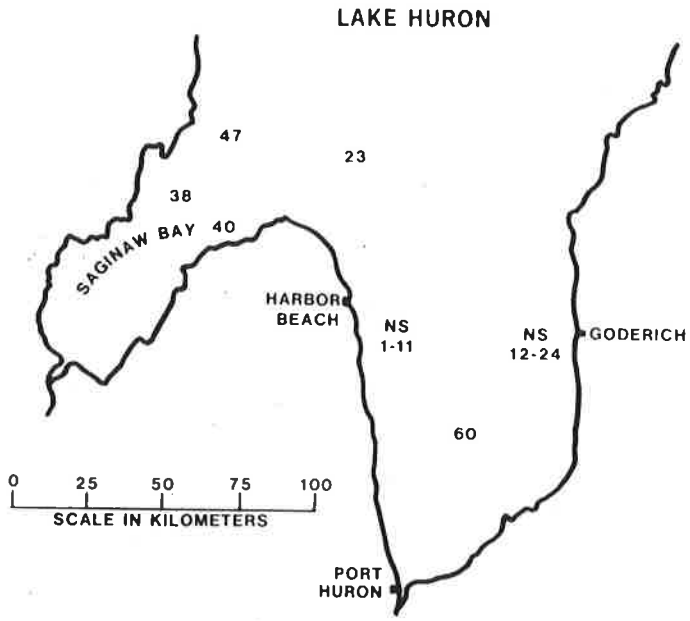


***FIG. 1. Map of southern Lake Huron showing sampling stations.***

locations on southern Lake Huron (see Fig. 1). Four cruises were conducted in 1975: Cruise 1 (29 April to 2 May), Cruise 2 (5 to 9 May), Cruise 3 (28 May to 2 June), and Cruise 4 (31 July to 5 August). At each location, a whole water sample was taken at 5 m using a 4-L Niskin bottle, and two zooplankton samples were taken by towing a number 20 mesh plankton net (67 $\mu$m aperture) vertically from 5 or 10 m to the surface. The contents of one net haul were carefully washed into a Mason jar and preserved with 4 percent formalin with sucrose (Haney and Hall 1973) for later determination of numbers and species composition of zooplankton. To separate zooplankton from phytoplankton retained in the net (typically large diatoms and blue-green algae), an aliquot of the living contents of the other net haul was placed in a darkened 1,000-mL separatory flask supported on a ring stand and filtered (0.45 $\mu$m pore size Millipore filter) lake water was added to bring the volume up to 800 mL. A blue light, placed near the top of the open flask, attracted live zooplankton to the upper layer of water. The apparatus was kept in this vertical position for up to 1 hr, after which time the contents were slowly poured out through the stopcock until about 200 mL of water remained. This water, containing relatively low concentrations of phytoplankton but teeming with active

zooplankton, was then poured through a 202 μm Nitex netting sieve to remove most of the phytoplankton from zooplankton except at infrequent times when large blue-green algae were abundant.

Initial water temperature was determined in the water sample taken from 5 to 10 m. Two 60-mL water samples, one filtered through a prerinsed 0.45 μm Millipore filter and the other unfiltered, were immediately frozen in plastic bottles and later transported to Ann Arbor, Michigan, for analysis of total soluble phosphorus (TSP) and total phosphorus (TP), respectively, using a Technicon AutoAnalyzer system I (Menzel and Corwin 1965). An additional 50-mL sample was filtered and frozen until analysis about 2 to 8 hr later on shipboard for soluble reactive phosphorus (Murphy and Riley 1962), nitrate + nitrite ($NO_3 + NO_2$), silica ($SiO_2$) (Armstrong *et al.* 1967), and ammonia ($NH_3$) (Slawyk and MacIssac 1972), using a Technicon AutoAnalyzer system II.

Although SRP and $NH_3$ are released directly by feeding zooplankton and are usually the major nutrients measured in studies of this type, the other nutrients (TP, TSP, $NO_3 + NO_2$, and $SiO_2$) were measured because it was believed that zooplankton would regenerate them by mechanically breaking cells apart with their mandibles or in their gut, resulting in leakage of these nutrients into the water.

Various numbers of zooplankton were added to lake water that had been filtered through a 0.45 μm Millipore filter and placed in either 310 mL BOD bottles or 30-mL test tubes. The BOD bottles were incubated in an on-deck incubator under artificial "cool white" fluorescent lights (118 $\mu Ein/m^2/sec$, Li-Cor quantum meter) and at the temperature of 1 m lake water continuously pumped through the incubator. The test tubes were incubated in the shipboard laboratory in a tub with 1 m lake water flowing through it and fluorescent lighting about 2 m overhead. Incubations lasted from 1 to 6.5 hr with most lasting about 2.5 hr. No animals died during the experiments. At the end of the incubation, the contents of the bottle or test tube were filtered into a clean container through a sieve made by attaching 102 μm Nitex netting to one end of a plastic cylinder. The sieve was immediately placed in distilled water at 100° C for approximately 10 seconds to kill the zooplankton. The dead zooplankton were rinsed from the netting with distilled water into a gridded petri dish for counting under a dissecting microscope. The water in the test tube was filtered through a 0.45 μm Millipore filter, poured into a water chemistry bottle, frozen, and analyzed within 2 to 8 hr for the various nutrients with the AutoAnalyzer on the ship. Sixty mL of the water from experiments using BOD bottles were poured into a water chemistry bottle and frozen for determination of TP. The rest of the liquid was filtered through a 0.45 μm Millipore filter. Sixty mL were frozen for determination of TSP, 60 mL were frozen for analysis of SRP, $NO_3 + NO_2$, $SiO_2$ and $NH_3$ by the AutoAnalyzer, and 100 mL were used immediately for determination of SRP with a Spectronic-20 (organic extraction method of Strickland and Parsons 1968). The extraction method measures lower concentrations of SRP than the AutoAnalyzer method (Range: 0.006-0.30 μM P and 0.03-5 μM P, respectively; Strickland and Parsons 1968).

Rates of nutrient regeneration were calculted as the difference between nutrient concentration in the experimental and control (average of two replicates with only 0.45 μm pore size Millipore-filtered lake water) vessels at the end of the incubation time. All rates were expressed per mg zooplankton dry weight and per hour of incubation.

To minimize contamination, all of the glassware used in the experiments was soaked in 10 percent hydrochloric acid and rinsed with double-distilled water before use, and gloves were worn when handling glassware. In addition, the BOD bottles and test tubes were capped during incubation.

A study was conducted to determine regeneration rates at various lengths of incubation time. Two sets of bottles, one with low and the other with high concentrations of zooplankton, were incubated for 1, 2, or 4 hr.

Two experiments were conducted at one station during a 24-hr period to document diel variation in rates of nutrient regeneration. Water and zooplankton samples were collected at 5 m every 4 to 8 hr for approximately 24 hr. The test tubes and bottles for the night experiments were incubated in the dark to simulate conditions of collection.

A radiotracer experiment was conducted during the last cruise (30 July to 5 August 1975) to compare chemical and radiotracer methods for measuring phosphorous release rates. Fifty μCi $^{33}P$ were added to a BOD bottle containing whole lake water collected at 10 m from Station 60. The bottle, containing about 0.16 μCi/mL, was placed in the on-deck incubator with alternating periods of 16 hr light/8 hr dark. After the phytoplankton were exposed to the tracer for 30 hr (for uniform labeling), zooplankton collected in a 5 m to surface

net haul at Station 38 were added to the bottle. The bottle was returned to the incubator for another 3 days to allow the zooplankton to incorporate the $^{33}P$ into their tissues. The zooplankton were then assumed to be uniformly labeled (cf. Peters and Lean 1973, Table 1). Most of these zooplankton remained healthy (as evidenced by their normal swimming patterns) and were used for the following two experiments. In the first experiment four zooplankton were placed in a beaker with unlabeled phytoplankton for about 30 min to empty their guts of radioactive algae. They were then transferred to another beaker with 0.45 $\mu$m Millipore-filtered lake water with 102 $\mu$m Nitex netting at the bottom. Following the method of Peters (1975), at certain time intervals the syringe was emptied (except for 0.5 mL to keep the zooplankton in suspension) into a scintillation vial with 10 mL Aquasol. The vials were stored in the dark with minimal disturbance until they were counted for radioactivity with a Beckman LS-230 liquid scintillaton counter in Ann Arbor. After each emptying, 2.0 mL of filtered lake water were drawn into the syringe containing the animal. Between emptyings the syringe was stored in a beaker with water at lake temperature (23.5°C). At the end of the experiment the zooplankton were killed in 100°C distilled water and placed on a precombusted and preweighed glass-fiber filter. They were dried for 24 hr at 70°C, stored in a desiccator, and weighed in Ann Arbor with a Cahn electrobalance. The second experiment was conducted in much the same way, except 10 zooplankton were used, and the syringe was incubated at 19.5°C. Excretion rates were calculated by the formula in Peters and Rigler (1973). Specific activity of the zooplankton was calculated by dividing $\mu$Ci/L $^{33}P$ (accounting for radioactive decay) by $\mu$mol/L $^{31}P$ (measured from a whole water sample from 5 m at Station 60 for total phosphorus).

Various parametric (2-sample t test, One-Way ANOVA, and Scheffé's multiple comparison test) and nonparametric (Mann-Whitney test and Kruskal-Wallis test) statistical tests were performed to test for differences in mean rates of regeneration of one nutrient between two or three groups of stations or cruises. The hypothesis for each test was that there were no differences in mean regeneration rate of that nutrient between the two or three groups being tested. Specific applications of these tests are discussed in the Results section. The nonparametric tests were used when the sample size was less then 10 or when the assumptions for parametric analysis were not met. These tests were conducted with various programs available on an HP 9845S computer and with MIDAS (Michigan Interactive Data Analysis System) on the University of Michigan Terminal System (MTS). Assumptions of normality and homogeneous variances for parametric tests were analyzed by several techniques using MIDAS. These assumption tests included residual plots, skewness, and kurtosis of the residuals, normalized plots of the residuals, Lilliefor's test for normality, and Bartlett's test for homogeneous variances. Considerable differences in concentrations of zooplankton, incubation time, time of day, temperature, and other factors generated large variablility in pooled rates of nutrient regeneration for each cruise. Based on the criteria of the models and the consequences of making either a Type I or Type II error, I decided on a compromise significance level of 0.10.

## RESULTS

The results of the preliminary study to determine the relation between incubation time and regeneration rate revealed that, at both concentrations of zooplankton, SRP regeneration rates generally decreased as incubation time increased. Similar results were found in laboratory experiments (Korstad, unpublished data). Since the zooplankton were essentially starved during experimental incubation, higher rates of nutrient regeneration in the first hour may have been caused by recent feeding prior to or during the time they were in the funnel, which may mean that these experiments initially measured excretion plus egestion. Lower rates after longer incubation times might thus reflect progressively lesser amounts of food in the animals' guts as shown by Jawed (1969). Experiments lasting several hours probably measured mostly rates of endogenous excretion. These results have been reported by other authors, leading them to use completely starved animals in some experiments (Marshall and Orr 1955, Rigler 1961, Corner and Newell 1967, Corner *et al.* 1967). I started the experiments using fed animals to determine more realistic rates of nutrient regeneration by zooplankton in Lake Huron. Incubation times used in the experiments following the preliminary experiments ranged from 1.0 to 6.5 hr, averaging 2.6 hr. Shortest incubation times were used on Cruise 4, followed successively by Cruises

3, 2, and 1. Constant incubation times were not used because two or three experiments were sometimes conducted at one station and times between sampling stations varied with distance and ship speed.

Regeneration rates in this preliminary study were generally higher in bottles with low concentrations of zooplankton than with high. This was also found in other laboratory and field experiments (Peters and Rigler 1973, Korstad unpublished data) and may reflect lower rates of regeneration resulting from physiological stress caused by crowding in the experimental containers with high numbers of zooplankton. Peters and Rigler (1973) believe that the low excretion rates reported by Barlow and Bishop (1965) may be partly explained by crowding of animals.

Rates of nutrient regeneration by zooplankton in the experiments are summarized in Tables 1, 2, and 4 to 6. The number of zooplankton used for all of the experiments ranged from 32 to 2,067 ($\bar{x}$ = 615; SE = 93) zooplankton/L during the first cruise, from 100 to 5,666 ($\bar{x}$ = 1892; SE = 639) zooplankton/L during the second cruise, from 132 to 7,366 ($\bar{x}$ = 1907; SE = 252) zooplankton/L during the third cruise, and from 33 to 8,599 ($\bar{x}$ = 1523; SE = 278) zooplankton/L during the fourth cruise. The results of the experiments using BOD bottles and test tubes are combined. Concentrations of zooplankton were generally two to three times higher in the test tube experiments than in the BOD bottle experiments. Watson and Carpenter (1974) found that the average number of crustacean zooplankton (>64 $\mu$m) per liter in Lake Huron ranged from 20 (early spring) to 100 (late spring) to 250 (summer). McNaught *et al.* (1980) conducted zooplankton feeding experiments during some of these cruises and estimate the abundance of zooplankton (>64 $\mu$m) in the top 5 m of the lake to be 33.2, 74.1, and 86.2 zooplankton/liter for Cruises 1, 3, and 4, respectively. My experimental concentrations of zooplankton therefore averaged about 17 to 26 times the lake concentration of zooplankton as determined by McNaught *et al.* These high concentrations of zooplankton were used to provide sufficient excreted nutrients for measurement. Since only healthy, actively swimming zooplankton were used in these experiments, sources of error in measuring rates of nutrient regeneration caused by leakage of nutrients from dead or injured zooplankton (Mullin *et al.* 1975) were minimal. Zooplankton concentrations (numbers and biomass) used in other studies equal or exceed these concentrations (Harris 1959, Pomeroy *et al.* 1963, Barlow and Bishop 1965, Corner *et al.* 1967, Peters 1975).

*Diaptomus sicilis*, *Eubosmina coregoni*, and *Bosmina longirostris* were abundant throughout the cruise season. *Diaptomus* commonly comprised more than 70 percent of the total number of zooplankton during the first three cruises (April to June). *Eubosmina* and *Bosmina* frequently accounted for the same percentage during the last cruise (July to August). Other less common genera found in Lake Huron during this study included *Daphnia*, *Ceriodaphnia*, *Holopedium*, *Moina*, and *Eurytemora*.

Stoermer and Kreis (1980) have described the seasonal abundance of the major groups of phytoplankton in southern Lake Huron. Diatoms are generally abundant during spring and late summer. Green and blue-green algae are generally low in abundance during spring and start increasing in late July, reaching their peak abundance in late summer-early fall. Microflagellates remain relatively scarce throughout the year. The increase of blue-green algae during the late summer months of my study had some impact on the nutrient regeneration experiments because blue-green algae were particularly difficult to separate from zooplankton owing to their large size (overlapping the zooplankton size range) and their flotation in the top layer of water. Blue-green blooms were encountered at Station 23 on 31 July and at Station 38 on 1, 3, and 4 August. On the first two dates the blooms were not too dense and some zooplankton could be separated from them. On 3 August the bloom was more dense and some zooplankton were separated from the algae only after passing the water through a 505 $\mu$m Nitex netting sieve, which retained only large zooplankton like *Daphnia*. The blue-green bloom was so dense on 4 August that separation was impossible and no experiments were conducted.

The nutrient regeneration experiments conducted during Cruise 1 (Table 1) were all done near either the Canadian (Stations NS 1-11) or USA (Stations 12-24) shorelines (see Fig. 1). Average rates of regeneration for all nutrients were higher at the Canadian stations than at the USA stations. Ambient lake concentrations are generally higher at the inshore Canadian than the inshore USA stations for all nutrients (Schelske *et al.* 1980). Average regeneration rates of each nutrient at the Canadian stations were compared to those at the USA stations using the Mann-Whitney test. Dif-

*TABLE 1. Rates of nutrient regeneration for Cruise 1, 29 April to 2 May 1975. All experiments were conducted near either the Canadian (Stations NS 1-11) or USA (Stations NS 12-24) shorelines.*

| | Zoopl. (#/L) | Zoopl. Dry Wt. (mg/L) | Incuba. Time (hr) | Nutrient Regeneration µmol/mg/hr | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | TP | TSP | SRP | $NH_3$ | $NO_3$+$NO_2$ | $SiO_2$ |
| | | | | Canadian Stations | | | | | |
| Range | 32–937 | 0.14–12.00 | 2.2–3.0 | U*–2.59 | U–0.790 | U–0.077 | U–0.736 | U–2.26 | U–3.11 |
| $\bar{x}$ | 378 | 3.33 | 2.71 | 0.471 | 0.162 | 0.019 | 0.075 | 0.211 | 0.312 |
| SE | 50 | 0.78 | 0.06 | 0.236 | 0.092 | 0.007 | 0.039 | 0.111 | 0.161 |
| n | 20 | 18 | 20 | 11 | 9 | 20 | 20 | 20 | 20 |
| | | | | USA Stations | | | | | |
| Range | 150–2067 | 1.0–90.66 | 3.0–4.33 | 0.003–0.158 | U–0.022 | U–0.021 | U–0.031 | U–0.696 | U–1.79 |
| $\bar{x}$ | 953 | 20.83 | 3.94 | 0.043 | 0.004 | 0.001 | 0.004 | 0.045 | 0.076 |
| SE | 182 | 4.89 | 0.08 | 0.023 | 0.003 | 0.001 | 0.001 | 0.030 | 0.074 |
| n | 14 | 24 | 24 | 8 | 8 | 24 | 24 | 23 | 24 |
| | | | | Results of Mann-Whitney test | | | | | |
| All data, p = | | | | 0.750 | 0.564 | +— | — | — | — |
| Only non-zero numbers, p = | | | | 0.002 | 0.022 | 0.018 | 0.010 | 0.004 | 0.856 |

*U = Undetectable

+Too many ties to analyze

ferences between mean rates of TP and TSP regeneration for these two areas of the lake were insignificant, while those of the other nutrients could not be analyzed because of too many ties (i.e., identical values). If all of the undetectable measurements were dropped, differences were significant except for $SiO_2$. Interpretation of these findings must be guarded, however, because most of the undetectable measurements were at the Canadian stations and eliminating these values caused the rates of nutrient regeneration at the Canadian stations to become significantly higher than those at the USA stations.

The nutrient regeneration experiments conducted during Cruises 2 to 4 (Table 2) were all done at either open lake (Stations 23 and 60) or Saginaw Bay (Stations 38, 40, and 47) stations. Average regeneration rates of each nutrient at the open lake stations were compared to those at the Saginaw Bay stations. The data were analyzed using the nonparametric Kruskal-Wallis test because the assumptions of normality and homogeneous variances were not met. The data were further analyzed graphically by plotting means and standard errors to see where, if any, differences in means were.

Average regeneration rates were significantly different for all of the nutrients for Cruises 2 to 4. Rates of $NO_3$ + $NO_2$ and $SiO_2$ regeneration were highest on Cruise 2, whereas rates of TP, SRP (AA and Extr.), and $NH_3$ regeneration were highest on Cruises 3 and/or 4. Rates of TSP regeneration were highest on Cruises 2 and 3. Regeneration rates were higher for TP and TSP relative to SRP and for $NO_3$ + $NO_2$ relative to $NH_3$ for Cruises 2 to 4 (as well as for Cruise 1). These results are summarized graphically in Figure 2.

Numbers of zooplankton per liter used in the experiments were not significantly different among the three cruises. Zooplankton dry weight and incubation time, however, significantly decreased as the cruise season progressed. This change reflected an attempt to decrease the zooplankton biomass and incubation time in later experiments. This change was thought to help minimize errors in measuring rates of nutrient regeneration caused by high concentrations of zooplankton and long incubation times (Peters and Rigler 1973, Mullin *et al.* 1975). Although these differences prevent exact comparisons among experiments, comparisons can still be made in a general way.

Rates of SRP regeneration measured with the AutoAnalyzer were not significantly different from those measured by extraction on the first and third cruises. On the second cruise, however, slightly higher measurements were obtained by the extraction method. This may have been caused by the

*TABLE 2. Rates of nutrient regeneration for Cruises 2–4, May to August 1975. All experiments were conducted at either open lake (Stations 23 and 60) or Saginaw Bay (Stations 38, 40, and 47) stations.*

| | Zoopl. (#/L) | Zoopl. Dry Wt. (mg/L) | Incuba. Time (hr) | Nutrient Regeneration µmol/mg/hr TP | TSP | SRP (AA) | SRP (Extr.) | $NH_3$ | $NO_3+NO_2$ | $SiO_2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Cruise 2 | | | | | | |
| Range | 100–5,666 | 0.27–154 | 3.0–6.5 | U*–0.094 | U–0.284 | U–0.030 | U–0.005 | U–0.066 | U–3.805 | U–1.637 |
| $\bar{x}$ | 1892 | 35.3 | 3.51 | 0.011 | 0.034 | 0.002 | 0.002 | 0.023 | 0.437 | 0.956 |
| SE | 639 | 5.4 | 0.18 | 0.007 | 0.022 | 0.001 | 0.001 | 0.005 | 0.179 | 0.243 |
| n | 11 | 34 | 34 | 13 | 13 | 25 | 6 | 20 | 30 | 8 |
| | | | | Cruise 3 | | | | | | |
| Range | 132–7366 | 0.33–60.7 | 1.12–4.5 | 0.011–0.229 | 0.005–0.134 | U–0.120 | U–0.025 | U–0.404 | U–1.217 | U–0.882 |
| $\bar{x}$ | 1907 | 8.38 | 2.60 | 0.069 | 0.028 | 0.010 | 0.005 | 0.051 | 0.087 | 0.075 |
| SE | 252 | 1.78 | 0.13 | 0.018 | 0.008 | 0.004 | 0.001 | 0.011 | 0.034 | 0.029 |
| n | 42 | 50 | 50 | 17 | 17 | 37 | 23 | 43 | 38 | 44 |
| | | | | Cruise 4 | | | | | | |
| Range | 33–8599 | 0.23–11.33 | 1.03–2.68 | U–0.213 | U–0.087 | U–0.117 | U–0.009 | U–0.974 | U–2.834 | U–2.94 |
| $\bar{x}$ | 1523 | 2.43 | 1.94 | 0.069 | 0.015 | 0.009 | 0.001 | 0.114 | 0.174 | 0.380 |
| SE | 278 | 0.36 | 0.07 | 0.010 | 0.004 | 0.005 | 0.001 | 0.025 | 0.083 | 0.096 |
| n | 46 | 46 | 46 | 26 | 26 | 26 | 26 | 46 | 44 | 46 |
| | | | | Kruskal-Wallis Test | | | | | | |
| p = | 0.113 | <0.001 | <0.001 | <0.001 | 0.017 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

*U = Undetectable

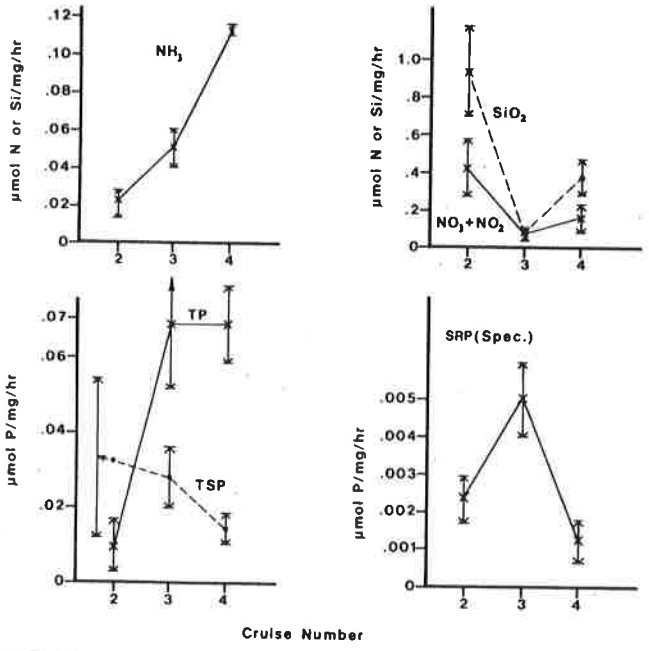


*FIG. 2. Graphical summary of Table 2. Rates of nutrient regeneration for Cruises 2–4, May to August 1975. Bars represent one standard error. SRP (Spec.) refers to soluble reactive phosphorus measured by the organic extraction method (see text for details).*

greater sensitivity of the organic extraction method, or it may merely reflect errors in measurement in either technique during that cruise.

Table 3 gives a summary of the surface nutrient concentrations measured in southern Lake Huron during Cruises 2 to 4. The average concentrations were 2.38 µM for TP, 1.10 µM for TSP, 0.11 µM for SRP, 0.90 µM for $NH_3$, 21.71 µM for $NO_3$ + $NO_2$, and 30.79 µM for $SiO_2$. These concentrations correspond closely to those reported by Schelske *et al.* (1980).

Average temperature at which the experimental containers were incubated on the four cruises was 7.16 (SE = 0.51), 8.43 (0.31), 16.29 (0.29), and 23.38 (0.18)°C for Cruises 1 to 4, respectively. This indicates that there was a narrow range in incubation temperature on each cruise, while the incubation temperature significantly ($p<0.001$, Kruskal-Wallis test)increased over the field season.

Tables 4, 5, and 6 give rates of nutrient regeneration averaged for the open lake and Saginaw Bay stations for Cruises 2, 3, and 4, respectively. On the second cruise (Table 4), rates of TP, TSP, and $NO_3$ + $NO_2$ regeneration were significantly higher ($p<0.05$, Mann-Whitney test) at the open

*TABLE 3. Summary of surface nutrient concentrations measured in southern Lake Huron for all stations during Cruises 2–4, May–August 1975.*

| | Nutrient Concentration (μM) | | | | | |
|---|---|---|---|---|---|---|
| | TP | TSP | SRP | $NH_3$ | $No_3+NO_2$ | $SiO_2$ |
| Range | 0.08–5.07 | 0.05–5.06 | U*–0.61 | U–2.79 | 6.69–90.44 | 5.00–107.86 |
| $\bar{x}$ | 2.38 | 1.10 | 0.11 | 0.90 | 21.71 | 30.79 |
| SE | 1.34 | 0.31 | 0.02 | 0.10 | 2.39 | 4.00 |
| n | 32 | 32 | 34 | 34 | 35 | 37 |

*U = Undetectable

lake than at Saginaw Bay stations. No significant differences were detected for rates of SRP (AA) and $NH_3$ regeneration. On the third cruise (Table 5), rates of regeneration of SRP (AA and Extr.) and $NH_3$ were significantly higher ($p<0.05$, Mann-Whitney test) at the Sagniaw Bay than open lake stations. Rates of TP and TSP regeneration were not significantly different. Differences in average rates of $NO_3$ + $NO_2$ and $SiO_2$ regeneration could not be analyzed by the Mann-Whitney test because too many of the values were tied. On the last cruise (Table 6), no significant differences for any of the nutrients were found, although rates of $NO_3$ + $NO_2$ and $SiO_2$ regeneration could not be analyzed because the nonparametric test on the HP 9845S computer was sensitive to too many ties.

The two 24-hr nutrient regeneration experiments were conducted at Stations 40 and 38 (Fig. 3). No statistical analyses were performed on the data because I wanted to look at only general trends in rates of nutrient regeneration. In both experiments, rates of TP and TSP regeneration were lowest at night (between 2400 and 0800 hr) and then progressively increased during the day (0800 to 2000 hr). Rates of SRP regeneration during the first experiment were highest at 0400 and 1800 hr and lowest at night. Soluble reactive phosphorus was not measured in the second experiment. In both experiments rates of $NH_3$ regeneration were highest beween 1600 and 2400 hr and lowest between 0400 and 1200 hr. Diel changes in rates of regeneration of the other nutrients were not analyzed. Neither diel experiment was run longer than 24 hr to see whether the pattern of nutrient regeneration repeated itself.

The results of both radiotracer experiments are listed in Korstad (1980). Because the animals were separated from radioactive algae for at least 60 min at the start of the experiments, most of the radioactive algae in their guts probably passed through by this time (Gauld 1953, Geller 1975). The regeneration rates are therefore expressed as excretion rates in this study. The rates of phosphorus excretion were plotted against incubation time on a semilog plot (Fig. 4) to obtain rates at the start of the experiments (time $t_o$). The regression equation for Experiment 1 is $Y = 0.0002\, e^{-0.0092x}$ ($R^2 = 0.407$; $p<0.025$), giving an excretion rate of 0.0002 μmol

*TABLE 4. Rates of nutrient regeneration at open lake (Stations 23 and 60) and Saginaw Bay (Stations 38, 40, and 47) stations for Cruise 2, 5–9 May 1975.*

| | Nutrient Regeneration μmol/mg/hr | | | | | | |
|---|---|---|---|---|---|---|---|
| | TP | TSP | SRP (AA) | SRP (Extr.) | $NH_3$ | $NO_3+NO_2$ | $SiO_2$ |
| | | | | Open Lake Stations | | | |
| Range | 0.004–0.094 | 0.004–0.284 | U*–0.030 | — | U–0.044 | U–3.81 | U–1.64 |
| $\bar{x}$ | 0.031 | 0.084 | 0.007 | — | 0.017 | 0.983 | 0.956 |
| SE | 0.021 | 0.054 | 0.006 | — | 0.009 | 0.366 | 0.243 |
| n | 4 | 5 | 5 | — | 5 | 13 | 8 |
| | | | | Saginaw Bay Stations | | | |
| Range | U–0.010 | U–0.005 | U–0.003 | U–0.005 | U–0.066 | U–0.114 | — |
| $\bar{x}$ | 0.002 | 0.003 | 0.001 | 0.002 | 0.026 | 0.019 | — |
| SE | 0.001 | 0.001 | 0.0002 | 0.001 | 0.006 | 0.008 | — |
| n | 9 | 8 | 20 | 6 | 15 | 17 | — |
| | | | | Mann-Whitney test | | | |
| p = | 0.014 | 0.010 | 0.30 | — | 0.41 | 0.022 | — |
| Result | OL>SB | OL>SB | OL=SB | — | OL=SB | OL>SB | — |

*U = Undetectable

*TABLE 5. Rates of nutrient regeneration at open lake (Stations 23 and 60) and Saginaw Bay (Stations 38, 40, and 47) stations for Cruise 3, 28 May to 2 June 1975.*

| | Nutrient Regeneration μmol/mg/hr | | | | | | |
|---|---|---|---|---|---|---|---|
| | TP | TSP | SRP (AA) | SRP (Extr.) | $NH_3$ | $NO_3$+$NO_2$ | $SiO_2$ |
| | | | Open Lake Stations | | | | |
| Range | 0.022–0.057 | 0.005–0.019 | U*–0.007 | U–0.002 | U–0.104 | U–0.075 | U–0.036 |
| $\bar{x}$ | 0.037 | 0.012 | 0.001 | 0.001 | 0.019 | 0.009 | 0.004 |
| SE | 0.008 | 0.003 | 0.001 | 0.0003 | 0.010 | 0.007 | 0.004 |
| n | 4 | 4 | 10 | 4 | 10 | 10 | 10 |
| | | | Saginaw Bay Stations | | | | |
| Range | 0.011–0.229 | 0.005–0.134 | U–0.120 | U–0.025 | U–0.404 | U–1.22 | U–0.882 |
| $\bar{x}$ | 0.079 | 0.03 | 0.013 | 0.006 | 0.061 | 0.115 | 0.095 |
| SE | 0.022 | 0.011 | 0.006 | 0.001 | 0.014 | 0.045 | 0.037 |
| n | 13 | 13 | 27 | 19 | 33 | 28 | 34 |
| | | | Mann-Whitney test | | | | |
| p = | 0.822 | 0.28 | 0.032 | 0.028 | 0.008 | 0.087+ | 0.092+ |
| Result | OL=SB | OL=SB | SB>OL | SB>OL | SB>OL | SB>OL | SB>OL |

*Undetectable
+Analyzed with the 2-sample t test because of too many ties for the Mann-Whitney test.

P/mg/hr at $t_o$. The regression equation for Experiment 2 is $Y = 0.0003\ e^{-0.0074x}$ ($R^2 = 0.694$; $p<0.025$), giving an excretion rate of 0.0003 μmol P/mg/hr at $t_o$.

## DISCUSSION

Rates of nutrient regeneration should be highest when zooplankton are feeding at maximum rates (Peters and Rigler 1973). Thus, when zooplankton encounter patches of phytoplankton, nutrient regeneration should be high. The higher rates at the Canadian nearshore stations compared to those near the USA shore, and the periodic higher rates at either the open lake or Saginaw Bay stations, may therefore be caused by greater numbers of phytoplankton in these areas at these times (Munawar and Munawar 1979, Schelske *et al.* 1980, Stoermer and Kreis 1980). Higher concentrations of phytoplankton in some areas may in turn be caused by higher rates of nutrient supply. Cycling of nutrients undoubtedly plays an intricate role in the distribution of both phytoplankton and zooplankton.

Rates of nutrient regeneration measured in this study are highly variable, even at one location at one time, for several reasons. Besides the influences of phytoplankton abundance, rates of nutrient regeneration also vary with changes in biomass and species of zooplankton, water temperature, incubation time, time of day, season, and other factors. Despite the variability, these rates are well within the range of rates of nutrient regeneration reported in the literature for freshwater zooplankton.

No clear seasonal trends in nutrient regeneration were observed in this study. Some nutrients (e.g., $NO_3$ + $NO_2$, $SiO_2$) were regenerated at higher rates on earlier cruises, while other nutrients (e.g., $NH_3$, SRP) were recycled faster on later cruises. Perhaps $NO_3$ + $NO_2$ and $SiO_2$ were regenerated at higher rates on the first cruise because this was when diatoms were at their peak. Zooplankton feeding on large colonial diatoms would be expected to break the frustules apart when feeding, thus releasing $NO_3$ and $SiO_2$ which are thought to be stored in vacuoles or other intracellular pools (Eppley and Coatsworth 1968, Kesseler 1974, Sullivan 1977, Chisholm *et al.* 1978). Silica released in this way would be in the dissolved form, whereas silica bound up in the broken frustules would be recycled at a much slower rate. Nevertheless, the role of zooplankton in recycling silica bound up in the frustules should not be minimized because bacterial degradation of diatom frustules is much more rapid on cells that are broken apart than on intact cells (Ferrante and Parker 1977, 1978; Parker *et al.* 1977; Ferrante and Ptaki 1978).

*TABLE 6. Rates of nutrient regeneration at open lake (Stations 23 and 60) and Saginaw Bay (Stations 38, 40, and 47) stations for Cruise 4, 31 July to 5 August 1975.*

| | Nutrient Regeneration µmol/mg/hr | | | | | | |
|---|---|---|---|---|---|---|---|
| | TP | TSP | SRP (AA) | SRP (Extr.) | $NH_3$ | $NO_3+NO_2$ | $SiO_2$ |
| | | | Open Lake Stations | | | | |
| Range | 0.010–0.104 | U*–0.022 | U–0.014 | U–0.009 | U–0.371 | U–0.165 | U–1.81 |
| $\bar{x}$ | 0.057 | 0.011 | 0.004 | 0.002 | 0.119 | 0.027 | 0.329 |
| SE | 0.018 | 0.003 | 0.001 | 0.001 | 0.029 | 0.014 | 0.146 |
| n | 6 | 6 | 14 | 6 | 14 | 14 | 14 |
| | | | Saginaw Bay Stations | | | | |
| Range | U–0.213 | U–0.087 | U–0.117 | U–0.009 | U–0.974 | U–2.83 | U–2.94 |
| $\bar{x}$ | 0.072 | 0.016 | 0.015 | 0.001 | 0.113 | 0.243 | 0.403 |
| SE | 0.012 | 0.005 | 0.010 | 0.001 | 0.034 | 0.119 | 0.124 |
| n | 20 | 20 | 12 | 20 | 32 | 30 | 32 |
| | | | Mann-Whitney test | | | | |
| p = | 0.586 | 0.564 | 0.878 | 0.350+ | 0.194 | 0.114+ | 0.365+ |
| Result | OL=SB | OL=SB | OL=SB | OL=SB | OL=SB | OL=SB | OL=SB |

*U = Undetectable
+Analyzed with the 2-sample t test because of too many ties for the Mann-Whitney test.

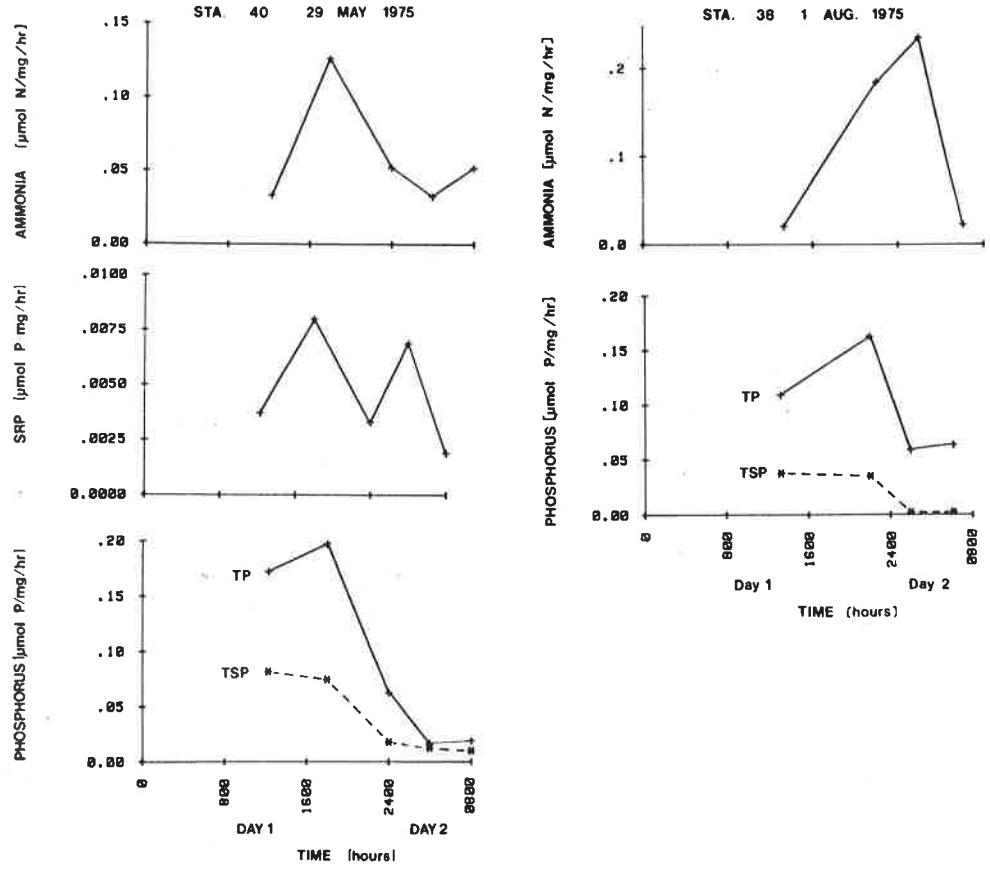


*FIG. 3. Rates of nutrient regeneration by zooplankton over 24 hr during the two diel studies at Station 40 on 29 May 1975 and at Station 38 on 1 August 1975.*

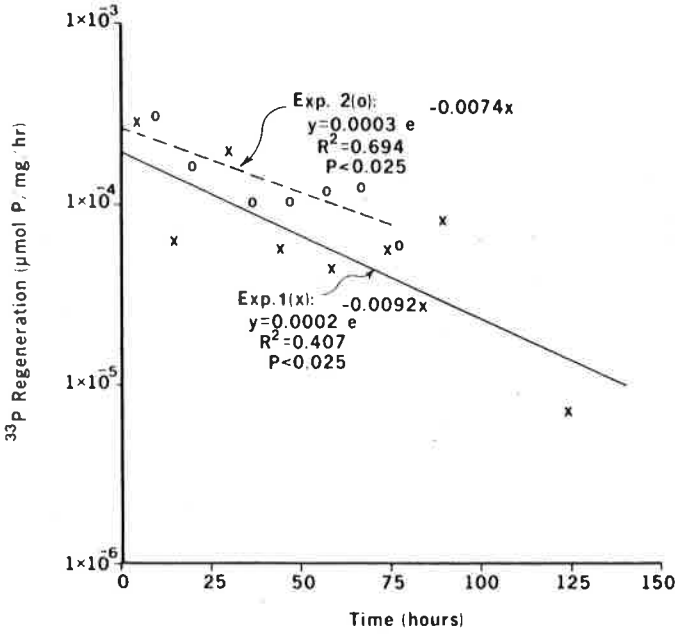


*FIG. 4. Rates of phosphorus excretion over time for the two $^{33}P$ experiments. Both experiments were conducted at Stations 38 and 60 on the last cruise (30 July–5 August 1975).*

Several mechanisms may help explain why regeneration rates of $NH_3$ and SRP were higher during the later cruises than during the earlier cruises. First, shorter incubation times were used during the later cruises. Because zooplankton regenerate more nutrients when they are feeding (Peters and Rigler 1973), the shorter incubation times may have misleadingly produced higher regeneration rates than during the longer incubation times used in the earlier experiments. Second, incubation temperatures progressively increased from the first to the last cruises. Higher metabolic rates of the experimental animals at these higher temperatures may have accounted for higher regeneration rates. Last, zooplankton may have been feeding more heavily on small green algae (nannoplankton) which were more abundant during the later cruises (McNaught *et al.* 1980, Stoermer and Kreis 1980). Zooplankton feeding on this type of food would be expected to ingest more cells intact, thereby reducing direct release of nutrients within the cells into the water. Furthermore, since nannoplankton have small vacuoles and nutrient concentrations are low during the summer when they are abundant, they should have relatively low concentrations of stored nutrients. Nutrient regeneration would therefore be primarily egestion and excretion. As discussed above, most of the phosphorus and nitrogen excreted by zooplankton is orthophosphate and ammonia, respectively (Butler *et al.* 1969, Peters and Lean 1973). Probably all three mechanisms are partially responsible for the higher regeneration rates during the later cruises.

The higher regeneration rates of TP and TSP relative to SRP and $NO_3 + NO_2$ relative to $NH_3$ for the four cruises may be a result of animals being fed prior to the start of experiments. Excretion of nutrients from food ingested before incubation may be higher in some forms of phosphorus (e.g., TP and TSP) and nitrogen (e.g., $NO_3$ and $NO_2$) than other forms of these nutrients (e.g., SRP and $NH_3$).

Ambient concentrations and supply rates of nutrients are generally higher near shore and at the mouth of Saginaw Bay than at open lake stations (Schelske *et al.* 1980). Because phytoplankton abundance is correspondingly higher at stations nearshore and at the mouth of Saginaw Bay (Munawar and Munawar 1979, Schelske *et al.* 1980, Stoermer and Kreis 1980), I expected rates of nutrient regeneration to be higher there, also. Rates of nutrient regeneration were generally higher at the nearshore (especially Canadian) stations sampled on the first cruise than at all other stations sampled on the other three cruises. On the third and fourth cruises, rates of nutrient regeneration were generally higher at the Saginaw Bay stations compared with the open lake stations. The higher rates of regeneration of some of the nutrients at the open lake stations during the second cruise were unexpected and may have been the result of differences in experimental methods, environmental variation, or some other factor(s).

During the diel study, regeneration rates of TP, TSP, and $NH_3$ were generally highest between late afternoon and evening (1600 to 2400 hr) and lowest during early morning to mid-daylight (0400 to 1200 hr). Regeneration rates of SRP during the first experiment were highest around 1800 and 0400 and lowest around 2400 and 0800. Since these studies were conducted with zooplankton collected between 0 and 10 m, these rates may reflect the diel fluctuations in feeding and/or vertical migration by certain species of zooplankton. The higher rates of nutrient rgeneration may result from different species of zooplankton actively feeding in the surface waters at night. During the first diel experiment (Sta. 40 on 29 May 1975) I observed a shift from a predominance of small copepods (1230 hr) to rotifers and other small zooplankton (1800 hr), and finally to *Bosmina*, rotifers, and other small zooplankton (2400 and 0400 hr). During the second diel experiment (Sta. 38 on 1 August 1975)

there was a shift from a predominance of *Bosmina* and *Daphnia* (1300 hr), to *Daphnia*, *Diaptomus*, and some *Bosmina* (2200 and 0200 hr), to *Daphnia*, *Diaptomus*, *Bosmina*, and some *Holopedium* and *Moina* (1600 hr). McNaught *et al.* (1980) reported that zooplankton grazing was slightly higher during hours of darkness. These higher grazing rates would account for higher rates of nutrient regeneration.

Another explanation for higher regeneration rates may be that phytoplankton contaminating the containers did not take up as many released nutrients in the dark as in the light. No noticeable accumulation of algae was noticed in the experimental containers until Station 38 at 0200 and 0615 hr when blue-green algae were abundant. Some authors (e.g., Hargrave and Geen 1968, LaRow *et al.* 1975, Ferrante 1976, and Gophen 1976) incubated all bottles in their nutrient regeneration experiments in darkened containers. I refrained from incubation in daylight experiments because 1) this might have caused some physiological change in the animals, producing spurious regeneration rates, and 2) uptake of ammonia and phosphate by algae has been reported to be extremely rapid even in the dark (Eppley and Coatsworth 1968, Ganf and Viner 1973). Further research must be done to support or refute these assumptions.

The magnitude and diel changes in rates of SRP and $NH_3$ regeneration measured in this study are quite similar to those reported by Ganf and Blazka (1974) for zooplankton in tropical Lake George (Fig. 5). Their rate measurements were converted to $\mu$mol/mg dry wt/hr using their estimate of nitrogen being 9 percent of zooplankton dry weight. The diel fluctuation in rates of nutrient regeneration reported by Ganf and Blazka are not as large as those in my study, probably because of the more uniform water temperature and less diel vertical migration by zooplankton in tropical lakes like Lake George than in large temperate lakes like Lake Huron. The diel ratios of $NH_3$/SRP (N/P) regenerated by zooplankton in both lakes are given in Figure 6. Because SRP was not measured at Station 38, N/P ratios for my study are reported only for Station 40. The differences in N/P ratios between the two studies probably reflect differences in species of zooplankton, temperature, food, and other factors. The N/P regeneration ratios in my study are much closer to those calculated by Lehman (1978, 1980a) for zooplankton in Lake Washington.

Rates of phosphorus excretion measured in the

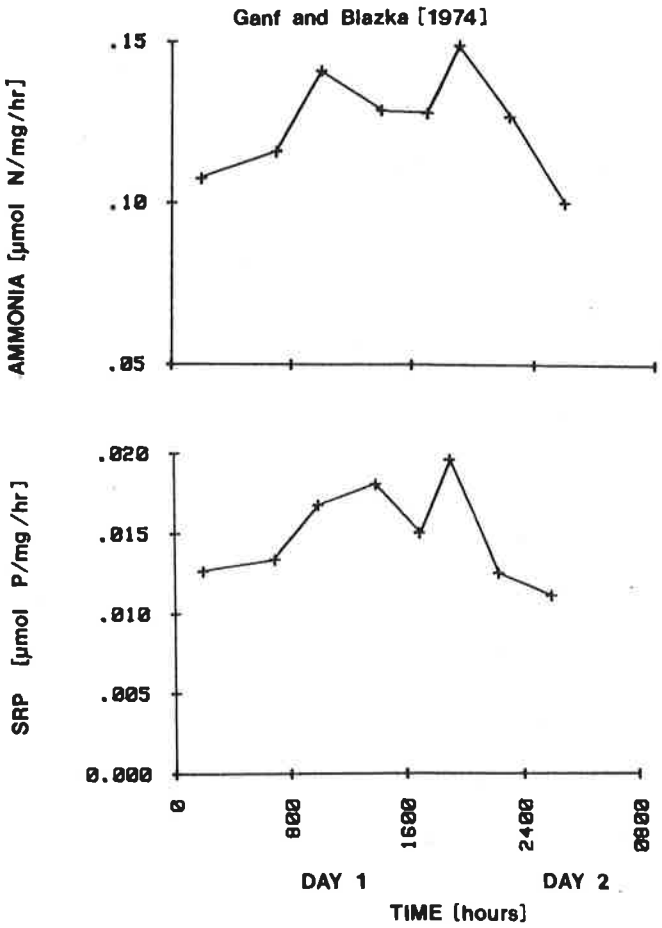


*FIG. 5. Rates of nutrient regeneration by zooplankton over a 24-hr period in Lake George, Uganda. Data have been modified from Ganf and Blazka (1974).*

$^{33}P$ experiments are at the lower range of rates of SRP regeneration measured chemically in southern Lake Huron, and are an order of magnitude lower than those measured by Peters and Rigler (1973) for starved *Daphnia rosea*. It is possible that zooplankton used in my study were not uniformly labeled with $^{33}P$, and that this accounted for the lower rates of excretion measured here compared with those measured by Peters and Rigler. If any P pool of the zooplankton used in my study was not uniformly labeled, however, it was probably the slow-turnover pool such as in the carapace and chitin, whereas the P pool that is rapidly metabolized was probably uniformly labeled with $^{33}P$. The differences between excretion rates in my study and Peters and Rigler's study may merely reflect different species of zooplankton and/or different experimental conditions. Lehman (1980b) has cautioned that Peters and Rigler (1973) may have

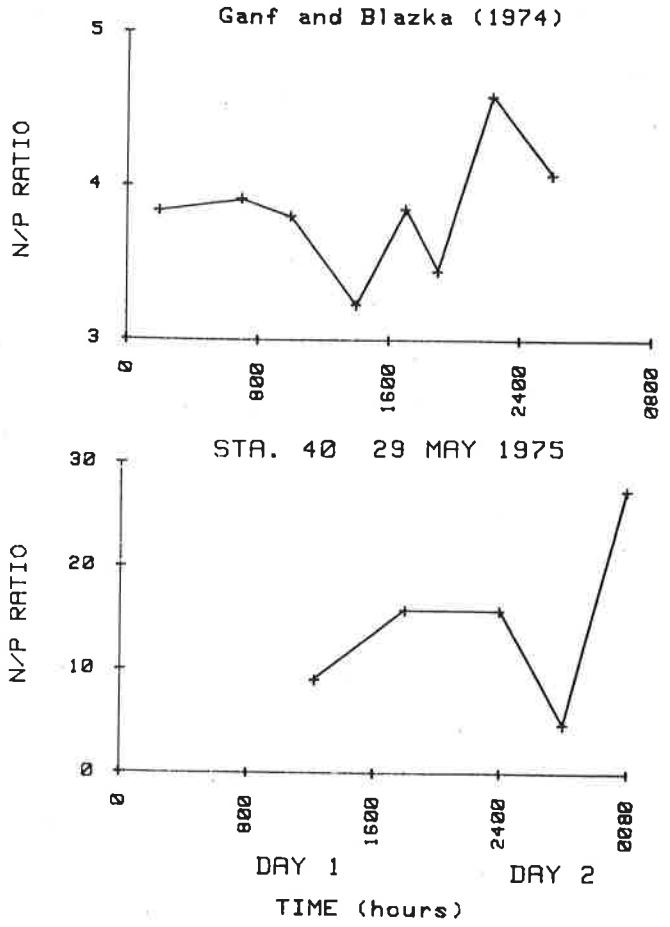


*FIG. 6. Comparison of the ratio of $NH_3$ to SRP (N/P) regenerated by zooplankton in Lake George (calculated from Ganf and Blazka 1974) and southern Lake Huron (Station 40 on 29 May 1975).*

overestimated phosphorus release rates because the *Daphnia* were mixed with living but unlabeled yeast cells in the experimental containers, and there may have been an exchange of $^{31}P$ for $^{32}P$ back and forth across the gut wall of the animals (Lampert 1977). Therefore, some of the $^{32}P$ released into the water may have resulted from isotope equilibrium and not excretion.

Several errors are involved in the methods of measuring nutrient regeneration used in my study. Since zooplankton were not feeding on natural concentrations of phytoplankton during the experiments and the remaining phytoplankton that were present in the experimental containers probably took up some of the regenerated nutrients, rates of nutrient regeneration measured in this study were probably underestimates of true regeneration in nature. Rates of nutrient regeneration by zooplankton in southern Lake Huron measured in this study are further underestimated because zooplankton smaller than 64 $\mu$m were not included in the experiments, and Johannes (1964) has shown that microzooplankton are important contributors to nutrient regeneration.

Lehman (1978; 1980a,b) has recently developed a method of more accurately measuring rates of nutrient regeneration by zooplankton. This method involves enclosing zooplankton with phytoplankton that have excess levels of ambient nutrients for about 24 hr. This method would be preferred over the one used in this study for accurately measuring rates of nutrient regeneration, but would be impractical for repeated experiements at various locations and times of day. Nevertheless, certain conclusions can be drawn from this study about rates of nutrient regeneration by zooplankton in southern Lake Huron.

If the rates of nutrient regeneration and concentrations of zooplankton are known for a lake, some indication of the importance of nutrient regeneration by zooplankton to productivity by phytoplankton can be ascertained (Peters and Rigler 1973, Ganf and Blazka 1974, Lehman 1978). In southern Lake Huron the calculated average rates of nutrient regeneration measured chemically were 0.056 $\mu$mol P/mg/hr for TP, 0.023 $\mu$mol P/mg/hr for TSP, 0.008 $\mu$mol P/mg/hr for SRP, 0.073 $\mu$mol N/mg/hr for $NH_3$, 0.215 $\mu$mol N/mg/hr for $NO_3 + NO_2$, and 0.290 $\mu$mol Si/mg/hr for $SiO_2$. The biomass of zooplankton in the surface waters probably averaged about 0.20 mg/L between April and August, using an average dry weight per zooplankton of 1.52 $\mu$g based on my calculation. Multiplying this average zooplankton concentration times the average nutrient regeneration rates, the calculated average concentration of nutrients regenerated would be 0.0112 $\mu$mol P/L/hr for TP, 0.0046 $\mu$mol P/L/hr for TSP, 0.0016 $\mu$mol P/L/hr for SRP, 0.0146 $\mu$mol N/L/hr for $NH_3$, 0.043 $\mu$mol N/L/hr for $NO_3 + NO_2$, and 0.058 $\mu$mol Si/L/hr for $SiO_2$. The actual levels of regeneration are probably greater than these values because of the underestimated rates of nutrient regeneration. Because concentrations of most of these nutrients in southern Lake Huron are usually low (Table 3), this suggests that nutrients regenerated by zooplankton in a 24 hr period are rapidly taken up by phytoplankton and bacteria.

The contribution of nutrient regeneration by zooplankton to the turnover of nutrients in the surface waters of southern Lake Huron can be calculated by dividing the average concentration of

the nutrient in the lake (μmol/L) by the average regeneration rate of that nutrient calculated above (μmol/L/hr). Turnover times were calculated as 212 hr for TP, 239 hr for TSP, 69 hr for SRP, 62 hr for $NH_3$, 505 hr for $NO_3 + NO_2$, and 531 hr for $SiO_2$. Although the turnover time for most of these nutrients is fairly slow, the pools for SRP and $NH_3$ are replenished in less than 70 hr by nutrient regeneration. Zooplankton thus appear to play a significant role in the availability of SRP and $NH_3$ in southern Lake Huron.

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