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A prospectus for periphyton: recent and future ecological research

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Abstract. The presence, abundance, composition, and growth of periphyton are controlled or influenced by 5 broad classes of environmental variation: disturbances, stressors, resources, hydraulic conditions, and biotic interactions. In turn, periphyton communities affect water chemistry, hydraulic conditions, habitat availability, and foodweb dynamics. This review focuses on responses of periphyton communities to environmental variation. A specific objective of the review is to identify robust periphyton–environment relationships and insightful concepts. Contributors to *J-NABS* have led the field in testing and expanding concepts in periphyton ecology. *J-NABS* papers about periphyton patch dynamics, light- and nutrient-limited periphyton growth, and the effects of disturbances on periphyton structure and function have been particularly influential. However, many topics in periphyton ecology remain unexplored and under-explored. These topics include resource colimitation, physiological responses to stressors, allelopathy, competitive inhibition and exclusion, and the effects of drag forces and turbulence. Periphyton ecology studies in *J-NABS* tend to be multivariable, phenomenological, and nonmechanistic. Such studies provide information about temporal and spatial patterns, but rarely provide evidence for the causes of those patterns. These studies are often impaired by low statistical power and insufficient experimental control. Periphyton ecology needs more rigorous manipulative experiments, particularly experiments that generate clear relationships between environmental drivers and ecological responses.

Key words: periphyton, physical disturbance, stressors, resource limitation, competitive interactions, hydraulic ecology.

Periphyton communities are solar-powered biogeochemical reactors, biogenic habitats, hydraulic roughness elements, early warning systems for environmental degradation, and troves of biodiversity. This abridged list gives some indication of the ecological and cultural importance of periphyton. The roles of periphyton in freshwater ecosystems and society have warranted several book-length reviews (Stevenson et al. 1996 [Fig. 1], Wehr and Sheath 2003, Azim et al. 2005). My review focuses on the responses of periphyton communities to variation in the chemical, solar, thermal, and hydraulic environment, and to competitive interactions. By advancing our knowledge of these responses, freshwater ecologists can contribute to the growth of ecological theory and to improvements in ecosystem management. Contributions of periphyton ecology to theory and management are partly based on the availability of robust mechanistic relationships, such as those linking diversity to flood frequency (Biggs and Smith 2002), and photosynthesis to light (Graham et al. 1995).

Further contributions from periphyton ecology will require a more diverse set of periphyton–environment relationships.

The term periphyton refers to assemblages of freshwater benthic photoautotrophic algae and prokaryotes. Heterotrophic and chemoautotrophic bacteria, fungi, protozoans, metazoans, and viruses inhabit periphytic communities, but are not included in this review. Symbiotic and endophytic algae and cyanobacteria also are excluded because they are partially isolated from the external environment by their hosts. The taxa that are included comprise a diverse group, represented by thousands of taxa, with a size range spanning 6 orders of magnitude (μm – m).

About 150 papers with periphyton ecology as a primary focus have been published in *J-NABS* (based on searches of Web of Science, Google Scholar, Biological Abstracts, and *J-NABS* bibliographies). Most of these papers can be classified into 7 broad topics: 1) effects of physical disturbances, 2) effects of exposure to stressors, 3) limiting abiotic factors, 4) competitive interactions, 5) effects of herbivores, 6) periphytic algae as environmental indicators, and 7)

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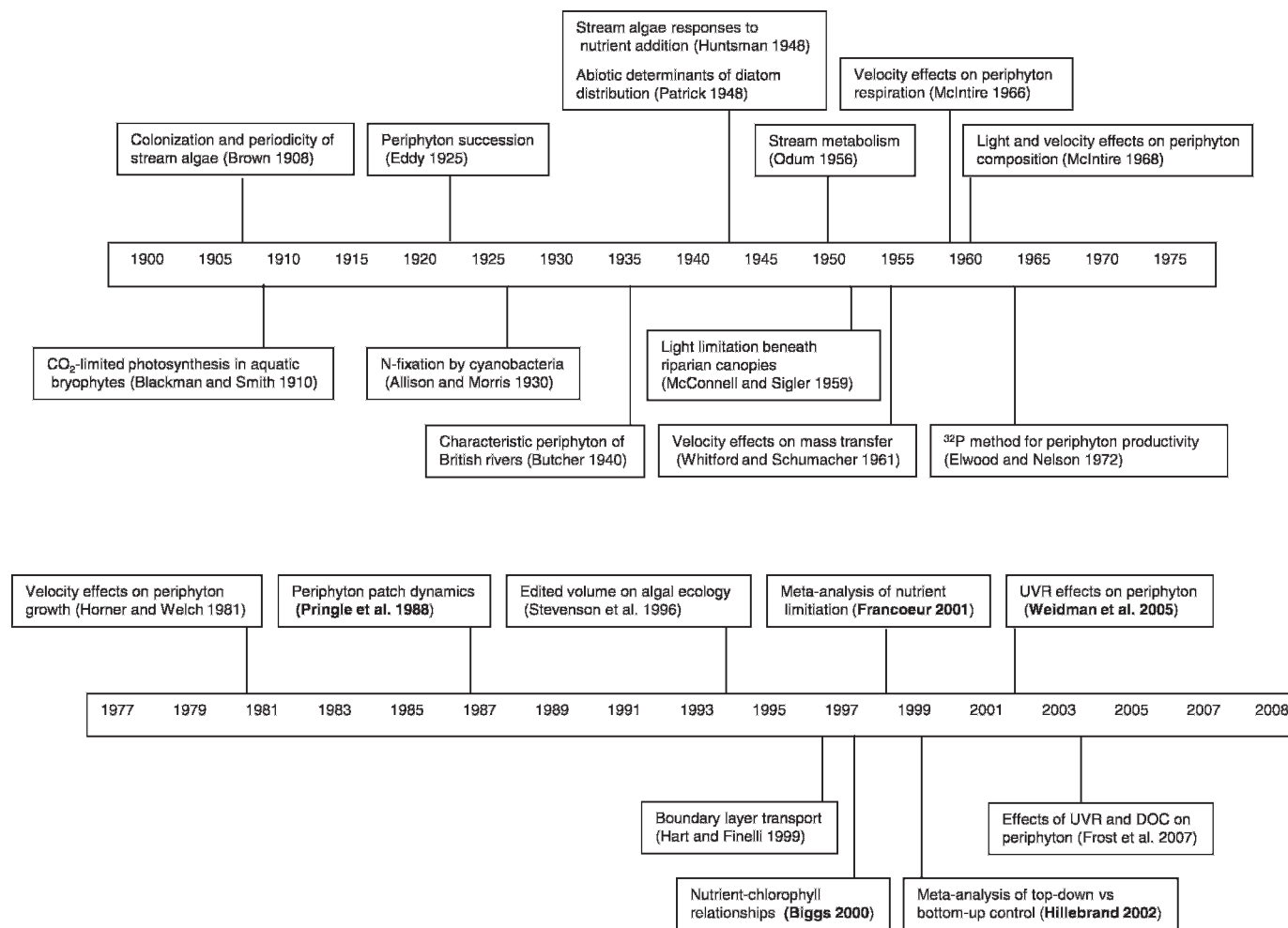


FIG. 1. Selected publications in periphyton ecology from the early 20th century to the present. This timeline illustrates the diversity of research topics, not the original, most important, or most highly-cited publications. Bold font indicates paper was published in *J-NABS*.

the roles of periphyton in nutrient cycling in food webs and between abiotic pools. The last 3 topics are covered in companion reviews on interspecific interactions (Holomuzki et al. 2010¹), biomonitoring (Dolédec and Stutzner 2010), and nutrient dynamics (Mulholland and Webster 2010), and are not discussed here. An additional topic in this review is the influence of hydraulic conditions (e.g., drag forces and turbulence) on periphyton. Despite an encouraging review in *J-NABS* (Statzner et al. 1988), studies of periphyton-hydraulic interactions are uncommon. Because *J-NABS* is one of the principal journals in periphyton ecology, the specific contributions of *J-NABS* articles to the topics in this review are highlighted at the end of each topic section.

¹ Boldface indicates paper was published in *J-NABS*

A Brief History

My review is focused on research in periphyton ecology over the last 25 y (since the start of *J-NABS* in 1986), but biologists have studied periphyton for far longer. The origins of periphyton ecology are difficult to identify precisely because benthic algae have been used for centuries as model systems for studies of phototropism, light limitation, and other problems in ecophysiology (e.g., Blackman and Smith 1910, Allison and Morris 1930; Fig. 1). Two of the earliest reports from periphyton field studies (Fritsch 1906, Brown 1908 [Fig. 1]) concern seasonal variation in the growth and composition of stream and pond algae. Similar descriptive studies dominated the field for several decades (e.g., Transeau 1916, Eddy 1925 [Fig. 1], Butcher 1932). In the 1940s, 2 new research areas emerged: the effects of abiotic factors on periphyton composition and abundance, and the use

of periphyton communities as indicators of stream health. Ruth Patrick (Academy of Natural Sciences, Philadelphia) and R. W. Butcher (British Ministry of Agriculture and Fisheries) were pioneers of both areas (Butcher 1940 [Fig. 1], 1947, Patrick 1948 [Fig. 1], 1949). Periphyton ecology in the modern sense (e.g., manipulative experiments and multiple response and explanatory variables) began in the 1950s and expanded rapidly. This period coincided with the development of radiotracers and other technologies, a growing awareness of human impacts on the environment, and a focus on freshwater ecosystems by systems ecologists (e.g., Odum 1956; Fig. 1). The new technologies facilitated research in stream metabolism and organic matter budgets (Odum 1956, 1957, Teal 1957, McIntire 1966 [Fig. 1]), light-limited primary production (McConnell and Sigler 1959; Fig. 1), and nutrient uptake by periphyton (Whitford and Schumacher 1961; Fig. 1). Some of the seminal field studies of lotic periphyton and grazing, succession, and nutrient cycling were published between the late 1950s and the early 1970s (e.g., Douglas 1958, Tippet 1970, Elwood and Nelson 1972 [Fig. 1], Horne and Carmiggelt 1975). During this period, the Hubbard Brook Ecosystem Study, the Walker Branch Watershed Project, and other ecosystems research programs provided logistical support for a large cohort of stream ecologists, including periphyton specialists. The mid-1970s to late 1990s were characterized by rapid growth in studies of natural disturbances and light and nutrient limitation. A remarkable number of these studies were published in *J-NABS*; among the most frequently cited are Lowe et al. (1986), Pringle et al. (1988; Fig. 1), Grimm and Fisher (1989), Mulholland et al. (1991), McCormick et al. (1996), and Biggs et al. (1999a). Since the late 1990s, the number of disturbance and resource-limitation studies in *J-NABS* and other aquatic ecology journals has declined, presumably because of shifts in research agendas and funding.

The last decade has seen continued growth in periphyton ecology and new conceptual models about the development of periphyton communities and their responses to the external environment. One of the most intriguing new models is the microbial (or periphyton) landscape, which views periphyton communities as dynamic structures with spatially distributed populations, shifting zones of biogeochemical activity, and continual community–environment feedback (Battin et al. 2003, 2007, Arnon et al. 2007, Besemer et al. 2007, Kühl and Polerecky 2008). A corollary of the periphyton landscape perspective is that processes traditionally associated with large-scale landscape ecology, such as metapopulation dynamics

and taxonomic turnover, can also be applied to periphyton landscapes at μm - or mm -scales (Battin et al. 2007).

Many of the advances in periphyton ecology in the last decade were made possible by parallel advances in technology. Microelectrodes and optodes allow researchers to make detailed biogeochemical profiles within periphyton mats (Kühl and Polerecky 2008). Acoustic and optical velocimeters are used to characterize hydraulic conditions near and within periphyton communities, and boundary-layer transport to and from periphyton (Hart and Finelli 1999 [Fig. 1], Larned et al. 2004). Confocal laser scanning microscopy has influenced the periphyton–landscape perspective by making fine-scaled studies of intact periphyton structures possible (Larson and Passy 2005). The development of pulse-amplitude modulated (PAM) fluorometers in the 1980s allowed ecologists to measure photosynthetic performance in periphyton communities in situ and without instrument interference. Applications of PAM fluorometry in periphyton ecology quickly diversified and now range from toxicology to light and nutrient limitation (Vopel and Hawes 2006, Muller et al. 2008).

Physical Disturbances

Ecologists generally define physical disturbances as episodic events that remove organisms at rates faster than rates of accrual or recruitment (Peterson 1996, Biggs et al. 1999a, Stanley et al. 2010). In earlier studies, including a widely cited *J-NABS* review (Resh et al. 1988), disturbances were defined as unpredictable events, and were distinguished from predictable events, such as spring snowmelt. The rationale for this restricted definition was that motile aquatic organisms might be genetically programmed to avoid deleterious predictable events (Townsend and Hildrew 1994). For immobile periphyton, no clear thresholds separate predictable and unpredictable disturbances, and the restricted definition is unnecessary.

In broad terms, physical disturbances that affect periphyton include desiccation, anoxia, freezing, rapid changes in osmotic potential, acute contaminant exposure, substrate movement, and rapid increases in hydraulic forces, heat, and light. Hydraulic forces, substrate movement, and desiccation are frequently studied by periphyton ecologists, and their effects are the focus of this section. Periphyton responses to long-term, sublethal exposure to contaminants and other stressors are discussed in the following section. Separating stresses and disturbances on the basis of

duration is artificial, but it highlights the need to consider disturbances in the context of periphyton generation times and rates of community succession. Taxa with generation times shorter than disturbance recurrence intervals are likely to be more resilient to those disturbances than taxa with longer generation times (Steinman and McIntire 1990). Similarly, periphyton communities characterized by rapid succession are likely to be more resilient than those characterized by slow succession or many seral stages (Fisher et al. 1982, Poff and Ward 1990).

Periphyton responses to physical disturbances are typically assessed in 2 phases, responses to the onset and duration of disturbance, and responses to the cessation of disturbance. Responses to the onset of disturbance are related to susceptibility or resistance (e.g., periphyton biomass loss and changes in metabolism and taxonomic composition). Responses to the cessation of disturbance are related to recovery and resilience (e.g., regrowth, recolonization, and the degree to which similar communities develop during each recovery phase).

Responses to the onset of disturbances

Field and laboratory investigations indicate that susceptibility to hydraulic disturbances (e.g., elevated shear stress) is influenced by periphyton growth form and age, magnitude of disturbance, rate of onset, and the hydraulic conditions under which periphyton communities develop (Peterson and Stevenson 1992, Biggs and Thomsen 1995). For a given community, a hydraulic threshold exists beyond which structural failure occurs. Biomass loss is rarely a linear function of disturbance intensity or duration; most biomass loss occurs immediately after the threshold is exceeded (Biggs and Thomsen 1995, Francoeur and Biggs 2006). Highly susceptible growth forms include chain-forming diatoms, uniseriate filaments, and loosely-attached cyanobacterial mats, and highly resistant forms include prostrate diatoms, and chlorophyte basal cells and rhizoids (Grimm and Fisher 1989, Biggs et al. 1998a, Benenati et al. 2000, Passy 2007). Susceptibility of periphyton to hydraulic disturbance generally increases as intervals between disturbances increase. When disturbances are infrequent, thick mats develop with weak attachment to substrata because of basal cell senescence; these mats can be removed by small increases in shear stress (Power 1990, Peterson 1996). Information about thresholds for periphyton removal is important for designing environmental flows intended to remove periphyton proliferations in regulated rivers (Biggs 2000 [Fig. 1], Osmundson et al. 2002).

In addition to the direct effects of increased shear stress, elevated flows affect periphyton by increasing sediment mobility, which leads to abrasion by suspended sediment and substrate tumbling (Grimm and Fisher 1989, Uehlinger 1991, Biggs et al. 1999a). In field studies, the direct effects of shear stress are rarely distinguished from the effects of sediment movement. However, Biggs et al. (1999a) identified natural conditions in which these factors vary somewhat independently. In armored stream reaches, sediment mobility at a given bed shear level is lower than in depositional reaches, and both reach types occur over a wide range of flood regimes. Biggs et al. (1999a) used 12 streams to create a natural factorial experiment with sites with high or low sediment mobility and high or low flood frequencies (a proxy for bed shear stress). Sediment mobility strongly affected periphyton biomass in their study, but flood frequency had no detectable effect. Subsequent field and flume studies with varied sediment and velocity levels support the view that sediment abrasion and tumbling dominate the negative effects of floods on periphyton (Francoeur and Biggs 2006, Lepori and Malmqvist 2007).

Periphyton responses to the onset of desiccation vary with mat or biofilm thickness, physiognomy, taxonomic composition, and production of extracellular mucilage, among other factors (Hawes et al. 1992, Blinn et al. 1995, Stanley et al. 2004, McKnight et al. 2007, Ledger et al. 2008). In some taxa, the onset of desiccation triggers protective physiological responses, such as encystment, cell-wall thickening, and synthesis of osmolytes that increase resistance to changes in osmotic potential. Broad taxonomic differences in desiccation resistance are clearly seen in dam tailwaters, which are alternately exposed and submerged by operating flows. Shallow tailwaters with frequent exposure often are dominated by sheathed cyanobacteria and deep, rarely exposed areas by susceptible taxa, such as *Cladophora* (Blinn et al. 1995, Benenati et al. 1998). In general, desiccation resistance is high in mucilaginous cyanobacteria and diatoms, and low in chlorophytes, rhodophytes, and nonmucilaginous diatoms. Exceptions include desiccation-tolerant chlorophytes that occur in both terrestrial and aquatic habitats, such as *Chlorella*, *Klebsormidium*, and *Trebouxia* (Morison and Sheath 1985, Gray et al. 2007).

Responses to the cessation of disturbances

Periphyton communities recover from hydrodynamic disturbances by recolonization or by regrowth from persistent cells. The relative importance of these

pathways has been partially evaluated by comparing periphyton biomass accrual on newly exposed substrata (colonization only) with that on substrata containing persistent tissue (colonization plus regrowth) (Hoagland et al. 1986, Dodds et al. 1996, Downes and Street 2005). Colonization dominates recovery when substrata are overturned during floods, exposing previously buried surfaces. Regrowth might dominate when substrata are abraded, but not overturned. Community succession on newly exposed substrata depends on the composition of the propagule pool (Peterson 1996). Succession on substrata with persistent cells depends on the rate of regrowth and interactions between resident taxa and propagules. In the latter case, macroalgae with persistent basal crusts (e.g., *Stigeoclonium*) often dominate early successional stages (Power and Stewart 1987).

Recolonization and regrowth are also the pathways by which periphyton recover from emersion and desiccation. Stanley et al. (2004) predicted that recolonization is the main recovery pathway following rapid drying (e.g., downstream of hydroelectric dams), because resident periphyton have insufficient time for protective physiological responses. Recovery by regrowth might be more important at sites with gradual water loss caused by seepage or evaporation.

Physiological recovery from desiccation has been measured in many environments and periphyton taxa. The premier examples are cyanobacterial mats in Antarctic and Mediterranean streams. Upon rewetting, these mats reach pre-emersion photosynthetic rates in minutes (Vincent and Howard-Williams 1986, Hawes et al. 1992, Romani and Sabater 1997, McKnight et al. 2007). Mechanisms that promote such rapid recovery include osmotic changes that reduce membrane and organelle damage and antioxidant production (Potts 1999, Gray et al. 2007).

Interactions between disturbances and resource availability

Several field surveys and laboratory stream studies have been motivated by observations of elevated nutrient concentrations during floods (Grimm and Fisher 1989, Mulholland et al. 1991, Humphrey and Stevenson 1992, Peterson et al. 1994, Biggs et al. 1999b, Biggs and Smith 2002, Riseng et al. 2004). In these cases, periphyton experiences both the negative effects of sediment movement and the positive effects of nutrient enrichment. Two general hypotheses have been tested: 1) that nutrient limitation increases periphyton susceptibility to disturbances, and 2) that nutrient enrichment hastens recovery following floods. In field surveys, the direct effects of flood

disturbances and nutrient levels have been confounded by variation in bed armoring and herbivory (Biggs and Smith 2002, Riseng et al. 2004). In laboratory experiments, the direct effects of increased flow or scour were significant, but the effects of nutrient concentrations on biomass loss during disturbances and on subsequent recovery were generally small or undetectable, particularly when concentration differences among treatments were relatively small (Mulholland et al. 1991, Humphrey and Stevenson 1992, Peterson et al. 1994). The study by Biggs et al. (1999b) was an exception; a 10-fold increase in NO_3^- concentration and a 4-fold increase in dissolved reactive P (DRP) concentration 10 d before and 2 to 9 d after a scouring flood significantly reduced periphyton biomass loss in experimental streams and reduced the time required for biomass to return to predisturbance levels. Most disturbance \times resource studies have addressed periphyton responses to floods and nutrient availability, but Wellnitz and Rader (2003) combined floods with variation in light level and grazing intensity and reported several 3-way (flood \times light \times grazing) interactions.

Contributions of J-NABS

The roles of physical disturbances in periphyton community structure and succession have been major themes in *J-NABS* for most of its history. This research began before *J-NABS* (e.g., Douglas 1958), but many of the subsequent experiments and syntheses were reported in *J-NABS* (e.g., Pringle et al. 1988, Grimm and Fisher 1989, Townsend 1989, Sinsabaugh et al. 1991, Cooper et al. 1997, Stevenson 1997a, Lake 2000). The patch dynamics concept was used in some of these papers to help explain complex community-level responses to disturbances (Winemiller et al. 2010). This concept has been the basis of several influential hypotheses in periphyton ecology, including: 1) spatial patchiness increases diversity at interpatch scales (Lake 2000, Hagerthey and Kerfoot 2005); 2) fine-scaled patchiness increases variability in larger-scale processes, such as nutrient spiraling (Pringle et al. 1988); 3) sizes and configurations of periphyton patches are determined by processes operating at multiple scales, including turbulent flow and sediment movement (Sinsabaugh et al. 1991). One limitation of the patch dynamics concept is that it is viewed from a planar perspective. Stream channels and lake basins are concave, and vertical gradients exist in the durations and frequencies of emersion and other disturbances. These gradients should produce vertical zonation in periphyton communities along channel and basin cross-sections. Vertical zonation

has been reported in dammed rivers, where operating flows for power generation cause frequent depth changes (Benetati et al. 1998, Burns and Walker 2000), and in lakes subject to wave disturbances (Hoagland and Peterson 1990). No comparable cases of flow-driven vertical zonation have been reported for natural streams and rivers.

Among the notable contributions of *J-NABS* papers to disturbance ecology are studies of simultaneous negative and positive effects of hydrological disturbances on periphyton (e.g., **Humphrey and Stevenson 1992**, **Biggs et al. 1999a**, **Riseng et al. 2004**). These disturbances remove organisms, but they also generate resources (e.g., nutrients and bare substrate), alleviate competition, and transport propagules. The responses of periphyton populations and communities to disturbances reflect the balance between increased mortality and emigration, and increased growth, reproduction, and immigration (**Stevenson 1990**). The *J-NABS* papers have contributed to the modern view of hydrological disturbances as complex phenomena with pervasive ecological effects in all but the most stable streams.

The intermediate disturbance hypothesis has also been used as a working model in periphyton studies published in *J-NABS* (**McCormick and Stevenson 1989**, **Suren and Duncan 1999**) and other journals (Fayolle et al. 1998, Biggs and Smith 2002). These studies focused on patterns of diversity-disturbance relationships, and whether those patterns confirmed the prediction of peak diversity at intermediate disturbance levels. Most of the studies were correlative, and the proximate causes of diversity-disturbance patterns could not be confirmed. As **Lake (2000)** noted, biodiversity is not controlled by disturbance alone, but by combinations of disturbance, resource supply, reproduction, and other processes. How disturbances interact with other biological and ecological processes, and how these interactions control species coexistence are central questions in community ecology (Agrawal et al. 2007). The high diversity and ease of manipulation of periphyton communities make them ideal systems for addressing those questions experimentally (**Steinman 1993**).

Exposure to Stressors

Ultraviolet radiation

Ultraviolet radiation (UVR) is a frequently studied stressor in phytoplankton ecology, but is less frequently studied in periphyton ecology. Current knowledge of UVR effects on aquatic autotrophs comes primarily from phytoplankton studies. For periphyton, UVR exposure varies with riparian

shading, water depth, and dissolved and particulate suspended matter (Vinebrooke and Leavitt 1998, **Kelly et al. 2001**, 2003, **Frost et al. 2005**, **Weidman et al. 2005** [Fig. 1]). UVR exposure also varies during succession in periphyton communities because of self-shading (**Kelly et al. 2001**, Tank and Schindler 2004). Variable exposure makes measuring UVR at realistic scales challenging. In most field studies, UVR measurements are made above periphyton surfaces with large (>50-cm tall) spectrophotometers. More realistic measurements at periphyton surfaces and within periphyton matrices will require microprobes (Garcia-Pichel 1995).

Molecular and physiological studies of the effects of UVR on aquatic photoautotrophs have focused on damage to deoxyribonucleic acid (DNA) and D1, the main structural protein of photosystem-2. DNA damage delays mitosis, and damage to D1 reduces electron transport and slows the generation of reducing power for C fixation (Grzymiski et al. 2001, Helbling and Zagarese 2003). Collectively, these changes can reduce growth rates, but studies of UVR-effects on periphyton growth have had mixed results. Growth in UVR-exposed periphyton was suppressed in some laboratory and field studies (Bothwell et al. 1993, **Kiffney et al. 1997**, Frost et al. 2007 [Fig. 1]), but no effects were detected in other field studies (**DeNicola and Hoagland 1996**, Hill et al. 1997, Hodoki 2005, **Weidman et al. 2005**). The generally weak effects of UVR on periphyton growth have been attributed to protective UVR-absorbing compounds, rapid repair of UVR-induced damage, self-shading, attenuation by tree canopies and water, and solar trophic cascades (Bothwell et al. 1994, Francoeur and Lowe 1998, Frost et al. 2007). Solar trophic cascades occur when the negative effects of UVR on herbivores reduce grazing losses in periphyton, compensating for direct negative effects of UVR on periphyton (Bothwell et al. 1994). As with periphyton growth, UVR exposure at natural levels appears to have moderate to undetectable effects on periphyton taxonomic composition (**DeNicola and Hoagland 1996**, Vinebrooke and Leavitt 1996, Tank and Schindler 2004). Long-term exposure to elevated UVR leads to shifts in periphyton communities to a predominance of UVR-tolerant taxa (Vinebrooke and Leavitt 1996, Navarro et al. 2008). A comparison of the responses of UVR-tolerant and UVR-sensitive periphyton to Cd exposure indicated that UVR-tolerant periphyton were also relatively Cd-tolerant (Navarro et al. 2008). UVR exposure and metal exposure both induce reactive O₂ in algal cells, and UVR-Cd cotolerance might be caused by similar physiological responses

to both stressors, including enhanced antioxidant activity (Prasad and Zeeshan 2005).

Thermal stress

Optimal temperatures for growth of hot-spring algae can be $>50^{\circ}\text{C}$ (Ciniglia et al. 2004, Liao et al. 2006), but optimal temperatures for most periphyton range from 10 to 30°C , and higher temperatures induce heat stress and reduce growth (DeNicola 1996). Direct physiological effects of high temperatures include protein and nucleic acid denaturation, photosystem degradation, and respiration in excess of C fixation (Davison 1991, Wahid et al. 2007).

Optimal growth temperatures and maximum temperatures for survival bracket the high-temperature tolerance ranges of periphyton. Some evidence indicates that heat tolerance varies among major taxa. Cyanobacteria generally tolerate higher temperatures ($>30^{\circ}\text{C}$) than do chlorophytes, which tolerate higher temperatures than do diatoms and rhodophytes (DeNicola 1996). Variation in tolerance suggests that thermal regimes influence spatial patterns in periphyton communities. Surveys along thermal gradients created by coolant water outfalls and geothermal springs provide some support for this proposition, with cyanobacteria dominant near thermal sources and diatoms dominant in cooler distal reaches (Squires et al. 1979, Bonny and Jones 2003). Additional support comes from heated artificial streams, in which rhodophytes were eliminated at temperatures 12.5°C above ambient, and cyanobacteria dominated at temperatures $>30^{\circ}\text{C}$ (Wilde and Tilly 1981). Last, the effect of water temperature is often significant in multivariate analyses of geographic or seasonal variation in periphyton composition (e.g., Wehr 1981, Griffith et al. 2002). However, other environmental factors covary with temperature, and controlled experiments are the best means of assessing direct thermal effects.

pH stress

Studies of stream and lake acidification generally focus on the effects of anthropogenic acidification caused by mine drainage and fallout from smelters and power plants. Many sources of natural acidification exist (e.g., wetland outflows, volcanic ashfall, pyrite weathering), but these have received less attention as stressors (for exceptions, see Sheath et al. 1982, Sabater et al. 2003, Baffico et al. 2004). Naturally acidic freshwater environments are inhabited by acidophilic periphyton (DeNicola 2000, Gross 2000). The taxa that make up these communities tend to share some physiological traits, including efficient

C uptake (to cope with low inorganic C concentrations), and tolerance or resistance to proton influx through cell membranes—a necessity in H^{+} -rich environments (Gross 2000). At sites of recent, anthropogenic acidification, the original periphyton communities are often replaced by depauperate communities of acidophilic chlorophytes and diatoms (Turner et al. 1991, Verb and Vis 2000, Greenwood and Lowe 2006). Recovery of algal diversity and reduction in acidophile dominance are indicators of success in remediation of acidified ecosystems (Vinebrook 1996, Vinebrooke et al. 2003).

The direct effects of acidification on algal cells are not well known, but might include osmotic stress and disruption of cell division (Gross 2000, Visviki and Santikul 2000). In addition to direct toxic effects, acidification increases exposure to other stressors. Stream acidification often is accompanied by metal dissolution and subsequent deposition of metal hydroxides downstream of the acid source. Acidic freshwater typically is enriched in dissolved Fe, Zn, Ni, Hg, Al, and other metals. Potential negative effects of dissolved metal exposure include alterations in membrane permeability, inhibition of photosynthetic electron transport, and metal–phosphate coprecipitation, which can reduce P availability (Pettersson et al. 1985, Genter 1996, Kinross et al. 2000). Deposition of oxidized metals in moderately acidic streams eliminates many periphyton taxa and favors a small number of tolerant taxa (e.g., *Ulothrix*, *Mougeotia*, and *Zygonium*) (Niyogi et al. 1999, 2002, Kleeberg et al. 2006). The properties of these algae that confer tolerance to oxidized metal deposition are unknown, but might include growth rates that exceed the rate of deposition, or mucilaginous sheaths that prevent deposition.

Contributions of J-NABS

Studies of abiotic stressors published in *J-NABS* tend to focus on multivariable problems, rather than direct effects of single stressors. For example, Fairchild and Sherman (1993) used nutrient-diffusing substrata in 12 lakes representing a broad acidity gradient (pH 4.4–8.8) to explore the combined effects of acidification and nutrient limitation on periphyton growth and composition. Their results suggested that C enrichment enhanced periphyton growth, which lends support to the hypothesis that acidification causes C limitation. Several *J-NABS* papers that addressed periphyton responses to multiple stressors (e.g., acidity, herbivory, and nutrient limitation) used exploratory multivariate analyses (Vinebrook 1996, Naymik et al. 2005, Cao et al. 2007, Stevenson et al.

2008). Responses to individual stressors were not identified or quantified in these studies because of covariance or because ordination axis scores were the only dependent variables reported. Vinebrook (1996) used reciprocal periphyton transplants and herbivore enclosures to study periphyton responses to a lake acidity gradient. This approach controlled for effects of herbivory and colonization sources, but the direct effect of acidity could not be separated from other abiotic factors that varied among lakes or from enclosure artifacts. Complex periphyton responses to multiple stressor gradients are important in environmental monitoring programs and indicator analyses, but it is also important to identify and quantify univariate periphyton–stressor relationships. The latter are needed to predict the effects of stressor exposure, detect trends, and identify mechanisms by which stressors affect periphyton.

Limiting Abiotic Factors

Periphytic organisms vary in their minimum resource requirements for survival because of differences in physiology and morphology, e.g., diatoms have high Si requirements and N₂-fixing cyanobacteria have high Mo requirements compared with other major taxonomic groups (Stal 1995). These differences are well established for many planktonic algae, for which minimum cell quotas for nutrients and compensation light intensities have been defined in culture (Reynolds 2006). Minimum resource requirements are unknown for most periphyton taxa, but these requirements are certain to vary as they do for phytoplankton (Hill 1996).

Transient changes in physiological condition and growth form lead to short-term variation in periphyton resource requirements (Graham et al. 1995, Hillebrand and Sommer 1999). For example, nutrient-replete periphyton might have higher light-saturated photosynthetic rates and higher photosynthetic efficiencies than nutrient-deficient periphyton (Taulbee et al. 2005, Hill and Fanta 2008). However, the scarcity of autecological studies of periphyton makes predicting changes in resource requirements difficult. Resource-limitation studies generally address responses of whole periphyton communities, not individual taxa. It is implicit in community studies that aggregate responses of multiple taxa are being measured, and these responses might include changes in taxonomic composition and relative abundance (e.g., Lohman et al. 1991, Hill and Fanta 2008). Specific responses depend on the time scale of resource variation. Responses to short-term (<1 d) variation in resources are primarily physiological

(e.g., Wellnitz and Rinne 1999). Responses to long-term variation, such as month-long nutrient additions, are dominated by biomass and taxonomic changes (e.g., Harvey et al. 1998). Responses to very long-term (mo–y) variation include secondary effects, such as species turnover and changes in foodweb structure (Blumenshine et al. 1997, Slavik et al. 2004). The following discussion considers the main effects of light-, temperature- and nutrient-limitation on periphyton communities, and pairwise interactions between these factors.

Light limitation

Most periphytic organisms are obligate photoautotrophs that use sunlight to generate reducing power and dissolved inorganic C to produce carbohydrates. Some periphyton taxa are facultative photoheterotrophs (sunlight + organic C substrates) or chemoor-ganoheterotrophs (organic compounds for reducing power + organic C substrates). Nutrient assimilation in photoautotrophs is catalyzed by chemical energy in C compounds, and light energy is required to produce those compounds. Consequently, nutrient limitation is detected frequently under high-light conditions and rarely under low-light conditions (Hill and Knight 1988, Bourassa and Cattaneo 2000, Larned and Santos 2000, Greenwood and Rosemond 2005).

Facultative heterotrophy has been proposed as a mechanism that allows periphyton communities to persist under severe light limitation (Tuchman 1996, Tuchman et al. 2006). Heterotrophy is energetically favored only at high dissolved organic C (DOC) concentrations, so facultative heterotrophy should be restricted to dark, DOC-rich environments, such as lake sediments and the interiors of dense periphyton mats.

The influence of riparian tree canopies on light transmission to stream periphyton has been a prominent research topic since the 1950s (e.g., McConnell and Sigler 1959, Hansmann and Phinney 1973, Hill and Knight 1988, DeNicola et al. 1992, Larned and Santos 2000, Hill and Dimick 2002, Ambrose et al. 2004). Most of these studies were categorical comparisons of periphyton under canopy gaps (high light) or dense canopies (low light). Studies that use continuous gradients in riparian light transmission provide more information about complex responses to light input. For example, Hill and Dimick (2002) measured in situ periphyton photosynthesis over the wide irradiance range created by a heterogeneous forest canopy and reported nonlinear effects of irradiance on photosynthetic efficiency, photosaturation, light utilization efficiency, and pigment concentrations. Heavily shaded photoautotrophs undergo a physio-

logical process of photoacclimation that increases photosynthetic efficiency at low light levels and reduces the irradiance required for maximum photosynthesis (Hill 1996).

At finer spatial scales, the 3-dimensional structure of periphyton communities causes variation in light transmission to cells within the community matrix. Vertical light attenuation increases with increasing periphyton density and thickness (Meulemans 1987, Dodds 1992, **Johnson et al. 1997**). Presumably, algae at the bases of periphyton mats are shade-acclimated. Supporting evidence for this assumption includes reports of increased photopigment concentrations at mat bases (Tuchman 1996) and a positive relationship between photosynthetic efficiency and depth in a filamentous periphyton mat (Dodds 1992).

Temperature limitation

Thermal energy is not a resource in the strict sense; it is not consumed and is not an object of competition. However, periphyton (like all organisms) requires thermal energy for enzyme-catalyzed reactions, and thermal energy deficits can limit growth and other physiological processes. Algal photosynthesis and growth respond unimodally to temperature variation, as they do to light variation (Graham et al. 1995, O'Neal and Lembi 1995). Temperatures corresponding to maximum photosynthesis and growth in freshwater algae (excluding extremophiles such as hot-spring algae) range from 10 to 30°C (Butterwick et al. 2005). This range suggests that thermal energy could be a limiting or colimiting factor in cold climates. Empirical models for periphyton indicate that photosynthetic rates increase with temperature over a 5 to 25°C range (**Morin et al. 1999**), and experimental results indicate positive relationships between light-saturated photosynthesis and temperature, with a rate of change caused by a 10°C increase in temperature ($Q_{10} \geq 2$) (DeNicola 1996). Temperature acclimation can reduce the severity of temperature limitation. Algae that are acclimated to low temperature have higher maximum photosynthetic rates, lower temperature optima for photosynthesis, and higher concentrations of C-fixing enzymes than nonacclimated algae (Davison 1991).

Thermal energy is unlikely to be the sole limiting factor for periphyton under natural light and nutrient levels. Temperature acclimation incurs nutrient costs for increased enzyme synthesis, and low temperatures might lead to nutrient limitation rather than temperature limitation per se. Thermal energy could be the sole limiting factor under light- and nutrient-

replete conditions (DeNicola 1996), but these conditions are rare in natural aquatic systems.

Nutrient limitation

Nutrient limitation is one of the best-studied topics in periphyton ecology. The high level of interest in nutrient limitation reflects concern about eutrophication and recognition of the role of nutrient limitation in community and ecosystem processes (Rosemond 1993, Smith et al. 1999, **Hillebrand 2002** [Fig. 1], **Holomuzki et al. 2010**). Studies of nutrient limitation in periphyton generally focus on macronutrients (e.g., N, P, Fe, Si), and rarely on micronutrients (e.g., Mo, B, Zn) (but see Pringle et al. 1986). Nutrients that are in low demand relative to availability (e.g., K, Mg) are rarely limiting. Other nutrients (e.g., N, P, Si) are frequently limiting because demand is high relative to availability. For a 3rd class of nutrients (e.g., Fe, Ca), great taxonomic and geographical variation in demand and availability suggests that limitation ranges from negligible to severe.

A common goal in nutrient limitation studies is to identify a single nutrient that controls periphyton growth because its availability relative to demand is lower than any other nutrient. The concept of single-nutrient limitation is enshrined in Liebig's Law of the Minimum, which states that plant yield declines as the scarcest nutrient is depleted (De Baar 1994). The expectation that periphyton growth will be limited by a single nutrient might have originated with influential studies of single-nutrient limitation in phytoplankton cultures (Droop 1974). Comparable results are not always observed in periphyton studies, in which N, P, or other nutrients can be colimiting (**Francoeur et al. 1999**, **Dodds and Welch 2000**, **Francoeur 2001** [Fig. 1]).

Discrepancies between Liebig's Law of the Minimum and experimental results for periphyton have several causes. In some studies, multiple-nutrient enrichment causes switching between single limiting nutrients. A more fundamental discrepancy is *community colimitation*, which occurs when periphyton communities contain taxa that are limited by different nutrients, and multiple-nutrient enrichment enhances growth in more taxa than single-nutrient enrichment. Community colimitation often occurs in natural phytoplankton communities, as indicated by differential nutrient limitation assays (Arrigo 2005, Danger et al. 2008, Saito et al. 2008). Community colimitation appears to be common in periphyton (**Francoeur 2001**), but differential nutrient limitation in periphyton is rarely tested (**Fairchild and Sherman 1993**).

Nutrient limitation has been assessed in many periphyton studies, using several different methods. Differences in methods can affect the outcomes of these studies, and obscure general patterns (**Francoeur 2001**). Examination of ambient nutrient concentrations is the most economical method for assessing nutrient limitation, but it has some short-comings. Periphyton growth rates are not always positively correlated with ambient nutrient concentrations. In fact, growth–nutrient relationships can be inverse because of ambient nutrient depletion by fast-growing periphyton (Welch et al. 1988, Stevenson et al. 2006). Different molecular forms of a given nutrient vary in bioavailability, which increases uncertainty in concentration–growth relationships (Saito et al. 2008). Ratios of 2 or 3 ambient nutrient concentrations (e.g., N:P:Si) provide information about their relative availability, but not about the nutrient requirements for periphyton growth (**Francoeur et al. 1999**, Stelzer and Lamberti 2001). Cellular nutrient concentrations and ratios may be used in lieu of ambient nutrients to assess nutrient limitation (e.g., Hillebrand and Sommer 1999), but these measures can also be unreliable. Periphyton taxa and communities vary in nutrient storage capacity, and it is rarely clear whether cellular nutrient levels reflect nutrient storage capacities or nutrient requirements for growth.

Experimental nutrient addition is generally a more reliable method for assessing nutrient limitation than examinations of nutrient concentrations. Nutrient additions have been used in periphyton studies for 60 y, starting with Huntsman (1948; Fig. 1). Most of these studies used nutrient diffusing substrata (NDS) that release dissolved nutrients from enriched media into porous substrata on which periphyton attaches and grows (e.g., **Coleman and Dahm 1990**, **Francoeur et al. 1999**). Limiting nutrients are then identified by comparing the biomass on substrata enriched with different nutrients. Other studies have used whole-stream nutrient enrichment (Peterson et al. 1993, Greenwood and Rosemond 2005). Two general issues are addressed in nutrient addition studies: whether periphyton growth is nutrient-limited (and by which nutrients), and the effects of nutrient limitation on periphyton community composition and succession. The 1st issue is usually addressed with NDS deployments that are brief enough to prevent switching between limiting nutrients, generally <1 mo.

The 2nd issue, concerning nutrient-limited community development, is addressed with long NDS deployments or whole-stream enrichment. The results of these studies indicate that nutrient availability influences periphyton succession and mediates inter-specific interactions. One of the clearest examples of

these effects comes from a comparison of NO_3^- -enriched and unenriched substrata in Sycamore Creek, Arizona (**Peterson and Grimm 1992**). In that study, unenriched substrata were dominated by diatoms with N_2 -fixing endosymbiotic cyanobacteria during early successional stages, and by N_2 -fixing cyanobacteria during later stages. NO_3^- -enriched substrata were initially colonized by non- N_2 -fixing diatoms and filamentous chlorophytes and later, by cyanobacteria. Seral stages were more apparent, and diversity higher, on NO_3^- -enriched substrata than on unenriched substrata. General relationships between periphyton diversity and the availability of limiting nutrients are still elusive; enrichment experiments have resulted in increased, decreased, and unchanged diversity (**Carrick et al. 1988**, Pringle 1990, Miller et al. 1992, **Peterson and Grimm 1992**, Greenwood and Rosemond 2005).

To sustain long-term growth, periphyton communities require nutrients from external sources to offset losses. The major pathways for external nutrient supplies are advection from the overlying water column and diffusion or upwelling from underlying substrata (Pringle 1987, **Henry and Fisher 2003**). Nutrient recycling within dense periphyton mats and biofilms can temporarily uncouple periphyton from external nutrient sources (Mulholland 1996, **Mulholland and Webster 2010**). Internal recycling cannot sustain periphyton indefinitely, but it can be surprisingly efficient over short time scales. In laboratory periphyton communities, recycling accounted for 10 to 70% of the P uptake, and daily P turnover was <15%/d (**Mulholland et al. 1995**, **Steinman et al. 1995**). Periphyton communities are likely to acquire nutrients from multiple sources simultaneously. Observations of vertical gradients in nutrient concentrations and enzyme activities within periphyton communities suggest that surface cells rely on water-column nutrient sources, whereas cells in the matrix rely on sediment-derived nutrients and recycling (Wetzel 1993, Mulholland 1996).

Calcareous periphyton mats have a unique mechanism for P recycling (Noe et al. 2003). Daytime photosynthesis raises pH levels within mats, which promotes rapid P precipitation with and adsorption to calcium carbonate. Respiration at night reduces pH levels within mats, which promotes calcium carbonate dissolution and P desorption. In a P tracer study, Noe et al. (2003) estimated that 80% of P uptake by periphyton was initially bound to Ca, and this fraction dropped to 15% after 1 d because of biotic uptake. P enrichment can lead to the replacement of calcareous cyanobacterial mats by filamentous chlorophytes, which lack the P adsorption–desorption

mechanism, but have higher growth potential (McCormick and O'Dell 1996).

Light × nutrient interactions

Tests of nutrient × light interactions have been made in natural streams with nutrient diffusing substrata and water-column enrichment beneath riparian canopy gaps and closed canopies (Lowe et al. 1986, Hill and Knight 1988, Larned and Santos 2000, Von Schiller et al. 2007) and in artificial streams with water-column enrichment and shade screens (Rosemond 1993, Bourassa and Cattaneo 2000, Hill and Fanta 2008). In the field studies, increased irradiance generally enhanced periphyton growth, nutrient enrichment had little or no detectable effect, and the nutrient × light interaction terms (when tested) were rarely significant. Possible explanations for the lack of detectable effects of nutrient enrichment included consumption of periphyton in enriched treatments by grazers and competitive inhibition by benthic heterotrophs. In contrast, Rosemond (1993), Hill and Fanta (2008), and Hill et al. (2009) reported significant main effects of both light and nutrient levels in artificial streams. Hill et al. (2009) used simultaneous gradients in DRP concentration and irradiance to quantify nutrient × light interactions. In that study, the positive effects of DRP enrichment on periphyton growth increased with increasing irradiance. Photoinhibition was apparent at high irradiance and low DRP concentrations, and DRP enrichment alleviated photoinhibition, presumably through increased synthesis of protective pigments. Colimitation at low light and DRP levels in these studies was less apparent, although a residual analysis in the study by Hill and Fanta (2008) indicated that P-enrichment enhanced growth at low light levels.

One of the predicted outcomes of nutrient-light colimitation is an increase in cellular nutrient levels with decreasing irradiance caused by the nutrient requirements of shade acclimation (Sternler et al. 1997, Hessen et al. 2002). Sternler et al. (1997) developed the light:nutrient hypothesis to explain how the balance of light energy and nutrient supplies controls algal productivity and stoichiometry in lakes. In its original formulation, the hypothesis was based on qualitative comparisons of low and high light:P ratios. High ratios were predicted to cause P limitation and low ratios to cause C limitation. The light:nutrient hypothesis was subsequently tested with periphyton by Frost and Elser (2002), Hill and Fanta (2008), and Hill et al. (2009). In these latter studies, variation in light intensity did not affect periphyton C:P ratios or

cellular P concentrations as predicted, although P-enrichment clearly increased productivity. However, Hill et al. (2009) reported a negative relationship between cellular N and light intensity, a result that suggested that N-light colimitation was in effect, not P-light colimitation. Support for the light:nutrient hypothesis as it applies to periphyton is equivocal at present, but further testing could be done by varying the concentrations of nutrients other than P.

Temperature interactions with light and nutrients

Temperature × light interactions in periphyton have been tested in several experiments (Graham et al. 1985, 1995, O'Neal and Lembi 1995). Graham et al. (1995) used a high-resolution design (58 temperature × light combinations) and reported that optimal and compensation irradiances for photosynthesis increased with temperature up to ~30°C. At higher temperatures, net photosynthesis decreased across the light gradient. Reduced photosynthesis at high temperatures is partly caused by photorespiration, as cellular CO₂ concentrations decrease with increasing temperature more rapidly than O₂ concentrations (Davison 1991).

The effects of temperature × nutrient interactions on periphyton communities have not been studied under controlled conditions. However, seasonal NDS deployments indicate that the frequency and severity of nutrient limitation increase during warm seasons (Allen and Hershey 1996, Francoeur et al. 1999). The most likely physiological basis for temperature-dependent nutrient limitation is that respiration and photosynthesis rates increase with temperature, which increases nutrient demand for C fixation, biomolecule synthesis, and other growth-related processes (Falkowski and Raven 2007).

Contributions of J-NABS

Resource-limited periphyton metabolism and growth have been the topics of many *J-NABS* papers. Several of the papers are from multivariable studies that tested for interactions between resource availability and physical disturbances or herbivory (Mulholland et al. 1991, Humphrey and Stevenson 1992, Gafner and Robinson 2007). These latter papers contributed to an emerging picture of the relative importance of processes that control periphyton growth and composition. Resource limitation is unlikely to have a strong influence if disturbances or grazing pressure maintain periphyton at low-biomass levels and early successional stages (Biggs 1996, Steinman 1996). In turn, light limitation is often more severe than nutrient limitation, as indicated by the

general lack of response to nutrient enrichment at very low light levels (e.g., **Lowe et al. 1986**, **Ambrose et al. 2004**). However, it should be noted that the primacy of light limitation in periphyton field studies might reflect the limited range of environments studied, not a strict physiological hierarchy of limiting factors. The most common environments used for comparisons of light and nutrient limitation in *J-NABS* papers were densely shaded, mesotrophic streams. Comparisons made over broader gradients (from ultraoligotrophic to hypereutrophic and from densely-shaded to full sun) might provide a more accurate view of resource limitation.

Nutrient limitation studies in *J-NABS* have focused on N, P, or both. In species-rich periphyton communities, community colimitation might involve >2 nutrients, simultaneously or sequentially (Passy 2008). Enrichment studies with multiple nutrients and tests of differential nutrient limitation among the populations in mixed-species communities have advanced our understanding of phytoplankton colimitation (Arrigo 2005). Similar studies are needed to advance periphyton ecology, although these studies could be challenging to design and interpret because of spatial variation in the forms and severity of nutrient limitation within periphyton communities (Burkholder et al. 1990, **Johnson et al. 1997**).

The NDS periphyton assay has been a popular tool for *J-NABS* contributors; NDS results appear in 15 *J-NABS* papers, and the results of 237 NDS assays were compared in a meta-analysis published in *J-NABS* (**Francoeur 2001**). In *J-NABS* papers, NDS assays were combined with a range of environmental variables, including riparian canopy removal (**Lowe et al. 1986**), lake acidification (**Fairchild and Sherman 1993**), salmon carcass addition (**Ambrose et al. 2004**), and zebra mussel invasion (**Pillsbury et al. 2002**). The NDS approach has been productive, but it has many limitations, including uncertainty about nutrient diffusion rates and whether the nutrient source simulated by NDS is the natural substrate or the overlying water (Pringle 1987, **Coleman and Dahm 1990**, **Hillebrand 2002**, **Rugenski et al. 2008**).

Hydraulic Conditions

The pervasive effects of flow on benthic organisms are evident to most aquatic ecologists. The paper that popularized the idea of flow as the master variable in lotic ecosystems has been cited >300 times (Poff et al. 1997). Experiments and field surveys have generated relationships between stream flow and periphyton for ~100 y (e.g., Brown 1908). However, it is not always clear in these studies which components of stream

flow directly affected periphyton or whether the researchers were measuring the most relevant variables. Two explanatory variables, volumetric discharge and velocity in the downstream direction, are used in most flow-biota studies. Velocity is usually measured at the water surface or at a depth thought to correspond to vertically-averaged velocity (e.g., 60% of total depth). In many cases, the measurement depth is in the outer or logarithmic portion of the benthic boundary layer (the region of water column influenced by friction at the benthos). These velocity measurements are referred to as free-stream velocities (e.g., **Poff et al. 1990**, Francoeur and Biggs 2006). Discharge and free-stream velocity might be correlated with hydraulic processes that affect benthic organisms, but they are rarely direct causes of biological changes (Biggs et al. 1998a, Hart and Finelli 1999). For example, periphyton detachment during periods of elevated discharge is not caused by free-stream velocity per se (e.g., Horner et al. 1990), but by drag and lift acting on periphyton. Spatially and temporally averaged metrics, such as discharge and free-stream velocity, do not accurately describe the hydraulic conditions that benthic organisms experience. Metrics that describe near-bed flow at spatial and temporal scales relevant to periphyton include bed shear stress and near-bed turbulence intensity (**Statzner et al. 1988**, Nikora et al. 1998a, Stone and Hotchkiss 2007).

The focus of this section is the influence of hydraulic conditions on periphyton communities. The term *hydraulic conditions* is used here to refer to the near-bed water movements that impinge on periphyton communities and is distinguished from *hydrological conditions*, which refer to stream flow regimes (**Stevenson 1997a**).

Solute transport

Studies of hydraulic effects on solute transport to or from periphyton have focused on N, P, and C uptake and O₂ release (Riber and Wetzel 1987, Borchardt 1994, Larned et al. 2004). These solutes move between the water column and periphyton in several steps: rapid, turbulent transport to and from the near-bed region, slower transport near and within periphyton matrices, mass-transfer through the viscous sublayers (VSLs) of benthic boundary layers, and transport through cell membranes. These steps can be viewed as resistors in series; the slowest step poses the greatest transport resistance and will control nutrient uptake rates (Larned et al. 2004). Transport through outer benthic boundary layers is mediated by turbulent diffusion and is rarely rate-limiting; either mass-

transfer through VSLs (by molecular diffusion) or membrane transport (by diffusion or carrier-mediated transport) limits uptake rates under most conditions. Nutrient mass-transfer rates increase as concentration gradients steepen and VSL thickness decreases. Membrane transport increases as concentration gradients steepen and carrier densities increase. Flow experiments indicate that mass-transfer can control uptake by benthic and epiphytic algae over a wide velocity range (Cornelisen and Thomas 2002, Larned et al. 2004). At low velocities, transport resistance is caused by thick VSLs that cover the benthos. At high velocities, most of the transport resistance is caused by individual VSLs that surround filaments and other structures that protrude into regions of turbulent flow (Røy et al. 2002, Larned et al. 2004).

Variation in uptake rate-limiting steps and their controls suggests that some periphyton taxa have morphological or physiological traits that maximize nutrient acquisition. For example, long filamentous and stalked algae with high surface–volume ratios (e.g., *Ulothrix*, *Audouinella*, *Didymosphenia*, *Rhizoclonium*) often occur in nutrient-poor streams (Biggs et al. 1998b, Shea et al. 2007). This pattern might be unexpected because large algae presumably have greater nutrient requirements than small algae. However, elongate algae often protrude from the near-bed region into the overlying turbulent flow, where mass-transfer resistance is lower (Steinman et al. 1992, Larned et al. 2004). In nutrient-rich water, light limitation, disturbances, and herbivory might be more important than nutrient acquisition, and elongate growth forms might not be optimal. In these environments, adaptive traits include rapid growth, shade tolerance, high reproductive output, and anti-herbivore defenses (Steinman et al. 1992, Biggs et al. 1998b).

Drag forces

Hydrodynamic drag affects periphyton colonization, growth, survival, and morphology. Some observational studies of periphyton have linked broad morphological classes (e.g., crustose, mucilaginous, densely-branched, and filamentous algae) to variation in free-stream or near-bed velocities (e.g., Parodi and Cáceres 1991, Biggs et al. 1998a). The results of these studies suggest that compact, prostrate forms represent adaptations to high-drag environments compared with filamentous and upright forms. A more rigorous approach for assessing morphology–drag relationships is to manipulate flows or transplant periphyton between hydraulic environments and observe subsequent changes in morphology and drag

forces. Such experiments are common in seaweed ecology (e.g., Koehl et al. 2008), but rare in periphyton ecology. Ironically, the sole *J-NABS* paper about effects of hydrodynamic drag on autotroph morphology concerned a terrestrial plant (Vogel 2006).

The drag force acting on periphyton has 2 components, both originating from fluid viscosity. Skin friction (or viscous drag) is caused by localized fluid shear across organism surfaces; form drag is caused by large-scale pressure variations over whole communities. Form drag is primarily influenced by the frontal area of periphyton patches, and skin friction by total surface area. Flexible periphyton reduces frontal area by bending downstream, and crusts, mats, and diatom films minimize frontal area by their low stature (Nikora et al. 1998b). Skin friction is reduced when filaments or other flexible appendages become compacted into streamlined bundles (Vogel 1994). Optimal morphologies for drag reduction (e.g., prostrate, low surface–volume ratio, compact branching, flexibility) might be different from morphologies optimized for nutrient acquisition and sun exposure (e.g., elongate, high surface–volume ratio, expansive branching, rigidity). Clearly, morphological tradeoffs are required to survive in high-velocity, resource-limited environments (Sheath and Hambrook 1988, Raven 1992). These tradeoffs can be analyzed in comparative morphology studies along resource and hydraulic gradients. Again, such comparative studies are common in seaweed and terrestrial plant ecology (e.g., Read and Stokes 2006, Haring and Carpenter 2007), but rare in periphyton ecology. The rarity of comparative studies of periphyton might be the result, in part, of the difficulties posed by manipulating small, freshwater algae, compared with large seaweeds and plants. Recent advances in instrumentation should improve the situation for periphyton ecologists (Callaghan et al. 2007).

Effects of hydraulic conditions on periphyton development

The relationship between periphyton species composition and prevailing hydraulic conditions is one of the original research problems in periphyton ecology (Butcher 1940, Patrick 1948). Hydraulic conditions affect many components of periphyton communities, not only composition. For simplicity, 2 general stages of community development are discussed here, immigration (including propagule dispersal and settlement), and post-immigration (including biomass accrual and changes in physiognomy).

The initial stages of periphyton community development are influenced by the composition and abundance of propagules in the water column, and

rates of propagule settlement (Peterson 1996). Cell division and sloughing create a constant flow of propagules to the water column (Hamilton and Duthie 1987, **Barnese and Lowe 1992**, Peterson 1996). Floods can substantially alter propagule composition and abundance in streams through increased sloughing and fragmentation and propagule dilution (Hamilton and Duthie 1987). Studies of flow-dependent periphyton dispersal are rare, and general relationships linking flow levels to propagule abundance, diversity, and settlement rates are lacking.

Negative relationships between periphyton colonization rates and free-stream or near-bed velocities have been reported in several studies, but whether these relationships reflect low rates of propagule attachment under high shear, or high rates of detachment following settlement is unclear (**DeNicola and McIntire 1991**, Stevenson 1996, Besemer et al. 2007). Another open question for periphyton ecologists is the importance of hydraulic conditions vs substrate suitability as determinants of colonization. Many benthic algae have motile, chemotactic, or phototactic propagules, which suggests that directed, reversible settlement interacts with hydraulic forces to deliver propagules to the benthos. Directed settlement has been observed in many marine algae (e.g., Callow and Callow 2000), but directed settlement also might occur in freshwater taxa with motile propagules, such as *Oedogonium* and *Vaucheria*.

Once a community has been established, relationships between periphyton biomass and free-stream velocity are highly variable; biomass increases with increasing velocity in some cases and decreases in others (McIntire 1968 [Fig 1.], Stevenson 1996). Positive biomass-velocity relationships have been attributed to velocity-dependent nutrient advection to periphyton (Horner and Welch 1981 [Fig. 1], Steinman and McIntire 1986, Stevenson and Glover 1993). Negative biomass-velocity relationships have been attributed to sloughing. Over wide velocity ranges, biomass-velocity relationships are likely to be monotonic; biomass initially increases with velocity because of increased nutrient supplies, then decreases because of sloughing (Biggs et al. 2005).

Periphyton communities and their hydraulic environments interact continually. As communities change in structure (i.e., size, density, and flexibility), they modify bed roughness and near-bed water velocity and turbulence (Nikora et al. 2002). In turn, the drag imposed by flowing water leads to changes in community structure, as discussed above. Continual feedback might lead to an equilibrium state with the maximum height and roughness of periphyton communities determined by local hydraulic condi-

tions. For communities that exceed these maxima, drag forces will exceed attachment strength and initiate sloughing. Circumstantial evidence for such equilibrium states come from comparisons of developing periphyton communities in which different starting values of shear stress and hydraulic roughness converge over time as the communities mature (Reiter 1989).

Contributions of J-NABS

Periphyton studies published in *J-NABS* that used hydraulic conditions as independent or dependent variables include studies of algal drift (**Barnese and Lowe 1992**), flow attenuation by periphyton (**Dodds and Biggs 2002**), and colonization and succession under varied free-stream velocities and turbulence levels (**Peterson 1986**, Poff et al. 1990, **DeNicola and McIntire 1991**, **Humphrey and Stevenson 1992**). Most of these studies used artificial streams where hydraulic conditions could be controlled by adjusting slopes and pump speeds and adding roughness elements. The experimental control and replication provided by artificial streams should be weighed against hydraulic artifacts and size constraints; these trade-offs are discussed in detail in a *J-NABS* special series on artificial streams (**Lamberti and Steinman 1993**).

The hydraulic data in most studies of periphyton-flow interactions, including those in *J-NABS*, are free-stream velocities (**Poff et al. 1990**, **Bourassa and Cattaneo 1998**). Free-stream velocities are not necessarily the appropriate hydraulic measurements for the research objectives, which include predicting periphyton biomass and prescribing flows that prevent or remove periphyton proliferations. The hydraulic forces that periphyton experience should be measured in the near-bed zones that periphyton occupy and at spatial scales that correspond to the ecological properties being studied. For example, if periphyton biomass or species composition vary at cm scales, hydraulic measurements intended to explain the biological patterns should be made at corresponding scales. In a special issue of *J-NABS* "Heterogeneity in Streams" (Volume 16, issue 1) focused on environmental heterogeneity in streams, Cooper et al. (1997) reviewed techniques for identifying the dominant scales of spatial variability. Matching scales in biological and hydraulic measurements should increase the precision and accuracy of periphyton-flow relationships. Stream ecologists were encouraged to adopt more relevant hydraulic variables than discharge and velocity in an early *J-NABS* review (**Statzner et al. 1988**). Useful guides for understanding and measuring near-bed hydraulic conditions in

periphyton studies include **Statzner et al. (1988)**, Carling (1992), Nikora et al. (1998a), Hart and Finelli (1999), and Stone and Hotchkiss (2007).

Competitive Interactions

Close packing among organisms and steep gradients in resources within periphyton communities create suitable conditions for interspecific and intraspecific competition. However, McCormick (1996) reported a near-absence of direct evidence for competitive inhibition or exclusion in periphyton studies. The situation has changed little in the decade since McCormick's review. Direct evidence of competition requires measurements of density- or biomass-dependent responses (Manoylov and Stevenson 2006). In one of the rare studies with such evidence, McCormick and Stevenson (1991) reported negative relationships between growth rates of some benthic diatom taxa and biovolumes of other taxa.

Studies of competitive interactions generally distinguish between exploitation (indirect inhibition caused by depletion of a resource pool) and interference (direct inhibition of access to resources). The distinction is not always clear, but overgrowth and pre-emption of space are usually considered forms of interference, and shading and nutrient depletion forms of exploitation. Allelopathy is a form of interference in which chemicals produced by some organisms inhibit colonization and growth of other organisms. Interspecific allelopathy has been documented in benthic cyanobacteria, charophytes, vascular macrophytes, and terrestrial bryophytes (Smith and Doan 1999, Juttner and Wu 2000, Gross 2003, Mulderij et al. 2003). Clear evidence that allelopathic substances are produced by other benthic algae or from natural periphyton communities is rare (**Leflaive and Ten-Hage 2009**), but the diversity of allelopathic taxa identified to date suggests that allelopathy is a widespread competitive strategy.

Exploitative competition among autotrophs for dissolved nutrients appears to be common in closed systems, such as ponds and lakes and laboratory flasks (e.g., Van der Grinten et al. 2004). In closed systems, nutrient uptake rates can exceed rates of nutrient input or remineralization and cause nutrient depletion. These conditions favor taxa with low half-saturation constants, high nutrient storage, and efficient conversion of nutrients to cellular material (Borchardt 1996). In streams, nutrient input rates often exceed uptake by orders of magnitude, so depletion is less common. Longitudinal nutrient depletion and corresponding changes in periphyton composition have been observed in natural and artificial streams

with high residence time, high periphyton biomass, and low nutrient input (**Mulholland and Rosemond 1992**, **Mulholland et al. 1995**, Vis et al. 2008, **Mulholland and Webster 2010**). Under these conditions, longitudinal changes in periphyton might be caused by changing nutrient availability. However, unidirectional stream flow prevents the periphyton upstream from exploiting the nutrient-limited periphyton downstream, and no competitive feedback occurs.

Intense nutrient competition is unlikely at the scale of stream reaches, but it might be prevalent within periphyton mats. Uptake by organisms in periphyton mats depletes dissolved nutrients as water passes through mats (Burkholder et al. 1990, Stevenson and Glover 1993, Wetzel 1993). Water flow through dense mats is limited by low porosity (De Beer and Kühl 2001). Nutrient depletion and low flow rates reduce nutrient supplies to cells deep within mat matrices and set the stage for competitive interactions. However, low nutrient supply rates alone are insufficient conditions for competition. Exploitative competition requires nutrient uptake rates to equal or exceed supply rates, and this situation has not been demonstrated (Stelzer and Lamberti 2001). Nutrient uptake rates might remain lower than supply rates because of severe light limitation. Alternatively, cells within periphyton mats might be supplied with nutrients from underlying sediments or from mat decomposition, in addition to the overlying water (Pringle 1990). Both situations would alleviate nutrient competition in mats.

As with nutrient competition studies, studies of light competition are rare in periphyton ecology. Dynamic light gradients in periphyton mats make these studies technically challenging (Dodds et al. 1999). As a first step, competitive hierarchies in periphyton could be inferred by ranking irradiance requirements for growth in different taxonomic groups (Steinman et al. 1989). Circumstantial evidence for exploitative competition between overstory and basal-layer taxa in periphyton mats comes from observations of taxonomic shifts during mat development and reduced irradiance and increased alkaline phosphatase activity in basal layers (**Johnson et al. 1997**). More compelling evidence for light competition would come from experiments in which periphyton canopy layers are removed. Canopy removal experiments are common in marine ecology (e.g., Clark et al. 2004), but not in stream ecology (Steinman 1996).

Assuming that competitive hierarchies do exist among taxa in periphyton communities, many processes could prevent competitive exclusion. Principal among these are disturbances and herbivory, which reduce populations of dominant taxa, and changing

resource availability. In a meta-analysis of studies of top-down (herbivory) and bottom-up (nutrient availability) effects on periphyton, Hillebrand (2002) reported that effects of herbivory were greater on average than nutrient effects. Differences in experimental designs confounded these comparisons, but the general pattern suggests that herbivory constrains periphyton growth more than nutrient availability, and presumably has a greater effect on competitive exclusion.

Contributions of J-NABS

Few papers in *J-NABS* have reported results of direct tests of hypotheses about resource competition in periphyton communities, and none have provided evidence for competitive exclusion. Scott et al. (2009) used a natural P gradient in 8 streams to test the hypothesis that covariation in benthic algal and bacterial production would decrease with decreasing P availability because of algae–bacteria competition. The opposite effect was observed; covariation between algal and bacterial production decreased with increasing P availability. These results suggested that low P availability induced mutualism, rather than competition.

Henry and Fisher (2003) suggested that the dominance of diatoms with N₂-fixing endosymbiotic cyanobacteria and free-living N₂-fixing cyanobacteria in DIN-poor habitats was caused by a release from nutrient competition with chlorophytes and nonsymbiotic diatoms. Presumably, the converse pattern reported by Henry and Fisher (2003), a scarcity of N₂-fixing algae and abundant chlorophytes in DIN-rich habitats, was caused by superior competition for space by the chlorophytes. The capacity for N₂-fixation alone does not ensure that cyanobacteria will dominate DIN-poor habitats. Light and P availability, water temperature, and grazing pressure all can limit the competitive prowess of benthic cyanobacteria (Marcarelli et al. 2008)

In the absence of information about competitive hierarchies at a detailed taxonomic level, authors of several *J-NABS* papers used a functional-form or size-based approach. These studies include comparisons of nutrient uptake, C-fixation, and spatial dominance among morphological groups (e.g., unicellular and colonial diatoms, branched and unbranched filaments) (Lowe et al. 1986, Steinman et al. 1992, DeNicola et al. 2006). The results of these studies were inconsistent (e.g., groups with high surface-volume ratios were not consistently associated with intense resource limitation). Some of the inconsistencies might have resulted from variation in functional

group definitions. A single widely accepted functional-group classification could increase comparability among studies and improve our understanding of periphyton competition, as the functional feeding group classification has for invertebrates (Mihuc 1997).

One reason for the scarcity of periphyton competition studies is the scarcity of conceptual models that posit roles for competition in community development and species coexistence (McCormick 1996). Useful conceptual models would generate hypotheses, synthesize current understanding, and identify research needs. Passy (2008) recently proposed one such model. The primary aim of this model was to explain why species richness in natural periphyton communities decreased as the number of limiting resources increased. In contrast to the negative relationship reported by Passy (2008), diversity in phytoplankton communities often increases with increasing numbers of limiting resources (Interlandi and Kilham 2001). The periphyton model predicts that severe resource scarcity leads to thin, depauperate periphyton communities dominated by stress-tolerant species. High resource supply leads to the establishment of thick mats, with canopies dominated by stress-sensitive, eutrophic species, and understories still dominated by stress-tolerant species. Nutrient uptake and shading by canopy species create vertical gradients of decreasing nutrient concentration and light in thick mats (Meulemans 1987, Johnson et al. 1997). Stress-tolerant species can persist in the understory of these mats, increasing overall diversity. An earlier conceptual model (Stevenson 1997b) predicted a similar increase in species richness at high resource levels, but did not account for the physical structure of periphyton communities. Tests of both models have been limited to observational studies (Passy 2008). Much scope exists for testing these models experimentally, refining or replacing them with improved versions, thereby improving our understanding of the roles of competition.

J-NABS and Periphyton Ecology: Strengths and Shortcomings

Papers in *J-NABS* have led the field in testing and expanding conceptual models in periphyton ecology. These models include patch dynamics (Pringle et al. 1988, Grimm and Fisher 1989, Sinsabaugh et al. 1991, Cooper et al. 1997), resource–stress relationships (Stevenson 1997b, Wellnitz and Rader 2003, Stevenson et al. 2008), and disturbance–biodiversity and disturbance–ecosystem function relationships (Grimm and Fisher 1989, Uehlinger and Naegeli 1998, Biggs

et al. 1999a). Most of the papers in the preceding list have been cited >50 times. The continuing role of *J-NABS* in the expansion of ecological theory depends on the imagination and fortitude of its contributors. New and improved theories evolve from new discoveries and new syntheses of research fields.

Periphyton ecology studies in *J-NABS* tend to be multivariable, phenomenological, and nonmechanistic (Creutzberg and Hawkins 2008). They provide information about temporal and spatial patterns in periphyton communities, but do not always identify the environmental or biological causes of those patterns (Stevenson 1997a, Beyers 1998). Combinations of explanatory variables in periphyton papers in *J-NABS* have included disturbances \times resources, herbivory \times substrata, stressors \times resources, resources \times substrata, and disturbances \times resources \times herbivory. Multivariable studies like these are more realistic than univariable studies because independent variables rarely act in isolation, but the effort needed to implement multivariable studies usually comes at the expense of statistical power and experimental control. For example, Ambrose et al. (2004) measured periphyton responses to nutrient \times light interactions with 2 levels of nutrient enrichment (salmon carcasses present or absent) and 2 light levels (canopy closed or open). No main effects or interaction terms were statistically significant. It is likely that variation within treatments, confounding variables, and low statistical power affected the study outcome. This example illustrates the need to weigh realism against information yield when designing periphyton studies. Experiments in which confounding variables are controlled and single explanatory factors are varied over broad ranges are likely to be more informative than poorly controlled multivariable experiments with few treatment levels and low replication.

The aims of most periphyton studies published in *J-NABS* are to describe patterns, detect correlations, or compare "treatments" in natural experiments, in which the treatments consist of naturally-occurring contrasts or unreplicated perturbations (Townsend 1989, Creutzberg and Hawkins 2008). Few studies in *J-NABS* aim to test hypotheses in a formal, deductive way. In a survey of *J-NABS* articles, Creutzberg and Hawkins (2008) concluded that *J-NABS* authors could advance freshwater benthic science best by shifting their emphasis from pattern descriptions and natural experiments to formal hypothesis testing and development of theory.

Many topics in periphyton ecology are unexplored or underexplored; the examples identified in this review (e.g., resource colimitation, competitive inhi-

bition and exclusion, effects of drag forces, and turbulence) are only a small sample. Because the field of periphyton ecology is defined by an assemblage, its domain includes many other fields of ecology (e.g., physiological, community, population, and ecosystem ecology). Rather than presenting an exhaustive list of research opportunities, I recommend 2 general approaches that might help integrate the disparate field of periphyton ecology and expand its range of inquiry. One is an increased focus on developing, testing, and refining conceptual models; the other is an increased emphasis on multidisciplinary research.

A century of field and laboratory studies has produced a large and diverse knowledge base for periphyton ecology. However, the development of conceptual models that provide context for data, contribute to ecological theory, and guide future research lags behind the empirical studies. This lag appears to apply to freshwater benthic ecology in general (Creutzberg and Hawkins 2008), not just periphyton ecology. The recent conceptual models discussed in this review (e.g., Battin et al. 2007, Passy 2008) could herald an era of rapid progress, if periphyton ecologists begin testing and revising those models and proposing new ones. These are critical steps if periphyton ecology is to progress from a largely descriptive and inductive discipline to a deductive and theory-based discipline. One of the primary aims of science disciplines is the construction of robust theory, and conceptual models are the basic units of scientific theories (Scheiner and Willig 2005).

To address increasingly complex research questions and environmental problems, ecologists need to adopt interdisciplinary approaches (Hannah et al. 2007). These approaches bring data, methods, theories and perspectives from different disciplines to bear on issues that span conventional science domains. Periphyton ecology is traditionally the domain of biologists with specializations in botany or ecology. Relatively little research in periphyton ecology has been undertaken by research teams from different disciplines. In contrast, collaborations among geologists, hydrologists, chemists, geneticists and ecologists have led to rapid advances in other areas of benthic ecology (e.g., Cover et al. 2008). Similar efforts would serve periphyton ecology well. Based on the knowledge gaps identified in this review, some of the most valuable collaborations would combine specialists in periphyton ecology, landscape ecology (Battin et al. 2007), fluid mechanics (Nikora et al. 1998a), and phytoplankton physiology (Saito et al. 2008).

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