Food web dynamics in open and closed systems

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AKADEMISK AVHANDLING

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Abstract

Most food webs in nature are open, and influenced by processes outside the focal habitat. The impact of an allochtonous subsidy on the dynamics in the recipient food web depends both on the trophic role of the recipient, and on heterogeneity within trophic levels. Heterogeneity within trophic levels allows for compensatory responses, as a decrease in one species can be compensated by an increase in another species at the same trophic level.

This thesis is a summary of enclosure and microcosm experiments that aimed to study the impact of allochtonous subsidies on food web dynamics in a heterogeneous food web. In the enclosure studies, a three trophic level littoral food web was used. The predator in the food web, young of the year (YOY) perch, can potentially affect two pathways in the in the food web, connected to the two growth forms of primary producer; phytoplankton and periphyton, and the associated herbivores to each of them; filtering and scraping herbivores. Manipulation of the openness for the different trophic levels to utilize the adjacent habitat showed that the inflow of phytoplankton and cross-habitat foraging by the herbivore level reinforced the compensatory response between the two growth forms of primary producers. Allowing YOY perch to utilize the adjacent habitat did not, however, affect the interactions within the food web, as the predation risk imposed by top predators in the adjacent natural lake habitat restricted the YOY perch to the littoral habitat.

In the microcosm experiment, the response of an herbivore food web and a microbial community to inflow of resources and food web configuration was studied, using a model littoral food web. The model food web consisted of two forms of primary producers, i.e. phytoplankton and periphyton, and two herbivores, i.e. *Daphnia pulex* feeding on phytoplankton, and *Chydorus sphaericus* feeding on both periphyton and phytoplankton. Three different food web configurations, all having the phytoplankton and periphyton, but either one of the herbivores, or both, were set up. The flow regimes consisted of an open treatment receiving a constant supply of phytoplankton, and a closed treatment with an initial resource pool, but no additional external input. The effect of the inflow of phytoplankton on the other organisms in the food web was clearly affected by the food web configuration. In the presence of *D. pulex*, the inflow of phytoplankton was made accessible to periphyton, and indirectly to *C. sphaericus*, which increased to such high densities that *D. pulex* was negatively affected. The inflow of phytoplankton had an indirect negative effect on the microbial community, since the biomass of herbivores increased, which imposed a higher grazing pressure on all parts of the microbial community.

Key words: Allochtonous input, cross-habitat foraging, donor control, heterogeneity within trophic level, compensation, food web, littoral

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This thesis is a summary and discussion of the following papers that will be referred to in the text by their Roman numerals.


II. Lövgren, J. Allochtonous input and cross-habitat foraging: impact on trophic interactions in a littoral food web. Submitted manuscript

III. Lövgren, J., Bertolo, A. and Persson L. Flexible behavior at different trophic levels: impact on trophic dynamics in a littoral food web. Manuscript

IV. Lövgren, J. Reinikainen M. and Persson L. Allochtonous input and trophic level heterogeneity: impact on an aquatic food web. Submitted manuscript

V. Reinikainen, M., Lövgren J. and Persson L. Associations between the microbial community and metazoan grazers as affected by allochtonous resources in aquatic microcosms. Manuscript

Paper I is reproduced with the permission from the publisher.
**Food web dynamics in open and closed systems**

**Introduction**

The basic concept on which a substantial part of the discussion on trophic interactions has focused is the Exploitation Ecosystem Hypothesis (EEH) (Oksanen et al. 1981, Hairston and Hairston 1993, Persson et al. 1996, Persson 1999). EEH in its original form assumes that a food web can be aggregated into a food chain where each trophic level acts as one single unit (Oksanen et al. 1981). The model by Oksanen et al. (1981) predicts that the equilibrium biomass of adjacent trophic levels would be unrelated to each other, whereas trophic levels two steps apart would be positively related to each other with increasing productivity. Although both comparative and experimental evidence suggest that enrichment may lead to patterns predicted by the model by Oksanen et al. (1981) (Wooton and Power 1995, Mazumder 1994, Kauntzinger and Morin 1998, Oksanen and Oksanen 2000), it is commonly observed that adjacent trophic levels respond positively to enrichment (McQueen et al. 1986, Leibold 1989, Hansson et al 1992, Brett and Goldman 1997, Leibold et al.1997, Persson 1997, Mikola and Setälaä 1998). There are several potential mechanisms for why adjacent trophic levels would increase in response to an increased productivity, such as interference among predators (Oksanen et al. 1995) and unstable predator-prey dynamics (Abrams and Roth 1994, see Persson 1999 for additional mechanisms). However, the general explanation for these observation is that heterogeneity within trophic levels (i.e. more than one species at each trophic level) causes consumer induced changes in the

Compensatory responses between organisms within a trophic level are likely to dampen the effects of predators on levels below and thus reduce the strength of a trophic cascade in terms of total density/biomass changes, where a trophic cascade is defined as a change in the biomass of the primary producer, induced by a change of species an even number of links above (Persson 1999).

An important reason for within trophic level heterogeneity is that food webs consist of organisms from different habitats. Furthermore, organisms connect habitats by movements and feeding in the different habitats (Carpenter and Kitchell 1993, Persson et al. 1996, Polis and Strong 1996, Polis et al. 1997, Persson and Crowder 1997). Most habitats and systems in nature are connected to each other, and even systems that seem to be closed are connected to other habitats, and influenced by processes taking place outside the system under study (Polis and Strong 1996, Polis et al. 1997). The connections between habitats can be due to abiotic factors such as wind and water movements that transport nutrients and detritus across habitat borders (Polis et al. 1996, 1997, Barko and James 1997, MacIntyre and Melack 1995). Mobile consumers may also connect habitats both in terms of prey consumption and nutrient translocation (Carpenter et al. 1992, Schindler et al. 1996, Vanni 1996, Jeppesen et al. 1997, Polis et al. 1996, 1997).

Recent papers have argued that input of resources produced outside the focal habitat (allochtonous input or subsidies) are common in a variety
of systems and can be received at any trophic level. Field observations (Power 1990, Polis and Hurd 1995, Polis et al. 1996, Rose and Polis 1998, Sabo and Power 2002a, b, Bustamante et al. 1995, Nakano et al. 1999, Nakano and Murakami 2001), and theory (De Angelis 1980, Polis et al. 1997, Huxel and McCann 1998, Huxel et al. 2002) have shown that the population dynamics can be dependent on the allochtonous inputs to the system, and that effects can propagate through trophic links and indirectly change the abundance of populations other than the recipient species. Theoretical studies suggest that the impact of an allochtonous input are depending on the magnitude of the input and on the trophic level that receives the input (Polis et al. 1996, Huxel and McCann 1998, Huxel et al. 2002). An allochtonous input can in some systems even exceed the total in situ production and decouple consumers from the renewal rate of its prey, resulting in donor controlled consumers (De Angelis 1980, Strong 1992, Persson et al. 1996).

This thesis focused on the impact of allochtonous subsidies on food web dynamics in a heterogeneous food web, and main questions asked were:

i) Do the trophic interactions in a food web differ depending on which trophic level that utilizes the adjacent habitat?

ii) How is the effect of allochtonous input affected by food web configuration?

The experiments conducted in order to answer the above questions were performed at different spatial scales (from aquaria to large sized enclosures in lakes) and with varied number of species at lower trophic levels (two or more). The rationale behind this was that field experiments have the advantage of including many aspects of the complexity of natural systems,
but on the other hand have the disadvantage of making it difficult to control for factors such as the form of the allochtonous input and the structure of the recipient food web. To delineate the effects of these factors, laboratory experiments are useful, as they will allow a high degree of control over both the allochtonous input and the structure of the recipient food web.

**Systems studied: The lake ecosystem**

Lakes are often used as model ecosystems because they are discrete, self-contained ecosystem with clearly defined boundaries, and with identifiable connections with adjacent habitats (Vander Zanden and Vadeboncoeur 2001, Vadeboncoeur et al. 2002, Schindler and Scheuerell 2002). A lake itself is however a complex ecosystem composed of at least three different habitats: the pelagic (open water), the benthic (bottom-associated) and the littoral (shoreline). These habitats have often been studied as distinct ecosystems due to the difference in physical structure, productivity and trophic structure (Lodge et al. 1988, Schindler and Scheurell 2002). Yet, these habitats are coupled in many ways, and for example, it has long been recognized that that the littoral and benthic are linked biogeochemically to the open water of lakes through wind and water movements that translocate nutrients between the habitats (Wetzel 1979, MacIntyre and Melack 1995, Barko and James 1997, Blumenshine et al. 1997). Mobile consumers, like fish and zooplankton, may transport nutrients between habitats in a variety of ways. Vertical and horizontal migrations of zooplankton link the benthic and littoral communities with the pelagic habitat (Vanni 1996, Jeppesen et al. 1997). Fish that feed in one habitat and excrete in another have been
argued to potentially translocate nutrients between all the habitats within a lake (Vanni 1996, Schindler et al. 1996, Vander Zanden and Vadebocoeur 2002). The consequences of the habitat couplings are pronounced. This can be illustrated by fish that induce pelagic trophic cascades, subsidized by benthic and littoral derived resources, which allow them to sustain high population numbers when they have driven their preferred pelagic prey to low densities (Schindler et al. 1996, Vanni 1996, Schindler and Scheurell 2002). A special case of habitat coupling is based on behavioral responses to predators. An example of this type of habitat coupling is when piscivorous fish restrict smaller fish to the littoral vegetated habitats. As a consequence zooplankton increase in the open water habitat, and prey resources in the refuge habitat decrease (Carpenter et al. 1987, Turner and Mittelbach 1990). A similar pattern is when zooplankton are utilizing the vegetated habitat as a daytime refuge from planktivorous fish, but at night migrate out in the pelagic where they control the phytoplankton communities, and thereby truncates the pelagic trophic cascade (Schriver et al. 1995). The above examples show that habitat coupling in lake ecosystems may create situations where the dynamics observed in one habitat may be driven by processes that occur in another habitat (Schindler and Scheurell 2002).

The results and conclusions from paper I-III comes from experimental studies conducted in two adjacent low productive lakes named lake Abbortjärn 2 and lake Abbortjärn 3, situated in central Sweden (64° 29′N, 19° 26 E). The lakes have low humic content and sparse natural vegetation. Both lakes contain perch (*Perca fluviatilis*) and Roach (*Rutilus rutilus*) in addition Lake Abbortjärn 2 also contains pike (*Esox lucius*). Both lakes have been subjected to a structure treatment where 40 % of the circumference was covered with artificial vegetation of a width of 2 m. The mats consisted of 1 m long floating lines anchored to the bottom. The
addition of artificial vegetation increased both the structural complexity and the food web complexity. The artificial vegetation also allowed for the development of a second form of primary producer, i.e. epiphytic algae/periphyton, and the associated consumers, i.e. scraping herbivores.

Food webs studied

The focal food web that I have studied in I-III was a heterogeneous littoral food web consisting of two principal forms of primary producers, i.e. phytoplankton and periphyton, and the herbivores associated with each of them, i.e. filtering herbivores and scraping herbivores (Fig. 1). The periphyton in the experimental lakes grows on a chemically inert substrate and competes with phytoplankton for nutrients in the water column. The predator in the food web young of the year perch, (YOY), (Perca fluviatilis) affects both filtering herbivores and scraping herbivores (Person et al. 2000). The two different pathways are connected at the top (YOY perch) and at the bottom (nutrients).

The aquaria experiment IV, V was in essence a simplified littoral food web where I used single species in each compartment (Fig. 2). The experiment was performed indoors in a light and temperature controlled laboratory environment.

The focus in IV was to study relationships between the organisms presented in (Fig. 2) in V we synthesized data on the microbial community from the experiment in (IV). The microbial community consisted of ciliates feeding on flagellates, which in turn are feeding on bacteria; in addition ciliates are able to utilize bacteria. The cladoceran grazers (D. pulex and C.
sphaericus) could potentially feed on all the organisms in the microbial community.

Fig. 1. The focal food web studied in the lake system was a littoral food web consisting of two primary producers (phytoplankton and periphyton), and the herbivores connected to each of them (scraping herbivores and filtering herbivores). The filtering herbivores consisted mainly of the cladocerans Ceriodaphnia sp., Bosmina sp., and Sida crystalline. The scraping herbivores in our study consisted of benthic cladocerans (Chydorid sp.) and macroinvertebrates (chironomids and trichopterans). The predator in the system was YOY perch.

Fig. 2. The model food web used in the microcosm experiment. In addition to theses experimentally controlled components, we also studied the microbial community that developed during the course of the experiment.
The impact of allochtonous inputs and cross habitat foraging in food webs

Cross-habitat foraging and inflow of resources to consumers may allow the consumer to persist at higher densities than is possible in isolated habitats. Furthermore, the higher consumer densities affect the in situ resources directly, and community structure indirectly, via food web effects (Polis et al. 1997). Potentially, a subsidized consumer can either dampen or reinforce trophic cascades depending on the magnitude of the inflow and which trophic level receives the input (Polis et al. 1997).

The impact of predation in an open littoral food web (I)

The aim of the experiment in I was to study the effect of predation in a heterogeneous food web open for the second trophic level (filtering and scraping herbivores) to potentially be subsidized. (Fig. 3.).
Fig. 3. Graphical representation of the food webs studied in I. Predator (Pred), Filtering herbivores (Filt. H.), Scraping herbivores (Scra.H), Phytoplankton (Phyt) and Periphyton (Peri). The dotted boxes indicate that the organisms were able to move in and out from the enclosures whereas filled boxes indicate that the organisms were enclosed.

We used net enclosures with and without fish in the littoral habitat. The mesh size of the net allowed the flow of phytoplankton, and filtering and scraping herbivores between the enclosures and the adjacent habitat (Fig. 3. A, B). The major results from the experiment were that although YOY perch reduced filtering and scraping herbivores, the top down effect did not cascade down to affect the primary producers. We found no difference in phytoplankton biomass between treatments, despite the large differences in biomass of filtering herbivores. This suggests that the inflow of phytoplankton into the enclosures compensated the loss through grazing by filtering herbivores. The biomass of periphyton was higher in the absence of fish, resulting in a positive correlation between scraping herbivore and epiphytic algae biomass. Our results suggest that the positive indirect effect of nutrient regeneration by filtering herbivores on periphyton was stronger than the direct negative effect of grazing by scraping herbivores. Thus, when a consumer in the food web was subsidized, it had a large impact on the interactions within the food web as the high inflow rate of phytoplankton allowed a large biomass of filtering herbivores in the fish free treatment to sustain. This further allowed a high and constant recycling of nutrients to be utilized by periphyton. The littoral food web that we studied, with two primary producers of different growth forms, enhances the potential for compensatory responses.

*The impact of predation in an open and closed food web (II)*
The results from (I) suggested that the allochtonous subsidy to the second trophic level (inflow of phytoplankton) influenced food web dynamics substantially. The purpose of this experiment was to study if the effect of fish predation differed in a system without exchange of the surrounding water (closed). The experimental set up involved an open system identical to the system in (I) with and without YOY perch (Fig. 3. A, B) and a closed system, consisting of enclosures covered in plastic, with and without YOY perch. (Fig. 4. A, B).

![Food Web Diagram](A B)

**Fig. 4.** Graphical representation of the food webs studied in II. Predator (Pred.), Filtering herbivores (Filt. H.), Scraping herbivores (Scra. H.), Phytoplankton (Phyt.) and Periphyton (Peri.). The dotted boxes indicate that the organisms were able to move in and out from the enclosures, whereas filled boxes indicate that the organisms were enclosed.

The impact of the predation of YOY perch in the open systems was to a large extent in correspondence with (I). The highest biomass of filtering and scraping herbivores was found in the fish free treatment, and correspondingly also the highest periphyton biomass. In contrast to (I), where we found that the biomass of phytoplankton was equal between the fish free and fish treatment, I found in II that the phytoplankton biomass
was lower in the open fish free treatment than in the open fish treatment. This was related to the fact that the biomass of filtering herbivores in II was five times higher than in (I). This higher biomass of filtering herbivores was probably due to filtering herbivores migrating into the enclosures.

The impact of predation by YOY perch in the closed system generally resulted in the same relationship at lower trophic levels between the fish and fish free treatment as in the open treatment. The highest biomass of periphyton was, in correspondence with the open treatment, also found in the closed fish free treatment. The major difference between the open and closed treatments was that the biomass of filtering herbivores did not differ between the closed fish free and fish treatment. This can be related to the fact that an initial high biomass of filtering herbivores in the closed fish free treatment decreased the phytoplankton to low levels, and that the closed design disabled inflow of phytoplankton and migration of filtering herbivores, which might have allowed a high biomass of filtering herbivores to persist. The higher biomass of periphyton in the closed fish free treatment, however, suggests that the initial higher biomass of filtering herbivores resulted in an overall higher positive indirect effect of filtering herbivores on periphyton growth in the closed fish free treatment than in the closed fish treatment.

The overall highest biomass of periphyton was found in the open fish free treatment, suggesting that the compensatory increase in one of the primary producers (periphyton) was reinforced in the open treatment, due to the potential for inflow of phytoplankton produced outside the habitat, and cross habitat foraging by filtering herbivores.
Impact of behaviorally induced habitat shifts on food web dynamics (III)

The impact of adjacent habitats can include more than allochtonous subsidies, as the presence of top predators in a specific habitat can induce prey to shift to low predation risk habitats, in turn inducing strong cascading effects both in non refuge (Carpenter et al. 1987) and in the refuge habitat (Power et al. 1989). The aim of this experiment was to study how the food web interactions in the open littoral food web studied in (I, II) (Fig 3.A, B) was affected by allowing the third trophic level (YOY perch) to flexibly utilize both the adjacent and the habitat under study. In one of the treatments that allowed flexible habitat use by YOY perch, we included two top predators, pike and perch, in the vegetation (Fig. 4. A, B.).

Fig. 5. Graphical representation of the food webs studied in III. Top predator (Top P), Predator (Pred.), Filtering herbivores (Filt. H.), Scraping herbivores (Scra. H), Phytoplankton (Phyt.) and Periphyton (Peri.). The dotted boxes indicate that the organisms were able to move in and out from the enclosures, whereas filled boxes indicate that the organisms were enclosed.
The major result from this study was that the biomass of lower trophic levels (herbivores and primary producers) was similar in the treatment where YOY perch was enclosed and the treatments where YOY perch was able to flexible habitat choice. The similar effects on lower trophic levels suggest in turn that YOY perch utilized the vegetated habitat extensively to avoid predation in the pelagic habitat. Additionally, it suggests that the predation risk in the pelagic was higher than the predation risk imposed by the top predators enclosed in the vegetation, which in turn could be related to the low efficiency of the top predators in structurally complex habitats (Christensen and Persson 1993). The compensatory response between the two growth forms of primary producers found in (I) and (II) was also present in this study, as we found a higher biomass of periphyton in the treatment without YOY, together with a high biomass of filtering herbivores.

Our results further suggest that the impact on food web dynamics by allowing the third trophic level (YOY perch) to utilize the adjacent habitat, did not change the dynamics compared to when the YOY perch was restricted to the focal habitat due to a high predation risk in the adjacent habitat.

Allochtonous input and food web configuration

A donor controlled consumers can increase to densities higher than if supported by in situ production, and inflict a large top down effect on in situ
prey (Polis et al. 1996, 1997). The overall food web effect by the allochtonous input depends on both the configuration of the recipient food web and the trophic role of the allochtonous input (Polis et al. 1997). Previous experiments have shown that food web configuration and within trophic level heterogeneity can have substantial effects on patterns of trophic biomass in response to an increased in situ productivity (Hansson et al. 1998, Leibold and Wilbur 1992, Steiner 2001, 2003, Bohannan and Lenski 1999, 2000, Persson 2001). In IV we studied the effect of food web configuration and within trophic level heterogeneity in response to a system where the consumers were partly decoupled from in situ productivity by an allochtonous input.

The microbial community has been argued to be regulated both by resource levels and by herbivorous cladocerans (Reimann and Christoffersen 1993). Previous studies that have delineated between these processes have manipulated in situ resources (nutrient addition) and measured the difference between herbivorous cladoceran grazing and protozoans (ciliates and flagellates) grazing by means of truncation experiments (Samuelsson et al. 2002, Samuelsson and Andersson 2003). In V we compared the effect on the microbial community consisting of ciliates, flagellates and bacteria in an open system with a system that was depending on in situ productivity. In addition, we studied how different food web configurations of herbivorous cladocerans affected the way in which the microbial community responded to the inflow of resources.

**Allochtonous input and different food web configurations:**

**Response of the herbivore food web (IV)**

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The impact of food web complexity in open and closed food webs was explored experimentally under controlled laboratory conditions. We used an aquatic model food web consisting of two forms of primary producers, i.e. phytoplankton (*Scenedesmus obtusiusculus*), and periphyton (*Nitzschia perminuta*), and two types of consumers, i.e. *Daphnia pulex* feeding on phytoplankton and *Chydorus sphaericus* feeding on both periphyton and phytoplankton. Three different food webs all having the phytoplankton and periphyton, but having either one of the consumers or both were set up. These food webs were studied in an open and closed environment. In the open environment, phytoplankton was continuously flowing through the aquaria, whereas in the closed environment all the phytoplankton was delivered at the start of the experiment.

The effect of the allochtonous input in our experiment depended substantially on the identity of the consumer in the recipient food web. In the absence of *Daphnia* (*Chydorus* only treatment), the biomass of *Chydorus* and periphyton did not differ from the same treatment in a closed environment. In contrast, in the presence of *Daphnia*, the allochtonous input was made accessible to periphyton and hence also to *Chydorus*. The positive effect of *Daphnia on Chydorus* was found both in the open and closed environment. The positive effect on *Chydorus* relates to that *Daphnia* increases the amount of nutrients for periphyton by grazing on phytoplankton, both by decreasing the competition of nutrients from phytoplankton, and by increasing the overall amount of nutrients through nutrient regeneration. In the open environment, *Chydorus* increased to very high numbers and was able to depress phytoplankton, and thereby negatively affect *Daphna*. There was, however, no effect of *Chydorus on Daphnia* in the closed environment. The contrast between the effect of *Chydorus* between the open and closed environment relates to that the renewal rate of
phytoplankton in the open environment was independent of the grazing rate in the recipient food web, resulting in a higher Daphnia biomass and a higher periphyton biomass in the open environment. Our study shows how the compensatory responses among the primary producers (increase in periphyton) had a strong feedback effect on the consumer densities, i.e. an increase in Chydorus which in turn lead to a decrease in Daphnia.

**Allochtonous input and different food web configurations:**

*Responses of the microbial community (V)*

The microbial community clearly responded to the different densities of D. pulex found in the open and closed environment (IV). As a result of the higher densities of Daphnia, the biomass of flagellates and bacteria was lower in the open food web configurations than in their closed counterparts. For the ciliates, the effect could not be elucidated however. The food web configuration also affected the results, as the lowest bacterial biomass was found in the open Chydorus only configuration, in spite of the fact that the biomass of ciliates and flagellates was similar to the open Daphnia configurations. The low bacterial biomass could also not be explained by a higher grazing on bacteria in the Chydorus treatment as Chydorus densities were low. This suggests that the presence of Daphnia was needed to make the allochtonous input accessible for the microbial community, probably by regeneration of nutrients from phytoplankton to the bacteria. Our results show that the allochtonous input had an indirect negative effect on the biomass of the microbial community, since the inflow of phytoplankton increased the biomass of the herbivorous cladocerans, which imposed a higher grazing pressure on all parts of the microbial community. This result
differs from the traditional view that microbial biomass increases with increasing phytoplankton concentrations.

**Concluding remarks**

My thesis demonstrates the importance of processes outside the focal habitat on food web interactions within a specific habitat. These effects of the adjacent habitat include allochtonous input of resources (I, II, IV, V), cross-habitat foraging by consumers (II), and behaviorally induced habitat use of consumers (II, III). My thesis also shows that heterogeneity within trophic level can have dramatic implications for food web dynamics (I, II, III, IV). These implications are the result of compensatory effects between two different growth forms of primary producers (I, II, III, IV) which can induce feedback loops between the consumers (IV). Furthermore, consumer identity affects the way in which allochtonous resources become available to the microbial community (V) and the herbivore food web (IV).

Previous studies have mainly viewed the littoral habitat as a source of input of nutrients to the pelagic (Lodge et al. 1988, Schindler et al. 1996, Schindler and Scheuerell 2002). This thesis identifies the opposite route where 1) horizontally migrating zooplankton may exert a strong grazing pressure on littoral phytoplankton, and 2) horizontally transported phytoplankton may form a renewing resource base for zooplankton in the littoral area. The pelagic zone may also function as a source consisting of nutrient containing phytoplankton that are grazed by littoral filtering cladocerans, whereby nutrients become available for littoral production by periphyton. The increase in periphyton can, in turn change the dominating
herbivore fauna from one associated with one primary producer towards the other (filtering herbivores toward scraping herbivores) and change the interactions between predators within the habitat.

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