

A review on the role of nutrients in development and organization of periphyton

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ABSTRACT:

Periphyton communities have not received wider attention and often misunderstood with 'biofilm' for their nature of development and role in aquatic ecosystem. To clarify its functional objective in aquatic ecosystem, present review proposes a functional definition for 'periphyton' in terms of ecological interactions and also outlines its ecological role in nutrient sharing with other aquatic components. The development and succession of periphyton is a function of nutrient and carbon (C) sharing with its constituent parts and ambient environment. Through mechanisms like entrapment, de novo synthesis, nutrient leakage, trophic upgrading etc., ambient nutrients are routed to periphyton and transferred to upper trophic levels. Periphyton communities stand next to phytoplankton for their contribution to primary productivity, in nutrient rich aquatic environment. Unlike phytoplankton, nutrient poor aquatic environment has no effect on periphytic primary productivity. As periphyton communities are attached to substratum, their ability to assimilate organic nutrient through substratum is an additional advantage over phytoplankton.

Keywords:

Aquatic ecosystem, Biofilm, carbon, primary productivity, phytoplankton.

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Article Citation:

Saikia SK, Nandi S, Majumder S.

A review on the role of nutrients in development and organization of periphyton.
Journal of Research in Biology (2013) 3(1): 780-788

Dates:

Received: 20 Nov 2012 **Accepted:** 10 Dec 2012 **Published:** 11 Feb 2013

Web Address:

[http://jresearchbiology.com/
documents/RA0307.pdf](http://jresearchbiology.com/documents/RA0307.pdf)

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INTRODUCTION

The term ‘periphyton’ (peri round; phyton plant) was proposed by (Behning, 1924) and popularized by several authors (Cooke, 1956; Sladeckova, 1962; Pieczynska, 1970). There exist a series of definitions proposed for ‘periphyton’ (Young, 1945; Neel, 1953; Wetzel, 1963). (Wetzel, 1983) defined it as the micro ‘floral’ community living attached to any substrate under water. (Stevenson, 1996) used it for describing microorganisms such as algae and bacteria growing in association with substrata. These communities play an important role in water bodies, not only as important primary producers and energy source for higher trophic levels, but also by affecting the nutrient turnover and the transfer of nutrients between the benthic and the pelagic zone (review Saikia, 2011). The substrates of periphyton commonly include submerged plants or plant parts, rocks and sediments. Such substrate selection designs periphyton as a medium in transferring and ‘trophic upgrading’ of nutrients. This property recognizes periphyton as a tool for biofiltering excess nutrients from polluted waters and for efficient nutrient transfer in aquatic food chain.

Aquatic ecosystems mainly comprise of freshwater and marine water bodies and their ecology discusses the relationship of aquatic organisms and its interaction with the immediate environment. The principle biotic components primarily explained in the recent past for their contributions to different interactions in aquatic ecosystem are macrophytes, plankton (Zooplankton and phytoplankton) and invertebrates (benthos, nekton and neuston). Till the mid of 19th century, periphyton or ‘associated organisms’ were not given any biological credit for their role in aquatic ecosystem. Probably, (Wetzel, 1963) in his evolutionary review paper ‘Primary productivity of periphyton’ in *Nature*, for the first time made convincing remark on the role of periphyton in aquatic ecosystem. Even today, periphytic communities are ignored as a major

contributor of most of the nutrient inputs to aquatic ecological cycles. The present review is an attempt to outline periphyton as an integral and essential component of aquatic ecosystem highlighting few areas recently addressed on the role of periphyton in nutrient sharing in aquatic processes.

Periphyton: A Nutrient Dependent Organization

(Whal, 1989) discussed settling pattern of ‘biofilm’ (Figure 1), in four phases: (i) surface conditioning or adsorption of dissolved organic compounds where macromolecules attach to submerged surfaces following a spontaneous physical-chemical process; (ii) primary colonization or bacterial settling following surface conditioning and after their colonization, bacteria start to produce EPS, (iii) secondary colonization to bacterial layer and EPS pool by eukaryotic unicellular microorganisms, mainly protozoan, microalgae and cyanobacteria and (iv) settling of eukaryotic multicellular organisms as a function of nutrient sharing, grazing and predation. According to (Wetzel, 1983), associated organisation from secondary colonization onwards can be designated as ‘periphyton’. In that way, it could be defined as an advanced successional stage of biofilm. However, there could be a fifth (v) phase; the tertiary colonization where bacterioplankton colonized on the surfaces of unicellular and filamentous secondary colonizer (e.g. diatom, *Oedogonium* etc.). Several bacteria different from early colonizer settle on algal surfaces at this stage (Alldredge *et al.*, 1993; Armstrong *et al.*, 2000).

Periphyton are rich Carbon source

TEP with rich Carbon sources of Glucopolysaccharides in aquatic environments initiates early colonization of bacteria through surface conditioning (Stoderegger and Herndl, 1999). The bacterial EPS from early biofilm exists as a part of dissolved organic matter (Lignell, 1990) as well as particulate matter (Decho, 2000). It acts both as rich organic Carbon storage (Freeman and Lock, 1995) and

chief supplier of Carbon demand for organisms that feed on periphytic aggregates (Decho and Moriarty, 1990; Hoskins *et al.*, 2003). Being polyanionic in nature (Costerton *et al.*, 1978), EPS further permits inorganic nutrient entrapment through ion exchange processes (Freeman *et al.*, 1995) leading to storage of organic Carbon in the biofilm. In addition, among the bacterial fractions, cyanobacteria are important primary producers and many of their species can fix atmospheric Nitrogen (Whitton and Potts, 1982). Chemical screening of laboratory grown, commercially viable cyanobacteria have revealed that they have a high nutritional value, in terms of protein (Choi and Markakis, 1981).

During tertiary phase of periphyton development, algal communities play indirect role in nutrient addition to periphytic complex through their surfaces. A study on algae-bacteria interactions on biotic surfaces revealed that bacterial abundance is significantly higher in areas of diatom colonization on substrates (Donnelly and Herbert, 1999). These bacteria contribute to the

management of community metabolism of periphytic matrix and can trap the metabolic products released by bacteria on algal surface (Makk *et al.*, 2003). Such algae-bacteria interactions enrich periphytic organic matrix with components of polysaccharides, proteins, nucleic acid and other polymers (Davey and O'toole, 2000).

Periphytic pathway of nutrient transfer

The periphytic nutrient transfer pathway (PNP) mainly involves ambient nutrient entrapment, storage and transferring it to immediate higher trophic level. The fate of PNP gets its initiation from the surface conditioning phase of periphyton formation. As soon as TEP prepares the substrate surface for colonization, bacteria as initial colonizer develops micro-colonies (Costerton, 1984) and through EPS, it supplies a significant source of Carbon to periphytic complex (Hobbie and Lee, 1980) (Figure 2). A PNP establishes between dissolved organic in periphytic complex and inorganic substances in the water column and the higher trophic levels of the ecosystem (Hynes, 1970). In general, the Carbon reserve of periphyton generates through three mechanisms. The first mechanism supplies energy through bacterial EPS. Bacterial EPS is rich in carbohydrate, and some time vitamins and other nutrients. During first-cryptic growth, the dying bacteria "leak" metabolizable energy to immediate environment (i.e. EPS) acting as nutrient source to neighbouring periphyton strata. This property not only protects the neighbours from starvation but also permits their multiplication (Postgate, 1976). In a growing periphytic assembly, cyanobacteria and other early algal colonizers share this Carbon source. In aged periphytic assembly, the old mostly filamentous periphytic layer receives such Carbon from overlying bacterial composition resulted from tertiary phase of colonization. The second mechanism consists of endogenous energy reserves. These reserves consist of Carbon that is accumulated and assimilated inside the microbial cell and can be

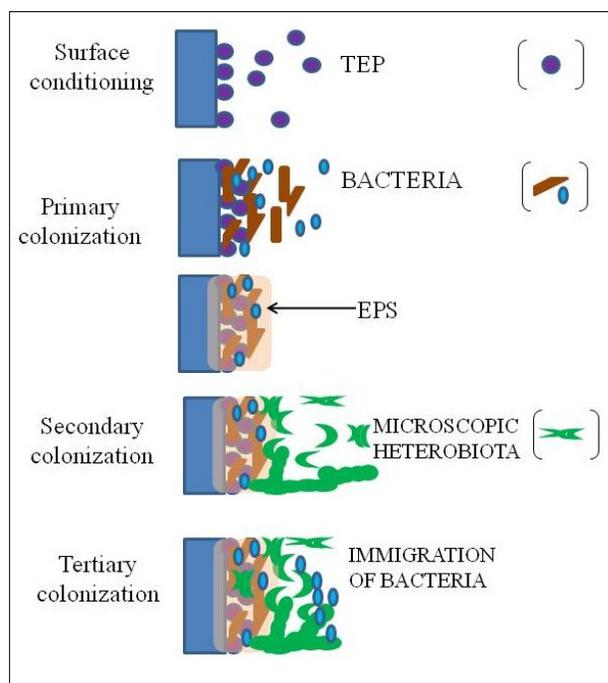


Figure 1. Formation of periphytic complex on natural substrate showing tertiary phase of colonization (Modified from Whale, 1989). TEP, Transparent Exopolymer Particles; EPS, Extracellular Polymeric Substances

mobilized to ensure survival during starvation (Dawes and Senior, 1973) and thereby recovery of periphytic aggregates due to senescence. The third mechanism of organic Carbon storage is the polysaccharide exudates (Freeman and Lock, 1995) released by algae at tertiary phase under nutrient (especially Phosphorus) limited condition. The algal components release polysaccharide exudates to EPS under Phosphorus limitation on which tertiary phase bacteria flourish. In return, these bacteria remineralize Phosphorus for algae. In addition, the ECM with polyanionic by nature (Costerton *et al.*, 1978) is believed to permit nutrient entrapment through ion exchange processes (Freeman *et al.*, 1995). (Freeman and Lock, 1995) proposed that the entrapment mechanism may also permit the storage of organic Carbon in the biofilm.

In transferring nutrient through PNP, the bacterial Carbon enters to organisms in the next trophic level as complex Carbon rich compounds. The Fatty acid (FA) component of algae is under extensive research now a day as Carbon rich compounds. Periphytic matrix is dominated by algae and hence FA contributes to the food quality of matured periphytic organization. In algae, FA increases as a result of exposure to stressful environmental conditions, such as high temperature, nutrient extremes and harsh light conditions. Polyunsaturated fatty acids (PUFAs) also affect many

physiological processes in living organisms and are major nutrient constituents of polar lipids, and are present in cell and chloroplast membranes. The dominance of algae in periphytic canopy acts as rich source of FA to animals grazing on periphyton.

Primary productivity of periphyton

The energetic relation of an ecosystem is principally regulated by primary production. In aquatic ecosystem, algae are dominant primary producers, and responsible for both Carbon fixation and sequestration. Periphyton with majority of algae might have significant contribution to primary production of aquatic ecosystem. However, very few investigations have been performed on measurements of photosynthetic rates of algal periphyton under natural conditions. (Wetzel, 1963) pointed out technical/methodological difficulty in assessing such parameters of periphyton under natural condition. From an analysis on nutrient limiting and nutrient rich lakes, it is obvious that periphyton productivity contributes more than 30% of primary productivity to the aquatic ecosystem (Figure 2a). On comparison, it seems evident that the nutrient limited aquatic ecosystems have more or less equal primary productivity levels to nutrient rich aquatic ecosystems. The same is not true in case of phytoplankton (Figure 2b).

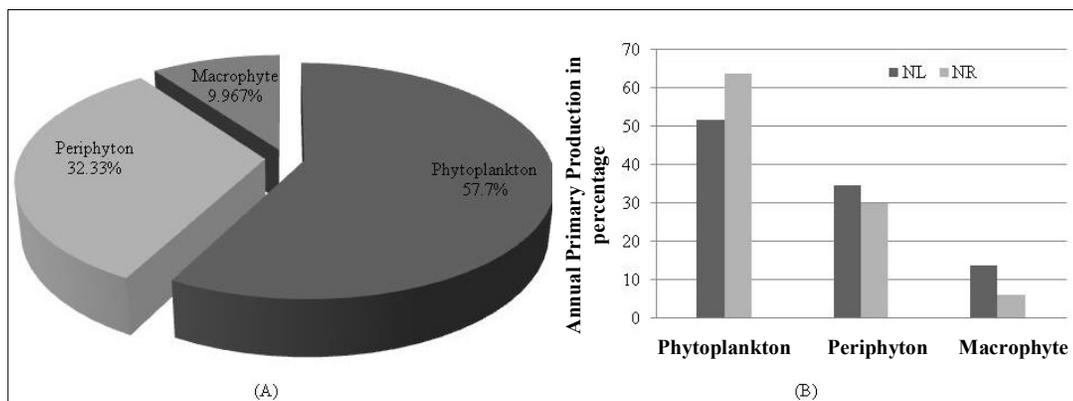


Figure 2. (a) Primary productivity of Phytoplankton, Periphyton and Macrophytes from aquatic ecosystems. (b) Primary productivity of Phytoplankton, Periphyton and Macrophyte in nutrient limited (NL, n=17) and nutrient rich (NR, n=10) aquatic ecosystems. Data from Vadeboncoeur and Steinman (2002).

Nutrient Regulated Biotic Interactions of Periphyton

Biotic interactions in aquatic ecosystems are more complex than any other ecosystems for its variable nature. Interactions between periphyton and biotic components in aquatic ecosystem are primarily regulated by nutrients and can be discussed under following subheadings-

- Plankton-periphyton interaction
- Periphyton-macrophyte interaction
- Grazer-periphyton interaction

Plankton-Periphyton interaction

The plankton-periphyton interaction is principally regulated by light and nutrient availability in the environment. Both the communities are composed of common members of bacterial, algal and zooplanktonic origin. However, on spatial ground, habitats of both plankton and periphyton have differences in receiving light and nutrients. Conceptual models revealed that nutrient limited environments are dominated by periphyton than plankton (Wetzel, 2001; Hansson, 1992). Nutrient limitation results thin planktonic cover that allows maximum light to pass through water column to reach the bottom of the ecosystem facilitating multiplication of periphytic population. Conversely, plankton rich aquatic ecosystems limit growth of periphyton due to limited light availability. Epiphytic communities can better adsorb nutrients from sediments or bottom of the system through macrophytes (Burkholder and Wetzel, 1990).

Periphyton-substrate interaction

Substrate type plays a driving role in growth and succession of periphyton. Being a substrate based organization, periphyton have access to both organic nutrients from substrate and inorganic nutrients from water column. In nutrient rich environments, it receives nutrients from water column (Eminson and Moss, 1980; Burkholder, 1996). Here, similar to planktonic cells, periphytic cells can use inorganic nutrients efficiently, specifically dissolved organic Phosphorus and in nutrient

limited environments, it relies mainly on organic nutrients from natural substrate. All artificial substrates cannot serve as organic nutrient supplier to periphyton. Substrates like sediments or seed grains acts as nutrient diffusing substrate releasing nutrients to overlying periphytic layer. (Hansson, 1989) showed that epipelion can significantly lower nutrient availability in the water column due to uptake of diffusing nutrients. (Hagerthey and Kerfoot, 1998) demonstrated that inflowing ground water is a significant source of nutrients for episammon in nutrient limiting environment. These sediments act as better nutrient source for periphyton (Burkholder, 1996). Substrate based nutrient uptake by periphyton is further related to depth, light availability, physical disturbances etc.

Grazer-Periphyton interaction

Studies reported that several herbivore types (e.g. gastropods, trichopteran larvae and fish) can dramatically reduce periphytic biomass to only a few percent of total biomass (Hillebrand *et al.*, 2000). Although grazing results reduction in periphytic biomass, the total productivity of the periphytic complex increases due to reduced competition among algal members (Carpenter, 1986; Mc Cormick and Stevenson, 1989). (Norberg 1999), using transparent incubation chambers, measured a 4-fold increase in periphyton specific productivity in grazed periphyton compared to ungrazed controls. Moreover, the grazer presence increased the Chlorophyll: biovolume ratio, especially reported from streams (Hill and Knight, 1987). In addition to increase in productivity, grazing and competition can modify the species composition of periphytic algal assemblages (Duffy and Hay, 2000; Nielsen, 2001), generating heterogeneity through temporal or spatial scale on the substrate. A top down effect of consumers on their prey can be further accelerated by grazer and grazer excretion of nutrients, removal of senescent cells, or increased uptake of nutrients by the remaining cells (Lamberti *et al.*, 1987; Kahlert and Baunsgaard, 1999). Grazers

may have strongest effects on Carbon:Phosphorus and Nitrogen:Phosphorus, but Carbon:Nitrogen and Carbon:Chlorophyll may remain unaffected (Hillebrand and Kahlert, 2001). Hillebrand *et al.*, (2008) described three pathways for grazer mediated periphytic interactions affecting nutrient stoichiometry. First, the non algal component, which could be a dominant part of the organic material of periphyton assemblage (Frost *et al.*, 2002) is reduced by unselective grazing. Benthic invertebrates graze upon both detritus and algal component of periphyton but only algae regenerate. Therefore, grazing not only reduces non algal component of periphyton, but also facilitates the growth of live component within it. (Jones *et al.*, 1999) suggested that epiphytes can influence the nutritional quality of the periphyton which grows on their surfaces, making it more nutritious for grazing by invertebrates, particularly snails. In return, these grazers might preferentially feed on the periphyton and clear the plants of a potential competitor for nutrients, with the plants and grazers both gaining from this relationship. Secondly, in streams, nutrient uptake of intact periphyton mats is often slower than cell specific uptake rates as boundary effects reduce the uptake ability of the benthic algae (Riber and Wetzel, 1987; Bothwell, 1989; Burkholder *et al.*, 1990). Grazer presence alters periphyton architecture, increases periphytic heterogeneity and relative availability of nutrients (through reducing Carbon: nutrient ratio) per unit biomass enhancing periphytic nutrient uptake. Thirdly, the excretion or egestion of nutrients or both by grazers also increase the supply of nutrients to the periphytic assemblages. Grazers may spatially recycle nutrients that increase the availability and uptake of nutrients by the periphyton. However, in streams, grazers may increase the export of nutrients (Mulholland *et al.*, 1991).

CONCLUSION

Disrupted nutrient cycling is a major problem both in freshwater and marine ecosystems and periphyton could be a non-point manager of nutrient cycle disruption and hence can overlay on plankton for nutrient cycling in aquatic ecosystem. During renovative practices, strategies of aquatic ecosystem health managers greatly ignore the role of these substrate based microorganisms. At the same time, it can play as an efficient supplier of nutrient to its grazer under controlled and well managed productive practices. It is observed that at traditional level, farmers from different parts of the world have been practicing periphyton to feed aquacrops to convert periphytic energy biomass to crop biomass (Saikia and Das, 2009). Such conversion of biomass is an outcome of increased assimilation of micro- and macro nutrients from periphytic complex in the fish body through trophic upgrading (Saikia and Nandi, 2010). Further researches on the mode of energy transfer through periphytic food chain, enhanced nutrient uptake under manipulative nutrient input, modelling on applied periphytic ecology, ecotoxicology, Carbon entrapment and delivery, directing nutrient and Carbon sequestration both in marine and freshwater are needed for better understanding of its role in aquatic ecosystem.

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