

Nutrient dynamics of Lake Tanganyika

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Introduction

The large and productive fishery of Lake Tanganyika is an important source of income and nutrition for the surrounding areas. This fishery, based primarily on pelagic clupeids (Kiswahili: *dagaa*), is very productive, and provides a readily available, nutritious, and inexpensive source of protein to the rapidly growing human populations in this area. The regional importance of the Lake Tanganyika fishery underscores the importance of the strict nutrient balance of the pelagic zone the lake, and any potential changes that might affect the nutrient dynamics of the lake. Global climate change appears to be affecting the productivity of the lake by reducing mixing and lowering nutrient availability (O'Reilly *et al.* 2003). As these changes develop and progress, it is increasingly essential to understand the nutrient dynamics of the lake.

Lake Tanganyika, like many other rift valley lakes, is characterized by steep vertical gradients in temperature and density, contributing to sharp vertical differences in oxygen and nutrient levels (Edmonds *et al.* 1993). The lake is completely anoxic below about 150 meters. The differences, by depth, that this creates in nutrient levels, mainly nitrogen and phosphorus, causes the epilimnion of the lake to be generally oligotrophic (Hecky and Fee 1981). This oligotrophic state of Lake Tanganyika creates a very tight balance of nutrients within the pelagic food web, which is highly responsive to change (Edmonds *et al.* 1993). Seasonal upwelling events, through the introduction of nutrients from the hypolimnion, thus have a potentially large impact on the nutrient balance of the lake and the pelagic food web.

The pelagic food web in Lake Tanganyika is quite simple, although it has been shown to vary between the northern and southern portions of the lake (Kurki *et al.* 1999). In the northern portion of the lake that this study focused on, the food web is dominated by two species of pelagic clupeids: *Limnothrissa miodon* and *Stolothrissa tanganyicae*, which make up approximately eighty percent of the fish yield, dominated by *Stolothrissa* in this area of the lake (Hecky and Fee 1981). These clupeids feed primarily on zooplankton, and are preyed upon by one major predator, *Lates stappersii*, which also feeds on plankton as a juvenile. Clupeid species are thought to have fast and large-scale horizontal migrations throughout Lake Tanganyika. *L. stappersii*, while thought to migrate to a lesser extent, have been occasionally found to migrate throughout the lake (Järvinen *et al.* 1999).

Seasonal upwelling events are the main source of new nutrients to the epilimnion. During the windy season (May-September), strong winds from the south cause seiche activity, resulting in a tilting of the thermocline, and periodic upwelling events. More localized and patchy upwellings, caused by Poincare internal waves, occur in some areas of the lake as well (Plisnier *et al.* 1999). These upwelling events introduce nutrients into the epilimnion of the pelagic zone of the lake from the anoxic hypolimnion, which is a sink for fixed forms of nitrogen and phosphorus (Edmonds *et al.* 1993). Upwelling events are thus important for returning nutrients above the oxycline and making them available to the pelagic food chain. For instance, Järvinen *et al.* (1999) suggested that the tight nutrient balance of Lake Tanganyika might impact phytoplankton populations and communities, a process that would likely be further impacted by an upwelling event.

The objectives of this study are to investigate the nutrient dynamics and interactions in the pelagic food web of northern Lake Tanganyika. First, nutrient concentrations and algal biomass were analyzed at two sites in the pelagic zone near Kigoma, Tanzania, (off of Kitwe Point and Nondwa Point) over a period of three weeks. Plankton samples were also collected for a future study to investigate the nutrient ratios (C:N:P) of zoo- and phytoplankton, thereby further understanding the issue of food quality. Third, to form a more complete understanding of the nutrient dynamics of Lake Tanganyika, fish nutrient excreta was studied to look at the potential role of fish in recycling nutrients and further contributing to lake productivity. It is expected that, if an upwelling does occur during the study period, we will see increased levels of nutrients in the epilimnion, and these increases in nutrients will be accompanied by increases in algal biomass (chlorophyll a). We hypothesize that the fish excretion study will show that pelagic fish

populations play a significant role in recycling nutrients, particularly nitrogen, by excreting nitrogen in a form that is usable by phytoplankton (NH₄).

Methods

The study was performed from 16 July 2005 until 6 August 2005 on northern Lake Tanganyika, based in Kigoma, Tanzania. Data were collected from the research vessel *R/V Echo* on approximately every third day at two offshore sites near Kigoma: Site 1 (Kitwe Point), to the south, and Site 2 (Nondwa Point), at the northern edge of Kigoma Bay. In addition to the offshore sites, at each site samples were collected at nearshore sites as well.

Table 1. Pelagic sampling dates and GPS points taken at start of sampling.

Date	Site 1 Kitwe Point GPS	Site 2 Nondwa Point GPS
16 July	S04°55'926 E29°36'325	S04°51'756 E29°35'658
20 July	S04°56'394 E29°36'139	S04°52'120 E29°35'662
24 July	S04 56'100 E29 35'470	unknown
26 July	S04°55'640 E29°35'024	S04°50'943 E29°34'364
28 July	S04°55''795 E29°35'209	S04°51'496 E29°35'316
1 August	S04°55'935 E29°35'179	S04°51'471 E29°35'433
3 August	S04°55'686 E29°35'202	S04°51'770 E29°35'376
5 August	S04°55'820 E29°35'072	S04°51'542 E29° ??

At each site, secchi depth was read by two or three different people using a 20 cm diameter secchi disk. Water quality parameters were measured at 0, 10, 20, 40, 60, 80, and 100 meters depth at each site, and at 0 and 10 meters at the nearshore sites. Two liters of water were taken at each depth with a Limnos water sampler and filtered upon return to the laboratory. Water samples were analyzed in the lab for nitrate, phosphate, silica, and chlorophyll a.

Nutrient analyses were carried out using the HACH Permachem spectrophotometer water analysis methods. For nitrate the cadmium reduction method for low range concentrations was used. The phosphate analyses were done using the amino acid method for low range concentrations. Silica was analyzed using the silicomolybdate method for high range concentrations of dissolved silica. For data collected 28 July through 5 August, nutrients were measured using HACH preparation methods and read using a calibration curve on a ThermoSpectronic Genesys20 spectrophotometer. During this period, silica was analyzed using the HACH heteropoly blue method for low range silica, and samples were diluted with ultrapure deionized water.

To measure chlorophyll a, two liters of each water sample were filtered on a 0.7 µm pore size filter, which was then inserted into a centrifuge tube containing 10 mL 90% ethanol. These were kept dark and refrigerated for approximately 24 hours. After 24 hours the filters were removed and the remaining extract was centrifuged for 15 minutes. Samples were analyzed on a Turner Designs AquaFLUOR version 1.3 fluorometer. A reading was taken of approximately 4 mL of extract in a glass cuvette on the fluorometer, then 3 drops of 0.1N HCl was added. After about one minute, the acidified sample was read again. The difference between these two readings, to correct for the presence of phaeopigments, was used to calculate chlorophyll a. The concentration of chlorophyll a was then calculated from these two readings using standard solutions read on a spectrophotometer and the fluorometer.

In addition, phytoplankton and zooplankton samples were collected with 100 µm and 48 µm nets. Four samples were collected at each site, two with each size net. Tows were taken from 80-0 meters, and 80-40 meters. The samples were filtered on 100 µm mesh (for the zooplankton samples) and 10 µm mesh after fractioning out 100 µm particles (for the phytoplankton samples). The meshes were dried and stored for future analysis of nutrient content.

Fish nutrient excretion was tested at night, when fishing is most dominant in Kigoma Bay. Fish were taken from fishing nets while still in the water, and placed in containers of filtered lake water, one fish per container, for between thirty and ninety minutes. Ziploc bags with 700 mL of water were used for small fish, while larger fish were placed in larger containers with 1 L or 4 L of water. Water samples taken after the fish had been in the containers for about twenty minutes, and initial samples of filtered lake water, were analyzed for nitrate and phosphate. Other nutrient analyses were carried out using the same methods as were used for pelagic water samples. Ammonium was analyzed in the field soon after samples were collected using the OPA reagent method (Taylor *et al.* submitted). Container controls were performed using distilled water. Initial and final samples were taken from each container an hour apart, and analyzed for ammonium and phosphate. Sampled fish were also collected and weighed, measured and dried for future analysis of nutrient content.

Results

Nutrient Profiles

When plotted across depth and date, the change in depth profiles of nutrients over time can be seen. Nitrate shows stable concentrations until 3 August, when an increase in concentrations at 80 to 100 meters was observed at both sites, although to a greater extent at Site 2 (Fig. 1). This pattern, however, was not observed with the other nutrients: phosphate and silica. At Site 1, phosphate levels were slightly elevated on 26 and 28 July at depths 80-100 meters and 40 meters (Fig. 2). Site 2 phosphate concentrations were high at all depths on 24 July, and showed slight elevations at depth on 3 and 5 August. Silica concentrations at both sites were elevated on 24 July at all depths, and showed increases at 80-100 meters on 3 August (Fig. 3) Chlorophyll a data show high concentrations at 20-40 meters on 28 July until 5 August at both sites (Fig. 4).

Fish Nutrient Recycling

Excretion rates of ammonium and phosphate from fish nutrient recycling experiments were compiled to examine relationships between fish species type, size, and excretion rate. It was found that *L. stappersii* excrete more mgN/hr/g wet weight on average than clupeid species (Fig. 5 ANOVA, $p < 0.0001$). Phosphate excretion rates were not found to be significantly different by fish type. An ANOVA analyzing total length, weight, and the interaction between total length and weight showed a significant overall effect on N excretion rate (mg/hr) (ANOVA, $p < 0.0001$), with significant individual effects of total length (ANOVA, $p = 0.0187$), weight (ANOVA, $p = 0.003$), as well as a significant effect of both total length and weight together on N excretion rate (ANOVA, $p = 0.0021$). For phosphate, there was not a significant overall effect, nor did the individual effects of total length, weight, and total length with weight significantly impact phosphate excretion rates. Container control tests showed that the containers used had no significant effects on nitrogen or phosphate concentrations.

Using fish biomass data from Sarvala *et al.* (1999), extrapolations were made to calculate estimated amounts of nitrogen and phosphorus that are recycled by *L. stappersii* and clupeids in the entire lake per year. We found that *L. stappersii* recycle $0.58 \text{ mol N/m}^2/\text{year}$ and $0.0056 \text{ mol P/m}^2/\text{year}$ in Lake Tanganyika. Clupeids are estimated to recycle $0.29 \text{ mol N/m}^2/\text{year}$ and $0.012 \text{ mol P/m}^2/\text{year}$. From these estimations, the N:P ratio of recycled nutrients was determined to be 48.5.

Discussion

Nutrient Profiles

Vertical nutrient profiles of both Kitwe Point (Site 1) and Nondwa Point (Site 2) show a lot of variability. Due to methodological difficulties, particularly concerning phosphate and silica, it is difficult to rely on these nutrient concentration profiles to understand the nutrient dynamics of pelagic Lake Tanganyika and interpret the findings.

Results from nitrate show very stable and consistent concentrations over the entire range of depths for the beginning of the sampling period. The increase in nitrate concentrations around 3-5 August is consistent with the findings of Andronicus Kiviyiro (pers. comm.), who found slight increases in dissolved oxygen on

the same days. Temperature, however, did not noticeably increase correspondingly, although there is a very slight increase at Site 2. Kiviyiro also found increases in temperature and dissolved oxygen on 28 August. These physical observations indicate that there may have been small upwelling events around 28 August and 5 August; however, nitrate concentrations do not correspond closely to both events. The most likely explanation for this is methodological error and inconsistency.

Phosphate and silica profiles are both largely inconsistent with physical data. Although small increases in phosphate and silica can be seen around both dates, where small increases in temperature and dissolved oxygen were also found, there are also larger discrepancies. Therefore, because of methodological issues, it is difficult to make any conclusions about phosphate and silica concentration gradients in Lake Tanganyika.

Chlorophyll a, a methodologically sound procedure throughout the sampling period, exhibited interesting trends. Chlorophyll a is used as an indicator for algal biomass, so the increases in chlorophyll a at both sites around 28 July and continuing until the end of the sampling period show an increase in phytoplankton biomass, which could be driven by increased nutrient concentrations from the small upwelling events that were recorded through physical data (Kiviyiro), but not captured by nutrient analyses. An interesting observation when comparing temperature and dissolved oxygen data with chlorophyll a is that chlorophyll a concentrations seem to peak later than temperature and dissolved oxygen. This shows that the response of phytoplankton to limnological changes is not immediate, rather it closely follows the physical changes. In a 2004 Nyanza Project study carried out at Nondwa Point, chlorophyll a followed a similar pattern in the presence of a more defined and closely tracked upwelling event, further suggesting that our results do indicate an upwelling, albeit a very small one (Kuboja 2004).

Overall, the nutrient concentration gradients in Lake Tanganyika are relatively sensitive to small physical limnological changes. Although a well-defined upwelling event did not take place during the sampling period, small 'waves' of upwelling resulted in variation in both nitrate and chlorophyll a concentrations.

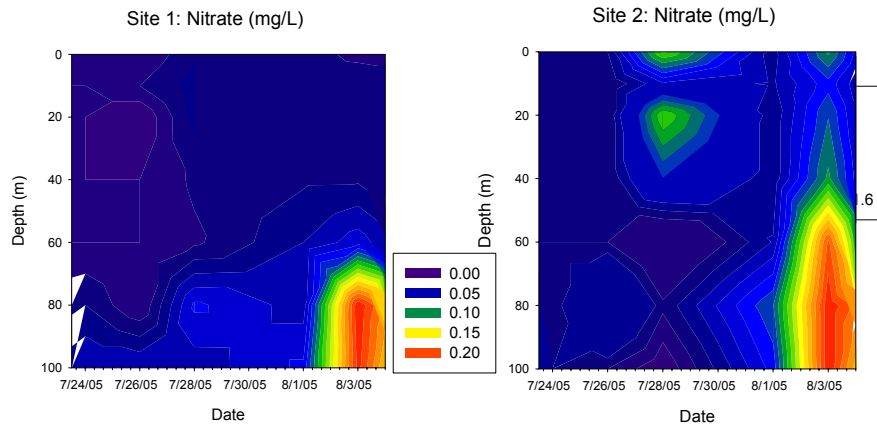
Fish Nutrient Recycling

Results from fish nutrient recycling experiments strongly indicate that pelagic fish populations play a large and significant role in nutrient, primarily nitrogen, recycling in Lake Tanganyika. Between the two types of fish studied, *L. stappersii* and pelagic clupeids (*S. tanganyicae* and *L. miodon*), *L. stappersii* was shown to recycle significantly higher concentrations of nitrogen than clupeids, but phosphate excretion rates were not different between fish types. A similar effect is seen in the relationships between fish size and excretion rates, and it is thought that the difference is based on the form that the different nutrients are excreted in.

The strong relationships between fish size (weight and total length) and nitrogen excretion rates for both fish types are not surprising. Although the internal processes that control nitrogen excretion are essentially metabolic, fish size is generally an effective indicator of basic metabolism of nitrogen. Phosphate excretion, on the other hand, was not as strongly related to fish size. This difference between trends in nitrogen and phosphate excretion is a function of the methods of excretion for these nutrients, and our sampling limitations. Nitrogen is excreted through fish gills in the form of ammonium, which is in dissolved form. Phosphate, however, is excreted in fecal matter, and thus is not dissolved and ready to be used by plankton. These differences are important because dissolved ammonium is a form of nitrogen that can be taken up immediately by phytoplankton and converted to nitrate, while phosphate excreted in fecal matter is not dissolved, so is not readily available to phytoplankton, and instead sinks down the water column, making it even less available. In this study, it is important to realize that the reason phosphate was not related to fish size is most likely because we were sampling water and not fecal matter; however, this is not a limitation of the study because excreted phosphate has very low immediate bioavailability.

Determining the lake-wide significance of nutrient recycling by *L. stappersii* and clupeids shows that nitrogen and phosphate inputs from fish excretion are very strong contributors to the nutrient cycle of Lake Tanganyika. Hecky *et al.* (in Coulter 1991) estimated the total nitrogen and phosphate loading into the lake from rain, rivers, and vertical mixing to be 0.091 moles N/m²/y and 0.209 moles P/m²/y. Compared to this value, nitrogen and phosphate recycling by pelagic fish species, 0.58 moles N/m²/y and 0.0056 moles

$P/m^2/y$ by *L. stappersii* and $0.21 \text{ moles N}/m^2/y$ and $0.012 \text{ moles P}/m^2/y$ by clupeids, shows that this process is extremely important in the nutrient balance of the lake, particularly for the nitrogen balance.



In an oligotrophic lake such as Tanganyika, it is generally expected that the system would be nitrogen-limited. With Lake Tanganyika, this is not the case, the system is limited by both nitrogen and phosphorus combined, a natural consequence of having low nutrient levels. By quantifying concentrations of nitrogen and phosphorus being recycled yearly by fish, the data strongly suggest that a possible reason for the lake not being nitrogen-limited is the recycling of nitrogen being done by fish. The high N:P ratio of fish nutrient excretions (48.5) for lake-wide estimates shows further evidence that the system is likely more limited by phosphorus than nitrogen.

To further understand fish excretion of nutrients, and its role in the overall nutrient balance of the lake, it will be important to better understand nitrogen and phosphorus metabolism in *L. stappersii* and clupeid species. The C:N:P ratios of the fish used in this study, as well as zoo- and phytoplankton samples will be determined upon return to the United States, which will hopefully elucidate some of the questions behind nutrient excretion and consumer-producer relationships on a stoichiometric level. An investigation into the impact of littoral nutrient inputs to the aquatic ecosystem of the lake, whether through the extensive cichlid populations in the littoral zone of Lake Tanganyika, stream or riverine inputs, or anthropogenic sources would also be interesting. While it is suspected that the effects of these inputs on the pelagic ecosystem are very small, it is important to understand the nutrient dynamics of the littoral ecosystem as well.

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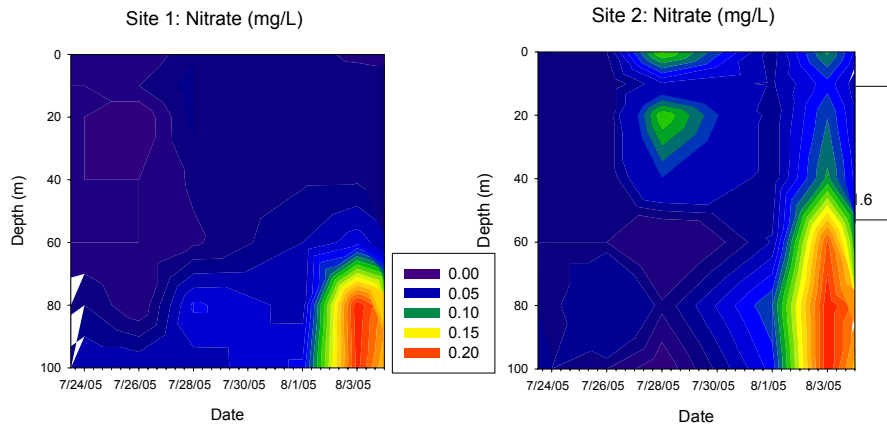


Figure 1. Nitrate concentrations (mg/L) over sampling depths and dates at two pelagic sites near Kigoma Bay.

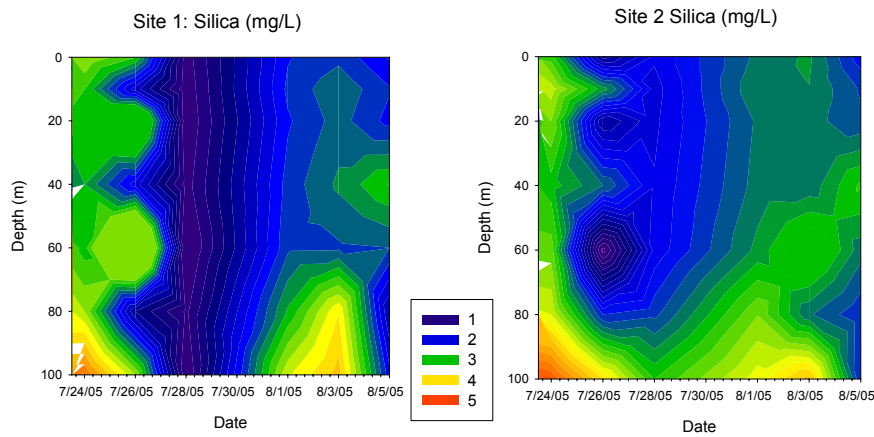


Figure 2. Silica concentrations (mg/L) over sampling depths and dates at two pelagic sites near Kigoma Bay.

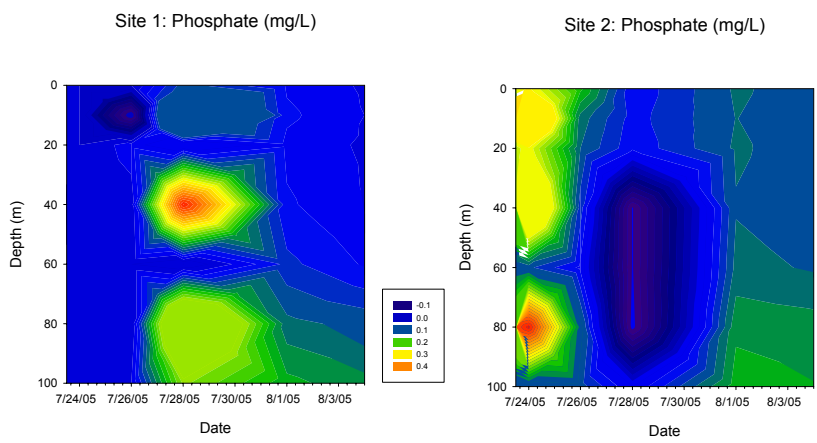


Figure 3. Phosphate concentrations (mg/L) over sampling depths and dates at two pelagic sites near Kigoma Bay.

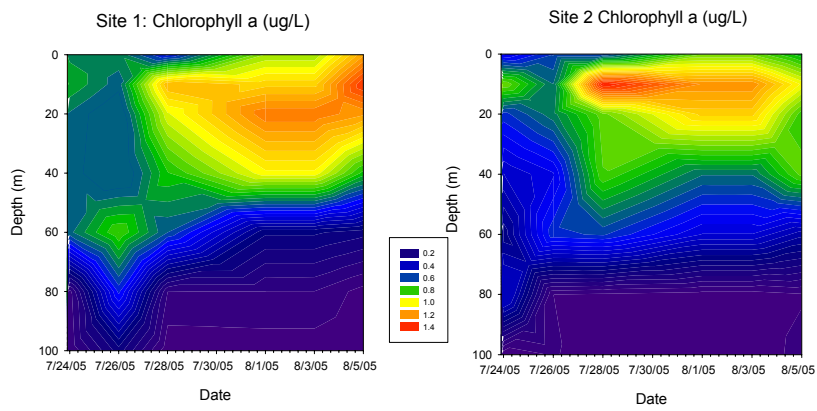


Figure 4. Chlorophyll a concentrations ($\mu\text{g/L}$) over sampling depths and dates at two pelagic sites near Kigoma Bay.

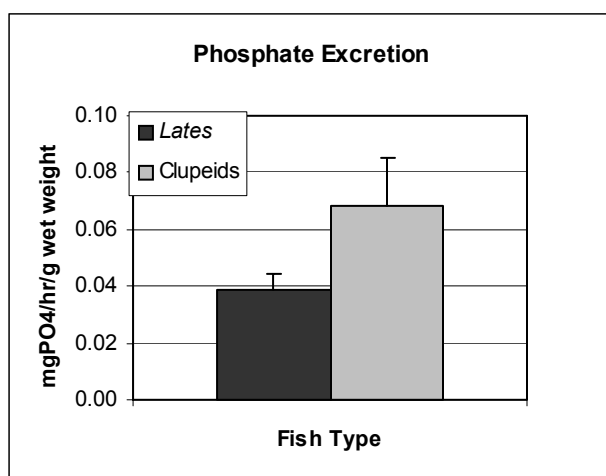
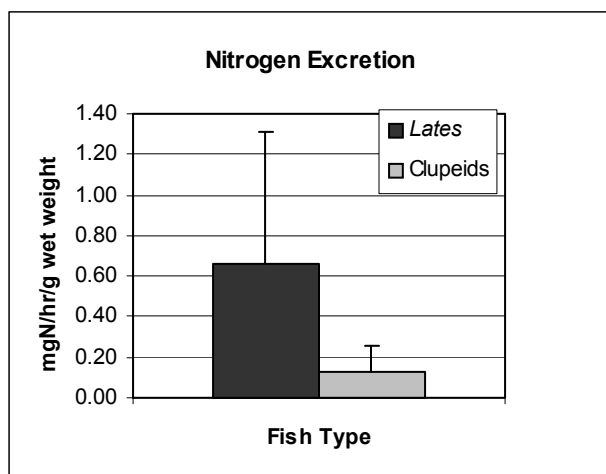


Figure 5. Nutrient excretion rates (mg/hr/g wet weight) of *L. stappersii* and clupeid species. *L. stappersii* excretes significantly higher levels of N than clupeids (ANOVA, $p=0.01$). *L. stappersii* excretes lower levels of PO_4^{3-} than clupeid species, but the difference is not significant (ANOVA, $p>0.05$).