Biomass and Nutrient Status
of Benthic Algae in Lakes

BY

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Abstract

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For a complete picture of the lake ecosystem, it is necessary to understand the mechanisms regulating
biomass and nutrient status (nutrient limitation, optimal supply, or surplus) of benthic algae, which are
important primary producers and a food resource for grazers. This thesis gives an overview of the
natural variation of benthic algae at different scales of space and time and on different substrates, and
unravels some of the underlying factors. Algal nutrient status was assessed using the C:N:P
(carbon:nitrogen:phosphorus) ratio of the entire natural benthic community. A review, observations,
and experiments confirmed that a C:N:P ratio of about 158:18:1 (molar basis) represented an optimal
nutrient supply, and that substantially higher C:N, N:P, or C:P ratios reflected algal growth limitation
caused by an N or P nutrient deficiency.

Horizontal variation of benthic algal biomass and nutrient status was patchy, of similar amount for
all investigated distances, substrates, and lakes, and constituted a dominant proportion of the total
variation. For example, patches of nutrient limited algae were found within only 10 m distance from
patches with a nutrient surplus. Thus, horizontal variation should not be neglected when sampling
benthic algae in lakes. Field observations suggested an impact of wind, nutrients, and grazers on the
horizontal variation. Light and nutrients might have caused the observed vertical and temporal
variation. Field experiments confirmed a simultaneous control of benthic algal biomass by nutrients
and grazing, mediated by light and temperature. Grazing effects were larger than nutrient effects, but
the comparison of natural communities in lakes of different trophy suggested that benthic algal
biomass was controlled by nutrients in the long run.

An important nutrient supply was animal excretions, causing a low C:N:P ratio of epizoon on
zebra mussels, and algal communities associated with macrograzers. A field experiment revealed that
[15]N circulated one week longer in epizoon associated with a sessile caddisfly than in surrounding
epilithon. In conclusion, the regulation of benthic algal biomass and nutrient status in lakes is
complex, and benthic animals should be looked at not only as grazers, but also as a nutrient source.

Key words: benthic algae; patchiness; C:N:P ratio; nutrient recycling; grazer

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'Viel zu lange rumgesessen,
überm Boden dampft bereits das Licht.
Jetzt muß endlich was passieren,
weil sonst irgendwas in mir zerbricht.

Dieser Kitzel auf der Zunge,
selbst das Abflußwasser schmeckt nach Wein.
Jetzt noch mal den Mund geleckt,
und dann tauch ich ins Gewühl hinein.'

(Konstantin Wecker)

dem schwedischen Himmel gewidmet

BIOMASS AND NUTRIENT STATUS OF BENTHIC ALGAE IN LAKES

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

I   MARIA KAHLERT (1998): C:N:P ratios of freshwater benthic algae. - Arch. Hydrobiol. (Suppl.) (Advanc. Limnol.). 51: 105-114.

II   MARIA KAHLERT, ANDERS T. HASSELROT, HELMUT HILLEBRAND AND KURT Pettersson: Spatial and temporal variation in the biomass and nutrient status of epilithic algae in Lake Erken, Sweden. – *(accepted by Freshwater Biology)*

III   MARIA KAHLERT AND KURT PETTERSSON: The impact of substrate and lake trophy on the biomass and nutrient status of benthic algae (*submitted*)

IV   MARIA KAHLERT: Horizontal variation of biomass and C:N:P ratio in benthic algal communities in lakes (*submitted*)

V   HELMUT HILLEBRAND AND MARIA KAHLERT: Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. – *(accepted by Limnology & Oceanography)*.

VI   MARIA KAHLERT AND MARIANNE BAUNSGAARD (1999): Nutrient recycling - a strategy of a grazer community to overcome nutrient limitation. - J. North Am. Benth. Soc. 18 (3): 363-369.

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EXPLANATION OF FREQUENTLY USED TERMS AND ABBREVIATIONS*

microphytobenthos	microscopically "small" algae such as diatoms
macrophytobenthos	"large" algae such as filamentous green algae (There is no clear demarcation between micro- and macrophytobenthos.)
benthic algae	microphytobenthos + macrophytobenthos
periphyton	microphytobenthos + fungi + meiofauna + bacteria + organic and inorganic detritus (nonliving material) (According to the definition of Wetzel (1983) and Stevenson (1996), macroscopic benthic algae would not be considered periphyton. Detritus is usually not included in the definition of periphyton (Wetzel 1983), but because of the difficulty in separating it from living material, it was always present in field studies.)
benthic algal community	benthic algal-dominated assemblage of periphyton and macrophytobenthos
epilithon	benthic algal community on stones, rocks, and similar substrates
epiphyton	benthic algal community on macrophytes
epizoon	benthic algal community on animals (Investigated substrates were the shells of the mussel *Dreissena polymorpha* (Pall.) and the galleries of the caddisfly *Tinodes waeneri* (L.).)
epipelon	benthic algal community on fine sediments
epipsammon	benthic algal community on sand
nutrient status	description of algal physiological status when growth is nitrogen (N) or phosphorus (P) limited, or when N and P are in optimal supply (special case: nutrient surplus)
C:N:P ratio	carbon : nitrogen : phosphorus ratio (molar basis)
chl *a*	chlorophyll *a*
APA	specific alkaline phosphatase activity (calculated per chl *a*)
top-down control	control of algal biomass by grazing (algae removal)
bottom-up control	control of algal biomass by nutrient supply (algal growth)
horizontal variation	variation of different sites sampled at the same depth
patchiness	horizontal variation showing an irregular texture
vertical variation	variation over depth
spatial variation	variation in space (three-dimensional expanse including horizontal and vertical variation)
temporal variation	variation over time

* definitions as used in the summary of this thesis

1 INTRODUCTION

This study gives an overview of the natural variation of biomass and nutrient status of benthic algae at different space and time scales, in different lakes, and on different substrates. Field observations and experiments were used to find factors regulating biomass and nutrient status of benthic algae in lakes, with special emphasis on variation at horizontal spatial scales, and on the importance of nutrient excretion by benthic animals as a nutrient source for benthic algae.

Benthic algae live in close connection with meiofauna, fungi, bacteria, and organic and inorganic non-living material (detritus) embedded in a mucopolysaccharide matrix (Burkholder 1996), an assemblage defined here as a "benthic algal community" (Fig. 1). Nutrient sources for a benthic algal community include the overlying water, an eventual nutrient release by the substrate, and internal nutrient recycling (Mulholland 1996). The access to the nutrients in the overlying water is, especially in lakes, often restricted by a "boundary layer" of quiescent water through which solutes can travel only by slow diffusion (Burkholder 1996). The investigated benthic algal communities were assemblages on rocks and stones (epilithon), on macrophytes (epiphyton), on mussel shells (*Dreissena polymorpha* Pall.), and on galleries of a caddisfly larva (*Tinodes waeneri* L.) (epizoon). It is necessary for a complete picture of the ecosystem lake to understand the mechanisms regulating nutrient content and biomass of benthic algae, because they can be dominant primary producers and are an important food resource for grazers (Wetzel 1983, Hecky & Hesslein 1995).
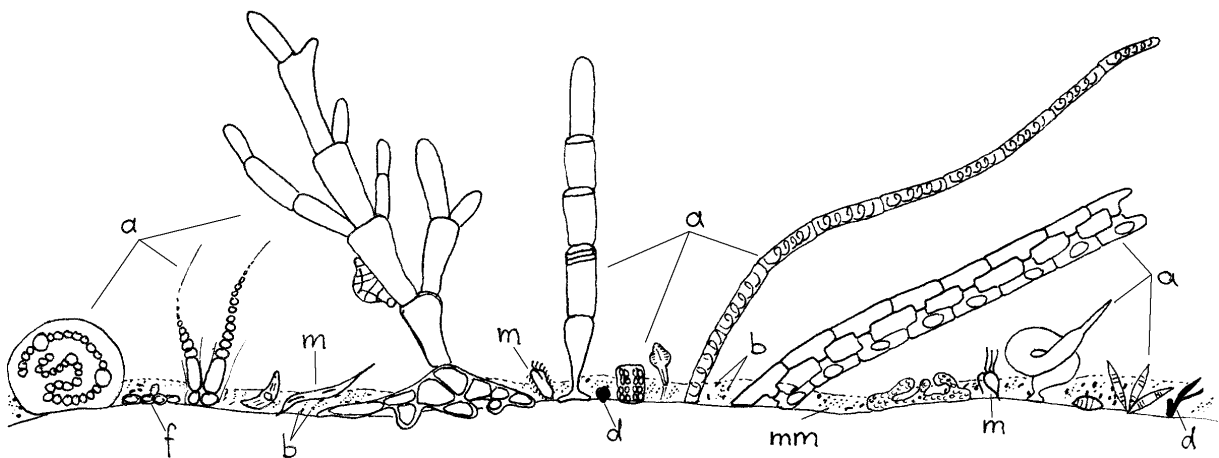

Figure 1. The benthic algal community, an assemblage dominated by benthic algae (a) associated with meiofauna (m), fungi (f), bacteria (b), and organic and inorganic non-living material (detritus) (d) embedded in a mucopolysaccharide matrix (mm).

A first step in my investigations was the analysis of spatial and temporal scales of variation in biomass and nutrient status of benthic algae in the littoral zone of lakes and a subsequent calculation of an optimal sampling design. Benthic algae in streams are patchily distributed, as indicated by high variation at different horizontal scales (Jones 1978, Stevenson 1997, Ledger & Hildrew 1998, Uehlinger *et al.* 1998, Pan *et al.* 1999). In lakes, however, similar information on amount of variation at different horizontal scales is available only for benthic algal biomass on sediment and sand (Downing & Rath 1988, Cyr 1998). Most studies focus on the variation of algal biomass at only a single spatial scale (distance).

Algal biomass on stones and rocks in lakes was shown to vary significantly between lake sites (Aloi *et al.* 1988, Cattaneo 1990), and within one lake site (Harrison & Hildrew 1998). If the variation at different scales is known, sampling effort can be minimized, and the probability of detecting significant differences between substrates or seasons, for example, can be maximized by calculating the number of samples needed at different scales (Sokal & Rohlf 1995). There are sampling recommendations for the number of required samples when analyzing sediments or macrophytes, but even these studies do not explicitly state which scales to repeat (Håkanson & Jansson 1983, Downing & Anderson 1985, Downing & Rath 1988). Although replicating the largest scale to include all variation and to minimize total variation is always correct (Sokal & Rohlf 1995), it is also costly. Thus, if high variation occurs at small scales, replicating sampling for these scales to minimize sampling costs might be more effective (Sokal & Rohlf 1995). Even less information than for biomass is available for variability of benthic algal nutrient status in lakes.

Knowing the temporal and spatial scales for variation, one can evaluate factors regulating benthic algal nutrient status or biomass. In marine environments (Blanchard 1990, Saburova *et al.* 1995, Burkovskii *et al.* 1996) and streams (Pan *et al.* 1999), researchers showed that biomass variance was coupled to environmental variance. Nutrient supply was patchily distributed in streams, and caused a patchy distribution of algal biomass (Uehlinger *et al.* 1998). However, this "bottom-up" control of algal biomass was only obvious when other factors that removed benthic algae were unimportant, such as "top-down" control by grazers or frequent physical disturbances (McIntire *et al.* 1996, Biggs *et al.* 1998a). Experiments and field observations in streams showed that grazer effects sometimes increased when algae were fertilized (Feminella & Hawkins 1995); and therefore, bottom-up control of benthic algae

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might even interact with top-down control by grazers. In this thesis, the term "bottom-up control" refers to "control of algal biomass by nutrient supply via algal growth," and "top-down control" refers to "control of algal biomass by grazing via algal removal."

The magnitude of bottom-up control can be deduced from benthic algal nutrient status. The nutrient status of an alga is a description of its physiological status, showing nutrient limitation, for example by N or P, or optimal nutrient supply for growth. A surplus of nutrients is a special case of a non-limiting status, when nutrients can be stored for later use. The macronutrients N and P frequently limit growth of phytoplankton and benthic algae in freshwater and marine environments (reviewed by Atkinson & Smith 1983, Hecky & Kilham 1988, Borchardt 1996). As for benthic algae in lakes, less is known about the frequency of N or P limitation.

A convenient way to assess algal nutrient status is to compare the community's C:N:P ratio with an "optimal ratio" (Healey & Hendzel 1980). This optimal ratio occurs when N and P do not limit algal growth. For phytoplankton, the optimal ratio is 106:16:1 (molar basis) (Redfield ratio) (Goldman *et al.* 1979, Goldman 1986). Under N or P limitation, the relative amount of N or P in the community decreases and causes an increase of the C:N:P ratio, e. g. an increase of the included ratios C:N, N:P, or C:P. For freshwater phytoplankton, N limitation is indicated by C:N > 8, and P limitation is indicated by C:P > 129 and N:P > 22 (Hecky *et al.* 1993, and the references therein). However, the use of the Redfield ratio for benthic algae was questioned, because the C:N:P ratio of a benthic algal community might indicate not only algal nutrient status, but also the proportions of non-algal material, such as detritus, which increases C, (Makarevich *et al.* 1993) or such as bacteria, which increases P (Rhee 1972). Moreover, it has not been clear if benthic algae have the same optimal C:N:P ratio as phytoplankton (Atkinson & Smith 1983). Yet many researchers used the C:N:P ratio successfully as an estimation of the nutrient status of benthic algae (e.g. Loeb 1981, Neil & Jackson 1982, Peterson *et al.* 1983, Lindstrøm 1994).

A special form of nutrient supply to benthic algae is that of animal excretions. In the pelagic food web in lakes, recycled nutrients originating from zooplankton are an important nutrient source for phytoplankton (Elser & Frees 1995, Sterner *et al.* 1995, Elser *et al.* 2000). Moreover, zooplankton influence the relative availability of N and P for phytoplankton, which can sometimes lead to changes in N and P limitation, and can even lead to subsequent

changes in the species composition of the phytoplankton (Sterner *et al*. 1992, Elser *et al*. 1996, Elser & Urabe 1999). So far, whether nutrient recycling by animals is as important in the benthic community of a lake as in pelagial phytoplankton, is unknown. As Steinman (1996) points out, benthic grazers might have not only a negative impact on their food because of algal removal while grazing, but also a positive impact, since they make nutrients re-available for algal uptake, and they remove senescent cells, resulting in an improved algal nutrient status. Such positive effects of grazers on algal nutrient content, sometimes coupled to increased algal growth, has been observed in streams (McCormick 1990, Rosemond 1993).

However, on benthic algal biomass in streams, a positive impact of grazers was seldom observed [see reviews in (Feminella & Hawkins 1995, Steinman 1996), which might be a consequence of nutrient spiraling in running water (e.g., nutrients released by grazers will be transported downstream) (Mulholland 1996). Lack of continuous water transport in lakes might cause a closer coupling of benthic algae and grazers than in streams, and might result in a more distinct improvement of algal nutrient status and biomass in lakes than in streams. Particularly close connections occur in epizoon, where benthic algae grow on animal substrates, such as on the shells of living mussels (Schreiber *et al*. 1998) or on galleries of caddisfly larvae (Hasselrot 1993). Thus, nutrient excretion by benthic animals in lakes is likely an important nutrient source both for algae attached to animal substrates and for other benthic algae receiving nutrients from mobile grazers.

Animal substrates might be just as important for the nutrient budget of epizoon as sediment is for epipelon and epipsammon, and as macrophytes are for epiphyton. The importance of substrates for nutrient supply to attached algae is seldom addressed (Vadeboncoeur *et al*. 2001), although it is known that benthic algae can also take up nutrients from macrophytes (see review of Wetzel 1996) and sediments (Jansson 1980, Carlton & Wetzel 1988, Hagerthey & Kerfoot 1998). Epiphytic algae can obtain over 60 % of their P from the macrophyte (Moeller *et al*. 1988), and similar values have been observed for the importance of grazer-supplied N to epilithon in streams (Grimm 1988). Thus, nutrient release by zebra mussels and reed, which are substrates found in many large lakes, might equally improve the nutrient status of algae attached to those substrates.

The importance of animals as a nutrient source might change with lake trophy, because benthic algae should be able to satisfy their nutrient demand mainly by uptake from lake water when the amount of available nutrients in the overlying water is high. Since low

nutrient concentrations are usually found in oligotrophic lakes, I expected the effect of a nutrient release by animals or macrophytes to be more pronounced in those lakes. In eutrophic lakes, the amount of available nutrients in the water can also be very low, despite high total nutrient concentration. During winter, however, and during stormy events in other seasons, the high total pool of nutrients in eutrophic lakes becomes available for algal uptake. However, benthic algae do not necessarily profit from a high nutrient concentration in lake water because the boundary layer prevents a fast nutrient uptake (reviewed in Borchardt 1996) and because of competition with lake phytoplankton (Cattaneo 1987, Hansson 1992, Havens *et al*. 1996, Vadeboncoeur *et al*. 2001). Moreover, if the main nutrient source of benthic algae is a recycling within the community (Mulholland 1996), nutrients from the overlying water might have little or no impact on benthic algal nutrient status.

The presented considerations led to the following hypotheses, which are tested in this thesis:

2   HYPOTHESES

1) Horizontal variation dominates the total variation of benthic algal biomass and nutrient status in lakes. The amount of horizontal variation varies for different scales, substrates, and lakes. An optimal sampling design must include replications of small as well as large horizontal scales.

2) The C:N:P ratio of natural benthic communities in freshwater reflects the benthic algal nutrient status (e.g., the C:N:P ratio is high when either N or P limit algal growth, and low when neither N or P are limiting).

3) The biomass of benthic algae is increased by nutrient enrichment and reduced by grazing. The contrasting effects of both controls are interactive (grazing reduces fertilization effects and vice versa).

4) Benthic algae benefit from nutrients released by animals. For algae attached to living mussels, the benefit is as large as for algae attached to macrophytes. The importance of animal substrate as a nutrient source for attached algae decreases with increasing lake trophy.

3 STUDY SITES

site	location	area (km^2)	mean depth (m)	T (ºC)	Secchi depth (m)	pH
Lake Ånnsjön	63º15'N 12º30'E Sweden	59	max depth: > 18 m	8.5	6.8	7.3
Lake Erken	59º50'N 18º35'E Sweden	24	9	8.3	5.8	8.0
Lake Limmaren	59º44'N 18º43'E Sweden	6.5	4.3	8.4	3.9	8.0
Lake Balaton, Tihany basin	47º04'N 18º10'E Hungary	228	2.3	12.5	0.7	8.2
Lake Balaton, Keszthely basin	46º62'N 17º15'E Hungary	38	3.7	13.0	0.5	8.4
Baltic coast embayment (Väddö)	59º56'N 18º55'E Sweden		1.5	10.3	3.4	7.8

site	phytoplankton chl a (µg l^{-1})	TN (µM)	TP (µM)	TN:TP (atomic ratio)	classification*	note
Lake Ånnsjön	1.2	11.7	0.2	73	oligotrophic	a)
Lake Erken	4.7	45.5	0.9	57.6	mesotrophic	
Lake Limmaren	18.3	74.8	1.8	57.3	eutrophic	b)
Lake Balaton, Tihany basin	8.8	62.9	2.0	41.0	eutrophic	
Lake Balaton, Keszthely basin	19.7	88.0	3.1	38.5	eutrophic	
Baltic coast embayment (Väddö)	5.9	26.9	0.7	44.0	mesotrophic	low salinity, c)

Table 1. Study sites. Values are calculated for the epilimnion as a yearly average (1994-2000). Exceptions: a) only single measurements were available for Lake Ånnsjön. b) values for Lake Limmaren are from 1991/92 and 1998-2000. c) Samples taken at the nearby Singöfjärden.

* Following Vollenweider & Kerekes (1982).

4 APPROACHES

4.1 FIELD SAMPLING AND EXPERIMENTS

Field samples of natural benthic algal communities were taken from the lakes Ånnsjön, Erken, and Balaton in 1996 and 1997 (**papers II, III, IV**). Biomass and nutrient status of algae attached to stones and rocks, living macrophytes, and mussels (*Dreissena polymorpha* Pall.) were estimated, at 1 m water depth. In 1997, stones and rocks in Erken were also sampled directly under the water surface (0 m) and at 4 m depth. A nested hierarchical design (Underwood 1981, Sokal & Rohlf 1995) was used to overcome the problem of different variation at different scales. I replicated sampling within one sampled object (cm scale), within a small area (dm scale), within a larger area (10 m scale), and within one lake (km scale). Sampling was also repeated in several seasons and on several days within a season. The nested design combines different scales, estimates the amount of variation for the respective scales, and requires a minimum of samples, in contrast to grid sampling, for example. Moreover, randomly placed single point-contacts like those used in a nested design have been shown to provide the best estimate of algal biomass (Miller & Ambrose 2000).

In 1999 and 2000, in the lakes Erken and Limmaren and at the Baltic coast of Väddö, experiments were run on the importance of top-down and bottom-up control of benthic algal biomass and nutrient status on hard substrate (**paper V**). Grazer presence was manipulated by using cages to exclude macrograzers. Nutrient supply was manipulated by adding N and P to the water column. Algal biomass and nutrient content were measured after four to five weeks. The experiments were repeated seasonally to encompass different abiotic conditions and seasonal changes in grazer species composition. Algal taxonomical composition on pre-colonized ceramic tiles used in this study resembled well the natural species composition, with the exception of a lower dominance of *Cladophora* in Lake Erken. The experiment was controlled for cage effects, which were low relative to grazer and nutrient effects.

One experiment was performed in Lake Erken in 1997 to study N recycling in the epizoon of *Tinodes waeneri* (L.) (**paper VI**). This grazer community consists of a sessile caddisfly larva plus its gallery. The gallery consists of a web spun by the larva plus the epizoon closely associated with the web. Applying ^{15}N in the field, uptake and retention time in the grazer

community were recorded, and then were compared to the fate of ^{15}N in the surrounding epilithon.

4.2 ESTIMATION OF BIOMASS

Biomass of benthic algae was estimated by measuring chl *a* and particulate C. Additionally, algal biovolume was measured for experiments that assessed the effects of top-down and bottom-up control (**paper V**), and for some of the field samples in Lake Erken (**paper II**). Being present only in the algal part of benthic algal communities, chl *a* reflects algal biomass. However, because the amount of chl *a* per cell is variable (Paerl *et al.* 1976, Stevenson 1996), a change in the amount of chl *a* in a benthic algal community does not necessarily reflect a change of benthic algal biomass. Particulate C, on the other hand, is a measure of all organic and inorganic material within the community containing C, and might therefore not only reflect a change of living organisms but also a change of the detritus mass and other non-algal material. However, algae dominated the investigated benthic algal communities (> 70%), non-algal material amount was low to moderate (< 30%), and the different measurements of biomass were highly correlated (**paper II, V**). Therefore, taken together, the measured biomass parameters gave good estimates of algal biomass at investigated sites.

4.3 ESTIMATION OF NUTRIENT STATUS

The validity of the use of the C:N:P ratio to estimate the nutrient status of natural freshwater benthic algae was shown in a review of field studies (**paper I**). The optimal C:N:P ratio of natural freshwater benthic algal communities (158:18:1 on molar basis), deduced from the literature, was slightly higher than the Redfield ratio (106:16:1) (**paper I**). Threshold ratios indicating severe N or P limitation were as high as for marine benthic algae (**paper I**, table 2). The C:N:P ratio usually reflected nutrient supply for the algae at some time before sampling, and indicated whether N or P or both were limiting algal growth (**paper I**). Other factors, such as light, grazing, shift of algal groups, or a change of detritus amount, also had an impact on the community C:N:P ratio, but their impact was, in natural communities, usually smaller than the impact of N or P supply (**paper I**). However, as a note of caution, a change of species composition of the algal assemblage can mask the effects of a nutrient supply, at least in artificial streams used for experiments (Stelzer & Lamberti 2001).

Table 2 Indicators of nutrient status of freshwater benthic algae

nutrient status		ratio (molar basis)
P limited	C:P	> 369
	N:P	> 32
N limited	C:N	> 11
P and N limited	C:N:P	all values relatively high

simplified from **paper I**

Field observations (**paper II, III**) and measurements in the experiments (**paper V**) confirmed the review's results (**paper I**). High benthic algal biomass was mainly found together with near optimal C:N:P ratio (Figure 2, values from **paper II**). Measurement of alkaline phosphatase activity (APA), another method to estimate P limitation (Pettersson 1980), mostly confirmed P limitation detected by C:P and N:P ratios (**paper II, III**). In the experiments, the C:N:P ratio decreased with a subsequent increase of algal biomass when nutrient supply was increased (**paper V**), a result also found in recent studies on benthic algae (Hagerthey & Kerfoot 1998, Hillebrand & Sommer 1999).
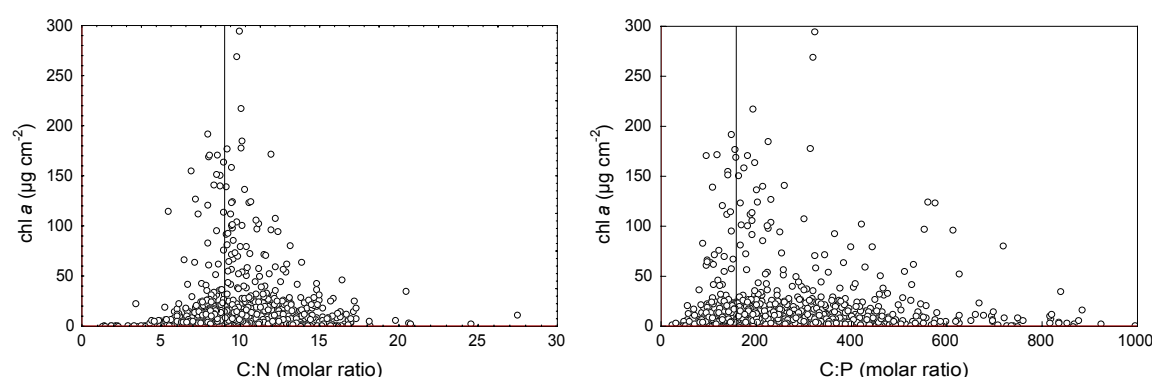

Figure 2. Biomass of epilithon versus C:N and C:P ratios. Optimal ratios (**paper I**) are indicated by lines. (Values of **paper II**)

The C:N:P ratio was used to evaluate benthic algal nutrient status in natural communities and in the experiments (**paper II, III, IV, V**). The proportion of detritus in natural communities and the algal groups present were similar during the field sampling (**paper II, III, unpublished data**), and therefore had no impact on change in the C:N:P ratio. In the top-down/bottom-up experiments, detritus amount was also constant, and the observed changes in algal groups could not explain the C:N:P changes (**paper V**). In conclusion, I am convinced that the observed C:N:P ratio reliably indicated whether supply of N or P was insufficient or sufficient, and therefore did or did not limit benthic algal growth.

5 THE VARIATION OF BIOMASS AND NUTRIENT STATUS

5.1 VARIATION WITH DISTANCE, DEPTH, AND TIME ON STONES AND ROCKS IN LAKE ERKEN

Biomass and nutrient status of algae attached to stones and rocks were distributed patchily in Lake Erken, as indicated by the significant and often high variation that was added by each of the investigated levels of distance (**paper II**). Patchiness was observed on a single stone, within a small area, within a sampled site and within the whole lake (**paper II**), consistent with the observation of small scale variation of benthic algal biomass in streams (Jones 1978, Ledger & Hildrew 1998) and of large scale variation in lakes (Aloi *et al*. 1988, Cattaneo 1990, Harrison & Hildrew 1998). Comparing horizontal, temporal, and laboratory variation, horizontal variation accounted for 50–80% of the total observed variation of algal biomass and the C:N ratio, and for 50% or less of the variation in parameters C:P, N:P, and APA for evaluating algal P status (**paper II**). Total horizontal variation was highest for algal biomass and APA values, followed by C:P and N:P ratios. C:N values varied least (**paper II, IV**). The observation of high biomass variation, and variation of P higher than of N, accord with the results of earlier studies on benthic algae, phytoplankton, and seagrass (Goldman *et al*. 1979, Duarte 1990, Morin & Cattaneo 1992, Hecky *et al*. 1993).

The importance of the variation at large horizontal scales is shown by the example of the C:N:P ratio on a single sampling day in fall 1996 (Figure 3): The median values of the sampling day indicated a trend toward N limitation and toward almost optimal P supply for the entire lake (**paper II**), but in reverse, single sampling sites indicated optimal N supply and P limitation. The occurrence of large-scale patchiness of the nutrient status of benthic algae indicates that benthic algae are not regulated in the same way as phytoplankton, where large-scale patchiness was less important (Sterner 1994, Pettersson *et al*. 1995). Earlier, Aloi *et al.* (1988) and Cattaneo (1990) proposed a large-scale difference of nutrient supply to benthic algae in lakes, based on the observation of large-scale biomass variation.
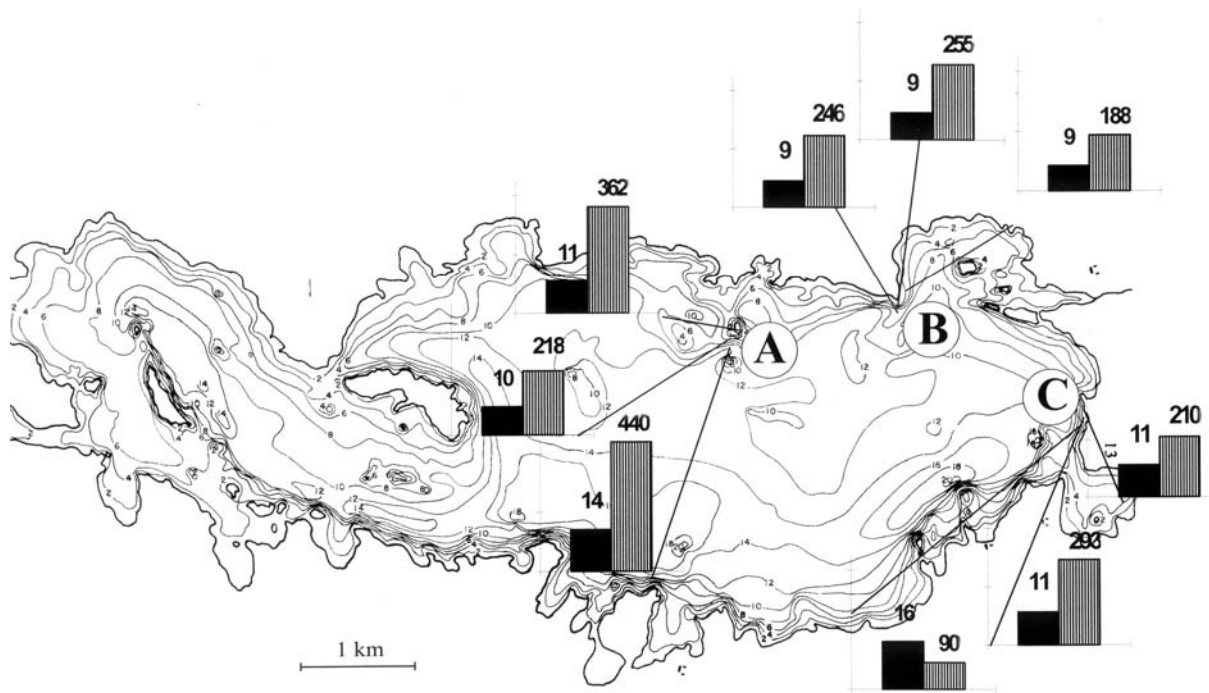
Figure 3. Example of the nutrient status variation of algae attached to stones and rocks on sampling day 13.10.1996 at large horizontal scales (10 m and km) (the three replicates taken at one lake site were about 10 m apart from one another). Black columns: C:N (atomic ratio). Striped columns: C:P (atomic ratio). (**paper II**)

Changes in depth and time contributed to the total variation in biomass and nutrient status of benthic algae attached to stones and rocks. Low biomass was observed directly under the water surface (0 m depth), and high N and P contents at 4 m depth (**paper II**). Algal biomass was more evenly distributed over the whole lake at 4 m than at 0 and 1 m, indicated by the absence of significant variation at large horizontal scales at 4 m (**paper II**). Temporal variation consisted of differences within and between seasons. Differences between the two sampled years were smaller than differences within one year (**paper II, IV**). Both N and P limitation occurred din the course of sampling time, but the pattern of variation varied for all investigated scales.

5.2   SIMILAR HORIZONTAL VARIATION FOR DIFFERENT SUBSTRATES AND LAKES

Horizontal variation of benthic algal biomass and nutrient status was substantial at most of the investigated scales, with no differences in the pattern of variation between substrates (**paper III, IV, V**). That is, biomass and nutrient status were more or less as patchily distributed on a

mussel, as on a reed stem, or stone. In addition, also at the dm, 10 m, and km scales, patchiness was about the same for all substrates (**paper IV**). The pattern of horizontal variation was even similar for the investigated lakes, despite the differences between them in morphology and lake trophy (**paper IV, V**).

The magnitude of horizontal variation was even similar regardless of the horizontal scale (**paper II, IV**, unpublished data). Chl *a* had, on average, a coefficient of variation (CV = standard deviation/mean) of 40%; C:P ratios, 25%; and C:N ratios, 15%. Similar algal biomass variation (CV for chl *a* $20 - 40\%$) regardless of scale was reported earlier in a review by Morin and Cattaneo (1992), and by others, who also listed the different horizontal scales of investigation (Jones 1978, Downing & Rath 1988, Cyr 1998). Thus, even though one might expect different regulating mechanisms for different horizontal scales, substrates, or lakes, apparently benthic algal variation is the same or similar for all.

5.3 CALCULATION OF AN OPTIMAL SAMPLING DESIGN

Because variation is already high at very small scales of space and time, it is important to take a sufficient number of replicates at appropriate scales to ensure discovering of true differences at the level of interest. For example, focusing on one sampling site can give biased estimates of nutrient limitation of benthic algae for the entire lake (see above). One can calculate an optimal sampling design that minimizes both variation and sampling costs, when variation at different sampling scales is known. In general, a replication of the largest sampling scales will minimize variation more than a replication of smaller subordinate scales (Sokal & Rohlf 1995); but replication of large scales is usually more expensive. Therefore, replicating subordinate scales can be worthwhile, if they add substantially to total variation. If, for example, a researcher follows the algal succession during one year, then finding significant differences between days is an important task. For this reason, in Lake Erken, at 0–1 m depth, the optimal number of sites to sample is 1–4, separated by at least 1 km. On each lake site, 2–6 locations, separated by about 10 m, should be sampled; and at each location, one stone should be taken and scraped once (**paper II**). Algae at 4 m depth are distributed more evenly; thus, sampling of only one lake site, and taking about six replicates in the dm scale to minimize sampling effort, is sufficient (**paper II**). Since laboratory replicates only slightly minimize total variation, they should be excluded (**paper II**).

To be conservative, a researcher should use the highest number of replicates in the respective scale suggested by the calculated optimal design. Pooling all samples taken at subordinate horizontal scales to form a composite sample for minimizing analysis costs is possible. One can also use the calculated optimal design for benthic algal communities other than epilithon, and for other lakes resembling Lake Erken, because horizontal variation was similar for different substrates and lakes (**paper III**). Between-lake comparisons must also include temporal variation, in days, seasons, and years, representing scales superior to the horizontal scales. In this case, sampling should concentrate on replicating mostly at temporal scales, because then within-lake variation of an estimated mean will be reduced most efficiently (Sokal & Rohlf 1995).

6   FACTORS REGULATING BENTHIC ALGAL BIOMASS AND NUTRIENT STATUS

6.1   INFERENCES FROM FIELD OBSERVATIONS

Field observations of this study indicated that bottom-up control likely was important for regulating the biomass of benthic algae in lakes. Nutrient effects were detected by plotting observed biomass versus C:N:P ratios, showing that a high algal biomass was mainly found together with an optimal C:N:P ratio (Figure 2). Bottom-up control in the form of nutrient limitation was, at times, also indicated by low dissolved nutrients in lake water, and by a community C:N:P ratio higher than the optimal (**paper I, II, III**). An impact of nutrients was also observed when comparing lakes of different trophy, with the highest biomass being found in the most eutrophic lake (**paper III**).

The higher P than N variation (**paper II, III, IV**), also observed for phytoplankton and seagrass (Goldman *et al*. 1979, Duarte 1990, Hecky *et al*. 1993), probably indicates a higher algal storage capacity for P than for N (Fitzgerald 1972, Lorenz & Herdendorf 1982, Lohman & Priscu 1992), which might have evolved because of a higher frequency of P than N limitation (Hecky & Kilham 1988, Planas *et al*. 1996). However, other factors often masked the effect of nutrient status on algal biomass, resulting in low biomass under optimal nutrient status, and high biomass occurring when nutrient status indicated limitation (Figure 2, **paper II, III**).

One factor causing an uncoupling of nutrient status and biomass is time, because time is required for an improved nutrient status to translate into new biomass via growth (Sakshaug & Holm Hansen 1977), and then growth can continue for some time after the N and P stores are emptied (Fitzgerald 1972, Gordon *et al*. 1981, Björnsäter & Wheeler 1990). Moreover, benthic algae, being accustomed to nutrient deprivation (Gordon *et al*. 1981, Pedersen & Borum 1996, Pedersen & Borum 1997), may well be genetically tolerant to it, through evolution. Thus, a fast decline in biomass due to nutrient limitation might be unusual under natural conditions, which might explain the high biomass found under obviously nutrient-limited conditions in Lake Balaton.

Factors preventing the development of high biomass under obviously non-limiting conditions include algal removal by grazing (top-down control), physical disruption, and factors limiting algal growth other than N and P, such as light or trace nutrients. Physical disruption includes high wind intensity over a short time period, which was significantly negatively correlated to algal biomass on stones and rocks at the km scale, indicating an effect of sloughing (**paper II**) (Kairesalo 1983, Lalonde & Downing 1991). Wind in form of waves or currents might also cause change in algal biomass in the dm scale, because of differing effects on stones of different size (see Jones 1978, and Ledger & Hildrew 1998, and the reviews of Biggs 1996, and Peterson 1996). Whereas small stones were subject to dislodging and abrasion, large stones nearby could withstand the waves and keep a high algal biomass. A direct coupling of low light intensity with low biomass, observed in other studies (Lalonde & Downing 1991, Hansson 1992, Vadeboncoeur 1998), and expected for turbid Lake Balaton (**paper III**) and for deep sampling points in Lake Erken, never occurred in this study (**paper II**). However, I did find indirect indications of light limitation. Light intensity was different between depths, and between the two sampling years, and was coupled to relatively low C:N:P ratios, possibly indicating a low nutrient demand due to light-limited growth (**paper II**) (Lorenz *et al*. 1991, Hill 1996). Other factors such as silicate concentrations (Wetzel 1996, Müller 1998), or maybe even iron concentrations (Hyenstrand *et al*. 2000), might also play a role in limiting algal growth, and therefore warrant further attention. Grazing is a biotic factor that might have caused the observed biomass patchiness (**paper II, IV**) at the cm scale (DeNicola *et al*. 1990) (Blanchard 1990, Sommer 2000), but also the observed variation at larger scales (Dall *et al*. 1990, Morrisey *et al*. 1992).

Why did we find nutrient limitation at all in Lake Balaton, a lake over-fertilized with nutrients (Herodek *et al*. 1988) (**paper III**)? And why was there an optimal C:N:P ratio in an oligotrophic lake, where nutrient limitation would be expected (**paper III**)? The surprisingly low C:N:P ratio observed in the oligotrophic Lake Ånnsjön (**paper III**) might be a consequence of an adaptation of the algal community to low nutrient concentrations by enhanced nutrient uptake and storage capabilities, similar to marine phytoplankton communities (Goldman *et al*. 1979, McCarthy & Goldman 1979).

Nutrient limitation in eutrophic Lake Balaton can be a result of transient low availability of dissolved nutrients despite high total N and P. Such low availability might in turn be caused by a large phytoplankton population, which is a better competitor for nutrients than benthic algae (Hansson 1992, Vadeboncoeur *et al*. 2001). Nutrient limitation might also be explained by the fact that algae in the understory of a thick mat have low access to nutrients in the overlying water (Burkholder *et al*. 1990) and that the boundary layer prevents the diffusion of nutrients into the community (Riber & Wetzel 1987). In general, lake trophy is a weak predictor of benthic algal biomass (Cattaneo 1987, Lalonde & Downing 1991) because of the mentioned factors.

6.2   EXPERIMENTAL TEST OF BOTTOM-UP VERSUS TOP-DOWN EFFECTS

The field observation that both bottom-up and top-down effects might both be important in the regulation of algal biomass and nutrient status in natural benthic communities were confirmed by field experiments manipulating grazer presence and nutrient supply over several weeks (**paper V**). Grazing reduced algal biomass, whereas nutrient supply increased algal nutrient content followed by an increase of algal biomass, a result found earlier in streams (McCormick & Stevenson 1991, Hill *et al*. 1992, Rosemond 1993). Top-down control was generally stronger than bottom-up control, possibly because bottom-up effects usually need more time for expression than top-down effects (Lampert & Sommer 1993). Most experiments revealed a combined influence of nutrients and grazers without an overriding importance of either manipulation (**paper V**). Top-down or bottom-up factors neither excluded nor intensified each other. Therefore, algae attached to hard substrate were simultaneously top-down and bottom-up regulated, probably because of the patchy distribution of grazing pressure (Blanchard 1990, DeNicola *et al*. 1990, Sommer 2000). Light, temperature, and background nutrient concentrations affected the importance of grazers and

nutrients, but no single abiotic variable alone produced a strong effect, indicating a complex interaction of regulating factors similar to the field observations.

6.3   ANIMALS IMPROVE THE NUTRIENT STATUS OF BENTHIC ALGAE

Animals had not only a negative effect on amount of benthic algal biomass, but also, as expected, a positive effect by increasing benthic algal nutrient content substantially. Field observations showed that algae attached to the shells of the mussel *Dreissena polymorpha* in lakes Erken and Balaton had lower C:N:P ratios than algae on stones and rocks (Figure 3, **paper III**), probably because of the release of N and P by the mussel (Arnott & Vanni 1996). Field experiments showed that mobile grazers also increased benthic algal nutrient content (**paper V**). Grazers mainly reduced C:P and N:P ratios, indicating a release of P, which was confirmed in the laboratory for the snail *Theodoxus fluviatilis* L.(Stendera 2000) and the caddisfly larva *Tinodes waeneri* (unpublished results). In addition, algae on the gallery of *Tinodes* had the advantage living close to the animal.

N supplied to the overlying water was taken up faster by epizoon than by epilithon and was recycled one week longer in the *Tinodes* community than in the epilithon (**paper VI**). Because mobile grazers usually are frequent in lentic ecosystems, and because the animal "substrates" *Dreissena* and *Tinodes* can reach high densities in a lake (Dall *et al*. 1984, Hasselrot 1993, Lowe & Pillsbury 1995), animal nutrient excretion is likely an important nutrient source for benthic algae in some lakes. In streams, nutrient recycling by grazers supplied 14–70% of the N demand of benthic algae, and 25% of the P demand (Grimm 1988, Mulholland *et al*. 1991, Jay 1993). It is possible that the amount of nutrients supplied by animal excretion is even higher in lakes, because of the closer coupling between animal and algae. One of the few studies dealing with benthic lake organisms showed that ammonia release by a snail stimulated the growth of the macrophyte *Ceratophyllum demersum* L. in laboratory experiments (Underwood 1991).
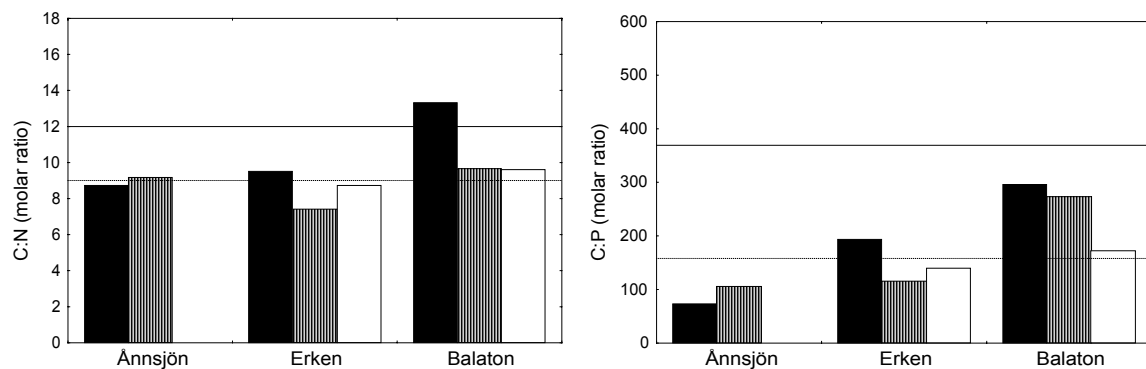
Figure 4. C:N and C:P ratios of benthic algae attached to stones and rocks (filled column), macrophytes (striped column), and mussel shells (open column) in Lake Ånnsjön (oligotrophic), Lake Erken (mesotrophic), and Lake Balaton (eutrophic). - - - = optimal ratio; — = severe nutrient limitation (simplified from **paper III**).

The largest differences in algal nutrient status between animal versus stone substrate occurred, as expected, when the C:N:P ratio of algae on stones and rocks were high, indicating that a nutrient release of the substrate is most important when benthic algae are nutrient limited (**paper III**). However, in contrast to expectation, nutrient limitation was found in the most eutrophic lake (**paper III**); therefore, the importance of a nutrient release by the substrate did actually increase instead of decrease with increasing lake trophy.

In the lakes Erken and Balaton, the nutrient status of benthic algae attached to zebra mussels (*Dreissena*) was almost as good as the nutrient status of algae attached to reeds (Figure 4, **paper III**), indicating that the animal excretions were as important as the nutrients leaching from the macrophyte. In Lake Erken, the C:N and C:P ratios of algae on reeds were slightly lower than those for algae on *Dreissena*; but in Lake Balaton, C:N ratios were the same for algae on reed and *Dreissena*, although C:P ratios were higher on reed (Figure 4, **paper III**).

However, improvement of algal nutrient status was seldom coupled to an increase in algal biomass. Only the field experiment with the *Tinodes* community indicated that an improved nutrient status resulted in a higher algal biomass on the galleries than on the surrounding bedrock (**paper VI**). In contrast, the field experiments in the lakes Erken and Limmaren, and at Väddö indicated that, although grazers improved the nutrient status of the algae, the top-down control of algal biomass was stronger than a possible positive response due to the improved nutrient status (**paper V**). In addition, the field observations showed that biomass of algae on mussels and on reed in Erken and Balaton was no higher than that on the

surrounding stones and rocks. In fact, biomass was lower despite the better nutrient status (**paper III**). Yet other studies of benthic algae in lakes did sometimes find a coupling of nutrient status and biomass (Hagerthey & Kerfoot 1998, Vadeboncoeur 1998), and sometimes not (Burkholder & Wetzel 1990). Clearly, other factors, such as top-down control by grazers or the longevity of the substrate, ultimately control algal biomass.

7 CONCLUSIONS

This thesis shows that biomass and nutrient status of benthic algae in lakes are patchily distributed at small and large scales of distance (**hypothesis 1**), and that substantial differences can occur between different depths and substrates, and between days, seasons, and years. In general, algal biomass varied most, followed by algal P content, and N content varied least. Horizontal patchiness accounted for a higher percentage of total variation than temporal variation for biomass and C:N ratios. Temporal variation was more important for the internal P content. Patchiness was similar for different substrates and different lakes, but not for different depths, such as benthic algae on stones and rocks were more evenly distributed over the entire lake at deep than at shallow locations (**hypothesis 1**). The observed patchiness indicated that different patches in the lake were regulated differentially. For example, nutrient limitation and nutrient surplus might occur within a distance of only 10 m. For experimental design, the observed patchiness requires replication at large sampling scales (km distance) to cover all variation in a lake when estimating benthic algal biomass and nutrient status. However, to minimize sampling effort and cost, the 10 m scale (and at 4 m depth, also the dm scale) should be replicated (**hypothesis 1**).

This thesis shows that the internal C:N:P ratio of an benthic algal community can be used to assess nutrient status of benthic algae in lakes (**hypothesis 2**). A review of natural freshwater benthic algal communities revealed an optimal C:N:P ratio of 158:18:1 (molar ratio), with C:N > 11 indicating severe N limitation, and with C:P > 369 and N:P > 32 indicating severe P limitation. Experimental studies confirmed that nutrient supply decreases the C:N:P ratio (i.e., decreases the C:N, N:P, or C:P ratio) in the benthic algal community, with a subsequent increase of benthic algal biomass. Field observations confirmed that highest benthic algal biomass occurs at the optimal C:N:P ratio. However, large variation occurs in the coupling of the C:N:P ratio and benthic algal biomass, indicating that often other factors mask the effect of nutrient supply.

This thesis shows that the regulation of benthic algae is a complex process, where bottom-up and top-down controls play important roles (**hypothesis 3**). Field experiments showed that top-down effects (grazing) and bottom-up effects (nutrient supply) control benthic algal biomass on hard substrate simultaneously, possibly because different patches are regulated differently. Grazing reduced biomass with and without fertilization (**hypothesis 3**), indicating that top-down and bottom-up control might be independent. Top-down effects were larger than bottom-up effects in the experiments, but the comparison of natural communities in lakes of different trophy suggested that benthic algal biomass was bottom-up controlled in the long run. A special case of bottom-up control is the effect of nutrient-releasing substrates. Physical factors such as light, temperature, and wind also control benthic algal biomass, but without a clear pattern.

This thesis shows that benthic algae in lakes benefit from nutrients released by animals (**hypothesis 4**). Benthic algae had a higher N and P content when associated with animal substrates (mussels shells and caddisfly larval gallery) and with mobile macrograzers than with inert substrates, such as stones and rocks (**hypothesis 4**). Nutrients were probably taken up as food by the grazers, excreted as feces, and dissolved as nutrients, and then remineralized into forms available for algae, causing frequent cycling of nutrients in close-coupled algal-animal assemblages, and low benthic algal C:N:P ratios. Nutrient supply by mussels was as important as nutrient supply by macrophytes (**hypothesis 4**). However, improvement of nutrient status by animals was seldom accompanied by a higher biomass, probably because of other factors controlling algal biomass, as for example, the longevity of the substrate. The importance of animal substrate as a nutrient source for attached algae did not decrease with increasing lake trophy (**hypothesis 4**), showing that simple explanations for changes in benthic algal biomass and nutrient status are missing.

8   FUTURE OUTLOOK

More research is needed analyze the causes of the observed enormous variation in nutrient status and biomass of benthic algae in lakes. For example, this thesis showed that the simple explanation of light limitation causing low biomass in eutrophic lakes, and N and P limitation causing low biomass in oligotrophic lakes, does not hold. How then were biomass and nutrient status controlled, and by which factors? A clear bottom-up effect was detected only

under controlled experimental conditions. In natural algal communities, other factors uncoupled algal nutrient status and biomass. One factor that should receive further attention is wind, because wind might have both positive (improving the nutrient status) and negative (sloughing) effects on algal biomass at small as well as large scales. Wind induced underwater currents in particular require more investigations, because not much is known about the effects of currents on benthic algae in a lake. Underwater currents might have caused the observed high horizontal patchiness of benthic algal nutrient status at large scales; but a groundwater impact might also be an important factor, although little is known about flow and nutrient contents of groundwater in the rocky littoral of a lake. In addition, the effect of grazers have been shown to be important both in regulating benthic algal biomass, but also as a nutrient source. A very interesting result of this study was the effect of benthic animals on algal C:N:P ratio. Are the nutrients excreted by benthic animals and the ratio of N and P in the excretions as important for a benthic algal population in an entire lake as the excretions of zooplankton for phytoplankton?

The use of multivariate analysis and modeling can help to analyze the relative importance of different abiotic and biotic factors on the regulation of benthic algal biomass and nutrient status. Multivariate analysis should use field data for the distribution of benthic algal nutrient status and biomass under a variety of different conditions (e.g. Pan *et al*. 1999, Kingston, 1983 #1108). Using models, it is possible to manipulate factors that might control algal biomass, and to watch and compare outcomes, even while the model is in process (e.g. McIntire *et al*. 1996, Biggs *et al*. 1998a, Biggs *et al*. 1998b). Still, experiments are needed to control *in situ* to empirically test the results of both multivariate analysis and modeling. In general, more knowledge is needed not only about the factors regulating benthic algal biomass and nutrient status, but also about causes resulting in the observed patchiness.

Future investigations should treat benthic algae in lakes as patchy, and not as homogeneously distributed random variation. The occurrence of patchiness can alter, for example, top-down effects if the grazers are smart enough to detect patches with high quantity or quality of food (see Power 1992, Nisbet *et al*. 1997). There are many fascinating paths to pursue for a better understanding of the ecosystem of a lake.

9 DEUTSCHE ZUSAMMENFASSUNG (GERMAN SUMMARY)

Ich habe in dieser Studie Biomasse und Nährstoffstatus (Vorhandensein von Phosphor- oder Stickstofflimitierung) von Aufwuchsalgen in Seen untersucht unter besonderer Berücksichtigung der horizontalen Verteilung. Untersuchungsobjekte waren Algen wachsend auf Stein und Algen auf lebenden Substraten wie Pflanzen, Muscheln und Gehäusen von seßhaften Köcherfliegenlarven.

Diese Doktorabeit zeigt, daß Biomasse und Nährstoffstatus von Aufwuchsalgen in Seen ungleichmäßig verteilt sind (so genannte 'Patchiness') über kurze und lange Distanzen und daß auch deutliche Unterschiede vorkommen zwischen unterschiedlichen Substraten, Wassertiefen, Tagen, Jahreszeiten und Jahren. Biomasse schwankte am meisten, gefolgt von Phosphorgehalt in den Algen. Stickstoffgehalt variierte am geringsten. Horizontale Patchiness machte einen höheren Teil der Gesamtvariation von Biomasse und Stickstoffgehalt aus als zeitliche Unterschiede. Zeitliche Schwankungen waren deutlicher im Phosphorgehalt. Die Patchiness der Aufwuchsalgen unterschied sich nicht zwischen verschiedenen Substraten oder Seen, war aber geringer in vier Meter Tiefe, da Aufwuchsalgen in dieser Tiefe gleichmäßiger über den ganzen See verteilt waren als Algen in flacherem Wasser. Die ungleichmäßige Verteilung des Nährstoffstatus der Aufwuchsalgen in einem See zeigte, daß verschiedene Stellen im See unterschiedlich reguliert waren. Zum Beispiel kamen Nährstofflimitierung und Nährstoffüberschuß mit einem Abstand von nur 10 m vor. Das Vorkommen dieser Patchiness erfordert Probennehmen an mehreren Stellen im See mit einem Abstand von mehr als einem Kilometer dazwischen. An jeder Stelle müssen wiederum von mehreren Punkten Proben genommen werden, um die gesamte horizontale Variation von Algenmasse und -nährstoffstatus zu erfassen. Nur in vier Metern Tiefe können weniger Stellen untersucht werden und statt dessen mehrere Proben an einem Platz genommen werden.

Diese Doktorabeit zeigt, daß C:N:P Quoten (Kohlenstoff : Stickstoff : Phosphor) einer Algenmatte den Nährstoffstatus von Aufwuchsalgen in Seen widerspiegeln. Eine Zusammenstellung von Literaturwerten von natürlichen Aufwuchsalgengemeinschaften ergab eine optimale Quote von 158:18:1 (Anzahl der Moleküle). War der Stickstoffgehalt einer Algenmatte zu niedrig zum Wachsen, stieg die C:N Quote auf über 11 und die N:P Quote sank auf unter 12. War der Phosphorgehalt zu niedrig, stieg die C:P Quote auf über 369 und die N:P Quote auf über 32. Experimente bestätigten, daß eine Nährstoffzufuhr die C:N:P Quoten in der Algenmatte senkt und die Algen dann eine deutliche Biomassezunahme durch bessere Wachstum zeigen. Beobachtungen an natürlichen Aufwuchsalgen zeigten ebenfalls, daß die höchsten Algendichten gemessen werden wenn C:N:P Quoten optimal sind. Häufig kann man jedoch umgekehrt nicht von den C:N:P Quoten auf die Biomasse schließen, das bedeutet, daß der Effekt von ausreichend Nährstoffen in der Algenmatte nicht unbedingt in höhere Biomass umgesetzt werden kann, weil andere Faktoren dies verhindern.

Diese Doktorabeit zeigt, daß die Kontrolle der Biomasse von Aufwuchsalgen kompliziert ist. Nährstoffe spielen eine zentrale Rolle, wenn zu wenig Nährstoffe vorhanden sind, ist die Biomasse gering. Ebenso spielen Weidegänger, also Tiere welche Algen vertilgen, eine große Rolle. In Experimenten konnte gezeigt werden, daß sowohl Weidegänger als auch Nährstoffzufuhr die Algenmasse einer kleinen Fläche gleichzeitig kontrollierten, möglicherweise weil einige Algenflecken abgeweidet wurden währden andere durch Nährstoffzufuhr wuchsen. Die Weidegänger verminderten die Algenmasse nicht stärker, wenn die Algen durch Düngung stärker wuchsen, was zeigt, daß beide Effekte unabhängig voneinander auf die Algen wirkten. Die Verminderung der Algenmasse durch Weidegänger war in den Experimenten stärker als das Ansteigen der Biomasse durch Nährstoffzufuhr, jedoch zeigten Vergleiche zwischen verschiedenen Seen mit unterschiedlichem Nährstoffgehalt, daß die Nährstoffzufuhr letztendlich über die Aufwuchsalgenbiomasse in Seen entscheidet. Licht, Temperatur, Wind, und die Eutrophierung eines Sees kontrollieren Aufwuchsalgen ebenfalls, jedoch ohne ein klares Muster.

Diese Doktorabeit zeigt, daß Aufwuchsalgen Nährstoffen aufnehmen welche durch Weidegänger oder Muscheln ausgeschieden werden. Aufwuchsalgen auf Muscheln und Köcherfliegengehäusen enthielten mehr Stickstoff und Phosphor als Algen auf Stein. Aufwuchsalgen enthielten auch mehr Stickstoff und Phosphor wenn sie im Experiment mit Weidegängern in Kontakt kamen. Die Nährstoffe waren vermutlich von den Tieren in Form von fester Nahrung aufgenommen worden, dann als Fäkalien oder lösliche Stoffe abgegeben worden, und in eine lösliche Form überführt worden, welche die Algen dann aufnehmen konnten. Die Nährstoffzufuhr durch Muscheln war fast so wichtig wie eine Zufuhr durch Schilf, welches ebenfalls Nährstoffe an die aufwachsenden Algen abgibt. Trotz besserer Nährstoffversorgung hatten die Algen auf Muschelschalen und Schilf jedoch keine höhere Biomasse als solche auf Stein, die Biomasse war sogar geringer. Möglicherweise haben Algen auf Stein einfach längere Zeit eine hohe Biomasse zu etablieren, da die untersuchten Muscheln nur drei Jahre alt werden und Schilfrohr sogar nur ein Jahr. Die Zufuhr von Nährstoffen, entweder experimentell übers Wasser oder natürlich durch Muscheln und Schilf, war entgegen aller Erwartung nicht am wichtigsten wenn die Nährtsoffkonzentration im See am geringsten war, auch dies zeigt, daß einfache Erklärungen nicht ausreichen um die Schwankungen von Aufwuchsalgenbiomasse zu deuten.

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