Benthic nutrient cycling: the role of fish in nitrogen and phosphorus regeneration in the rocky littoral zone of Lake Malawi/Nyasa/Niassa, Africa

by

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A thesis
presented to the University of Waterloo
in the fulfilment of the
thesis requirement for the degree of
Master of Science
in
Biology

Waterloo, Ontario, Canada, 1999

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Abstract

The interaction between the cichlid fishes of the nearshore rocky littoral zone of Lake Malawi with the epilithic periphyton community is addressed in this study, looking specifically at fish grazing rates and importance of the fish community in recycling of nitrogen and phosphorus through excretion, defecation and mortality.

To determine rates of nitrogen and phosphorus regeneration through excretion and defecation, a series of *in situ* fish incubations in 13L plexiglas chambers were performed at two islands of Lake Malawi. Fish grazing rates were assessed by determination of fish consumption rates using Kraft's (1992) bioenergetics model where defecation and excretion rates were derived from the in situ experiments and growth rates were determined in the lab by rearing 30 fish specimens for 22 days under controlled conditions. Mortality was assessed by the assumption that it is equal to growth as fishing is negligible and there is no long-term fish biomass change in the nearshore rocky littoral zone of Lake Malawi.

This study provides evidence that rock dwelling cichlids, through excretion and defecation, recycle substantial amounts of nitrogen and phosphorus that can support measured rates periphyton photosynthesis. However the uncertainty about the N and P composition of the living algae hamper assessment of whether N and P recycled by the rocky dwelling cichlids meet periphyton demand for these nutrients. This study also provides evidence that fish may be important in structuring the epilithic periphyton by recycling N and P at low ratios, and therefore favouring dominance of nitrogen-fixing blue-green algae species in the periphyton community. Estimates of consumption rates indicate that the fish community is a major grazer of the periphyton community as about 70% and 103 % respectively of nitrogen and phosphorus uptake by periphyton is consumed by fish. Results also suggest that periphyton production can meet the nutritional requirements of the fish community. This observation supports the hypothesis put forward by Fryer (1959) that co-existence of many species in high densities is due to high availability of food (periphyton).

Acknowledgements

I am very grateful to Dr. Robert E. Hecky for having believed that I could succeed in this project, despite the language barrier, and having recruited me as his graduate student. Much of what I have learned I owe to his constant encouragement and intelligent advice that were always available throughout the program.

I could never asked for better supervision than what Dr. Hamish Duthie and Dr. Robert Hecky provided to me. Their advice in the good and difficult moments contributed very much to make this thesis possible, for that, I am sincerely grateful.

Dr. William Taylor and Dr. David Barton with their expertise and experience helped overcome many of the difficulties faced during the preparation of the thesis proposal. Their very interesting discussion, contributions and criticism, not only in the early stages, but during the data processing stages of the project are very much appreciated.

Dr. Harvey Bootsma provided invaluable assistance and advice in Malawi. His experience in tropical limnology and especially the limnology of Lake Malawi, his experience in dealing with logistical problems, capacity to solve problems, and especially his willing to transmit his expertise to students simplified many of the technical problems that I faced when I was in Malawi for the field season. No water chemistry analysis background I had when I first arrived at Senga Bay. I am especially grateful to him for all he has done to make this work possible.

I am grateful to Dr. Tony Ribbink and Dr. Fabrice Duponchele for the very constructive discussions and co-operation offered, especially for having provided me with abundance data for cichlids.

This research would never been possible if CIDA and World Bank have not given their financial support. I am especially grateful for that support.

I am very grateful to my wife Isabel and my children Sheila and Jason for their great understanding and patience in all those moments during the last three years that I had to leave home to pursue this research.

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The role of predators such as fish in regulating aquatic food web interactions through recycling of nutrients has only been recently realised by ecologists (Hunter and Price 1992; Power 1992; Strong 1992). Fish can alter the rates and ratios of nutrient supply through several mechanisms, thereby driving alterations in food web abundance and structure, particularly to primary producers (Elser et al. 1988; Huntly and Inouye 1988; Naiman et al. 1988; Whicker and Detling 1988; Sterner 1986, 1990; Lehman and Sandgren 1985). In the past, ecologists believed that fish could only regulate food web interactions through direct predation (top-down) effects (Persson et al. 1988; Oksanen et al. 1981; Fretwell 1977; Hairston et al. 1960). Models of food web interactions assumed that the effect of the top predator could affect the lowest trophic level (primary producers) by means of propagation of the top predator consumption derived mortality throughout the food web until it reaches the base (primary producers). However, on several occasions these models failed to explain observed food web dynamics. The realisation that predators can regulate food webs through resource-based forces (nutrients) brought in new elements in the better understanding and interpretation of trophic cascading effects in aquatic food webs. Currently, many ecologists claim (e.g. Vanni 1996) that new food web models should account for resource-based effects of predators on food web dynamics.

Debate in the literature regarding the role of predators (fish) in altering rates and ratio of nutrient supply culminated with several mechanisms being put forward to explain how predators effect these changes. The first mechanism is that the fish directly alter the rate and ratio of nutrient supply through excretion and egestion (defecation). Fish digestion results in a portion of the consumed food items being converted into soluble inorganic nutrients (e.g. ammonium, phosphate, etc.) that are released into the water column and thereby available to pelagic food webs. The portion of the consumed food that is not digested is recycled through defecation (egestion) in particulate form. This portion sediments to the bottom and may enter bacteria mediated remineralization processes culminating with liberation of nutrients that may be available to benthic food webs if the defecation takes place in the littoral zone. If defecation takes place in the pelagic zone, nutrients contained in the fish faeces may be lost from pelagic

food webs because of sedimentation through the thermocline. Excretion and defecation rates as well as the ratios of nutrient supply are generally affected by allometric growth (Vanni 1996; Mather et al. 1995). Therefore alteration in fish abundance and size structure may lead to alteration in rates and ratios of nutrients available to primary producers and thereby drive alterations in the food web structure through resource competition.

Zooplankton nutrient regeneration is recognised by most ecologists to be perhaps the most important source of nutrients for phytoplankton in the pelagic zones of marine and fresh water ecosystems (Lehman and Sandgren 1985; Lehman 1980; Goldman et al. 1979). However, planktivorous fish can regulate indirectly zooplankton nutrient regeneration rates and ratios of nutrient supply by regulating zooplankton abundance, size structure and species composition. In pelagic food webs were zooplanktivorous fish are not abundant, large zooplankton species are abundant. However, when zooplanktivorous fish are abundant, small zooplankton species are more abundant. However zooplankton nutrient regeneration studies have shown that small zooplankton species have higher mass specific excretion rates than larger species (Bartell 1981) and small species may excrete nutrients at different ratios than the larger species (Sarnelle 1992; Andersen and Hessen 1991; Sterner 1990). There can also be specie-specific effects with copepods and cladocerans having different C, N and P composition.

Littoral and pelagic food webs used to be considered by ecologists as separate compartments in the aquatic ecosystems. However with understanding of the link that the fish establish between the two food webs, currently littoral (benthic) food webs are often regarded as subsystems of the pelagic food webs (Vanni, 1995). Several mechanisms coupling these two habitats have been reported (Lodge et al. 1988; Wetzel 1979). Fish may transport nutrients between pelagic and benthic zones in two general mechanisms: when they feed in the littoral (acquire nutrients) and swim to the pelagic and excrete some of the nutrients, they functionally translocate nutrients from the benthos to the pelagic. These nutrients may then impact the phytoplankton community (Schindler et al. 1993; Carpenter et al. 1992a, 1992b). Alternatively, fish may depart from the littoral benthos, move to the pelagic zone, feed (acquire nutrients), return to the benthic to rest and excrete nutrients. In this case, there is a net flux of nutrients from the pelagic to the littoral benthic zone.

Alternatively, fish may transport nutrients from the littoral to pelagic without necessarily moving between the habitats. When the fish feed on the benthic prey and acquire nutrients they convert some into soluble inorganic form by excretion within the littoral. The excreted nutrients may be transported by turbulent mixing and or convective circulation (James and Barko 1991) to the pelagic zone was they are available to the phytoplankton. The defecated portion of nutrients that are in particulate (in faeces) form may be deposited in the sediments and enter bacteria-mediated remineralization process. Eventually, fish faeces may release nutrients to support the periphyton productivity.

Fish nutrient regeneration is not a continuous process (Mather et al. 1995); it is affected by diurnal behavioural cycles. Therefore, temporal variation in nutrient supply by fish may affect phytoplankton community structure by favouring species that are adapted to sequester nutrient pulses. The frequency at which nutrients are supplied to phytoplankton can determine how many species coexist and which species will dominate the assemblage (Sommer 1989).

Lake Malawi surface waters are very low in dissolved inorganic nitrogen (DIN) concentration, DIN external input, and are a sink of nitrogen due to the anoxic hypolimnion that can lead to significant losses of fixed nitrogen denitrification to nitrogen gas (Bootsma and Hecky 1999). However, phosphorus external input and internal loading are quite significant and are showing increasing loading trends. Nevertheless, recent phytoplankton nutrient status assessment performed by Guildford (in preparation) indicates phytoplankton are not exhibiting extreme nitrogen or phosphorus deficiency. This is quite surprising given the apparent imbalance in the nitrogen and phosphorus supply to the epilimnion (Bootsma and Hecky 1999). There is potential for a nitrogen subsidy from the littoral zone to meet the nitrogen deficit in the pelagic food webs. However quantification of the proportion of nitrogen export from the littoral to the pelagic zone has never been addressed in Lake Malawi. Higgins (1999) determined benthic nitrogen fixation rates and assumed that export from the littoral zone should be equal to these rates as no major losses of nitrogen within the littoral food webs are expected besides losses that actually represent exportation to the pelagic food webs. My research complements the study of Higgins (1999) on nitrogen fixation by providing better understanding of the coupling of pelagic food webs with the

littoral zone and the central role that the rock-dwelling cichlids are playing in maintaining the linkage.

Objectives

Understanding of the trophic functional relationships within the littoral food webs is important not only for the better environmental management of the littoral zone, but also for the better management of to the whole lake ecosystem as the littoral is coupled with the pelagic ecosystem in the flow of energy and matter. Therefore, the overall aim of this study is to contribute to improved understanding of the interaction of the epilithic periphyton community growing on surfaces of rocks in the littoral habitats of Lake Malawi with the fish community living in the same habitat. In particular this study will 1) determine fish grazing pressure on the epilithic periphyton community and 2) determine rates of nutrient recycling by the fish community. The processes of fish excretion and defecation by which nutrients are regenerated and made available for the periphyton and phytoplankton will be quantified. These processes will determine the potential for nutrient export set by excretion and the potential for retention in the littoral by defecation. Fish consumption on epilithic periphyton community will be estimated. This will be important for understanding first, the proportion of nutrients assimilated by the periphyton that actually is consumed by the fish. Second, it will help determine how efficient the fish community is in utilising the nutrients acquired from the periphyton as well as setting the potential for export to the pelagic zone.

Study area

Lake Malawi/Nyasa located between 9.5 and 14.5 S, in the Western Rift Valley (Figure 1.1) is one of the African Great Lakes. Detailed description of this lake can be found in Eccles (1974, 1984). Lake Malawi has a maximum depth of 700 m. It is the ninth largest by area, 30800 km^2 (Hutchinson 1957), and is the fourth largest freshwater body in the world, by volume, 8400 Km^3. Lake Malawi is a "Great Lake" not only for its large dimensions, but also for its unique and large

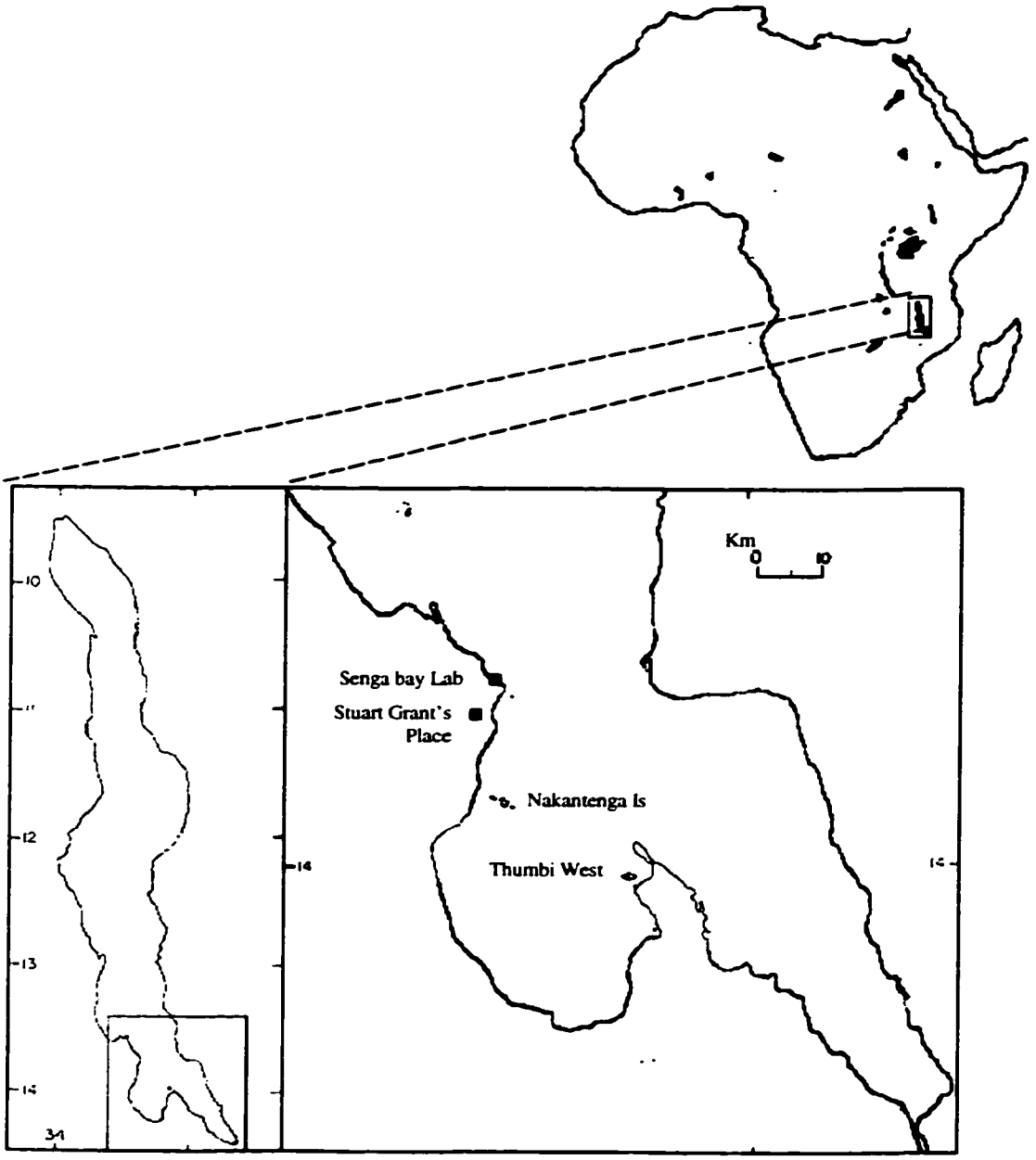


Figure 1.1: Geographic location of Lake Malawi and locations of sampling sites and land based laboratories.

fish fauna currently estimated to be about 500-1000 species. Over 90 % of these species are endemics belonging to the family Cichlidae.

The littoral zone of Lake Malawi is very productive system (Bootsma 1993). It is composed of approximately 70 % of sandy beaches and 30 % of rocky substrata (Ribbink et al. 1983). About 50 % of total number of species found in Lake Malawi live in the rocky littoral zone habitats (Ribbink et al. 1983). The major proportions of these species are associated with the rocky substrates and are locally known as "Mbuna". Many species of the Mbuna community are found to feed directly on the epilithic periphyton that is found to be growing on surfaces of rocks (Bootsma et al. 1996; Reinthal 1990; Ribbink et al. 1983).

Lake Malawi, with relatively low external inputs and concentration of limiting nutrients (Hecky at al. 1996; Bootsma and Hecky 1993), low phytoplankton productivity (Bootsma 1993), and outstanding water clarity with a euphotic zone greater than 30 m depth (Bootsma and Hecky 1998), is considered as an ultra-oligotrophic lake. Because of high water transparency in conjunction with high solar irradiance characteristic of the region of the lake, benthic primary production can be among the highest in the world (Bootsma 1993), and occurs up to approximately 50-60 meters depth making a significant contribution (30% according to Bootsma in personal communication) to the lake primary productivity.

The weather regime of the region has three distinct seasons. A cool and dry season, which starts by May and ends by August, is characterised by air temperatures in between 20 – 22 °C although some times temperatures may drop to as low as 15 °C. From September to November the weather is hot and dry. Daily average air temperatures during that period are 28 °C. In late November, the rainy season starts. During December to April northerly winds are persistent and rains are frequent although usually for only short periods.

These weather patterns together with the great depths of the lake maintain a permanent stratification, allowing only limited water exchange between surface and deep waters below 200 m. One of the consequences is a development of an anoxic boundary that allows recycling of

phosphorus from the deep water to the epilimnion, however it acts as a permanent sink for nitrogen because of denitrification (Hecky et al. 1996).

Due to population increase on its catchment area and altered land use practices that are resulting in increasing nutrient (especially phosphorus) loading, the lake is at serious risk of suffering a major trophic change in the future. Malawi, Mozambique and Tanzania (the riparian countries) share responsibilities for management of the lake ecosystem. A serious concern about conservation of the lake has led the countries to undertake the SADC/GEF Lake Malawi/Nyasa/Niassa Biodiversity Conservation Project with sponsorship from the Southern African Development Community (SADC) and the Global Environmental Facility (GEF).

Chapter 2: Nitrogen and phosphorus regeneration by rock-dwelling cichlids of Lake Malawi/ Nyasa/Niassa, Africa

Introduction

In ecosystems characterised by low external inputs and low concentrations of major nutrients such as nitrogen and phosphorus, recycling of those elements within the ecosystem becomes crucial if productivity in the ecosystem is to be maintained. In Lake Malawi, because nutrients in the water column are low, and external inputs are also low, recycling of these elements by consumers is important for the primary producers. Guildford et al. (in press) have observed that phytoplankton are in nitrogen deficit if regeneration by consumers is not included in the phytoplankton nutrient budget. Guildford et al. (in press) suggests that regenerated nutrients make up the major proportion of the phytoplankton demand for N and P.

Although, limiting nutrients (nitrogen and phosphorus) are low in surface waters of Lake Malawi, primary productivity by the epilithic periphyton community in the littoral is very high. Bootsma (1993) estimates benthic algal primary production rates of about 1 g C m^{-2} d^{-1}. These rates are comparable to highly productive coral reef ecosystems. Such high rates of production require high rates of nutrient supply to maintain them. Where does the epilithic periphyton derive nutrients to sustain such high productivity? This is the central question that is being addressed in this chapter.

According to Ribbink et al. (1983), the rocky littoral zone of Lake Malawi harbours a very large fish community. About 50 % of the total number of species of the lake and densities as high as 10 individuals per meter square can be found in this habitat. Because of this, it is generally assumed that the high periphyton productivity is related to high abundance of fish that through excretion and defecation regenerate abundant nutrients that maintain high rates of periphyton productivity. However, actual measurements of fish nutrient recycling in the rocky littoral have never been performed.

Epilithic periphyton of the rocky littoral zone of Lake Malawi is also found to exhibit high rates of atmospheric nitrogen fixation (Higgins 1999). Selective nutrient regeneration by the fish community may be the reason for this. It is hypothesised that fish through defecation, concentrate high amounts of phosphorus relative to nitrogen in the benthos as faeces are found to be richer in phosphorus relatively to nitrogen. If true, this may lead to periphyton community being nitrogen limited, and thus dominated by algal species that can cope with relatively high concentrations of phosphorus but less nitrogen, such as the heterocystous filamentous cyanoprokaryotes (Higgins 1999). However, evidence in support of such selective recycling in Lake Malawi has not been available.

Available literature (Schindler et al. 1993; Kraft 1992; Carpenter et al. 1992a, 1992b; Brabrand et al. 1990; Vanni and Findlay 1990) indicates fish-excreted nutrients (in soluble form) can support phytoplankton productivity. Therefore, fish excretion is potentially a significant contribution of nutrients to pelagic food webs. Quantification of nitrogen and phosphorus excretion by fish is extremely important because it will provide insights into quantification of potential nitrogen and phosphorus export from the littoral food webs to pelagic food webs, thereby elucidating the strength of the nutrient interaction between littoral and pelagic food webs in Lake Malawi.

Experimental design

To determine how the fish community in the rocky littoral zone of Lake Malawi is important in recycling nutrients, a series of 19 excretion and defecation *in situ* experiments were conducted at Thumbi and Nakatenga Islands (Figure 1.1) from July of 1998 to February of 1999. Experiments were conducted in more than one station because of uneven distribution of species. For example *Cynotilapia afra*, one of the targeted species in the study, was not available at Nakatenga Island but occurred at Thumbi Island. The experimental sites were very similar: both were exposed areas of the islands, with rocky substrate ranging from boulders and rocks in the shallows to smaller rocks as depth increased. Most of the experiments were performed at Thumbi Island although it was desirable to perform the experiments at Nakatenga Island due to its proximity to the mainland laboratory. However, Nakatenga was abandoned due to the arrival of crocodile at the sampling location part way through the field season.

In each experiment, live fish specimens were incubated underwater in 13-liter Plexiglas chambers for an average 3-hour incubation time. Experimental apparatus consisted of three 13-liter watertight clear plexiglass chambers used for incubating fish and an additional 13-Liter chamber used as a control. These chambers were carried to the depth, usually 2 meters, with the aid of SCUBA gear and anchored on the surface of pre-selected flat rocks. The chamber was anchored with weighted bags by placing them on top of the chamber. The weighted bags consisted of a nylon fabric bag stuffed with about 1 kg of small lead pellets. After anchoring the chambers, fish specimens were collected and introduced to the chamber. The control chamber was left without fish in order to control for other factors that may change nutrient concentrations of the water in the chambers.

Before the actual collection of specimens started, a "Mbuna" net of monofilament nylon was set-up. After the target specimens were selected, the catch strategy was to chase the specimens (slowly) towards the net at an angle close to 90 degrees. Because the fish couldn't see the net,

eventually the fish movement would be blocked, and that is the exact moment that the specimen were caught by either using net bags or by hands. Once the specimen was caught, it was immediately taken to the chamber. The exact time the specimens were introduced in the chambers was recorded marking the start of the experiment. Care was taken to avoid injuring the specimens during capture and transportation to the chambers by minimising as much as possible the time of contact with the specimens.

The "Mbuna" net is modified gillnet (approximately 10 m long by 2 m wide) designed to catch the nearshore cichlids. It had a sinking rope tied to it at the bottom side and a floating rope at the top. These two ropes allowed the net to sink and anchor it at the bottom at the same time it is spread vertically in the water column. The mesh size used varied from 0.6 to 1.2 cm.

Water samples were collected for nutrient analysis from each chamber at the beginning of the experiment and every hour during the 3-hour incubation period using 50cc syringes. At each collection time 200 ml of water were collected from each chamber by sucking water using syringes equipped with hypodermic needles through the rubber stoppered ports already set up in the chambers. The rubber stoppers were equipped with two or three-way valves attached to needles. This set-up allowed samples to be taken by just opening and closing the valve without having to spend too much time trying to insert the needles in the rubber stoppers.

Faeces produced during the experiment in the experiment chambers were also collected either hourly underwater or at the end of the experiment period at the surface. When faeces were collected underwater, special 50cc syringes were used to suck up faecal material. This collection syringe was inserted in a special chamber port that was previously set-up for this purpose. The port consisted of a circular opening at the bottom of the chamber with the diameter of approximately 1.5 cm. When not in use the port was closed using vacutainer rubber stoppers. At the surface, the faeces were collected by filtering the water from the chambers after excess water had been decanted off from the chamber.

Analytical Methods

Immediately after returning to the boat, water samples were filtered and stored in either 50 cc syringes or 150 ml polyethylene flasks. NH_4^+ and total dissolved nitrogen (TDN) water samples were stored in syringes and the filtration was done in such a way that the water samples never had contact with the atmosphere. This was accomplished by transferring the water sample from one syringe to another, having an in-line Millipore filtering apparatus in between the two syringes that filtered out particulate material from the samples. The filtration was done using an in-line Millipore apparatus with 25mm GF/F filters. After filtration, samples were stored in a cool-box to avoid sample deterioration.

In the laboratory at the Senga Bay station, water samples were immediately kept in the deep freezer at temperatures close to minus 20 °C until they were analysed for nutrient concentrations. The water samples were not usually kept in the cool-box for more than 8 hours after collection. Faeces samples were immediately put in a desiccator containing dry silica gel. After two to three days the faeces samples were weighted into mg approximation with aid of a microbalance, and then kept frozen until they were shipped to the Freshwater Institute for analysis of nitrogen and phosphorus concentration.

In the Lab the fish specimens were killed, measured for their length and weight, dried for 3-4 days at 60 °C, and weighted again. Dried specimens were kept in the freezer appropriately labelled until they were sent to Freshwater Institute for C, N and P content. Water samples were analysed for Ammonium (NH_4^+), Soluble Reactive Phosphorus (SRP), Total Dissolved Nitrogen (TDN), and Total Dissolved Phosphorus (TDP). NH_4^+ was analysed by the modified Phenol method; soluble reactive phosphorus (SRP) was analysed by the molybdate method (Stainton 1977). Total dissolved nitrogen (TDN) was determined by the modified phenol method after photo-oxidising and passing the water samples through zinc columns in order to reduce nitrate and nitrite that result from photo-oxidation. TDP was done by the molybdate method after photo-oxidising the water samples to digest soluble organic matter in the samples.

Fish Species

Five different Mbuna species were selected for this study. Each species represented one of the five feeding habits that Reinthal (1990) found nearshore cichlid to exhibit. Due to their differences in feeding habit nearshore cichlids show differences in their food sources. Obligate benthic feeders like *Pseudotropheus tropheops* feed preferentially on epilithic algae while *Pseudotropheus zebra* and *Cynotilapia afra* feed in the water column, eating mainly pelagic diatoms (Bootsma et al. 1996; Reinthal 1990). Intermediate feeding were also identified by Reinthal (1990) and species that were allocated to these categories show some level of overlap with benthivorous and pelagic feeders species, e.g. *Petrotilapia* "Mumbo blue", *Labeotropheus fuelleborni* (Table 2.1). These species allowed estimation of nutrient regeneration that were representative of the whole fish community as whole range of food sources were covered. Different food sources are known to influence excretion rates (Schindler and Eby 1997) as their N and P composition may vary. The species selected were collected at Thumbi and Nakatenga Islands and these species are particularly abundant in these locations. The only exception is *Cynotilapia afra*, which was not seen at the Nakatenga Island.

Table 2.1: List of cichlid fish species selected for the study and their major food sources according to the references given.

Species	Preferred food sources	Reference
Pseudotropheus zebra	*Melosira* and *Nitzschia epiphyticoides*	Reinthal 1990
Petrotilapia "mumbo" *blue*	Diatoms, *Calothrix* and *Oscillatoria*	Reinthal 1990
Labeotropheus fuelleborni	*Calothrix*, *Oscillatoria* and *Cladophora*	Reinthal 1990
Cynotilapia afra	Pelagic diatoms	Ribbink et al. 1983; Reinthal, 1990
Pseudotropheus tropheops	*Calothrix* and *Oscillatoria*	Reinthal 1990

Determination of fish community excretion and defecation

Species and size specific rates of nitrogen and phosphorus excretion and defecation determined experimentally were scaled-up to the community level by combining them with fish abundance and size distribution data. The first procedure in the calculations was to derive fish biomass per size class (B_i) from the counts and size frequency data that were obtained from visual censuses and gilnet catches. This was accomplished as represented in the formula 2.1 by multiplying fish counts (A) by fish weight frequency data (F_i) (Figure 2.1), and mean weight of each size class established *a priori:*

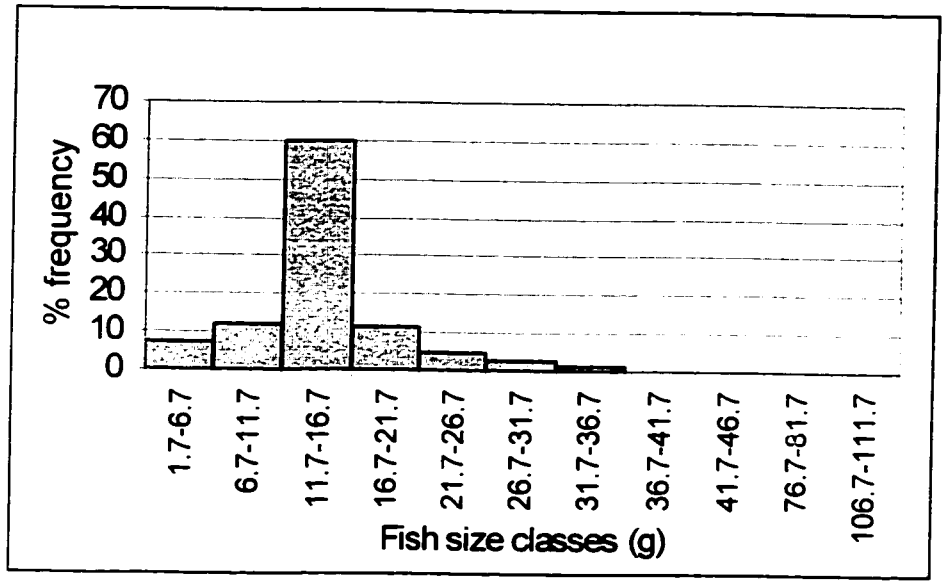


Figure 2.1: Size frequency distribution of cichlid fish specimens collected with gill nets at Thumbi and Nakatenga Islands (from F. Duponchelle, unpublished data).

$$Fi \times A \times Wi = Bi \qquad (2.1)$$

In the second step excretion or defecation rates were multiplied by the fish biomass (B_i) to obtain size classes excretion (Ce_i) or defecation (Cd_i) rates (formula 2.2):

$$E_i \times B_i = Ce_i \text{ or } D_i \times B_i = Cd_i \qquad (2.2)$$

Summing the size classes excretion or defecation rates across size classes we obtain the community excretion (Ce) or defecation rates (Cd) in grams of nitrogen or phosphorus per square meter per day (e. g. g N m^{-2} d^{-1}) (formula 2.3).

$$\sum Ce_i = Ce \text{ or } \sum Cd_i = Cd \qquad (2.3)$$

Periphyton nitrogen and phosphorus demand

The rationale for the calculation of algal nutritional demand was entirely stoichiometric. It is known from the primary production measurements done by Bootsma (1993) that algae fix carbon at a mean rate of approximately 1 g $C{\cdot}m^{-2}{\cdot}d^{-1}$. I assumed that as the algae photosynthesise and fix carbon they also take up nitrogen and phosphorus from the water in the same proportions as these elements appear in the periphyton. Therefore, element specific algal demand was calculated by first determining the C, N and P stoichiometry in the algal biomass and then calculating N and P uptake from carbon fixation rates (1 g $C{\cdot}m^{-2}{\cdot}d^{-1}$). The C, N and P stoichiometry of the algal biomass was assumed to be equal to C:N:P ratios determined in the epilithon scrapings (642:47:1) collected from the surface of rocks (Higgins 1999). Alternatively, N and P demand of algae were also calculated assuming Redfield ratio of C, N and P as it seems that C, N and P stoichiometry of the epilithon scrapings might not accurately represent the living algal cells due to detritus, extracellular organic excretions, bacteria and other organisms that are associated with the algae mats. It was impossible to separate the living algae cells for the C, N and P analyses.

Mass-specific excretion and defecation rates

Mass-specific rates of fish nitrogen excretion measured across 19 experiments and 5 different fish taxa varied between 10 – 100 μg N g^{-1} h^{-1} (Figure 2.2A), while phosphorus excretion rates ranged from 0.1 to 10 μg P g^{-1} h^{-1} (Figure 2.2B). Both nitrogen and phosphorus mass specific excretion rates were strongly influenced by allometry, which agrees with fish nutrient regeneration studies carried out by Schindler and Eby (1997), Mather et al. (1995), Schindler et al. (1993), Kraft (1992), and Peters (1983). Excretion rates of ammonium (NH_4^+), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) were significantly correlated with mean fish weight in the incubation chambers ($P<0.001$). Smaller fish tended to have higher mass specific excretion rates than bigger fish. While specimens of about 10 g had N excretion rates of about 100 μg N g^{-1} h^{-1}, 90-g specimens had rates of about 10 μg N g^{-1} h^{-1}. For phosphorus, 10-g specimens excreted about 10 μg P g^{-1} h^{-1}, while 90-g specimens had excretion rates of about 0.1 μg P g^{-1} h^{-1}.

Mass-specific nitrogen defecation rates were between 5 – 50 μg N g^{-1} h^{-1} (Figure 2.3A), while phosphorus mass-specific defecation rates were between 0.2 – 7 μg P g^{-1} h^{-1} (Figure 2.3B). Both excretion rates and defecation rates were dependent on fish size, although the relationship between nitrogen defecation rates and mean fish weight was not as well defined due to high variability of nitrogen defecation rates. Nitrogen defecation rates did not correlate significantly with mean fish weight in the incubation chambers ($p=0.079$). However phosphorus defecation rate correlated significantly with mean fish weight ($p<0.05$).

Night-time mass-specific nitrogen excretion rates measured in 6 incubations of fish specimens ranging in weight from 3 to 33 g varied in between 3.87 and 15.43 μg N g^{-1} hr^{-1} (Table 2.2). Phosphorus mass specific excretion rates varied from 0.47 to 1.64 μg P g^{-1} hr^{-1} (Table 2.2). Although my sample size was small, nocturnal data showed the same pattern of relationship

between excretion rates and fish size as in daytime. Smaller specimens had higher mass-specific excretion rates that the bigger specimens. Nocturnal rates of N and P are lower when compared to diurnal rates. This is because fish at night were not feeding.

Table 2.2: Nocturnal excretion rates of nitrogen and phosphorus measured in two experiments. Mean fish weight is given in g, while N and P excretion forms are given in $\mu g\ g^{-1}\ h^{-1}$

Experiment	Mean fish weight (g)	NH_4^+	TDN	SRP	TDP
19	12.55	3.68	3.87	0.30	
19	3.49	10.50	15.43	1.87	0.90
19	28.22	4.09	5.24	0.53	0.47
20	5.04	9.93	9.24	1.53	1.64
20	33.36	8.12	7.69	0.35	0.64
20	12.94	5.88	6.14	1.32	1.23

Daytime mass specific excretion rates of nitrogen and phosphorus were consistently three times higher than their nocturnal counterparts. Lower excretion rates at night might be related to the fact that fish do not feed at nigh (Ribbink, personal communication). Mather et al. (1995) observed that time since feeding and feeding history affect excretion rates. Night time defecation rates were not measured directly; they were estimated from the assumption that they are 3 times lower than daytime defecation rates as it was observed with N and P excretion rates.

Ammonium (NH_4^+) was found to be the most predominant nitrogen fraction excreted. It accounted for 90 % of total dissolved nitrogen excreted (Figure 2.2A). Ammonium excretion rates were significantly different from TDN excretion rates (paired t-test, df=33; p= 0.003). Soluble reactive phosphorus (SRP) was practically the only phosphorus fraction excreted. Although SRP seems higher than TDP this differences are due to analytical errors. A paired t-test of SRP against TDP showed SRP to be not significantly different from TDP at 95% confidence level and 34 degrees of freedom (p= 0.499) (Figure 2.2B).

The combined species-specific and size effects on the excretion and defecation rates (Table 2.3) were tested statistically by ANOVA. The ANOVA results did not show a significant difference

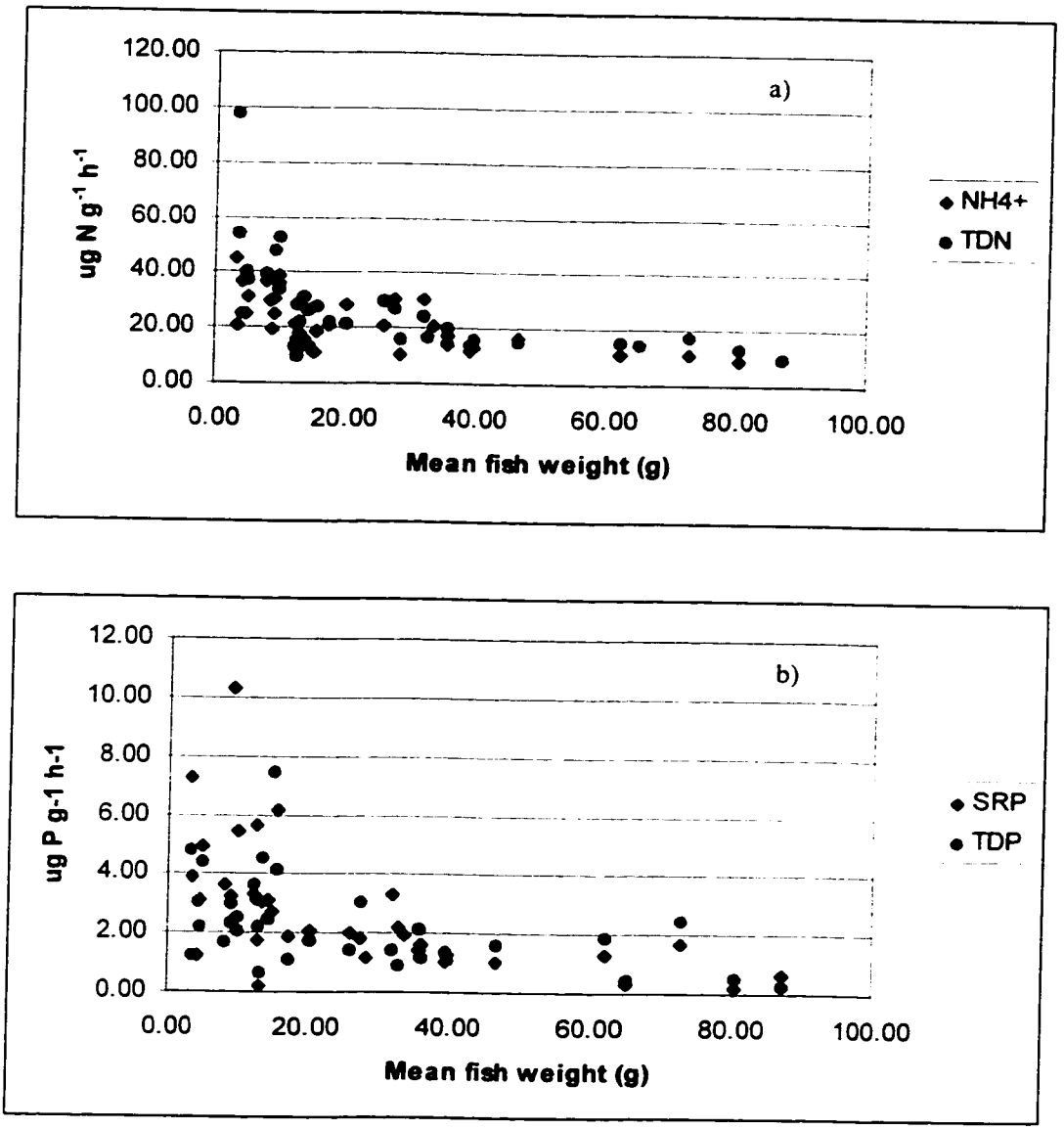
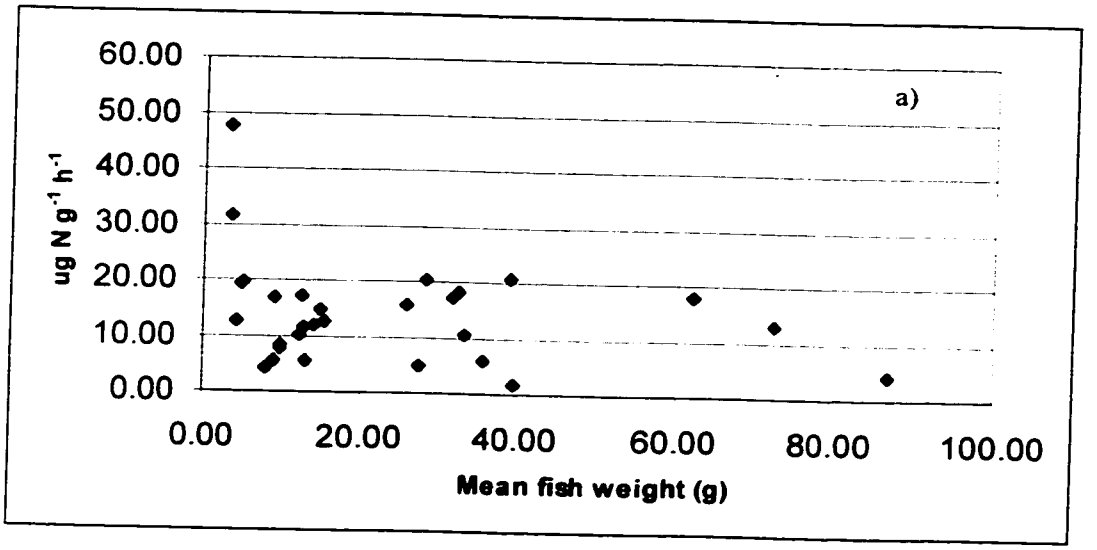


Figure 2.2: Effect of fish weight on mass specific rates of excretion of *Pseudotropheus zebra*, *Pseudotropheus tropheops*, *Petrotilapia* "mumbo" *blue*, *Labeotropheus fuelleborni*, and *Cynotilapia afra* combined. a) Solid squares represent total dissolved nitrogen (TDN) excretion rates and solid circles represent ammonia excretion rates. b) Open squares represent total dissolved phosphorus (TDP) excretion rates and open circles represent soluble reactive phosphorus (SRP) excretion rates.



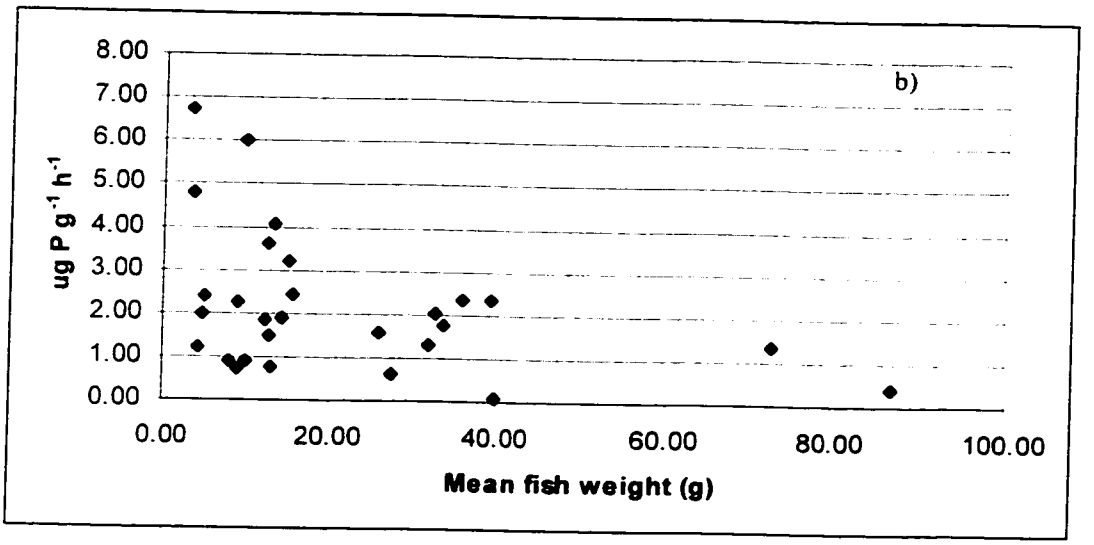


Figure 2.3: Effect of fish weight on mass specific rates of N and P defecation of *Pseudotropheus zebra*, *Pseudotropheus tropheops*, *Petrotilapia* "mumbo"*blue*, *Labeotropheus fuelleborni*, and *Cynotilapia afra* combined. a) particulate nitrogen defecation. b) particulate phosphorus defecation rates

for N and P excretion rates and N defecation rates. P defecation rates were the only exception (Table 2.4). ANOVA test excretion and defecation N:P ratios resulted also not significant (Table 2.4). The individual effects of fish size and taxa on the mass specific excretion, defecation and N:P ratios were not shown to be significantly different because it was extremely difficult to obtain specimens of the same size across taxa in the field.

Regeneration rates

Mass-specific rates of nutrient excretion and defecation varied allometrically. Therefore calculation of whole fish community excretion, and defecation, hereafter grouped as regeneration or recycling or re-supply rates, required estimates of fish biomass and the size structure of the fish community. Fish regenerated more N and P through excretion than defecation. Fish regenerated two times more N by excretion than by defecation (Table 2.5). Total N excreted was about 3.0 mmol N m^{-2} d^{-1} during daytime at 6-m depth, while defecation yielded 1.5 mmol N m^{-2} d^{-1}. During night-time N excretion was about 1.0 mmol N m^{-2} d^{-1} while defecation yielded 0.5 mmol N m^{-2} d^{-1}. Total N regeneration for 24 hr was about 5.8 mmol N m^{-2} d^{-1} for 6-m stations (Table 2.5). In contrast, P excretion rates exceeded P defecation rates by only 25%. About 0.15 mmol P m^{-2} d^{-1} of P were excreted during daytime at 6-m depth while defecation only yielded about 0.12 mmol P m^{-2} d^{-1}. At night P fish excretion yielded 0.05 mmol P m^{-2} d^{-1}, while defecation produced about 0.04 mmol P m^{-2} d^{-1}. The total P fish regeneration for 24 hr was determined to about 0.35 mmol P m^{-2} d^{-1} (Table 2.5). At 10 m stations fish N and P regeneration rates were lower than 6 m stations due to lower fish abundances. N fish excretion yielded about 2.0 mmol N m^{-2} d^{-1}, while defecation produced about 1.0 mmol N m^{-2} d^{-1} during daytime at 10m stations. At night time N excretion yielded 0.6 mmol N m^{-2} d^{-1} while defecation produced 0.4 mmol N m^{-2} d^{-1}. Total N fish regeneration for 24 hr was estimated to be 4.0 mmol N m^{-2} d^{-1}. P excretion and defecation yielded respectively 0.101 and 0.081 mmol P m^{-2} d^{-1} during daytime, at night time P excretion and defecation yielded respectively 0.034 and 0.024 mmol P m^{-2} d^{-1}. Total fish P regeneration for 24 hr at 10 m stations was estimated to be 0.231 mmol P m^{-2} d^{-1} (Table 2.5)

Table 2.3: Mass-specific rates of N and P excretion and defecation, N to P ratios of excretion and defecation, weight of the five species experimented and number of cases used for the averages and standard deviation calculations. For each variable data given in the format: mean ±standard deviation. Averages and standard deviations given for each species were calculated from all experimental observations; experiment with missing data were omited before calculating N:P ratios. N and P rates of excretion and defecation are given in $\mu g\ g^{-1}\ h^{-1}$

Taxa	Weight (g)		Excretion						Defecation					
			n	N		P		N:P	n	N		P		N:P	
Cynotilapia afra	9.2	±0.86	3	43.36	±8.20	2.33	±0.56	19.5 ±5.8	4	6.49	±2.01	2.11	±2.58	5.6	±3.3
Pseudotropheus zebra	10.53	±4.19	8	26.96	±14.76	1.78	±1.27	15.44 ±5.13	9	15.84	±7.03	2.76	±1.10	6.2	±2.4
Pseudotropheus tropheops	23.60	±11.29	2	26.19	±2.32	2.81	±1.91	11.77 ±7.19	2	14.87	±3.29	1.87	±0.81	9.2	±5.8
Labeotropheus fuelleborni	25.67	±13.04	10	26.99	±25.35	1.78	±1.27	15.44 ±5.13	10	15.93	±12.94	2.57	±2.33	8.4	±4.9
Petrotilapia "mumbo" *blue*	68.94	±14.32	6	14.28	±2.59	1.20	±0.91	19.65 ±12.74	3	11.63	±6.92	3.16	±3.96	7.3	±4.3

Table 2.4: Results of analysis of variance (ANOVA) of species effects on N and P excretion and defecation rates as well as on N to P ratio of excretion and defecation. df represent degrees of freedom, P is the probability, NS mean test not significant and S mean test significant.

	Excretion			Defecation		
	N	P	N:P	N	P	N:P
df	32	28	30	29	29	28
P	0.230	0.098	0.192	0.824	0.000	0.595
Significance	NS	NS	NS	NS	S	NS

Table 2.5: Regeneration rates of soluble forms of nitrogen (ammonia (NH_4^+) and total dissolved nitrogen (TDN)) and phosphorus (soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP)) and particulate forms of nitrogen (particulate nitrogen (PN)) and phosphorus (particulate phosphorus (PP)) represented in mmol m^{-2} d^{-1}at 6, and 10-m depth of Nakatenga and Thumbi Islands.

	Thumbi West Is.						Nakatenga Is.					
	6m			10m			6m			10m		
	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr
NH_4^+	2.323	0.847	3.170	1.276	0.465	1.741	2.396	0.874	3.270	1.814	0.661	2.475
TDN	2.930	0.955	3.885	1.610	0.525	2.135	3.023	0.986	4.009	2.285	0.746	3.031
PN	1.466	0.466	1.932	0.805	0.268	1.073	1.512	0.504	2.016	1.145	0.381	1.526
Total N	4.396	1.421	5.817	2.415	0.793	3.208	4.535	1.490	6.025	3.430	1.127	4.557
SRP	0.152	0.052	0.204	0.084	0.028	0.112	0.157	0.053	0.210	0.119	0.040	0.159
TDP	0.148	0.043	0.191	0.080	0.023	0.103	0.150	0.044	0.194	0.114	0.033	0.147
PP	0.122	0.041	0.163	0.067	0.020	0.087	0.126	0.042	0.168	0.095	0.031	0.126
Total P	0.270	0.084	0.354	0.147	0.043	0.190	0.276	0.086	0.362	0.209	0.064	0.273

Table 2.6: Percentages of calculated regenerated nutrients from fish community to periphyton total nitrogen and phosphorus demand calculated from photosynthesis. The periphyton demand was calculated assuming C, N and P composition of periphyton equal to C, N and P measured in epilithic mass scraped from the surface of rocks at 6, and 10-m depth of Nakatenga and Thumbi Islands. NH_4^+=Ammonum; TDN = total dissolved nitrogen; PN = particulate nitrogen, SRP = soluble reactive phosphorus; TDN = total dissolved phosphorus; PP = particulate phosphorus.

	Thumbi West Is.						Nakatenga Is.					
	6m			10m			6m			10m		
	day	nigh	24 Hr	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr
NH_4^+	31.3	11.4	42.7	17.2	6.3	23.5	32.3	11.8	44.1	24.4	8.9	33.3
TDN	39.4	12.9	52.3	21.7	7.1	28.8	40.7	13.3	54.0	30.8	10.0	40.8
PN	19.7	6.3	26.0	10.8	3.6	14.4	20.4	6.7	27.1	15.4	5.1	20.5
Total N	59.2	19.1	78.3	32.5	10.7	43.1	61.1	20.1	81.1	46.2	15.2	61.3
SRP	125.8	42.8	168.6	69.1	23.5	92.6	129.8	44.1	173.9	98.3	33.4	131.7
TDP	122.2	35.2	157.4	66.0	19.3	85.3	124.0	36.3	160.3	93.9	36.3	130.2
PP	100.9	33.9	134.7	55.4	16.5	71.9	104.0	34.7	138.8	78.8	25.6	104.1
Total P	223.1	69.4	292.6	121.5	35.5	157.0	228.1	71.1	299.2	172.7	52.9	225.6

Algal Demand and Regeneration Supply

Based on N and P periphyton demand determined assuming C, N and P stoichiometry of periphyton was equal to measured epilithic periphyton mass C, N and P ratios, at 6m on all stations, daytime N fish excretion could account for 40 % of the algal N demand. Defecation could supply an additional 20% of algal N demand. At night-time, fish excrete at much slower rate, contributing only 10 % to the daily demand. Night-time defecation rates were not measured, however if we make an assumption that the defecation rates at night were three times less than daytime rates as observed with N and P excretion rates, then the contribution of defecation would be about 7 % of demand. Therefore, the total nitrogen regenerated by fish at 6 m should account for about 77 % of daily algal demand (Table 2.6). At 10 m daytime N excretion accounted for only 25% and defecation accounted 13%, 15% and 7 % less compared to 6m depth excretion and defecation rates respectively. Night time N excretion averaged only 8 % the daily algal demand, and defecation contributed with 4 % given the assumption above. Hence, the 24 hour regeneration could account for 50% of daily algae N demand at 10 m (Table 2.6). Bootsma (1993) measured photosynthesis rates at 4 m. These rates were used to determine the algal demand at 6 and 10 m depth. However, due to light extinction, photosynthetic rates at 10 m should be lower and not as much lower at 6 m. So it is likely that fish supply as much of N and P demand at 10 m as at 6, because algal demand will decline with depth and light availability

At 6m, average daytime P excretion rates accounted for 122 % of P periphyton demand, while defecation accounted for 102 %. At night-time, excretion accounted for another 35 %, and defecation accounted for about 33 %. Therefore, over 24 hours P regeneration accounted for 292%, about three times more than periphyton requires. At 10-m depth, daytime excretion accounted for on average 80%, and defecation accounted for 67%. Night-time excretion of P accounted for an average of 28% of daily algae demand. Defecation contributed 22% so the total regeneration for a 24-hour period accounted for 197 % of periphyton P demand (Table 2.6). Because algal demand decreases with depth, these percentages may be underestimates.

Table 2.7: Percentages of calculated regenerated nutrients from fish community to periphyton total nitrogen and phosphorus demand at 6, and 10-m depth of Nakatenga and Thumbi Islands. Periphyton demand calculated assuming C, N and P composition of periphyton equal to theoretical Redfield ratios. NH_4^+=ammonia; TDN = total dissolved nitrogen; PN = particulate nitrogen, SRP = soluble reactive phosphorus; TDN = total dissolved phosphorus; PP = particulate phosphorus.

	Thumbi West Is.						Nakatenga Is.					
	6m			10m			6m			10m		
	day	nigh	24 Hr	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr
NH4+	18.4	6.4	25.1	10.1	3.7	13.8	19.0	6.9	25.9	14.4	5.2	19.6
TDN	23.3	7.6	30.9	12.8	4.2	17.0	24.0	7.8	31.8	18.1	5.9	24.0
PN	11.6	3.9	15.5	6.4	2.1	8.5	12.0	4.0	16.0	9.1	3.0	12.1
Total N	34.9	11.5	46.4	19.2	6.3	25.5	36.0	11.8	47.8	27.2	11.9	36.1
SRP	19.4	6.6	26.0	10.6	3.6	14.2	20.0	6.8	26.8	15.1	5.1	20.2
TDP	18.8	5.4	24.2	10.2	3.0	13.2	19.1	5.6	24.7	14.5	4.2	18.7
PP	15.5	5.2	20.7	8.5	2.8	11.3	16.0	5.3	21.3	12.1	4.0	16.1
Total P	34.4	10.6	44.9	18.7	5.8	24.5	35.1	10.9	46.0	26.6	8.2	34.8

Table 2.8: Percentages of excreted nutrients (ammonia (NH_4^+), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP)) and defecated (particulate nitrogen (PN) and particulate phosphorus (PP)) nutrients to total regenerated nitrogen or phosphorus pools at 6, and 10-m depth of Nakatenga and Thumbi Islands

	Thumbi West Is.						Nakatenga Is.					
	6m			10m			6m			10m		
	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr
NH4+	52.8	59.6	54.4	52.8	58.6	54.2	52.8	58.6	54.2	52.8	58.6	54.3
TDN	66.7	67.2	66.8	66.7	66.2	66.6	66.7	66.2	66.5	66.6	66.2	66.5
SRP	56.3	61.9	57.6	57.1	65.1	58.9	56.9	61.6	58.0	56.9	62.5	58.2
TDP	54.8	51.2	54.0	54.4	53.5	54.2	54.3	51.2	53.6	54.5	51.6	53.8
PN	33.3	32.8	33.2	33.3	33.8	33.4	33.3	33.8	33.5	33.4	33.8	33.5
PP	45.2	48.8	46.0	45.6	46.5	45.8	45.7	48.8	46.4	45.5	48.4	46.2

Comparing N and P periphyton demand calculated assuming C, N and P stoichiometry equal to theoretical Redfield C, N and P stoichiometry, daytime N fish excretion at 6 m was on average 24 % of periphyton N demand, while N defecation was12 %. Night-time excretion contributed 7.5 %, and defecation added another 4% of N periphyton demand. Therefore, 24 hr N regeneration by fish accounted for 47% of daily periphyton nitrogen demand at 6 m (Table 2.7). At 10 m during daytime, N excretion contributed an average of 15%, and defecation contributed 7.6 %. Night-time excretion accounted for 5%, and defecation accounted for 2.5 %. Therefore, 24 hr fish N regeneration accounts for 30 % of daily periphyton nitrogen requirement at 10 m (Table 2.7). Daytime P fish excretion could account for 20% of daily P periphyton requirement, while defecation added another 16%. Night-time fish excretion accounted for 7 % and defecation contributed with 5 %. Fish regeneration could supply 48 % of 24-hr periphyton P requirement at 6 m(Table 2.7). At 10-m depth stations, daytime excretion could supply 13 % of daily periphyton P requirement and P defecation contributed 10 %. Night-time P excretion would yield only 4% and defecation 3% of daily demand. Over 24 hrs fish regeneration would account for 30% of daily P periphyton requirement (Table 2.7), if Redfield stoichiometry is assumed.

The major proportions of regenerated N and P were in soluble form. For nitrogen, 67 % of total regenerated nitrogen was in soluble form, the rest in particulate form. Soluble and particulate forms supplied approximately equal proportions of total recycled phosphorus (Table 2.8). In all cases the assumptions for the calculation are that all N and P regenerated are consumed by benthic algae, while in fact losses to phytoplankton also occur but are undefined.

C, N and P stoichiometry in periphyton, fish and regenerated products

Fish faeces were much richer in phosphorus relative to nitrogen in excretory products (Table 2.9). N:P molar ratio of faeces were averaged about 12, while excretory products had a N:P ratio of about 21. Pooling excretory products and faeces, the N:P ratio calculated rose to 16, equalling the theoretical Redfield ratio. This excretory N:P ratio was in the range frequently reported in the literature for fishes (Schindler and Eby 1997; Mather et al. 1995), while defecated N:P ratio

Table 2.9: Molar N:P fish recycling ratios for soluble inorganic forms (NH_4^+:SRP), total soluble forms (TDN:TDP), Particulate forms (PN:PP), and all recycled forms combined (TN:TP) at 6 and 10-m depth of Nakatenga and Thumbi islands.

	Thumbi West Is.						Nakatenga Is					
	6m			10m			6m			10m		
	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr	day	night	24 Hr
NH4+:SRP	15.3	16.3	15.5	15.2	16.6	15.5	15.3	16.5	15.6	15.2	16.5	15.6
TDN:TDP	19.8	22.2	20.3	20.1	22.8	20.7	20.2	22.4	20.7	20.0	22.6	20.6
PN:PP	12.0	11.4	11.9	12.0	13.4	12.3	12.0	12.0	12.0	12.1	12.3	12.1
TN:TP	16.3	16.9	16.4	16.4	18.4	16.9	16.4	17.3	16.6	16.4	17.6	16.7

were not compared because no data were found in the literature. The pooled excretion and defecation N:P ratio was considerably lower than the N:P ratio measured in algal scrapings from the rocky surfaces.

Fish abundance and structure

Fish abundance determined by Ribbink (personal communication) based on visual counts at Nakatenga and Thumbi West stations is presented in Table 2.10. These results agree with the observations of Ribbink et al (1983). Fish densities as high as these are quite rare in natural fresh water ecosystems. Data on fish species diversity (not presented here) were unusual for fresh water ecosystems as Ribbink et al. (1983) also found. A decreasing pattern of fish abundance with depth was also observed in this study and that pattern was consistent over the two sites where the estimates were performed. Interestingly fish densities and biomass were similar at Nakatenga and Thumbi Islands, suggesting the locations may have similar carrying capacities because of similar algal productivities (Bootsma 1993). Fish consumption data (presented in Chapter 3) also suggest similarity in that the fish community consume nearly all the periphyton productivity. Unfortunately due to lack of replicate observations no statistical comparisons between the sites and between depths could be performed to validate statistically the observed differences.

Table 2.10: Rocky dwelling cichlid fishes densities and biomass measured in units of ind m^{-2} and g m^{-2} respectively at 6, and 10-m depth of Nakatenga and Thumbi islands.

Depth	Thumbi west Is.		Nakatenga Is.	
	Density	Biomass	Density	Biomass
6 m	9.5	140.6	9.8	145.04
10 m	5.2	77.26	7.0	109.81

Small-bodied fishes characterise the nearshore cichlid fish communities, only a few species of *Petrotilapia* attain substantial size either in length or in weight,. The median fish size (in g) observed in a sample of about 2000 specimens collected by Duponchele (personal

communication) (Figure 2.4) was located in the range between 12 to 17 g. The biggest specimen captured was 112 g and the smallest was 1.2 g (Figure 2.1). The size histogram obtained from the fish sample (Figure 2.1) showed a normal distribution, shape although slightly skewed to the left because juveniles are underrepresented in gill net catches. However, this does not seem to have influenced significantly the scaling of regeneration rates and consumption rates (Chapter 3) to the community level as the missing juveniles represent only a very small part of the fish community, as can be observed from the histogram (Figure 2.1).

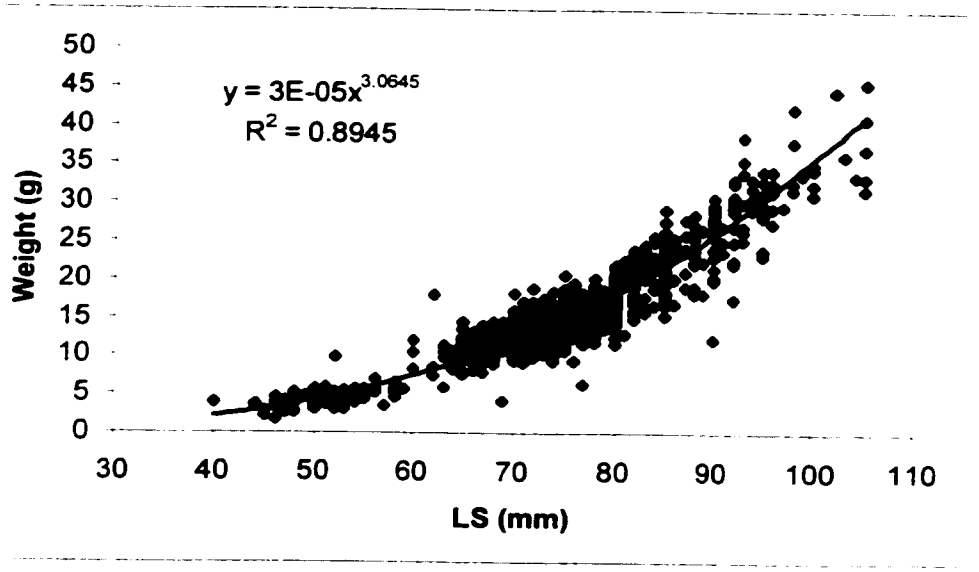


Figure 2.4: Standard Length (LS) and Weight relationship of cichlid specimens of several species collected by Duponchele (personal communication) with gillnet at Thumbi and Nakatenga Islands. All Mbuna species captured are pooled. The line represents a regression curve which regression function and coefficient is given in the figure.

Pelagic and littoral food webs of Lake Malawi receive low rates of nutrient loading and depend on locally recycled nutrients to support their productivity (Bootsma 1993, Guildford (in press)). The role of organisms in mediating recycling of nutrients is undoubtedly critical to maintaining stability of the food webs. Data produced by this study strongly suggest that fish mediate a major nutrient recycling process and contribute a major portion of the flux of inorganic nitrogen and phosphorus to the littoral zone of Lake Malawi. Whether fish nutrient regeneration satisfies periphyton nutrient demand requires further study. Definitive assessment of the importance of nutrients recycled by fish in meeting periphyton nutritional requirements will only be possible when more precise determinations of periphyton nutrient demand have been achieved. Based on our initial determinations of periphyton demand, fish recycle P and N in excess, about 5 times more P and 1.25 more N, than periphyton actually require to achieve currently measured rates of photosynthesis. Obviously, because the fish feed primarily on periphyton, they cannot regenerate more nutrients than are assimilated by periphyton. This would be thermodynamically impossible if these fishes rely completely on periphyton as concluded by Bootsma et al. (1996) for two of these species.

There is high likelihood that the source of this error lies in the determination of periphyton demand. As detailed elsewhere in this chapter the determination of periphyton demand was based on carbon fixation rates measured by Bootsma (1993) and C, N and P stoichiometry measured from the epilithic mat scraped from surfaces of rocks. The stoichiometric data are a potential problem because the epilithic mat contains live algae cells, as well as dead organic matter, bacteria, and inorganic. C, N and P ratios determined in epilithic mass were higher than the theoretical Redfield ratios. In fact because the epilithic periphyton community is nitrogen limited and dominated by *Calothrix* which fix atmospheric nitrogen (Higgins 1999), we would expect their ratios (especially N:P) to be lower than 16 (the ratio of rapidly growing algal community).

Calculation of periphyton demand applying the theoretical Redfield C, N and P ratios were also performed. Obtained demand figures were higher that fish regeneration rates, therefore holding

thermodynamic balance as fish community feed on periphyton and energy flows from periphyton to fish. Nitrogen excretion and defecation accounted for about 47% of periphyton nitrogen demand, using Redfield stoichiometry, leaving room for fish mortality to contribute 23% (Chapter 3), while, atmospheric nitrogen is fixation estimated to account for 30% (Higgins 1999). Benthic macroinvertebrates are also potential sources of recycled nutrients. However, quantification of their contribution to nutrient recycling has not been done. It is unlikely that this source can be significant. Phosphorus excretion and defecation accounted for about 50% of periphyton phosphorus demand while fish mortality (56 % of periphyton demand) and benthic macroinvertebrates (undetermined) should account for the remainder. These estimates assume all nutrients recycled are available to the periphyton. Any loss from the littoral to the pelagic would reduce these percentages, perhaps substantially.

The potential contribution of fish natural mortality in providing nutrients that may be utilised by periphyton was also considered. Mortality was assessed by assuming growth to equal mortality as the rocky dwelling cichlids are not practically harvested by local people and in the long term, this community are not documented to be undergoing substantial increase in their size. The haplochromine cichlids are well known to be philopatric, so local abundances are expected to be static. Therefore, if fish populations are not changing, it is quite reasonable to assume that mortality rate is equal to growth or production. Fish community growth and production estimation will be addressed in Chapter Three. The flux of nitrogen and phosphorus from the fish community due to mortality is estimated to be about 2.848 mmol N m^{-2} d^{-1}, corresponding to 22.6 % of periphyton N demand, and 0.455 mmol P m^{-2} d^{-1}, corresponding to 55.7 % of periphyton P demand. Fish mortality is therefore a major flux of nutrients to the periphyton, assuming nutrients are fully available. This is especially true for phosphorus because the proportion of phosphorus that is released from dead fish exceeds the major fish regeneration component (excretion). However, the fate of nutrients tied to dead fish biomass is uncertain. The possibility that these nutrients may be lost from the benthic food web. If this is the case this might be a path of significant export of nutrients, especially by migratory predators, from the littoral to elsewhere, especially for phosphorus. The likelihood that this export is occurring seems low, as littoral food webs may not have significant sources of P that would compensate for this loss of phosphorus due to fish mortality. In addition phosphorous seems relatively more

available to the periphyton which leads to the dominance of nitrogen fixing heterocystous blue green algae.

C, N and P stoichiometry

Haplochromine fishes in Lake Malawi regenerate N and P at the ratio of about of 16, a ratio similar to the theoretical Redfield for phytoplankton growing in optimal conditions of N and P supply. If periphyton N:P ratio were higher than the fish's, then regeneration N:P ratio should be higher than the food sources (periphyton). Sterner and George (1999) observed that for fish to maintain constant elemental stoichiometry in their tissues, they must regulate element specific retention efficiency in proportion to the concentration of the elements in their food sources. As a consequence, when fish feed upon a diet that has, for instance, an N:P ratio that is higher than the fish's N:P ratio, the fish regeneration N:P ratio will be even higher than the N:P ratio of the food sources. In the case where the food source has a lower N:P ratio than the fish N:P ratio, the regeneration N:P ratios will be even lower than the food sources. There are at least two explanations for the total regenerated N:P ratios to be about 16: 1) fish might be very selective in feeding from the periphyton mat to the point that they can actually select living algal matter with C, N and P that might be close to Redfield ratios. 2) Alternatively, N to P ratio measurements on scraped periphyton samples might be higher than what the living algal cell actually are; they might not reflect the stoichiometry of these elements in the living cells for the reasons explained above. It is important to note that using the C, N and P ratios from benthic scrapings gave rise to a large imbalance between periphyton nutrient requirements and nutrient supply by fish. Also fish maintaining a constant stoichiometry could not regenerate at Redfield ratios if they were consuming a diet of such a high N:P.

N:P supply ratios and periphyton community structure

N and P regeneration ratios may have important effect on the periphyton community of the rocky littoral of Lake Malawi, because N and P re-supply has been shown to be critical in determining algae community structure in other studies (Helal and Culver 1991; Sterner 1990; Elser et al. 1988; Smith 1983). Nitrogen-fixing blue green algae often dominate in lakes where N:P ratios are low (Smith 1983; Tilman et al. 1982) and blue green algae are rare in lakes with N:P molar ratios higher that 64:1 (Smith 1983). In the littoral zone of Lake Malawi, nitrogen-fixing blue green algae dominate the epilithic periphyton community (Higgins 1999; Bootsma, 1993). This has been considered to be a result of fish defecation and mortality, which contribute in the phosphorus rich but nitrogen poor faecal material. My data indicate that the N:P ratio of fish faeces is about 12:1, and dead fish might re-supply N and P at the ratio of 11:1. These are ratios that can competitively favour dominance of nitrogen fixing blue green algae (Tilman et al. 1982; Smith 1983). The fact that N-fixation rates are high in the littoral suggests that fish debris and defecation are more likely to be more retained in the littoral than excretory products which have a higher N:P.

Comparison of mass-specific excretion rates with other studies

The range of mass-specific P excretion rates measured in this study (0.1 – 10 μg P g^{-1} h^{-1}) is broader than those reported by Mather et al. (1995) (0.03 – 0.44 μg P g^{-1} h^{-1}), Lamarra (1975) (0.8 – 4.7 μg P g^{-1} h^{-1}), Nakashima and Leggett (1980) (0.78 – 3.16 μg P.g^{-1}.h^{-1}), and Brabrand et al. (1990) (2.0 – 7.6 μg P g^{-1}.h^{-1}), although it spans the range of values reported in the literature. Similarly, the range of rates of N excretion measured in this study were much broader (10 – 100 μg N g^{-1} h^{-1}), and generally higher than rates reported by Mather et al. (1995) (12.0 – 47.0 μg N g^{-1} h^{-1}). The Mather et al. (1995) range falls in the lower half portion of this study's range. Rates of N excretion of unfed fish measured by Brett and Zala (1975) (4.75 μg N g^{-1} h^{-1}) and Savitz (1969) (4.75 and 3.08 μg N g^{-1} h^{-1}) were below my minimum rate. A bibliographic yielded data on mass specific rates of defecation on cichlid fishes or other species, therefore comparisons of this study defecation rates with others were not performed.

Potential availability of excreted nutrients to the phytoplankton

Fish-excreted nutrients may not be retained only in benthic food webs, although calculations presented here have been based on the assumption that all regenerated nutrients are eventually taken up by periphyton. The physical/chemical State of recycled nutrients may determine their relative availability to periphyton or phytoplankton. The nutrients recycled in particulate form can settle onto the immediate substrata and be processed as detritus, slowly liberating nutrients that may be taken up by the adjacent periphyton. However, nutrients recycled from fish in soluble inorganic form, excreted directly to the water column, are subjected to advective water circulation. This may reduce their availability to the periphyton but increase their accessibility to phytoplankton. Dissolved excretory products may represent a net loss to the attached algal community, especially compared to nutrients recycled from faeces.

If we assume that excreted nutrients are exported to the pelagic zone, and that periphyton only have access to nutrients in particulate form (faeces and dead fish), then the fish community re-supply about 4.864 mmol N m^{-2} d^{-1}, corresponding to about 39 % of periphyton N demand, and about 0.615 mmol P m^{-2} d^{-1}, 77.1 % of periphyton P demand, and N:P ratio drops from 16:1 to 8:1. It is important to note that P therefore would be relatively better re-supplied to periphyton than N. The excreted portion lost from the littoral zone would have a higher N:P. This pattern of N and P cycling would impose N limitation on the benthic algae as observed by (Higgins 1999).

This study provides evidence that excretion and defecation by rock dwelling cichlids recycle substantial amounts of nitrogen and phosphorus that may support currently measured rates periphyton photosynthesis. However the uncertainty of the nutrient composition of living periphyton hampers assessment of whether N and P recycled by the rock dwelling cichlids of Lake Malawi meet periphyton demand for these nutrients. This study also provides evidence that fish may be important in structuring the epilithic periphyton by imposing a low N to P ratio on the benthic algae and therefore favouring dominance of nitrogen-fixing blue-green algae species in the periphyton community.

Chapter 3: Energy and nutrient balance of rock dwelling cichlids grazing on epilithic periphyton of the littoral zone of Lake Malawi, Niassa, Africa

Introduction

Bootsma (1993) performed initial measurements of periphyton primary production in the rocky littoral zone of Lake Malawi. He found this community to exhibit one of the highest rates of benthic primary production in fresh water ecosystems (1 g C m^{-2} d^{-1}), a rate that is comparable to coral reef ecosystems. Besides high rates of carbon fixation, Higgins (1999) reported high rates of atmospheric nitrogen fixation by benthic algae in Lake Malawi.

Despite high C, N and P assimilation by the periphyton and production of organic matter, accumulation of epilithic periphyton biomass has not been observed in these habitats. This suggests that loss of organic matter from periphyton through respiration, organic compound release, and grazing must balance these high periphyton productivity rates. Of these loss processes, only grazing can lead on to high rates of secondary production

A diverse and dense cichlid fish community that feeds directly on periphyton (Bootsma et al. 1996; Reinthal 1990; Ribbink 1983; Fryer 1959) characterises the littoral zone of Lake Malawi. Therefore, fish consumption may account for a major portion of organic matter losses from the periphyton community to meet the nutritional demand of the dense fish community (up to 10 fish m^{-2}). It is thought that the existence of this unique diversity of fishes sharing limited space is made possible by high periphyton productivity that provides virtually unlimited food, eliminating the possibility of food resource competition (Fryer 1959).

The objectives of this chapter are to answer the following questions: 1) what is the fish community grazing or consumption rate? 2) Is the periphyton primary production able to meet fish community nutritional requirements? 3) What proportion of benthic algae

production can be consumed by fish? 4) What proportion of nutrients consumed by fish can be recycled to the algae community.

The hypothesis put forward is that the fish community, due to its great size and stability, mediates the major loss flux of nutrients from the periphyton community by consuming a major proportion of periphyton production. In addition fish are able to derive most of their nutritional requirements from periphyton consumption and so maintain their current abundance.

Fish community consumption rates were determined using the nutrient mass balance form of the bioenergetic model described by Kraft (1992) by balancing the terms of the equation of the model. The bioenergetic mass balance model for N and P defines that of all food consumed (C), a portion of N and P will be lost as faeces (U), another portion is fixed in the tissues as the fish grow (G), and another portion is lost through excretion (E). Mathematically the representation of the nutrient balance equation is:

$$C = U + E + G \qquad (3.1)$$

Excretion and defecation rates of the fish community were determined experimentally as described in the last section. The growth rates were determined in the lab by rearing specimens of two herbivorous cichlid species, *Pseudotropheus zebra* and *Labeotropheus fuelleborni*, for about 22 days under controlled conditions. Both species rely on periphyton as their primary food in their natural environment (see Chapter two).

To start the rearing experiment a number of specimens of both species were caught from the wild, as described in the materials and methods section of the last chapter, and brought into the lab. In the lab the specimens were sorted into species, and then each species divided into three size classes of five individuals. After this the fish were transferred into six aquariums of about 160 litres in volume and acclimatised for about a week. During the acclimatisation the fish were fed twice a day ration of commercial fish food that was proportional to the total biomass present in each aquarium. Usually the daily ration provided was about three percent of their wet body weight. This amount of food seemed to provide them satiation as very often food was left until following day. Usually the food was provided in the morning, between 8-10 hours of local time; and again at dusk, in between 16-18 hours of local time, if no food was found remaining. To protect the fish from ammonium intoxication the aquariums were equipped with ammonium filters, these filters were shown to efficiently remove most of the ammonium produced by fish excretion. In addition the water in the aquariums was changed every

two days. Water temperature was monitored on a daily basis and an effort was made to never let water temperature rise above 28 °C. This was accomplished by exchanging water more often when tendency towards temperature increase was noticed.

When the experiment started, all fish specimens were weighed and after 11 and 22 days from the start of the experiments all specimens were weighed again. The treatment of the fish was kept as similar as possible to the acclimatisation phase. Every two days all fish faeces produced were collected from the aquarium by siphoning the bottom of the aquarium. The faeces were then dried and weighed.

When the experiment finished, two specimens from each aquarium were sampled randomly. The specimens were then killed, dried, measured for their dry weight, and stored in the deep freezer for later analysis of nitrogen and phosphorus content. Unfortunately these samples were lost when they were being shipped to Canada.

Some deaths occurred during the rearing experiment. Dead fish were replaced with one of similar size if available from the surplus tank (containing specimens not being used in the experiments). If specimens for replacement were not available, no replacement was carried out, but adjustment in food supply was immediately made in other to keep the same food supply rate.

As individual growth rates were measured directly, and averaged into size class groups, the next step was to determine the community growth or fish community production (P). This was performed by multiplying the growth rates (Gi) measured as increase in mass per unit of individual weight per unit of time ($g\ g^{-1}\ d^{-1}$) by fish biomass (Bi) of the corresponding size class and integrating the production across the size classes.

$$P = \sum Gi \times Bi \qquad (3.2)$$

Consumption was determined by adding the community production to community excretion and defecation rates already determined *in situ* in Lake Malawi (Chapter two).

However, before consumption was determined, production was first converted to quantity of nitrogen and phosphorus incorporated into fish biomass by multiplying production by a factor of 0.0091 for phosphorus in fish tissues, and by 0.025 for nitrogen (Sterner and George 1999; Davis and Boyd 1978).

These experiments didn't cover all the entire size range of fish collected from the field. Therefore, a relationship between the fish size and growth rates was developed (Figure 3.1) and used for estimating growth rates of size classes not covered in the experiments.

Individual growth rates

Individual growth rates measured in *Pseudotropheus zebra* and *Labeotropheus fuelleborni* specimens between 5 – 30g ranged in between 0.005 – 0.035 $g.g^{-1}.d^{-1}$(Figure 3.1). Individual growth rates were affected by allometry; small specimens exhibited higher growth rates than the larger specimens. A strong correlation was found between fish weight and individual growth rates ($p<0.05$). Taxa effects on the growth rates were difficult to assess as the specimens of the two species were quite different in size.

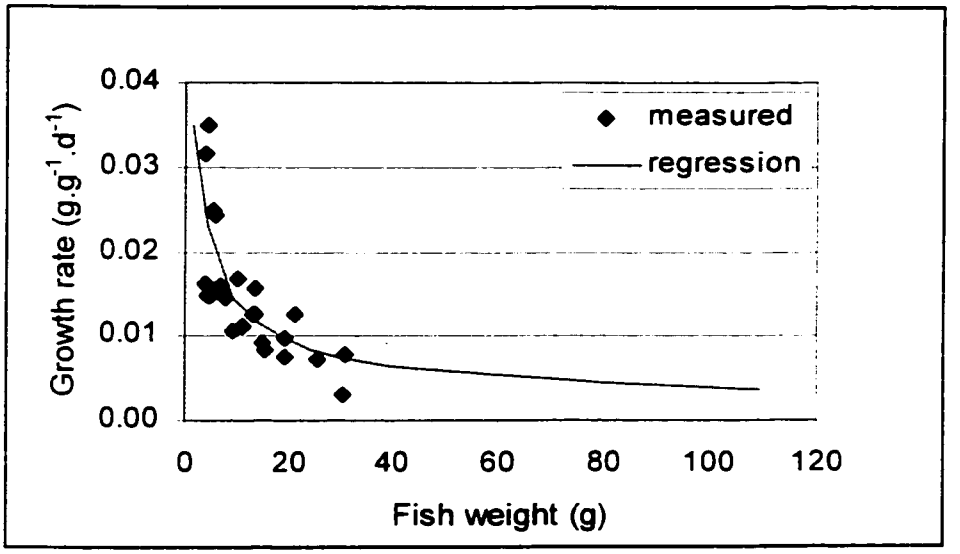


Figure 3.1: Relationship between individual growth rates and fish body weigh of *Pseudotropheus zebra* and *Labeotropheus fuelleborni*. The line represents the regression of the two variables ($p<0.05$).

Community production

Estimated fish community production or growth, determined by scaling up individual growth rates to observed fish densities and size (see Chapter two), was about 1.59 $g\ m^{-2}\ d^{-1}$, corresponding to about 2.848 $mmol\ N\ m^{-2}\ d^{-1}$ of nitrogen and 0.455 $mmol\ P\ m^{-2}\ d^{-1}$ of

phosphorus. This suggests that fish growth incorporated about 22.6 % of the nitrogen and 57.9 % of the phosphorus assimilated by the periphyton community, assuming that periphyton C, N and P assimilation stoichiometry was at Redfield ratios (Figure 3.2). If we use the measured C, N and P stoichiometry from scraped periphyton samples (Figure 3.2), fish production correspond to 38.3% of nitrogen and 375.9% of phosphorus assimilated by algae through photosynthesis. The P demand for by fish growth would be excessive if fish diet were comparable to scrapings.

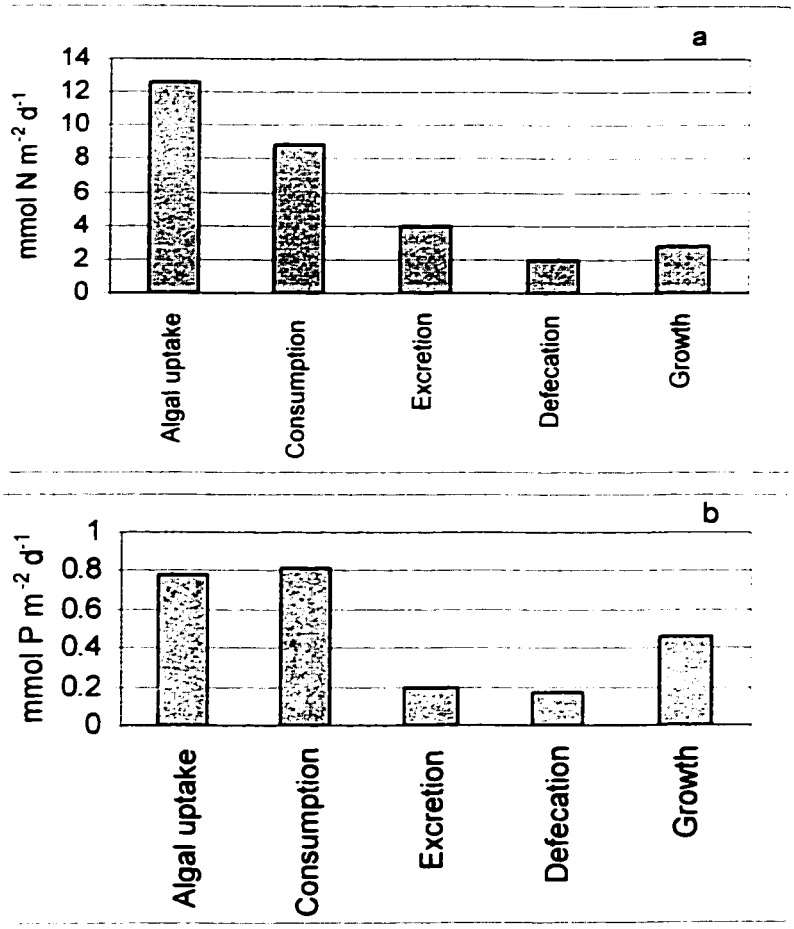


Figure 3.2: Comparison of fish a) nitrogen and b) phosphorus consumption estimate with periphyton uptake, with uptake assumed to be in Redfield C, N and P ratios. The three components of the estimate of fish consumption are indicated by the bars for excretion, defecation and growth.

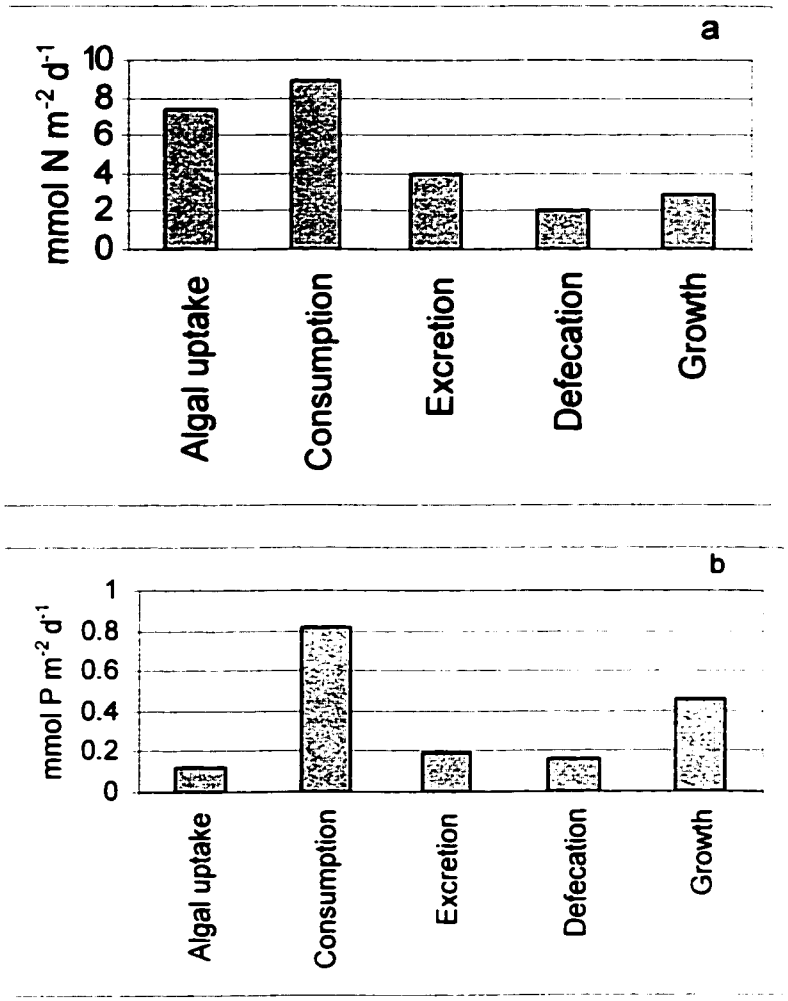


Figure 3.3: Comparison of fish a) nitrogen and b) phosphorus consumption estimate with periphyton uptake, with uptake assumed to be in measured C, N and P ratios on epilithon scrapings. The three components of the estimate of fish consumption are indicated by the bars for excretion, defecation and growth.

Fish consumption rates

From the bioenergetics mass balance model, we estimated fish consumption rates to be about 8.873 mmol N m^{-2} d^{-1} (0.124 g N m^{-2} d^{-1}) and 0.747 mmol P m^{-2} d^{-1} (0.019 g P m^{-2} d^{-1}), which correspond to about 70% of periphyton nitrogen assimilation and 103% of periphyton phosphorus assimilation, assuming that periphyton community C, N and P assimilation stoichiometry is Redfield (Figure 3.3). Fish nitrogen consumption is 119.4 % and phosphorus consumption is 675.1% of periphyton assimilation if C, N and P assimilation stoichiometry by periphyton is assumed to be equal to measured C, N and P ratios on periphyton samples (Figure 3.2). This results in a even greater distortion of the P balance between algal growth and fish consumption.

Bioenergetic models have been shown to be very useful in providing insights about growth processes (Rice et al. 1983), predator-prey interaction dynamics (Stewart et al. 1981), nutrient recycling (Kraft 1992), bioaccumulation of pollutants (Borgamann and Whittle 1992), and fish management strategies (Stewart et al. 1981). However, because bioenergetic models are based on equations that describe physiological processes, equations that are usually derived from laboratory experiments, they might not adequately represent field situations. In their widespread use, bioenergetics models have been evaluated by comparing their outputs with field observations. However, the adequacy of these models remains subject for debate (Boisclair and Leggett 1991; Hewett et al. 1991). Some evaluations have produced good fits (Rice and Cochran 1984; Olson and Boggs, 1986; Beauchamp et al. 1989; Brodeur et al. 1992; Kraft 1992; Ruggerone and Rogers 1992; Hewett and Kraft 1993) and others produced poor fits (Minton and McLean 1982; Diana 1983; Boisclair and Leggett 1989; Post 1990; Fox 1991; Wahl and Stein 1991; Madon and Culver 1993).

In this study, because only one term of the bioenergetics equation (Growth) was derived from laboratory experiments, the likelihood that estimates of consumption might be biased from the actual field situation is minimised. The growth term in the bioenergetics equation described in the materials and methods is 32% and 55 % respectively of nitrogen and phosphorus of the total consumption estimates. Excretion and defecation make up the rest. Excretion and defecation were measured in the field, therefore although certain margins of errors might exist, these terms should closely reflect the field situation. Criticism about growth rates determined in the laboratory is that higher growth rates than are usually obtained if better quality food is provided in captivity compared to natural food. In this study the fish were not provided natural food, therefore this factor might have influenced growth rate estimates. There is a potential that higher rates than field situation might have been estimated. However due to the scarcity of literature sources for comparison, it is difficult to compare my estimates with others on rock-dwelling cichlids of Lake Malawi. Nevertheless, my estimates of conversion efficiencies for phosphorus

were in the range observed by Penczak (1985), although those for nitrogen were slightly higher (Table 3.1), indicating that my growth rate estimates are acceptable within acceptable ranges. The fact that fish regeneration N:P ratio is near the Redfield ratio suggests the nearshore fishes of Lake Malawi may have a balanced nutrient diet, which should allow efficient N and P retention. The systems studied by Penczak (1985) may have been P limited; and therefore the fishes may be more efficient in use of P while inefficient in use of N. Food conversion efficiencies of this study were calculated as percent proportion of growth relative to fish consumption. Consumption rates were estimated from formula 3.1 using field estimates of excretion and defecation and laboratory estimates of growth.

Table 3.1: Comparison of N and P conversion efficiencies of rocky dwelling cichlids with some riverine fishes. The conversion efficiencies are given in percent.

Species	N	P	Author
Loach	18.54 ±4.38	42. 84 ±9.83	Penckzac 1985
Gudgeon	13.32 ±1.91	34.00 ±7.03	Penckzac 1985
Three-spined Stickleback	14.50 ±2.12	42.50 ±1.71	Penckzac 1985
Nine-spined Stickleback	13.20 ±2.85	36.47 ±3.38	Penckzac 1985
Malawi Cichlids	32.09	40.79	This study

The other aspect that might have influenced my estimates of growth rates, and consequently the fish community consumption rates, is the fact that we have assumed that species-specific variability on growth rates of the two species chosen for experiments is sufficient to represent all species in the community. How this assumption might affect the results can not be evaluated at present , but rock-dwelling cichlids are very genetically similar and therefore it is likely that differences in growth rates across different species might be of less significance. Previous studies of these fishes by Reinthal (1990), Bootsma et al. (1996) and Ribbink (1983) have shown that these species share common morphometric and even physiologic attributes, making the task of distinguishing different species extremely difficult.

A very important assumption made when evaluating fish grazing pressure on the periphyton community is that the rock-dwelling cichlid species are totally dependent on periphyton as their food, and are not consuming other resources. This assumption has great implications for the estimates of grazing; if these species have alternatives food sources, then the actual grazing pressure on algae will be lower than current estimates. However, stable isotope analyses of these species performed by Bootsma et al. (1996) showed that they rely primarily on periphyton as food sources. If there are alternatives, they must be of negligible importance in their diet in order not to alter our estimates of grazing pressure on periphyton.

Estimates of nitrogen and phosphorus accumulated as fish biomass through growth, and amounts of nutrients released through fish mortality (discussed in chapter 2) were based on published data on the nitrogen and phosphorus content of fish tissues. However this is not expected to have a great influence as fish C, N and P content do not show great variation (Sterner and George 1999; Penczack 1985). Malawi cichlid fishes like centrarchid fishes, are bony, so I used average P concentrations for centrarchid fishes, published by Sterner and George (1999) and Davis and Boyd (1978).

Our estimates of consumption rates (Figure 3.3) suggest that the fish community exerts a substantial gazing pressure and must be the major grazer of the periphyton community. If we consider an hypothetical situation where the periphyton community cease photosynthesising but the fish community continues feeding, based on current measurements of periphyton density and fish density, the fish community would need, in theory, only 5 days to deplete the nitrogen and 1.5 days for phosphorus from the periphyton organic matter pool. Continuous high rates of primary production are essential to maintain the fish community, and any decline in benthic primary production would have immediate consequences for the fish community.

If Redfield ratios are assumed for the periphyton being consumed, periphyton productivity is found to be higher than fish consumption (Figure 3.3); and apparently it would be able to meet the nutritional requirements of the fish community. This

observation supports the hypothesis put forward by Fryer (1959) that co-existence of many species in high densities is due to high availability of food (periphyton). However, the periphyton appear to depend heavily on nutrient regeneration from the fish community to maintain these high rates of primary productivity. Loss of the benthic grazing fish community would eliminate the major nutrient flux to the periphyton.

Cooper (1973) successfully showed that grazers can enhance productivity of primary producers independently from the grazer-regenerated supply of nutrients. He observed though that productivity increases could only be achieved within certain margins of grazing pressure, above or below which productivity decreased. However he didn't explain the mechanism by which higher productivity rates were achieved by producers under those circumstances. Lambert et al. (1989) observed that primary productivity was enhanced by additional gazing intensity only when the productivity is biomass or density dependent, suggesting self shading as the factor that limits productivity at high producer densities or biomass.

The fish community in the rocky littoral of Lake Malawi consumes about 70% and 103 % of respectively nitrogen and phosphorus production by epilithic periphyton. If these estimates (after all assumptions made) are correct, this grazing intensity according to Lambert et al. (1989) is quite significant. However its unlikely that the grazing effect alone determines the high periphyton productivity rates of the rocky littoral zone of L. Malawi. It is more probable that the combined effect of grazing and grazer-nutrient supply through regeneration give rise to the rates of periphyton that we observe. Removal of the fish community would quickly lead to extreme nutrient limitation of the periphyton because fish regeneration dominates P supply to the periphyton.

The fish community exerts a substantial gazing pressure and is the major consumer of the epilithic periphyton community of Lake Malawi. Consumption rates of about 8.873 mmol N m^{-2} d^{-1} of nitrogen and 0.747 mmol P m^{-2} d^{-1} correspond to about 70% of periphyton nitrogen assimilation and 103% of periphyton phosphorus assimilation, assuming that periphyton community C, N and P assimilation stoichiometry conforms to Redfield ratios and all regenerated nutrients from fish are available to the periphyton community. This suggests periphyton production is able to meet the nutritional requirements of the fish community, an observation that supports the hypothesis put forward by Fryer (1959) stating that co-existence of many species in high densities is due to the high availability of food (periphyton). Because defecated nutrients are richer in P and more likely to be retained by sedimentation in the near vicinity of the periphyton, the nutrient supply ratio of N:P to periphyton from fish may be lower than the above estimates. Consequently the realised nutrient supply ratio will result in a nitrogen deficit for benthic algal growth which is apparently met by N-fixation in the benthic algal community (Higgins 1999).

Fish community nutrient regeneration by N and P excretion, defecation and mortality (Chapter 2) as well as fish consumption of periphyton (Chapter 3) are summarised diagrammatically in figures 4.1 and 4.2 to emphasise: 1) the current view of nitrogen and phosphorus cycling in the littoral; 2) the interactions between the fish community and its food source (periphyton) in the flow of materials and energy and 3) the role of the fish in the littoral N and P cycling and even overall lake N and P cycle.

The P flow in the littoral is extremely unbalanced when P periphyton demand is calculated assuming C, N and P assimilation stoichiometry of periphyton equal to C,N and P content of benthic scrapings (Figure 4.2b). Fish community consumption for P appears to be much greater than what periphyton P production can provide, i.e. fish P consumption would be 675 % of P periphyton supply. Similarly in the N cycle, N periphyton production was lower than fish N consumption (Figure 4.2b), with fish N demand being 119 % of N periphyton supply. These unbalanced flows of N and P in the N and P cycles are due to low N and P periphyton demands that are obtained when C, N and P concentrations measured on algal scrapes are considered in calculation of demand of periphyton for these nutrients. However, Redfield C, N and P ratios allow determination of N and P demand that is more realistic, allowing fluxes in the N and P cycles (Figure 4.1a and 4.2a) to balance. These different assumptions about the stoichiometry of consumed rations by grazing fish result in very different conclusions. For Redfield proportions to be possible in the diet of grazing fishes, they must feed selectively in the benthic algal mat. This has been observed by H.J. Kling (personal communication) and others (Table 2.1). If the measured stoichiometry of benthic mat is assumed to represent the diet, the observed regeneration ratios are not possible. Consequently the Redfield stoichiometry in the diet and selective grazing are the most plausible assumptions.

In the phosphorus cycle fish biomass is the major reservoir of P. It was proportionally 35.6 times higher that the algal P pool but had a relatively low turnover rate (50 d)

compared to the turnover rate of P in the periphyton (1.5 d). This ensures steady supply of P to the periphyton community through defecation and mortality while minimising losses of P from the littoral zone. The excretion flux, measured to be 24.7 % of periphyton P demand (assuming Redfield ratios), could represent a loss of P from the littoral zone and may contribute to the pelagic food webs. Fish P defecation and mortality fluxes of P supplied periphyton with respectively 21.4 % and 55.7 % of periphyton P demand totalling P supply to 77.1% assuming Redfield ratios. With this supply, fish are the major P source for the periphyton. However, fish P supply leaves a deficit of about 22.9 % relative the periphyton P demand. This deficit must be met by uptake of nutrients from the water and from invertebrate regeneration. According to the fish consumption of periphyton flux (103 % of periphyton production), invertebrates must be consuming insignificant proportion of P periphyton production. Therefore invertebrate regeneration must be also an insignificant to supplement the deficit left by fish regeneration, given the present understanding of fluxes and the mass balance constraint. P uptake from the water column must account for the major portion of the deficit. However, it is not obvious that periphyton can derive the 22.9 % of their P demand from the soluble P pool given the low concentrations of soluble P in the surface waters of Lake Malawi. However algae can obtain P at very low concentrations if renewal of the water is rapid, as may be the case in this large lake.

The littoral N cycle (Figure 4.1a) differs from the P cycle because N_2 from the inexhaustible atmospheric reservoir can be made available to the biota through periphyton N-fixation. Fish defecation and mortality supplied 16 % and 22.6 %, respectively, of periphyton N demand (assuming Redfield ratios. Fixation of atmospheric nitrogen supplemented the fish supply with 30% of periphyton demand, leaving a deficit of 31.4 % to be met from other sources. Fish consumption of periphyton N flux is estimated to be 70 % of periphyton N production. Other losses may be invertebrate consumption, erosive transport of N rich detrital material, etc. The excess of N in the periphyton production to consumption may account for the high N:P in the benthic scrapings. The fish excretion flux (31.8 % of periphyton N demand), like P excretion may represent a loss to pelagic food webs.

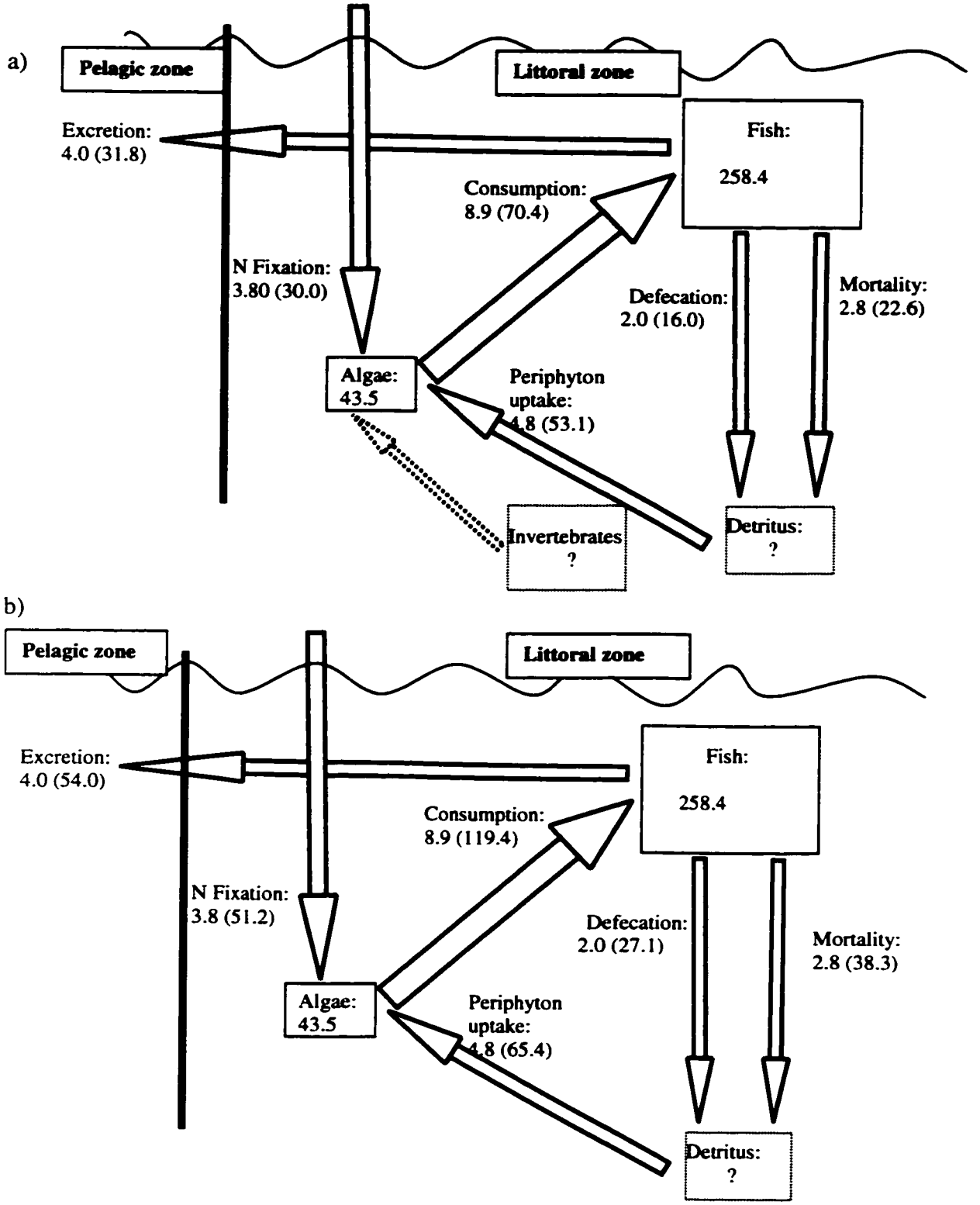


Figure 4.1: Nitrogen flow through a rocky littoral food web of Lake Malawi/Nyasa. Periphyton demand calculated assuming a) Redfield ratios and b) measured C,N and P ratios on benthic scrapes. Area of rectangles is proportional to pool size except the rectangles in dashed lines that pool sizes are unknown. Width of arrows is proportional to fluxes except dashed line arrows for which fluxes are unknown. The pool sizes are given in mmol N m^{-2} while fluxes are given mmol N m^{-2} d^{-1} and percent N periphyton demand given in brackets. Data presented is for 6 m depth.

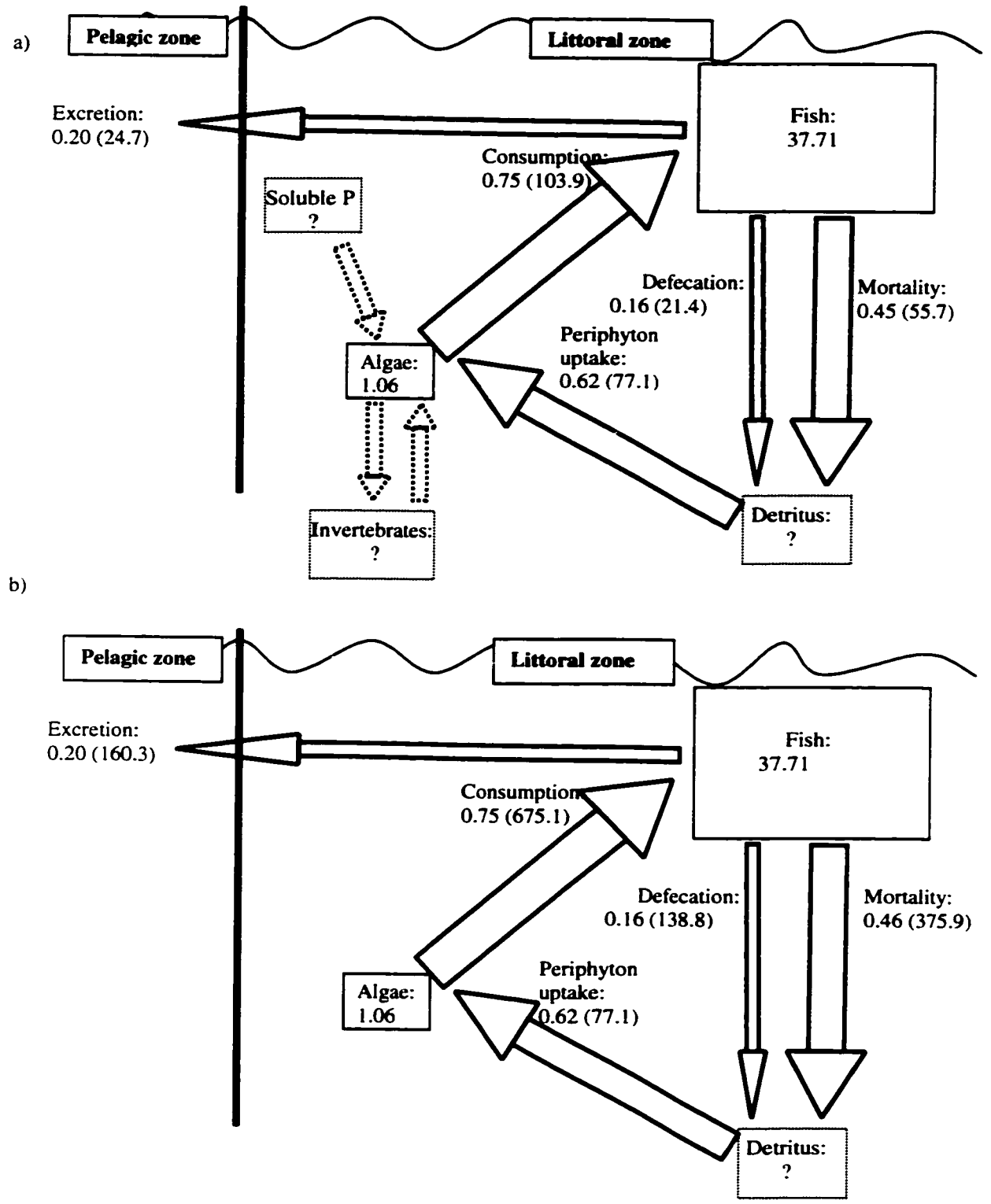


Figure 4.2: Phosphorus flow through a rocky littoral food web of Lake Malawi/Nyasa. Periphyton demand calculated assuming a) Redfield ratios and b) measured C,N and P ratios on benthic scrapes. Area of rectangles is proportional to pool size except the rectangles in dashed lines that pool sizes are unknown. Width of arrows is proportional to fluxes except dashed line arrows which fluxes are unknown. The pool sizes are given in mmol P m^{-2} while fluxes are given mmol P m^{-2} d^{-1} and percent P periphyton demand given in brackets. Data presented is for 6 m depth.

Data presented in Chapter Two and Three suggest that the fish community and the epilithic periphyton community exist in a very delicate inter-dependent relationship. The diversity and density of fishes seem to depend on the high productivity of the algae community. The fishes in turn, through recycling of grazed nutrients, appear to provide most of the nutrients that algae require to maintain high organic matter production. They may even enhance productivity by triggering compensative algal growth by effectively removing slow growing algal species. Higgins (1999) reports a low diversity of algal species in the periphyton, and these are selected for by the grazing and nutrient regime imposed by fish.

In the littoral zone of Lake Malawi we can not choose between keeping the algal community and discarding the fish community or the opposite. The two communities are inter-dependent and must be considered together for conservation, or neither of them can be maintained. Any disturbance that would directly affect the fish community abundance, and probably the diversity, such as over-fishing, will cause changes to the nutrient recycling and grazing pattern, and affect periphyton productivity and its biomass. On the other hand, any disturbance that might affect directly the periphyton community (e.g. eutrophication, sedimentation, etc.) will result in alteration of periphyton productivity and biomass, which will cascade to the fish community. Any management strategies to be put in place to conserve the rocky littoral zone habitat should strongly emphasise considering the fish and periphyton as an ecosystem unit, and must consider together abiotic and biotic external factors which can affect either the algae or fish elements of this association.

Among the most important threats to conservation of these important habitats are the human activities in the lake (fishing) and in the lake's catchment (eutrophication and sedimentation). The rocky littoral zone of Lake Malawi is generally easily accessible by the subsistence fishery due to its nearshore location. With the now rapidly growing population living in the watershed of Lake Malawi, and consequently increasing demand for resources, it is likely that fishing pressure upon the nearshore rocky dwelling cichlids

will increase. Currently, probably for cultural reasons, most of the Mbuna species are not preferred by the local people and the fishing pressure on these species is low.

Bootsma and Hecky (1999) have observed an increasing loading of limiting nutrients from the lake watershed, and correlated these trends with shifts in land use practices in the catchment areas. Therefore, eutrophication is a potential threat in the long-term perspective if management measures are not put in place. As Higgins (1999) noted, eutrophication will affect strongly the light penetration in the water column resulting in less light reaching the bottom and consequently reducing periphyton productivity. Less productivity will mean less food available for fish, a smoller number of species to be sustained and lower fish densities. Eutrophication, due to its effect on light penetration, will also interfere with the mechanism of fish diversification, leading to decrease in fish diversity. Seehausen et al. (1997) found the eutrophication impact on light penetration to relax sexual selection of these cichlids. Eutrophication will affect the composition of the benthic algae assemblages generally reducing the diversity of algal species. This should also impact the fish community because the rock-dwelling cichlids exploit differentially different algal taxa (Bootsma et al. 1996; Reinthal 1990).

With the increasing population demand for land for subsistence agriculture, more land is being cleared of natural vegetation cover and is more vulnerable to erosion during periods of strong rainfall. This is a another potential threat to the algae-fish association because a portion of the increased loads of sediments transported to the lake through rivers will be deposited on nearshore rocky shores, burying the algal mats, mainly at greater depths due to lower wave energy. The consequence of this is reduction of foraging surface area, resulting in more fish species accumulating in the shallows and leading to more competition for space and food. The sediments transported to the lake by the rivers, while still in suspension, affect transmission of light. Less light will be able to reach the bottom affecting the algal community and cichlid fishes in similar way that eutrophication does.

Management measures to avoid such human impacts must not only be applied at the lake scale, they should also be applied at the basin scale because not only fishing destabilise the periphyton-Mbuna association but also land use associated impacts on lake ecosystems such as eutrophication and sedimentation.

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