Biomass patterns in boreal-subartic lake food webs along gradients of light and nutrients

Gustaf Thomsson

Department of Ecology and Environmental Science
Umeå University
Umeå 2015
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Abstract

There is large natural variation in light and nutrient conditions across lakes. In the boreal-subarctic region most lakes are small, shallow and nutrient poor. In such lakes there is often sufficient light to support primary production at the lake bottom. An expectation for the future is that colored dissolved organic matter (cDOM) of terrestrial origin will increase in these lakes. cDOM depresses the underwater light climate but is often associated with elevated pelagic nutrient concentrations.

A dynamical model of a coupled benthic-pelagic food web was explored for how lake ecosystems might respond to altered light and nutrient regimes. The model predicts that mobile carnivores (fish) control grazers and release primary producers from grazing pressure. Primary producers are therefore limited by their resources and cross-habitat interactions are dominated by spatially asymmetric competition for light and nutrients. At high light and low nutrient supply benthic algae out-compete pelagic algae for nutrients diffusing from the sediment, whereas pelagic algae shade out benthic algae at lower light and/or higher nutrient supply. Biomass patterns of benthic and pelagic consumers follow the patterns of primary production. In contrast, habitat coupling through carnivore movement has only a weak impact on biomass patterns in the model food web.

Model predictions were compared with data from boreal-subarctic lakes covering a broad range of cDOM concentrations. In agreement with model expectations the following relationships with increasing light attenuation were observed: benthic primary and secondary production decreased, pelagic primary production showed a unimodal trend, and pelagic nutrient concentrations as well as the proportion of fish feeding in the pelagic habitat increased. As a consequence, both primary and fish production were negatively related to pelagic nutrient concentrations across lakes.

In a comparative study of boreal-subarctic lakes covering a broad range of cDOM concentrations, a similar negative relationship was found between pelagic total nutrient concentrations and the biomass of epilithic algae. This was surprising, because epilithon cannot access nutrients from the sediment. Patterns in epilithon biomass were largely driven by nitrogen fixing cyanobacteria, which in turn were positively related to light supply. The data suggest that nitrogen fixing autotrophs may have a competitive advantage over other epilithic primary producers in low-cDOM, low-nutrient, high-light environments, and that patterns in epilithic biomass, nutrient sequestration and elemental stoichiometry depend upon which functional group is dominant in the epilithic biofilm.
List of papers

This thesis is a summary of the following two articles, which are referred to by their roman numerals.

I. Diehl S., Thomsson G., Wickman J., Vasconcelos F.R., Uszko W., Ask J., Karlsson J. and Byström P. Resource and consumer control of cross-habitat trophic interactions in shallow lakes. manuscript

II. Thomsson G., Diehl S., Kahlert M., Karlsson J. and Liess A. Inverse relationship of benthic algae and pelagic phosphorus in unproductive lakes: roles of N₂ fixers and light. manuscript
**Author contributions**

**Paper I.**

SD conceived the study and developed and parameterized the model, with input from GT, JW and WU. GT and JW wrote the computer code with input from WU. GT performed all numerical simulations and produced the data figures. SD verified numerical simulations. PB, JA, FV, WU and JK contributed unpublished data. GT and SD analyzed data. SD wrote the article using extensive draft material produced by GT. All authors gave input on the manuscript.

**Paper II.**

GT and AL conceived the study and the sampling design. GT did most of the sampling, sample processing and water and seston chemical analyses. MK performed the microscopic analyses and calculations of algal biovolume. GT analyzed the raw data with input from AL, JK and SD. SD, GT and JK conceived, and GT performed the statistical analyses. GT and SD wrote the manuscript with input from all authors, especially AL.
**Introduction**

Primary production in lakes is fundamentally dependent on light and nutrients. The supply of light and nutrients is in turn related to the input of dissolved and suspended matter (nutrients, dissolved organic matter, clay etc.) (Thomas 1997), lake morphology (e.g. depth profile; Wetzel 1992) and internal nutrient recycling (MacIntyre et al. 1999). Until recently it has been widely held that primary and secondary production are limited by phosphorus in most freshwater environments (Schindler 1977, Sterner 2008). Even so it has recently been discovered that whole-lake production of both algae and fish is negatively correlated with total phosphorus over a relatively narrow TP gradient in low-productive boreal-subartic lakes (Karlsson et al. 2009). It has also been shown that the light environment is important for benthic algal growth (Hill et al 2008).

This thesis is concerned with a further exploration of trends in how biomass and production in shallow lakes are related to variation in the supply with light and nutrients and the investigation of underlying mechanisms. Special emphasis has been put on the interplay between benthic and pelagic processes and on how the biomass of benthic algae is related to light and nutrient conditions as driven by variation in colored dissolved organic matter (cDOM).

**Resource limitation of primary producers**

Pelagic primary production is often co-limited by nutrients and light. The upper part of a lake’s water column is generally exposed to relatively high radiation while it often holds relatively low nutrient concentrations. The opposite is true for the lower part of the water column, where the light is attenuated because of absorbance and scatter in the overlaying water column. Hence primary production is often nutrient limited in the upper part of the water column but is often light limited in the lower part of the water column (Brauer et al 2012). The nature of the limiting nutrient may vary between systems. A vast number of studies have shown that pelagic primary production is mainly limited by phosphorus (Schindler 1977, Sterner 2008). Even so other research has shown that primary production in boreal-subartic lakes tends to be limited by nitrogen (Bergström et al. 2005, Elser et al. 2009).

Benthic algae can be associated with lake sediment (epipelon) or be attached to hard substrates (epilithon). Epipelon intercepts the nutrient directly from
the sediment. As so epipelon is not nutrient limited but rather limited by light reaching the bottom of the lake (Vadebonccouer 2000). The limitation of epilithon is far less clear. Epilithic algae have no direct access to nutrients in the sediment but are typically associated with shallow littoral environments where light is relatively abundant. They have access to nutrients recycled within the biofilm layer (Riber et al 1987). Fertilization experiments with nutrient-diffusing substrates in a Canadian Shield lake have shown that epilithic growth can increase with increasing phosphorus concentration (Frost et al. 2002). A comparative lake study from Sweden provided evidence that epilithon in boreal lakes tended to be nitrogen limited at high latitude and phosphorus limited at decreasing latitude (Liess et al 2009).

**Benthic-pelagic coupling**

Habitat coupling is typically caused by passive flow of resources and active movement of consumers between habitats (Schindler & Scheurell 2002, Genkai-Kato et al. 2012). In lake ecosystems light gets filtrated through the pelagic zone before it reaches the benthic habitat. Limiting nutrients could reach the pelagic zone of lakes either as surface flow from the catchment or through diffusion from the lake sediments. Thus, primary producers in the pelagic zone could control the level of light reaching the bottom of the lake, while benthic primary producers could regulate the concentration of nutrients diffusing from the sediment into the water column. This relationship makes primary producers in the pelagic and benthic zones competing for light and nutrients in a spatially asymmetric way (Jäger et al. 2014).

A classic benthic food web consists of benthic algae, macroinvertebrates and fish as top consumers. The macroinvertebrate grazes on benthic algae and is turn fed upon by the top consumer. In a pelagic food web the top consumer is often a fish preying on zooplankton, which in turn feeds on phytoplankton. Top consumers such as fish could be specialized on prey in either the benthic or the pelagic zone but many fish species feed in both the benthic and the pelagic zones and move readily between them (Schindler & Scheurell 2002).

Even though a large amount of research has been devoted to how nutrient and light supply affect lake ecosystems, most studies have focused on either the benthic or the pelagic food web. Yet, because benthic and pelagic habitats are linked through both the passive transport of resources (nutrients, light) and through movement by top consumers, the dynamics of these two food webs are coupled. It is therefore of interest to understand the relative importance of these links and how they affect the biomass patterns in lake
ecosystems. In this thesis it was focused on how the dynamic coupling of benthic and pelagic food web in conjunction with variation in light and nutrient supply affects patterns in production and biomass of primary producers and consumers in the two habitats.

**Light and nutrient environment in boreal subarctic lakes**

Boreal and subarctic lakes are relatively nutrient poor. In these lakes nitrogen deposition and total phosphorus concentrations are fairly low while the concentration of dissolved organic carbon (DOC) varies widely from lake to lake (see paper II). In the clearest nutrient poor lakes a large part of the incoming light can reach the bottom, while in lakes with higher dissolved organic carbon concentration a large fraction of the light is attenuated on the way to the benthic habitat (Karlsson et al. 2009). Both decreased light supply and increased nutrient supply can shift a lake’s food web from dominance of benthic to dominance of pelagic pathways of energy flow. In shallow clear water lakes at high latitudes the majority of the whole-lake production is derived from the benthic habitat (Vadeboncoeur et al. 2003). In contrast, lakes that receive high loading of DOC or high nutrient input through surface inflow are often dominated by pelagic production (Hansson 1992, Ask et al. 2009a).

Dissolved organic carbon can act as driver for the light environment and is also often associated with an increased nutrient concentration across lakes (Seekell et al. 2015). Because DOC is such an important driver of light and nutrient conditions in boreal-subarctic lakes, this thesis studies the importance of DOC as a potential driver of biomass patterns with a special emphasis on benthic producers.
Materials and methods

Food web model

Paper I explores how light and nutrient supply can influence the dynamics within a food web where benthic and pelagic habitats are coupled through flow of resources and via movement of top consumers. To investigate these patterns, the algal resource competition model described by Jäger and Diehl (2014) was extended with predation of grazers and carnivores. To facilitate conceptual understanding of the system dynamics and to simplify the interpretation of results, a highly simplified, one-dimensional spatial structure of the two habitats was assumed (see figure 1). In the model the pelagic habitat is located on top of the benthic habitat, which in turn is situated on top of the sediment surface. Light enters the system through the surface of the pelagic habitat and the nutrient enters the system both through surface flow to the pelagic habitat and through diffusion from the sediment into the benthic habitat (see figure 1). The movement of fish between the two habitats is assumed to be more or less adaptive. Highly adaptive fish react instantly to shifts in food availability and choose to be in the more profitable habitat. Less adaptive fish are slower in their response and tend to spend most of their time in the habitat which has the largest volume. Among other parameters it was investigated what consequences different fish behaviors may have for the whole food web. Literature data were used to provide an initial baseline parameterization of the model.

Model analyses

To explore the influence of light and nutrient supply on biomass patterns in the model food web the model was run to equilibrium over large ranges of background light attenuation (mimicking shading by colored DOC) and sediment nutrient concentration. To explore the generality of the resulting patterns I ran 1000 model iterations where consumer parameters were collected randomly from 10-fold intervals. For a comparison of model predictions to data I selected model output representative of lakes with relatively low sediment nutrient content but with highly variable background light attenuation. This model output was subsequently compared to data collected from lakes along a gradient in DOC loading in the boreal-subarctic region of Sweden (Karlsson et al. 2009).
Figure 1. One dimensional habitat arrangement (a) and food web structure (b) assumed by the model. $A$ stands for pelagic algae, $Z$ for pelagic grazer, $B$ benthic algae, $G$ for benthic grazer, $C_{pel}$ and $C_{bent}$ for top consumer in pelagic and benthic habitats, respectively. $R_{surf}$ is the inorganic nutrient in the surface flow, $R_{pel}$ the limiting inorganic nutrient in the pelagic habitat and $R_{bent}$ the limiting inorganic nutrient in the benthic habitat and $R_{sed}$ is the inorganic nutrient in the sediment. $I_0$ is the incoming light to the water surface, $I_{z,\text{max}}$ is the light reaching the top of benthic habitat and $I_{z,\text{sed}}$ is the light reaching the bottom of the benthic habitat. Solid lines represent flow of energy within respective habitat while broken lines represent flow of energy/nutrients between habitats.

Comparative study of epilithic biofilms

To investigate how biomass and stoichiometry of benthic primary producers are related to light and nutrient conditions I collected epilithic biofilms from littoral lake environments. In total 20 lakes located at latitude 68°27' to 59°49' were sampled on three occasions during 2010-2011. Lakes were chosen to cover a large DOC gradient. There was a four-fold difference in atmospheric nitrogen deposition between the lakes (100 to 450 mg m$^{-2}$ yr$^{-1}$). Dissolved organic carbon ranged 14-fold (2.2 to 29.6 mg L$^{-1}$) and total phosphorus ranged 20-fold (2-40 µg L$^{-1}$). In each lake I collected samples for periphyton and lake water chemistry (DOC; total nitrogen, TN; total phosphorus, TP) and measured vertical light attenuation. On each sampling
occasion epilithic biofilm was taken at five littoral sites, where five stones were collected and pooled together. These samples were used to determine elemental composition, taxonomic/functional composition and biovolume of benthic algae. The data was then averaged over the growing season. To investigate how biovolume and elemental stoichiometry of benthic algae were related to the physiochemical environment we used simple and multiple linear regression with lake water nutrients (TN, TP) and light attenuation as explanatory variables, and biovolume of benthic primary producers as well as epilithic elemental composition as response variables.

Results and discussion

Dynamics of the model food web and comparison with data

How food webs respond to altered light and nutrient condition is to a high degree dependent on their trophic structure. For instance primary producers in a food web with one trophic level are often controlled by their resources (e.g. light and/or nutrients) while in a two-trophic level food web the primary producer could be controlled by grazing. In our model we varied the trophic structure of the food web to see how it responded to altered supply with light and nutrient. As an inherent condition of our model benthic and pelagic primary producers could not survive above a certain level of background light attenuation. This condition did not change with trophic structure of the food web. With that said we can compare how the existence boundary of primary producers changed with both the trophic structure of the food web and with variation in light and nutrient supply.

In a food web with one trophic level benthic and pelagic primary producers are coupled through their resources. When background light attenuation is high pelagic primary producers dominate the system. With increasing nutrient concentration in the sediment and increasing background light attenuation pelagic producers reach high enough densities to shade out benthic producers. While benthic producers are outcompeted under low light climate and high concentration of nutrient in the sediment, benthic producers intercept the nutrient leaking from the sediment under high light conditions, leading to that less nutrient reaches the pelagic zone and resulting in a depressed density of pelagic primary producers.

In a food web with two trophic levels primary producers are controlled by grazers. Because of the grazing pressure primary producers are held at low constant levels resulting in that pelagic producers cannot reach high enough
abundances to out-shade benthic producers. This leads to that benthic producers can exist over a larger range of light and nutrient supply. Yet, benthic primary producers are kept at low densities by their own grazers, which in turn leads to that more nutrients are diffusing from the sediment to the pelagic zone where they stimulate pelagic primary production. Thus, pelagic and benthic grazers act as indirect mutualists that release each others food from resource limitation.

In a food web with three trophic levels where the habitat choice behavior of the top consumer is highly adaptive the grazing pressure on primary producers is released. Top consumers control the density of grazers which in turn do not reach high enough abundance to control the primary producer. Instead primary producers are limited by their resources and their existence boundaries are close to the ones seen in a one-trophic level food web. Due to nutrient competition from abundant benthic producers, pelagic primary producers are held at low densities under high light conditions. These densities are not sufficient to support pelagic consumers. Therefore pelagic grazers and carnivores can only exist under relatively low light supply when pelagic producers are released from nutrient competition by benthic producers. Under these conditions pelagic producers out-compete benthic producers.

A general pattern that was seen in our model is that resource competition between benthic and pelagic producers rather than coupling through movement of top consumers explains the overall biomass patterns in the ecosystem. A system where top consumers cannot move between habitats (i.e. where benthic and pelagic top consumers are separate populations) exhibits close to identical biomass patterns as the system where top consumers can adaptively choose in which habitat to feed.

When background light attenuation increases, a large part of the benthic production will get lost and the ecosystem will shift from benthic to pelagic processes. We compared our model with field data from boreal-subarctic lakes that covered a broad gradient in colored dissolved organic matter. For comparison we chose a model transect along the full range of background attenuation while holding the concentration of nutrient in the sediment fixed at 0.05 g P / m$^3$. This concentration was close to what has been seen in field data from subarctic lakes.

The data produced from the model were largely consistent with data collected in field. For instance benthic primary production and the biomass of benthic grazers and carnivores decreased with decreasing light supply both in the model and the data. In the model, pelagic production and the
biomasses of grazers and carnivores showed a unimodal trend with decreasing light supply. In the field data similar, but less distinct trends were seen for pelagic producers and carnivores, while pelagic grazers only showed an increasing trend with decreasing light supply. As predicted by the model, total primary production and total biomass of carnivores decreased with increasing light attenuation, whereas the proportional use of the pelagic habitat by fish increased.

Production terms were also related to the total nutrient concentration in the pelagic habitat. In both the model and the lake data total (= benthic + pelagic) primary production and fish production were negatively related to total nutrient concentration in the water column. In the model, the mechanism behind these correlations is that high background attenuation reduces benthic (and total) primary production and consequently also fish production, but increases the leakage of nutrients from the sediment to the pelagic habitat. To which extent this mechanism also operates in the study lakes remains to be investigated. Because background attenuation in boreal-subarctic lakes is primarily driven by cDOM supply, it is likely that nutrients bound to cDOM contribute to the negative relationship between production and pelagic nutrient concentrations in the study lakes.

**Comparative study of epilithic biofilm**

Shallow, nutrient-poor clear water lakes have been shown to be dominated by benthic processes (Ask et al. 2009b). With this in mind we studied how biomass, stoichiometry and functional groups of epilithon (periphyton on rocks) shifted along a boreal-subarctic cDOM gradient. The light supply in these lakes was negatively correlated with the concentration of dissolved organic carbon (DOC), while pelagic total nitrogen (TN) and total phosphorus (TP) were positively correlated with DOC. These cross-correlations make it difficult to draw conclusive inferences on the impact of light, phosphorus and nitrogen supply on epilithic algae. Still, a number of interesting patterns emerged that suggest novel hypotheses.

In a multiple regression analysis we found that the biomass of epilithon was negatively related to TP but positively to TN when the relationship to phosphorus was accounted for. This suggests that nitrogen rather than phosphorus was the more strongly limiting element for epilithic producers in the study lakes. In line with this nitrogen fixing cyanobacteria made on average up c. 60% of epilithic biovolume. The correlation patterns of epilithic
total biovolume with environmental variables were therefore to a large degree driven by nitrogen fixing cyanobacteria.

With increasing water clarity both total periphytic N and the biovolume of nitrogen fixing bacteria increased. It can therefore be suggested that nitrogen fixing cyanobacteria disproportionally benefit from increased light supply and then more than compensate for the low availability of dissolved nitrogen by assimilating atmospheric nitrogen, which leads to high periphytic N sequestration in nutrient-poor, clear lakes. Overall, nitrogen fixing cyanobacteria also showed a strong positive correlation with light supply and an even stronger negative correlation with pelagic total phosphorus. As so it could be argued that epilithon was mainly limited by light but not by phosphorus. Nitrogen fixing cyanobacteria were also strongly positively correlated with periphytic carbon, and periphytic C:P and N:P ratios increased with increasing proportional contribution of nitrogen fixing cyanobacteria to total epilithic biomass. Hence environmental conditions that increase the relative contribution of nitrogen fixing cyanobacteria to total periphytic biomass could alter the elemental stoichiometry of epilithon and partly explain how epilithon responds to altered light and nutrient conditions.

**Concluding remarks**

The model of a coupled benthic-pelagic food web developed in paper I can serve as a useful tool for exploring how altered light and nutrient conditions affect the relative importance of benthic and pelagic processes in lakes. For instance increased runoff of allochtonous colored dissolved organic matter increases light attenuation in the water column which, beyond some critical threshold, can strongly depress benthic production. Similarly, increased loading of the pelagic habitat with nutrients from the surrounding catchment will stimulate pelagic production and thus shade the benthic habitat. Hence increased runoff of allochtonous dissolved organic matter and/or nutrients can shift a lake ecosystem from being dominated by benthic processes to become dominated by pelagic production. The shift could also lead to a depressed whole-lake primary production and in the end suppress the production and biomass of fish.

Predictions from the model are qualitatively largely compatible with patterns of production and biomass observed in lakes covering a broad DOC gradient. Yet, the model makes some simplifying assumptions that should be relaxed in future work. For example, the model assumes a lake of uniform depth. A more realistic assumption would be to incorporate a gradually sloping bathymetry including both shallow and deep lake areas. This would likely
lead to a smoother transition between benthic and pelagic processes along gradients in light-nutrient supply. In our model pelagic producers out-compete benthic producers at fairly low levels of background attenuation. In a model with more realistic lake morphology I would expect that benthic producers persist in very shallow lake habitats even when light attenuation is strong. This suggests that benthic and pelagic producers could coexist over a larger light-nutrient supply space when a more realistic lake bathymetry is assumed.

We also assumed that the coupling of benthic and pelagic habitats by carnivores is driven by foraging decisions of individuals that are free to choose either habitat and are only constrained by the accuracy of their foraging decisions. However, the most prominent habitat couplers in lakes are fish, many of which go through pronounced ontogentic diet and habitat shifts during their life cycle. A very interesting and relevant scenario to explore in the future would therefore be to include ontogenic shifts in fish feeding behavior.

We also compared lakes along a cDOM gradient to explore how associated light and nutrient conditions are related to epilithic biofilms. In general it was seen that the biovolume of epilithic primary producers was positively correlated with both light supply and to some degree with total pelagic nitrogen concentration. The data suggest that epilithic nitrogen fixing cyanobacteria benefit strongly from a combination of high light and low pelagic nutrient supply, which paradoxically leads to epilithic carbon, nitrogen and biovolume being highest in the most nutrient-poor lakes. Many key environmental factors were, however, correlated across lakes. As a consequence it is difficult to convincingly infer causality. Even so the study gave a plausible picture and suggests hypotheses for underlying mechanisms that could be tested in the future. To explore these mechanisms properly it could be of interest to use mesocosm studies where environmental factors are manipulated independently.
References


Thanks!

First of all I would like to thank Antonia Liess for giving me the opportunity to work in science. I also want to thank Sebastian Diehl for encouraging debates, for his patience and for showing interest in my early work. I am also grateful to Sebastian for supervising me during the later part of my thesis work and for evoking my interest in modelling. Jan Karlsson has been a good mentor and helped me out when needed.

I would not have been able to conduct my field study without help from Junwen Guo, Fernanda Miranda and Anne Deininger. Especially I want to thank you for all your hard work and for keeping a good mood even during late hours. Thanks to you my field season felt as a long holiday.

Jonas Wickman has been a source of inspiration and helped me out when I got stuck in matlab. I appreciate your patience and I am grateful for the pedagogic way you introduced me to modelling.

Wojciech Uszko and Francisco Vasconcelos have been of great support and have always been up for good scientific discussion. Thank you for good discussions and for giving me advice regarding both modelling and statistical analyses.

I am also grateful to the staff at CIRC and Erken Laboratory who supported me with accommodation and with facilities where I could run laboratory analyses during my field work.

Thanks to Daniel Karlsson for good conversations and for letting us share your accommodation in Abisko.

I also want to thank my family. Without you I would not have been able to make it this far. I am also grateful for your patience, for inspiring me and for always believing in what I am doing.