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# Attached Algae: The Cryptic Base of Inverted Trophic Pyramids in Freshwaters

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## Keywords

cyanobacteria, diatoms, *Cladophora*, microphytobenthos, periphyton, grazers, lakes, rivers, primary consumer, primary producer

## Abstract

It seems improbable that a thin veneer of attached algae coating submerged surfaces in lakes and rivers could be the foundation of many freshwater food webs, but increasing evidence from chemical tracers supports this view. Attached algae grow on any submerged surface that receives enough light for photosynthesis, but animals often graze attached algae down to thin, barely perceptible biofilms. Algae in general are more nutritious and digestible than terrestrial plants or detritus, and attached algae are particularly harvestable, being concentrated on surfaces. Diatoms, a major component of attached algal assemblages, are especially nutritious and tolerant of heavy grazing. Algivores can track attached algal productivity over a range of spatial scales and consume a high proportion of new attached algal growth in high-light, low-nutrient ecosystems. The subsequent efficient conversion of the algae into consumer production in freshwater food webs can lead to low-producer, high-consumer biomass, patterns that Elton (1927) described as inverted trophic pyramids. Human perturbations of nutrient, sediment, and carbon loading into freshwaters and of thermal and hydrologic regimes can weaken consumer control of algae and promote nuisance attached algal blooms.

## 1. INTRODUCTION

Compared with terrestrial food webs, algal-based, trophic-level biomass pyramids are upside down: The mass of aquatic grazing animals and predators often exceeds the mass of their algal food (Elton 1927). Ironically, the strongly inverted pyramids of trophic-level biomass (see the sidebar titled Inverted Pyramids of Trophic-Level Biomass) that typify many unimpaired freshwaters confer an invisibility on attached algae that belies their critical role in aquatic food webs and ecosystem function. Algae attached to submerged surfaces typically represent only a small fraction of the standing stock of organic carbon in unpolluted lakes and rivers (Mayer & Likens 1987, Vadeboncoeur et al. 2008, Brett et al. 2017). However, these diminutive standing stocks are often due to intense consumption rather than low algal primary production. In addition, turnover rates of algae (whether attached or planktonic) are high relative to the rates of longer-lived animals that consume them (Elton 1927, Lindeman 1942). Processes or perturbations that reduce the ability of grazers to efficiently consume and digest new attached algal production lead to bottom-heavy biomass pyramids that humans often view as nuisance algal blooms. In this review, we challenge the notion that we can overlook attached algae because they make up a small proportion of the organic carbon pool in lakes or rivers. Rather, recalling Elton (1927), we argue that attached algae are a small proportion of the organic carbon pool because they are the trophic foundation of many aquatic ecosystems.

**Primary production:** production of autotrophic organisms that fix their own carbon by reducing inorganic carbon ($CO_2$, $HCO_3$) to biomolecules like carbohydrates

**Production:** elaboration of new tissue by an organism or a group of organisms over a given (often annual) time period [mass area$^{-1}$]

**Trophic efficiency:** the fraction of production within a trophic level that is converted into new production in the subsequent trophic level

Interactions between grazers and their attached algal food have been widely studied (Stevenson et al. 1996), but attached algae are often treated as a minor component of energy flow in aquatic ecosystems. In lakes, the sheer volume of water column habitat relative to benthic habitat caused researchers to emphasize food chains founded on phytoplankton (Vadeboncoeur et al. 2002). Attached algae are well studied in rivers, but their role in food webs was thought to be relatively minor, particularly near headwaters (Vannote et al. 1980, Junk et al. 1989). In river and lake watersheds, most plant biomass is terrestrial, and gravity pulls matter downslope. Therefore, terrestrial carbon inputs to freshwaters often dwarf standing crops of algae. Indeed, the abundance of terrestrial carbon in inland waters, and its contribution to microbial respiration, led investigators to suggest that apparently inverted biomass pyramids in ecosystems with high trophic efficiency were merely heavily subsidized by terrestrial carbon (Cole et al. 2011). However, natural tracers, such as stable isotopes and fatty acids, are providing compelling evidence that attached algae

### INVERTED PYRAMIDS OF TROPHIC-LEVEL BIOMASS

Ecologists aggregate organisms into trophic levels to depict energy fluxes in ecosystems. The number of trophic (feeding) transfers that occur between an organism and the base of the food web determines an organism's trophic level. Ecologists aggregate primary producers such as plants and algae into the first trophic level because they transform inorganic carbon into living cells. Algivores and herbivores that eat primary producers compose the second trophic level (primary consumers). Predators that feed on primary consumers are the third trophic level, and so on. Metabolic costs preclude any animal from converting 100% of the energy in its food into new biomass. This inefficiency in energy transfer means that the production (biomass produced per area or volume per time) of any trophic levels is necessarily smaller than production of the preceding trophic level. Counterintuitively, biomass accrual may increase with trophic level; the biomass of consumers can exceed that of their resources. These inverted pyramids of trophic-level biomass occur when animals can efficiently harvest resources and efficiently convert food into growth. Inverted biomass pyramids occur in aquatic ecosystems in part because consumer lifespans encompass many generations of their resource organisms.

provide a trophic foundation for lake and river ecosystems. This is so even though attached algae are typically a small proportion of carbon standing stocks.

Attached algae grow in lakes and rivers on virtually all submerged, illuminated surfaces including sand, mud, rocks, wood, aquatic animals, and anthropogenic structures and debris (Stevenson et al. 1996). Attached algae thrive under high light conditions in shallow water of lakes, in midsized streams with open canopies, and in gutters and farm ditches. However, attached algal assemblages also persist in low light environments deep in lakes (Vadeboncoeur et al. 2001) and in headwater streams heavily shaded by riparian vegetation (Mayer & Likens 1987). For instance, living attached algae have been collected from depths >70 m in Lake Baikal, Russia, where researchers thought that low light precluded algal viability (Vadeboncoeur et al. 2011). Even in very low light habitats, attached algae are an important resource for consumers (Finlay 2001, Devlin et al. 2013).

The key to understanding the efficient use of attached algae in aquatic food webs is to appreciate (*a*) the nutritional value of algae relative to terrestrial detritus, (*b*) the concentration of attached algae relative to suspended phytoplankton, and (*c*) the indirect positive effects of grazers on attached algae that limit the detrimental effects of consumption. We begin with a brief overview of the natural history and taxonomy of attached algae in lakes and rivers and the abiotic factors that control attached algal biomass and productivity. We then discuss the nutritional characteristics of attached algae that contribute to their efficient assimilation by grazers and subsequent conversion into consumer biomass. We show that, in the face of very high consumption efficiencies, grazers have many positive indirect influences on attached algal production. We then integrate these effects to consider how light, nutrient, and disturbance regimes influence grazer–algal interactions, sometimes with counterintuitive outcomes that depend on the balance of direct and indirect effects. Understanding the tight trophic coupling between attached algae and aquatic grazers is critical if we are to understand the consequences of environmental stresses that are weakening these linkages and impairing aquatic ecosystems.

**Disturbance:** a discrete event that removes or kills organisms and frees space and other resources (Sousa 1984)

**Biofilm:** a thin layer of microorganisms (bacteria, microalgae) that grows over and adheres to a surface

**Raphid:** a group of diatoms with raphes (longitudinal slits in the silica shell, or frustule); the raphe allows diatoms to glide over surfaces

## 2. ATTACHED ALGAL DIVERSITY

Three divisions (phyla) dominate attached algal assemblages in freshwaters: Cyanobacteria, green algae (Chlorophyta), and diatoms (Bacillariophyta). Cyanobacteria evolved more than 2.3 billion years ago (Falkowski et al. 2004) in a low-oxygen atmosphere and in the absence of metazoan grazers (for simplicity, we include the prokaryotic photosynthetic cyanobacteria under the linguistic canopy of algae). Modern cyanobacteria thrive over a wide range of light intensities and temperatures (Komárek et al. 2003). Highly motile members of the family Oscillatoriaceae form thin biofilms over a range of light environments, whereas members of the tightly attached family Rivulariaceae can be a dominant feature in well-lit benthic habitats (Whitton & Mateo 2013). Chlorophytes (green algae) evolved more than 1 billion years ago when ancient protists incorporated endosymbiotic cyanobacteria into their cells (Falkowski et al. 2004). Both single-celled and filamentous green algae are common in lentic freshwater environments, whereas filamentous taxa in the orders Cladophorales and Zygnematales can form long attached streamers and dense canopies in flowing water. Filamentous Chlorophytes are often epiphytized by the latest evolutionary arrival, diatoms. Diatoms arose less than 250 million years ago by the incorporation of an endosymbiont from the red algal lineage into a eukaryotic cell. Diatoms rapidly diversified over the last 25 million years in association with global mobilization of silica by grazer–grass interactions (Falkowski et al. 2004). Adnate diatoms grow closely appressed to the substrate; stalked diatoms excrete mucilaginous stalks that elevate cells above the substrate; and motile raphid forms glide over surfaces and through silt and biofilms, tracking light and nutrients. Diatoms are ubiquitous in the benthos and remain ecologically important throughout much of the year, unlike diatoms in the plankton. Physiological and biochemical differences among the three major phyla of attached algae have a profound effect on consumers and on ecosystem function in freshwaters.

Grazing and abiotic factors interact to determine attached algal biomass and taxonomic composition. Worldwide, three attached algal assemblages commonly recur on hard substrates: (*a*) Thin skins (<0.1 mm thick) of small, tightly appressed (adnate) or motile diatoms (Lowe & Hunter 1988, Steinman 1996); (*b*) tightly attached felts (0.1–1 mm thick) of nitrogen-fixing cyanobacteria in the family Rivulariaceae (Higgins et al. 2001); and (*c*) long streamers (10s of centimeters to many meters) of attached filamentous Chlorophytes (**Figures 1*a*,*b*** and **2**). The first two assemblages persist in the face of intensive grazing, yielding strongly inverted biomass pyramids. However, the third assemblage emerges when green algae have escaped grazing in space or time and have

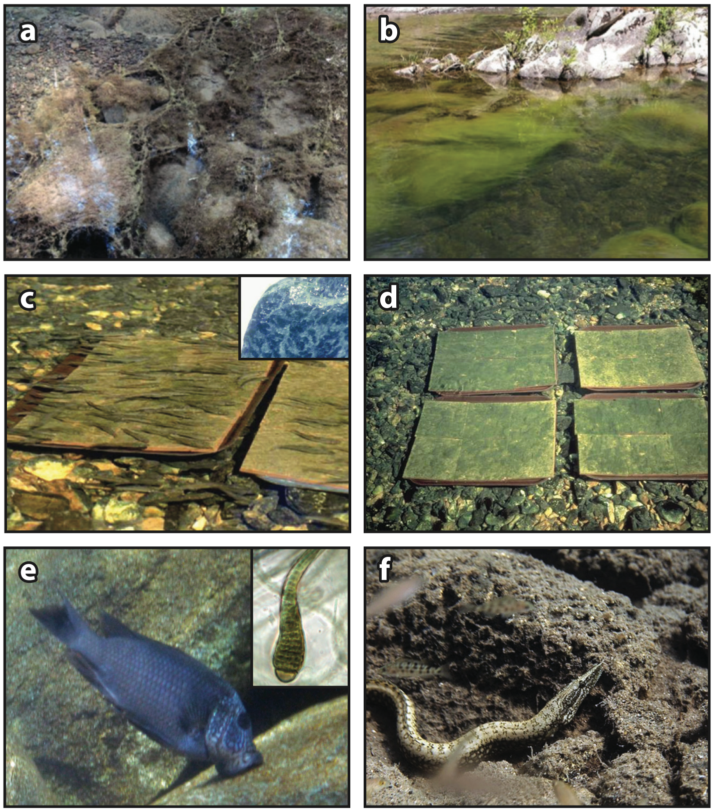

**Figure 1**

Grazed (*left column*) and ungrazed (*right column*) algal assemblages. (*a*) Chironomid midges in the Eel River of Northern California weave tuft retreats into the macroalga *Cladophora*, fragmenting it and grazing off its epiphytic diatoms. (*b*) *Cladophora* in the Eel River can form dense canopies during the summer of high flow years because scouring winter floods reduce abundances of large, predator-resistant grazing caddisflies during the subsequent summer growing season. Algivorous minnows (*c*) maintain black felts of cyanobacteria (*inset* shows dark grazing scars). (*d*) Felts are rapidly overgrown with turfs of the filamentous colonial diatom *Melosira* when grazers are excluded. (*e*) In Lake Tanganyika, East Africa, high densities of algivorous cichlids, such as *Petrochromis* sp., maintain thin biofilms comprising the nitrogen-fixing cyanobacteria *Calothrix* (*inset*) and stalked diatoms. (*f*) In nearby areas receiving high sediment loads from deforested riparian areas, algivorous cichlid densities are low and predators such as the spiny eel (*Mastacembelus moorii*) thrive. In this photograph, thick, sediment-encrusted turfs of filamentous green algae cover the rocks. Photo credits: (*a–d*) Mary E. Power, (*e*), Ryan Satchel, (*e*, *inset*) Paula Furey, and (*f*) Saskia Marijnissen.

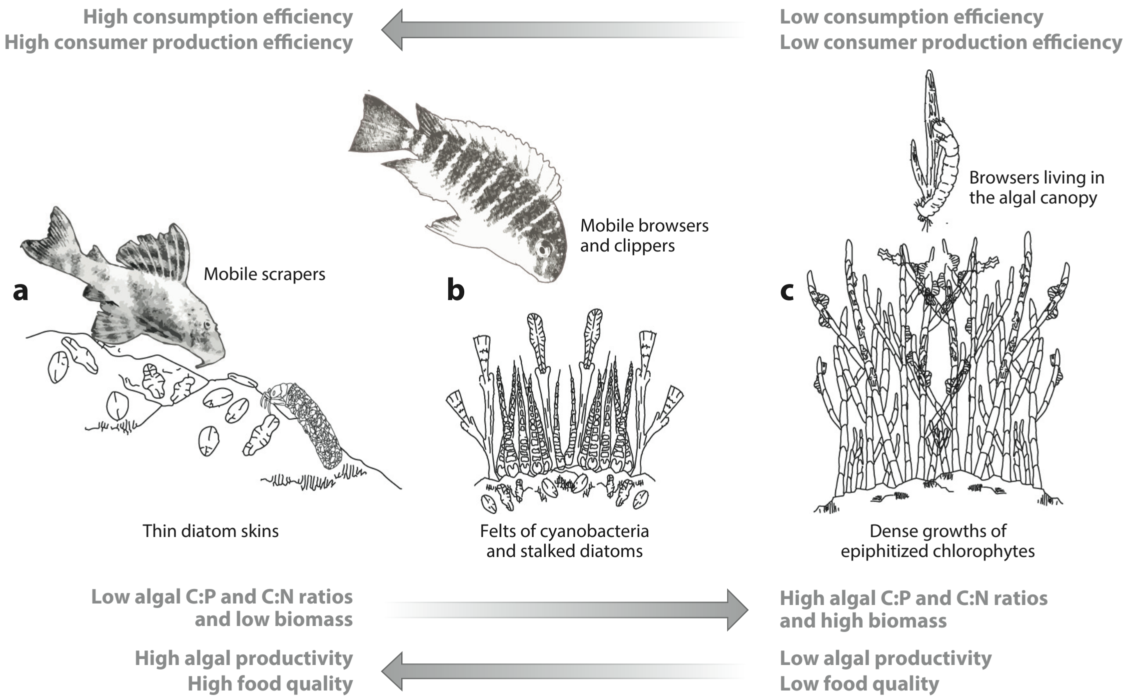

**Figure 2**

Grazers, in conjunction with disturbance, strongly determine algal taxonomic composition and biomass accumulation. (*a*) Mobile grazers with scraping mouth parts can maintain barely perceptible, thin skins of rapidly growing, nutritious diatoms. Although biomass is low, algal quality is high due to high concentrations of nitrogen and phosphorus relative to carbon (low C:N). (*b*) Cyanobacteria in the family Rivulariaceae and stalked diatoms persist in the presence of grazers that avidly tear and comb loose algae from the low-growing felts that coat rocks. (*c*) When grazing pressure is relaxed for periods of weeks, green algae such as *Cladophora* form dense canopies that provide habitat for small grazers but yield a bottom-heavy biomass pyramid. As biomass accumulates, algal quality declines because there are high concentrations of carbon in the algae relative to nitrogen and phosphorus. Note, organisms are not to scale.

attained lengths or girths that are unwieldy for many grazers. These filamentous green proliferations underlie bottom-heavy trophic pyramids dominated by primary producer biomass as in most terrestrial food webs. We first describe general features of these three algal assemblages and then discuss how light, nutrients, and disturbances affect their development and persistence.

## 2.1. Diatom Skins

Submerged rocks that look barren, or are tinged with red or gold, typically harbor thin skins of adnate diatoms (e.g., *Achnanthidium minutissimum*, *Cocconeis placentula*). Epilithic diatoms dominate early algal assemblages that persist or recover after substrates are scoured by ice or sediment transport. The tight attachment and low profiles of adnate diatoms that allow them to resist abrasion also allow them to find refuge from grazing within the microtopography of rocks. Long after scouring flood waters have subsided, the thin skins of these diatoms are maintained by grazers including invertebrates with robust scraping mouthparts such as trichopteran larvae (Lamberti 1996, Steinman 1996, Wootton et al. 1996) and algivorous fishes such as *Campostoma* minnows or loricariid catfish (Gelwick & Matthews 1992, Power 1984b, Power et al. 1985) (**Figures 1*c*,*e*** and **2**).

## 2.2. Cyanobacterial Felts

**Heterocyte (aka heterocyst):** a specialized, structurally distinct, nitrogen-fixing cell in cyanobacteria colonies that maintains a low oxygen microenvironment to protect the nitrogenase enzyme

**Time:** a resource, in the sense of Begon et al. (2006), in that it can be used up by an organism

In high-light, low-nutrient lakes and rivers worldwide (Power et al. 1988, Peterson & Grimm 1992, Higgins et al. 2001, Whitton & Mateo 2013), early successional diatom skins can be replaced by ∼1-mm-thick tufts (**Figure 1*e***) or dense felts (**Figure 1*c***) of nitrogen-fixing cyanobacteria in the order Rivulariales (e.g., *Calothrix*, *Rivularia*). Each tightly adhered rivularian filament has a basal, nitrogen-fixing heterocyte and, above this cell, an attenuating trichome (**Figure 1*e***, *inset*). Adnate (*A. minutissimum*, *Cocconeis*), stalked (*Gomphonema*), nitrogen-fixing (Rhopalodiaceae), and filamentous (*Melosira*) diatoms can grow over the basal cyanobacterial layer, but grazing by algivorous fish removes diatom overgrowths (Power et al. 1988). Experimentally excluding grazing fish from rivularian cyanobacterial felts leads to visible overgrowths of diatoms within days or weeks, but diatoms are stripped off within minutes of re-exposing the assemblage to fish (figure 1*c* in Power et al. 1988; Y. Vadeboncoeur, personal observation).

## 2.3. Green Macroalgal Turfs

If epilithic assemblages do not experience heavy grazing or physical abrasion, adnate epilithic diatoms and low-profile cyanobacteria are overgrown by erect, stalked, and filamentous taxa, especially chlorophytes such as *Stigeoclonium* and *Cladophora* (Steinman 1996). *Cladophora glomerata*, an attached, branched filamentous cholorophyte, is arguably the most widespread freshwater benthic macroalga in the world and often dominates attached algal biomass in sunlit temperate lakes and rivers (Whitton 1970, Higgins et al. 2008). Cladophorales can grow from a few residual basal cells to lengths of several meters in weeks, increasing the surface area of benthic habitats available to microalgae by five or more orders of magnitude (Power et al. 2009) (**Figure 1*b***). The rough, cellulose-rich cell walls of *Cladophora* become heavily epiphytized by diatoms (Stevenson & Stoermer 1982, Dodds & Gudder 1992, Stevenson et al. 1996). Many grazers including cichlid fish (Takamura 1984), mobile insect larvae (Dodds 1991, Harrison & Hildrew 2001), and retreat-dwelling chironomid midges (Power 1991) selectively browse on epiphytic diatoms, sometimes benefitting the underlying host (Dudley 1992, Furey et al. 2012).

## 3. ABIOTIC CONTROLS

Attached algae are the most important in-stream primary producer from small headwater streams to midsized rivers (Ogdahl et al. 2010). Phytoplankton assemblages occur only in larger river pools when long residence times permit persistence (Talling & Rzoska 1967). Attached algae can dominate whole-lake primary production in small oligotrophic lakes and dominate littoral zone primary production in clear lakes of all sizes (Vadeboncoeur et al. 2001, 2003, 2008; Malkin et al. 2010). The role of nutrients in determining algal productivity is a fundamental concept in limnology and has given rise to the notion that water bodies can be arrayed along gradients from nutrient-poor, unproductive oligotrophic waters to nutrient-rich, productive eutrophic ones. Although this concept applies well to phytoplankton, whose biomass exhibits conspicuous positive response to nutrients, the conflation of oligotrophic with unproductive is misleading in the context of attached algae. Oligotrophic ecosystems are often characterized by high water clarity, a necessary condition for high attached algal production (Wetzel 2001; Vadeboncoeur et al. 2003, 2008). Rather than use these familiar categories, we carefully distinguish between the roles of light and nutrients in controlling specific growth rates of attached algae. A third resource, time, determines the duration of biomass accumulation, which is curtailed by disturbance and grazing.

Attached algae grow in place, and the ambient light environment profoundly influences their taxonomic composition and biomass accumulation (Hill 1996, Hill et al. 2011). Light availability accounts for most of the variation in maximum photosynthetic rates of attached algae within specific lakes and rivers (Hill 1996; Hill et al. 2001, 2010; Vadeboncoeur et al. 2003, 2014; Godwin et al. 2014). Latitude, season, cloud cover, topography, and riparian vegetation determine the amount of light hitting the water surface (Bode et al. 2014). The water and its suspended and dissolved constituents further attenuate incoming light (Hill 1996). However, self-shading produces by far the most rapid decrease in light. Indeed, 99% of light hitting an attached algal assemblage does not penetrate deeper than 5 mm into the assemblage (Hill 1996, Krause-Jensen & Sand-Jensen 1998). Attached algal biofilms colonize bare surfaces by forming new thin skins of adnate taxa, but subsequent growth occurs by new cells growing on or over these early colonizers (**Figure 2**). Surface cells reduce light availability to deeper cells, and this strong self-shading within the assemblage means that large increases in biomass are not accompanied by similar increases in overall primary production (Dodds et al. 1999, Higgins et al. 2008).

**Extracellular enzymes:** enzymes excreted into the environment by bacteria or algae to sequester nitrogen or phosphorus atoms from organic molecules dissolved in the water

Within a given light environment, the availability of the macronutrients nitrogen and phosphorus strongly determines attached algal productivity (Hill & Fanta 2008, Hill et al. 2011). Assessing nutrient flux to attached algal biofilms is nontrivial due to the diverse sources from which attached algae obtain nutrients. Abiotic adsorption and microbial growth concentrate nutrients on surfaces, creating local microzones of enrichment on biofilms that are difficult to quantify. Algae sequester dissolved nutrients from the water column and the substrate upon which they grow (Borchardt 1996, Mulholland 1996). Algae on the surface of biofilms can meet a substantial amount of nutrient demand by recycling nutrients from senescent understory cells and use extracellular enzymes to scavenge organic phosphorus and nitrogen (Mulholland 1996, Rier et al. 2007, Whitton & Mateo 2013, Smucker et al. 2014). When water column nutrient concentrations are very low, attached algal assemblages are often dominated by nitrogen-fixing cyanobacteria and diatoms with cyanobacterial endosymbionts (Peterson & Grimm 1992, Marks & Lowe 1993, Power et al. 2009) that contribute substantially to whole-ecosystem nitrogen budgets (Higgins et al. 2001). Diverse nutrient sources and acquisition strategies, together with flow effects on nutrient fluxes, weaken the relationship between attached algal biomass and total nitrogen or total phosphorus concentrations in the water column (Dodds 2007, Vadeboncoeur et al. 2003).

Although light and nutrient availability determines attached algal growth rate (Hill et al. 2011, Hill & Fanta 2008), local biomass is determined by the intensity and frequency of disturbance or grazing, which limit time for accrual. The effects of disturbance depend on substrate stability, which increases with substrate particle size and decreases with shear stress on these particles imposed by moving fluids. In river networks, bed mobilization and sediment scour are rare in mountain headwater streams where bedrock, boulders, and large cobbles provide stable persistent substrates for attached algae. Attached algae grow faster in wider, better-lit main stem channels, but algae are periodically scoured off cobble and smaller bed sediments when these are mobilized by floods. In large lowland rivers, fine sand and silt bed loads are constantly shifted and transported (Dietrich et al. 1979, Benda & Dunne 1997) and turbidity lowers light penetration. Persistent attached algal communities develop on submerged or floating wood (Benke et al. 1985) or on macrophytes (Engle & Melack 1993) but not on the river bed.

Wave action at the margin of lakes mobilizes and sorts shoreline sediments, determining habitat distribution for attached algae (Lowe 1996). Sand and boulder habitats dominate at wind-exposed lake edges, and mud habitats occur in deeper or sheltered areas (Wetzel 2001). Attached algae grow on all these surfaces, but biomass accumulation appears to be limited by disturbance in shallow areas subjected to ice scour and wave action, and limited by light at depths beyond the zone of physical disturbance (Vadeboncoeur et al. 2014). In cold climates, winter ice periodically scours algal biomass from lake margins and river beds. Conversely, during warm summers, vascular macrophytes and macroalgae (e.g., *Cladophora*) proliferate, and these ephemeral substrates are colonized by epiphytic algae. As macrophytes and macroalgae elongate, they become increasingly susceptible to drag, such that even minor disturbances can detach entire host–epiphyte assemblages.

## 4. ATTACHED ALGAE AS A FOOD RESOURCE

Resources available to primary consumers in lakes and rivers include terrestrial vascular plants that enter aquatic ecosystems as detritus, aquatic vascular plants (e.g., pondweeds), attached macroalgae (e.g., filamentous chlorophytes), and attached (benthic) microalgae and planktonic microalgae (phytoplankton). Each of these resources has different costs and benefits as a food source. Detritus deposits, living aquatic macrophytes, and attached algae are concentrated resources relative to planktonic algal cells, which are widely dispersed in the water column. In terms of food acquisition, ingesting phytoplankton is clearly different from and potentially more costly than ingesting other resources. However, both attached algae and phytoplankton are more digestible and nutrient rich than vascular plants (terrestrial detritus and aquatic macrophytes). Within algae, there are differences in food quality associated with evolutionary groups but not necessarily habitat (benthic or planktonic). In the following text, when the term "algae" appears without a modifier, we are not distinguishing between phytoplankton and attached algae.

**Consumption efficiency:** the proportion of new production in a trophic level that is eaten by the trophic level immediately above it

**Assimilation efficiency:** the proportion of ingested food that the consumer successfully digests and transfers across its gut wall into its body

**Production efficiency:** the proportion of assimilated food that the consumer converts into growth or reproduction (rather than using it for metabolism or movement)

**Functional responses:** the variation in ingestion rate of a consumer as a function of the density of its prey

### 4.1. Acquisition and Assimilation

The proportion of primary production that is converted to production of grazers (trophic efficiency) is highest in microalgal-based food chains (Elton 1927, Lindeman 1942). Trophic efficiency between two adjacent trophic levels is the product of consumption efficiency, assimilation efficiency, and production efficiency (Lindeman 1942). The proportion of attached algal primary production consumed by grazers (consumption efficiency) is approximately 2 times higher than in terrestrial grasslands and approximately 40 times higher than in terrestrial forests (Cebrian 1999). The fraction of consumed algal biomass that is digested and assimilated by consumers (assimilation efficiency) and converted into secondary (consumer) production is also higher than for consumed vascular plant tissue (Cebrian et al. 2009). Most consumers in freshwater food webs do not regulate body temperature, so they can allocate a large proportion of assimilated food to growth (high production efficiency) (Humphreys 1979). Because freshwater algae are more palatable, nutritious, and digestible than vascular plants (Cebrian 1999, Sterner & Elser 2002), consumers are able to convert a high proportion of their algal food into new growth.

Unlike dispersed phytoplankton, attached algae colonize and accrue along surfaces. A typical attached algal biofilm growing on sediments or rocks in the midlittoral zone of an unpolluted lake has as much algal production, biomass, and nutrients as the column of water above that has the same area but is 10–30 m deep (O'Reilly 2006, Malkin et al. 2010, Vadeboncoeur et al. 2014). Therefore, grazers of attached algae do not need to concentrate their food, which is a significant energetic and time cost for animals that feed on phytoplankton (Koehl & Strickler 1981). Zooplankton ingestion rates increase with phytoplankton concentration (Peters & Downing 1984). Although we lack similar data on the functional responses of attached algivores to variation in food concentration, the limited data that have been published suggest that consumers can feed on attached algae at a much higher rate than they can ingest phytoplankton. Ingestion rate (mass/individual/day) scales with body size for detritivores, grazers on algal biofilms, and zooplankton that graze phytoplankton (Cattaneo & Mousseau 1995). However, for any given body mass, daily ingestion rates by zooplankton feeding on phytoplankton are 10–100 times lower than for organisms feeding on benthic detritus or algal biofilms (Cattaneo & Mousseau 1995) concentrated on surfaces. Furthermore, animals consuming attached algae can ingest much larger cells (relative to body size) than filtering zooplankton can (Tall et al. 2006). Grazers consume a high proportion of both attached algal and phytoplankton production as living biomass (Cebrian 1999). However, if time and energy costs associated with consuming attached algae are lower than those associated with phytoplankton, trophic efficiencies for attached algal diets may be higher. To our knowledge, this has not been quantified explicitly, but it has important implications for aquatic food webs. Phytoplankton and attached algae are both more nutritious than terrestrial detritus. If a diet of attached algae has lower consumption costs than that of phytoplankton, trophic efficiencies may be higher in food chains based on attached algae compared with suspended algae.

**Catabolism:** processes within an organism that break down complex organic molecules and capture useable energy in the synthesis of adenosine triphosphate

The nitrogen, phosphorus, and protein contents of algae are higher than those of vascular plants but lower than those in animal prey (Sterner & Elser 2002), resulting in intermediate assimilation efficiencies. Both terrestrial and aquatic primary consumers must feed and digest nearly continuously to meet their caloric and nutrient requirements. Many algivorous fish forage nearly nonstop during daylight hours (Moriarty 1973, Fowler & Taber 1985, Sturmbauer & Dallinger 1995, Munubi 2015), and some also forage at night (Power 1983). Ingested algae must be digested and assimilated, and there is a tradeoff between ingestion rate and assimilation efficiency (Calow 1975, McCullough et al. 1979b, Karasov & Martínez del Rio 2007). Assimilation efficiency increases with increasing total gut length, and gut development within some species is responsive to dietary nutrient concentrations. For example, gut length:body length ratios of the grazing cichlid *Tropheus brichardi* decrease with algal nutrient content (Wagner et al. 2009, Munubi 2015). Such plasticity of consumers' behavior, physiology, and morphology in response to algal nutrient content suggests that consumers balance nutrient and net calorie acquisition to increase growth.

Both attached algae and phytoplankton are more easily assimilated than terrestrial detritus, but the molecular composition of algal cell walls differs among phyla and influences assimilation efficiency. Cyanobacteria cell walls are proteinaceous, with a peptidoglycan layer, a lipopolysaccharide layer, and often a mucilaginous sheath (Komárek et al. 2003). The lack of cellulose as a structural component of cyanobacterial cell walls may make them more digestible (at least in guts with low pH; see Moriarty 1973) than green algae, whose cell walls contain an inner structural layer of cellulose (John 2003). The thin silica shells (frustules) of diatoms have many perforations (punctae), through which cell contents can be digested. Assimilation efficiencies for larval aquatic insects fed the cyanobacteria *Lyngbya* and *Anabaena* were 33%, whereas assimilation efficiencies for diatoms ranged from 35% to 60% (McCullough et al. 1979a,b). In another study, nearly 100% of single-celled and filamentous chlorophytes passed through the guts of primary consumers in streams with intact chloroplasts (i.e., were not digested), but <10% of diatoms did (Moore 1977). There are many biochemical reasons why diatoms are a high-quality food resource for primary consumers, but high digestibility relative to other algal groups is likely important. Taxonomic differences in assimilation efficiencies are likely more important than whether a particular alga is benthic or planktonic. However, highly nutritious diatoms are both more dominant and more persistent in attached algal assemblages than they are in planktonic assemblages (Lowe 1996).

## 4.2. Indices of Consumer Metabolic Demand: Carbon-to-Nutrient Ratios

As food, algae are stoichiometrically superior to terrestrial plants and more digestible. Whether they consume living cells or detritus, primary consumers must build their protein-rich bodies from nitrogen-dilute foods. Animals allocate assimilated materials toward two broad categories of use: basic catabolic requirements (respiration) and structural requirements for anabolic processes of tissue repair, growth, and reproduction. Catabolism oxidizes energy-yielding carbon-rich compounds such as carbohydrates and lipids for fuel. In contrast, anabolism requires nitrogen and phosphorus for building structural macromolecules necessary for growth. A plant-based diet is low in the nitrogen and phosphorus necessary to synthesize the molecular building blocks of proteins, DNA, RNA, phospholipids, and bones (Sterner & Elser 2002). The nitrogen content (percentage dry weight) of microalgae ranges from 3.5% to 6% compared with 0.1% to 2% for terrestrial plants; microalgal phosphorus concentration ranges from 0.4% to 0.8% compared with 0.01% to 0.15% for terrestrial plants (Cebrian 1999). Although the nutrient content of forage often limits terrestrial grazers, the relatively high quality of algae makes it difficult to predict a priori whether the carbon (energy) or macronutrient (nitrogen, phosphorus) content of algae limit the growth of aquatic grazers.

**Anabolism:** organismal processes that synthesize complex organic macromolecules (e.g., proteins, lipids) from simpler molecules using adenosine triphosphate as an energy source

Algal C:N and C:P ratios are indices of nutrient limitation for algae (Hillebrand & Sommer 1999), but consumer elemental ratios cannot be used to infer demand unless they are combined with budgets that quantify allocation of elements to catabolism, excretion, and growth (Wagner et al. 2013, Halvorson et al. 2015). Primary consumers grow better on algal diets with high nitrogen and phosphorus content (Sterner & Elser 2002), but carbon, nitrogen, and phosphorus have different turnover times in a consumer's body. Thus, a discrepancy between the stoichiometry of the consumer and its diet is not necessarily indicative of a dietary imbalance. Aquatic primary consumers oxidize 60–97% of ingested carbon for catabolic processes (Humphreys 1979). Consumers respire this carbon as $CO_2$, and it is not reflected in the stoichiometric ratio of their body tissue. Variation in the digestibility of different foods, combined with behavioral, physiological, and morphological plasticity in consumers, means that algivores thrive on diets over a range of nutrient ratios rather than showing sharp decreases in growth across nutrient ratio thresholds (Benstead et al. 2014, Halvorson et al. 2015). Stoichiometry provides an informative first assessment of consumer nutritional constraints in freshwater ecosystems, but algal calorie, protein, and fatty acid content are better measures of food quality. The best measure, of course, is the rate of consumer growth or reproduction on various diets (Kupferberg et al. 1994).

### 4.3. Metabolic Necessities: Calories, Proteins, and Fatty Acids

The emphasis on carbon dynamics that defined early ecosystem ecology is rooted in the understanding that life depends on capturing and transforming energy from the sun (Lindeman 1942). From individuals to ecosystems, carbon flux is an index of these processes. Yet, the influence of caloric density of food on aquatic primary consumers is not well understood. Algae, whether benthic or planktonic, have about twice the caloric density of terrestrial detritus (Bowen et al. 1995). Algal taxa differ in the quality and accessibility of their carbon compounds. Chlorophytes have starch reserves, but they come packaged in cellulose. Diatoms are rich in lipids, but isolating the importance of diatoms as an energy-dense food is confounded by the essential fatty acids (EFAs) that they provide as nutrients to consumers. Many freshwater invertebrate grazers are relatively sedentary (e.g., certain chironomids, snails, and caddisflies), so calorie demand may be low relative to macronutrient requirements for growth. However, highly active, often territorial algivores dominate tropical fish assemblages (Hori et al. 1983, Sturmbauer & Dallinger 1995, Munubi 2015), and they may need foods with both high calorie content and high macronutrient density. Feeding activity of marine algivorous fish correlates positively with daily variation in the soluble carbohydrate (energy) content of their algal food (Bruggemann et al. 1994), but to our knowledge, this is not documented for freshwater grazers. Recent research on tadpoles demonstrates that when exposed to higher temperatures, these omnivores increase consumption of plant material relative to animal protein, presumably because carbon demand for catabolism increases faster than nutrient demand for growth (Carreira et al. 2016).

Digestible protein is strongly correlated with primary consumer growth, and algae have about twice the protein content of terrestrial detritus (Bowen 1979, Bowen et al. 1995). Protein content of detrital aggregates in a South African lake ranged from 1.8% to 14.2% and declined with depth, primarily because of a concomitant decline in diatoms growing on the detritus (Bowen 1979). Adult fish feeding deeper in the lake were stunted by protein deficiency. Laboratory comparisons of the protein content of different algal taxa need to be extrapolated to natural ecosystems with caution, but up to 70% of cyanobacteria dry weight is protein, whereas the range in green algae is 35–55%. Lipid-rich diatoms have only 25–35% protein (González-López et al. 2010, Tibbetts et al. 2015, Barka & Blecker 2016). Some algivorous fish that actively select for diatoms also consume and grow well on protein-rich cyanobacteria (Nagarkar et al. 2004, Abe et al. 2007).

**18:2ω-6:** linoleic acid has 18 carbons and 2 double bonds; the last double bond occurs 6 carbons from the terminal carbon

Brett & Müller-Navarra (1997) demonstrated that primary consumers require specific, algal-derived EFAs to grow and reproduce. Their researched transformed our understanding of how the molecular composition of fixed carbon affects aquatic primary consumers and how these effects propagate through food webs to the ecosystem level. Most animals cannot synthesize certain essential vitamins, amino acids, or EFAs and must acquire these from their diet. EFAs are more efficiently transferred between trophic levels than other carbon compounds because they are necessary for growth (Gladyshev et al. 2011). Research on EFAs has deepened our understanding of how algal food quality determines the growth, reproduction, and development of zooplankton and fish. Now, fatty acid analysis is increasingly used to characterize benthic food webs (Torres-Ruiz et al. 2007; Lau et al. 2009, 2014; Guo et al. 2016a,b; Makhutova et al. 2016).

Fatty acids are structural components of cell membranes and key building blocks for neurological development. Polyunsaturated fatty acids (PUFAs) are critical for growth and reproduction of many animals, especially vertebrates. Cholorophytes, and to a lesser extent cyanobacteria, are rich in the shorter chain PUFAs: linoleic acid (LIN; 18:2ω-6) and α-linoleic acid (ALA; 18:3ω-3), which some consumers can elongate to the highly unsaturated EFAs eicosapentaenoic acid (EPA; 20:5ω-3), arachidonic acid (ARA; 20:4ω-6), and docosahexaenoic acid (DHA; 22:6ω-3). Algae in the lineage arising from the second incorporation of endosymbionts synthesize the longer chain EFAs de novo (Falkowski et al. 2004). This lineage includes diatoms, a major component of attached algal assemblages that are rich in EPA and ARA, and the predominantly pelagic cryptophytes that are rich in EPA and DHA. Although light, temperature, and nutrients affect algal fatty acid content (Guo et al. 2016b), fatty acid profiles reflect taxonomic composition of attached algal assemblages and the relative food quality of these assemblages for consumers (Torres-Ruiz et al. 2007, Strandberg et al. 2015, Guo et al. 2016a). Fatty acid analysis of stream invertebrate assemblages across systems points to a strong reliance on attached algae despite the abundance of terrestrial organic matter in rivers (Torres-Ruiz et al. 2007; Lau et al. 2009, 2014; Guo et al. 2016a; Brett et al. 2017). Benthic insects in both lakes and rivers have high levels of EPA relative to other EFAs (Lau et al. 2009, 2014; Guo et al. 2016a). Gut content analysis demonstrates that grazers selectively ingest and digest diatoms, and the prevalence of EPA in the tissues of zoobenthos is further evidence of the outsized importance of attached diatoms to consumers. The high fatty acid concentrations in attached algae, especially diatoms, make attached algae a higher quality food than terrestrial detritus in aquatic ecosystems.

## 4.4. Metabolic Monkey Wrenches: Toxins and Mucoidy

Although it is well established that planktonic cyanobacteria and some dinoflagellates in lakes produce toxins that can severely limit grazing, toxic attached algae are less well documented in literature. Feeding assays suggest that some aquatic grazers may avoid cyanobacteria [e.g., *Lyngbya* (Camacho & Thacker 2006) and *Phormidium* (Fialkowska & Pajdak-Stós 1997)] more for their mechanical challenges than their toxins. Crayfish concentrate cyanotoxins in their hepatopancreas (Liras et al. 1998, Wood et al. 2012). No harmful impacts on the crayfish have been detected, but these toxins are of concern for humans that eat the crayfish (Wood et al. 2012). Some fish that ingest cyanobacteria accumulate toxins in their liver but are able to detoxify and excrete them (e.g., Smith & Haney 2006). Cyanobacterial mats along shorelines of a Kenyan hot spring have poisoned flamingos (Krienitz et al. 2003), and neurotoxic cyanobacteria in rivers have killed dogs in Northern California (Puschner et al. 2008). Food web impacts of benthic cyanotoxins need more investigation, but limited evidence to date suggests that benthic cyanotoxins may be more of a threat for homeotherms than for freshwater invertebrates or fish.

Some benthic diatoms can become non-nutritious because of their copious secretion of carbon as gelatinous stalks or other forms of extracellular mucopolysaccharides. The diatom *Didymosphenia geminata* accumulates as masses of mucilaginous so-called river snot in ultraoligotrophic cold rivers (Bothwell et al. 2014). In controlled experiments, tadpoles ingested *Didymosphenia* but failed to grow. The tadpoles in this study grew rapidly on a diet of other diatoms with lower C:N ratios (Furey et al. 2014).

## 5. INFLUENCE OF GRAZERS ON ATTACHED ALGAE

The reduction in algal biomass associated with high consumption efficiency in attached algal food chains (Cebrian 1999) is only the most obvious influence of grazers. Grazers also alter the taxonomic composition of algal biofilms through active selection and because algal taxa are differentially susceptible to particular algivores (Steinman 1996, Geddes & Trexler 2003). Biomass removal by grazers increases light availability to underlying algal cells, and grazers fertilize attached algae through excretion and defecation (Andre et al. 2003). The combined positive effects of enhanced light penetration and accelerated nutrient turnover substantially offset the negative effects of biomass removal. Thus, grazing usually increases biomass specific–primary productivity (Liess & Hillebrand 2004). Basal algal cells commonly persist under even heavy grazing and subsequently replenish food for consumers (Bein 2012). These combined effects of grazers result in rapidly growing algal assemblages that provide nutritious, stable food supplies.

### 5.1. The Primary Consumers: A Bestiary

Protozoans, rotifers, crustaceans, nematodes, annelids, snails, clams, diverse aquatic insect larvae, fish, frog tadpoles, and turtles all consume attached algae. Invertebrates dominate the grazer assemblage in temperate latitudes, but at least 45 species of freshwater fish in North America have attached algae as a major dietary component (Lee et al. 1980, Matthews et al. 1987). Algivores dominate fish assemblages in tropical waters (Vadeboncoeur et al. 2011) and strongly reduce attached algal biomass (Power 1984a, Flecker et al. 2002). We use the term grazer collectively for all animals that consume attached algae but distinguish among grazers on the basis of their feeding mode (**Figure 2**). Scrapers (e.g., glossosomatid caddisfly larvae) have robust mouthparts that non-selectively gouge attached algae off hard substrates; clippers (e.g., *Tropheus* cichlids) shear or tear clumps of algae from surfaces; browsers (e.g., poeciliid fishes, chironomid midge larvae) selectively remove loosely attached algae from the surfaces of soft sediments or macrophyte or macroalgal hosts; and suction feeders (e.g., catostomid suckers, mussels) pump respiratory structures to slurp up loosely attached or deposited cells. Some small invertebrate grazers make their homes within algal assemblages, whereas larger, more mobile grazers actively track algal productivity over scales of kilometers.

## 5.2. Direct Effects of Grazing on Attached Algal Biomass

The consumption efficiency of attached algae is high because, as outlined above, attached algae are spatially concentrated, nutritious, and digestible. Forty percent (range, 15–90%) of net annual benthic microalgal primary production is directly consumed by grazers, compared with 25% for terrestrial grasslands and <5% for forests and shrublands (Cebrian 1999). A meta-analysis of field experiments revealed that grazers remove, on average, 55% of attached algal biomass measured as chlorophyll (Hillebrand 2009). Grazers also reduce spatial variation in algal biomass, in part because they convert increased algal productivity directly into secondary production rather than allowing it to accrue (Marks et al. 2000, Hill et al. 2010). In his meta-analysis of almost 600 field experiments comparing benthic grazer impacts with grazer-free controls, Hillebrand (2008) found that on average, grazers reduced absolute variation (log response ratio of the standard deviation of biomass) by 50%.

**Secondary production:** production of heterotrophs (organisms that get their energy and raw materials from biomolecules fixed by other organisms)

**Donor control:** consumer–resource dynamics in which consumption has no effect on the rate of supply of that resource

When grazers are resource limited, attached algal biomass is less variable than algal growth rates because grazers track benthic primary productivity at multiple scales. At small patch scales, individual grazers increase feeding rates and their residence times in patches with high algal standing crops (Hart 1981, Kohler 1984). At larger scales, if mobile grazers perceive differences in food availability among habitats and are free to settle in the best habitat available at any time, they may track food renewal rates so closely that they exhibit an ideal free distribution (Fretwell & Lucas 1970, Royama 1971), in which consumer fitness and food abundance are equalized across habitats of different primary productivity.

Densities of highly mobile algivorous fish can be particularly responsive to variation in attached algal primary production. Free-living loricariid catfish were monitored for 3 years over 16 pools spanning a 3-km reach of a forested Panamanian stream (Power 1983, 1984a). Attached algal growth rates in individual pools varied with forest shading and consequent light limitation. Armored catfish biomass and abundance tracked this variation quantitatively. Catfish numbers and biomass increased linearly with algal growth rates in pools, but standing crops of algae and growth rates and survivorship of prereproductive loricariids were similar across pools. When tree fall increased light, loricariid densities increased within weeks, eliminating the biomass response of algae. Similarly, in Lake Tanganyika, Tropheini cichlids aggregate in shallow waters where light and algal productivity are highest. Depth-dependent changes in attached algal photosynthesis and algal phosphorus content together explained 97% of the variation in densities of *T. brichardi* with depth; however, variation in algal chlorophyll with depth was minor (Munubi 2015). Under ideal free conditions, the ability of grazers to track algal productivity closely, and to limit algal biomass, generates positive relationships between grazer densities and area-specific productivity of attached algae but flattens the relationship between algal productivity and attached algal biomass (Oksanen et al. 1995, Steinman 1996, Marks et al. 2000, Munubi 2015).

Despite algivores' ability to track variation in algal primary production closely, little evidence has been found that they overexploit their resource (but see Power 1990a). Algivores reduce attached algal biomass more than productivity (Liess & Hillebrand 2004), and this finding appears to be especially true when grazers move freely or are only minimally impeded (Power 1984a, Munubi 2015). In a model that parameterized primary production and grazing using data from Lake Tanganyika, attached algal productivity was stable over a wide range of algivore densities. In contrast, variation in zooplankton density generated strong oscillations in phytoplankton production (Bein 2012). The benthic algal food chain in Lake Tanganyika exhibited dynamics consistent with donor control of resources, which stabilizes consumer–resource dynamics. This finding is consistent with many studies that demonstrate that attached algal productivity controls consumer density and growth rates, even when consumers control attached algal biomass (e.g., Rosemond et al. 1993; Steinman 1996; Hill et al. 1995, 2010).

Release from grazing by predation (Power et al. 1985, Forrester et al. 1999, McCollum et al. 1998), scouring floods (Power 1992, Wootton et al. 1996, Power et al. 2008), or experimental exclosures (Lamberti 1996, Steinman 1996) produces dramatic change in algal biomass. In a Panamanian stream where algivorous fish abound, substrates appeared barren at depths greater than ~20 cm, but so-called bathtub rings of attached filamentous green algae developed along river margins. This sharp vertical gradient in algal biomass marked a transition from three-level trophic control in shallow water, where wading birds effectively preyed on grazing fish, to two-level food chains in deeper water, where grazing catfish were safer (Power 1984b, Power et al. 1989). In an Oklahoma stream, predation on algivorous minnows by piscivorous bass released filamentous green algae from grazing over entire pools. Along a uniformly sunlit prairie stream, pools containing bass were filled with lush filamentous green macroalgae (*Rhizoclonium* sp., a close relative of *Cladophora*), whereas pools without bass had high densities of grazing minnows and scant algal biomass (Power & Matthews 1983). When floods or experimentalists rearranged grazing minnows and bass, pools switched from green to barren or vice versa within 5 weeks (Power et al. 1985).

**Biomass-specific primary production:** total primary production per mass of algae; chlorophyll is an imperfect surrogate for attached algal biomass

**Area-specific primary production:** total primary production per area of substrate, stream bottom, or lake bottom

Phenology and physical controls can also release attached algae from grazing. Following seasonal disturbances like floods (Wootton et al. 1996, Power et al. 2008) or ice scour (Lorenz & Herdendorf 1982), attached algae typically recover before animals and have time to proliferate while grazer densities are low. Between floods, spatial refuges where filamentous green algal biomass can accrue occur where high flow velocity impedes grazers (DeNicola & McIntire 1991, Hart & Finelli 1999, Lamberti 1996). Because higher flow velocities and floods can also stimulate algal growth, however, both bottom up and top down effects of flow require evaluation to assess their relative importance for algal accrual (Stevenson et al. 1996).

### 5.3. Indirect Effects of Grazing: Alleviating Light Limitation

Grazed attached algal assemblages often have higher biomass-specific primary production, and sometimes area-specific primary production, than assemblages that are shielded from grazers (Steinman 1996, Liess & Hillebrand 2004). Rapid light attenuation within algal biofilms (Krause-Jensen & Sand-Jensen 1998) and a consequent inverse relationship between biofilm thickness and biomass-specific photosynthetic rates are consistent with an alleviation of light limitation by grazing for residual algal cells (DeNicola & McIntire 1991). Grazers also clear off silt and sediments (Power 1984a, Flecker & Taylor 2004). This may be especially important for algae in deeper river pools or lake strata, where light and turbulence are lower.

### 5.4. Indirect Effects of Grazing: Nutrient Recycling

Biomass removal by grazers accelerates nutrient turnover in algal biofilms (Andre et al. 2003). Grazers live in close proximity to their algal food, and the residual ungrazed algae rapidly sequester nutrients from urine and feces from grazers and other consumers. Larval chironomids living within proliferations of the macroalga *Cladophora* had a positive indirect effect on nonselected (tightly attached) epiphytic diatoms and *Cladophora* host filaments near their retreats (Furey et al. 2012). Sedentary trichopteran larvae "garden" by fertilizing and then preferentially consuming algae growing on their retreats (Ings et al. 2010). These positive fertilizing effects can more than compensate for losses due to grazing. For instance, area-specific attached algal primary production on sediments in mesocosms increased linearly with stocked chironomid density; area-specific primary production in mesocosms with the maximum stocking density of 140,000 larvae per $m^2$ was 71% higher than in mesocosms with no chironomid larvae (Herren et al. 2017). Consumer nutrient recycling also alters the stoichiometry of algal biofilms. Grazed biofilms have lower C:N and C:P ratios and higher phosphorus concentrations than their ungrazed counterparts (Liess & Hillebrand 2004, Evans-White & Lamberti 2006). Thus, nutrient recycling by grazers can stimulate primary productivity (Abe et al. 2007, Herren et al. 2017) and enhance food quality of residual attached algae (Liess & Hillebrand 2004, Evans-White & Lamberti 2006).

When grazers live within the algal assemblage, indirect effects of algivorous guests change with life stage of the grazer and host. The tuft-weaving midge, *Pseudochironomus richardsoni*, densely infests proliferations of the green filamentous macroalga *C. glomerata*. Despite ingesting relatively little *Cladophora*, younger midge instars fragment *Cladophora* as they weave it into retreats, reducing long streamers to prostrate, knotted remnants (Power 1990b) (**Figure 1*a***). However, as midges near pupation, destructive tuft-weaving stops, and their accumulated nitrogen-rich feces promote *Cladophora* viability (Power 1991).

Consumer effects can contribute substantially to nutrient cycling at the ecosystem scale, especially when ambient nutrients are low. Recycling by fish accounted for 75% of whole ecosystem nitrogen demand in a tropical river (McIntyre et al. 2008). Invasive snails, *Potamopyrgus antipodarum*, controlled both carbon and nitrogen cycling in the Yellowstone River. High densities of snails consumed >75% of primary production and supplied 67% of algal nitrogen requirements (Hall et al. 2003). Both extinctions and invasions of algivorous fish in tropical rivers altered spatiotemporal availability of nutrients for algae and changed the relative availability of nitrogen and phosphorus (McIntyre et al. 2008, Capps & Flecker 2015).

## 6. ATTACHED ALGAE: A CRYPTIC FOUNDATION OF AQUATIC FOOD WEBS

Advances in stable isotope and fatty acid analyses have transformed our ability to identify the sources and fates of carbon inputs to aquatic ecosystems. Stable isotope analysis provides information on whether metazoan bodies are made of carbon fixed by terrestrial plants, phytoplankton, or attached algae (Vander Zanden & Rasmussen 1999, Finlay 2001), whereas fatty acid analysis tracks essential compounds produced by algae through food webs (Brett & Müller-Navarra 1997). Careful budgets that quantify primary and secondary production and trace their sources demonstrate that attached algae support a disproportionate fraction of metazoan production in freshwaters (Lewis et al. 2001; Vander Zanden et al. 2006, 2011; Karlsson et al. 2009; Lau et al. 2009, 2014). This is so irrespective of whether the ecosystem as a whole is a source or a sink for carbon (Thorp & Delong 2002, Brett et al. 2017).

Brett et al. (2017) reviewed the evidence for attached algal support of metazoan production (both grazers and higher trophic levels) in rivers. Here, we briefly summarize several studies across a range of river sizes. Forested streams have high inputs of terrestrial organic carbon and low light penetration. Nevertheless, more than 60% of snail and shrimp biomass in shaded Hong Kong streams was derived from carbon fixed by attached algae, and fatty acid profiles of these organisms indicated a diet of cyanobacteria and diatoms (Lau et al. 2009). In the Eel River in Northern California, benthic macroinvertebrates were built of carbon from attached algae in their local riffle or pool (Finlay et al. 2002). Larger steelhead and rainbow trout resided in deep pools that had low algal productivity, but they ate macroinvertebrates drifting in from the shallow habitats, where these prey had fed on attached algae (Finlay et al. 2002). Fish and invertebrates in the large (7,000 km$^2$) floodplain habitat of the Orinoco River depended on algal carbon (both phytoplankton and attached algae), not the macrophytes and terrestrial detritus that made up 98% of the available carbon (Lewis et al. 2001). To examine carbon sources for consumers, Finlay (2001) reviewed stable isotope data from 70 rivers, many of which were heavily forested. Scraping grazers relied on attached algae as far into the headwater tips of river networks (drainage areas $<1$ km$^2$) as they could be collected. In river channels that drained more than 10 km$^2$, all consumers except shredders relied in large part on algal carbon.

The historic focus on phytoplankton as the trophic basis of production in lakes has given way to the recognition that attached algae and terrestrial detritus are also important food sources for primary consumers (Vadeboncoeur et al. 2002, Devlin et al. 2013). Zooplankton are largely dependent on phytoplankton (Brett et al. 2009, Kelly et al. 2014) but supplement their diets with attached algae in shallow lakes (Rautio & Vincent 2006). Littoral invertebrates and fish in lakes throughout the world rely on carbon fixed by attached algae (Hecky & Hesslein 1995; Vander Zanden & Vadeboncoeur 2002; Vadeboncoeur et al. 2003; Vander Zanden et al. 2006, 2011; Karlsson et al. 2009; Devlin et al. 2013). Vander Zanden et al. (2011) synthesized stable isotope data of macroinvertebrates and fish from 75 lakes and combined these with estimates of whole-lake (benthic plus planktonic) primary production. The contribution of attached algae to whole-lake primary production declined with the average depth of the lake and with increasing nutrient concentrations. Regardless of lake size, most fish species relied roughly equally on food chains based on attached algae and on phytoplankton. Only a few fish species fed exclusively on a phytoplankton-based food chain. Most species of fish and zoobenthos live in, or exploit, the littoral zone, even in the world's largest lakes (Vadeboncoeur et al. 2011). This concentration of fish and invertebrate diversity in the littoral zone gives rise to the strong reliance on attached algal carbon by fishes, irrespective of lake size. However, it is also notable that most fish species consume resources derived from both attached algae and phytoplankton (Vander Zanden et al. 2011). Benthic–planktonic resource coupling may increase growth efficiency in fishes through ontogenetic diet shifts (Vander Zanden & Vadeboncoeur 2002;Vander Zanden et al. 2006) and help stabilize ecosystems (Vadeboncoeur et al. 2005).

In summary, interactions of attached algae and grazers often produce ecosystems that are characterized by a highly productive, low biomass (cryptic) algal production that is efficiently transferred to primary consumers. Attached algae are a concentrated food source, and algivores, from single-celled protozoans to large tropical fish, efficiently consume a high proportion of new algal production. However, rough surfaces (Dudley & D'Antonio 1991) provide spatial refuges for low-profile and tightly adhered basal algal cells that allow them to escape even the most determined grazers. Thin algal residues, when stimulated by grazer enhancement of light and nutrient availability, often show increased biomass-specific primary productivity, and sometimes area-specific primary productivity (Power 1990a, Steinman 1996, Herren et al. 2017), and regrow rapidly enough to sustain a resource base. Diatoms, in particular, appear to thrive even when intensively grazed and continue to supply highly nutritious, easily digestible food that promotes rapid growth in most consumers.

## 7. FRESHWATER TROPHIC PYRAMIDS IN A CHANGING WORLD

Benthic grazers in low-nutrient, unpolluted freshwaters commonly maintain inverted pyramids of trophic level biomass, unless grazers are excluded by predators, removed or diluted by floods, or constrained by other factors. Some interesting exceptions include calcium carbonate–encrusted cyanobacterial assemblages that dominate food web biomass in unpolluted areas of the Florida Everglades (Gaiser et al. 2005, 2006; Trexler et al. 2015) and mucoid masses of stalked diatoms that accumulate in cold oligotrophic streams, described above (Bothwell et al. 2014, Furey et al. 2014). Grazing can continue to suppress attached algal accrual under moderate nutrient enrichment (Marks et al. 2000). Beyond a critical nutrient-loading threshold, however, phytoplankton or floating scums proliferate, extinguishing light for attached algae below. Light limitation then flips clear-water ecosystems fueled by attached algae to phytoplankton-based ecosystems (Vadeboncoeur et al. 2003, 2005, 2008). The threshold for this flip, or conversely, the resilience of the clear-water inverted pyramid in the face of eutrophication, depends in large part on the water retention time in lakes (Carpenter et al. 1999) and the flushing rate in rivers (Power et al. 2015).

**Photosynthetic efficiency:** the amount of carbon fixed per unit light flux

Removal of riparian forests near waterways is a common agricultural practice. The resultant increases in light and temperature reduce the ability of grazers to control nuisance algal blooms (Sturt et al. 2011). Riparian vegetation removal also increases sediment delivery to inland waters (Cohen et al. 1993). The direct and indirect effects of sediment on attached algae and their grazers deserve more study. Sediment accumulation on attached algae immediately reduces photosynthetic activity of the covered cells (Power 1990a, Izagirre et al. 2009). However, area-specific photosynthetic rates can recover over time through increases in cellular chlorophyll content and photosynthetic efficiency (Izagirre et al. 2009). Over the long term, increased sediment deposition on benthic surfaces appears to have a stronger effect on attached algal species composition than on area-specific primary productivity (Cohen et al. 1993, Wagenhoff et al. 2013). Deposition of silt and fine sediments favors filamentous and stalked algae and motile diatoms and cyanobacteria (Izagirre et al. 2009, Wagenhoff et al. 2013). Riparian deforestation is associated with species loss in many phyla in Lake Tanganyika, East Africa (Cohen et al. 1993). Grazing fish are particularly vulnerable to increased sediments and have experienced persistent declines relative to predatory fish (Takeuchi et al. 2010). The negative effects of sediments on growth of algivorous fish has weakened top-down control of algal biomass in Lake Tanganyika (Munubi 2015) (**Figure 1*e*,*f***).

Over much of our history, humans have been diverting and extracting water from lakes and rivers while adding nutrients, xenochemical pollutants, excessive fine sediments, and light and summer heat (by removing riparian shade or groundwater). These impacts leave lakes and rivers turbid (with suspended sediment or phytoplankton) and periodically hypoxic owing to biomass decomposition, which exacerbates nutrient regeneration. In recent decades, warming, stagnation, and eutrophy in freshwaters have led to outbreaks of harmful algal blooms. Hypoxia and fish kills often follow, as well as toxic cyanobacterial blooms, which have long raised public and environmental health concerns in lakes (Wood et al. 2011) and are of increasing concern in rivers worldwide (McAllister et al. 2016, Power et al. 2015). Further warming and nutrient loading will increase the frequency and intensity of harmful blooms, favoring harmful cyanobacteria over more edible algae (Paerl et al. 2016).

Aquatic ecosystems with food webs characterized by inverted pyramids of trophic-level biomass sustain both clean water supplies and populations of fish, birds, and wildlife. Clear freshwater ecosystems are highly prized by society and are thought to represent a pre-European historical state in North America, Europe, and Australia (Stoddard et al. 2006; but see Moss 2015). Appreciating that these inverted biomass pyramids are supported by small, cryptic algae should inform our efforts to maintain or restore the conditions that allow them to thrive.

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