Ecology of Blue-Green Algae in Aquaculture Ponds

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Abstract

Cyanobacteria (blue-green algae) in the genera *Anabaena, Aphanizomenon, Microcystis,* and *Oscillatoria* often form extensive and persistent blooms in freshwater aquaculture ponds. Bloom-forming cyanobacteria are undesirable in aquaculture ponds because: 1) they are a relatively poor base for aquatic food chains; 2) they are poor oxygenators of the water and have undesirable growth habits; 3) some species produce odorous metabolites that impart undesirable flavors to the cultured animal; and 4) some species may produce compounds that are toxic to aquatic animals. Development of cyanobacterial blooms is favored under conditions of high nutrient loading rates (particularly if the availability of nitrogen is limited relative to phosphorus), low rates of vertical mixing, and warm water temperatures. Under those conditions, dominance of phytoplankton communities by cyanobacteria is the result of certain unique physiological attributes (in particular, N_2 fixation and buoyancy regulation) that allow cyanobacteria to compete effectively with other phytoplankton. The ability to fix N_2 provides a competitive advantage under severe nitrogen limitation because it allows certain cyanobacterial species to make use of a source of nitrogen unavailable to other phytoplankton. The ability to regulate cell buoyancy through environmentally-controlled collapse and reformation of intracellular gas vacuoles is perhaps the primary reason for the frequent dominance of aquaculture pond phytoplankton communities by cyanobacteria. Cyanobacteria that can regulate their position in the water column gain a distinct advantage over other phototrophs in poorly mixed bodies of water. In addition to the physicochemical interactions that influence phytoplankton community dynamics, cyanobacterial-microbial associations may play an important regulatory role in determining community structure. Cyanobacteria are always found in close association with a diverse array of microorganisms, including eubacteria, fungi, and protozoans. These associations, which in the past have often been viewed as antagonistic, are increasingly seen as mutualistic and may function in a positive manner during bloom development.

Phytoplankton communities are an essential component of most pond aquaculture systems. Primary production by phytoplankton is the base of the food chain in pond cultures that depend upon natural foods to support fish or crustacean production. Plant nutrients may be intentionally added to these ponds in manures or chemical fertilizers to enhance phytoplankton growth and, ultimately, increase aquaculture yield. On the other hand, phytoplankton-based food chains may be relatively unimportant in pond cultures that rely upon manufactured feeds to promote rapid growth of the fish or crustaceans. Nevertheless, phytoplankton communities are considered beneficial even in those systems because they are part of the pond microbial community that acts to maintain adequate environmental conditions for culture. For example, phytoplankton communities at moderate standing crops are net producers of dissolved oxygen, and they assimilate ammonia as a nitrogen source for growth, thereby reducing the accumulation of un-ionized ammonia, which can be toxic to aquatic animals at relatively low concentrations. Notwithstanding the beneficial aspects of phytoplankton in aquaculture ponds, it is com-

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monly accepted that most water quality problems in aquaculture ponds are the result of unmanaged growth of phytoplankton communities (Smith 1988, 1991). One important result of that unmanaged growth is the tendency for phytoplankton communities in freshwater aquaculture ponds to be dominated by noxious species of cyanobacteria ("blue-green algae").

In this review we will briefly summarize the occurrence of cyanobacteria in aquaculture ponds and the consequences of their presence. The discussion will then focus on the functional linkages that may act to promote and maintain blooms of nuisance genera. Such linkages include the relationships between physicochemical "forcing features" and biotic factors. An important example of such a linkage is that between water column turbulence and cell buoyancy regulation.

Research on the ecology of cyanobacteria in aquaculture ponds is meager, so most of the information in this review is drawn from work in other ecosystems. Nevertheless, a better understanding of interactions between cyanobacteria and their immediate physical, chemical, and biotic environment on relevant microbial scales will hopefully yield ecologically and environmentally relevant information useful in devising effective bloom control measures in aquaculture ponds.

Cyanobacteria in Aquaculture Ponds

Cyanobacteria are widely distributed and represent at least 22 genera, including over 90 species, that have been identified from freshwater habitats (Gibson and Smith 1982). Relatively few studies of aquaculture pond phytoplankton assemblages have been conducted, but it appears that the cyanobacterial flora is as diverse as that in other habitats. As is true of other freshwater ecosystems, most of the cyanobacterial species encountered in freshwater aquaculture ponds occur as rare or minor components of the plankton community (Boyd and Scarsbrook 1974; Munawar 1974; van Rijn

et al. 1986; Tucker and Lloyd 1984; Tucker 1985; Hariyadi et al. 1994). Relatively few species, principally in the genera *Anabaena, Aphanizomenon, Microcystis,* and *Oscillatoria* (Table 1), are responsible for nuisance blooms. All of the noxious, bloom-forming cyanobacterial species are relatively large, multicellular colonies or filaments (Fig. 1) and all have the ability to change cell buoyancy through environmentally-controlled collapse and reformation of intracellular gas vacuoles.

The importance of cyanobacteria in aquaculture ponds, in the most basic terms of occurrence and biomass, has been amply demonstrated in channel catfish *Ictalurus punctatus* culture ponds in Mississippi, USA (Tucker and Lloyd 1984; Tucker and van der Ploeg 1993; Millie et al. 1992, in press). During the summer growing season, pond water temperatures are relatively warm (25–35 C) and nutrient loading rates are high as large amounts of manufactured feed are added to ponds to promote rapid fish growth. Over the 6-mo period of warm water temperatures, cyanobacteria are present in nearly all catfish culture ponds and account for over 75% of the total phytoplankton biomass in most ponds.

Aside from the obvious importance of cyanobacteria as contributors to much of the phytoplankton biomass in freshwater aquaculture ponds, the presence of bloom-forming species assumes added significance because they are generally undesirable components of the plankton community. Bloom-forming cyanobacteria are not a readily utilized source of primary production for food chains in most aquaculture systems, they are relatively poor oxygenators of the water, they have undesirable growth habits, certain species may produce odorous metabolites that confer undesirable flavors to the cultured animal, and some species may produce compounds that are toxic to fish.

The common, bloom-forming cyanobacteria found in warmwater aquaculture ponds are K-selected organisms (Reynolds 1984; Kilham and Hecky 1988). K-selected or-

TABLE 1. *Characteristics of four common genera of cyanobacteria with species that may form nuisance blooms in freshwater aquaculture ponds.*

Genus	Morphology	Comments
Anabaena	Straight, coiled, or twisted filaments of spherical or barrel-shaped cells with intercalary heterocysts. Filaments often entangled and inclosed in an amorphous mucilage.	Most species are planktonic, heterocystous, N_2-fixers. Some species produce the odorous compound, geosmin, or potent toxins. The nuisance species are gas-vacuolate and may form extensive blooms in eutrophic, stratified, warm, fresh waters.
Aphanizomenon	Relatively short filaments of cylindrical cells with intercalary heterocysts. The filaments lie parallel in plate-like bundles or flakes, which are free-floating.	Gas-vacuolate, heterocystous, N_2-fixer that can form massive bright green surface blooms in nutrient-enriched waters. May produce geosmin or potent neurotoxins.
Oscillatoria	Simple, usually solitary, filaments without sheaths. The filaments are usually straight but may be curved at the apex.	A genus with many species that inhabit a wide variety of aquatic habitats. Some species are gas vacuolate and may form extensive blooms in nutrient-enriched waters. Some species produce the odorous compounds geosmin or 2-methylisoborneol. Some species are non-heterocystous N_2-fixers.
Microcystis	Numerous spherical cells irregularly aggregated within copious mucilage to form an irregular, globose, free-floating colony. Cells often have gas vacuoles.	A non-N_2-fixing genus that is very common in nutrient-enriched (N + P) fresh waters, especially those of high hardness and pH. The highly buoyant colonies can produce spectacular surface blooms. Certain strains produce potent toxins.

ganisms have relatively slow growth rates but compete well for limited resources: they tend to be "climax" organisms that are able to dominate relatively stable environments. The slow growth rate of bloom-forming cyanobacteria may affect aquaculture production in ponds where the food for fish or crustaceans originates entirely from in-pond primary production. In essence, the low biomass-specific rates of net carbon fixation by cyanobacterial communities relative to most eukaryotic phytoplankton (diatoms, green algae, and dinoflagellates) should translate into reduced aquaculture yields. The efficiency of food transfer in phytoplankton-based food chains may be further reduced when bloom-forming cyanobacteria are present because they are acknowledged to be poorly utilized as food by herbivorous crustacean zooplankton (Ryther 1954; Paerl 1988b). Cyanobacterial biomass is inefficiently utilized by zooplankton herbivore populations because the colonies or filaments may be too large to be effectively processed or the biomass may be undigestible, toxic, or of poor food quality (Crowley 1973; Porter and Orcutt 1980). The transfer of carbon from primary production to herbivores in cyanobacteria-based food chains may rely heavily on detritus pathways or grazing by rotifers and protozoans to convert this biomass into food more readily utilized by herbivorous zooplankton (Paerl 1988b). The additional steps in cyanobacteria-based food chains may reduce the efficiency of transfer of organic matter and nutrients from primary production to aquaculture crop.

The slow growth rates of bloom-forming cyanobacteria also mean that they are poor oxygenators of the water on a per unit biomass basis compared to most eukaryotic species of phytoplankton. Furthermore, under extreme light-limited conditions for photosynthesis and low rates of water column turbulent mixing, persistent positive
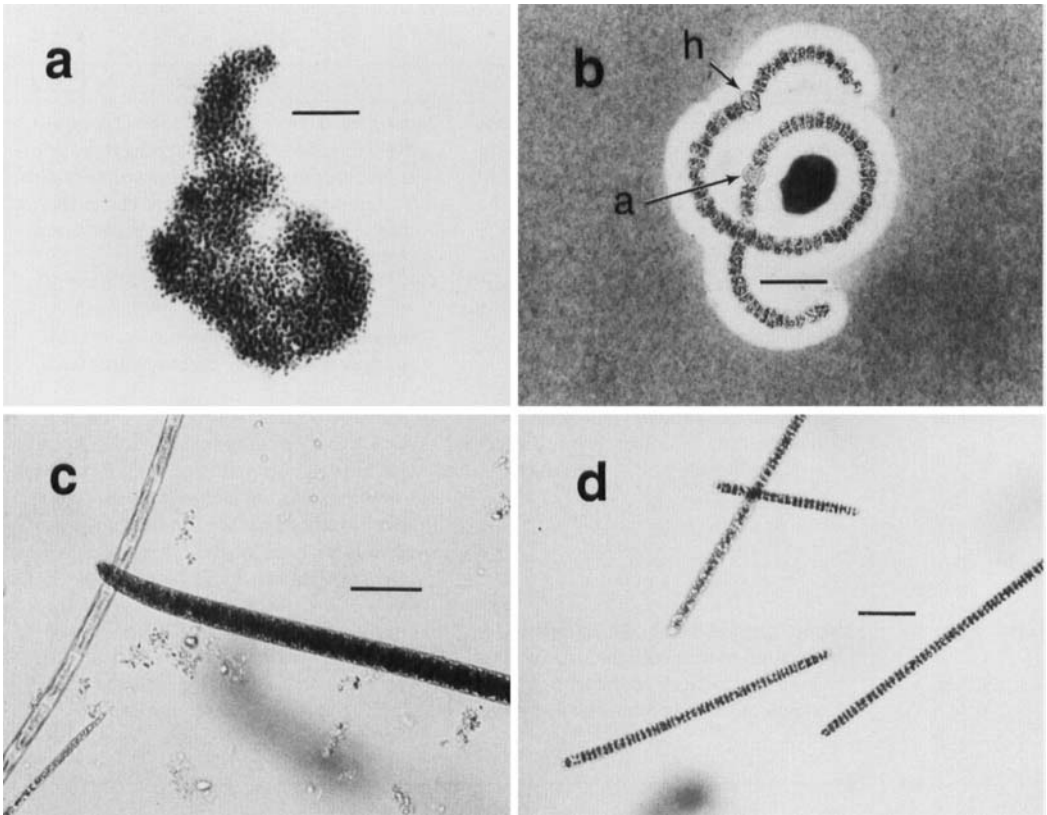
FIGURE 1. *Four typical bloom-forming cyanobacteria found in freshwater aquaculture ponds. (a) A colony of*
Microcystis aeruginosa, *the most common cyanobacterium in plankton communities of channel catfish culture
ponds in northwest Mississippi, USA (Tucker 1985). Bar = 50 μm. (b) A filament of* Anabaena sp. *from a
channel catfish pond in east Alabama, USA (van der Ploeg et al. 1992). This species produces geosmin, a highly
odorous, earthy-smelling compound, and was photographed in India ink to show the mucilage around the
filament. Bar = 25 μm, h = heterocyst, a = akinete. (c) A filament of* Oscillatoria cf. chalybea, *a species that
produces the musty-smelling compound 2-methylisoborneol in Mississippi catfish ponds (Martin et al. 1991).
Bar = 25 μm. (d) Filaments of* Oscillatoria agardhii var. isothrix (= O. mougeotii), *the most common species
of Oscillatoriaceae found in Mississippi catfish ponds (Tucker 1985). Bar = 20 μm.*

buoyancy of bloom-forming cyanobacteria may result in formation of surface scums. Development of surface scum communities further reduces net input of dissolved oxygen to the pond because oxygen production during photosynthesis is restricted to the upper few centimeters of the water. Oxygen produced in the surface layer may be rapidly lost to the atmosphere by degassing and thus not be available for eventual use in fish respiration. Surface scums of cyanobacteria also are more prone to massive die-offs than are mid-water blooms of eukaryotic phyto-plankton (Boyd 1990). The sudden death of dense, nearly mono-specific cyanobacterial communities can have disastrous consequences in aquaculture ponds because photosynthetic oxygen production nearly ceases and large amounts of dissolved oxygen are consumed as dead algal cells are decomposed (Boyd et al. 1975, 1978).

Perhaps the most economically important attribute of cyanobacteria in aquaculture ponds is the production by certain species of highly odorous metabolites that are released into the water when cells lyse. The

water-borne compounds may then be absorbed by fish, imparting an undesirable "off-flavor" to the flesh. Two metabolites of cyanobacteria, geosmin (trans-1, 10-dimethyl-trans-9-decalol) and 2-methylisoborneol (1, 2, 7, 7-tetramethyl-exo-bicyclo [2.2.1]heptan-2-ol), have earthy-musty odors and are responsible for most episodes of off-flavor in pond-cultured fish (Martin et al. 1991; Tucker and Martin 1991; van der Ploeg and Boyd 1991; van der Ploeg et al. 1992; van der Ploeg and Tucker 1994). The occurrence of earthy-musty off-flavors in pond-raised fish is episodic, coinciding with the appearance and eventual disappearance of the cyanobacterial species responsible for synthesis of the odorous compounds. Problems with off-flavor are most common in freshwater pond systems receiving large additions of feed or fertilizer because environmental conditions in those ponds tend to favor the growth of odor-producing taxa such as species of Oscillatoria or Anabaena. Earthy-musty off-flavors are relatively rare in brackishwater or marine cultures because odor-producing cyanobacterial species do not appear to thrive in waters of salinity greater than 5 to 10 ppt. Off-flavors may, however, develop in fish or crustaceans cultured in coastal areas when high river discharges cause the salinity in estuarine water supplies to decline to levels permissive for blooms of odor-producing cyanobacteria (Lovell and Broce 1985).

Off-flavor fish should not be harvested and marketed because consumer dissatisfaction with product quality may adversely affect market demand. Most episodes of cyanobacteria-related off-flavors eventually resolve as natural changes in the phytoplankton community result in the disappearance of the offending species from the community. After production of geosmin or 2-methylisoborneol ceases, the compound (and the associated flavor) is rapidly purged from the fish. However, the costs associated with delayed harvest of off-flavor fish can be substantial. For example, it has been estimated that environment-derived off-flavors may add 10–20% to the cost of producing channel catfish in the southeastern United States (Keenum and Waldrop 1988; Engle et al., in press).

Several species of cyanobacteria produce compounds that are extremely toxic to warm-blooded animals (Carmichael and Mahmood 1984) but little documentation of the importance of cyanobacterial toxins in aquaculture ponds is available. One toxigenic cyanobacterial species, Aphanizomenon flos-aquae, is known to have caused large losses of pond-raised channel catfish in South Carolina, USA (English et al. 1993). Species of Microcystis and Anabaena, two bloom-forming cyanobacterial genera common to freshwater aquaculture ponds, also are known to produce potent toxins and may be responsible for some unexplained losses of fish or crustaceans.

Environmental Factors Controlling Cyanobacterial Bloom Formation

Despite the ubiquity and persistence of nuisance blooms of blue-green algae, there exists little information linking the physical, chemical, and biological conditions in the environment to the onset and persistence of blooms. Equally obscure are cyanobacterial physiological and ecological "strategies" that have evolved to optimize growth and persistence during physically and chemically favorable bloom periods. Physicochemical factors controlling freshwater bloom potentials are numerous and complex (Table 2). Physical factors are frequently of overriding importance in determining which genera and species become established and dominant in specific ecosystems. Frequently mentioned physical factors are the size and volume of the system, the mean hydraulic retention time (the degree of "flushing"), stability of the water column (vertical mixing), and water transparency. Cyanobacteria exhibit relatively slow growth rates (< 1 division per day). Therefore, lengthy periods of physical stability (i.e., stable hydraulic, climatic, and hydrologic conditions) are a prerequisite for the development of bloom

TABLE 2. *Physicochemical factors potentially controlling cyanobacterial bloom formation.*

Factor	Effects or impacts
Physical	
Flushing/low hydraulic retention time	Prevents bloom establishment or removes bloom if flushing rate exceeds growth rate of bloom taxa
Large scale vertical mixing	Prevents surface bloom accumulations and forces competition for light and nutrients with non-buoyant eukaryotic taxa
Small-scale turbulence (shear)	May disrupt filaments, colonies, and mutualistic associations with other microorganisms
Temperature	Generally warm water temperatures accompanied by a stratified water column and high nutrient loading rates promote blooms
Chemical	
Nutrient (N and P) inputs	High N and P inputs favor bloom formation, especially if the ratio of N to P loading is low
Salinity	Salinity in excess of a few ppt may be an effective barrier to the development and persistence of nuisance species
Environmental pH	Generally low pH (<6) favors eukaryotic phytoplankton, high pH favors cyanobacteria
Trace metals	Under high N and P loading, restricted availability of Fe may favor cyanobacteria

populations (Reynolds and Walsby 1975). Beyond that, nutrient availability and water temperature are the ultimate determinants of population size, assuming persistent physical stability.

Water Column Turbulence

In examining the suite of physical and chemical factors potentially controlling establishment and persistence of planktonic cyanobacteria, water column turbulence assumes an eminent role. It is well known that vertical water column mixing can be a strong determinant of dominance of the plankton community by heterocystous and non-heterocystous cyanobacteria (Reynolds and Walsby 1975; Paerl 1988a, 1988b; Vincent 1987). This realization has fostered the application of artificial mixing strategies aimed at reducing and eliminating cyanobacterial dominance and nuisance blooms. To be effective as a bloom mitigation tool, destratification must operate more or less continually during the favorable cyanobacterial growth periods. Even when intermittent weak stratification is experienced during these periods, cyanobacterial blooms can quickly re-emerge, leading to long-term dominance throughout the entire spring-summer period (Paerl 1987). Shallow, periodically mixed lakes such as Clear Lake (California, USA), Klamath Lake (Oregon, USA), embayments of Lakes George and Victoria in Africa, brackish segments of the Baltic Sea, and many agricultural and urban impoundments exhibit such tendencies (Reynolds and Walsby 1975; Horne 1977; Paerl 1988b) and illustrate the importance of continuous vertical mixing of the water column as a means of suppressing dominance by cyanobacterial bloom taxa.

Both the magnitude and duration of turbulence are known to alter phytoplankton (bloom-forming dinoflagellates and diatoms) growth rates and structural integrity (Thomas and Gibson 1990a, 1990b). Among cyanobacterial taxa, non-disruptive (to cell, colony, or filament integrity) low-level turbulence is known to promote localized "phycosphere" nutrient cycling, alleviate certain forms of nutrient limitation (carbon dioxide, orthophosphate, or trace metals) and generally promote cell growth (Fogg et al. 1973; Rhee et al. 1981). Gently stirred laboratory cultures of bloom-forming heterocystous genera, including *Anabaena, Aphanizomenon, Nostoc,* and *Gloeotrichia* often show better growth than static cultures.

Subtle increases in turbulence (either as stirring or shaking) can, however, inhibit growth, with excessive turbulence causing disaggregation, cell and filament damage, and rapid death or "crashes" among diverse colonial genera in culture and in nature. Optimal N_2 fixation, photosynthetic rates, and growth in these genera have been shown to be strongly reliant on mutually beneficial microbial (heterotrophic-autotrophic) consortial interactions functioning in close physical association with filaments and aggregates of colonial genera (Paerl 1990). Interactions may include nutrient and vitamin exchange and localized removal of inhibitory metabolites such as molecular oxygen and hydrogen sulfide. Phototrophic growth and N_2 fixation are often strongly suppressed in filamentous and colonial genera when they are grown axenically (i.e., bacteria-free; Fig. 2). It is suspected that turbulence can disrupt beneficial consortial interactions and thus act as a negative growth factor.

Excessive small-scale, cellular-level turbulence or shear (Hunt 1982), generated by stirring or shaking at high speeds, can physically disrupt filaments of heterocystous N_2-fixing cyanobacteria. The junctions between heterocysts and adjacent vegetative cells are narrow, fragile, prone to disruption, and are sites of filament breakage (Fig. 3). This phenomenon is particularly evident in common bloom-forming species existing as solitary filaments, such as *Anabaena cylindrica, A. circinalis,* and *A. oscillarioides,* whereas intertwined, aggregated species such as *Anabaena flos-aquae, Aphanizomenon flos-aquae, Gloeotrichia* spp., and *Nostoc* spp. may be better protected from shear. When filament breakage involving heterocysts occurs, affected heterocysts lose their ability to fix N_2, senesce, and are shed from the filament (Paerl and Bland 1982) (Table 3).

While small-scale shear can lead to disaggregation and structural damage, large-scale mixing induced by wind or tides affects vertical and horizontal distributions and transport of cyanobacterial bloom taxa.
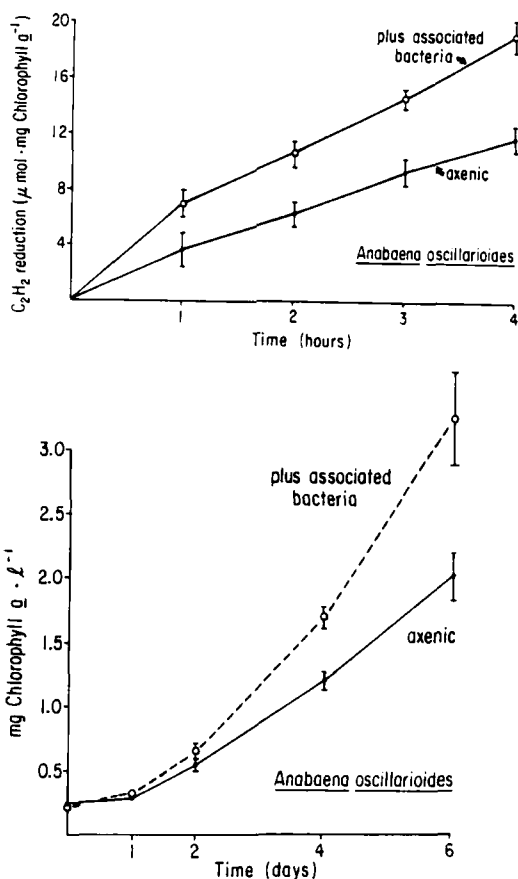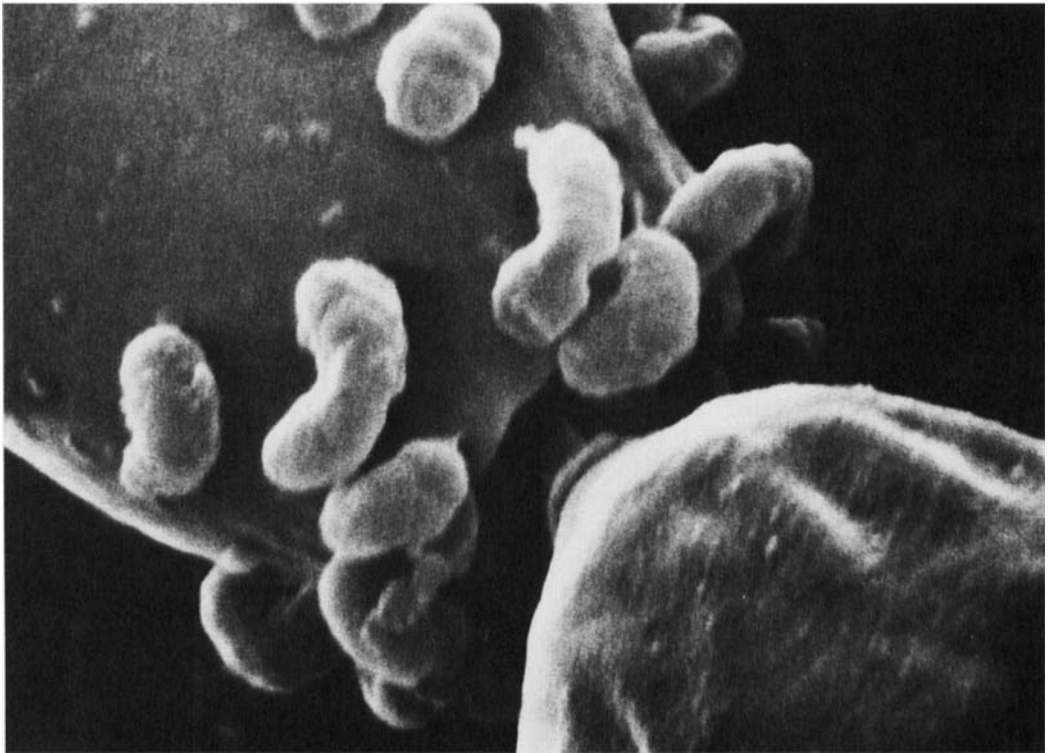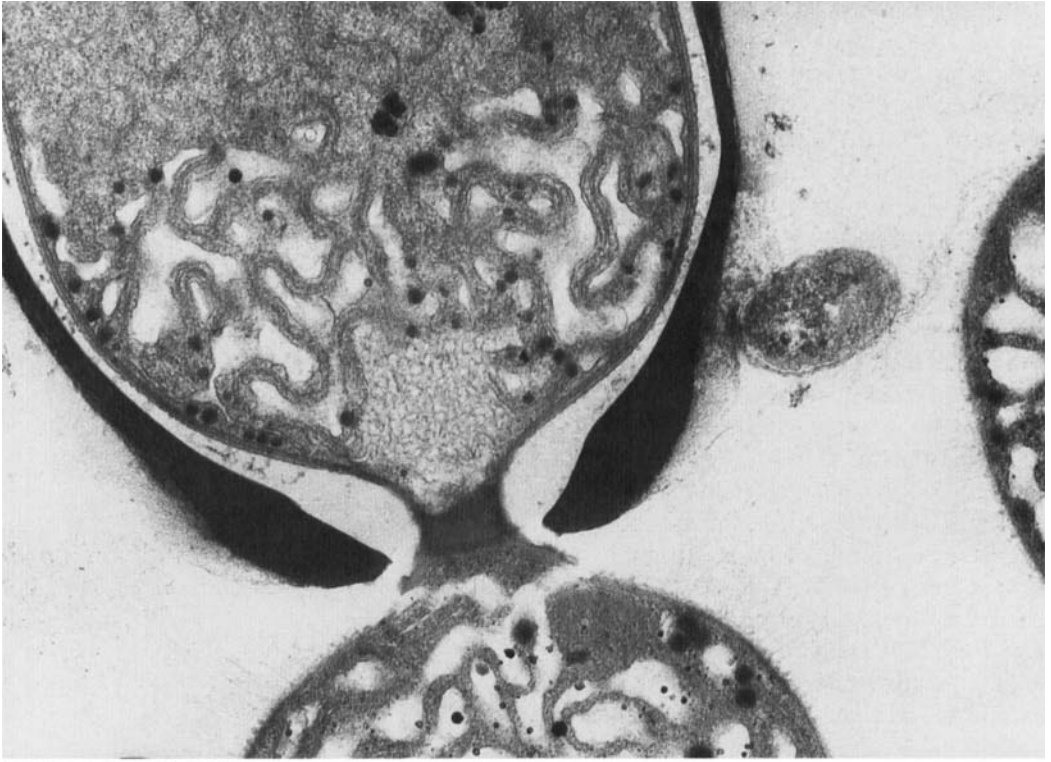

FIGURE 2. *Nitrogen fixation (top) and growth (bottom) of bacterized and axenic cultures of* Anabaena oscillarioides *(Paerl 1990). The heterotrophic bacterium* Pseudomonas aeruginosa *is associated with the heterocysts of this species of cyanobacterium (Gallucci and Paerl 1983).*

Many heterocystous and non-heterocystous genera (*Anabaena, Aphanizomenon, Microcystis, Oscillatoria*) can regulate buoyancy, a feature aimed at assuring optimal (for growth) vertical orientation in the water column. In highly turbulent waters, the ability to maintain optimal vertical positioning can be overcome by turbulent mixing, which negatively affects cyanobacterial growth and forces buoyancy-regulating taxa to compete directly with eukaryotic phytoplankton (diatoms, chlorophytes, chrysophytes, etc.) which thrive under conditions of variable light and nutrient regimes. Physical forcing of this sort is considered to play an impor-

tant role in shaping phytoplankton resource competition, community composition, and succession on short-term (diel) and longer-term (seasonal or interannual) bases (Reynolds and Walsby 1975; Paerl 1988a).

In summary, water column turbulence at varying scales, magnitudes, and durations is a strong, and at times overriding, determinant of phytoplankton growth and community composition. With regard to heterocystous cyanobacterial bloom genera, there is evidence that both large-scale mixing and small-scale shear yield negative direct (filament breakage, aggregate disruption) and indirect (vertical and horizontal displacement) impacts on N_2 fixation, photosynthetic performance, growth and reproduction of these genera in waters exposed to continual and high turbulence.

Nutrient Supply

The relationship between high nutrient loading rates and dominance of the plankton community by cyanobacteria is well known. In general, availability of nitrogen and phosphorus is most often implicated as the primary factor constraining phytoplankton growth and biomass accumulation, and in influencing phytoplankton community structure in freshwater. Low N : P ratios have been implicated as a major factor favoring cyanobacterial dominance in a variety of lakes. Smith (1983) concluded that cyanobacteria were either rare or absent when the ratio (by weight) of water column total N to total P exceeded 29. That conclusion has fostered interest in manipulating the N : P ratio as a means of controlling cyanobacterial dominance and bloom formation. This hypothesis is consistent with the fact that certain cyanobacterial bloom genera are capable of fixing atmospheric N_2, which would certainly afford a competitive advantage when N : P ratios are low due to nitrogen deficiency.

TABLE 3. *Effect of stirring speed on nitrogenase activity in* Anabaena oscillarioides. *Nitrogenase activity is expressed as mean chlorophyll a-specific acetylene reduction rate ± SEM for three replicate samples. Cultures were grown under N-limited conditions with constant illumination (200 μEinsteins/m^2 per sec) at 25 C. Stirring speeds that resulted in filament breakage are indicated by an asterisk.*

Stirring speed (rpm)	Nitrogenase activity (μmoles C_2H_4/mg Chl a per hour)
50	7.5 ± 0.5
100	7.2 ± 0.7
250	5.8 ± 1.2
400*	3.2 ± 0.5
550*	2.4 ± 0.7
750*	1.2 ± 0.4

The practical implications of N : P ratios in fish ponds as a determinant of cyanobacterial dominance are not clear because many aquaculture ponds have high nitrogen loading rates which should not favor N_2-fixing cyanobacteria, yet ponds often have an abundant cyanobacterial flora. For example, the average total N : total P ratio in Mississippi channel catfish ponds during the summer months ranges between 4 and 16 (Tucker and van der Ploeg 1993). Such N : P ratios are usually well within the range of N : P ratios postulated by Forsberg et al. (1978) to be indicative of nitrogen-limiting conditions. By extension, the low total N : P ratios in catfish ponds should favor the presence of cyanobacteria and, in fact, the plankton flora of most channel catfish ponds is dominated by cyanobacteria. The low N : P ratios of channel catfish pond waters are not, however, due to low total nitrogen levels (they are quite high: 4–8 mg N/L), but rather to extraordinarily high concentrations of total phosphorus (0.5–1 mg P/L). In this instance, cyanobacterial dominance is not due to conditions that favor organisms that compete well in nitrogen-limited environments, but rather to conditions that favor the presence of phototrophs with the

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FIGURE 3. *Transmission (top) and scanning (bottom) electron micrographs of the junction between heterocyst and vegetative cell of the N_2-fixing, bloom-forming cyanobacterium* Anabaena oscillarioides.

ability to regulate vertical position in the water column. Phytoplankton in catfish ponds grow luxuriantly in response to generally abundant nutrients (both phosphorus and nitrogen) and the resultant spatial separation of resources (light and nutrients) tends to favor phototrophs with the ability to regulate vertical position in the water column.

Water Temperature

Water temperature regimes also play a critical role in cyanobacterial bloom formation. Generally, as water temperatures increase, so does the degree of cyanobacterial dominance. This is particularly true for nutrient-enriched water bodies. In laboratory chemostat culture studies, Tilman and Kiesling (1984) were able to demonstrate that temperature was the most important factor controlling phytoplankton taxonomic groups. In particular, they showed temperature and N : P supply ratio to be the most important variables controlling cyanobacterial dominance. The fact that highest nutrient loading rates in most aquaculture ponds also coincide with the period of warmest water temperatures simply provides another growth advantage to bloom-forming cyanobacteria over eukaryotic phytoplankton.

Dissolved Organic Matter

Early studies (Fogg 1969) cite dissolved organic matter as a factor potentially controlling cyanobacterial blooms. However, close scrutiny of the relationship between dissolved organic matter and such blooms yields no clear trends (Paerl 1988b). In fact, it is pointed out by Fogg (1969) and others that elevated levels of dissolved organic matter is more than likely a result rather than cause of cyanobacterial blooms. Furthermore, the waters in question are frequently enriched with dissolved organic matter derived from terrestrial sources or produced autochtonously (the Albemarle-Pamlico Sound and adjacent coastal waters of North Carolina, USA, for example).

Salinity

Cyanobacteria are found in environments ranging from dilute freshwaters (>0.001 ppt salinity) to brines with salinities exceeding 100 ppt (Walsby 1982). It appears, however, that certain species adapted to a specific environment may be remarkably intolerant of changes in salinity. For example, in the nutrient-enriched Neuse River estuary (North Carolina, USA), relatively minor changes in salinity have profound effects on phytoplankton community structure (Paerl et al. 1984). At less than 2 ppt salinity, massive blooms of *Microcystis aeruginosa, Anabaena* spp., or *Aphanizomenon flos-aquae* are common. At salinities exceeding 5 ppt, blooms of these nuisance genera are rare. Salinity (or, more appropriately, the ionic composition of water) may also affect rates of N_2 fixation, and is discussed later.

The effects of salinity on the presence of certain species of cyanobacteria may have considerable economic significance for the culture of animals in brackish aquaculture ponds. For example, the salinity of the water in penaeid shrimp culture ponds in Ecuador ranges from less than 5 to over 30 ppt depending upon rainfall and river discharge into estuaries where most shrimp farms are located. Musty off-flavors in cultured shrimp (found to be caused by geosmin, a metabolite of certain cyanobacteria) are absent when the salinity of pond waters is greater than about 10 ppt. When salinity decreases to very low levels as a result of high river discharge, dense blooms of blue-green algae develop with the coincident occurrence of geosmin-related off-flavors in the shrimp (Lovell and Broce 1985).

Ecophysiological Factors Affecting Bloom Formation and Proliferation

Buoyancy Regulation

While many factors have been implicated as critical in explaining cyanobacterial dominance in nutrient-enriched ecosystems, it appears that buoyancy regulation,

a physiological mechanism unique to cyanobacterial bloom genera, is of paramount importance (Reynolds and Walsby 1975; Walsby et al. 1983). The ability to regulate vertical position in the water column is an advantageous attribute for a phototroph living in an environment with strong vertical gradients of light, temperature, and nutrients.

Irradiance (Walsby 1972; Konopka et al. 1978), carbon dioxide availability (Paerl and Ustach 1982), and inorganic nitrogen concentrations (van Rijn and Shilo 1983) have been implicated as major environmental factors controlling cyanobacterial buoyancy. Irradiance usually plays the dominant role and appears to regulate buoyancy through its effect on rates of photosynthesis. This is accomplished in two ways. First, high rates of photosynthesis occurring under conditions of high irradiance increase intracellular turgor pressure, leading to the collapse of gas vacuoles which provide buoyancy (Walsby 1972). Conversely, low levels of irradiance lead to suboptimal photosynthetic rates, which in turn reduce cell turgor pressure and promote gas vacuole formation and buoyancy. In this manner, cells are capable of regulating their position in the water column in relation to photosynthetic needs. Second, active photosynthesis can also lead to the production of relatively dense polysaccharides, which lead to a loss of buoyancy (Konopka et al. 1978). Both mechanisms interact to control buoyancy in natural waters where irradiance, transparency, inorganic carbon (dissolved carbon dioxide plus bicarbonate), and nitrogen supplies can vary greatly in time and space.

There is some evidence that surface accumulation of cyanobacterial blooms facilitates interception of atmospheric carbon dioxide (Paerl and Ustach 1982) and inorganic nitrogen from dry or wet atmospheric deposition (Lewis 1983), both of which could provide a competitive advantage over purely planktonic forms. Environmentally controlled buoyancy can additionally provide biological advantages by allowing cyanobacteria to exploit favorable nutrient gradients within the water column, including nutrients located at the bottom of the euphotic zone (Reynolds and Walsby 1975; van Rijn and Shilo 1983).

The ability to regulate cell buoyancy is clearly advantageous in an aquaculture pond environment and is perhaps the primary reason for the frequent dominance of the aquaculture pond phytoplankton communities by cyanobacteria. Aquaculture ponds receive large additions of plant nutrients either intentionally from manures or fertilizers or unintentionally as a result of fish feeding practices. The high nutrient loading rates stimulate the development of large phytoplankton standing crops which, in turn, causes rapid attenuation of photosynthetically active radiation with depth. The metabolic activities of the phytoplankton community also result in reduced availability of carbon dioxide, inorganic nitrogen, and other nutrients in near-surface waters where favorable conditions for photosynthesis (adequate light availability) induce high rates of nutrient uptake. Meanwhile, bottom waters tend to be nutrient enriched by the continuous release of phosphate and ammonia produced during the decomposition of detritus at the sediment-water interface. During periods of calm weather, the spatial separation of resources becomes pronounced because the water column remains poorly mixed. Under such conditions, the ability to migrate between well-lit, carbon dioxide-rich surface waters and nutrient-rich bottom waters provides a distinct advantage over eukaryotic taxa lacking an efficient means of vertical migration (van Rijn et al. 1986).

Nitrogen Fixation

A unique (to photosynthetic prokaryotes) and particularly advantageous ecophysiological trait is the ability of certain cyanobacterial taxa to fix atmospheric N_2 (diazotrophy), thereby circumventing nitrogen limitation. Diazotrophy has allowed these

taxa to periodically invade and dominate waters sufficient in phosphorus but deficient in nitrogen supply (Fogg 1974; Gibson and Smith 1982; Healy 1982). In numerous freshwater ecosystems, tropical reefs, salt marshes, and benthic microalgal mats, cyanobacterial N_2 fixation can constitute a highly significant fraction (10 to nearly 100%) of "new" nitrogen input, sustaining primary and secondary production (Horne and Goldman 1972; Horne 1977; Lean et al. 1978; Howarth et al. 1988).

The ability to fix N_2, however, is not without environmental constraints. Molecular oxygen (O_2) is a potent inhibitor of nitrogenase, the enzyme mediating this process (Bothe 1982). When nitrogen limitation exists in aquatic ecosystems, it generally prevails in near-surface, oxic waters. Ironically, as oxygenic phototrophs, cyanobacteria themselves are in large part (during blooms) responsible for creating and maintaining high dissolved oxygen concentrations in these waters. To solve this paradoxical and perplexing ecophysiological problem, certain genera, including *Anabaena, Aphanizomenon, Gloeotrichia,* and *Nostoc,* form biochemically and morphologically-distinct, O_2-devoid cells, called heterocysts (Fig. 1), that harbor the oxygen-sensitive nitrogenase enzyme complex (Wolk 1982). This adaptive feature has opened up diverse phosphorus-sufficient aquatic ecosystems to exploitation by heterocystous taxa. In particular, many eutrophic lakes and ponds are sites of extensive N_2-fixing heterocystous cyanobacterial blooms that may significantly impact the nitrogen budget of those systems.

Some cyanobacterial species not endowed with heterocysts, but possessing N_2-fixing potential have evolved additional structural, physiological, and ecological strategies that facilitate limited exploitation of oxygenated, nutrient-sufficient waters. These include species of filamentous and coccoid nonheterocystous genera such as *Oscillatoria, Lyngbya, Trichodesmium,* and *Synechococcus.* Characteristically, members of these genera exist in colonies, including aggregated bundles, laminar mats, and biofilms. In certain freshwater and marine habitats, including submersed sediments, intertidal sands and mudflats, reefs, and biofilms, where localized dissolved oxygen depletion occurs, these genera can be dominant diazotrophs.

Biological N_2 fixation provides certain cyanobacteria with a direct source of nitrogen unavailable to other prokaryotes and all eukaryotes. Hence, during periods of severe nitrogen limitation, diazotrophic cyanobacteria should enjoy a competitive advantage. During periods of nitrogen sufficiency, the ability of diazotrophs to compete and proliferate will depend on their growth rates relative to other microorganisms competing for common resources (other macro and micronutrients) and to removal rates (e.g., grazing, sinking). Under conditions of high ambient levels of combined inorganic nitrogen, expression of nitrogenase may be repressed and the success of diazotrophs will be dependent upon their ability to efficiently utilize sources of combined inorganic nitrogen.

Nitrogenase synthesis and, in several photosynthetic diazotrophs, nitrogenase activity, are regulated by intracellular nitrogen concentrations. For gene expression (most thoroughly studied in *Klebsiella pneumoniae*), there is a complex interaction between several operons (nif, ntr and pln) with several sites of sensitivity to intracellular combined nitrogen which combine to provide a mechanism of induction during nitrogen deficiency and repression during nitrogen sufficiency (Gallon 1992). Howarth et al. (1988) cite studies finding 0.002 to 0.02 mg/L nitrate-nitrogen and 0.02 to 0.17 mg/L ammonium-nitrogen as repressing heterocyst formation in cyanobacteria. Similarly, N_2 fixation in sediments can be inhibited by as little as 0.7 mg/L (but generally higher) ammonium-nitrogen.

Despite their spectacular success in many nitrogen-limited freshwater ecosystems, diverse heterocystous cyanobacterial genera

are frequently absent as significant contributors of fixed nitrogen or carbon in large nitrogen-limited lakes, estuaries, and coastal waters that otherwise appear favorable for cyanobacterial dominance (Smith 1983; Niemi 1979). Ironically, such phosphorus-sufficient, nitrogen-limited waters cover vast stretches of the globe, including much of the oceans and estuaries. On the face of it, it would appear that a potential niche for these diazotrophs remains largely unoccupied in such waters. Interestingly, these aquatic ecosystems are not a priori incapable of supporting heterocystous, N_2-fixing cyanobacteria. For example, two often-cited cases of oligotrophic, nitrogen-limited large lakes, Lake Tahoe on the California-Nevada (USA) border and Crater Lake in Oregon (USA), contain benthic/periphytic heterocystous N_2-fixing genera, including Nostoc, Calothrix, and Scytonema (Reuter et al. 1985). Also, chronically nitrogen-deficient estuaries and coastal lagoonal environments worldwide (including the Albemarle-Pamlico Sound, adjacent estuaries, and barrier island lagoons of North Carolina, USA) support benthic heterocystous taxa showing relatively high N_2-fixation rates.
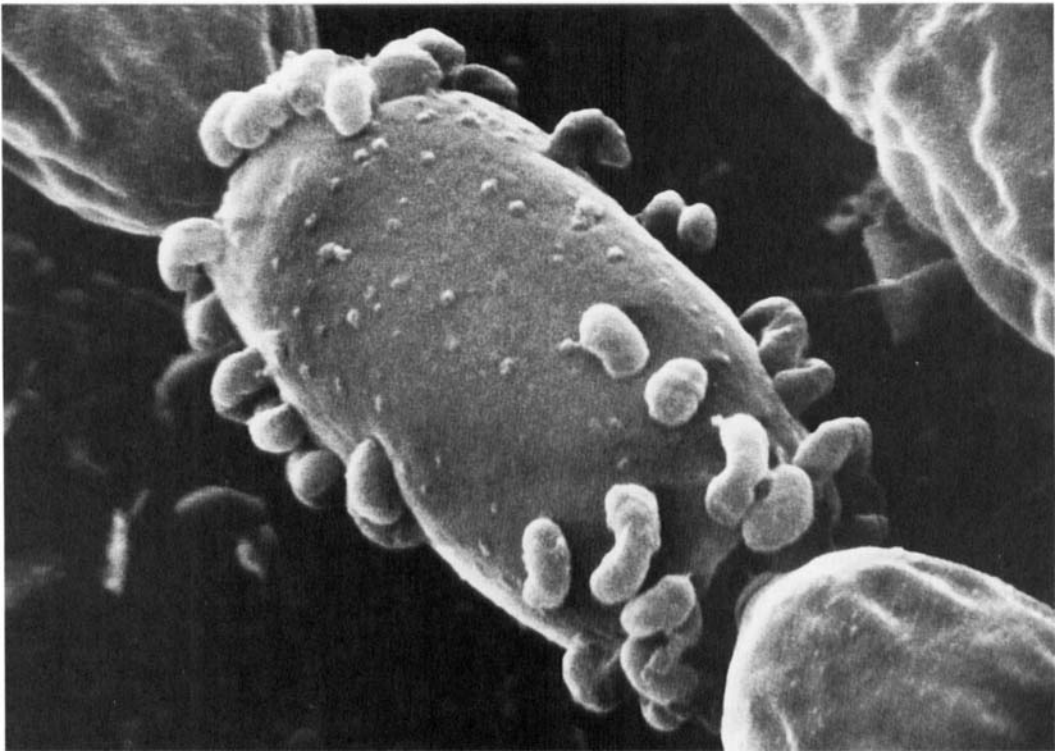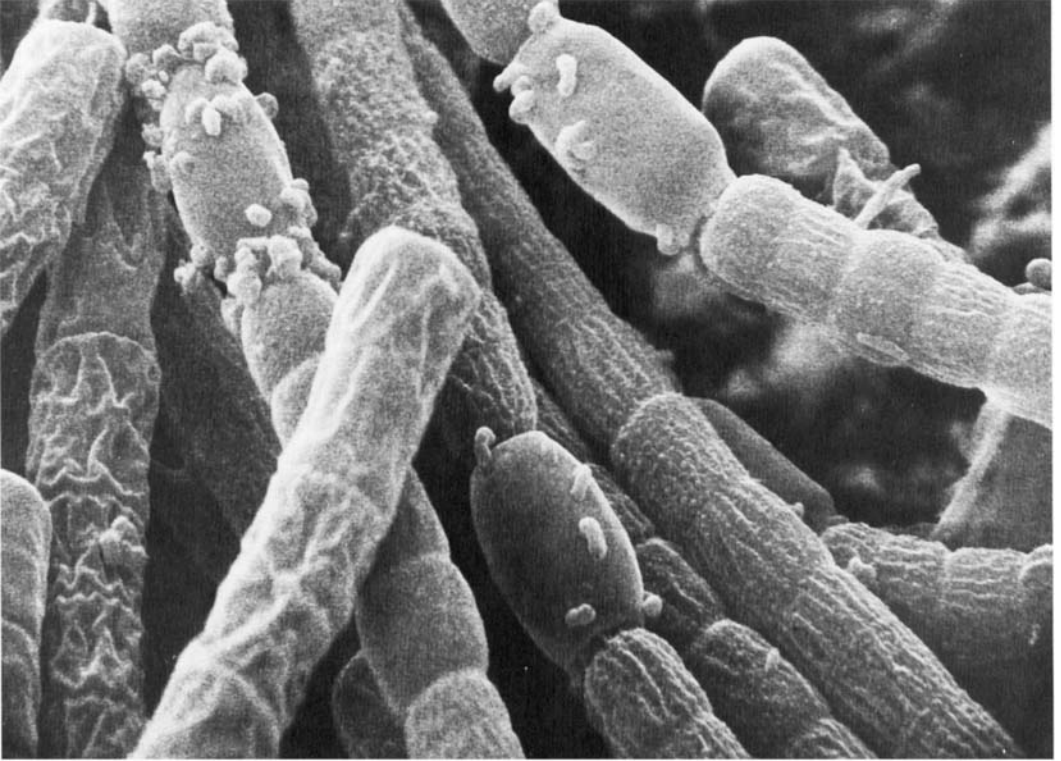
Salinity or, more specifically, ionic composition and strength of waters has been mentioned as a potential effector of N_2 fixation (Thomas et al. 1988) and hence a barrier to the establishment and proliferation of diazotrophic cyanobacteria and eubacteria. Fixation of N_2 seems particularly susceptible to osmotic stress, and organisms unable to adjust by production of compensatory factors exhibit inhibition of activity with increasing salt concentrations (Dubois and Kapustka 1981). In addition, Howarth and Cole (1985) and Howarth et al. (1988) proposed that relatively high concentrations of sulfate (SO_4^{2-}), which is a structural analogue of molybdate (MoO_4^{2-}), present in seawater and saline lakes might competitively (via the uptake process) inhibit molybdate uptake. Molybdenum is a component of the nitrogenase complex and is required for N_2 fixation. While competitive inhibition of molybdate uptake by sulfate at concentrations found in seawater is operative (Cole et al. 1993), the N_2-fixing potentials of marine diazotrophs appear unaffected by this competition (Paulsen et al. 1991). The small cellular molybdenum requirements for N_2 fixation have been shown to be met by reduced but sufficient uptake and storage (Ter Steeg et al. 1986; Paulsen et al. 1991).

Salinity as such does not appear to be a barrier to the establishment and proliferation of N_2-fixing cyanobacteria in estuarine and oceanic waters because many chronically nitrogen-deficient estuaries and coastal lagoonal environments worldwide support benthic heterocystous taxa showing relatively high N_2-fixation rates. For example, oceanic coral reef, shelf, and coastal mangrove habitats are often richly endowed with diverse heterocystous genera Scytonema, Nostoc, Anabaena, Cylindrospermum, and Calothrix (Frémy 1933; Potts 1980; Whitton and Potts 1982). Therefore, it is difficult to invoke salinity or "unusual" ionic ratios as barriers per se to the development and proliferation of diazotrophs. It is striking, however, that the examples cited above are all benthic or otherwise attached. There are a few examples of brackish and full-salinity systems where planktonic heterocystous genera thrive. Most obvious are the invasions of N_2-fixing Nodularia and Aphanizomenon blooms in the Baltic Sea (Grontved and Steeman Nielsen 1957; Niemi 1979), and blooms of Nodularia in the Peel-Harvey Estuary in Australia (Huber 1986).

Cyanobacterial-Microbial Consortial Interactions

With few exceptions, freshwater cyanobacterial bloom species are generally found associated with diverse microorganisms both in nature and in the laboratory. Associated microorganisms include a variety of heterotrophic eubacteria, fungi, phytoflagellates, and ciliated and amoeboid protozoans (Whitton 1973; Paerl 1978, 1983, 1985, 1988a). Cyanobacterial-microbial as-

sociations are commonly observed inside colonies, aggregates of filaments, and within the mucilaginous sheaths, capsules, and slimes located outside cyanobacterial cell walls. Collectively such regions have been referred to as the "phycosphere."

In nature, the diversity of phycosphere-associated microbial associations as well as specificities of microbial attachment sites are striking. Bacterial, flagellate or protozoan species may appear randomly attached to cyanobacterial filaments and colonies, or scattered throughout mucilagenous matrices bordering cells. In contrast, one can encounter highly specific associations, where a single microbial species may exclusively inhabit morphologically and physiologically differentiated cyanobacterial host cells such as akinetes and heterocysts (Fig. 4).

A review of the recent literature addressing cyanobacterial-microbial interactions in nature and in the laboratory yields numerous contradictory research findings and conclusions regarding their ecological significance (Whitton 1973; Paerl 1982). Much confusion stems from the fact that no common mechanisms or sets of ecophysiological interactions characterize cyanobacterial-microbial interactions *per se*. Among investigators who have examined bacterial interactions with the nuisance cyanobacterial genera *Anabaena, Aphanizomenon,* and *Microcystis*, no clear consensus has arisen as to unifying themes typifying either antagonistic or mutualistic properties of such interactions. The pioneering studies of Safferman and Morris (1964) and Bershova et al. (1968) were designed to detect antagonism among a wide range of bacteria commonly found associated with cyanobacteria. However, both studies indicated that relatively small proportions of associated bacteria (as well as viruses) exhibited antagonistic behavior. Likewise, examinations of natural and laboratory cyanobacterial-bac-

terial associations by Lange (1967), Kuentzel (1969), Straskrabova (1974), and others (see Caldwell 1977) have failed to reveal bacterial antagonism.

Cyanobactericidal activity by lytic bacteria has been documented (Shilo 1970; Reim et al. 1974). However, this form of antagonism requires rather high densities of lytic bacteria (Stewart and Daft 1976), and protection from such a fate can be provided by the thick mucilaginous coatings exhibited by many cyanobacterial nuisance taxa (Bershova et al. 1968). Nevertheless, bacterial lysis has been invoked to explain sudden declines or "crashes" of cyanobacterial blooms. Detailed, long-term studies have, however, shown that episodes of bacterial lysis of bloom-forming cyanobacterial populations are rare events (Paerl and Ustach 1982; Paerl and Keller 1978; Gallucci and Paerl 1983). Moreover, "crashes" of such blooms were often preceded not by bacterial lytic attack, but rather by sudden perceptible changes in ambient nutritive or climatic conditions which led to suboptimal cyanobacterial growth. Such environmental "stresses" preceded both autolysis and bacterial lytic events. Hence, rather than inducing cyanobacterial senescence, direct bacterial attack and lysis appeared to be a result of senescence brought on by deteriorating physical-chemical growth conditions (Paerl 1988a).

Phycosphere-associated bacteria have, in fact, been implicated as mutualistic cohorts during cyanobacterial bloom development and proliferation. Diverse freshwater and marine studies have noted relatively high densities of planktonic and phycosphere-associated bacteria during peak cyanobacterial bloom conditions (Paerl 1978, 1988a). In some cases, phycosphere-associated bacteria appeared both loosely and randomly associated with cyanobacterial filaments and colonies, whereas highly specific associa-

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FIGURE 4. *Scanning electron micrographs showing the specific associations between heterotrophic bacteria and heterocysts of the N_2-fixing, bloom-forming cyanobacterium* Aphanizomenon flos-aquae.

tions have also been noted (Paerl and Kellar 1978). In either case, associations remain intact during weeks and months of bloom development and proliferation. Axenic laboratory isolates of the bloom species *Anabaena oscillarioides* and *A. flos-aquae* have consistently revealed lower biomass-specific N_2 fixation and growth rates than bacteria-colonized populations (Fig. 2). Some cyanobacterial bloom species, including a *Microcystis aeruginosa* strain from the Neuse River (North Carolina, USA) and an *Aphanizomenon flos-aquae* strain from the Chowan River (North Carolina, USA), have not been successfully grown free of bacteria in laboratory cultures. Such findings are not unique and the freshwater literature abounds with reports on differential growth of axenic and bacterized culture conditions; with few exceptions, bacterized freshwater cyanobacterial genera have revealed higher growth rates and are easier to maintain in culture than axenic strains.

Phycosphere-associated bacteria are suspected of recycling essential (for photosynthetic growth) carbon dioxide and phosphate supplies during periods of dense bloom formation. For example, Lange (1967) demonstrated that the addition of readily metabolized carbohydrates (sugars) led to enhanced cyanobacterial growth, especially under inorganic carbon-limited conditions. He attributed such photosynthetic stimulation to rapid mineralization of the sugars followed by carbon dioxide release among phycosphere associated bacteria. Schiefer and Caldwell (1982) using carbon dioxide-limited continuous cultures of *Anabaena* sp. and the epiphytic heterotrophic bacterium *Zoogloea* sp., demonstrated that phycosphere-associated carbon dioxide recycling by *Zoogloea* sp. readily optimized the photosynthetic performance and growth of host *Anabaena* sp. Paerl and Kellar (1978) and Kellar and Paerl (1980) have additionally shown that bacteria commonly associated with heterocysts of bloom-forming *Anabaena* and *Aphanizomenon* enhance N_2-fixation potentials of these genera,

when compared to axenic conditions (Fig. 2). Subsequent examination of this specific association (Lupton and Marshall 1981) confirmed the positive impact of associated bacteria on *Anabaena* growth. Bacterial colonization of heterocysts led to high rates of oxygen consumption in microenvironment surrounding heterocysts. Since N_2-fixation potentials among various *Anabaena* and *Aphanizomenon* species are to some extent regulated by ambient dissolved oxygen concentrations (despite the presence of heterocysts), it was concluded that respiratory uptake of oxygen by heterocyst-associated bacteria helped optimize N_2-fixation among these cyanobacterial genera, especially during dissolved oxygen-supersaturated bloom conditions (Paerl 1978).

Situations do arise where cyanobacteria and bacteria may directly compete for resources, including growth-limiting nutrients. In particular, limited availability of dissolved inorganic (and organic) phosphorus can lead to direct competition between planktonic bacteria and cyanobacteria (as well as other phytoplankton), both under controlled laboratory conditions (Rhee et al. 1981) and in nature (Paerl and Lean 1976). Furthermore, it is commonly accepted that decreased phosphate availability can lead to declines in cyanobacterial bloom potentials, particularly for N_2-fixing genera. Hence, the ability of bacteria to outcompete cyanobacteria for this critical nutrient might *a priori* be interpreted as a potential agent modifying magnitudes and duration of blooms. Effective microbial competition for available phosphate (or other inorganic nutrients, including iron and other trace metals), is, however, reliant on a variety of interacting physicochemical and biotic factors, including availability of photosynthetically active radiation, water temperature, pH, ionic properties, concentrations and supply rates of growth limiting nutrients relative to microbial uptake affinities, intracellular storage capabilities, nutrient exchange-recycling characteristics of cyanobacterial-microbial associations, as

well as nutrient regeneration of micro- and macro-zooplankton and fish communities.

Even if bacterial antagonism, in the form of effective nutrient uptake competition, were to prove a barrier to cyanobacterial bloom development, many bloom species can potentially avoid long-term competition by rapidly migrating (vertically) in the water column. This facilitates the ability to periodically migrate upwards into light-rich surface waters or downwards into nutrient-rich metalimnetic and hypolimnetic waters at appreciable speeds.

Periodic vertical migration into phosphorus-rich hypolimnia in eutrophic lakes allows for ready access to this nutrient. Planktonic bacteria, which may effectively compete with cyanobacteria in light-rich epilimnia, are not capable of extensive short-term vertical migrations into nutrient-rich deeper waters. As a result, cyanobacteria need not directly compete with planktonic bacteria for epilimnetic phosphate supplies, since periodic migration into phosphate-rich hypolimnia followed by storage of assimilated phosphorus as polyphosphates assures long-term access to that nutrient. In that manner, cyanobacteria may coexist with bacteria exhibiting higher affinities for this growth-limiting nutrient.

Cyanobacteria (as well as eukaryotic phytoplankton) are known to actively and passively excrete a variety of organic compounds (Fogg and Westlake 1955; Walsby 1974). Although the functional significance of extracellular organic matter production remains unclear, and is a subject of continuing dispute among phycologists, limnologists, and oceanographers (Sharp 1977), a variety of excretion products have been shown to both attract (chemotactically) and readily support the growth of phycosphere-associated bacteria (Paerl and Kellar 1978; Paerl and Gallucci 1985). Products identified include a variety of organic and amino acids, peptides, carbohydrates and small amounts of lipopolysaccharides.

From a physiological perspective, the excretion of such compounds might represent a "wasteful" process in that recently fixed carbon and nitrogen are disposed of shortly after synthesis. However, from both evolutionary and ecological perspectives, extracellular production may, in the long run, benefit host cyanobacteria during active growth and bloom periods. Since blooms often occur in near-surface waters, radiant energy required for carbon and nitrogen fixation is seldom limiting. Potential carbon limitation is also minimized among surface-dwelling cyanobacteria, since they are capable of intercepting atmospheric carbon dioxide at the air-water interface. Assuming little, if any, radiant energy or carbon limitation, extracellular photosynthate production may be an "affordable" process (from a bioenergetic standpoint) among surface dwelling cyanobacteria. In this regard, extracellular production may actually be enhanced (as a shock response) under excessively high surface solar radiation and dissolved oxygen conditions (Fogg 1971). Since extracellular production can attract and support the growth of heterotrophic bacteria, which in turn leads to enhancement of host cyanobacterial growth, such production may represent a "trade-off" mechanism among cyanobacteria faced with potential growth limitations that can be alleviated through the formation of mutually beneficial microbial consortia. Clearly, extracellular production is of benefit to aquatic heterotrophic bacteria, whose growth rates are often limited by organic matter (including organic nitrogen) availability.

Mutual benefits may also exist among cyanobacterial-protozoan associations. Several functional roles of phycosphere protozoan grazers appear to be analogous to those previously described for heterotrophic bacteria. Localized removal of dissolved oxygen and nutrient recycling are two likely "positive feedback" factors benefitting host cyanobacteria. Protozoan members of these consortia have a readily available and virtually inexhaustible food source, barring toxic, and hence inedible, properties of host cyanobacteria (Collins 1978). Certain pro-
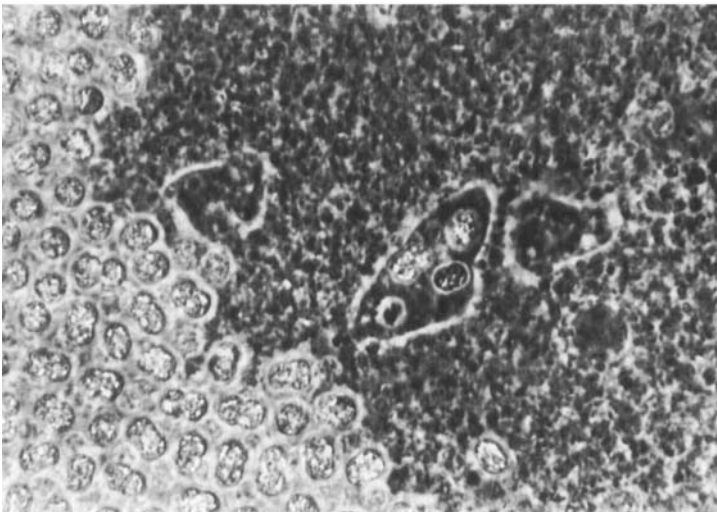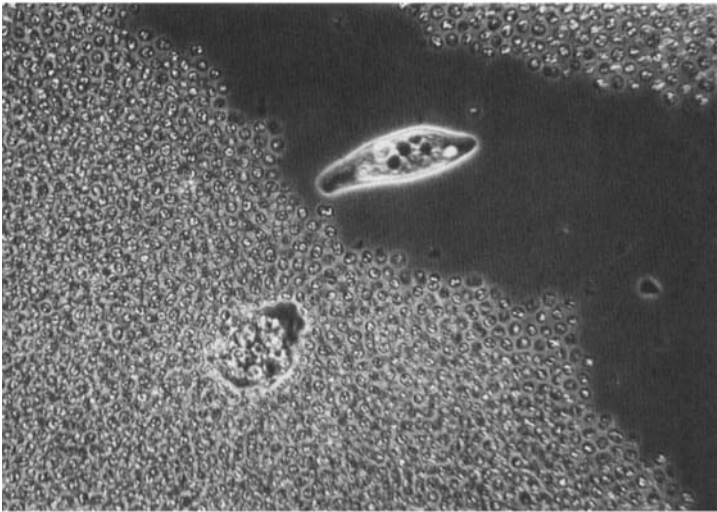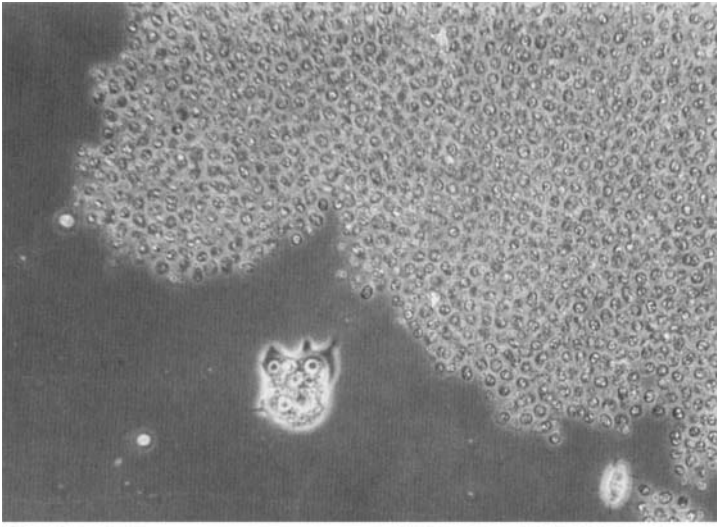
TABLE 4. *Effects of microbial associations on cell-specific carbon fixation rates in colonies of the non-N_2 fixing, bloom-forming cyanobacterium* Microcystis aeruginosa. *Results are expressed as mean ± SEM picograms of carbon fixed/cell per hour for three replicate samples in three independent experiments. Microautoradiographic determinations of carbon dioxide fixation rates were made on axenic (bacteria- and protozoa-free),* Amoeba *spp.-associated, and bacteria-associated (bacteria were largely confined to the mucilaginous sheath) populations of* M. aeruginosa. *Original cultures were obtained from the Neuse River (North Carolina, USA) and were cultured at 25 C on ASM + N medium with continuous illumination at 250 μEinsteins/m^2 per sec of photosynthetically active radiation.*

	pg C/cell per hour		
Date	Axenic	*Amoeba*-associated	Bacteria-associated
10 October 1985	0.11 ± 0.01	0.25 ± 0.02	0.23 ± 0.01
12 November 1985	0.14 ± 0.01	0.31 ± 0.01	0.22 ± 0.01
25 November 1985	0.12 ± 0.01	0.27 ± 0.02	0.31 ± 0.01

tozoans are known to consume some cyanobacterial bloom species directly or indirectly, by grazing phycosphere-associated bacteria which utilize host cyanobacteria as carbon, nitrogen, phosphorus and other nutrient sources.

Amoeboid protozoans often co-occur with bloom forming cyanobacteria (Fig. 5), being active grazers of host cyanobacteria even when higher-ranked crustacean zooplankton find such cyanobacteria either inedible, distasteful, or toxic (Fulton and Paerl 1988). Host cyanobacterial (*M. aeruginosa*) colonies being partially grazed by *Amoeba* sp. contain ungrazed cells having maximum (relative to cells in *M. aeruginosa* colonies free of grazers) cell-specific rates of photosynthesis (Table 4). Such associations may represent a microbial consortium exhibiting mutually beneficial maintenance of high growth rates of host cyanobacteria and *Amoeba* sp. grazers. Interestingly, it appears that *Amoeba* sp. grazing is not intense enough to eliminate *Microcystis aeruginosa* bloom proliferation. However, as is the case with cyanobacterial-bacterial associations, when cyanobacterial senescence (due to adverse or unfavorable physicochemical con-

ditions) is evident, *Amoeba* sp. resorts to extreme antagonism, rapidly consuming inactive and lysing cyanobacterial cells.

In conclusion, examinations and evaluations of recent studies reveal that cyanobacterial-bacterial and cyanobacterial-protozoan associations may yield more mutualistic (as opposed to antagonistic) characteristics than previously assumed. Such associations appear to function in a positive synergistic manner throughout various stages of bloom development and proliferation and may play a regulatory (and at times positive) role during the development, proliferation and maintenance of such blooms. These interactions co-occur with the well-known physicochemical factors promoting freshwater cyanobacterial nuisance blooms (nutrient enrichment, water column stability, high levels of irradiance and surface water heating, organic matter enrichment, etc.). Consideration of the functional roles cyanobacterial-microbial interactions play in regulating bloom potentials complements the more traditional antagonistic (bacterial attack, lysis and mineralization and protozoan grazing and assimilation of cyanobacteria) relationships thought to be embodied

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FIGURE 5. *Phase contrast micrographs of amoeboid protozoan colonization of the colonial, bloom-forming cyanobacterium* Microcystis aeruginosa. *These samples were collected from the Neuse River (North Carolina, USA) during a surface bloom exhibiting relatively high rates of carbon dioxide fixation per unit chlorophyll a. Top and middle: Initial colonization by ciliate and amoeboid protozoans. Bottom: Amoeboid protozoan "grazing" inside a* Microcystis *colony.*

in such associations. It is therefore cautioned that bloom eradication and mitigation approaches utilizing biological control measures based on bacterial lysis and protozoan/metazoan grazing (of cyanobacteria) require careful and critical evaluation prior to deployment on the natural community and ecosystem level. Such measures may in fact yield water quality and trophic results contrary to those desired, both in the short and long term.

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