

Review on Periphyton as Mediator of Nutrient Transfer in Aquatic Ecosystems

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Abstract. In the studies of aquatic ecology, periphyton has been uncared for despite its vital role in nutrient uptake and transfer to the upper trophic organisms. Being the component of food chain as attached organism it takes part in nutrient cycling in the ecosystem like that of suspended planktonic counterparts. The present review, with an aim to understand the role of periphyton in nutrient transfer from benthic environment to upper trophic level, focuses many aspects of periphyton-nutrient relationship based on available literatures. It also attempts to redefine periphyton, as a part of biofilm, harboring nutrient components like protein, fat and carbohydrate preferably in its extracellular polymeric substance (EPS), cyanobacteria, diatom and other algal communities. In addition to physical processes, nutrient uptake by periphyton is catalyzed by enzymes like Nitrogen Reductase and Alkaline Phosphatase from the environment. This uptake and transfer is further regulated by periphytic C: nutrient (N or P) stoichiometry, colonization time, distribution of periphyton cover on sediments and macrophytes, macronutrient concentration, grazing, sloughing, temperature, and advective transport. The Carbon (C) sources of periphyton are mainly dissolve organic matter and photosynthetic C that enters into higher trophic levels through predation and transfers as C-rich nutrient components. Despite of emerging interests on utilizing periphyton as nutrient transfer tool in aquatic ecosystem, the major challenges ahead for modern aquatic biologists lies on determining nutrient uptake and transfer rate of periphyton, periphytic growth and simulating nutrient models of periphyton to figure a complete energy cycle in aquatic ecosystem.

Key words: Biofilm, bacteria, algae, nutrient stoichiometry, diffusive boundary layer, periphytic succession.

Introduction

In an aquatic food chain, the significance of food quality of primary producers for well-being of zooplankton and fishes has always been the focus of applied research. In determining food quality, attention was paid on two parameters, firstly, nitrogen (N): phosphorus (P) stoichiometry (URABE *et al.*, 1997) and secondly, Carbon (C) as DOC, carbohydrate and long-chain polyunsaturated fatty acids (PUFAs) (BRETT & MÜLLER-NAVARRA, 1997; WEERS & GULATI, 1997). The sestonic algal community has already

been characterized as rich source for ω -3 PUFAs for higher trophic levels through extensive studies (See review of SAIKIA & NANDI, 2010). However, the epiphytic or attached life forms on aquatic substrates/plants (i.e. periphyton), being similar in genetic origin but occupying different ecological grade, requires wider attention in the context of food quality. The recently developed aquaculture technologies (KESHAVANATH *et al.*, 2001; SAIKIA & DAS, 2009) have experimentally proved the potentiality of periphyton as good source of quality food for stocked fish. On this

background, certain basic questions need critical review in comprehending the nature of nutrient transfer ability of the periphytic life forms in aquatic food chain viz., (i) How does epiphytic or periphytic community act as food source for the grazers/detritus feeders? (ii) How the uptaken C, N and P in periphyton are being transferred into aquatic food chain and (iii) What are the stoichiometric consequences for uptake and transfer of nutrients in a periphyton based food chain? The present review is an effort to realize all those questions in detail as well as to present a comprehensive synthesis of fact on the background of available literature.

Biofilm or periphyton?

The terms 'biofilm' and 'periphyton' are often used interchangeably for all epiphytic microorganisms. While reviewing the present topic, it becomes a dilemma in referring the terminology is to be used throughout the discussion and therefore, both the terms need justified clarification to start with. Even though both the terms are used mostly as synonymous, however there exists narrow but significant difference from compositional as well as ecological point of view. The term 'biofilm' was coined and described in 1978 (COSTERTON *et al.*, 1978) that denotes to an aggregation of bacteria, algae, fungi and protozoa enclosed in a matrix consisting of a mixture of polymeric compounds, primarily polysaccharides, generally referred to as extracellular polymeric substance (EPS). The formation of biofilm is a prerequisite for the existence of all microbial aggregates (FLEMMING & WINGENDER, 2001a; SUTHERLAND, 2001) and it is an essential step in the survival of bacterial populations (VAN HULLEBUSCH, 2003). The proportion of EPS in biofilms can comprise between approximately 50-90% of the total organic matter (DONLAN, 2002; FLEMMING & WINGENDER, 2001b). In addition to polysaccharide, biofilms also consist of proteins, nucleic acids, lipids and humic substances. The composition and quantity of the EPS may also vary depending on the type of microorganisms, age of the biofilms and the different

environmental conditions under which the biofilms exist (MAYER *et al.*, 1999). To its true meaning, microbial biofilms, which 'may' exclude eukaryotic primary producers, and thereby mostly includes decomposers and pioneer colonizing groups of early successional stages, can develop on a number of different surfaces, such as natural aquatic and soil environments, living tissues (e.g. gut lumen), medical devices or industrial or potable water piping systems (DONLAN, 2002; FLEMMING & WINGENDER, 2001a) etc.

However, the term "periphyton" though often used to describe microorganisms such as algae and bacteria growing in association with substrata (STEVENSON, 1996), has specificity, mostly in terms of nutrient dynamics in ecosystem. Close to such objectivity, WETZEL (1983a) defined it as the micro 'floral' community living attached to the substrate inside water. These micro flora plays an important role in water bodies, not only by being important primary producers (VADEBONCOEUR *et al.*, 2001; LIBORIUSSEN & JEPPESEN, 2003) and serving as an energy source for higher trophic levels (HECKY & HESSLEIN, 1995), but also by affecting the nutrient turnover (WETZEL, 1993) and the transfer of nutrients between the benthic and the pelagic zone (VANDER ZANDEN & VADEBONCOEUR, 2002). The substrate selectivity of periphyton commonly includes submersed plants or plant parts, rocks and sediments. Such substrate selection denotes periphyton's role in transferring and 'trophic upgrading' of nutrients available in the benthic environment either directly or indirectly. This property embodies periphyton under extensive research to design as a tool for biofiltering excess nutrient from polluted waters and for efficient nutrient transfer from primary to higher trophic levels. Therefore, periphyton, though a form of biofilm appears at a later stage of succession should be discussed under the preview of nutrient exchange between benthic and pelagic ecosystems. However, bacterial colonization and EPS formation are preconditions for periphyton colonization on any substrate. The commonly referred

periphytic groups in relation to nutrient transfer through trophic levels are algae.

Nutrient composition of Periphyton

The basic foundation of ecosystem lies on the availability of food as C and macronutrients (viz. N and P). According to WHAL (1989), periphyton is formed following a settling pattern, which can be divided into four phases: (i) adsorption of dissolved organic compounds, i.e. macromolecules that attach to submersed surfaces, being a spontaneous physical-chemical process; (ii) bacterial settling - after colonization, bacteria start to produce extracellular polymeric substances (EPS), that protect them against predators, and increase their resistance to the radiation and dehydration; (iii) colonization by eukaryotic unicellular microorganisms, mainly protozoan, microalgae and cyanobacteria and (iv) settling of eukaryotic multicellular organisms. Therefore, the succession procedure of periphyton initiates accumulation of variable sources of nutrients as C, microbial protein, lipid and P in its complex.

In aquatic environments, bacterial EPS which is a precondition of periphyton colonization on natural substrate exist as a part of dissolved organic matter (LIGNELL, 1990) and in particulate matter (DECHO, 1990, 2000; PASSOW *et al.*, 1994). FREEMAN & LOCK (1995) proposed that EPS of bacterial component acts as rich organic C storage. It has been shown to be polyanionic by nature (COSTERTON *et al.*, 1978) and is believed to permit nutrient entrapment through ion exchange processes (FREEMAN *et al.*, 1995). Such entrapment mechanism permits the storage of organic C in the biofilm. That is why EPS acts as an important supplier of C demand for many organisms that feed on periphytic aggregates (DECHO & MORIARTY, 1990; BAIRD & THISTLE, 1986; HOSKINS *et al.*, 2003). Among the bacterial fractions, Cyanobacteria are important primary producers, many species of which are able to fix atmospheric N₂ (STEWART, 1973; WHITTON & POTTS, 1982). Chemical screening of many laboratory grown, commercially viable, marine cyanobacteria has revealed that they have a high

nutritional value, in terms of protein (VENKATARAMAN, 1993). CHOI & MARKAKIS (1981) found 63% of crude protein content from *Anabaena flos aqua*, a very common periphytic candidate.

Other algal communities also play a key role in periphyton formation and nutrient addition to periphytic complex through their surfaces that provide potential habitats for several bacteria from early successional stages. A study on algal bacterial interactions revealed that in the case of submerged plant surfaces, bacterial abundance is significantly higher in areas of diatom colonization (DONNELLY & HERBERT, 1999). These bacteria involved in the community metabolism of periphyton can trap not only dissolved organic materials and debris drifting from the water body but also the metabolic products released by bacteria in algal species (MAKK *et al.*, 2003). Such algal bacteria interaction turns periphytic organic matrix as a source of polysaccharides, proteins, nucleic acid and other polymers (DAVEY & O'TOOLE, 2000).

In algal-based food webs the abundances of essential elements (e.g. N, P) and organic compounds (e.g. fatty acids and amino acids) are thought to play a large role in determining algal food quality (STERNER & HESSEN, 1994; BRETT & MÜLLER-NAVARRA, 1997). Being dominated by algal members as secondary colonizer in periphyton formation, food webs regulated by these eukaryotic components are not a deviation of such possibility. Therefore, all microorganisms present in the periphyton regime represent a complementary food source, providing essential nutrients like polyunsaturated fatty acid (PUFA), sterols, amino acids, vitamins and pigment that help a better development of post successional organisms (THOMPSON *et al.*, 2002).

The nutrient quality and availability on periphyton varies with several factors like grazing pressure, algal and bacterial taxonomic composition, nutrient level of environment, environmental purity, and most significantly to substrate type (MAKAREVICH *et al.*, 1993; AZIM *et al.*, 2002). MONTGOMERY & GERKING (1980) reported proximate composition of 16 periphytic

algae grown on granite boulders suspended in the Gulf of California. Protein, lipid, carbohydrate and ash contents of these epilithic algae were 8-10, 2-5, 52-60, and 25-38% respectively. An average protein content of 15% was estimated in periphyton collected from coral reef (POLUNIN, 1988). DEMPSTER *et al.* (1995) reported 28-55% protein and 5-18% lipid in some algal species of periphytic nature. AZIM *et al.* (2001a) estimated 27.19% crude protein from periphyton grown on bamboo substrate. He also recorded 14.63% protein in Hizol (*Barringtonia* sp.) branches, 18.74% on Kanchi (bamboo side shoot), and 12.69% protein on jute stick. KESHAVANATH *et al.* (2004) also recorded protein level of 19.27-35.56% in periphyton. LEDGER & HILDREW (1998) recorded as low as 2-3% protein, 0.04-0.29% lipid, and 29-33% carbohydrate in periphyton grown on stones. BECKER (2007), in a recent study, reported protein, lipid and fat content of some algae as 35-63%, 10-57% and 2-22% respectively.

AZIM *et al.* (2001a) observed periphytic fat content as 5.43%, 0.35%, and 2.75%, respectively on substrates Hizol, Kanchi, and Jute stick. The ash content also shows variation with a range from 17.45-41%. AZIM *et al.* (2001b) observed ash content from periphyton on bamboo (29%), Hizol (41%), Kanchi (29%), and jute stick (31.12%). Ash content of periphyton is known to increase as the community grows older (HUCHETTE *et al.*, 2000). NIELSEN *et al.* (1997) found the EPS of biofilm accounted for 50-80% of the total organic matter, therefore, high amount of carbohydrate.

Thus, all sorts of nutrient components make their representation on the periphytic microhabitat. As periphytic microhabitat is constituted of heterogeneous prokaryotic as well as eukaryotic epiphytic microbial communities, the interactions of periphytic microhabitat might be more intraspecific than interspecific. Such interactions could enable addition of variable food qualities to the periphytic communities as a whole. Probably, these anthropogenic natures of periphyton stimulates survival and growth rates of several cultivated organisms on consumption (AZIM *et al.*, 2002; BRATVOLD &

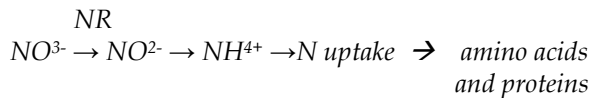
BROWDY, 2001; MRIDULA *et al.*, 2003; KESHAVANATH *et al.*, 2004). AZIM *et al.* (2001a) reported that periphyton alone can support fish production of 5000 kg/ha¹year⁻¹. BALLESTER *et al.* (2007) demonstrated that the consumption of periphyton by the pink-shrimp *Farfantepenaeus paulensis* can enhance its survival and growth rates. ABREU *et al.* (2007) by using stable isotope analysis (d13 C and d15 N) demonstrated that periphyton contribution to the pink-shrimp *F. paulensis* growth represents 49% of carbon and 70% of nitrogen of shrimp demand.

How does periphyton uptake nutrients?

Periphyton assemblages can play significant roles in uptake of ambient macronutrients since they can trap particulate material from the water column (ADEY *et al.*, 1993). Such macronutrient uptake values are potentially influenced by the degree and distribution of periphyton cover on substrate in addition to ambient macronutrient concentration, grazing, sloughing, temperature, and advective transport. Such macronutrient uptake by periphyton and other benthic autotrophs is controlled by three principal processes that occur in series: (1) diffusion from the ambience into the viscous sub layer of the periphytic boundary layer; (2) slower transport, dominated by molecular diffusion, through the inner portion of the viscous sub layer (the diffusive boundary layer, or DBL) to periphyton cell surfaces; and (3) membrane transport from cell surfaces into cells. In relation to streams, LARNED *et al.* (2004) proposed three criteria of periphytic nutrient uptake. These are: (1) when the canopy is submerged within the DBL covering the substratum, uptake is controlled by the thickness of this DBL; (2) when canopy height is greater than DBL, but comparable with the substratum DBL thickness, uptake is controlled jointly by the substratum DBL and by individual DBLs surrounding the periphyton elements that protrude above the substratum DBL; and (3) when the substratum DBL is very thin and most of the canopy protrudes above it, uptake is controlled by the DBLs surrounding periphyton elements.

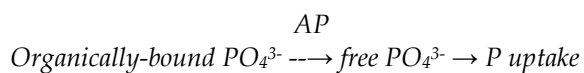
The rationale of nutrient uptake is further influenced by the activity of enzymes prevalent in periphytic body. The enzymatic uptakes of N and P by periphyton in algae are regulated in response to available macronutrients and are thus act as a physiological index of nutrient status (BEARDALL *et al.*, 2001).

Inorganic N assimilation by algae follows the following pathway:



Nitrate Reductase (NR) catalyzes the initial reduction of NO_3^- to NO_2^- , mostly available from decomposers from understory and overstory bacterial components, which is believed to be the rate limiting step in uptake and assimilation of NO_3^- into amino acids and proteins. The activity of NR is regulated in response to available NO_3^- , NO_2^- and NH_4^+ ; NR expression dependent on NO_3^- and light and is suppressed by high ambient concentrations of NH_4^+ in most algae (BERGES *et al.*, 1995; YOUNG *et al.*, 2005).

Growth of microalgae consumes P as an essential element needed for cellular constituents such as phospholipids, nucleotides, and nucleic acids (MIYACHI *et al.*, 1964). Much of the P-fraction available in the aquatic environment is not available for uptake by algae because it is bound to organic chelators. A widely distributed enzyme which helps cleave orthophosphate from the organic chelator is alkaline phosphatase (AP). The expression of AP activity is greatly elevated under conditions of low P availability, means when it is P limiting (DYHRMAN & PALENIK, 1997). The overall process is



These uptake qualities of periphyton help it to act as a bioeliminator to improve water quality (SLÁDEČKOVÁ & MATULOVÁ, 1998). This is why the periphytic communities serve important regulatory functions that can drastically alter rates and

pathways of ecosystem biogeochemical cycling (WETZEL, 1983b). CRISPIM *et al.* (2009) reported that periphyton is highly effective in removing nutrients through nutrient uptake efficiency, and, to a less extent, macrophytes sheltering epiphytes also play an important role. In a comparative study, they observed that macrophytes efficiently capture dissolved N, but not P from the water, whereas periphyton is efficient in capturing both.

A second biological mechanism of nutrient uptake is luxury P-uptake. Luxury P-uptake is the storage of P within the biomass in the form of polyphosphate. Polyphosphate can be present as acid-soluble or acid-insoluble polyphosphate. Acid-soluble polyphosphate is actively involved in metabolism, while acid-insoluble polyphosphate is stored for when the external phosphate concentration becomes limiting (MIYACHI *et al.*, 1964).

Periphytic nutrient transfer

C source and transfer

Aquatic macrophytes and periphyton remove soluble nutrients from the ambient water during their growth phase. Nutrients acquired by periphyton may be released to the environment back via several processes. First, macrophyte and epiphytes release soluble nutrients by respiration and lysis and particulate nutrients back into the water column by sloughing, scour and dislodgement. A fraction of the senescence and periphytic detritus as dead particulate organic matter is mineralized either within the periphyton mat or in the water column to release soluble nutrients. Nutrients released into the water column are subjected to downstream transport while those retained in the periphyton mat are not. In stream, this phenomenon is called "nutrient spiralling" (NEWBOLD *et al.*, 1981). Nutrients retained in the periphyton, in this way, could have two possible fates, viz. total loss to the sediment or transfer to upper trophic levels. Further, the transfer of periphytic nutrient to upper trophic levels has two possible pathways. First, direct nutrient uptake from environment and natural

substrate and transfer to immediate grazer (SAIKIA *et al.*, in press). Second, through de novo synthesis of metabolic products as raw material and trophic upgrading to immediate predator (SAIKIA & NANDI, 2010).

The colonization of bacterial biofilms is the first phase towards periphyton growth on all wetted surfaces in aquatic ecosystems. The source of C in periphyton establishes from the time of initiation of bacterial biofilm formation. The bacteria, as initial colonizer on substrate develop micro-colonies with EPS (COSTERION, 1984). Through this EPS, bacteria provide a significant source of C to biofilm complex (PEARL, 1978; HOBBI & LEE, 1980) (Fig. 1). It thus represents a trophic link between dissolved organic and inorganic substrates in the water column and the higher trophic levels of the ecosystem (HYNES, 1970). Two such substrates, the colloidal and dissolved organic C (DOC) are known to relocate as energy source for the microorganisms in those biofilms (LOCK & FORD, 1985). In general, the bacterial C reserve of biofilm generates through three mechanisms. The first mechanism supplies energy during substrate scarcity. During first-cryptic growth, the dying bacteria “leak” metabolizable substrates to immediate neighbours of periphyton strata. This property not only protects the neighbours from starvation but may also permit their multiplication (POSTGATE, 1976). In a growing biofilm, cyanobacteria and other early colonized algae share this C source. In aged periphytic assembly, the old mostly filamentous periphytic layer receives such C from bacterial decomposition. The second mechanism consists of endogenous energy reserves such as poly- β -hydroxy alkanoate (PHA). These reserves consist of C that is accumulated inside the microbial cell and which can be mobilized to ensure survival during starvation (DAWES & SENIOR, 1973). This mechanism could also play an important role in the starvation responses of biofilm bacteria. The third organic C storage, is the polysaccharide matrix (FREEMAN & LOCK, 1995). The matrix is polyanionic by nature (COSTERTON *et al.*, 1978) and is believed to permit nutrient

entrapment through ion exchange processes (FREEMAN *et al.*, 1995). FREEMAN & LOCK (1995) proposed that the entrapment mechanism may also permit the storage of organic C in the biofilm.

The bacterial C may enter to next trophic group as complex C rich compound (Fig. 1). The C rich compound under extensive research now a day is the Fatty acid (FA) component of algae. Being dominated by algae, FA contributes to food quality in the mature periphytic assembly. Although the biosynthesis of FA is just beginning to be understood, it is well known that saturated fatty acids (SAFA) and monounsaturated fatty acids (MUFA) are the major components of neutral lipids. These lipids function mainly as energy storage reserves, which, in algae, generally increase as a result of exposures to stressful environmental conditions, such as high temperature, nutrient extremes and harsh light conditions. In contrast, PUFAs affect many physiological processes and are major constituents of polar lipids, which are present in cell and chloroplast membranes. Although recent studies have shown that some organisms, such as the nematode *Caerhabditis elegans*, can synthesize PUFA containing more than 20 carbon atoms directly from SAFA and MUFA (WALLIS *et al.*, 2002), most animals cannot synthesize essential fatty acids (EFA) de novo from linoleic acid (18:2 ω 6) and α -linolenic acid (18:3 ω 3) in sufficient amounts to achieve optimal physiological performance (CUNNANE, 1996; ARTS *et al.*, 2001). The dominance of algae in periphytic canopy provides a rich source of C in the form FA to periphyton grazing animals.

As food chain proceeds, C is transferred from periphyton to grazers through predation (Fig. 1). The trophic interactions between periphyton and consumers (predators) are mediated through direct and indirect predation mechanisms (ELSER & URABE, 1999; HILLEBRAND & KAHLERT, 2001). Several studies, on questioning the uniformity of C utilization by predators from periphyton, instead of being rich source of nutrients at this stage, observed consumers to show a disproportionate relia-

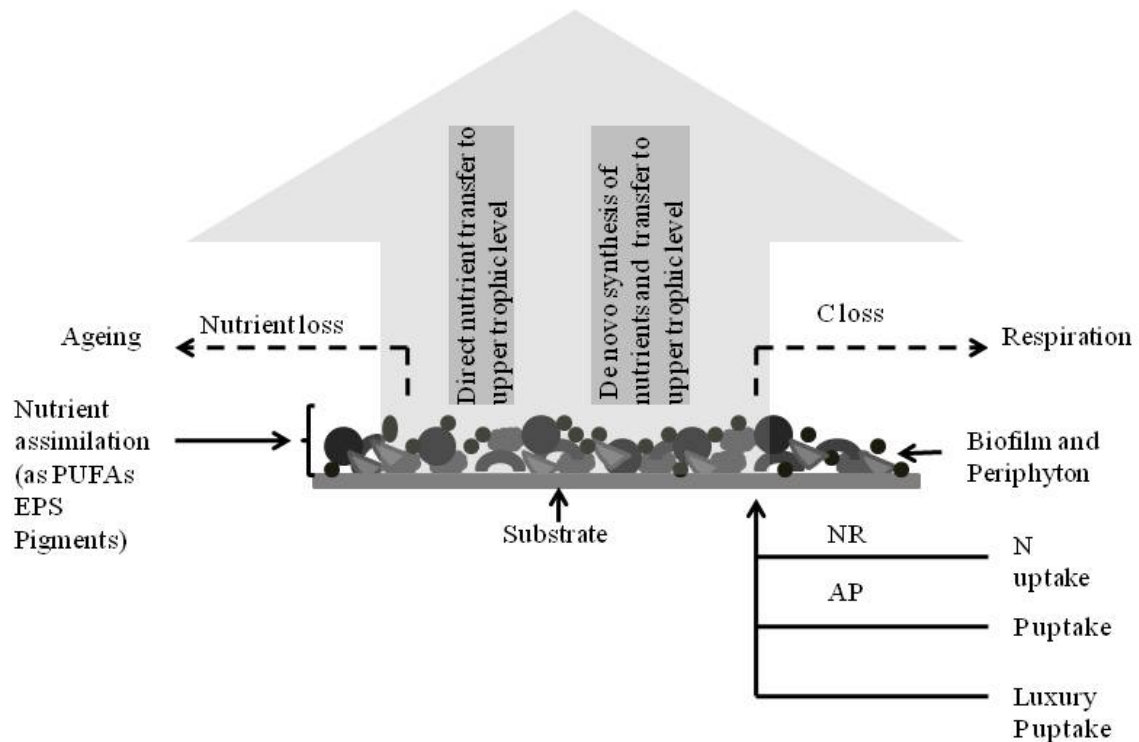


Fig 1. Periphyton as source and mediator of nutrient transfer between environment and higher trophic levels. Here NR, Nitrate reductase, AP, Alkaline phosphatase, N, nitrogen, P, Phosphate and C, Carbon.

nce on periphyton C, even when standing consumer biomass is low (HECKY & HESSLEIN, 1995; JAMES *et al.*, 2000).

Such reliance, especially of littoral zone food webs on algal periphytic sources of C contrasts with findings from the pelagic zones of several lakes, wherein allochthonous carbon sources have often been shown to fuel planktonic food webs (JONES *et al.*, 1998; JANSSON *et al.*, 2000). However, in shallow lakes with low planktonic productivity, periphyton is often the dominant C source for consumers (HECKY & HESSLEIN, 1995; JAMES *et al.*, 2000). Some invertebrate taxa (such as aquatic insects, Hemiptera and Trichoptera, and the freshwater shrimp, Caridina) that are generally reported to use allochthonous C sources (MIHUC & TOETZ, 1994) attain up to 65% of their dietary C from periphyton.

The PUFAs, in particular 20:5 ω 3, seem to be ubiquitous among aquatic insects in temperate streams (HANSON *et al.*, 1985; BELL *et al.*, 1994; GHIONI *et al.*, 1996; SUSHCHIK *et al.*, 2003). Evidence from marine and lacustrine systems indicates that invertebrates in these systems obtain PUFAs

primarily from algae (AHLGREN *et al.*, 1992). At some times of the year, benthic algal communities, which are composed of a variety of taxa over an annual cycle (WEHR, 1981), can be a greater C source and, in particular, a higher-quality food source (i.e. PUFA rich) than terrestrial matter for the proper development and reproduction of macroinvertebrates (LAMBERTI, 1996). Algal food sources, especially the benthic algae, can remain qualitatively important throughout the year, even when their quantities are small, because of their higher protein and lipid content (LAMBERTI, 1996).

Nutrient (N:P) stoichiometry and transfer

Ecological nutrient stoichiometry considers how the relative proportions of nutrients affects their biological transformation in ecological interactions. In case of aquatic ecosystem, the elemental composition of N and P are mostly considered as nutrient stoichiometry measure with special reference to producers and consumers. In natural phytoplankton, the critical supply ratios of nitrogen to phosphorus (N: P) varies roughly from 7:1

to 45:1 atomic ratio i.e. 4.4:1 to 19.4:1 mass ratio (SUTTLE & HARRISON, 1988). The optimal ratio of N: P varies among species. The typical atomic ratio of 16:1 (Redfield ratio) is found in phytoplankton (REDFIELD, 1958). Generally the mass ratio of 7.2 1(N:P) is used as optimal ratio. Macro-algae tend to be more enriched in N, with an N: P ratio of 30:1 (ATKINSON & SMITH, 1983). Low ratios of N: P (usually <10:1) may indicate N-limitation, whereas higher values (>20-30:1) may indicate P limitation (RHEE, 1978; VYMAZAL, 1995).

As periphytic heterobiota (bacteria and other heterotrophs) are closely attached to organic and inorganic substrates, the organisms expose to all resources from bottom as well as upper aquatic column. The three major nutrient sources for periphytic heterobiota are water column, substrates and groundwater (BURKHOLDER, 1996; WHITE & HENDRICKS, 2000). A change in nutrient availability in any of these sources changes the N:P ratio of periphytic heterobiota. In addition, heterotrophic bacteria that are growing rapidly tend to have lower C:N ratio (CHRZANOWSKI *et al.*, 1996). During initial colonization phase, r-strategic bacterial species generally predominant on substrates (KRIŠTŮFEK *et al.*, 2005). In this case, bacterial C:P ratio shows less variation to C:N ratio (KIRCHMAN, 2000). The bacterial periphytic heterotrophs, therefore, can reduce the elemental stress not only among themselves but also between them and the substrates (CHRZANOWSKI *et al.*, 1996). The luxury P-uptake of bacteria adds additional dimension for P storage in bacterial cell influencing P uptake and transfer. FROST *et al.* (2002), therefore, justified periphytic bacteria as elastic elemental manager for nutrient stoichiometry.

Periphytic bacteria serve as important nutrient source at the base of periphytic food web even though allochthonous C input to benthic habitat is low and light penetration is high. According to light: nutrient hypothesis (STERNER *et al.*, 1997) light influence the autotrophic input of C (C fixation) and then effects C:N and C:P ratios of periphytic community itself and to

consumers. However, to hypothesize that autotrophic input of C to effect C:N and C:P ratios, light: nutrient hypothesis received little experimental support (FROST & ELSER, 2002; HUGGINS *et al.*, 2004). However, the light: nutrient hypothesis may be, undoubtedly, effective in shallow wetlands.

Accumulation of organic matter along with periphyton colonization on substrates is another way to regulate nutrient stoichiometry through periphyton. The particulate organic matter (POM) tends to exhibit lower C:P ratio with decrease in particle size (SINSABAUGH & LINKINS, 1990). The fine particulate organic matter (FPOM) acquires higher nutrient content and lower C: nutrient ratio (BONIN *et al.*, 2000; CROSS *et al.*, 2003). The littoral organic matter with <1mm in diameter, therefore, a source of nutrient input to periphyton. During the late successional stages of periphyton in pond and rice fields, when decomposition rate is high, decrease in chlorophyll-a indicates possibility of accumulation of such organic particle on substrate (KESHAVANATH *et al.*, 2001; SAIKIA & DAS, 2009). Detritivory on periphyton at an optimum accumulation period of FPOM could ensure higher rate of nutrient transfer to consumers.

Conclusion

The overall transfer of nutrient through periphyton is highly dependent on consumer's feed selectivity and it's type, homeostasis, resistance or preference etc. Despite all these functional forces, periphyton ultimately forms an ecologically quantifiable as well as additional trophic level in all the aquatic ecosystems. Further, compared to suspended phytoplankton, periphyton complex plays more significant role in most of the functional aspects of aquatic ecosystem like regulation of eutrophic condition, maintenance of a two dimensional stable nutrient resource flow, performing as nutrient retention tool and excess nutrient removal agent, indicator of pollution and nutrient levels in the system as a whole. However, the major challenges, towards sustainable utilization of knowledge on periphyton and developing the models of application of the knowledge,

lie primarily with progresses in quantifying parameters like its growth rate, nutrient uptake and transfer rate, C recycling rate etc. Therefore, current need of modern aquatic ecologists is to focus on exploration of less basic ecological processes linked with periphytic (attached) life forms for formulating utilizable ecological designs with simulative approach, rather confining only to the planktonic (Suspended) life forms. In the aquatic ecosystem, the knowledge of 'nutrient cycling' and 'trophic energy transfer' seems to remain incomplete if study on periphyton is ignored. Therefore, the contribution of periphyton must be accounted in addition to zooplankton and phytoplankton for evaluating over all material recycling and energy flow to the food web in any aquatic ecosystem in general .

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Received: 10.05.2011
Accepted: 18.10.2011