I. WHAT IS FRESH WATER?

The study of freshwater algae is really the study of organisms from many diverse habitats, some of which are not entirely “fresh.” Although the oceans are clearly saline (≈ 35 g salts L⁻¹) and most lakes are relatively dilute (world average < 0.1 g L⁻¹; Wetzel, 1983a), there is enormous variation in the chemical composition of the nonmarine habitats that algae occupy. Conditions in lakes and rivers vary not only in salinity, but also in size, depth, transparency, nutrient conditions, pH, pollution, and many other important factors. Aquatic ecologists also use the term “inland” waters to encompass a greater range of aquatic ecosystems. Even this term may be unsatisfactory, because algae occupy many other habitats, such as snow, soils, cave walls, and symbiotic associations (Round, 1981).

Organisms grouped together in this volume as freshwater algae fall into a large, but ecologically meaningful collection of environments: all habitats that are at least slightly wet, other than oceans and estuaries. One reason for such a broad scope is that inland saline lakes, snow and ice, damp soils, and wetlands are studied by phycologists and ecologists who also examine more traditional freshwater environments. Some genera with terrestrial species, such as *Vaucheria*, *Nostoc*, *Chlorella*, and *Prasiola*, also have species found principally in streams or lakes (Smith, 1950; Whitton, 1975). In North America, the variety of freshwater habitats colonized by algae is very rich, and offers an enormous and fascinating range of environments for their study.

The distinction between marine and freshwater habitats is revealed in the variety of algae that occur in these environments. There are no exclusively freshwater divisions of algae, but certain groups exhibit...
greater abundance and diversity within fresh waters, especially Cyanobacteria, Chlorophyta, and Charophyta (Smith, 1950). Within the green algae, conjugating greens and desmids (Zygnematales, Chap. 9) comprise a very rich collection of species that almost exclusively occupy fresh water. Other groups, such as the diatoms and chrysophytes, are well represented in both spheres. Other groups, particularly the Phaeophyta, Pyrrophyta, and Rhodophyta, exhibit greater diversity in marine waters (Smith, 1950; Bourrelly, 1985). Most freshwater algae are best described as cosmopolitan, although there are reports of endemic chrysophytes, green algae, rhodophytes, and diatoms (Tyler, 1996; Kociolek et al. 1998), and at least some species of cyanobacteria (Hoffmann, 1996). Many algal taxa have particular environmental tolerances or requirements, and are ecologically restricted, but still geographically widespread. The euglenophyte Colacium is almost exclusively epizoic on aquatic invertebrates, but is widely distributed throughout North America (Smith, 1950; Chap. 10). The chrysophyte Hydrurus foetidus is an exclusive inhabitant of cold mountain streams, but is distributed worldwide (Smith, 1950; Whitten, 1975, Chap. 12). Even specialized taxa such as Basicladia chelonum (Chlorophyceae), which is restricted mainly to the shells of turtles, has been collected from many habitats throughout eastern North America (Smith, 1950; Prescott, 1962; Colt et al., 1995). The actual distribution of apparently disjunct freshwater species must therefore be viewed with some caution until detailed surveys have been conducted (see, for example, Linne von Berg and Kowallik, 1996; Müller et al., 1998).

Inland waters represent only about 0.02% of all water in the biosphere, and nearly 90% of this total is contained within only about 250 of the world’s largest lakes (Wetzel, 1983a). Nonetheless, it is fresh water that is most important for human consumption and is most threatened by human activities. Algal ecologists play an important role in the understanding of aquatic ecosystems, their productivity, and water quality issues (Round, 1981; Brock, 1985a; Hoffmann, 1998; Dow and Swoboda, 2000; Oliver and Ganf, 2000, Chaps. 23 and 24). This chapter examines the habitats of freshwater algae and how differences in these systems affect algal communities.

II. LENTIC ENVIRONMENTS

Lentic environments include standing waters from the smallest ponds (a few square meters) to enormous bodies of water (e.g., Laurentian Great Lakes: 245,000 km²). Their formation, geography, limnology, and conservation have been covered in several texts (Hutchinson, 1957, 1967, 1975; Frey, 1963; Wetzel, 1983a; Cole, 1994; Abel et al., 2000). This section summarizes some features of lentic environments as they pertain to the ecology and distribution of freshwater algae.

A. Major Lakes of North America

Worldwide, the single largest volume of freshwater — nearly 20% of the world’s total — is located in Lake Baikal, Siberia (23,000 km³), but the North American Great Lakes (Fig. 1A) collectively represent the largest total volume of nonsaline water on Earth, approximately 24,600 km³ (Wetzel, 1983a). North America is home to many spectacular large and deep freshwater systems, nearly half of all the world’s lakes greater than 500 km² (Hutchinson, 1957). Two of the most impressive lakes are subarctic: Great Slave Lake (28,200 km²; 614 m deep; deepest in North America) and Great Bear Lake (30,200 km²; > 300 m deep) in the Northwest Territories (Hutchinson, 1957). Crater Lake in Oregon (Fig. 1B) is much smaller (64 km² in area), but is the deepest lake in the United States (608 m) and seventh deepest in the world (Edmondson, 1963). The largest lakes on the continent are located in northern and temperate regions, although Great Salt Lake (Utah) is a massive remnant lake (> 6000 km²) that has a mean depth (~ 9 m) and very high salinity (130–280 g L⁻¹) that fluctuate with available moisture, and occupies a portion of the Pleistocene Lake Bonneville, which had an area > 51,000 km² and a depth of 320 m (Hutchinson, 1957).

B. Lake Basins

Sizes and shapes of lake basins (their morphometry) have profound effects on the physics, chemistry, and biology of lake ecosystems, and influence the composition of algal communities and their productivity. Lake basins differ in morphometry as a result of the forces that created them, many of which were catastrophic events from the past, principally glacial, seismic, and volcanic activity. Hutchinson (1957) distinguished 76 different lake types based on their origins; these were classified into a simpler scheme by Wetzel (1983a) that is summarized in Table I.

Glacial activity is the most important agent in North America. It created millions of small and large basins from the arctic south to the southern extent of the Wisconsin ice sheet. In this period (15,000–5000 years BP), many basins became closed by morainal deposits, including the Laurentian Great Lakes. Some morainal lakes occur at the ends of long valleys after glaciers have receded, including the Finger Lakes of...
New York (Fig. 1C), which are elongate, radially arranged basins that range from small ponds to large lakes, such as Seneca (175 km² area, 188 m depth; Hutchinson, 1957; Berg, 1963). However, most glacially formed lakes are small kettles scattered across the continent (Fig. 1D and E). Glacial scouring in mountainous terrain may form deep amphitheater-like cirques (Fig. 1F), which are common from Alaska through the western mountain ranges south to tropical locations in Costa Rica (Haberyan et al., 1995). Glacial basins within narrow valleys may form deep fjord lakes (Fig. 2A), or a chain of smaller lakes known as paternosters. Several forces, including glacial scour and lava flow, combined to form the small (9.9 km²) but deep (259 m) fjordlike Garibaldi Lake (Northcote and Larkin, 1963; Fig. 2B). Ice-formed (thermokarst) lakes, which result from freezing and thawing action in ice and soil, are common in the Arctic. All are shallow but vary from large elliptical basins (up 70 km² area) to small (10–50 m diameter), “polygon” ponds (Fig. 2C).
which are estimated at more than a million in number (Livingstone, 1963; Sheath, 1986).

Tectonic basins are formed by movements of the Earth’s crust. Among these, grabens form when fault lines create often enormous depressions, such as Lake Tahoe, a symmetrical, deep (505 m), and steep-sided lake (Fig. 3A). Tahoe (double fault lines) and Lakes Baikal and Tanganyika (single faults) include the deepest lakes in the world, although less spectacular examples also occur. Lago de Peten (Guatemala) is

<table>
<thead>
<tr>
<th>Type of forces</th>
<th>Basins</th>
<th>Principal force</th>
<th>North American examples</th>
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<tbody>
<tr>
<td>Catastrophic</td>
<td>1. Glacial</td>
<td>Glacial scouring</td>
<td>Great Slave Lake, NWT</td>
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<td></td>
<td>Moraine deposits</td>
<td>Finger Lakes, NY; Moraine Lake, AK</td>
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<td>Kettles</td>
<td>Linsley Pond, MA; Cedar Bog Lake, MN</td>
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<td></td>
<td>Cryogenic</td>
<td>Many polygon lakes, AK</td>
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<td></td>
<td>2. Tectonic</td>
<td>Graben</td>
<td>Lake Tahoe, CA-NV</td>
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<td></td>
<td>Uplift</td>
<td>Lake Okeechobee, FL</td>
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<td></td>
<td>Landslide</td>
<td>Mountain Lake, VA</td>
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<td>3. Volcanic</td>
<td>Caldera</td>
<td>Crater Lake, OR</td>
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<td></td>
<td>Maar</td>
<td>Zuni Salt Lake, Mexico</td>
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<td></td>
<td>4. Meteor</td>
<td>Meteor</td>
<td>New Quebec Lake, PQ</td>
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<td>Noncatastrophic</td>
<td>5. Solution</td>
<td>Doline</td>
<td>Deep Lake, FL; limestone areas of KY-IN-TN</td>
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<td></td>
<td>Salt collapse</td>
<td>Montezuma Well, AZ; Bottomless Lakes, NM</td>
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<td>6. Rivers</td>
<td>Oxbows</td>
<td>Lake Providence, LA</td>
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<td></td>
<td>Plunge</td>
<td>Fayetteville Green Lake, NY</td>
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<td></td>
<td>7. Coastal</td>
<td>Shoreline</td>
<td>Along Laurentian Great Lakes; Cape Cod area</td>
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<td></td>
<td>8. Wind</td>
<td>Deflation</td>
<td>Moses Lake, WA; Sandhills region, NB</td>
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<td></td>
<td>9. Organic</td>
<td>Beaver</td>
<td>Many locations in northern regions</td>
</tr>
<tr>
<td></td>
<td>Human</td>
<td>Lake Mead, AZ-NV; Cherokee Reservoir, TN</td>
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**FIGURE 2** Other glacial and ice-formed lakes: A, Okanagan Lake (BC), a fjord lake; B, Garibaldi Lake, formed by glacial scour and lava damming; C, arctic polygon ponds. Photos A courtesy of NASA, reproduced with permission; photos B and C by R. J. Cannings, reproduced with permission.
the largest (567 km$^2$) and deepest (> 32 m) lake on the Yucatan Peninsula (Covich, 1976), and the largest lake in Mexico, Lago Chapala (1109 km$^2$), is also a tectonic trench (Serruya and Pollingher, 1983). Landslide lakes form when water flows through an existing depression and is blocked by rock or other material, as in as Spirit Lake, near Mount St. Helens (WA; Fig. 3B) and Mountain Lake (VA; Parker et al., 1975). In the Pliocene, shallow marine areas were raised above sea level and existing depressions filled with freshwater, as with Lake Okeechobee (Fig. 3C), a large (1840 km$^2$), shallow (4 m) subtropical lake in Florida.

Volcanic lakes are among the deepest and most steep-sided lakes on the continent. The exceptionally clear water in Crater Lake (OR), a collapsed caldera (Fig. 1B), has Secchi depths between 20 and 30 m, with 1% surface light down to 100 m (Larson et al., 1996). Lake Atitlán in Guatemala is an alpine tropical caldera (8.2 km$^2$; 1550 m elevation) that reaches a depth of 341 m, making its ratio of depth to surface area four times greater than better known Crater Lake. Lake Nicaragua (Fig. 4A; 7700 km$^2$ area; depth = 60 m) was formed by volcanic lava damming an existing valley (Cole, 1963). Some volcanic lakes, such as Yellowstone Lake (WY) and Surprise (AK) Lake, have hydrothermal vents that influence temperature, pH, and O$_2$ conditions, and may contribute trace metals (Pierce, 1987; Larson, 1989; Cameron and Larson, 1993). Other volcanic lakes formed from violent explosions of cinder cones (maars) and are often nearly circular in outline, such as Big Soda Lake in Nevada, Lago Chamiuc in El Salvador (Cole, 1963), and Laguna Hule in Costa Rica (Umama-Villalobos, 1993). Volcanic lakes also occur in Mexico, Guatemala, Nicaragua, and El Salvador (but not all are deep), and some were formed as recently as 500 year ago (Hutchinson, 1957; Cole, 1963).

In limestone regions, solution or sinkhole lakes form from the dissolution of bedrock by surface and underground waters charged with CO$_2$ (Cole, 1994). Sinks may be circular, elliptical, or irregular in outline, and occur throughout Kentucky, Indiana, Tennessee, Florida, Mexico, and Guatemala (Fig. 4C). Florida is especially rich in sinkholes, with several hundred lakes and ponds ranging from less than 1 ha to several square kilometers (Fig. 3C). In north Florida, some lakes are relatively dilute and colored with organic matter from pine litter, whereas others are clear,

![Figure 3](image-url)
hardwater systems (Shannon and Brezonik, 1972). Spring-fed sinkholes may become isolated or thermally constant, such as Montezuma Well (AZ; Fig. 4D), creating an environment with high algal productivity (600 g C m⁻² y⁻¹; Boucher et al., 1984) and unusual communities. Montezuma is a collapsed travertine system with several endemic invertebrates, but no fish, rotifers, or cladocerans (Cole, 1994).

Lakes may form through wind action, whereby deposited sand blocks existing valleys (e.g., Moses Lake, WA) or forms depressions in dunes, as in Nebraska and Texas (Cole, 1963; Edmondson, 1963). River-formed lakes, including oxbows, occur across North America where rivers traverse level terrain, enabling siltation of meandering valleys (Fig. 5A). Other small basins form in the plunge pools of waterfalls (Fig. 5B). Fayetteville Green Lake is a relatively deep (59 m; 0.3 km² area) plunge-pool lake in central New York that apparently has never fully mixed; it was formed during the Pleistocene when melting glaciers formed a vast waterfall (Berg, 1963; Brunskill and Ludlam, 1969).

For many centuries the principal biological agent responsible for creating lakes in North America was the beaver (Castor canadensis), which dams smaller rivers to form lakes and ponds (Hutchinson, 1957; Fig. 5C). Today, reservoirs are a more important group of lentic ecosystems, the size and number of which are increasing worldwide (Fig. 5D). The physical and chemical properties of reservoirs differ from natural lakes with respect to dendritic or eccentric morphology (deepest near the dam), shorter flushing period, irregular water level, greater dissolved and suspended solids, and less stable littoral zone (Wetzel, 1990). Because reservoirs serve hydroelectric, flood control, or drinking water uses, they occur in many biomes.

A few lakes may have been formed by meteor impact, such as New Quebec Lake, a nearly perfectly circular basin (3.4 km diameter) in a region of irregular, glacially formed lakes in northern Quebec (Cole, 1994). Carolina Bays, which are not truly bays, are a series of roughly 150,000 small, shallow, elliptical basins, with a distinctive NW–SE orientation, and concentrated along the Atlantic coast from New Jersey south to Florida. It is their directional orientation that has caused some to speculate that their origin may be from meteor showers, whereas others have suggested wind action or artesian springs (Hutchinson, 1967; Cole, 1994).
Cole, 1994). Many are now filled, but those with aquatic habitats are shallow and have extensive macrophyte beds and low algal production (Schalles and Shure, 1989).

C. Lake Community Structure and Productivity

1. Lake Zones and Thermal Patterns

Regions within lakes exhibit physical and chemical differences that affect algal communities. The open water region of lakes is termed the pelagic (or limnetic) zone, whereas close to shore is the littoral zone, where the greatest exchange between nutrient-rich sediments and the water occurs (Fig. 6). The littoral zone is colonized by submersed (e.g., Ceratophyllum, Potamogeton, and Vallisneria) and emergent (e.g., Scirpus and Typha) flowering plants, although some macroalgae (e.g., Chara, Nitella, and Batrachospermum) and nonflowering plants (mosses, liverworts) also occur (Hutchinson, 1975). Vertical zones also develop in temperate regions. In early spring, most temperate lakes are well mixed, with similar temperatures and chemical conditions from top to bottom. As temperatures increase, upper mixed waters become thermally isolated from deeper and colder waters, a process which is termed stratification. The upper epilimnion continues to become warmer, receives greater irradiance, and is well mixed and oxygenated; deeper waters remain cool (ca. 4°C in deep lakes) and dissolved gases are consumed by microbial activity. At an intermediate depth (the metalimnion), temperature declines, often sharply, with reduced heat penetration and reduced mixing (= thermocline if ≥Δt° m−1). Density gradients formed by this thermal barrier may be sufficient to support dense algal populations (Pick et al., 1984); here light is adequate for photosynthesis coupled with a greater supply of nutrients. Algal production may create metal-
imnetic oxygen maxima in clear oligotrophic lakes (Wetzel, 1983a; Parker et al., 1991). The hypolimnion is a deeper, cooler region with greater nutrient supply, but reduced (approaching zero) oxygen levels; light may be too low for photosynthetic algal growth except in very clear lakes.

Patterns of thermal stratification and mixing differ with altitude and across biomes. A dimictic pattern, in which lakes stratify in the summer, mix in the autumn, stratify in the winter after ice cover, and mix in the spring after ice-out, is most common in temperate climates. Warm monomictic lakes (stratification and one mixing period; summer epilimnion > 4°C) occur in warmer climates or in large basins without ice cover (Wetzel, 1983a). Examples include the Great Lakes, larger Finger Lakes, Lake Tahoe, lakes in warm or coastal climates, and subtropical, high altitude lakes. Cold monomictic lakes, with a single turnover in summer or late spring, occur mainly in alpine and arctic areas (temperatures ≤ 4°C). Oligomictic lakes have rare mixing periods (less than once per year), where temperature strata (summer epilimnion > 4°C) may remain for some years; this pattern is most common in deep tropical lakes (Wetzel, 1983a). Polymictic lakes are shallow systems with frequent or continuous mixing, and occur in tropical and equatorial areas such as Lake Managua (Xolotlán), Nicaragua (Erikson et al., 1997). Amictic lakes, uncommon in North America (some in Greenland; common in the Antarctic), are perennially ice covered and do not turn over. A special class of lakes in which upper waters (mixolimnion) mix, but deeper waters (monimolimnion) never circulate, are termed meromictic (Wetzel, 1983a). These lakes have a very stable chemical and temperature density gradient, known as a chemocline, that results in anoxic conditions, H₂S, and purple sulfur bacteria in

![Figure 6: Diagram that represents the zones and algal habitats within typical oligotrophic and eutrophic lakes (EZ = euphotic zone).](image-url)
the water column. A strong depth to surface area ratio is usually necessary to maintain meromixis; Fayetteville Green Lake in New York and Hot Lake in Washington are examples (Hutchinson, 1957).

2. Lake Productivity

Limnologists distinguish lakes according to a gradient of primary production (¹⁴C uptake, algal growth) or biomass, from oligotrophic (annual average < 50–300 mg C m⁻² d⁻¹; < 0.05–1 µg chlorophyll-a L⁻¹) to eutrophic (> 1000 mg C m⁻² d⁻¹; 15–100 µg chlorophyll-a L⁻¹), and these levels are influenced, at least in part, by the properties of lake basins (Wetzel, 1983a; Likens, 1985). Oligotrophic lakes are poor in nutrients, usually deep and steep-sided, and have high transparency, a narrow littoral zone, abundant dissolved oxygen with depth, and larger relative hypolimnion volume. Lake Tahoe is an ultra-oligotrophic lake that has exceptional water clarity, although average Secchi depths have declined from about 30 to 23 m and primary productivity levels have more than doubled (40–100 mg C m⁻² d⁻¹) since the late 1950s, following increased nutrient loading from regional development (Goldman, 1988). Eutrophic lakes are nutrient-rich, often shallower with a broad littoral zone, and have depleted summer hypolimnetic oxygen and reduced transparency. Eutrophication of lakes often result when nutrients are added as sewage, detergents, or fertilizers (Wetzel, 1983a). Lake Mendota, Wisconsin, is an example of a larger lake (39 km²) that has an average depth of only 12 m and receives substantial input from agricultural and urban sources. The lake has experienced algal blooms and high nutrient levels for more than a century, and water transparency has been consistently low for more than 80 years (Brock, 1985a).

D. Ponds, Temporary Pools, and Bogs

Smaller lentic environments, often called ponds, may seem very similar to lakes except for their size, but they have distinct properties. Ponds are shallow enough either to support rooted aquatic vegetation across the entire basin or to fail to stratify during the summer. The term “pond,” however, is not a precise concept, despite its frequent usage. In New England, the word is often applied to fairly substantial lakes, such as Linsley Pond (9.4 ha, max depth 14.8 m; Brooks and Deeye, 1963) and Long Pond (40 ha, 22 m; Canavan and Siver, 1995), both of which stratify in summer. Small limnetic systems can be divided into those that contain water year round, often called permanent, and temporary waters that become dry each year and are termed vernal ponds (Wetzel, 1983a).

Temporary ponds are located in low-lying areas that fill with snow melt or spring runoff, but dry up in the summer (Wetzel, 1983a); resident algal populations may be quite substantial during the growing season and rely on resistant resting stages (e.g., dinoflagellate cysts [Chap. 20], cyanobacterial akinetes [Chap. 4], and zygospores of Zygnematales [Chap. 9]) capable of surviving extended adverse conditions (Reynolds, 1984a, b). Arctic tundra ponds typically freeze solid for many months, resulting in a growing season of only 60–100 days (Wetzel, 1983a; Sheath, 1986). Algal communities often consist of small flagellates (particularly Cryptophyceae and Chrysophyceae; see Chaps. 21 and 12–14) that bloom during the brief summer of long daylight, although many species apparently do not form resting stages and survive freezing conditions in their vegetative condition (Sheath, 1986).

E. Phytoplankton of Lakes and Ponds

Assemblages of planktonic algae vary greatly among lake basins and biogeographic regions. They include members of all algal divisions except the Rhodophyta and Phaeophyta. Their ecology has been the subject of many reviews, including Hutchinson (1967), Kalf and Knoechel (1978), Round (1981), Reynolds (1984a), Munawar and Talling (1986), Sandgren (1988), Munawar and Munawar (1996, 2000), Stotner and Smol (1999), and Whitton and Potts (2000).

1. Phytoplankton Diversity, Composition, and Seasonal Succession

Every collection of freshwater algae is characterized by a fascinating and perplexing diversity of species, many of which are potential competitors for common resources. Up to several hundred algal species may coexist in a relatively uniform habitat was proposed by Hutchinson (1961) to be possible because of the numerous niches within a lake, as well as variation within the environment over time. Many factors contribute to phytoplankton diversity and production, including temporal and spatial variations in nutrient supply, grazing, temperature, and parasitism (Turpin and Harrison, 1979; Crumpton and Wetzel, 1982; Sommer, 1984; Bergquist and Carpenter, 1986). The biomass of phytoplankton is thought to be driven mainly by nutrient supply and herbivory in all lakes, but their temporal dynamics differ in eutrophic and oligotrophic systems (Walters et al., 1987; Carpenter et al., 1993).
Ecosystem-level studies of lake food webs in some cases have ignored phytoplankton species composition, and instead treat this component as a black box. This approach is incomplete because the functional properties of algal assemblages vary strongly with species composition. Taxonomic information is important for ecological studies because many of the features used to classify algae, such as photosynthetic pigments, storage products, motility, reproduction, cell ultrastructure, and even DNA sequence information, have functional importance. For example, among freshwater phytoplankton, only cyanobacteria and some cryptomonads possess the red accessory pigment phycocyanin, which has an absorption maximum (540–560 nm) that broadens the photosynthetic capacity of cells and may facilitate growth at greater depths (Goodwin, 1974, Chap. 21). Similarly, only certain species of cyanobacteria are able to fix N\textsubscript{2}, mainly those that possess heterocysts (e.g., *Anabaena*, *Aphanizomenon*, and *Nostoc*), although some non-heterocystous forms with thick sheaths or that form dense aggregations, although some non-heterocystous forms with *Nostoc*, are involved in the capture of bacterial prey (Andersen and Wetherbee, 1992).

Diversity in size is also an important property of phytoplankton communities. One scheme (Sieburth et al., 1978) categorizes sizes into groups that differ over orders of magnitude: picoplankton (> 0.2–2 µm), nanoplankton (> 2–20 µm), microplankton (> 20–200 µm), and mesoplankton (> 200–2000 µm) include most algal cells and colonies in freshwater. Expressed in terms of volume, the sizes of freshwater phytoplankton span at least 8 orders of magnitude (Reynolds, 1984b). The bacteria-sized picoplankton have attracted recent interest because they have been found to dominate (at least numerically) many phytoplankton communities in lakes and marine systems (Stockner et al., 2000). They occur in great numbers (10\textsuperscript{5}–10\textsuperscript{10} mL\textsuperscript{–1}), possess rapid growth rates, and are highly productive; most often reported are cyanobacteria (e.g., *Cyanobium*, Cyanophyceae, Synechococcus, and Synechocystis; see Chap. 3) and some green algae (e.g., *Nannochloris*). Their importance (percentage of biomass or primary production) seems to be greatest in oligotrophic and least in eutrophic lakes (Burns and Stockner, 1991; Hawley and Whitton, 1991; Wehr, 1991), although there are exceptions (Wehr, 1990; Weisse, 1993). Autotrophic picoplankton have a strong competitive ability in P-limited conditions (Suttle et al., 1987, 1988; Wehr, 1989) and are grazed mainly by micro-zooplankton (ciliates, flagellates), rather than cladocerans or copepods (Pernthaler et al., 1996; Hadas et al., 1998), making them important links between microbial and classical food webs (Christoffersen et al., 1990; Sommaruga, 1995).

Size affects sinking rate and thus the ability of cells to remain in the euphotic zone. Smaller cells tend to be spherical or ellipsoidal and thus sink more slowly, whereas larger forms have more elongate or complex shapes to reduce sinking. The dinoflagellate *Ceratium hirundinella* is a large planktonic alga (up to 400 µm) common in mesotrophic and eutrophic lakes with stable stratification (Chap. 20); the alga regulates its position in the water column by active migration and perhaps by changes in the shape and size of hornlike projections (Heaney and Furness, 1980; Pollingher, 1987; Heaney et al., 1988). The silica walls of diatoms result in heavier cellular densities, making them susceptible to sinking. Diatoms are estimated to have 3–16 times faster sinking rates than nonsiliceous algae of equivalent sizes (Sommer, 1988). Larger colonial diatoms, such as *Asterionella formosa*, *Fragilaria crotonensis*, and *Tabellaria fenestrata* (see Chap. 16), have more elongate or elaborate morphologies, which may reduce sinking rates or cause some cells to rotate (Smyda, 1970; Barber and Haworth, 1981). Planktonic cyanobacteria and desmids produce extracellular mucilage, which may aid in buoyancy (Round, 1981). Some cyanobacteria, such as *Anabaena flos-aquae* and *Microcystis aeruginosa*, also maintain their position in the water column using gas vacuoles (Chaps. 3 and 4). Observed changes in the population size may be the result of differences in vertical migration and sinking to lower strata, rather than actual changes in numbers.

Regular seasonal changes (seasonal succession) in phytoplankton populations over many years have been observed widely and reported in long-term limnological records. Few species have been documented as thoroughly as *Asterionella formosa*, a diatom found in mesotrophic, temperate lakes (Round, 1981; Reynolds, 1984a, Chap. 16). In Lake Windermere, populations increase after turnover and peak in the spring when light levels and temperatures are increasing and the Si:P ratio is near maximum (Fig. 7). Populations decline over the summer and have a second (usually smaller) peak in the autumn (Lund, 1964; Reynolds, 1984a; Neale et al., 1991). *Asterionella* was the spring dominant in Lake Erie from at least 1931 until about 1950, when nutrient enrichment selected for diatom genera such as *Stephanodiscus*, *Aulacoseria* (Melosira; see Chap. 15), and *Fragilaria*, and filamentous cyanobacteria such as *Anabaena* and *Aphanizomenon* (Davis,
As eutrophication receded, there was a 70–98% reduction in numbers of *Stephanodiscus* spp. and *Aphanizomenon flos-aquae*, and the reappearance of *Asterionella* (Makarewicz, 1993). Further details are given in Munawar and Munawar (1996).

Population dynamics generally follow predictable changes in temperature, sunlight, nutrients, and other factors. However, algal population dynamics exhibit more abrupt changes than these gradual trends predict, suggesting that other factors may drive seasonal succession. Round (1971) described these as “shock” periods: times in the lake cycle, such as turnover, that lead to sharp changes in chemical or physical conditions. Lakes with less predictable conditions or more shock periods exhibit frequent changes in species composition and shorter growth peaks (Fig. 8A), but when conditions are more stable, populations may persist over longer time periods (Fig. 8B). Furthermore, coexistence (temporal overlap) among species will result if a greater variety of habitats are available, perhaps through stratification, basin complexity, or multiple inflows (Fig. 8C). These temporal patterns repeat only if nutrient conditions remain stable.

**FIGURE 7** Seasonal periodicity in the abundances (cells per liter) of *Asterionella formosa* (solid line), *Fragilaria crotonoensis* (dashed line), and *Tabellaria flocculosa* (dotted line), and concentrations of dissolved silica (upper, black; milligrams per liter) in Windermere, English Lake District 1945–1960. Reproduced with permission from A. Horne and C. R. Goldman, Limnology, 2nd ed. Copyright © 1994, McGraw–Hill, New York.
or other conditions are stable and other disturbances are kept to a minimum. For example, in Lake Michigan Tabellaria sp. and Asterionella formosa exhibited regular peaks in the spring phytoplankton community for several decades, but Asterionella numbers have declined in more recent years, while Stephanodiscus and filamentous cyanobacteria have increased following increases in P supply (Makarewicz and Baybutt, 1981).

Laboratory experiments with Stephanocyclus (Cyclotella) meneghiniana and Asterionella formosa, which have different Si and P requirements and consumption rates, have indentified the levels of these nutrients at which the two species may coexist (Fig. 9, Tilman, 1977, 1982). Studies have quantified resource competition among other species and with other resources, such as C:P and N:P (Kilham and Kilham, 1978; Rhee and Gotham, 1980; Sommer and Kilham, 1985; Olsen et al., 1989). In situ manipulations of phosphorus and light have demonstrated clear differences among species: some respond positively to P addition alone (e.g., Synedra radians), whereas others, such as chrysophytes (e.g., Dinobryon sertularia and Synura uvella), increase under greater light (de Noyelles et al., 1980; Wehr, 1993). Species composition and size structure each can be influenced by nutrient supply. With higher N:P supply ratios, assemblages in an oligotrophic lake were dominated by pico-cyanobacteria (Synechococcus sp.; see Chap. 3), but at lower supply ratios, larger diatoms (Nitzschia and Synedra) dominated (Suttle et al., 1987). Whole-lake N and P additions to oligotrophic Kennedy Lake (BC), used to enhance production of sockeye salmon, also affected competitive interactions among phytoplankton (Stockner and Shortreed, 1988). Loadings at N:P ratios between 10 and 25 increased algal biomass with a summer community dominated by N2-fixing Anabaena circinalis; increasing the N:P ratio to 35 retained the higher biomass, but shifted the community dominance to small-celled Synechococcus spp.

Manipulations of fish densities in a small Wisconsin lake varied predation pressure on zooplankton, which in turn created different levels of grazing pressure on phytoplankton; nested nutrient-permeable chambers separated effects of recycled nutrients from relaxed herbivory (Vanni and Layne, 1997). Phyto-

FIGURE 8 Diagrammatic representation of seasonal growth curves of freshwater phytoplankton species in lakes with different ecological conditions and habitat complexity: A, variable ecological conditions or frequent shock periods, with short peaks and low overlap; B, more stable conditions or longer stratification periods, with greater temporal overlap; C, complex lake basins with more habitats and peaks of different duration, overlap, and frequency. Redrawn and adapted from Round (1972).

FIGURE 9 Predicted (lines) and observed (points) outcomes of competition between Asterionella formosa (stars = dominant) and Cyclotella (Stephanocyclus) meneghiniana (diamonds = dominant) under varying levels of Si and P, indicating that coexistence (solid circles) is possible in an intermediate range of Si:P ratios (From Tilman, D.; Resource Competition and Community Structure. Copyright © 1982 by Princeton University Press. Reprinted by permission of Princeton University Press.)
plankton biomass and the abundance of many algal taxa (e.g., *Peridinium inconspicuum*, *Chrysocyanobium* sp., and *Staurastrum defactum*) increased with greater fish biomass, although a similar effect was seen in grazer-free diffusion chambers for some species, which suggested that the positive effect of fish may have been mediated through recycled nutrients, rather than lower grazing pressure.

Some algae occupy both planktonic and benthic habitats at different periods of the year or even daily. This strategy may involve overwintering as inactive stages (e.g., algal cysts) or active recruitment of benthic forms into the pelagic zone. In many systems, flagellates such as *Ceratium*, *Cryptomonas*, and *Euglena*, exhibit diurnal vertical migrations toward the surface by day and into deeper strata at night (Palmer and Round, 1963; Heaney and Talling, 1980; Hansson et al., 1994), responding to patterns in light availability, temperature cues, mixing conditions, or nutrient supply. In spring and early summer, the cyanobacterium *Gloeocystis echinula* colonizes shallow sediments or submersed plants in eutrophic lakes, but in late summer, gas-vacuolate colonies migrate into the pelagic zone, representing as much as 40% of the planktonic assemblage (Barbiero and Welch, 1992). In subtropical Lake Apopka, Florida, benthic and settled planktonic diatoms (and their resting stages) are regularly resuspended into the water column by wind action, making a major contribution to the chlorophyll budget of the lake (Schelske et al., 1995). In these shallow lakes, buoyant cyanobacteria contribute to recycling phosphorus (internal loading) from sediments back into the water column (Salonen et al., 1984; Pettersson et al., 1993; Moss et al. 1997).

### 2. Factors That Regulate Phytoplankton Production in Lakes

A large body of data clearly indicates that phytoplankton production and biomass in most lentic systems is controlled by P supply (Schindler, 1978; Wetzel, 1983a; Hecky and Kilham, 1988). Although other factors (e.g., grazing, light availability, temperature) are clearly involved in regulating phytoplankton production, only nutrients are amenable to regulation (Schindler, 1978). This concept was demonstrated in Lake Washington, which received secondary sewage (a source of P) from the city of Seattle. Blooms of planktonic cyanobacteria, especially *Planktothrix* (*Oscillatoria* rubescens), were common in past decades (Edmondson, 1977). Today eutrophication in Lake Washington has been largely reversed through monitoring and sewage diversion, which reduced P inputs to near zero, summertime chlorophyll-α from about 45 to 5 μg L⁻¹ and the percentage of phytoplankton as cyanobacteria from ≈100 to 10% or less (Edmondson and Lehman, 1981).

Eutrophic lakes with low N:P ratios favor blooms of N₂-fixing cyanobacteria; hence, nutrient cycling within these lakes is closely coupled these organisms (Schindler, 1977, 1985). Algal species have different micronutrient requirements, such as Si, Mg, Ca, Fe, Mo, and Se. Diatom dominance in phytoplankton assemblages is dependent on recycled Si following spring turnover; lakes with lower Si levels may lack a springtime diatom pulse altogether. The haptophyte *Chrysocyanobium breviturrita* develops large populations in dilute lakes undergoing the early stages of acidification (Nicholls et al., 1982, Chap. 13). Its requirement for Se and NH₄⁺, and its inability to use NO₃⁻ favor its success in oligotrophic lakes within the pH range 5.5–6.5 (Wehr and Brown, 1985; Wehr et al., 1987). Nutrient requirements may have important interactions, for example, Mo, which is an essential micronutrient for some cyanobacteria as a co-factor for N₂ fixation; its assimilation may be inhibited by elevated SO₄²⁻, which is common in saline lakes (Howarth and Cole, 1985; Marino et al., 1990).

Light supply within the water column is a critical factor that also affects phytoplankton production and species composition in lakes. Although the abundance of many species is greatest in the epilimnion where irradiance is greatest, other species, including several algal flagellates are adapted to deeper waters (Lund and Reynolds, 1982). Under relatively warm and calm conditions in Blelham Tarn, more than 90% of *Uroglena* sp. colonies and *Eudorina elegans* aggregated in the upper 2 m, but in October, *Trachelomonas* occupied a narrow band near the thermocline (6–8 m depth). In eutrophic or highly turbid waters, some algae remain buoyant using gas vesicles (e.g., *Anabaena*, *Aphanizomenon*, *Coelosphaerium*, and *Microcystis*; see Chaps. 3 and 4) or flagella (e.g., *Ceratium*, *Chlamydomonas*, and *Euglena*). Species also exhibit different photosynthesis–irradiance and temperature optima. Some species, such as *Asterionella formosa*, have especially high photosynthetic efficiency at low light (Reynolds, 1984a), whereas others, including species of *Oscillatoria*, may vary their chlorophyll-α levels and employ accessory pigments that saturate at lower and spectrally altered light levels (Mur and Beisendorf, 1978). Flagellates such as *Dinobryon*, *Poterioochromonas*, *Cryptomonas*, and *Ceratium* may ingest bacteria under low light conditions or under ice; these mixotrophic species switch between photosynthetic and bacterivorous metabolism (Bird and Kalff, 1987; Porter, 1988; Berninger et al., 1992; Caron et al., 1993). This strategy may also serve to supplement inorganic nutrients as well as organic-C needs.
F. Benthic Algal Assemblages of Lakes

Benthic algae—those attached to or closely associated with various substrata or bottom surfaces—occupy an enormous variety of microhabitats, including stones, macrophytes, sediments, sand grains, and logs, as well as a variety of artificial substrata. Many divisions of algae have benthic representatives, although many fresh water species in Chrysophyta (Chaps. 12–14), Xanthophyta (Chap. 11), Cryptophyta (Chap. 21), and Pyrrophyta (Chap. 20) are planktonic, whereas all species of freshwater Phaeophyta and Rhodophyta are benthic (but rare in lakes). Perhaps the most widely used term for benthic algae is periphyton, a word that has obscure etymology and debatable usage (Sládecková, 1962; Round, 1981; Wetzel, 1983a; Aloï, 1990; Stevenson, 1996a). The term may have been coined in the 1920s by Russian limnologists (Sládecková, 1962) to refer to a collection of organisms (bacteria, fungi, protozoa) and detritus (Wetzel, 1983c). The word is analogous to the German aufwuchs, which means “to grow upon,” but some authors (e.g., Round, 1981) argue against using it because it is often used incorrectly to describe only the algal community and is imprecise with regard to habitat. Its use probably will not be abandoned, however. We recommend the use of the most precise and descriptive terminology for particular algal communities (e.g., epilithic diatom) that includes the nature of the substratum. Otherwise the term “benthic” is perhaps most suitable for general uses or when the substratum is not defined.

Modes of algal attachment are diverse. Some are firmly attached or encrusting, such as Chamaesiphon, Coleochaete, and Cocconeis, making them resistant to wave scour or other disturbances, but susceptible to competition from canopy-forming morphologies, such as Stigeoclonium or Ulothrix (Hoagland and Peterson, 1990; Maltais and Vincent, 1997; Graham and Vinebrooke, 1998). Diatoms, such as Frustulia, Navicula, Nitzschia, Pinnularia, and Staurosira, maintain contact with various surfaces (and glide among these microhabitats) by means of a slit in the wall that is termed a raphe (Chaps. 16–19). Other diatoms (e.g., Cymbella and Gomphonema) attach by means of gelatinous pads or stalks. Some filamentous cyanobacteria, such as Oscillatoria, Hapalosiphon, Lyngbya, and Microcoleus, exhibit motility by gliding, although the mechanisms are not clear (Castenholz, 1982). Filamentous green algae, such as Cladophora, Oedogonium (see Chap. 8), Spirogyra, and Zygnema (Chap. 9) produce holdfast-like rhizoids that enable them to remain attached in turbulent conditions. Other benthic forms are loosely associated with plants or sediments, and include filamentous species like Mougeotia, flagellates such as Cryptomonas, Euglena, and Eudorina, and chains of cells such as Tabellaria (Hutchinson, 1975; Graham and Vinebrooke, 1998).

The range of sizes in freshwater benthic algae exceeds that of planktonic forms. The smallest include unicells like Nannochloris or Synechococcus (0.8–2 μm diameter) to actual macrophytes, such as Chara, Cladophora, and Hydrodictyon, which range from a few centimeters to more than a meter in length. In terms of length, this range is more than 6 orders of magnitude, and in biovolume, perhaps as great as a factor of $10^{10}$. The tremendous variety of microhabitats, morphologies, sizes, and architectures found in benthic algal associations has led to the suggestion that these organisms may represent a more diverse community and greater trophic complexity than phytoplankton (Havens et al., 1996; Stevenson, 1996a). In shallow lakes, production of epiphytic algae often equals or exceeds that of phytoplankton per unit area (Wetzel, 1983a). Much of the literature on freshwater benthic algae has been reviewed in several important works, including Hutchinson (1975), Round (1981), Wetzel (1983b), and Stevenson et al. (1996).

1. Epiphytic Communities

Epiphytic algae colonize submersed and emergent plants. These are the most widely studied group of benthic algae in lakes, perhaps because of their obvious accumulation in the littoral zone. Larger forms, such as Cladophora, Chara, Hydrodictyon, and Oedogonium, serve as additional substrata for microalgae. Epiphytic algae are important in macrophyte communities, because greater densities may cover and shade their hosts (Losee and Wetzel, 1983). Evidence includes negative relationships between epiphyte and macrophyte biomass (Sand-Jensen and Soendergaard, 1981; Cattaneo et al., 1998) and more rapid host senescence with greater epiphyte cover (Neely, 1994).

There are often differences in species composition and biomass of epiphytic algae among different macrophyte species. Prowse (1959) recognized that densities of three common epiphytes, Gomphonema gracile, Eunotia pectinalis, and Oedogonium sp., differed among three macrophyte species in one small pond. Many subsequent studies have reported differences in epiphyte biomass or species composition on different plant hosts (Gough and Woelkerling, 1976; Eminson and Moss, 1980; Lodge, 1986; Blindow, 1987; Douglas and Smol, 1995; Hawes and Schwarz, 1996), although not in all cases (Siver, 1977). In one shallow lake, epiphyte biomass on submersed macrophytes (Myriophyllum spicatum, Ceratophyllum demersum, and Najas marina) was 10–40 times greater than on floating-leaved plants (Trapa natans), but
species diversity was less (Cattaneo et al., 1998). In the Great Lakes, Cladophora glomerata is a host to many microalgal epiphytes, but the red alga Chroodactylon ornatum (as C. ramosum) is attached only to this species (Sheath and Morrison, 1982). The three-dimensional architecture of epiphyte assemblages also varies with the type of substratum. Colonization by epiphytic algae has been compared to terrestrial plant succession, which comprises temporal changes in vertical structure and diversity, an increase in the dominance of larger organisms, and possible facilitative effects of earlier colonizers (Hoagland et al., 1982).

The reasons for differences in epiphytic communities among host plant species can be attributed to features of the macrophyte, such as leaf orientation, texture, or chemical properties. One survey revealed a correspondence between epiphytic communities and species of submersed macrophytes in less productive lakes, but little pattern was observed in eutrophic lakes where nutrient macrophyte interactions might be less (Eminson and Moss, 1980). However, plants may inhabit different zones within lakes that indirectly offer different ecological conditions for algal colonization. Nonetheless, direct evidence shows that living macrophytes translocate and release small quantities of P (about 3.5 µg P g⁻¹ macrophyte shoot), which can be taken up by algal epiphytes, and that algal species differ in their ability to sequester released P (Moeller et al., 1988). A Synedra–Fragilaria complex obtained more than 50% of released P, but erect forms such as Mougeotia and Lyngbya, and stalked Gomphonema obtained most of their P from the surrounding water. Alkaline phosphatase activity of epiphytic algae on artificial (plastic) plants was shown to be greater than on natural plants under similar conditions (Burkholder and Wetzel, 1990).

Epiphytic communities are important and complex components of lake food webs. In mesotrophic Lake Mann (WI), herbivorous snails consume and regulate benthic algal biomass, but pumpkinsed sunfish also exert predatory control on snails (Brönmark et al., 1992). Algal-feeding snails, benthic insects, and other invertebrates also have a qualitative impact on epiphytic communities, because many consumers graze more effectively on erect or filamentous forms, thereby shifting the community toward more compact or adherent forms like Cocconeis placentula and Coleochaete spp. (Kesler, 1981; Lodge, 1986; Marks and Lowe, 1993). In eutrophic lakes, snails similarly avoid larger colonies of epiphytic Gloeotrichia (Cattaneo, 1983; Brönmark et al., 1992). In contrast, the limpet Ferrisia fragilis grazes mainly understory species, such as Epithemia spp., Cocconeis placentula, and Achnanthes minutissimus, and avoids upright forms such as Synedra ulna and Fragilaria vauchariensis (Blinn et al., 1989). Grazers of epiphytic algae may have indirect effects on host plants by reducing shade and enhancing plant growth (Lodge et al., 1994).

Because of the difficulties of sampling epiphytic algae, artificial substrata, such as glass slides, plastic flagging, styrofoam floats, plexiglas plates, and plastic aquarium plants, are employed. Advantages include reduced variability, known surface area, standardized conditions, and no nutritional or chlorophyll artifacts from the host. An implicit assumption in their use is that the community sampled is representative of the “true” epiphyte community on aquatic plants, but studies suggest this is rarely true (Tippet, 1970; Robinson, 1983; Aloi, 1990; Cattaneo and Amireault, 1992). Glass microscope slides were among the first materials used (Sládecková, 1962), but differences in biomass, seasonal patterns, and community structure (different species proportions) suggest this approach may provide unreliable estimates (Tippet, 1970). Evidence suggests that biomass of most epiphytic algae is overestimated when some types of artificial substrata are used, although green algae and cyanobacteria may be undersampled (Aloi, 1990; Cattaneo and Amireault, 1992). Synthetic materials are much simpler in surface texture and chemistry than natural substrata, and this is likely to affect the grazing, production, and community structure of epiphytes. Although artificial substrata should not be assumed to mimic natural habitats fully, they can be useful in comparative analyses or replicated studies on the effects of disturbances on benthic algal communities (Robinson, 1983; Aloi, 1990).

2. Epilithic Communities

Epilithic algae colonize stones, boulders, and bedrock in lakes, and may dominate wave-swept littoral zones and oligotrophic lakes that have minimal macrophyte cover (Loeb et al., 1983). Species composition differs more strongly from phytoplankton than do epiphytic communities, but do exhibit pronounced seasonality in response to changes in nutrients, temperature, and other factors (Hutchinson, 1975; Lowe, 1996).

Epilithic communities in turbulent littoral habitats are distinct from epiphytic communities within the same lake and comprise species known mainly from streams, such as Chamaesiphon spp., Gongrosira incrustans, Hildenbrandia rivularis, Tolyphothrix distorta, or Heribaudiella fluviatilis (Kann, 1941, 1978; Auer et al., 1983). Vertical zonation is often observed. Many epilithic species are restricted to the upper littoral zone, whereas others occur in deeper waters where wave action is less severe (Hoagland and Peterson, 1990; Lowe, 1996). Bangia atropurpurea and Ulothrix zonata...
occur on rocks in the upper splash zone of the Laurentian Great Lakes, just above a mat of *Phormidium* sp., whereas a *Cladophora glomerata* zone is found in deeper water (Sheath and Cole, 1980). In Lake Traunsee (Austria), Kann (1959) documented that zonation patterns can differ among regions in a lake according to differences in slope. Epilithic algae form distinct communities in different regions of oligotrophic Lac à l’Eau Claire (subarctic Quebec), that are influenced by ice scour and wave action (Maltais and Vincent, 1997). A *Gloeocapsa*-dominated community colonized shallow areas, while a filamentous community dominated by *Ulotrix zonata* occurred in open, south-facing shores. In a study of 35 arctic ponds, freezing and other habitat factors were found to be of greater importance to benthic communities than were chemical variables (Douglas and Smol, 1995). Light or other factors may interact with the effects of wave action. An epilithic population of *U. zonata* exhibited a greater photosynthesis irradiance optimum (1200 μmol photons m⁻² s⁻¹) than *C. glomerata* (300 μmol photons m⁻² s⁻¹) isolated from the same region of Lake Huron (Auer et al., 1983). Temperature tolerances and nutrient requirements may further interact with irradiance optima, and affect local and regional distributions (Graham et al., 1985). *Bangia*, recent invader to the Great Lakes, has displaced *Ulotrix zonata* in many locations, perhaps because of its ability to produce more durable holdfasts (Lin and Blum, 1977) or an ability to resist epiphyte cover by sloughing its cell wall (Lowe et al., 1982). Interestingly, Kann (1959) similarly observed *Bangia* occupying rocks in the splash zones of the Traunsee, but co-occurring with another filamentous green alga, *Mougeotia*. In the calmer epilithic community of Montezuma Well (AZ), only 8 of the 83 benthic diatom taxa identified were restricted to this habitat (Czarnecki, 1979). The upper littoral zone can be a harsh habitat, where algal cells experience abrasive turbulence or desiccation during an annual cycle.

Controls on epilithic production vary among different lake types. The epilithon of softwater, oligotrophic Lakes in the Experimental lakes Area (ELA; ON) was dominated by diatoms and filamentous green algae; production levels tended to be low but quite variable (Stockner and Armstrong, 1971; Schindler et al., 1973). Comparing nutrient-amended, pH-manipulated, and reference lakes in the ELA, Turner et al. (1994) concluded that epilithon production is unrelated to N or P supply (despite positive effects on phytoplankton), but is limited by dissolved inorganic carbon (DIC). Experiments using nutrient-diffusing substrata determined that DIC and P supply were the most important influences on biomass and species composition in another oligotrophic, softwater lake in Pennsylvania (Fairchild et al., 1989). The epilithon of meso-oligotrophic Flathead Lake (Marks and Lowe, 1993) was limited principally by N and P, but individual species differed in their response to nutrient and shading manipulations. In sublittoral Lake Tahoe, epilithic populations of *Calothrix, Tolypothrix*, and *Nostoc* were strongly N-limited and exhibited N-fixation activity, in contrast to resident phytoplankton (Reuter et al., 1986). Recent increases in atmospheric N deposition may change the nutrient economy toward P limitation (Jassby et al., 1995).

Grazing by benthic invertebrates is also important to epilithic algae. Snails (*Planorbis contortus*) and limpets (*Ancylus fluviatilis*) that inhabit the stony littoral zone of a small calcareous lake consumed substantial quantities of algae and detritus, and each preferentially grazed certain algal species (Calow, 1973a, b). Selectivity and more intense grazing activity by limpets exerted greater effects on algal community structure than did snails. Light availability and grazing pressure are factors that logically would be expected to be more important than nutrients for epilithic algae in eutrophic lakes, but grazing had minor impacts on biomass and seasonal patterns of epilithic algae in Crosmere, a eutrophic lake in the English Midlands, although caddisfly larvae may have contributed to spatial patchiness of *Cladophora* (Harrison and Hildrew, 1998). Studies on epilithic food webs that consisted of crayfish, invertebrates, and macrophytes in one Swedish lake found little top-down control by crayfish on epilithic algae (Nyström et al., 1996). The general importance of benthic algae in lake food webs is not well established, in part because of difficulties in their quantification. However, a study of arctic, temperate, and tropical lakes using stable isotopes suggests that previous efforts may have underestimated the importance of algae in benthic food webs (Hecky and Hesselin, 1995). Prior studies were based on net production of phytoplankton, benthic algae, and macrophytes, instead of ease of grazing, edibility, or nutritional quality; all of these qualities were predicted to be greatest in benthic algae. The importance of epilithic algae in some lakes may be increasing, due to the expansion of filamentous algae in many acidifying lakes (Stokes, 1986; Turner et al., 1995). In one neutral lake, tadpoles suppressed the growth of filamentous algae on tiles, and favored communities of adherent and encrusting species (*Coleochaete scutata, Achnanthes minutissimus*); grazers had no such effects on epilithic communities in acidified lakes (Graham and Vinebrooke, 1998). Transplants of epilithic algae (on natural quartz tiles) across lakes of varying acidity, coupled with grazer exclosures confirmed that pH was the key factor that regulated algal communities,
but grazer control was important in neutral lakes (Vinebrooke, 1996).

3. Epipelic and Epipsammic Communities

Algal communities that colonize sediments (epipellic) and sand (epipsammic) are among the least studied benthic associations. This knowledge gap is surprising, considering the large area of many lakes not covered by stones or aquatic plants. It is difficult to separate epipelic from epipsammic habitats because these substrata are often mixed and, due to wave action, are especially unstable (Hickman, 1978; Kingston et al., 1983). Methods used to quantify living algal cells from lake sediments require considerable care and may still result in fairly high relative error (30% or greater), which may not be consistent among taxa (Éaton and Moss, 1966).

Epipelic and epipsammic communities occur in all lake types, but their relative importance is greatest in small, shallow systems. Diatoms are the most common algal group in most systems (numbers and biomass), although cyanobacteria, cryptomonads, desmids, euglenoids, and colonial and filamentous green algae often are observed (Gruendling, 1971; Round, 1972; Hickman, 1978; Roberts and Boylen, 1988). Epipelic algae may live on or within the first few millimeters of sediment and so must be able to tolerate conditions of very low light or oxygen, making motility a distinct advantage. Nonmotile epipelic and epipsammic forms may be capable of heterotrophic growth, which allows them to tolerate dark conditions and utilize greater levels of dissolved nutrients. Despite these constraints, epipelic and epipsammic communities are often very diverse. In a study of arctic ponds, Moore (1974) identified 357 algal taxa from sediments, of which 226 were benthic diatoms. Very high standing crops were also measured, some exceeding \(10^8\) cells cm\(^{-2}\), which perhaps was influenced by long photoperiods during arctic summers. A diverse assemblage of 255 taxa was observed along a depth gradient in Lake Michigan, where benthic forms predominated in shallow and mid-depth communities (6–15 m) and settled, living planktonic forms were more common in deep (23–27 m), low light conditions (Stevenson and Stoermer, 1981).

Patterns of seasonal succession seem to differ from those observed for lake phytoplankton. Over a three-year period, Round (1972) observed that populations of epipelic algae in two shallow ponds had distinct and reproducible periods of abundance peaks, but their duration was longer (months rather than weeks) and varied markedly among species. *Stauroneis anceps* and *Oscillatoria* sp. persisted for several winter months, whereas other species like *Navicula hungarica* and *N. cryptocephala* maintained sizeable populations for more than nine months. In acidified Woods Lake (NY), several epipelic species were abundant from May through October, such as *Navicula tenuicephala* at 1 m and *Hapalosiphon pumulis* at 7 m (Roberts and Boylen, 1988). Following liming, several acidophilic species were replaced by other taxa, but diatom species still dominated the epipelon (Roberts and Boylen, 1989). Round (1972) suggested that epipelic habitats provide greater habitat diversity than the water column, enabling more species to coexist.

4. Benthic Macroalgae

Several species of macroalga, those that form macroscopic or plantlike morphologies, can be important in benthic lake communities. Some investigators (e.g., Hutchinson, 1973) restrict this category to taxa that are attached by means of rhizoids, which include only charophytes (*Chara, Lamprothamnium, Nitella, Tolypella, and Nitellopsis*). From an ecological perspective it makes sense to include other algae, such as *Cladophora, Enteromorpha*, and *Nostoc*, which also may function as structuring elements within the benthic zone and as hosts for epiphytic microalgae. Astounding colonies of *Nostoc* greater than 30 cm in diameter (“mare’s eggs”) have been observed (Dods et al., 1995), and tubes of *Enteromorpha* may exceed 1 m in length (Wehr, unpublished). *Chara* may form large underwater meadows in the littoral zone of calcareous, nutrient-poor lakes and frequently is encrusted with marl (CaCO\(_3\)).

In clear, oligotrophic lakes, charophytes colonize lake bottoms down to depths of 30 m or more. In nonturbid systems, wave action is suggested to be the primary limiting factor, rather than light (Schwarz and Hawes, 1997). Various species of *Chara* and *Nitella* differ in their depth distributions, presumably as a function of individual light requirements (Wood, 1950). The lower depth boundary for *Nitella* meadows in more productive lakes is influenced by total irradiance and the supply of red light; in deep, clear lakes, their distribution is limited by the availability of blue light (Stross et al., 1995). Reduced charophyte abundance in lakes with eutrophication has been attributed to excessive or even toxic levels of P (Hutchinson, 1975; Phillips et al., 1978). However, the macrophyte community of eutrophic Lake Luknajno (Poland) is dominated (90% of total dry mass) by seven charophyte species (codominants: *C. aculeolata* and *C. tomentosa*), where the mean biomass is greater than 1 kg dry mass m\(^{-2}\) (Krolikowska, 1997). *Nitella hookeri* was found to grow best at very high P concentrations, about 20 mg L\(^{-1}\) (Starling et al., 1974). Reduced charophyte abundance in eutrophic lakes may be the result of light limitation, given that some species do grow at greater
physical and geological attributes of river systems are the watershed to downstream areas. Descriptions of the environment (Likens), water and chemical balances within the aquatic environment, which is responsible for regulating the watershed, is responsible for regulating water and chemical balances within the aquatic environment (Likens et al., 1977). Rivers are open systems that transport materials and energy from one part of the watershed to downstream areas. Descriptions of the physical and geological attributes of river systems are given in the treatises by Leopold et al., (1964) and Morisawa (1968), and in syntheses by Hynes (1970) and Beaumont (1975). Several important reviews discuss ecological feature of rivers, in particular, those by Hynes (1970), Whitton (1975, 1984), Lock and Williams (1981), Allan (1995), and Petts and Callow (1996).

III. LOTIC ENVIRONMENTS

Running water ecosystems, from headwater streams to the largest rivers, are termed lotic environments and differ from standing waters in several important respects. Lotic systems are turbulent and generally well mixed; hence stratification is uncommon except for brief periods in slowly flowing, lowland rivers (Hynes, 1970). Waters with greater current velocity tend to have abundant dissolved oxygen; even large rivers with substantial current speed, such as the Ohio, are generally well mixed (Thorpe et al., 1994). In shallow rivers or littoral regions of large rivers, organisms experience less temperature fluctuation than organisms in lakes of comparable depths. Many organisms adopt a benthic habit and are attached to a variety of substrata, the sizes of which are a function of current velocity and discharge. Rapid rivers are typified by large stones and boulders, whereas the bottom material in more slowly flowing systems consists of sand and silt.

Rivers are intimately connected with the surrounding watershed, which is responsible for regulating water and chemical balances within the aquatic environment (Likens et al., 1977). Rivers are open systems that transport materials and energy from one part of the watershed to downstream areas. Descriptions of the physical and geological attributes of river systems are

A. Major Rivers of North America

The Mississippi–Missouri River system is longest in the world (6970 km), has the third largest drainage area (3270 × 103 km²), and is the sixth largest in terms of discharge (18,390 m³ s⁻¹; Hynes, 1970; Milliman and Meade, 1983). At least 10 other rivers in North America exceed 1000 km in length. Most of them have been altered substantially by navigation or hydroelectric dams, channelization, wetland removal, and pollutants (Sparks, 1995; Wehr and Descy, 1998). The Missouri River (3770 km) has six major impoundments over 1230 km (33%) of its length; another 1200 km (32%) have been channelized. Only 35% (1330 km) of all river sections remain free-flowing, although discharge still is influenced by reservoir conditions upriver (Hesse et al., 1989). No major impoundments are located on the Ohio or Mississippi Rivers, but navigation dams and channelization have been built throughout their lengths to facilitate ship traffic.

B. Geomorphology of Rivers

Streams and rivers are part of a network of connected, increasing tributaries that have hydrological features that vary in predictable ways. Many features, such as discharge, substratum size, stream width, and depth, affect the species composition and productivity of lotic algae and their consumers. For example, sizes of substrata available for colonization vary with differences in current velocity (Table II). Physical features of rivers may be described in a system of stream orders, which assign increasing numbers to streams when two tributaries of equal order join. The most widely adopted system (Strahler, 1957) defines a headwater stream or spring with no (permanent) tributaries as first order and the junction of two such streams a second order (Fig. 10). A second-order stream increases only when it is joined by another second-order stream and so on. Larger order streams are wider and longer segments, drain larger areas, and have a more gradual slope than smaller streams. The network of these stream segments forms a treelike structure that is used in hydrological models to predict average discharge, behavior of flood events, and quantity of suspended matter (Beaumont, 1975). A simpler scheme divides rivers into three zones...
(Schumm, 1977). Zone 1 (erosional) includes headwater and small order streams that function as the source of water and sediments for downstream reaches. In Zone 2 (conveyance), water and sediments are transported along the mainstem with no net gain or loss of materials. Zone 3 (deposition) includes lower reaches that receive sediments from upriver, including river deltas and estuaries. Some studies suggest that benthic algal communities differ similarly along these zones (Rott and Pfister, 1988).

Although many aspects of drainage basins follow an ordered structure within an individual watershed (catchment), physical conditions and biological communities in streams of equal order at two locations may be quite different. Current velocity, stream width, and substrata in a second- or third-order mountain stream in New England differ from a similar order cool-desert stream in the western Great Basin (Minshall, 1978; Minshall et al., 1983; Benke et al., 1988). Landscape factors such as climate, terrestrial vegetation, and external nutrient supplies, may exert a substantial effect on the biological properties of rivers. For example, rivers that flow through a limestone region will possess greater concentrations of certain ions (Ca, Mg) than would be found in streams flowing through a region composed of granite or basalt.

River basins also differ in the amount of interaction between river channels and their watershed, which is mainly influenced by geological features of the region and amount of interface between groundwater and surface waters (Dahm et al., 1998). Some rivers are geologically constricted, such as the Hudson River and large sections of the Ohio and Columbia. Floodplain rivers have substantial watershed interaction, such as the lower Mississippi. The floodplain includes portions of the watershed (tributaries, adjacent wetlands, flood-

**TABLE II** Relationship between Minimum Current Velocity and Mean Size of Stone Substrata That Can Be Moved along a Streambed (based on Hynes, 1970; Reid and Wood 1976)

<table>
<thead>
<tr>
<th>Current velocity (m s⁻¹)</th>
<th>Particle size (cm)</th>
<th>Stream bed characteristics</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>180</td>
<td>Bedrock</td>
<td>Torrential</td>
</tr>
<tr>
<td>2.0</td>
<td>80</td>
<td>Boulders</td>
<td>Rapids</td>
</tr>
<tr>
<td>1.0</td>
<td>20</td>
<td>Large stones</td>
<td>Riffles</td>
</tr>
<tr>
<td>0.8</td>
<td>10</td>
<td>Stones and gravel</td>
<td>Riffles</td>
</tr>
<tr>
<td>0.5</td>
<td>5</td>
<td>Gravel &amp; coarse sand</td>
<td>Run</td>
</tr>
<tr>
<td>0.2</td>
<td>1</td>
<td>Sand</td>
<td>Run</td>
</tr>
<tr>
<td>0.1</td>
<td>0.2</td>
<td>Silt</td>
<td>Pool</td>
</tr>
</tbody>
</table>

**FIGURE 10** Structure of tributaries in a watershed, indicating numbering of stream orders.
plain lakes, riparian zones) that are seasonally inundated during periods of high flow. Meandering rivers and those with more islands have greater littoral and floodplain interaction, and more complex and varied current regimes than rivers with less sinuous courses (Fig. 11A and B). This increased habitat complexity may offer refuge to larger, more slowly growing algae. Small “islands” also form in lowland rivers from large stands of submersed angiosperms (Butcher, 1933; Holmes and Whitton, 1977).

Within a given reach, there are alternating regions of erosion and deposition. Bottom materials are eroded from river margins and deposited downstream in point bars. Differences in current velocity and substratum also create regular, alternating patterns of riffles and pools (Fig. 11C and D). Riffles are shallow sections with larger substrata and greater current velocity, and are spaced at fairly regular intervals, about five to seven stream-widths apart (Hynes, 1970). These regions have greater turbulence and concentrations of dissolved gases, which may provide a physiologically richer habitat for benthic algae. Deeper pools form downstream of riffles, where organisms experience reduced current velocity, possibly depleted dissolved gases, and perhaps light limitation. Bottom materials consist of smaller particles, primarily sand and silt, and current velocity is reduced during average flow periods. However, during flooding, pools lack stable substrata, which makes them susceptible to scouring and erosion.

C. The River Continuum and Other Models

For many decades ecologists lacked broad conceptual models for describing and testing patterns in the structure and function of river communities. Early concepts, some of which were developed by algal biolo-
gists, borrowed ideas from lake systems, such as the concept of oligotrophic–eutrophic gradients and climax communities (Blum, 1956; Hynes, 1970). These ideas do not adapt easily to lotic ecosystems, and a recent synthesis of nutrient and chlorophyll data from more than 200 temperate streams suggest that nutrient–algal biomass relationships are weaker than in lakes, perhaps because of the effects of nonalgal turbidity in running waters (Dodds et al., 1998). Some ecologists recognize different zones along the length of a river that possess different physical conditions and habitats for riverine organisms (Hawkes, 1975). A river’s features, however, do not fall into discrete zones, but rather vary continuously along a river’s course. The combination of hydrological principles with changes in biological and chemical processes along river gradients led to the development of the river continuum concept (RCC; Fig. 12; Vannote et al., 1980).

The RCC characterizes lotic ecosystems as a network of streams with a continuum of longitudinally linked environmental (e.g., width, depth, flow) and resource (nutrients, light) gradients. Biological communities respond to longitudinal changes in geomorphology, water chemistry, and energy sources in several ways. In addition, organisms, by their own activities, influence conditions and communities downstream (Fig. 12). This is evidenced by changes in the types of invertebrate consumers that are localized in rivers of different sizes. The model was based on data largely from smaller, temperate forest streams, and broadened into a theory for rivers as a whole. Many other ideas and studies concerning nutrient spiraling, benthic invertebrates, fish production, and the influence of dams have emerged from the general framework laid out in the RCC (Newbold et al., 1981; Welcomme et al., 1989; Minshall et al., 1983; Ward and Stanford, 1983; Thorp and Delong, 1994).

The role of algae and other primary producers was also considered in the RCC. The metabolism of first- to third-order streams was viewed to be largely dependent on external or allochthonous sources of terrestrial carbon. Hence, consumers in smaller streams were mainly shredders and collectors of coarse particulate matter. Algae were viewed as a minor component of food webs in headwater communities because of light limitation due to heavy riparian shading and subsidies of terrestrial organic matter. The overall effect is a net heterotrophic community, in which system-level respiration \((R)\) exceeds in situ primary production \((P; P : R < 1)\). Long-term studies confirm that the mass of allochthonous litter (leaves, wood) forms the dominant organic carbon source for small streams (Benke et al., 1988; Findlay et al., 1997), although food web studies suggest that benthic algae still may be an important or even dominant food source for some benthic animals, perhaps because of greater assimilation efficiency with algae than detritus (Fuller et al., 1986; Mayer and Likens, 1987). Algal production is predicted to increase in mid-sized (fourth to sixth order) rivers, in response to greater sunlight and a reduction in subsidies of allochthonous organic matter, resulting in \(P : R \geq 1\). In such systems, consumers are likely to be dominated by grazers of (mainly benthic) algal material and collectors of finer organic matter transported downstream from upper reaches. The model suggests that algal (plus macrophyte) primary production still may not come to dominate river metabolism in mid-sized rivers if the reach receives substantial supplies of allochthonous organic matter from smaller tributaries, which would increase system-level respiration and reduce light penetration. In larger rivers (greater than sixth order), the RCC predicts that even though the river basin is open to full sun, higher levels of fine particulate matter from upstream, greater depth, and resuspended sediments

![Diagram](image-url)
limit algal production. Although phytoplankton usually dominate the algal community in large rivers, these systems are predicted to be too turbid and too deep to support high levels of algal production. This forecast appears to be the case in the Hudson River, where depth and tidally driven mixing create a light-limited environment for phytoplankton (Cole et al., 1992), but studies on other large rivers have found that substantial phytoplankton populations can develop (e.g., Descy and Gosselain, 1994; Lair and Reyes-Marchant, 1997; Wehr and Descy, 1998).

Ideas from the RCC have stimulated a great increase in research on and discussion of lotic ecosystems, but several exceptions have been raised (Wetzel, 1975; Lock and Williams, 1981; Benke et al., 1988). Rivers in different biomes have different climate, lithology, and amounts of riparian vegetation, which may shift the relative importance of autochthonous versus allochthonous production for river metabolism (Minshall, 1978; Minshall et al., 1983; Wetzel and Ward, 1992). Not all rivers (small or mid-sized) in North America are shaded heavily (e.g., high altitudes, deserts, agricultural areas) nor do they receive large subsidies of terrestrial organic matter from their watershed. In more open rivers, algal production may be substantial. A metaanalysis of studies on 30 streams from five biomes showed that gross primary production (GPP) levels varied by more than 4 orders of magnitude; the greatest rates were in desert areas (Lamberti and Steinman, 1997). Variations in GPP were related to variables such as watershed area, inorganic P, temperature, discharge, and canopy cover, but not to stream order or latitude, further suggesting that variation among rivers may be greater than predicted by the RCC. River systems are also very patchy, from differences in sunlight within a local reach to watershed-level differences in sources of carbon or inorganic nutrients (Pringle et al., 1988). Subsequent syntheses have emphasized that lotic ecosystems also can be regulated by biotic interactions, such as predator–prey dynamics, competition, and food-chain length, rather than solely controlled by physical (e.g., hydraulic) factors (Power et al., 1988). In turn, physical factors, such as the frequency of floods, have significant effects on food web interactions at several levels, including algal biomass (Wotton et al., 1996).

Other syntheses have focused on large rivers (greater than sixth order). Sedell et al. (1989) and Junk et al. (1989) pointed out that many large rivers receive materials, energy, and organisms from the adjacent floodplain, often in greater quantity than may have been transported from upriver. The influence of algal production was regarded as minimal because large rivers were generally turbid and light-limited. In their flood-pulse model, Junk et al. (1989) suggested that large river metabolism may be driven more by batch processes—the pulses of resources from flood events—than by the continuous processes emphasized in the RCC. This process is undoubtedly true for rivers such as the Amazon and the lower Mississippi. However, not all large rivers occur in extensive floodplains. River basins also flow through constricted channels that have minimal floodplain influence. Thorp and Delong (1994) proposed a river productivity model that suggests that local autochthonous production may have been underestimated in large, constricted-channel rivers, which have firm substrata and less turbid water. In such systems, for example, a 350 km stretch of the Ohio River, substantial phytoplankton biomass and production have been observed, and during some seasons may be the principal carbon source for planktonic consumers, such as small-bodied cladocerans and rotifers (Thorp et al., 1994; Wehr and Thorp, 1997). Also, many, if not most large rivers worldwide have been altered substantially due to industrialization, which has had profound influence on ecological conditions. Flow regulation and nutrient inputs favor greater phytoplankton productivity in large rivers, such that $P:R$ ratios may exceed 1.0, at least during the spring and the summer (Admiraal et al., 1994; Descy and Gosselain, 1994; Wehr and Descy, 1998).

D. Benthic Algal Communities of Rivers

Most studies of river algae concern benthic species. The necessity to remain in a stable position while water flows downstream is an important selective force for all benthic organisms in lotic environments. Earlier reviews pointed out the paucity of studies on lotic algae relative to those on lakes (Blum, 1956; Hynes, 1970; Whittton, 1975), yet the pace of work on benthic algae in streams and rivers has increased substantially. Much of what has been learned in the interim has been summarized in several reviews (Lock et al., 1984; Reynolds, 1996; Biggs, 1996; Steinman, 1996), which reveal an evolution from mainly descriptive studies to structural and functional analyses of benthic algae and their importance in lotic food webs.

1. Benthic Algal Diversity, Composition, and Biogeography

In streams, diatoms often comprise the dominant algal group in terms of species number and biomass (Blum, 1956; Douglas, 1958; Round, 1981; Kawecka, 1981). Their diversity in species and growth form (upright frustules, short- and long-stalked, rosettes, tube-dwelling, filamentous, mucilaginous matrix, and
prostrate cells) enables them to colonize a variety of microhabitats. In more slowly flowing or less flood-prone systems, filamentous species like Melosira varians and upright, stalked forms such as Gomphonema berculeana may predominate, along with filamentous nondiatom species (Stevenson, 1996a; Biggs, 1996). In very rapid water, firmly attached diatoms, such as Cocconeis placentula, Achnanthes minutissimum, and Hammelia arcus, may occur with encrusting nondiatoms, such as Hildenbrandia rivularis, Gongrosira spp., and Chamaesiphon spp., and corticated forms like Lemanea spp. (Fritsch, 1929; Whitton, 1975; Kawecka, 1980; Kann, 1978).

One of the fascinations of studying benthic algae in rivers is that many species (although not the majority) are macroscopic and recognizable in the field (Holmes and Whitton, 1977; Kann, 1978; Entwisle, 1989; Sheath and Cole, 1992). These include cyanobacteria, and green and red algae, as well as chrysophytes, xanthophytes, and brown algae (Whitton, 1975; Sheath and Cole, 1992). Morphologies are diverse and include encrusting, turflike, filamentous, cartilaginous, mucilaginous, tubular, and bladelike thalli (Fig. 13). In some instances, diatoms, including species of Eunotia, Fragilaria, and Melosira, and stalked forms, such as Didymosphenia geminata and Cymbella spp., may be recognized by their gross appearance, but are identified only using microscopy (Holmes and Whittton, 1981; Steinman and Sheath, 1984; Sheath and Cole, 1992).

Some benthic stream algae have limited distributions. Prasiola mexicana, a seaweed-like green alga (Fig. 13B), thus far has been recorded only in streams located in the arctic tundra and western coniferous biomes, whereas the encrusting brown alga Heribaudiella flaviatilis has been confirmed in North America from streams in western Canada and the United States only (Sheath and Cole, 1992; Wehr and Stein, 1985). Some taxa have been regarded to be limited in geography or habitat, only to be found later in other locations. Thorea violacea is a large red alga that was thought to be restricted to streams in warmer biomes or in temperate areas only during the summer (Smith, 1950; Sheath and Hambrook, 1990, Chap. 5), but it was discovered growing profusely in the upper Hudson River in cool (15°C), rapidly flowing water (Pueschel et al., 1995).

Few long-term studies of benthic stream macroalgae exist that may help to explain the dispersal patterns of these organisms. In one of the few cases of...
Ecological endemism in some species of river algae may be caused by the spread of marine taxa into estuarine environments, followed by adaptation to lower salinity. Such may be the case with genera such as *Audouinella*, *Hildenbrandia*, *Prasiola*, and *Enteromorpha*: genera that each has marine and freshwater species and are found in rivers but only rarely in lakes (Flint, 1955; Whitton, 1975; Sheath and Cole, 1980; Sheath et al., 1985; Hamilton and Edlund, 1994). However, other species appear to be human-accelerated invaders from other freshwater systems. Populations of the red alga *Bangia*, which invaded North American freshwaters in the 1960s through the St. Lawrence River, are not closely related to any marine populations (based on *rbc*-*L*, RuBisCo spacer, and 18s rDNA sequences) and show strong affinities with freshwater European populations (Müller et al., 1998). These data suggest that some vector, such as a ship’s ballast water, enabled invasion, rather than gradual spread and adaptation from a marine environment.

Biogeographic data suggest that green algae are the most common group of stream macroalgae across all biomes in North America. Based on 1000 stream segments studied, the lowest species diversity was found in streams in arctic tundra and the greatest in boreal forests (Sheath and Cole, 1992). There was no increase in macroalgal species diversity from the arctic to the tropics (contrary to marine species), which may be the result of periodic flooding common in streams across all regions. Arctic streams tend to have more species of macroalgal cyanobacteria, whereas tropical streams have more species of Rhodophyta (Sheath and Cole, 1992; Sheath et al., 1996; Sheath and Müller, 1997).

### 2. Factors That Regulate Benthic Algae in Rivers

Several reviews (Blum, 1956; Hynes, 1970; Whitton, 1975; Biggs, 1996; Stevenson, 1997) discuss many ecological factors, including current velocity, substratum, geology, nutrient conditions, grazers, temperature, pollutants, and light availability, and their effects on benthic algae in rivers. Factors often interact to affect algal growth and survival, and multivariate analyses have been useful in determining the key environmental factors that affect species composition (e.g., Hufford and Collins, 1976; Wehr, 1981; Lowe and Pan, 1996). The following discussion provides a brief overview of current perspectives on the influence of habitat variables on benthic stream algae and, in particular, efforts to integrate structural aspects (species composition, diversity, architecture) with functional studies (production, food web dynamics, nutrient cycling).

In all river systems, there are proximate variables (those we measure) that affect organisms, such as light availability or nutrient supply, and larger scale factors such as climate, watershed features, and land use practices, that drive proximate variables (Stevenson, 1997). Biggs (1996) and Biggs et al. (1998) proposed a conceptual, disturbance-resource supply–grazer model that categorizes controls on benthic algal production in streams in terms of two processes: factors that affect (1) biomass accrual and (2) biomass loss. The model recognizes how ecosystem-level changes, such as floodplain modifications, can affect proximate controls, such as current velocity. An energetic balance sheet is constructed for each side of the ledger that can be used to predict to algal production and species composition (Fig. 14). In this scheme, biomass accrual increases as a function of resource supply, whereas biomass losses are a function of disturbance and grazing. In rivers with infrequent, low-intensity floods (= disturbance) and modest grazing intensity, the model predicts that biomass accrual dominates to a level dictated by resources. Under low resource supplies, growth continues at lower rates, favoring an adnate and turflike community dominated by filamentous cyanobacteria (e.g., *Schizothrix*, *Phormidium*, and *Tolyphothrix*; Chap. 4), red algae (e.g., *Audouinella*; Chap. 5), and many benthic diatoms (e.g., *Epithemia* and *Navicula*; Chaps. 17–19). Under similar hydraulic and grazing conditions but greater nutrient supply, a greater biomass of filamentous taxa, such as *Cladophora*, *Ulothrix*, or *Melosira*, is expected. For each combination of plus and minus factors, specific predictions can be made about the most important variables that drive algal production and community composition.

Empirical evidence supports these predictions. In the Colorado River, where nutrients and sunlight are generally nonlimiting, release of water from Glen Canyon Dam (greater disturbance) decreased the biomass and relative importance of *Cladophora glomerata*, and reduced total benthic primary productivity (Blinn et al., 1998). The physiognomy of epiphytic algae changed from upright assemblage (*Diatoma vulgaris*, *Rhoicosphenia curvata*) to more closely adherent forms (*Achnanthes* spp. and *Cocconeis pediculus*; Hardwick et al., 1992). Herbivorous invertebrates have been widely shown to reduce the density and biomass of benthic algae, but losses due to grazer activity come from scouring as well as consumption (Allan, 1995). Furthermore, ingestion and assimilation of benthic algae vary widely (30–70%), depending on the species of both the alga and the consumer (Lamberti et al.,...
Food supply, but differences in irradiance also affect the ed. Abundances of algal grazers are often driven by shaded conditions, while other species were unaffected. Grazers (e.g., *Gymnagama nigricula*) declined significantly in shaded conditions, whereas a community consisting of long filamentous algae (*Oedogonium* sp. and *Phormidium* sp.) experienced decreased biomass accrual (Biggs, 1989; Pandian and Marian, 1986). Resultant biomass and compositional changes, in turn, have effects on benthic food webs, because many invertebrates find an adherent community less easily grazed (Colletti et al., 1987). The Rivière de L’Achigan (Quebec) is an unshaded stony stream interspersed with a chain of small lakes that alter flow conditions immediately downstream (lower disturbance; Cattaneo, 1996). Biomass and species composition of benthic algae on gravel varied inversely with distance from lake outlets, yet this impoundment effect was unimportant for algae that colonize boulders. Only boulders supported communities of large filamentous and plumose forms such as *Draparnaldia* (Chlorophyceae), *Stigonema* (Cyanobacteria), and *Batrachospermum* (Rhodophyta). An experimental study in Big Sulphur Creek (CA) demonstrated the interactive effects of shading (resource supply) and invertebrate grazing on epilithic algal communities (Feminella et al., 1989). Algal biomass in low-grazer conditions declined by 75% with greater (15–95%) canopy cover, but was unaffected by light availability at normal grazer densities. The food web—resource supply interaction in Big Sulphur Creek is complicated by the fact that densities of trichopteran grazers (e.g., *Gymnagama nigricula*) declined significantly in shaded conditions, while other species were unaffected. Abundances of algal grazers are often driven by food supply, but differences in irradiance also affect the chemical composition of algal assemblages, including changes in protein, total lipids, and fatty acid composition (Steinman et al., 1988). In general, cyanobacteria have different complements of fatty acids, including greater oleic, linoleic, and linolenic acids than diatoms (McIntire et al., 1969). Reductions in light availability to Kingsley Creek (NY) caused significant reductions in epilithic algal biomass and densities of a herbivorous mayfly (*Baetis tricaudatus*), but did not affect densities of a filter-feeding blackfly larva (*Simulium* spp.), which mainly consumed detritus (Fuller et al., 1986). However, most field studies on grazing are conducted under summer base-flow conditions when disturbance is low and resource factors are less important (Feminella and Hawks, 1995).

Current velocity is of great importance to benthic algae. Species that colonize areas of rapid current velocity are firmly attached to substrata using rhizoidal or holdfast-like structures (Israelson, 1949; Whitton, 1975). Greater current velocity provides a continuous replenishment of nutrients from upstream and a steeper diffusion gradient near the cell surface (Whitford, 1960; Horner et al., 1990). Species restricted to riffles with strong current velocity (e.g., *Hydrurus foetidus* and *Lemanea fluviatilis*) may have a higher metabolic demand for nutrients, which must be met by a greater physical supply. Studies suggest that there is no simple positive relationship between current velocity and algal metabolism or growth rate; greater current speed may also decrease algal biomass through scouring (Borchardt et al., 1994; Stevenson, 1996b). Few correlative studies are able to attribute differences in algal communities to current velocity effects because many variables change along a river’s course. A more clear-cut study of parallel streams draining the same reservoir found that the regulated stream had greater diatom cover and large populations of *Prasiola fluviatilis*, while the stream that lacked flood control had populations of *Hydrurus foetidus* and *Ulothrix zonata*, and greater species number, but a lower biomass of diatoms (Kawecka, 1990).

Current velocity affects the growth form of individual algae, such as in *Cladophora*, which develops compact tufts with narrow branching in greater current velocity and develops plumose forms with widely branched filaments in calmer flow (Whitton, 1975; Dodds and Gunder, 1992, Chap. 8). The architecture of algal communities affects their response to current speed. A mucilaginous, stalked diatom community (e.g., *Gomphonene berculeana* and *Navicula avenacea*) exhibited increased production with greater near-bed current velocity, whereas a community consisting of long filamentous algae (*Oedogonium* sp. and *Phormidium* sp.) experienced decreased biomass accrual (Biggs et al., 1989; Stevenson, 1996a).
et al., 1998). The morphology of Nostoc parmelioïdes (a filamentous colonial cyanobacterium) in stony streams is altered from spherical to ear-shaped colonies by the presence of an endosymbiotic midge larva (Ward et al., 1985), and only ear-shaped colonies exhibit greater photosynthesis and N₂-fixation rates with greater current velocity (Dodds, 1989). Such studies that aim to link metabolic patterns with differences in community composition or form are needed to improve our understanding of the factors that regulate lotic communities.

Several studies of benthic stream algae also have considered the influence of substratum. Several decades ago, Douglas (1958) recognized that different sizes of stones supported different densities and species of epilithic algae, which was likely the result of differences in their susceptibility to flood disturbance. A comparison of epilithic communities on different substratum sizes and similar in nutrient conditions found that most of the variation in algal biomass was explained by total-P and seston levels, but size of the substratum also exerted a significant effect (Cattaneo et al., 1997). Stones that are disturbed or scoured during floods may have algal crusts or propagules that still remain on their surfaces (Power and Stewart, 1987). The degree to which algae can recolonize disturbed substrata in a stream is a function of (1) their resilience, through immigration and greater growth rates, or (2) their resistance, as influenced by the species’ morphology and community physiognomy (Peterson, 1996). Benthic algal biomass and species composition are also influenced by substratum–current interactions. Diatom immigration onto bare substrata may increase with either reduced current speed or greater surface complexity (Stevenson, 1983). Substrata conditioned with a simulated mucilage (agar coating) were colonized twice as rapidly as clean surfaces, but responses were species-specific; some increased (Navicula gregaria and Synedra ulna), while others declined (Achnanthidium minutissimum and Diatoma vulgare) or were unaffected (Diatoma tenue and Gomphonema olivaceum). A matrix of organic matter and bacteria probably facilitates colonization by most benthic algae in rivers (Karlström, 1978; Korte and Blinn, 1983; Sheldon and Wellnitz, 1998). A comparison of benthic diatom assemblages that colonize natural rocks, sterilized rocks, and clay tiles in Fleming Creek (MI) found greater total densities and species diversity on natural rocks (Tuchman and Stevenson, 1980). Otherwise identical natural substrata constructed from three rock types (basalt, sandstone, and limestone) that occur in Oak Creek (AZ) were compared for their effects on diatom colonization of riffles (Blinn et al., 1980). Densities on sandstone substrata were 60–80% greater than on basalt and limestone, but species composition and diversity were similar. In Mack Creek (OR), greater biovolume (but not chlorophyll-a) and diversity of benthic algae were observed colonizing pieces of wood than clay tiles (Sabater et al., 1998). Certain taxa, such as Cymbella minutula, Hannaea arcus, and Zygnema sp., were more abundant on wood, while some closely adherent forms, such as A. minutissima and A. lanceolata, were more abundant on clay tiles. The physical structure of the stream bed also influences benthic communities. Experimental manipulations of rocks and bricks with different density and surface texture resulted in significant changes in the diversity and the abundance of benthic invertebrates and epilithic algae in the Steavenson River, Australia (Downes et al., 1998). Greater densities of Audouinella hermannii were observed on substrata without large crevices, but total biomass was greatest on surfaces that were roughened, independent of the presence of crevices.

E. Phytoplankton Communities of Rivers

Although benthic algae typically dominate rocky streams and smaller rivers, phytoplankton become important in larger rivers and lowland streams (Rosemarin, 1975; Reynolds and Descy, 1996). A long history of studies on river phytoplankton dates back to at least the 1890s, when Zacharias (1898) coined the term “potamoplankton,” to refer to the suspended organisms in flowing waters. In North America, phytoplankton have been studied since the early years of limnological research in rivers including the Illinois (Kofoid, 1903, 1908), Mississippi (Reinhard, 1931), Ohio (Eddy, 1934), San Joaquin (Allen, 1921), and Sacramento (Greenberg, 1964). Much of the early research focused on whether a true phytoplankton community (populations that survive and reproduce within rivers) actually existed, as opposed to dislodged benthic forms or plankton washed in from lakes within the watershed. Indeed, plankton in most rivers consists of all three components in varying proportions (Reynolds, 1988), but in a single river sample, it is difficult to distinguish these sources, although certain algal taxa may be considered typical of each.

Many benthic algae become suspended. These meroplanktonic forms can be washed out from sediments, plants, or other substrata. A metanalysis of 67 studies suggests that about 50% of suspended algal taxa in rivers are either benthic or meroplanktonic (Rojo et al., 1994). Among diatoms, most raphe-bearing species are likely nonplanktonic, but it is difficult to distinguish true potamoplankton from those that originated from lakes (Reynolds, 1988). One distinction may be found in species’ responses to flow regime and other physical factors, as has been attempted for phyto-
plankton species in the Ohio River (Peterson and Stevenson, 1989; Wehr and Thorp, 1997). The abundances of most species were negatively related to discharge, but tributary rivers were found to have little effect on species composition. However, during low flow (summer to early autumn), there were significantly greater amounts of colonial cyanobacteria (e.g., *Aphanocapsa saxicola*) and certain diatoms (e.g., *Stephanocyclops* [= *Cyclotella meneghiniana*) in the river downstream of these tributaries, suggesting that some populations may have originated from outside the main river.

The fact that chlorophyll-*a* concentrations in large rivers usually vary inversely with discharge (Schmidt, 1994) strongly suggests that potamoplankton is not derived primarily from benthic habitats. This pattern was observed for individual species in the River Thames, although smaller cells were less affected or even increased with greater discharge (Ruse and Love, 1997). In general, smaller forms appear to be more successful members of the potamoplankton, perhaps due to greater growth rates and surface area to volume ratios (Reynolds, 1988; Rae and Vincent, 1998). Diatoms are clearly the most diverse and abundant group, with *Cyclotella* and smaller species of *Stephanodiscus* especially common in larger rivers worldwide (Chap. 15). Algal flagellates rarely achieve large numbers in river plankton, except some cryptomonads, chrysophytes, and members of the Volvocales (see Chap. 6). In some instances, poor preservation techniques may cause underreporting (see Chaps. 12 and 21).

Two major limitations to survival and growth of river phytoplankton are the continuous removal of organisms by downstream flow (so-called washout) and mixing within the water column, which places cells in variable and often aphtotic light fields. Hence, most studies conclude that riverine phytoplankton production is controlled by discharge (Baker and Baker, 1979; Soballe and Kimmel, 1987; Cole *et al*., 1992; Reynolds and Descy, 1996). Assuming no other limiting resources, rivers must be sufficiently long and/or the flow rate sufficiently low for net positive algal growth rates. This principle was demonstrated clearly in early studies on the Sacramento River in which peaks of abundance in potamoplankton became progressively more pronounced further downstream, a region that provided reduced current velocity and more time for populations to develop (Greenberg, 1964). A similar increase was seen along the Rhine (Germany–Netherlands; de Ruyter van Steveninck *et al*., 1992). In the lowland River Spree (Germany; Köhler, 1993, 1995), phytoplankton biomass declined in mid-river in response to increased turbidity and Fe precipitation of P, but then increased further downstream as a result of impoundments and flow regulation. A rather different longitudinal pattern is seen in the St. Lawrence River, in which a gradient of increased P and reduced current velocity is counterbalanced by greater suspended matter, causing a net decrease in river plankton densities downstream (Hudon *et al*., 1996). The contrary and complex influences of discharge and algal growth rates have been discussed in detail by Reynolds (1988, 1995). Despite these limits on algal growth, large accumulations of phytoplankton frequently develop in summer and other low-flow periods. With greater nutrient supplies, surface blooms of cyanobacteria (*Microcystis*, *Anabaena* and *Aphanizomenon*) may occur, although their prevalence appears to be greater in warmer climates or in temperate zones under low-flow conditions (Baker and Baker, 1979; Krogmann *et al*., 1986; Paerl and Bowles, 1987). Unlike many lakes, nutrient limitation is uncommon in larger rivers (Reynolds, 1988; Reynolds and Descy, 1996; Wehr and Descy, 1998). Therefore, the principal factor that regulates phytoplankton production in rivers is discharge, which regulates dilution rates, turbidity, and mixing of cells within the water column (Reynolds and Descy, 1996).

Algal productivity in larger and lowland rivers can be substantial despite frequent turbidity and continuous mixing of algal cells within the water column (Descy *et al*., 1987, 1994; Reynolds and Descy, 1996). A delicate balance exists between phytoplankton production and respiratory losses during periods of higher turbidity (Descy *et al*., 1994; Reynolds and Descy, 1996). In freshwater tidal sections of the Hudson River, turbidity is further complicated by tidally driven mixing, resulting in a net heterotrophic balance for most of the year (Cole *et al*., 1992). Following invasion of the Hudson by zebra mussels (*Dreissena polymorpha*), phytoplankton biomass declined from a summertime mean of about 30 to about 5 µg chlorophyll-*a* L⁻¹ and species composition shifted from colonial cyanobacteria to diatoms (Caraco *et al*., 1997; Smith *et al*., 1998).

In the River Spree, a positive autotrophic balance is established during the spring (mainly diatoms), but in the summer, cyanobacteria dominate (Köhler, 1995). How large river systems maintain large phytoplankton populations throughout the year is still something of a mystery, but the main channel may receive subsidies of algae and nutrients from tributaries, wetlands, or backwaters (Owens and Crumpton, 1993; Reynolds, 1996). Species composition may provide a clue: slower growth rates of larger colonial species (e.g., *Aphanizomenon* and *Planktothrix*) may have higher respiratory costs (P : R < 1) for maintaining populations than smaller centric diatoms (e.g., *Cyclotella* spp. and...
Stephanodiscus hantzschii; see Chap. 15), but may be stable if they are ineffectively grazed by small-bodied zooplankton (Gosselain et al., 1998). Only zebra mussels, which utilize a wider particle size range, may crop these larger forms, as in the Hudson River. In the Meuse, Rhine, Danube, and upper Mississippi Rivers, higher levels of nutrients coupled with less turbid conditions enable high levels of phytoplankton production to be sustained for several months of the year (Baker and Baker, 1979; Descy et al., 1987; Lange and Rada, 1993; Admiraal et al., 1994; Kiss, 1994). With greater primary production, potamoplankton influence the biogeochemical properties of large rivers, including dissolved O_2 (Köhler, 1995; Reynolds and Descy, 1994; Kiss, 1994). With greater primary production, potamoplankton influence the biogeochemical properties of large rivers, including dissolved O_2 (Köhler, 1995; Reynolds and Descy, 1996), dissolved Si (Admiraal et al., 1993), and dissolved organic matter (Wehr et al., 1997).

Phytoplankton are an important food source for zooplankton in rivers, even if grazers do not regulate algal biomass or production as effectively as in lakes. Grazing pressure is less important because the zooplankton community is usually dominated by small-bodied cladocerans and rotifers (Winner, 1975; Köhler, 1995). Rivers select for small-bodied zooplankton because of their ability to grow rapidly enough to compensate for downstream losses (Viroux, 1997). Biomass and density of zooplankton in larger rivers also may be less than in lakes (Pace et al., 1992; Thorp et al., 1994). Although discharge and turbidity typically drive phytoplankton production in rivers on an annual basis, zooplankton grazing may still be an important loss factor during summer low-flow periods (Gosselain et al., 1994). Grazing activity in the River Meuse (mainly Bosmina and rotifers) appears to exert strong control over summertime phytoplankton numbers and to cause a shift in phytoplankton size structure toward larger celled forms (Gosselain et al., 1998).

Models designed to predict phytoplankton production in large rivers primarily have been devised for specific conditions, such as the influence of temperature and irradiance on phytoplankton production in one reach of the Great Whale River, Quebec (Rae and Vincent, 1998). Light and temperature explained between 74 and 98% of the variation in photosynthetic activity in this subarctic river. A larger model for the Rhine, which included the effects of irradiance, light attenuation, flow, nutrients, phytoplankton biomass, and grazing, was successful in predicting the fate of algal production, although some parameters (e.g., zooplankton grazing) were based on data from lakes (Admiraal et al., 1993). Efforts to develop nutrient- algal biomass models have been less effective than in lakes, owing to weaker relationships between N or P and chlorophyll-a, and the complicating effects of discharge and turbidity (Van Nieuwenhuyse and Jones, 1996; Dodds et al., 1998). Even more difficult to predict are changes in species composition of phytoplankton communities in rivers. This information is important for water management agencies, because certain algae affect taste and odor conditions of water that may ultimately be used for domestic consumption. Despite the inclusion of many physical and chemical variables, only about 20% of the total variation in phytoplankton species composition for the River Thames could be explained using a canonical correspondence model (Ruse and Hutchings, 1996). One model, which incorporates several physical factors and river order, found that hydrological conditions exert an overriding effect on potamoplankton development, but biological controls (mainly grazers) are important during low-flow conditions (Billen et al., 1994). Reynolds (1988, 1995) has suggested that more fundamental work is still needed to acquire the necessary data to build meaningful predictive models for plankton communities in rivers.

IV. WETLANDS

Wetlands regulate nutrient fluxes between terrestrial and aquatic systems, serve as nurseries for many of the world’s fisheries, and are among the most productive and threatened ecosystems worldwide (Whittaker, 1975; Mitsch and Gosselink, 1993). Freshwater wetlands occur from arctic to tropical biomes across North America. Many are situated in the upper littoral zone of lakes and rivers, and also include marshes, peat bogs, fens, wet alpine meadows, cypress swamps, and forested lowlands. Unifying features of wetland include more or less continuously saturated soils, shallow water depth (≤ 2 m), fluctuating water levels, an accumulation of plant detritus and organic matter, and vegetation adapted to wet conditions (Mitsch and Gosselink, 1993; Goldsborough and Robinson, 1996).

A. Functional Importance of Algae in Wetlands

Most wetland algae are benthic, loosely associated with emergent plants (metaphyton), attached to plants, or colonized in sediments; most suspended forms have been dislodged from various surfaces. A five-year study of epipelic, epiphytic, metaphytic, and planktonic primary production in Delta Marsh, Manitoba, determined that metaphyton contributed roughly 70% of the total algal productivity, compared with only 6% for phytoplankton (Robinson et al., 1997). Values for algal productivity (400–1100 g C m⁻² y⁻¹) over the year are comparable to or exceed that of the emergent
macrophytes present (aboveground: 100–1700 g C m⁻² y⁻¹). Among several constructed wetlands in Illinois, benthic algae are estimated to contribute between 1 and 65% of the total system primary production (Cronk and Mitsch, 1994). However, not all wetland algal communities are highly productive, presumably a result of nutrient limitation (Murkin et al., 1991; Goldsborough and Robinson, 1996).

Algal production is important for many invertebrate consumers that preferentially consume algal material over either live or detrital macrophyte tissues (Campeau et al., 1994; Goldsborough and Robinson, 1996). Attached algal material may be especially important in winter when emergent macrophytes are dead or senescent (Meulemans and Hienis, 1983). In a wetland along western Lake Superior, δ¹³C data suggest that entrained algae are an important primary food source for the grazing food web in addition to macrophyte detritus (Keough et al., 1998). Given the greater proportion of structural tissues in emergent plants and the greater turnover rates among algal cells, the importance of algae in wetland food webs is often substantial. Nutrient additions designed to enhance algal biomass in wetland enclosures also resulted in greater densities of cladocerans and copepods in nearshore water, as well as benthic invertebrates such as snails and chironomids (Gabor et al., 1994). Using pigment tracers, Bianchi et al. (1993) estimated that benthic diatoms comprise a major food source for invertebrates in Hudson River wetlands and, combined with lower C:N ratios, may be a better resource for benthic consumers than detritus. Algal biomass may, however, be spatially variable. In wetlands of Lake Gooimeer (Netherlands), stable isotope data indicate that within Phragmites beds, macrophyte detritus is the major carbon source for benthic invertebrates, but algal material dominates littoral food webs outside the reed bed (Boschker et al., 1995). The littoral zone of lakes is an important region of nutrient exchange between nearshore and pelagic zones, and attached algal communities are important components of this exchange (Mickle and Wetzel, 1978; Aziz and Whitton, 1988; Moeller et al., 1988). During decomposition of wetland plants, attached algae may enhance breakdown (Neely, 1994), although other data suggest that dissolved organic carbon (DOC) released during this process may inhibit algal growth (Cooksey and Cooksey, 1978).

B. Algal Diversity in Freshwater Wetlands

The communities of algae in freshwater wetlands are nearly as diverse as those found in lakes. In other systems, nutrient conditions, climate, and geology influence species composition, but in wetlands, water level, macrophyte plant composition, and degree of mixing with other water bodies are also important (Goldsborough and Robinson, 1996). In the Everglades, benthic algae colonize many macrophyte and sediment surfaces; species composition and production vary with species of macrophyte, water level, nutrient inputs, and degree of CaCO₃ incrustation (Browder et al., 1994). Filamentous cyanobacteria, including Sytonema, Schizothrix, Oscillatoria, and Microcoleus, are often abundant. Filamentous green algae (Spirogyra, Bulbochaete, and Oedogonium), desmids, and diatoms (Cymbella, Gomphonema, and Mastogloia) are common in less calcareous conditions. Algae represent between 30 and 50% of primary producer biomass in these systems, and their activity is apparent in the large diurnal changes in dissolved O₂ and CO₂. Because of their close connection with water chemistry, benthic algae help regulate water quality in wetlands, especially P loading from agricultural and urban runoff (McCormick and Stevenson, 1998).

In nutrient-rich wetlands, the algal flora is typified by filamentous green algae such as Stigeoclonium, Oedogonium, and Cladophora, cyanobacteria such as Lyngbya, Oscillatoria, and Nostoc, and many diatoms, including species of Amphora, Epithemia, Navicula, Nitzschia, and Surirella (Chaps. 17–19). Filamentous cyanobacteria Rivularia, Calothrix, Microcoleus, and Gloeotrichia (Chap. 4), and meadows of Chara (Chap. 8) typically dominate systems that have greater Ca²⁺ levels. In more oligotrophic systems, filamentous members of the Zygnematales (Chap. 9), including Mougeotia, Zygnema, and Spirogyra, commonly occur, along with epiphytic diatoms such as Tabellaria, Eunotia, and Fragilaria (see Chaps. 17 and 18), sediment-dwelling species such as Frustulia and Pinnularia (Chap. 17), and many desmids (Hooper-Reid and Robinson, 1978; Livingstone and Whitton, 1984; Goldsborough and Robinson, 1996; Pan and Stevenson, 1996, Chap. 9). Similar to patterns in softwater lakes, wetlands too may be impacted by acidic precipitation, leading to increases in Mougeotia, Zygnema, and, in severely impacted systems, Zygoonion (Stokes, 1986; Turner et al., 1995). Invertebrate grazers mediate species composition. Experimental removal of cladocerans and copepods from marsh enclosures resulted in a shift from a simple community dominated by Stigeoclonium to a more diverse and structurally complex assemblage of diatoms, filamentous green algae, and cyanobacteria (Hann, 1991).

An important reason for the success of certain algal species in wetland habitats is their ability to tolerate variations in water level and desiccation. One model predicted specific wetland algal communities that depend on varying water level: dry, sheltered, or
lakelike (Goldborough and Robinson, 1996). Water levels may fluctuate several times in a few months or persist for several years. Algae that occupy a variable moisture regime must have adaptations to tolerate extremes of conditions. Some epipelic desmids (Closterium and Micrasterias species) are capable of surviving extended periods of drying and darkness (Brook and Williamson, 1988). Other filamentous forms (e.g., Oscillatoria, Lyngbya, and Oedogonium) may form thick mats during the open (flooded) state that protect algal cells during a later dry phase.

C. Algal Communities of Bogs

Bogs are a special class of algal habitats, and include wetlands, streams, and ponds where water retention and chemistry are usually influenced by Sphagnum. Most bogs have lower pH (4.0–5.5), low Ca²⁺, are poor in nutrients, and have high levels of dissolved organic matter, which casts a yellow or brown stain to the water (Gorham et al., 1985; Cole, 1986). These dystrophic systems, along with lakes high in humic materials, accumulate poorly decomposed organic matter as peat. Ombrotrophic bogs are hydrologically isolated and depend on precipitation as their water source. Bogs are scattered throughout North America, especially in cool or cold regions that have an excess of moisture most of the year (Wetzel, 1983a).

Algal communities of bogs are typically species-poor, although diversity, especially that of the desmids, may be much greater in systems connected to other lakes or streams (Woelkerling, 1976; Hooper, 1981; Mataloni and Tell, 1996). A tangle of filamentous green algae (Zygnematales and Ulotrichales) and desmids (see Chap. 9) are common, but contrary to common wisdom, although desmids are numerous and diverse, they are rarely important in terms of algal biomass (Yung et al., 1986). Further details on their distribution and ecology are given in Chapter 9. At least three major algal habitats are found in bogs: (1) pools and open water, (2) habitats associated with Sphagnum, and (3) epiphytic habitats of Nuphar or other macrophytes. Data for 31 eastern bog systems demonstrated that algal species richness increases (especially desmids) with proximity to the Atlantic coast, and is less in systems with greater color and lower pH (Yung et al., 1986). The flagellate Gonyostomum (Raphidophyceae; Chap. 11, Sect. III) and the red alga Batrachospermum turfosum (as B. keratophyllum; Chap. 5) are two unusual species that are characteristic of boggy systems (Prescott, 1962; Bourelly, 1985; Yung et al., 1986; Sheath et al., 1994).

Diatoms are generally less diverse than desmids, but certain species are frequently observed, including Anomoneis brachysira, Frustulia rhomboides var. saxonica, Eunotia elegans, E. exigua, Navicula subtilissima, Pinnularia viridis, and several types of Stauroneis spp. (Kingston, 1982; Cochrane-Stafira and Andersen, 1984; Mataloni and Tell, 1996). Diatom species composition may change with successional stage of the surrounding vascular plant community, and apparently are responsive to many of the same variables, such as Ca, pH, and specific conductance (Cochrane-Stafira and Andersen, 1984). Although it has been argued that cyanobacteria may be unable to tolerate lower pH, especially values less than 4.0 (Brock, 1973), there are several species that are common in these waters, including species of Aphanocapsa, Chroococcus, Dactylococcopsis, Hapalosiphon, Microchaete, Nostoc, and Stigonema. Because many of these species are heterocystous, their N-cycling role in these nutrient-poor environments deserves attention. Some species of dinoflagellates, chrysophytes and synurophytes also may be found, although their abundance is usually low.

V. THERMAL AND ACIDIC ENVIRONMENTS

A. Thermal Springs

Thermal springs and streams (hot springs) are extreme environments in geologically active regions where temperatures are influenced by geothermal
sources and can range from 35 to 110°C. In North America, thermal springs are common from Alaska south to Costa Rica, and in scattered locations in Arkansas, Florida, Georgia, Virginia, and north to Massachusetts. Among the best known for aquatic organisms is the spectacular thermal area of springs, geysers, and fumaroles in Yellowstone National Park. Some thermal springs are less obvious, exerting their chemical and thermal effects on larger lakes and rivers, as in Yellowstone Lake (and adjacent lakes), and several streams and lakes in eastern Costa Rica (Pringle et al., 1993; Theriot et al., 1997).

The geology, chemistry, and organisms of hot springs have been reviewed by Castenholz and Wickstrom (1975), Brock (1986), and Ward and Castenholz (2000). Temperatures can be fairly constant near the source, but can range from about 110°C (with a high concentrations of salts) to just above ambient, depending on the temperature and volume of thermal water, distance from the source, and volumes of non-thermal surface water entering a system. Temperature is not the only extreme condition for thermal organisms; most springs have elevated concentrations (50–150 mg L⁻¹) of inorganic ions (Ca²⁺, Mg²⁺, Na⁺, HCO₃⁻, Cl⁻, Si, and H₂S) and elevated pH (8–10). These conditions select for highly adapted organisms, especially chemoautotrophic and heterotrophic bacteria in very hot (>70°C to ≈94°C) conditions (Brock, 1985b). Among photosynthetic organisms, cyanobacteria are most common, with an upper limit between 70 and 73°C; eukaryotic algae are restricted to a maximum of about 55°C. Along a thermal stream, distinct zones of bright colors and morphologies that correspond to different species along the thermal gradient can be observed.

A diversity of cyanobacteria dominate thermal waters. They include masses of coccolid species of Aphanocapsa, Chroococcus, Cyanobacterium, and Synechococcus, and filamentous species of Mastigocladus, Oscillatoria, and Phormidium (Ward and Castenholz, 2000, Chaps. 3 and 4). In cooler waters further from the source (35–50°C), diatoms (Achnanthes and Pinnularia) and green algae (Spirogyra and Mougeotia) proliferate (Stockner, 1967; Castenholz and Wickstrom, 1975). Cyanobacterial assemblages may form mats several centimeters thick and have extremely high rates of primary production (>10 g C m⁻² d⁻¹; Castenholz and Wickstrom, 1975). In one hot spring in Costa Rica (62°C, pH 7.0), a species of Oscillatoria dominated, while nearby streams with less extreme temperatures (35–36°C; pH 7.8–8.0) had a greater diversity of algal species, including cyanobacteria (Oscillatoria, Phormidium and Lyngbya) and diatoms (Pinnularia; Pringle et al., 1993). Unusual consumers are associated with hot springs, because few metazoa tolerate temperatures greater than about 50°C. Invertebrates include ostracods, water mites, and rotifers, but little is known of their dynamics or food webs. Adult beetles and flies are successful in some systems. Brine flies (Paracoenia and Epiphydra) lay eggs in microbial mats found in springs in Yellowstone Park within the 30–40°C range. Both adult and larval stages consume algal and bacterial material, which may in turn enhance primary productivity (Brock, 1967; Brock et al., 1969).

Some thermal springs are highly acidic, which further limits their species diversity. A notable eukaryote, the red alga Cyanidium caldarium, is often the sole photosynthetic organism in very acid (pH 2–4) hot springs up to about 55°C. This somewhat enigmatic organism was variously classified as a cyanobacterium, green alga, cryptomonad, and an evolutionary link between red and green algae (Seckbach, 1991); today it is placed in the division Rhodophyta based on pigments, chloroplast structure, and molecular features (Steinmüller et al., 1983; Pueschel, 1990). In acid hot springs, other enigmatic rhodophytes including Cyanidoschyzon merolae and Galdiera sulphuraria (DeLuca and Moretti, 1983), also have been reported, also have. It seems to be unlikely that either high temperature or low pH is solely responsible for this peculiar flora, because alkaline hot springs and nonthermal acid springs have very different algal communities.

B. Acid Environments

Most highly acid springs and streams are non-thermal and support a characteristic algal flora that is unlike those in other aquatic environments. Although bogs may exhibit relatively low pH (4.0–5.0), highly acidic environments typically are regarded as systems with H⁺ concentrations at least an order of magnitude greater, that is, pH values ≤3.0, and they usually receive acidic inputs from either geological or anthropogenic sources (Hargreaves et al., 1975). Nearly all have elevated concentrations of metals, including Al, Fe, Mn, Pb, Co, Cu, and Zn, which may be near saturation levels even for very low pH, resulting in the formation of metal salt precipitates along stream margins or on algal colonies. Acid springs with very high Fe concentrations also may have very low dissolved O₂, due to Fe(OH)₂ and FeO(OH)₂ precipitates (Van Everdingen, 1970). Laguna de Alegria, a crater lake in El Salvador, is influenced by sulfur-rich fumaroles and exhibits pH values as low as 2.0 (Cole, 1963).

The earliest detailed studies of algae in highly acidic systems in North America were conducted in acid mine drainages in Indiana, Kentucky, Ohio,
Pennsylvania, and West Virginia (Lackey, 1938; Bennett, 1969; Warner, 1971). These studies, as well as those in the United Kingdom (Hargreaves et al., 1975), all reveal low species diversity and a remarkable similarity in composition. *Euglena mutabilis* is the most widespread and often most abundant species, occurring in systems as acidic as pH 1.5. *E. mutabilis* is also common in naturally acidic streams, such as the Rio Agrio (pH 2.3) in Costa Rica (Pringle et al., 1993), and in acidic ponds in the Smoking Hills region of the Northwest Territories (Sheath et al., 1982). The latter site also supports populations of *Chlamydomonas acidophila*. *E. mutabilis* is not apparent in natural acid springs in Kootenay Paint Pots (BC) although a few diatoms and green algae are present (Wehr and Whittom, 1983). Other common elements in many highly acidic environments include *Klebsormidium* (previously Hormidium) *rivulare*, *Eunotia tenella*, *Pinnularia microstauron*, *P. braunii*, and *Gloeochrysis turfosa*. Acid sites in West Virginia contain many of the same species found in the United Kingdom. (Bennett, 1969), although an apparent absence of *G. turfosa* from North American sites may be the result of the alga being overlooked. No studies report cyanobacteria in these highly acidic environments, in agreement with Brock’s (1973) recommendation for a lower pH limit of less than 4.0. Isolates of *E. mutabilis*, *Chlamydomonas acidophila*, *Klebsormidium rivulare*, *Gloeochrysis turfosa*, and *Stichococcus bacillaris* from one acid stream (pH 2.6–3.1) were able to tolerate and grow at pH levels less than the lowest measured in their collecting site (Hargreaves and Whitton, 1976a). In addition, an acid strain of *Klebsormidium rivulare* tolerated greater Zn and Cu concentrations in the pH range 3.0–4.0, than at pH ≥ 6.0, suggesting a H⁺–metal interaction (Hargreaves and Whitton, 1976b).

VI. UNUSUAL ENVIRONMENTS

A. Saline Lakes and Streams

Saline lakes and streams make up a large and heterogeneous collection of water bodies that have elevated total dissolved salts (> 500 mg L⁻¹; Williams, 1996). Many are closed basins or desert playas that gain salinity over the year as they lose water (Hammer, 1986; Evans and Prepas, 1996). The term “saline” does not mean simply greater concentrations of NaCl. The ion content of inland saline lakes is influenced by Na⁺, K⁺, Ca²⁺, and Mg²⁺, and the major anions are typically Cl⁻, SO₄²⁻, HCO₃⁻, and CO₃²⁻ (Wetzel, 1983a; Hammer, 1986; Cole, 1994). Systems are usually well buffered (high in HCO₃⁻ and/or CO₃²⁻) and neutral to alkaline in pH (7.5–10.0). Among 47 saline lakes in the western United States and Canada, anion and cation chemistries vary significantly with latitude: lakes north of 47° latitude are dominated by SO₄²⁻ and either Na⁺ or Mg²⁺, whereas lakes in more southern locations are dominated by CO₃²⁻ or Cl⁻ in conjunction with Na⁺ ions, reflecting climatic as well as geological characteristics of each region (Blinn, 1993).

Saline lakes of athalassic (nonmarine) origin differ from oceanic systems in several important ways. Total dissolved salts vary considerably more (0.5–600 g L⁻¹) than in oceans (35–40 g L⁻¹), both among systems and over time. Most athalassic lakes are shallow, which makes seasonal and longer term (climatic, anthropogenic) changes in salinity important for algal survival, and results in low biotic diversity (Cole, 1994). A few are large and relatively deep, such as Pyramid Lake (532 km²; 102 m deep) and Big Soda Lake (1.5 km²; 64 m deep) in Nevada (Hutchinson, 1957), Mono Lake (150 km²; 40–50 m deep) in California (National Academy of Sciences 1987), and Soap Lake (3.6 km²; 27 m deep) in Washington (Castenholz, 1960). Because of differences in concentrations of salts with depth, many of the deeper saline lakes, such as Soap and Mono Lakes, are meromictic. Water level in Mono Lake varies substantially as a function of water diversion for human usage. In Redberry Lake, Saskatchewan, mean depth has decreased by about 37%, while salinity has increased by roughly 41% since the 1940s, due to changes in land use (Evans et al., 1996).

Saline lakes are concentrated in arid environments, especially in the U.S. Southwest, Mexico, and interior regions of California, Oregon, Washington, northern prairies, and British Columbia. Some of the most extensive surveys of the chemistry and biology of saline lakes were conducted in Saskatchewan (Rawson and Moore, 1944; Hammer et al., 1983). Few inland saline lakes are found in eastern North America, although Onondaga Lake (12 km², 20.5 m depth) is a saline lake in the New York Finger Lakes region. Levels of [Na⁺ + K⁺] and Cl⁻ exceeded 500 and 1400 mg L⁻¹, respectively, in part from salt springs, plus pollution from an adjacent soda ash facility (Berg, 1963; Sze and Kingsbury, 1972). Controls on salt waste have resulted in reduced total salinity (450 mg Cl⁻ L⁻¹), although levels are still greater than pre-industrial times (ca. 230 mg Cl⁻ L⁻¹). Effler and Owens, 1996; Rowell, 1996).

Algal communities of saline lakes differ among systems and their diversity varies inversely with salinity (Blinn, 1993; Cole, 1994). Because many saline lakes are shallow and subject to wind-driven mixing, it is often difficult to distinguish between benthic and planktonic forms. Several studies have evaluated the influences of salinity and ion composition on algal communities (Castenholz, 1960; Hammer et al., 1983;
Blinn, 1993; Fritz et al., 1993; Evans and Prepas, 1996; Wilson et al., 1996). In mildly saline (total salts 500–2000 mg L–1) lakes, the algal flora is fairly rich and composed of a variety of diatoms (e.g., species of *Amphora*, *Campylocystis*, *Cyclotella*, *Epithemia*, *Fragilaria*, *Navicula*, *Nitzschia*, and *Rhopalodia*), green algae (*Crucigenia*, *Pediastrum*, *Oocystis*, and *Sphaerocystis*), and cyanobacteria (e.g., species of *Anabaena*, *Aphanizomenon*, *Chroococcus*, *Lyngbya*, *Merismopedia*, *Microcystis*, and *Oscillatoria*), especially if N and P are high. In more strongly saline conditions (2–20 g L–1), many species are eliminated, but the community still includes taxa found in nonsaline waters, like *Cladophora glomerata*, *Botryococcus braunii*, *Cocconeis placentula*, *Mastogloia spp.*, *Nitzschia palea*, *Plagioselmis* (as *Rhodomonas*) *minuta*, and several cyanobacteria (*Aphanizomenon flos-aquae*, *Anabaena* spp., *Microcystis aeruginosa*, and *Oscillatoria* spp.).

Species typical of higher salinities also co-occur within this range, probably because concentrations can vary by an order of magnitude or more over a year in many lakes. Under hypersaline conditions (20–600 g L–1), diversity is very low, and includes some species that are restricted to higher salt levels, such as the diatoms *Amphora coffeiformis*, *Anomoneis sphaerophora*, *Navicula subinflatoidea*, *Nitzschia communis*, and *N. frustulum*, cyanobacteria *Nodularia spumigena* and *Aphanothece halophytica*, and the filamentous green alga *Ctenocladus circinatus* (Blinn, 1971; Herbst and Bradley, 1989; Wurtsbaugh and Berry, 1990; Kociolek and Herbst, 1992; Reuter et al., 1993). A few taxa that have marine distributions, such as *Enteromorpha intestinalis*, diatoms *Dunaliella salina*, *D. viridis*, *Chaetoceros muelleri*, and *Thallasiosira pseudonana*, and the coccolithophorid *Pleurochrysis carterae*, have been observed (Sze and Kingsbury, 1972; Stephens and Gillespie, 1976; National Academy of Sciences, 1987; Johansen et al., 1988). Experiments in which salinity was varied within Mono Lake mesocosms determined that diatom domination, algal diversity, chlorophyll-a, and photosynthesis in benthic communities all declined at higher salinities, while *Ctenocladus circinatus* and an *Oscillatoria* spp. dominated, although the diatom *Nitzschia monensis* increased (Herbst and Blinn, 1998).

Primary production by algae is often high (300–1000 g C m–2 year–1), along with very high chlorophyll-a levels (50 to > 500 mg L–1), because many saline lakes are located in sunny locations and have surplus P levels (total P: 50 to > 1000 mg L–1; Hammer, 1981; National Academy of Sciences, 1987; Robarts et al., 1992). Much of this production comes from epipelic and epilithic assemblages (e.g., *Ctenocladus*) rather than phytoplankton (*Wetzel*, 1964). Surface blooms of cyanobacteria may at times represent a significant portion of total production (Sze and Kingsbury, 1972; Robarts et al., 1992). Many lakes in the Canadian prairies have lower algal biomass and primary productivity than would be predicted using standard nutrient models (Campbell and Prepas, 1986), apparently because of greater densities of macrozooplankton that flourish in saline waters and perhaps due to fewer zooplanktivorous fish (Evans et al., 1996). In Great Salt Lake, weather-induced decreases in salinity (250–50 g L–1) resulted in an increase in grazers from one species (*Artemia*) to four, where rotifers and copepods were dominant (Wurtsbaugh and Berry, 1990).

Paleoecological studies have considered whether these systems were saline in the past (Fritz et al., 1993; Rowell, 1996). A study of the diatoms from 219 lakes in British Columbia indicated that some species are limited by salinities as dilute as 0.02 g L–1 (e.g., *Achnanthes pusilla*), whereas others tolerate more than 500 g L–1 (*Amphora coffeiformis* and *Nitzschia frustulum*; Wilson et al., 1996). Models from these data have been used to infer temporal and spatial differences in precipitation, which in turn influences salinity in these closed basins. Long-term changes in fossil algal pigments suggest that as prairie lakes became more saline, phytoplankton communities have shifted from a diatom–chrysophyte–dinoflagellate community to one dominated by greens, cyanobacteria, and diatoms (Vinebrooke et al., 1998). Due to possible effects of global warming, semiarid regions of North America may experience an increase in the number of saline waters in the next few decades (Evans and Prepas, 1996).

B. Snow and Ice

People who have hiked in alpine regions are familiar with red snow, especially where snowfields accumulate for most of the year. Aristotle also apparently observed red snow many centuries ago (Kol, 1968). This phenomenon is most often caused by the green alga *Chloromonas* (previously recorded as *Chlamydomonas* *nivalis* (see Chap. 6). The red color is the result of an accumulation of secondary carotenoids, mainly astaxanthin, in resting cells (Round, 1981; Bidigare et al., 1993). Not all snow communities are colored red: orange, brown, and green patches are also seen, depending on the species present, dominant pigments, exposure to sunlight, and perhaps pH (Stein and Amundsen, 1967; Kol, 1968; Hoham and Blinn, 1979). Cells aggregate near the surface, and as successive snowfalls accumulate, layers or bands of pigmented algal communities can be seen in vertical cuts through a snow bank (Hoham and Mullet, 1977). Although motile stages can be found in snow, most cells occur either as thick-walled resting zygotes or as asexual
hynospores (Stein and Amundsen, 1967). Cryophilic flora include other algal flagellates, such as Chloromonas nivalis, C. brevispina, Carteria nivalis (= planozygotes of Chloromonas sp.), Scotiella cryophila, and Chromulina chionophila, and nonflagellated green algae, such as Raphidonema nivale and Stichococcus spp. (Stein and Amundsen, 1967; Kol, 1968; Hoham, 1975; Hoham and Blinn, 1979). The life cycles of many snow algae are incompletely known; thus, some cells previously identified as new taxa have been shown to be zygotes of other known species (Hoham and Blinn, 1979; R.W. Hoham, personal communication).

Snow algae exhibit measurable but low photosynthesis rates, many of which reach a maximum near 10°C, although some peak near freezing and decline at higher temperatures (Mosser et al.; Round, 1981). A strain of Chloromonas pichinchae from snowfields in Washington state grew best at 1°C and pH 6.0, whereas the optimum for an isolate of Raphidonema nivale from the same location was 4–5°C, with a pH optimum ≥ 7.0, despite lower environmental pH (ca. 5.0) and temperature (near 0°C; Hoham, 1975). Strains of Chloromonas isolated from snowfields in the Adirondack Mountains (exposed to decades of acid deposition) have significantly greater (1.5- to 2.2-fold greater) growth yields at pH 4.0 than Chloromonas isolated from the (less acidic) White Mountains of Arizona (Hoham and Mohn, 1985). Algal cells that colonize snow surfaces at high altitude experience extreme levels of solar (including UV) radiation. Carotenoid pigments provide photoprotection by reducing total radiation and filtering certain shorter wavelengths from photosynthetic pigments (Bidigare et al., 1993). Experiments with snow algae from Tioga Pass in the Sierra Nevada found that UV radiation inhibited photosynthesis in green snow by 85%, but only 25% in red snow (Thomas and Duval, 1995). Snow algal communities also are influenced by the amount of wind-blown soil (plus factor: nutrient source), exposure (plus or minus factor: direction and quantity of sunlight), snow albedo (usually minus factor: reflective property), and water content (plus factor) of the snow (Stein and Amundsen, 1967; Hoham and Blinn, 1979; Thomas and Duval, 1995). These communities have cryophilic food webs with protozoan consumers, and bacterial and fungal decomposers that are active at very low temperatures (Felip et al., 1995; Thomas and Duval, 1995).

C. Other Unusual Habitats

Algae form thick mats on tank walls, outflow weirs, pipes, and other substrata in sewage treatment plants, where concentrations of nutrients greatly exceed requirements (N: 1–20 mg L⁻¹, P: 0.1–2 mg L⁻¹). The most common taxon appears to be Stigeoclonium tenue; lesser abundances of Chlorella spp., Nitzschia palea, Oedogonium sp., Oscillatoria spp., Pleurocapsa minor, Pseudanabaena catanata, Scenedesmus quadricauda, and Tribonema spp. also are observed (Palmer, 1962; Sládecková et al., 1983; Davis et al., 1990a). Communities exhibit seasonal changes in composition: Tribonema dominates in the spring, and Oscillatoria, Scenedesmus, and Stigeoclonium reach their maxima in warmer months. These shifts are largely driven by changes in light and temperature, not nutrient supply (Davis et al., 1990a). Substantial biomass and rapid growth rates have made algae candidates for nutrient removal plans (Sládecková et al., 1983; Davis et al., 1990b). Treatment ponds have been devised in which > 95% of P may be removed by algal assemblages alone (Hoffmann, 1998).

Algae colonize caves in many limestone or dolomite regions where fractures or underground streams form underground pockets or large caverns. Some cave-dwelling algae, including species of Gloeocapsa (Cyanobacteria), survive very low light levels by having densely packed thylakoids in their cells and very slow growth rates (Pentecost and Whitton, 2000). By some observers caves may be considered to be dark, unproductive environments, but substantial algal florals develop where surface are open to the sunlight (fissures, mouths) or in show caverns where artificial lighting has been added. Cyanobacteria (e.g., Aphano-capsa, Calothrix, Chroococcus, Gloeocapsa, Hapalo-siphon, and Schizothrix) may be especially abundant near light sources (Claus, 1962; Round, 1981). Species diversity is typically low: Timpanogos Cave (UT) and Seneca Cavern (OH) each support an algal flora of fewer than 30 species (St. Clair and Rushforth, 1976; Dayner and Johansen, 1991). Species include diatoms (Navicula tantula and N. contenta), unicellular green algae (Chlorella miniata), and the xanthophyte Pleurochloris communata. CaCO₃ from cave walls may become incorporated into algal colonies and thalli, which is why artificial lighting and the resultant algal colonization has been cited as a prime cause of cave wall destruction in show caves (Gurnee, 1994).

The calcareous cave flora are similar to wet limestone seepages above ground, and exhibit an abundance of calcified cyanobacteria and diatoms (Pentecost, 1982; Pentecost and Whitton, 2000). Algae from pools adjacent to caves may be an important carbon source for food webs inside caves (Pohlman et al., 1997). Noncalcareous, temporary rock pools that form in weathered bedrock along lake and river margins also become algal habitats. These small systems (a few liters or less) experience great variations in water level and...
nutrients, and extremes in solar radiation. The most common inhabitant is the algal flagellate *Haematococcus lacustris*, which accumulates red secondary carotenoids much like snow algae. This adaptation serves a similar photoprotective role and is not influenced by nutrient levels (Yong and Lee, 1991; Lee and Soh, 1991). Humans have created a widespread habitat for *H. lacustris*, namely birdbaths (Canter-Lund and Lund, 1995); hence, many people report red water in their birdbaths after a year or so of use.

Endophytic algae live in cavities of higher plants or colonize plant tissues intracellularly. Algae colonize microhabitats created by bromeliad cups, and colonized by algae, and differ in pH and dissolved O2 levels among different plants (Laessle, 1961). Perhaps the most ecologically important endophytic algae in freshwaters are species of cyanobacteria that colonize various aquatic plants and bryophytes. The best known is *Anabaena azollae*, a symbiont within the water fern *Azolla*, which is used as a nitrogen source or “green fertilizer” for rice crops worldwide (Bothe, 1982). Roots of some cycads (*Cyas, Encephalartos*, and *Macrozamia*) are colonized by several cyanobacteria, especially *Anabaena*, *Calothrix*, and *Nostoc* (Huang and Grobbelaar, 1989); when sectioned, cyanobacteria appear as a healthy blue-green color. Green algae (e.g., *Chlorella*, *Chlamydomonas*) and some xanthophytes (see Frost et al., 1997, Chaps. 6 and 7) are symbionts in a variety of aquatic organisms, including freshwater sponges (e.g., *Spongilla lacustris* and *Corvomeyenia everetti*), ciliates (e.g., *Euplotes* and *Ophrydium*), and other organisms (Slobodkin, 1964; Frost and Williamson, 1980; Berninger et al., 1986; Sand-Jensen et al., 1997). In the spring, green, baseball-sized (up to 20 cm) green masses can be observed in ponds and lake outflows that are actually mucilaginous sized (up to 20 cm) green masses can be observed in ponds and lake outflows that are actually mucilaginous masses of amphibian eggs (*Amblystoma* and *Rana*) colonized by the green alga *Chlamydomonas* (syn. *Osiophila*) amblystomatis. This association appears to provide N for the alga and added O2 for developing amphibian eggs (Goff and Stein, 1978; Bachmann et al., 1986; Pinder and Friet, 1994). Much more intimate symbioses are found among algae and cyanobacteria with fungi, as lichens. The treatise by Ahmadjian (1993) can be consulted for further information.

Many algae colonize terrestrial habitats such as soils, trees, and other surfaces, and serve important ecological functions in soil and moisture retention, seed germination, nutrient dynamics, and succession of terrestrial vegetation (Carson and Brown, 1978; Bell, 1993; Vazquez et al., 1998). Many of the more common terrestrial species, appear as a green “felt” on stone walls, tree bark, and wooden fences such as *Apatococcus* and *Trentepohlia* (Chlorophyta), that may be mistaken for moss (Canter-Lund and Lund, 1995). Epiphytic green algae have been used as biological indicators of air quality (Hanninen et al., 1993). A number of genera that colonize plant leaves, walls, stones, or soils are also common in fresh waters, including many cyanobacteria (*Nostoc, Oscillatoria, Lyngbya*, and *Plectonema*), green algae (*Chlamydomonas, Chlorella, Chlorococcum*, and *Klebsormidium*), and diatoms (*Achnanthus, Hantzschia*, and *Navicula*; Segal, 1969; Cox and Hightower, 1972; King and Ward, 1977; Hunt et al., 1979). Diatoms from these habitats are often desiccation-resistant and many are regarded as obligate aerial taxa (Johansen, 1999). Other genera, such as *Prasiola* and *Zygogonium*, have very distinct ecological requirements. *Prasiola* colonizes N-rich (e.g., guano) rocks and walls in aerial (often shaded) and even urban environments (Jackson, 1997; Rindi et al., 1999), whereas aquatic species colonize cool, nutrient-poor streams (Sheath and Cole, 1992; Kawecka, 1990; Hamilton and Edlund, 1994). A few terrestrial species colonize the interstitial spaces within crystalline rocks in arid or semiarid regions, where water supply may be limited (Bell, 1993; Johansen, 1993). Further details on the algal flora of soils and terrestrial habitats can be found in reviews by Fritsch (1922), Starks et al. (1981), and Johansen (1993). Some algae are parasitic within plant tissues (leaves and twigs), such as *Cephaleuros*, which is the cause of red rust disease in higher plants (Thompson and Wujek, 1997). Perhaps one of the most unusual of all algal habits is that of the red alga *Rufusia*, which lives within the hairs of two- and three-toed sloths, but apparently does not colonize nearby vegetation (Chap. 5).

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LITERATURE CITED


Andersen, R. A., Wetherbee, R. 1992. Microtubules of the flagellar apparatus are active during prey capture in the chrysophycean alga 
Euglena pulchra.
Protoplasma 166:8–20.

Glosteria pium
in field and laboratory. Microbios 53:7–19.


Blinn, D. W. 1971. Aecotrophy of a filamentous alga, 
Cladophora cinnamatoidea


Blinn, D. W., Truitt, R. T., Pickart, A. 1989. Feeding ecology and radular morphology of the freshwater limpet 
Ferrissia fragilis.


Brock, T. D. 1969. Feeding by 
Paracocemia
and 
Ephedia


Brooks, J. L., Deevey, E. S. 1963. New England,


Brönmark, C., Klosiewski, S. P., Stein, R. A. 1992. Indirect effects of


