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# Nutrient Stoichiometry in Benthic Food Webs – Interactions Between Algae, Herbivores and Fish

ANTONIA LIESS
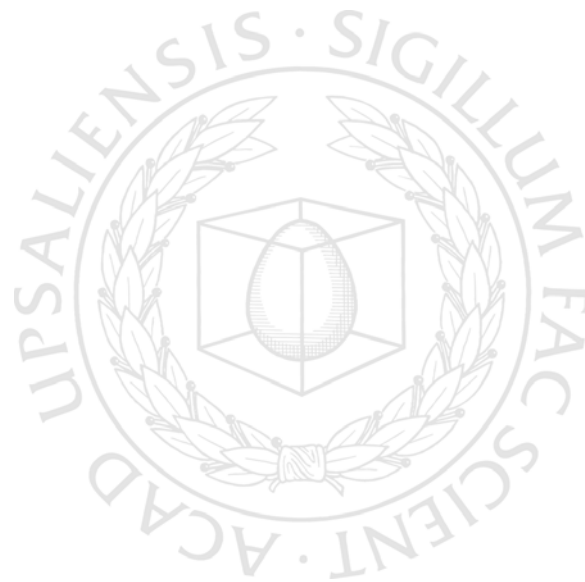
Dissertation presented at Uppsala University to be publicly examined in Friessalen, Kärnhuset, EBC, 752 36 Uppsala, Friday, September 8, 2006 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

**Abstract**
Liess, A. 2006. Nutrient Stoichiometry in Benthic Food Webs – Interactions Between Algae, Herbivores and Fish. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 197. 44 pp. Uppsala. ISBN 91-554-6592-7.

The aim of this thesis was to identify general structuring mechanisms in benthic food webs within the framework of ecological stoichiometry theory. Ecological stoichiometry is defined as the balance of multiple chemical substances in ecological interactions and explicitly considers the combined dynamics of key elements such as carbon (C), nitrogen (N) and phosphorus (P). Ecological stoichiometry theory was developed for pelagic environments, thus it must be tested whether the same mechanisms are applicable to benthic environments.

In this thesis, ecological stoichiometry theory was used as a framework to investigate nutrient pathways in benthic littoral ecosystems. I conducted one invertebrate field sampling and six experiments. In the experiments, factors such as grazing, light, nutrients and fish presence were manipulated.

The results showed that stoichiometric variability in consumers could mostly be explained by taxa. However, there was some stoichiometric variability due to sampling season, site, and nutrient enrichment.

Grazing mostly increased periphyton N and P content, although nutrient recycling effects were dependent on grazer stoichiometry. Grazing changed benthic algal community composition by increasing the proportion of grazing resistant algae species. Additionally, grazing decreased algal diversity, especially under nutrient poor conditions. The manipulation of fish presence revealed that fish affected primary producer biomass and stoichiometry through nutrient recycling.

The manipulation of abiotic factors, such as light and nutrient addition could affect periphyton nutrient content, biomass and benthic algal chlorophyll a content. The separate addition of N or P led to an increase of the added nutrient in the periphyton. Increased light intensities led to a decreased cellular chlorophyll a content and increased C:nutrient ratios.

This thesis arrives at the conclusion that periphyton-grazer-predator interactions in the benthic are bound by stoichiometric constraints. Nutrient recycling by benthic invertebrates and fish are important mechanism in benthic littoral ecosystems.

*Keywords:* ecologial stoichiometry, periphyton, grazer, benthos, trophic interactions, nutrient, algae

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*To the memory of my father*

*Cover picture:* Suzanne Viot.

# List of Papers

This thesis is based on the following papers, which will be referred to by their roman numerals.

I    Liess A., and H. Hillebrand. 2005. Stoichiometric variation in C:N, C:P and N:P ratios of littoral benthic invertebrates. Journal of the North American Benthological Society, 24: 256-269.

II    Hillebrand H., G. DeMontpellier, and A. Liess. 2004. Effects of macrograzers and light on periphyton stoichiometry. Oikos, 106: 93-104.

III    Liess A., and H. Hillebrand. 2006. The role of nutrient stoichiometry in grazer periphyton interactions at high P supplies. Journal of the North American Benthological Society, accepted.

IV    Liess, A., and M. Kahlert. The effects of gastropod grazers, nutrients and light on periphytic algal diversity. Oecologia, under revision.

V    Liess A., M. Quevedo, J. Olsson, T. Vrede, P. Eklöv, and H. Hillebrand. 2006. Food web complexity affects trophic interactions. Oikos, in press.

# Contents

# Abbreviations

| | |
|---|---|
| ANOVA | Analysis of variance |
| C | Carbon |
| Chl *a* | Chlorophyll *a* |
| DIN | Dissolved inorganic nitrogen |
| DIP | Dissolved inorganic phosphorous |
| MANOVA | Multivariate analysis of variance |
| N | Nitrogen |
| P | Phosphorus |
| RNA | Ribosomal nucleic acid |

# Introduction

The aim of this thesis is to identify general structuring mechanisms in benthic food webs within the framework of ecological stoichiometry theory. Because ecological stoichiometry theory was developed for pelagic environments, it is not self-evident that the mechanisms which regulate nutrient interactions in pelagic habitats are also applicable to benthic environments. Pelagic and benthic communities differ in fundamental ways. Perhaps the most important difference between the two is that pelagic primary producers, in contrast to their benthic equivalents, float freely in the water column, and thus can easily access available nutrients. Benthic algae are constrained by the shape and nutrient uptake kinetics of the periphyton matrix (Riber and Wetzel 1987). Thus, the same mechanisms that structure predator-grazer-producer interactions in the one habitat are not automatically applicable to the other.

## Ecological stoichiometry theory and trophic interactions

Trophic interactions are important in determining distribution and abundance of organisms. Hairston et al. (1960), in their famous theory about "why the world is green", envisioned food webs as consisting of three trophic levels: producers, herbivores, and predators. The theory states that abundant green plants dominate terrestrial landscapes because predators limit herbivores. Producers are consequently limited by their resources (bottom-up limitation). Since then, ecologists have been debating whether the primary control is by resources (bottom-up forces) or by predators (top-down forces) (reviewed in detail by Power 1992).

An alternative to the top-down versus bottom-up debate is to focus on the constraints of matter. This is called the theory of ecological stoichiometry. Ecological stoichiometry is defined as the balance of multiple chemical substances in ecological interactions and processes, or the study of this balance (Sterner and Elser 2002) and explicitly considers the combined dynamics of key elements such as carbon (C), nitrogen (N) and phosphorus (P). Ecological stoichiometry theory has not only increased the mechanistic understanding of trophic interactions (e.g. Elser et al. 1998; Sterner et al. 1998), but also of nutrient cycling (Elser and Urabe 1999; Vanni 2002) and population

dynamics (Andersen et al. 2004; Moe et al. 2005) as well as the role of species in ecosystems (Vanni et al. 2002).

A central premise of ecological stoichiometry is that animals are more stable (homeostatic) in their body nutrient composition and usually have lower C content than their plant prey (Sterner and Elser 2002). Thus, when a nutrient element in the plant biomass is in short supply relative to consumer requirements, the specific recycling rate of that element decreases (Sterner and Hessen 1994; DeMott et al. 1998; Elser and Urabe 1999). The nutrient composition of the consumers and that of their food influence the ratio at which nutrients are recycled. This was first noticed in pelagic communities (Olsen et al. 1986; Elser et al. 1988; Urabe 1993).

The amount of the element in short supply in the primary producer compared to consumer requirements also puts constraints on consumer growth (reviewed by Cross et al. 2005). High growth rates are predicted to require high P uptake, since organisms with higher growth rates require more P to produce P-rich RNA for protein synthesis as stated in the "Growth Rate Hypothesis" (Elser et al. 2000). This link has been found across species, during ontogeny, and under physiological P-limitation (Elser et al. 2003). When P was limiting, P-addition has led to increased growth rates and increased RNA and P-content in *Daphnia* (Vrede et al. 2002; Acharya et al. 2004) showing that body P-content and RNA content are coupled to growth rate under P-limiting conditions. This connection between organism stoichiometry and its growth rate as formulated in the "Growth Rate Hypothesis" is central to ecological stoichiometry theory.

## Ecological stoichiometry applied to benthic food webs

The benthic littoral food web usually consists of three to four tropic levels, with periphyton at the base, invertebrate grazers at the second trophic level and predatory macroinvertebrates and fish on top (Fig. 1).
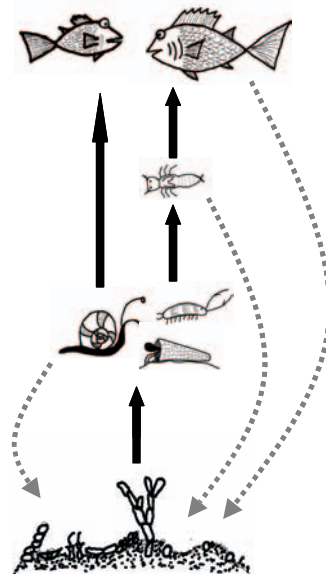
Figure 1: Benthic food web interactions between periphyton at the bottom, benthic grazers as consumers and macroinvertebrates and fish at the top. Solid arrows symbolize flow of matter through ingestion and dotted arrows symbolize the flow of recycled nutrients.

Periphyton is an assemblage of algae, bacteria and eukaryotic microorganisms covering almost all littoral substrates. Previous studies have shown that the growth and architecture of periphytic biofilms is constrained by the availability of light (Hill 1996) and nutrients (Borchardt 1996; Hillebrand and Sommer 1997), and by consumption from herbivores (Nicotri 1977; Feminella and Hawkins 1995; Hillebrand et al. 2000).

Nutrients, light, and grazers play important antagonistic roles for the development of algal biomass. Nutrient and light supply increases algal growth and biomass (Hillebrand and Sommer 1997; Stelzer and Lamberti 2001; Hillebrand 2005) and natural grazer densities strongly limit periphyton biomass (Feminella and Hawkins 1995; Steinman 1996; Hillebrand 2002). When the combined effects of nutrient enrichment and grazing on algal biomass and nutrient composition were investigated experimentally, it was found that both grazing and nutrient supply affected periphyton biomass. Thus both factors had strong direct effects, but they were also interacting noticeably, since nutrient addition could weaken or strengthen grazing effects (Rosemond 1993; Hillebrand et al. 2000). The same was true for the combined effects of grazing and light (Steinman 1992; Hillebrand 2005).

Herbivores also affect periphyton indirectly. They disrupt the periphyton matrix, revert the succession by removing the overlying canopy layer and maintain higher algal diversity (Rosemond 1993; Feminella and Hawkins 1995; Steinman 1996; Hillebrand et al. 2000; Liess and Hillebrand 2004). Grazing can also increase periphyton growth rates, since grazers increase resource availability through the regeneration of nutrients from detritus and the canopy layer (McCormick and Stevenson 1991; Steinman 1996; Liess and Hillebrand 2004).

Predation on herbivores and nutrient recycling by predators may change top-down (Dahl 1998; McCollum et al. 1998) and bottom-up limitation (Andre et al. 2003) of periphyton. Trophic interactions in the littoral zone are thus characterised by direct negative effects on lower trophic levels through consumption, and by nutrient mediated positive effects of higher trophic levels on autotrophs and consumers.

Ecological stoichiometry was first developed for pelagic communities, but has been applied to all parts of the benthic food web in recent years (reviewed in Cross et al. 2005). Periphyton nutrient stoichiometry was used to identify nutrient limitation for algal growth (Kahlert 2002; Kahlert et al. 2002) and benthic invertebrate nutrient content and flexibility were determined (Cross et al. 2003; Evans-White et al. 2005). Several studies investigated the effects of grazers on periphyton nutrient stoichiometry (Hillebrand and Kahlert 2001; Hillebrand and Kahlert 2002; Hillebrand et al. 2002; Stelzer and Lamberti 2002; Elser et al. 2005a; Evans-White and Lamberti 2005) and vice versa (Elser et al. 2005b) as well as nutrient recycling of invertebrates (Frost and Tuchman 2005) and fish (Vanni et al. 2002).

Stoichiometric interactions between benthic herbivores and primary producers are similar in many ways to those in the pelagic. The type of zooplankton affects which nutrient is limiting because zooplankton re-supply nutrients in different ratios depending on their body nutrient composition, e.g. cladocerans have lower body N:P ratios and resupply nutrients at higher N:P ratios compared to copepods (Elser et al. 1988; Sterner et al. 1992). Recent studies dealing with benthic grazer N:P ratios have shown that, similar to zooplankton, benthic grazers have relatively stable and taxon specific nutrient stoichiometry (Evans-White et al. 2005), thus P-rich benthic grazers are likely to be similar in their recycling properties to pelagic cladocerans. For example, P-rich grazing catfish were shown to have very low P recycling rates (Hood et al. 2005). Thus, parallel to their pelagic equivalents, benthic grazers with low N:P ratios and high N:P excretion rates might induce P limitation of periphyton. Nutrient deficient algae, on the other hand, can limit grazer growth. In pelagic systems, nutrient poor phytoplankton has been shown to limit zooplankton growth and reproduction (Van Donk and Hessen 1993; Elser and Hassett 1994). Recently the same mechanism has

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been shown to apply to benthic producer-consumer dynamics (Elser et al. 2005b).

The effects of grazing and nutrient regeneration on benthic microalgae have been investigated alone (reviewed in Liess and Hillebrand 2004) or in combination with nutrient addition (Evans-White and Lamberti 2005). Several studies provide indicative support for the importance of nutrient recycling in periphyton. Internal biomass stoichiometry of benthic microalgae can be influenced by nutrient supply ratios (Hecky et al. 1993; Stelzer and Lamberti 2001; Bowman et al. 2005; Elser et al. 2005a), and by grazer presence (Hunter and Russell Hunter 1983; Rosemond 1993; Liess and Hillebrand 2004). An unbalanced regeneration of nutrients might be due to differential retention of nutrients by consumers according to their physiological demands and reflected in their body nutrient composition (Hillebrand and Kahlert 2001).

Nutrient cycling in benthic food webs might lead to the following nutrient dynamics (Fig. 2): High inflow ratios of N:P leads to high N:P ratios in periphyton, since periphyton stoichiometry is flexible and reflects dissolved nutrient ratios. Grazers ingest high N:P periphyton and compensate through higher ingestion rates of periphyton biomass. Thus excretion of C and N is high and excretion of P is low. This scenario does not usually drive plants into P-limitation (Daufresne and Loreau 2001); grazers however might experience nutrient limitation even though food is abundant. The low P content in periphyton leads to low grazer densities and growth rates. In the case of severe P limitation of grazers, overall grazer densities are low and grazing impact is weak (Elser et al. 2005b). Another limiting factor can be light. It has been shown that high light intensities increases the C:nutrient ratio of algae. This was first shown for phytoplankton (Urabe and Sterner 1996; Hessen et al. 2002; Urabe et al. 2002). High C:nutrient ratios can limit herbivore growth, as has been shown in the pelagic for *Daphnia* (Hessen et al. 2002) and in littoral systems for snail (Stelzer and Lamberti 2002) and mayfly (Frost and Elser 2002b) grazers. By contrast, Hill et al. (1995) found increased growth of snails in streams with increased light intensity.
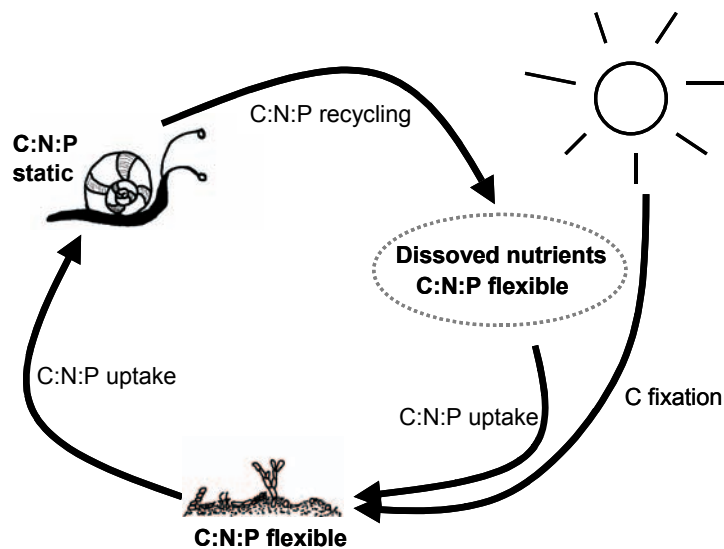
Figure 2: Stoichiometric dynamics in grazer - periphyton interactions. Grazers ingest periphyton C, N and P undifferentially but can take up needed nutrient and recycle surplus of others. Grazer stoichiometry remains stable, but dissolved nutrients change in their C:N:P stoichiometry depending on grazer recycling (and inflow into the system). Periphyton stoichiometry is flexible, and depends on the availability of dissolved C, N and P, and light.

Benthic grazer densities can be top-down limited by predators, relieving periphyton from grazing pressure. However, predators (mostly fish) can also lead to increased nutrient availability for producers through nutrient recycling, as has been shown in pelagic studies (Attayde and Hansson 1999; Attayde and Hansson 2001b). Also in the benthos, nutrient recycling by fish produce a significant part of the nutrients required by producers. In Lake Malawi, cichlid fish supplied 46-48% of the N and P required for production by epilithic algae in the littoral zone (Andre et al. 2003).

Ecological stoichiometry in benthic habitats has been examined less well compared to pelagic habitats, and most studies that apply ecological stoichiometry theory to benthic ecosystems have been conducted in recent years. By testing predictions derived from "pelagic" ecological stoichiometry theory in benthic systems, this thesis will increase the understanding of trophic interactions and nutrient pathways in benthic littoral ecosystems.

# Aims of this thesis

The aim of this thesis is to identify general structuring mechanisms in benthic food webs and to examine the applicability of ecological stoichiometry theory to nutrient interactions in benthic food webs. The focus of paper I is on benthic invertebrate grazer stoichiometry, whereas papers II, III and IV deal with the interactions between grazers and periphyton under different abiotic conditions (nutrients, light). In Paper V, the role of fish in benthic nutrient interactions is examined.

A field survey, laboratory and field experiments were conducted to describe patterns in invertebrate C:N:P stoichiometry and to test the nutrient imbalances that constrain grazer-periphyton interactions in the benthos. Thus, it can be determined whether the same nutrient imbalances in crucial elements (C, N and P) exist in benthic, as in pelagic producer-grazer interactions.

This thesis addresses four specific questions:

1. Do benthic invertebrates have taxon-specific body nutrient stoichiometry? (Paper I)

2. What effects do grazing, nutrient enrichment and light have on the periphyton nutrient stoichiometry, algal biomass and community composition? (Papers II, III, IV)

3. Does nutrient addition influence the body nutrient composition of benthic consumers? (Paper III)

4. How does nutrient recycling by predators affect the biomass and nutrient composition of periphyton? (Paper V)

# Material and Methods

Paper I is a field survey while Papers II-V are experimental studies. In the following I will describe the analytical methods used in the studies, while sampling and experimental setup will briefly be described in the Results section.

The field sampling strategy was designed to partly correspond to a previous periphyton survey at lake Erken in 1996-1997 (Kahlert et al. 2002). The laboratory experiments were all conducted in climatised rooms with GF/C filtered lake water, a natural periphyton community and snail densities in the snail treatments corresponding to natural densities in Lake Erken.

## Lake Erken

All these studies were conducted at Lake Erken or in the Erken laboratory. Lake Erken in Sweden (lat 59º50'N, long 18º35'E; area = 24 km$^2$; mean depth = 9 m) is dimictic, alkaline and mesotrophic. Most of the shoreline is stony or rocky and the littoral substrata consist of bedrock, cobble, and sediments (Kahlert et al. 2002).

## Invertebrate and periphyton nutrient content and dissolved nutrients

Invertebrates were frozen and freeze-dried. When possible, invertebrates were analyzed whole. Whole snails were difficult to sample, so we used muscle tissue for the analyses of particulate C, N, and P. We measured C and N with a CHN-Analyzer. I measured P as $PO_4$ after hot hydrolysis with potassium persulfate (Grasshoff et al. 1983). Snail C, N, and P content were expressed as % dry mass. C, N, and P results were converted into molar C:N, C:P, and N:P ratios.

Periphyton was removed from experimental tiles with a razor blade and the slurry was adjusted to a defined volume. I filtered the suspension from each aquarium onto 3 precombusted GF/C filters (3 subsamples/aquarium), and stored all subsamples frozen until analysis of particulate C, N, and P, and chlorophyll *a* (Chl *a*). I measured particulate C, N, and P in the same

way as for snail tissue (see below). Periphyton C, N, P, and Chl *a* were expressed as $\mu g/cm^2$ of substrate. C, N, and P results were converted into molar C:N, C:P, and N:P ratios.

Water samples were removed from each experimental unit and filtered (0.2-$\mu$m filter) for analyses of dissolved $NO_3 + NO_2$ (DIN) and dissolved inorganic P (DIP). I analyzed DIN with the sulfanilamide method and DIP with the ammonium–molybdate method (Grasshoff et al. 1983) in a Flow Injection Analyzer. The excretion product $NH_4^+$ was only measured in some experiments because concentrations of $NH_4^+$ are affected by freezing.

## Algal chlorophyll a, biovolume and taxonomic diversity

Chl *a* was used as a proxy for algal biomass. Chl *a* data must be interpreted cautiously as an indicator of algal biomass because increases in light can decrease cellular Chl *a* content (Steinman and Lamberti 1996). However, where light was constant, Chl *a* probably is a robust indicator of algal biomass. Chl *a* is measured after acetone extraction according to Strickland and Parsons (1972) and normalized it per unit area of the tiles ($\mu$g cm$^{-2}$).

For estimations of algal biovolume, algal cell numbers were counted at 400 times magnification in a 2 ml counting chamber under an inverted microscope. Algae were identified to genus level with the exception of diatoms, which were partitioned into the following groups: single (< 20 $\mu$m), single (20 - 80 $\mu$m), single (> 80 $\mu$m), colonies, bands, fragmented colonies. Cell numbers were multiplied by the taxon-specific biovolume. This was calculated from the mean of 20 cell size measurements of each taxa, using the equations of Hillebrand et al. (1999). I used the Simpson diversity (Magurran 2004) index to estimate diversity of algae and presented diversity as $D^{-1}$.

# Results

## Invertebrate stoichiometry (Paper I)

To assess the inter- and intraspecific variation in benthic invertebrate C:N:P stoichiometry, a field survey was performed in 3 seasons and at 5 sites, in the littoral zone of Lake Erken. At each site, 5 stones were carefully removed from a water depth between 5 cm and 1 m and put in a submerged bucket to minimize loss of loosely attached invertebrates. Samples were transported to the laboratory where invertebrates were identified and frozen for C, N and P analyses.

### Taxon specific stoichiometry

Invertebrate taxa differed in nutrient stoichiometry. The most conspicuous difference was between. Coleoptera with high C:N, C:P, and N:P ratios and Isopoda with low C:N, C:P, and N:P ratios. Taxonomic identity accounted for 30 - 40% of the variability in C:N, C:P, and N:P ratios.

### Stoichiometric variation among seasons and sites

C:N, C:P, and N:P ratios of different taxa differed among seasons and sites, and both season and site interacted strongly with taxonomic group. In particular, season explained > 35% of the variation in C:P and N:P ratios across all taxa, and interactions among season and/or site and taxonomic group explained > 46% of the variation in C:N ratios.

Season – Invertebrate N:P ratios were lower in autumn than in spring and summer. C:N:P dynamics were similar among *Teodoxus fluviatilis*, *Dreissena polymorpha*, and Polycentropodidae, the 3 taxa in which C:N:P ratios varied significantly with season. Their C:N ratios were higher and their C:P and N:P ratios were lower in autumn than in summer (Fig. 3).

Site – Sampling site explained far least of the variability in nutrient ratios (3–6%).

### Periphyton vs invertebrate stoichiometry

Benthic invertebrates had higher N and P content and smaller ranges of C:N and C:P ratios than periphyton, even though the standard deviation of periphyton and invertebrates was approximately equal (Fig. 3). Mean periphy-

ton C:N and C:P ratios were twice as high and N:P ratios were slightly lower than mean invertebrate ratios.



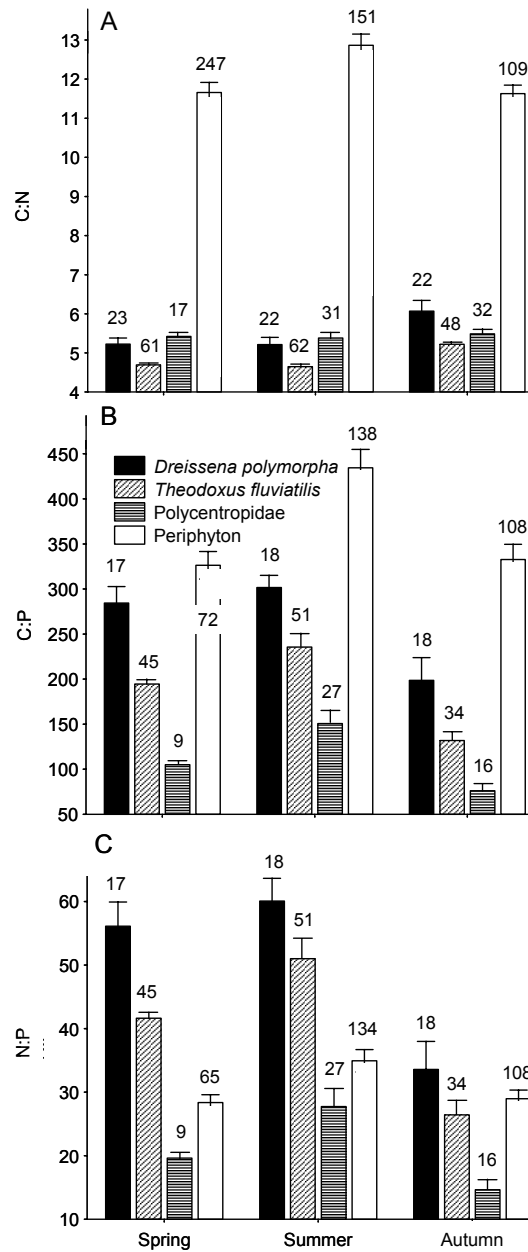Figure 3: Seasonal mean (±1 SD) C:N (A), C:P (B), and N:P(C) molar ratios of *D. polymorpha*, *T. fluviatilis*, and Polycentropodidae from the field survey and of periphyton sampled in 1996 (Kahlert et al. 2002). Numbers over the bars show the sample size (Figure 3 in Paper I).

# Periphyton - grazer interactions (Paper II-IV)

To study the periphyton-grazer interactions under variable environmental conditions, such as changes in irradiance and nutrient supply, 4 laboratory experiments were executed (Paper II-IV).

## Grazing and light

In two experiments (Paper II) it was tested how grazing and light influenced periphyton nutrient content and algal abundance. The first experiment had 3 treatments (no snails, *Bithynia*, *Theodoxus*). For the second experiment, aquaria were subjected to high and low light treatments factorially combined with the same 3 grazing treatments.

The results showed that both grazer presence and light reduction increased the nutrient content of the periphyton. Besides reducing periphyton biomass, grazers increased the relative concentration of the limiting nutrient in the periphyton and decreased particulate C:nutrient ratios. The two grazers differed in their body mass composition, which influenced their indirect effect on periphyton nutrient content. The consumer with lower N-demand (*Bithynia*) had stronger positive effects on periphyton N content. Light reduction increased periphyton nutrient content without affecting algal biomass, but did not alter the effects of grazer presence on periphyton nutrient content.

### Effects of grazers and light on periphyton biomass

Grazer significantly reduced algal biomass in both experiments, consuming between 80 and 95% of algal biovolume. Light reduction did not affect algal biomass. Moreover, light did not change the grazer effects on algal biomass. Light reduction increased algal Chl a content.

### Effects of grazers and light on periphyton stoichiometry and dissolved nutrients

The availability of nutrients in the dissolved phase and the relative incorporation of nutrients in prey biomass were both affected by consumer presence. Nutrient-related consumer effects were strongest for the nutrient being least available for the producers, i.e. N in the first and P in the second experiment.

Consumer effects on periphyton C:N:P partly depended on consumer nutrient content. In these experiments, the two snail species *Bithynia* and *Theodoxus* differed with respect to their C:P ratios and to their C:N ratios. Differences in the C:N ratios of the snails showed that per unit C, *Theodoxus* required 25% more N than *Bithynia* in the first experiment. Subsequently, *Bithynia* had stronger effects on dissolved and particulate N than *Theodoxus*. In the P-limited second experiment, both grazers affected periphyton P content, but only *Bithynia* had additionally positive effects on the N content.

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The reduction of light decreased the C:nutrient ratios. However, even at low light the periphytic C:P ratios still indicated strong P-deficiency. At high light, P limitation increased and no further algal growth was supported.

## Grazing and nutrients

The influence of grazing and nutrient addition on the nutrient status of the periphyton community and grazers under high-P conditions were tested (Paper III). A laboratory experiment was conducted in which a 4 × 4 factorial design was used. The manipulated factors were water-column nutrient concentrations (+N, +P, +N+P, unenriched) and grazers (*Theodoxus*, *Bithynia*, *Valvata*, no grazers). I examined a situation in which P concentration in the water column was high, in contrast to previous experiments in which P was the limiting nutrient.

The results showed that N enrichment decreased periphyton C:N ratios (in the absence of snails) and P enrichment decreased periphyton C:P ratios. The addition of the potentially limiting nutrient (N) decreased snail C:P and N:P ratios and increased % P in *Valvata*. Grazers increased periphyton C:P and N:P ratios.

### Algal biomass

N or P enrichment alone had no effect on Chl *a*, but combined N and P enrichment resulted in higher Chl *a* per area, which indicates possible colimitation of algal growth by N and P, a result found in other studies (Francoeur 2001). Higher Chl *a*:C ratios in the +N+P treatment compared to other treatments indicate that autotrophic material made up a greater proportion of the periphyton in the +N+P treatment than in the other nutrient-enrichment treatments. Grazers had no effect on algal biomass.

### Periphyton stoichiometry

P enrichment (+P and +N+P) reduced periphyton C:P and N:P ratios, showing that P was assimilated or absorbed by the periphyton. In this study, periphyton C:P and N:P ratios at ambient nutrient concentrations were 91 and 8.2, respectively, and C:N ratios were 10.4. These ratios indicate high P content and low N content in the periphyton. Periphyton C:P ratios increased in the presence of grazers, but N:P ratios remained very low (Fig. 4).
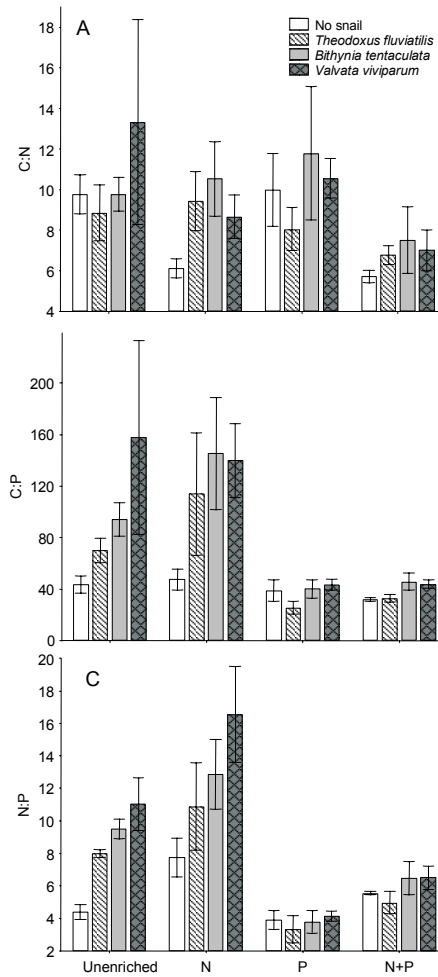
Figure 4: The C:N (A), C:P (B) and N:P (C) molar ratios of periphyton under different enrichment (ambient, N-addition, P-addition, N+P-addition) and grazing conditions (no snail, *T. fluviatilis*, *B. tentaculata*, *V. viviparum*). Bars indicate the mean and the whiskers +/- standard error of mean of 4 samples (Figure 3 in Paper III).

## Snail stoichiometry

Snails had higher P content in treatments enriched with N (+N and +N+P) than in unenriched or +P treatments. Snail N:P ratios ($55 \pm 2.4$) were much larger than periphyton N:P ratios ($7.5 \pm 0.99$) in all treatments. All 3 species had consistently higher N:P ratios (40) in field surveys (see Paper I) than the periphyton N:P ratios observed in this experiment (7.5).

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## Grazing, nutrients and light

In a fourth laboratory experiment (Paper IV) it was tested how grazing, nutrients and light interact in determining algal taxonomic diversity and composition, periphyton nutrient stoichiometry and biomass. This was achieved by factorially combining the addition of nutrients, light and grazing. Grazers and periphyton were kept under different light and nutrient conditions in a $2 \times 2 \times 2$ factorial design. The factors were grazing (snails, no snails), nutrients (ambient, N and P enriched) and light (low, high).

Grazing and nutrients interacted in determining algal diversity. Grazing decreased benthic algal diversity through biomass removal whereas the addition of nutrients weakened this grazing effect, probably by increasing autotrophic growth. Increased light decreased the C:nutrient ratios of the periphyton in the ungrazed treatments, but not in the grazed treatments. However, increased light availability did not significantly increase the strength of the interactions between grazing and nutrients.

### Periphyton and algal biomass

Grazing decreased periphytic Carbon and Chl *a* per unit area. Nutrient addition had no effects on periphyton biomass parameters. Light had no effects on diversity and taxonomic composition. Chl *a* and Chl *a*:C increased under low light intensities.

### Periphyton nutrient state

Grazing, but not nutrients and light changed the nutrient content of periphyton (Fig. 5). However nutrients interacted with grazing in determining the C:P ratio. Grazing increased the C:P and N:P ratios of periphyton, especially in the ambient nutrient treatments.
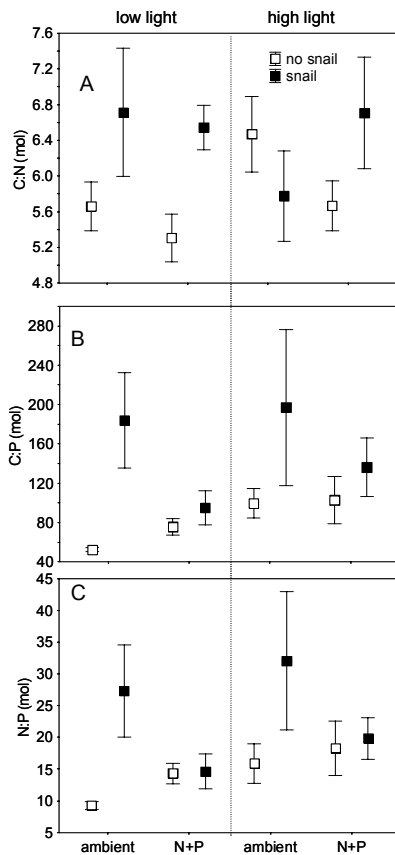
Figure 5: C:N (A), C:P (B) and N:P (C) ratios of periphyton in the different experimental treatments. Point labels represent the mean and whiskers the standard error (Figure 3 in Paper IV).
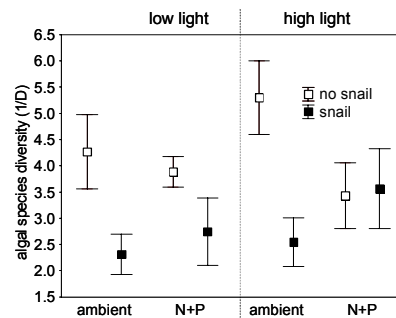


Figure 6: Diversity index (Simpsons diversity index $D^{-1}$) at the different experimental treatments. Bar graphs represent the mean and whiskers the standard error (Figure 4 in Paper IV).

**Algal diversity and taxonomic composition**

Algal species diversity decreased with grazing (Fig. 6). Light and nutrient enrichment did not affect algal species diversity. However nutrient addition counteracted the negative effects of grazing on algal diversity. The taxonomic composition of benthic algae was affected only by grazing, but not by light climate or nutrient enrichment. Grazing reduced the relative abundance of the easily ingestible *Spirogyra sp.* and increased the abundance of the grazing resistant *Chaetophora sp.*

# Periphyton – grazer – fish interactions (Paper V)

I examined trophic interactions in two food webs of different complexity to address the influence of food web complexity on trophic interactions and on nutrient-mediated pathways. A field enclosure experiment and an aquarium experiment were conducted. The food web in the enclosures consisted of

perch (*perca fluviatilis*) and a natural community of benthic and pelagic primary producers and grazers. The food web in the aquaria consisted of perch, grazers and periphyton.

The set up in the complex food web was a nested 3 x 5 design with 3 grazer treatments (present, absent, a cage control) inside 5 fish enclosures (0, 2, 4, 6, 8 perch per enclosure). Enclosures were placed in the littoral zone of Lake Erken and the grazer treatments were placed inside the enclosures. Grazers were excluded through closed cages (absent) and had ambient densities in the absence of cages (present) and in the cage control. Periphyton-covered tiles were put inside the grazer treatments.

The simple food web in the laboratory experiment had periphyton as primary producers, the snails *Theodoxus fluviatilis* and *Valvata viviparum* as consumers and perch. Perch were fed with brine shrimp. The design was a 2 x 3 factorial design with 4 replicates, using 2 fish treatments (fish, no fish) and 3 snail treatments (*Valvata*, *Theodoxus*, no snails).

### Grazer effects on periphyton biomass and stoichiometry

Benthic grazers exerted a limiting top-down effect on periphyton biomass in both food webs. In the complex food web, benthic grazers increased periphyton P-limitation. In the simple food web, benthic grazers improved periphyton nutrient state, as indicated by the decreased C:P ratios in grazed treatments (Fig. 7B). Grazing also reduced periphyton biomass in both food webs (Fig. 7D).

### Fish effects on primary producer biomass and stoichiometry

The results showed that fish affected primary producers through nutrient recycling. However, the effects of fish differed between the two experiments. Fish decreased periphyton biomass in the complex system, but did not affect periphyton stoichiometry. In the simple system, fish had positive effects on periphyton biomass and nutrient content. Fish presence decreased periphyton C:P ratios significantly in the simple food web (Fig. 7B), but not in the complex food web. In the simple food web, increased DIP concentrations (Fig. 7F) led to reduced periphyton C:P ratios. On the other hand, fish presence did not change periphyton C:N and N:P ratios (Fig. 7A and C), although DIN concentrations increased (Fig. 7E) and periphyton C:N and N:P ratios indicated N limitation. In the simple system we found that fish increased dissolved nutrient concentrations and probably increased periphyton biomass through nutrient-mediated pathways.
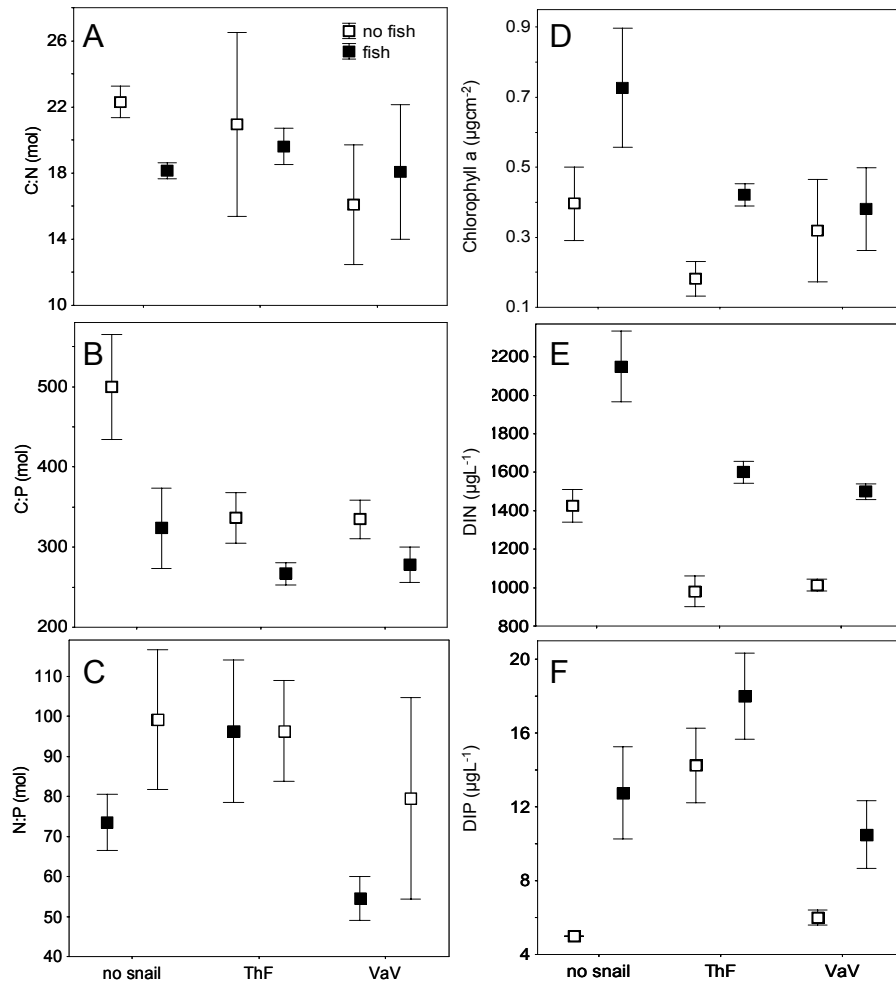
Figure 7: Stoichiometry and biomass of periphyton and dissolved nutrients in the simple laboratory experiment. The C:N (A), C:P (B), N:P (C) ratios (mol) and biomass (in Chl a in mg cm$^{-2}$) (D) of periphyton and under different grazing conditions (no snails; ''ThF'': T. fluviatilis and ''VaV'': V. viviparum) and with ''no fish'' / ''fish'' treatments. The content of DIN (E) and DIP (F) under different grazing conditions (no snails; ''ThF'': *T. fluviatilis* and ''VaV'': *V. viviparum*) and with ''no fish'' / ''fish'' treatments. Error bars represent the standard error of the mean (Figure 4 in Paper V).

# Discussion

## Benthic compared to pelagic consumer stoichiometry

Invertebrate nutrient ratios (Paper I) and frequency distributions were similar to those presented in another study of benthic invertebrates (Frost et al. 2003). Frost et al. (2003) reported medians of 5.5, 141, and 25.8 for C:N, C:P, and N:P ratios, respectively, whereas the medians of the same ratios in this study were 5.3, 171.2, and 32.8. Pelagic studies of crustacean zooplankton species found pronounced variation in interspecific content of P, while intraspecific variations were restricted (Andersen and Hessen 1991; Hessen and Lyche 1991). *Daphnia* had a far higher specific P-content (> 1.5% P of dry weight) compared with carnivorous cladocerans and copepods (approximately 0.5% P) (Hessen and Lyche 1991). Benthic invertebrates had between 1% (Bivalvia) and 0.4% P of dry weight (Polycentropidae) with low intraspecific variation (Paper I). For benthic invertebrates mean N content was between 8 - 11% of dry weight and mean C content was between 30 - 49% of dry weight for different species. N and C content of pelagic consumers showed less interspecific variations with means close to 9-10% and 45-50% of dry weight, respectively, for most species (Hessen and Lyche 1991). Thus, interspecific variation was higher in benthic habitats. These findings suggest that the species composition of the benthic invertebrate community can have a strong influence on the N:P ratio of recycled nutrients and thus periphyton nutrient composition.

The variability of invertebrate nutrient content due to seasonal and spatial variation (Paper I) and nutrient enrichment (Paper III) indicates that invertebrates were not strictly homeostatic and showed some intraspecific variation. Seasonal variation in invertebrate C:N:P stoichiometry was probably also a consequence of seasonal differences in nutrient concentrations in the water column and the periphyton (Paper I). In Paper I, invertebrate N:P ratios were lowest in autumn, the season when periphyton N:P and dissolved inorganic N:P ratios are low in Lake Erken (Hillebrand and Kahlert 2001, Kahlert et al. 2002). Spatial variation in invertebrate C:P and N:P ratios may have reflected differences in nutrient availability among sites. Similar results have been found in earlier benthic studies (Frost and Elser 2002b; Cross et al. 2003), where the nutrient stoichiometry of benthic grazers changed in response to the nutrient content of their food. Similar dynamics are also known

from pelagic studies, for example, the P content of *Daphnia* increased with increasing food P content (DeMott et al. 1998).

In all studies, variability in invertebrate nutrient content was due to a change in the C:P and N:P ratios but not in C:N ratios. This indicates, that the element that is most variable in the body is P. Higher growth rates require higher invertebrate P-content, since growth requires the production of P-rich RNA as stated in the growth rate hypothesis (Elser et al. 2000). Thus, the increase in P-content under some conditions, such as nutrient enrichment, might have been due to an increase in invertebrate growth rate.

Nutrient enrichment might lead to decreased invertebrate nutrient limitation. The comparison of periphyton and invertebrate stoichiometry and stoichiometric variability indicate that invertebrates might be frequently N or P limited, since they mostly graze on periphyton with higher C:P and C:N ratios than their own body stoichiometry.

I conclude that benthic consumers, like their pelagic counterparts, have taxon specific nutrient composition. Some variability in body P content due to dietary P content was found in benthic as well as in pelagic consumers, whereas the consumer C:N ratios appear to be very stable within taxa.

# Factors influencing nutrient interactions in the benthos

## Grazing

Nutrient recycling by benthic grazers did not induce enough extra periphyton growth to compensate for grazing losses (Paper IV and V). This is in accordance with the majority of benthic grazing studies (reviewed by Feminella and Hawkins 1995; Hillebrand 2002; Liess and Hillebrand 2004).

However, grazers can even have such strong positive effects on algal growth rates that they compensate for grazing losses (Paper III) (McCormick and Stevenson 1991). Moreover, grazer-resistant growth forms, such as cyanobacteria, *Chaetophora* and the basal cells of *Stigeoclonium* (green algae), tend to dominate benthic algae under grazed conditions (Paper IV) (Steinman et al. 1987; DeNicola et al. 1990; Hill et al. 1992).

Grazers affect the periphyton nutrient content (Papers II-V) as has also been shown in previous studies (Hunter and Russell Hunter 1983; Rosemond 1993; Hillebrand and Kahlert 2001; Frost et al. 2002). However, nutrient-related consumer effects were strongest for the nutrient being least available for the producers. In support of predictions from ecological stoichiometry, consumer effects on periphyton C:N:P partly depended on consumer nutrient content. Thus, benthic grazers with low N:P increased periphyton P limita-

tion, whereas benthic grazers with higher N:P ratios improved the periphyton nutrient state (Paper II and V). Differences in N:P ratios are important, since grazers with lower N:P ratios differentially recycle more N than P, thereby increasing P-limitation of primary producers, as has been shown in pelagic habitats (Sterner and Hessen 1994; Elser and Urabe 1999). Similar dynamics were found in models of the interactions between zooplankton and phytoplankton (Hessen and Bjerkeng 1997) predicting increased nutrient limitation in primary producers due to grazing. On the other hand, grazing can improve periphyton nutrient state. Since grazing reduces periphyton biomass, competition for nutrients decreases, and nutrients availability for the remaining periphyton increases.

An alternative explanation of grazer effects on periphyton stoichiometry, is that grazer-induced structural changes in periphyton were more important than grazer-recycled nutrients. In this case, one would not expect predictions based on ecological stoichiometry theory to apply. Exposure to grazers with different feeding modes can cause periphyton communities to have different physiognomies (Mulholland et al. 1991; Rosemond et al. 1993; Steinman 1996) and possibly different C:P ratios. For example, if a grazer ingests components of the periphyton matrix with high C:P ratios, the resulting community may consist of small, fast-growing taxa with high P content, leading to a decreased C:P ratio in the periphyton.

In conclusion, grazing can affect periphyton biomass and stoichiometry. However, it is not always easy to predict which direction grazer effects have, since grazers can affect periphyton biomass, stoichiometry and algal species composition both via nutrient recycling and biomass removal. Which effects are strongest and which nutrients are recycled depend on ambient nutrient conditions, grazer density and grazer stoichiometry.

## Enrichment

Nutrient enrichment has been shown to affect periphyton stoichiometry (Hillebrand and Kahlert 2001; Frost and Elser 2002a) if it is supplied in sufficient quantities (Paper III). The results in Paper IV showed no effects of nutrient enrichment on periphyton stoichiometry, probably due to the longer duration of the experiment, since additional N and P were only supplied at the beginning. P enrichment in Paper III reduced periphyton C:P and N:P ratios as also shown by Frost and Elser (2002a). In Paper III, periphyton C:P and N:P ratios at ambient nutrient concentrations were 91 and 8.2, respectively, and C:N ratios were 10.4. These ratios indicate high P content and low N content in the periphyton and N limited algal growth.

Nutrient enrichment had no effects on algal taxonomic composition or diversity (Paper IV). This was probably due to the fact that nutrients were

added only once, at the beginning of the experiment, which is in contrast to earlier studies, where nutrients were added more often and where fertilisation decreased species evenness (Hillebrand 2003) or changed species composition (Bourassa and Cattaneo 2000).

Snail stoichiometry changed due to nutrient enrichment (Paper III). An increase in invertebrate P content due to P-enrichment has also been shown by Cross et al. 2003. Surprisingly, in Paper III, snail P content increased in response to N addition. That is, snails had higher P content in treatments enriched with N (+N and +N+P) than in unenriched or +P treatments. A possible explanation is that grazers grew faster in N-enriched treatments, producing more RNA and leading therefore to higher P content as stated in the Growth Rate Hypothesis (Elser et al. 2000). Snails were potentially N-limited in Paper III because snail N:P ratios (55 ± 2.4) were much higher than periphyton N:P ratios (7.5 ± 0.99) in all treatments.

N and P addition in sufficient quantities usually leads to increases of the added nutrient in the periphyton biomass, since benthic algae can take up and store excess nutrients. The effects of nutrient addition on grazers can lead to changes in P content probably due an increase in the relative allocation of P to RNA and other biochemicals (Vrede et al. 2004) to be able to support higher growth rates.

## Light

In Paper II (but not in Paper IV), higher light intensities increased the C:nutrient ratios of periphyton in accordance with predictions from ecological stoichiometry theory (Sterner et al. 1997). On the other hand, the reduction of light decreases the light:nutrient supply ratios, which reduces the relative nutrient limitation, and allows the incorporation of more P and N into periphyton biomass, thus decreasing C:nutrient ratios (Elser et al. 2002; Urabe et al. 2002). The Chl *a* and Chl *a*:C or Chl *a*:biovolume ratios increased under low light intensities (Paper II and IV), due to increased production of Chl *a* to compensate for decreased photosynthetic rates under low light conditions (Steinman and Lamberti 1996).

High light intensities can increase algal biovolume if algal growth is not limited by nutrients and/or grazing (Rosemond 1993; Hillebrand 2005). Thus, the absence of light effects on algal biovolume in Paper II. This can be explained by the very strong P-limitation, as indicated by the very low dissolved P concentrations measured throughout the experiment. Thus, increased light could not be transformed into increased algal growth. In Paper IV no effects of light on periphyton of benthic algal biovolume were found due to top down limitation by grazers.

The conclusion is, that increased light intensities can increase the C:nutrient ratios and decrease algal Chl $a$:C ratio. Positive effects of light on benthic algal biomass are only seen when grazing pressure is low and nutrients are available.

## Interactions between the factors grazing, nutrients and light

Grazing, but not nutrients and light changed the nutrient content of periphyton, when grazing, nutrient addition and light intensities were factorially combined in a laboratory experiment (Paper IV). However nutrients interacted with grazing in determining the C:P ratio. Contrary to other grazing studies (Hillebrand and Kahlert 2001; Frost and Elser 2002b; Frost et al. 2002), grazing increased the C:P and N:P ratios of periphyton, especially in the ambient nutrient treatments. These findings are consistent with my earlier experiments, were snails also increased the C:P ratios of periphyton even though their body C:P ratios were higher than that of the periphyton (Paper III). The nutrient content of the periphyton did not change due to addition of N or P (Paper IV), suggesting that periphyton was not strongly limited by any of these nutrients, or more probable, that the one nutrient addition at the start of the experiment was not detectable after 3 weeks.

Light decreased periphyton nutrient content only in the ungrazed treatments, since the strong negative effects of grazing on periphyton nutrient content masked the light effects. However, in the treatment without nutrient nor grazer addition we can see almost a doubling of the mean C:P and N:P ratio with higher light intensities. Thus, in accordance with earlier studies (Frost and Elser 2002a; Hessen et al. 2002; Urabe et al. 2002) increased light intensities further increased the C: nutrient ratio in nutrient poor conditions.

Algal species diversity decreased with grazing. Light and nutrient enrichment did not affect algal species diversity. However nutrient addition decreased the negative effects of snail presence on algal diversity (Paper IV). This was probably due to the fact that nutrient addition increased the capability of grazed species to regrow (Worm et al. 2002). I expected light to influence diversity through the interactions with other factors (such as grazing) as previously found by (Wellnitz and Rader 2003), but found no such interactions.

The taxonomic composition of benthic algae reacted only to the grazing treatment, but not to light and nutrient enrichment. As expected, grazing reduced the relative abundance of the easily ingestible *Spirogyra sp.* and increased the abundance of the grazing resistant gelatinous *Chaetophora sp.* (Paper IV).

In conclusion I found that grazing and nutrient addition interacted in determining periphyton nutrient state (N:P ratio) and algal taxon diversity. Light

showed no such interactions. However, more studies about the effects of light on periphyton nutrient content and on the interactions between light, grazing and nutrient addition are needed to clarify the role of light in structuring benthic algal communities.

## Effects of fish on periphyton biomass and stoichiometry

Fish increased dissolved nutrient concentrations and probably increased periphyton biomass through nutrient-mediated pathways (Paper V). The results suggest that fish made nutrients more accessible for periphyton. The same was found in a pelagic study, where fish excreted N and P at ratios close to the optimum for enhancing phytoplankton growth (Attayde and Hansson 1999). In the complex food web, two different mechanisms could have been responsible for the decrease of periphyton biomass in fish treatments:

(1) In the complex food web, fish probably increased the amount of dissolved nutrients, thus enhancing phytoplankton growth. Dissolved nutrients are supposed to favour phytoplankton more than periphyton. Increased phytoplankton biomass leads to increased turbidity, thus less light will reach the benthic community (Hansson 1988; Havens et al. 2001; Vadeboncoeur et al. 2001). In our study, phytoplankton abundance increased in fish treatments, probably leading to light limitation of periphyton growth.

(2) Fish decreased the zooplankton abundance, thus reducing nutrient recycling by zooplankton and nutrient availability of periphyton and phytoplankton. Lövgren and Persson (2002) found that fish affected zooplankton nutrient recycling. In our study however, fish led only to an insignificant decrease in zooplankton biomass. Several studies have found that fish exert a top-down effect on periphyton and phytoplankton through predation on herbivores, and facilitate periphyton and phytoplankton growth through nutrient recycling, (McCollum et al. 1998; Romare et al. 1999; Andre et al. 2003). Fish increased dissolved nutrient concentrations and phytoplankton biovolume in pelagic habitats (Attayde and Hansson 2001a; Attayde and Hansson 2001b). However, nutrient recycling by fish is more important under nutrient limited conditions. In eutrophic lakes, fish predation on zooplankton has stronger effects on the structure and dynamics of plankton communities than fish nutrient excretions (Attayde and Hansson 2001b).

In conclusion, in mesotrophic Lake Erken, where phytoplankton is nutrient limited (mainly by N) during the summer months (Vrede et al. 1999), fish nutrient excretion might be very important for phytoplankton growth. Trophic cascading effects on phytoplankton through fish predation on zooplankton are probably less important, especially for the grazing resistant cyanobacteria *Gloeotrichia sp.*

# Conclusions and perspectives

In summary, this thesis arrives at the following conclusions:

1. Do benthic invertebrates have taxon-specific body nutrient ratios?
   - Benthic invertebrates have taxon-specific C:N and C:P ratios, but there is significant seasonal variability especially in the C:P and N:P ratios. This variation in taxon-specific grazer nutrient content must be taken into account when applying stoichiometric theory to benthic food webs.

2. What effects do grazing, nutrient enrichment and light have on periphyton nutrient stoichiometry, algal biomass and community composition?
   - Indirect effects of grazers on periphyton are bound by stoichiometric constraints of nutrient incorporation and excretion.
   - The positive effects of nutrient recycling through grazing on periphyton biomass can compensate for periphyton biomass removal through ingestion.
   - Grazing and nutrients interact in determining benthic algal community composition and periphyton nutrient ratios.
   - Light can affect periphyton C:nutrient and Chl $a$:C ratios, but did not affect algal biovolume or periphyton community composition.

3. Does nutrient addition influence the body nutrient composition of benthic consumers?
   - Variation in the nutrient content of periphyton can influence benthic grazer C:P and N:P ratios. Even the addition of N can increase invertebrate P content.

4. How does nutrient recycling by predators affect the biomass and nutrient composition of periphyton?
   - Predators increase resource availability and thus biomass and nutrient content of benthic primary producers if there is no nutrient competition from pelagic primary producers.
   - Resource competition plays an important role in complex food webs with several species or functional groups at the same trophic level. Resource competition with pelagic primary producers can switch the expected effects of nutrient recycling by predators on periphyton.

The present thesis arrives at the conclusion that periphyton-grazer-predator interactions in the benthos are bound by stoichiometric constraints. Nutrient interactions in benthic food webs depend on nutrient state, grazing pressure and grazer identity, light, and food web properties. Periphyton ingestion by grazers and nutrient recycling by benthic invertebrates and fish are important mechanisms in benthic ecosystems and influence all aspects of the benthic food web.

Benthic habitats are subjected to drastic environmental changes through anthropogenic influences. Changed land use can increase the nutrient input into aquatic ecosystems through the use of fertilisers, whereas the use of pesticides can change lake food webs by killing more sensitive species. Climate change can lead to changes in temperature and irradiance levels due to changing weather patterns. Thus, it is essential to know how eutrophication, irradiance regime and food web construction affect benthic as well as other ecosystems. Merging biodiversity research, food-web theory and ecological stoichiometry is an important frontier for ecologists.

More research directed towards assessing dynamics of ecosystems is needed. Thus, ecological stoichiometry is an important tool to facilitate better risk assessments, which will help to manage, conserve and 'rehabilitate' biodiversity and ecosystems in a sustainable manner for future generations.

# Summary in German (Zusammenfassung)

Das Ziel dieser Doktorarbeit ist es, die Nährstoffinteraktionen im Benthos aufzuschlüsseln. Als Benthos bezeichnet man den Grund eines Gewässers im Gegensatz zum freien Wasser, das Pelagial genannt wird. Da Seen und Flüsse zunehmend unter Verunreinigungen - insbesondere durch Stickstoff und Phosphor - zu leiden haben, ist es von allgemeinem Interesse, die Wirkung dieser Nährstoffe auf alle aquatischen Habitate zu untersuchen. Pelagische Systeme sind bereits weitgehend untersucht, und allgemeine Regeln für Nährstoffinteraktionen im Pelagial sind aufgestellt. Im Benthos sind erst in den letzten Jahren verstärkt Studien durchgeführt worden, die die Regeln, die für das Pelagial gelten, in benthischen Habitaten testen. Diese Studien sollen durch die vorliegende Doktorarbeit vertiefen werden.

Um Nährstoffinteraktionen zu quantifizieren war es zuerst wichtig, die Nährstoffbedürfnisse der einzelnen funktionellen Einheiten in benthischen Habitaten zu messen. Dies geschieht, indem man sowohl den Stickstoffgehalt (N) und den Phosphorgehalt (P) der Organismen misst als auch deren Kohlenstoffgehalt (C). Daraufhin setzt man N, P und C in Relation zueinander. Für Aufwuchsalgen existieren bereits Daten zu den Quoten N:P, C:N und C:P. Deshalb fing ich damit an, benthische Invertebraten (wirbellose Tiere, unter anderem Insektenlarven und Schnecken) zu sam-meln und deren Quoten N:P, C:N und C:P zu bestimmen.

Benthische Invertebraten haben genau wie pelagische Konsumenten artspezifische Verhältnisse von N:P, C:N und C:P. Die Flexibilität dieser Nährstoffverhältnisse ist im Vergleich zu Aufwuchsalgen relativ gering. Aufwuchsalgen dienen benthischen Invertebraten als Nahrung. Aufwuchs-algen haben proportional mehr C in ihrer Biomasse als benthische Invertebraten. Das kann bedeuten, dass benthische Invertebraten mit ihrem Futter mehr C und möglichweise auch mehr N oder P aufnehmen als sie verwerten können. Diese überflüssigen Nährstoffe müssen wieder ausgeschieden werden. Um die Nährstoffinteraktionen zwischen Inverte-braten und Aufwuchsalgen zu untersuchen, wurden Experimente durchge-führt. In ihnen wurden An- und Abwesenheit der Invertebraten, ihre Art sowie Nährstoffzufuhr und Lichtintensität manipuliert. Es zeigte sich, dass grasende Invertebraten die Nährstoffkonzentrationen ihres Futters verändern konnten. In einem System, in dem Nährstoffe (N oder P) die begrenzenden Faktoren waren, konnten grasende Invertebraten die N:P Quoten in den

Aufwuchsalgen verändern. Invertebraten, die relativ wenig N im Vergleich zu P brauchen, regenerieren N und erhöhen dadurch den Anteil von N im Aufwuchs. Invertebraten, die relativ wenig P im Vergleich zu N brauchen, regenerieren proportional mehr P und erhöhen dadurch den Anteil von P im Aufwuchs.

Die Veränderung von Licht und Nährstoffzufuhr hatte auch einen Effekt auf die Nährstoffkonzentration im Aufwuchs. Hohe Lichtintensität führte zu einer Erhöhung des C Anteils im Aufwuchs. Das bedeutete also eine Verschlechterung der Futterqualität für die grasenden Invertebraten. Düngung mit N und P konnte dann partiell auftretende Licht- und Invertebrateneffekte auf den Nährstoffgehalt der Aufwuchsalgen wieder ausgleichen. Möglicherweise hatte ein erhöhter Nährstoffgehalt im Aufwuchs einen positiven Effekt auf die Wachstumsraten ihrer Konsumenten.

Ebenso kann die Gegenwart von Fischen für eine erhöhte Nähstoffzufuhr sorgen. Fische fressen andere Tiere und sorgen damit für zusätzlich verfügbare Nährstoffe. Die Gegenwart von Fischen kann daher zu höherer Aufwuchsalgenbiomasse führen und damit zu einem höheren Nährstoffge-halt in den Algen. Allerdings sind Aufwuchsalgen nicht die einzigen Algen, die um Nährstoffe konkurrieren. Da Fische ihre Nährstoffe ins Wasser abgeben, können auch pelagiale Algen davon profitieren. Pelagiale Algen können diese Nährstoffe aufnehmen und ihre Biomasse erhöhen. In diesem Fall haben die Aufwuchsalgen einen Konkurrenznachteil, da eine erhöhte Algenbiomasse im Wasser über ihnen  zur Beschattung der Aufwuchsalgen führt.

Diese Arbeit zeigt, dass für Nährstoffinteraktionen im Benthos Regeln aufgestellt werden können, wenn in der konkreten Situation vor Ort folgende Fragen geklärt werden können:

Fragen:
- Welcher Nährstoff begrenzt das Wachstum der Aufwuchsalgen?
- Ist Licht limitierend?
- Welcher Nährstoff begrenzt das Wachstum der Invertebraten?
- Wie sieht das Nahrungsnetz aus?

Regeln:
- Benthische Invertebraten haben artspezifische Verhältnisse von N:P, C:N und C:P.
- In einem System, in dem Nährstoffe begrenzend sind, können Invertebraten den Nährstoffgehalt in den Aufwuchsalgen verändern.
- Erhöhte Lichtintensität führt zu einer Erhöhung des C Anteils im Aufwuchs, wenn Licht begrenzend war.
- Genügend Düngung mit N und P kann Licht- und Invertebrateneffekte auf den Nährstoffgehalt der Aufwuchsalgen ausgleichen.
- Die Gegenwart von Fischen erhöht die Nähstoffzufuhr und kann daher zu höherer Aufwuchsalgenbiomasse und zu einem höheren Nährstoffgehalt in den Algen führen, wenn pelagiale Algen abwesend sind.

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