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# Ecological Relationships Between Periphyton Composition and Benthic Invertebrate Distribution in Shallow Lakes

[1*] Daniel Martin, Canadian Institute for Northern Innovation, Toronto, Canada.

[2] Claire Tremblay, Canadian Institute for Northern Innovation, Toronto, Canada.

**Abstract:** Shallow lakes are some of the most productive and sensitive of freshwater systems, with most of their benthic food web being supported by periphyton, the adhering association of algae, cyanobacteria, bacteria, fungi, and detritus that is found covering sediment, stone, and submerged vegetation. Despite intensive work having been carried out separately into periphyton and benthic macroinvertebrates, the coupling of these two components as an integrated whole has not been explored in detail for use in shallow lake assessment and management. This paper summarises information gained through field surveys, enclosures and mesocosm experiments as well as quantitative meta-analyses to explore the effects of periphyton community structure on benthic invertebrate distributions and the feedbacks from invertebrates on periphyton community structure. A structured literature synthesis was conducted using peer-reviewed papers that included both periphyton and invertebrate characteristics (periphyton biomass, growth form, taxonomic composition and substratum type, density, functional feeding group and spatial distribution of invertebrates), focusing on lakes with a mean depth less than 3 m. Evidence was arranged on a nutrient and light gradient ranging from clear water to turbid water with domination of macrophytes and phytoplankton. Periphyton biomass showed an unimodal response to enrichment, which increased with increasing nutrients and decreased with increasing shading from phytoplankton. Clear water states were associated with diatoms forming adnate epipelic and epiphytic films that supported a large number of scrapers such as gastropods and mayflies, while turbid water states changed the benthic energy pathway to detritus-based, with dominance of chironomids and oligochaetes. Grazing always resulted in a decrease in periphyton biomass and favored growth forms that were resistant to grazing pressure, while predation by fish on grazers created a fish-invertebrate-periphyton cascade causing further loss of macrophytes.

**Keywords:** Periphyton; Benthic Macroinvertebrates; Shallow Lakes; Grazing; Alternative Stable States; Eutrophication; Functional Feeding Groups; Benthic–Pelagic Coupling.

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## I. Introduction

"Shallow lakes are lakes in which the entire water column mixes often, and light reaches a great portion of the bottom." These lakes are considered the most common type of lake on Earth. As the ratio of sediment surface area to volume of water is relatively high in such ecosystems, the benthic community becomes especially important for productivity, nutrient dynamics, and food web organization in them. One of the key characteristics of shallow lakes is the presence of two opposite states in which such systems can exist. Thus, in addition to the state in which the water body contains many submerged macrophytes and benthic primary producers, there is also the condition in which turbidity prevails due to dominance of phytoplankton and suspended particles (Scheffer et al., 1993). These alternative stable equilibria, divided by mechanisms of feedback and hysteresis, have become an integral part of the ecological science of shallow lakes and their management. Moreover, comparative studies of lakes differing in phosphorus content indicate significant differences in trophic structure, number of species, and biodiversity of several biological communities along the nutrient gradient.

Periphyton plays an important role as part of the benthic community in shallow lakes. Periphyton refers to the mixture of microalgae, cyanobacteria, heterotrophic bacteria, fungi, protozoa, and organic and inorganic compounds that grow on subaqueous surfaces. Depending on the substrate, it may be classified as epipelon (growing on soft sediments), epilithon (growing on stones), epiphyton (growing on plants) and episammon (growing on sand particles). Traditionally, pelagic processes were of prime interest in limnology; however, it is now known that benthic algal production forms a significant fraction of the lake's

total primary production, and benthic pathways contribute a significant part of the energy reaching invertebrates and fishes (Vadeboncoeur et al., 2002). Studies of whole-lake comparison and fertilization show that anthropogenic eutrophication leads to a decrease in the contribution of benthic algae in the total production of lakes mainly due to the fact that phytoplankton reduces light penetration into the lake bottom; therefore, it leads to the elimination of benthic pathways in lakes (Vadeboncoeur et al., 2003).

The role of the periphyton is not just being a food source but also a microhabitat with intensive processes of transformation of nutrients as well as an indicator of environmental conditions. The taxonomic and structural composition of periphyton varies from the low-profile adnate film of diatoms to erect filamentous mats and loosely attached aggregations of cyanobacteria, and defines the ability of this biota to be used as food for consumers (Larned, 2010). On the other hand, benthic macroinvertebrates are some of the key consumers of periphyton. There are gastropods, nymphs of mayflies, larvae of caddisflies, and numerous larvae of chironomids consuming attached algae, as well as collector-gatherers, filterers, and burrowers consuming the litter and organic debris beneath and in periphyton mats. As such, interactions among benthic organisms like grazing, facilitation, competition, and predation play a vital role in benthic ecosystems in freshwater bodies (Holomuzki et al., 2010).

In spite of this large body of information, the interactions between the periphyton community structure and benthic invertebrates' distribution in shallow lakes have been studied in a fragmented fashion. Periphyton studies are usually more focused on nutrient and light effects on biomass production, while invertebrates have more often been studied with regard to sediment features, oxygen, and fish predation. However, the two systems are tightly linked, because periphyton regulates food availability and habitat quality for invertebrates, while invertebrates affect periphyton biomass, structure and taxonomic composition by grazing. The interactions between the two are crucially important for shallow lakes because even small changes in the periphyton-grazer balance may affect macrophyte survival and thus clear water conditions.

1. Assess the variability of periphyton biomass, morphology, and species composition according to the nutrient and light gradients found in shallow lakes in their clear and turbid conditions.
2. Identify how this variability in periphyton species composition is linked to the abundance, functional feeding guilds, and distribution of benthic invertebrates.
3. Assess the feedback of invertebrate grazing and fish predation on the periphyton species composition and macrophytes' survival.
4. Conclude about the ecological significance of the study findings and their implications for the management of shallow-lake systems.

Structure of the paper: In Section I, the shallow lakes, periphyton, and benthic invertebrates are discussed. Section II outlines the methodology that was employed for conducting the evidence synthesis. In Section III, the results pertaining to periphyton and benthic invertebrates are presented. Section IV discusses the ecological processes and managerial aspects, while Section V draws conclusions.

# II. Materials and Methods

## *2.1 Scope and Definitions*

Synthesis has concentrated on natural and semi-natural lakes, where the mean depth is usually below 3 m and that have a polymictic regime and a well-developed littoral zone. Periphyton has been studied within the four main compartments (epipelon, epiphyton, epilithon and episammon) and its structure has been characterized in terms of the total biomass (chlorophyll a, ash-free dry weight or algal biovolume), dominant algae species (diatoms, green algae and cyanobacteria), and physiological types (adnate or prostrate unicells, stalked and rosette diatoms, and erect or loosely attached filaments). Benthic invertebrates have been categorized according to their functional feeding groups: scrapers and grazers,

collector-gatherers, filter feeders, shredders, and predators. Such a categorization has been chosen because it allows one to relate the consumer distribution pattern to the available food resource represented by periphyton and detritus.

### *2.2 Literature Identification and Selection*

The peer-reviewed literature was identified by performing a search of Web of Science, Scopus, and Google Scholar for various combinations of the terms periphyton, epiphyton, epipelon, benthic algae, macroinvertebrate, grazer, zoobenthos, shallow lake, alternative stable states, and eutrophication. The reference lists of relevant papers were also checked. Articles were included in the analysis if they (i) were published in peer-reviewed journals prior to 2022; (ii) concerned either lakes or experimental systems that explicitly mimicked lake littoral and/or benthic conditions; (iii) contained quantitative or qualitative information about periphyton and at least one benthic consumer or about light and nutrients regulating periphyton; and (iv) had relevance to ecosystem-level issues such as partitioning of production, trophic relations, or regime shifts. Articles that studied rivers were included in the review only if they contained quantitative synthesis of grazer-periphyton interactions that were frequently used to interpret grazer-algal dynamics in lakes. The duplicate articles, conference abstracts, and papers without sufficient methodological details were not considered. After the screening, twelve papers that fully satisfied the inclusion criteria became the core of the evidence base.

### *2.3 Data Extraction and Synthesis*

For each study, the information was obtained about the study system, the gradient studied (nutrients, light, grazer density or fish density), the periphyton characteristics studied, the invertebrate characteristics studied, and the nature and significance of the observed relationships. Due to the different designs, units, and response variables of the studies, no effect size meta-analysis was attempted. A narrative and semi-quantitative synthesis of the results was conducted, placing them in relation to a common gradient of lake trophic state ranging from clear, nutrient-limited to clear, macrophyte-dominated and turbid, phytoplankton-dominated lakes. Whenever the studies presented numerical values, these were preserved for the purposes of the synthesis. The patterns generated were summarized into a comparison table (Table 1) and an expected response model (Figure 1).

### *2.4 Appraisal of Evidence Quality*

The potential strength of inference in each study was assessed. Three levels of evidence were defined. Level I evidence included manipulative experiments and quantitative meta-analyses where either grazer densities, nutrient supply or light were manipulated and the effect on the periphyton community was quantified. This evidence represented the strongest support for the hypothesis that consumers and resources can regulate periphyton abundance (Hillebrand, 2002; Feminella & Hawkins, 1995; Hillebrand & Kahlert, 2001). Level II evidence included comparative surveys and lake-wide measurements where relationships between nutrients and lake condition and the algal community have been studied. In this case, have the evidence for the pattern, but not necessarily for the mechanism of regulation since multiple variables change along the trophic gradient (Jeppesen et al., 2000; Vadeboncoeur et al., 2003) Level III included conceptual models and narrative reviews that integrate the previous evidence and provide the basis for interpretation (Vadeboncoeur et al., 2002). Conclusions presented in this article were valued higher if they were based on more than one level of evidence. Conclusions based only on one level of evidence will be noted in the Discussion section.

## III. Results

### *3.1 Periphyton Composition Along Nutrient and Light Gradients*

Non-linearity of the relationship between periphyton biomass and lake productivity was another key characteristic of all available empirical studies. Specifically, in a comparative field investigation of the

effect of lake productivity on sediment-associated periphytic algal biomass ranging from extremely oligotrophic meltwater lakes to eutrophic lakes, a curvilinear relationship of sediment periphyton biomass with lake productivity was observed, suggesting a shift from nutrient limitations at low productivity levels to light limitation due to phytoplankton at high productivity levels; temperature, substrate type, and food web composition seemed relatively unimportant factors (Hansson, 1992). Another proof of this tendency was provided by whole-lake studies, demonstrating that the proportion of whole-lake primary productivity attributable to benthic algae decreases with increased productivity of lakes due to decreased light penetration in the sediments.

Measurements taken directly in shallow Danish lakes have highlighted how this change is realized in the shift between the alternative states. During a year-round measurement made at 0.5 m depth, the joint production by phytoplankton and epipelic species was 190 g C $m^{-2}$ $year^{-1}$ in a turbid lake and 141 g C $m^{-2}$ $year^{-1}$ in a clear lake; nevertheless, phytoplankton production made up around 96% of total production in a turbid lake, while epipelic algae made up about 77% of total production in the clear lake (Liboriussen & Jeppesen, 2003). The importance of epipelon production increased in winter due to higher transparency of water, but decreased to very low levels during summer months. Epiphytic production in reed stands was low and did not show any significant differences between the lakes. Thus, it can be seen that the total amount of autotrophic production might differ insignificantly between the states, while its distribution between the benthic and pelagic fractions changes dramatically.

Table 1: Periphyton Composition, Dominant Benthic Invertebrate Guilds and Governing Mechanisms Along the Shallow-Lake State Gradient

| Lake Condition | Periphyton Composition | Dominant Benthic Invertebrates | Principal Mechanism | Sources |
|---|---|---|---|---|
| Clear, Nutrient-Limited (Low TP) | Epipelon and Epilithon; thin, Adnate Diatom Films; Biomass Limited by Nutrients | Scrapers (Gastropods, Ephemeropteran Nymphs); Moderate Total Density | Nutrient Limitation; Benthic Algae Dominate Whole-Lake Production | Vadeboncoeur et al., (2003); Hansson, (1992) |
| Clear, Macrophyte-Dominated (Intermediate TP) | Epiphyton on Submerged Plants Plus Epipelon; Mixed Adnate, Stalked and Filamentous Forms; High Surface Area | High Density and Diversity of Grazers (Snails, Mayflies, Caddisflies) and Plant-Associated Chironomids | Habitat Complexity and Grazer Control of Epiphyton; Epipelon ≈77% Of Benthic + Pelagic Production in a Clear Lake | Scheffer et al., (1993); Holomuzki et al., (2010); Liboriussen & Jeppesen, (2003; Jones & Sayer, 2003) |
| Turbid, Phytoplankton-Dominated (High TP) | Light-Limited, Reduced Epipelon; Loosely Attached Filamentous Green Algae and Cyanobacteria | Collector-Gatherers and Burrowers (Chironomids, Oligochaetes); Few Scrapers | Phytoplankton Shading; Phytoplankton ≈96% Of Production in a Turbid Lake; Detrital Pathway Dominates | Jeppesen et al., (2000); Vadeboncoeur et al., (2003); Liboriussen & Jeppesen, (2003) |
| High Grazer Density (Any Trophic State) | Low Biomass; Adnate, Prostrate and Grazer-Resistant Cells; Altered C: N:P | Grazers Abundant and Food-Limited | Selective Consumption; Grazer Effects Comparable to or Stronger Than Nutrient Effects | Hillebrand, (2002), Feminella & Hawkins, (1995), Hillebrand & Kahlert, (2001) |
| High Fish Predation on Grazers | Accumulation of Epiphyton and Erect Filaments on Plants | Grazers Suppressed; Predator-Tolerant Taxa | Fish–Invertebrate–Periphyton Cascade Causing Macrophyte Shading and Loss | Holomuzki et al., (2010); Jones & Sayer, (2003) |

The same gradients were reflected in the changes in the taxonomic and structural composition of periphyton. In water bodies characterized by the absence of nutrients and transparency, the periphyton usually consisted of diatoms that formed tightly attached films on sediments and plants. In conditions of

medium nutrient concentration and high abundance of submerged macrophytes, epiphyton became more important, consisting of adnate, stalked and filamentous periphyton due to the availability of large surface of the plant organs (Vadeboncoeur et al., 2002; Larned, 2010).

In the case of eutrophication and turbidity, light was a limiting factor in periphyton, so that the tightly attached periphyton was replaced by shade-adapted and loosely attached periphyton, including filamentous green algae and cyanobacteria, often of low nutritional value for herbivores (Larned, 2010).

TP = total phosphorus. Percentages refer to annual phytoplankton plus epipelic production reported for one clear and one turbid shallow lake (Liboriussen & Jeppesen, 2003).

### *3.2 Distribution of Benthic Invertebrates in Relation to Periphyton*

The distribution of benthic invertebrates followed the pattern of periphyton communities discussed in table 1. In clear waters where macrophytes predominated, the high epiphyton surface area, presence of diatomaceous biofilms, and structural shelter promoted the occurrence of grazing and scraping animals, including snails, ephemeropteran nymphs, trichopteran larvae, and phytophilous chironomids. These consumers were abundant in the littoral zone and within macrophyte beds, where periphyton production is highest. On the other hand, in turbid waters, where the quality of the attached algal community was poor, there was a prevalence of collector-gatherers and burrowers like chironomid larvae and oligochaetes that rely more on sedimented phytoplankton and detritus rather than living periphyton (Jeppesen et al., 2000).

Supporting this interpretation, comparative evidence from shallow lakes exists. In general, the density of the grazing invertebrates on the submerged plants has been strongly and inversely correlated with the biomass of periphyton present on the surface of the plants, suggesting the existence of a relationship between grazer distribution and the standing crop of periphyton (Jones & Sayer, 2003). In cases where the benthic algal biomass forms the bulk of the production, like in the case of the clear lake mentioned earlier, a greater fraction of high quality, attached food would be available to the grazers than in the case of turbid lake with the production being dominated by phytoplankton. Based on the information from the literature on the benthic pathway, the zoobenthos fed by the periphyton contribute a lot to the diet of the fish inhabiting the lake, and any variation in the periphyton community would have an effect on the diet of the fish via invertebrates (Vadeboncoeur et al., 2002). As a result, the distribution of the invertebrate community with respect to depth and habitats followed that of light-saturated periphyton and was characterized by higher grazer densities in shallow, well-lighted littoral zones and decreasing densities with increased depths and shading of sediments.

### *3.3 Feedback Effects of Invertebrate Grazing on Periphyton*

Invertebrates are not just tracking the periphyton. In a meta-analysis of studies that manipulated periphyton through consumer removal and nutrient enrichment, consumer manipulations were shown to impact autotrophic biomass, while grazer manipulation had the same strength as nutrient manipulation, with grazers having sometimes even more impacts (Hillebrand, 2002). A quantitative review of experimental studies on the effects of herbivores on periphyton biomass revealed that, in most cases, grazers negatively impacted periphyton biomass, and the degree of the impact varied depending on the type and density of grazers, with mollusks and caddisflies being among the most efficient grazers (Feminella & Hawkins, 1995). Studies conducted in the field and in experiments have proven that grazing and nutrient supply interactively control the biomass and carbon: nutrient stoichiometry of periphyton (Hillebrand & Kahlert, 2001).

Periphyton architecture was affected by grazing as well. Grazing by scrapers caused loose and upright filamentous algae to disappear and promoted low-lying and adnate diatoms and prostrate cells, which were difficult to remove, while in the absence of grazers upright filaments and stalked forms built up (Larned, 2010). In this manner, the invertebrate fauna reacts to the periphyton community, which defined the distribution of the invertebrates in the first place. Such a reciprocal relation results in a positive feedback loop in clear lakes with many grazers producing thin productive periphyton films.

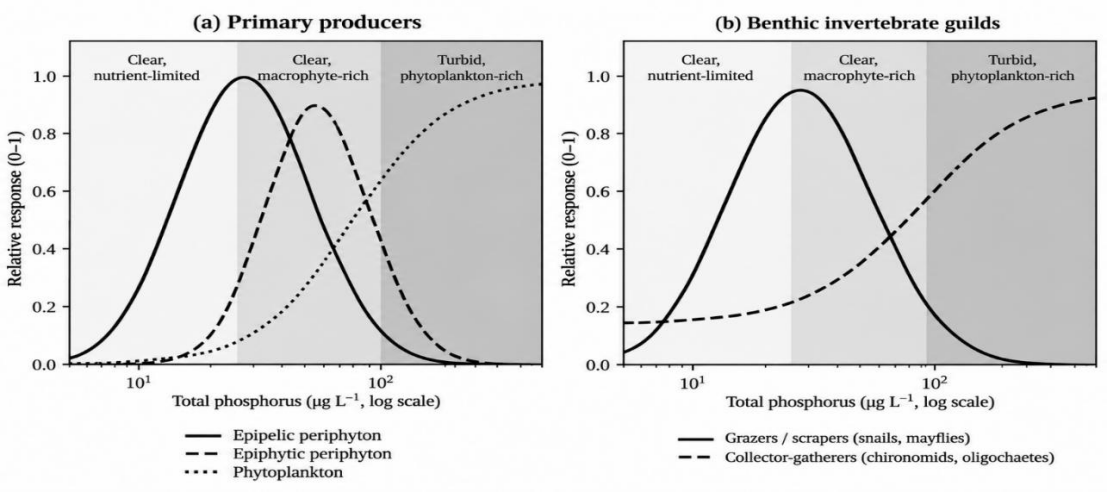



Figure 1: Conceptual Responses of Periphyton and Benthic Invertebrate Guilds Along the Phosphorus Gradient in Shallow Lakes

The conceptual response model resulting from the synthesis is illustrated in figure 1. Figure 1(a) provides the relative responses of epipelic periphyton, epiphytic periphyton, and phytoplankton; figure 1(b) provides the relative responses of grazer/scraper and collector-gatherer invertebrates. These curves are illustrative and normalized from 0 to 1 and depict the trend of the results obtained from references (Scheffer et al., 1993; Jeppesen et al., 2000; Vadeboncoeur et al., 2003; Hansson, 1992); they are not based on any particular dataset (Liboriussen & Jeppesen, 2003). Approximate regions of clear nutrient-limited, clear macrophyte-rich, and turbid phytoplankton-rich are shaded accordingly.

### *3.4 Trophic Cascades and Macrophyte Interactions*

The clearest evidence for the importance of periphyton-invertebrate coupling at the ecosystem level was found from studies involving fish, grazers, periphyton, and macrophytes. An investigation of shallow lakes found that there was an inverse relationship between macrophyte biomass and periphyton biomass, an inverse relationship between periphyton biomass and grazing invertebrate density, and an inverse relationship between grazer density and fish density; nutrient concentration was not responsible for declines in macrophyte biomass directly. This demonstrates that there is a cascading effect between fish, invertebrates and periphyton, whereby increased predation by fish on the grazers decreases periphyton biomass by releasing it from grazing pressure, enabling it to shade out and compete with the macrophytes. Since the macrophytes stabilize the clear-water state through sediment stabilization, nutrient removal, and shelter, the removal of the grazers is likely to destabilize the feedbacks that maintain clear water (Scheffer et al., 1993). The trends of cyprinid fish dominance and decreasing macrophyte cover as phosphorus increases in Danish lakes suggest that such a mechanism applies throughout lake eutrophication.

## IV. Discussion

### *4.1 Bottom-up and Top-down Regulation of the Periphyton–Invertebrate Interface*

In the case of shallow lakes, the relationship between periphyton and invertebrates is controlled by bottom-up and top-down forces that act in tandem. Bottom-up control is exhibited at the beginning when nutrients promote periphyton growth, but in cases of excess enrichment, the effect of increased phytoplankton shading causes a decrease in benthic production. Invertebrates control periphyton biomass and composition, while fish predation regulates the density of grazers. High grazing pressure allows nutrients to increase the turnover rate of periphyton without increasing biomass significantly. At low grazing pressure, filamentous algae may grow (Hillebrand & Kahlert, 2001). Therefore, the distribution of invertebrates shows reciprocal effects between food availability, grazing, habitat, and predation.

### *4.2 Implications for Alternative Stable States*

Interactions between periphyton and invertebrates help to stabilize and shift alternative ecological states. Clear water lakes have a high abundance of macrophytes, diatom periphyton, and invertebrates that graze the plants. In turbid lakes, light penetration is low, there is low coverage of macrophytes, and detritivores predominate. Shifts in fish predation may speed up the process by decreasing grazer abundance. The figure shows conceptual responses along the clear-to-turbid gradient with lower abundance of scrapers and increased phytoplankton dominance. Nevertheless, threshold values differ based on lake depth, nutrient content, climatic conditions, and fish community composition.

### *4.3 Spatial Heterogeneity and Substratum Effects*

Periphyton communities and invertebrate distribution are highly variable across different lake habitats, with fine sediments forming the basis for epipelic, stones supporting epilithic, and plants allowing for epiphytic colonization. Highly illuminated littoral zones often contain grazers, while deeper, organic sediments tend to favor collectors. Thus, sampling conducted within individual habitats might fail to provide an accurate representation of the whole lake benthic function. Stratified sampling across multiple substrates and depths, combined with measurements of both periphyton and invertebrates, could increase the ecological understanding and separate food effects from structural habitat effects.

### *4.4 Indicators for Monitoring and Restoration*

Periphyton community and invertebrate distribution vary greatly between different habitats of the lake, with fine sediments serving as a basis for epipelic, stones – epilithic, and plants providing conditions for epiphytic periphyton growth. Littoral areas with high illumination usually have grazers present, whereas organic sediments found at greater depths can be suitable for collectors. Consequently, sampling carried out in particular habitats can give an inadequate picture of the functioning of the entire lake benthos. Sampling using a stratified approach in various habitats and depths, coupled with determination of both periphyton and invertebrates, will enhance ecological knowledge and isolate food from habitat effects.

### *4.5 Climate Change and Emerging Pressures*

Climate warming may affect periphyton-invertebrate interactions by promoting greater algal production, metabolic changes, expansion of cyanobacteria, and modification of the fish assemblage. Increased predation pressure on grazers may lead to reduction of biological control and enhanced susceptibility to shifts into the turbid state. Variable water levels may also affect the availability of littoral habitats for colonization. While these predictions are in line with known ecological processes, they need to be tested in long-term observations and multifactorial experiments (Jones & Sayer, 2003).

### *4.6 Limitations and Research Gaps*

Limitations of the current review arise from the lack of a sufficient number of observations, geographic limitation of studies to temperate lakes, and differences in methods applied in various research works. Different sampling techniques used by researchers prohibited performing meta-analysis of the data; moreover, some publications only provide information on the biomass of periphyton without analyzing the structure of communities. Evidence regarding tropical and subtropical lakes is scarce. Future research must include measurement of standardized parameters of periphyton, invertebrate functional traits, stable isotopes, and fatty acid biomarkers.

## V. Conclusion

This study demonstrates that periphyton community structure and benthic invertebrate distribution in shallow lakes are mutually interrelated and play an important role in the functioning of the ecosystem as a whole. Periphyton biomass exhibits a unimodal dependence on the increase in nutrients: when nutrients are deficient, biomass increases; when phytoplankton shading prevails, the biomass decreases. The

composition of the community varies from palatable, adherent diatoms to filaments and cyanobacteria. Benthic invertebrates respond to these changes accordingly: clear lakes with a predominance of macrophytes have large and diverse grazing and scraping fauna, including gastropods, mayflies and caddisflies; turbid lakes contain mostly collector-gatherers and burrowing organisms such as chironomids and oligochaetes. Meanwhile, grazers control periphyton biomass, stoichiometry and morphology; predation of grazers by fish leads to a cascade of effects in the form of a fish-invertebrate-periphyton interaction, which results in the removal of macrophytes and disruption of the clear-water state. From an ecological point of view, these results indicate that benthic consumer-resource relationships should be considered as seriously as pelagic ones. In practical terms, the integration of periphyton community measures and invertebrate functional feeding guilds forms a cheap but highly sensitive measure for the identification of degradation in its initial phases and the monitoring of results achieved through nutrient removal and biomanipulation efforts. Hence, managers should strive to ensure good light penetration into the water bodies, preserve structurally diverse littoral areas, and regulate the size of the fish stocks in order to keep grazers healthy. Additional research with the use of standardized techniques, trophic tracers and long-term observations, particularly in tropical and subtropical zones and in a warming environment, is essential.

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**Conflict of Interest:** The authors state that there is no conflict of interest involved in the publishing of this paper.

**Data Availability:** No new data were collected for this study. All data analyzed are accessible through references in the reference list.

**Ethics Approval:** Not applicable, since there were no experiments involving human or animal subjects.

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