

28. *Aphanizomenon* Blooms: Alternate Control and Cultivation by *Daphnia pulex*

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Abstract

Dense blooms of the blue-green alga, *Aphanizomenon flos-aquae*, are often associated with populations of the large filter-feeder, *Daphnia pulex*. These blooms are always characterized by colonies of "grass-blade" morphology. *Daphnia* may prevent the development of an *Aphanizomenon* bloom when the alga is unable to grow colonies large enough to avoid being grazed. However, once a grass-blade bloom is established, *Daphnia* may prolong the bloom's existence by removing potential algal competitors.

Recent proposals for improving water quality have included the suggestion that management for populations of large herbivores, such as *Daphnia*, will enhance water transparency by increasing the intensity of grazing on phytoplankton (Brooks 1969; Shapiro et al. 1975). However, while many algae may be depressed to very low levels by large herbivores, some phytoplankters directly benefit from such grazing activity (Porter 1977). One species in particular, *Aphanizomenon flos-aquae*, often reaches bloom proportions in the presence of dense *Daphnia pulex* populations. The morphology of this alga is unique; it grows from single cells (akinetes) into single filaments which may aggregate into large colonies (up to 3 by 30 mm) resembling small "grass-blades." All blooms of *Aphanizomenon* which I have seen co-occurring with *D. pulex* in Minnesota lakes and ponds have grass-blade morphology. Furthermore, grass-blade blooms rarely occur when *Daphnia* is not abundant.

The frequent association of *Aphanizomenon* with *D. pulex* is not restricted to Minnesota. Hrbáček (1964) studied the development of blue-green algal blooms in a variety of Czechoslovakian backwaters, fish ponds, and reservoirs. He found that while the intensity of *Aphanizomenon* blooms was related to the level of enrichment, their presence could not be explained in terms of nutrients alone. Rather, the blooms were generally associated with the presence of *Daphnia pulicaria* (a species nearly identical in morphology to *D. pulex*). The colonies had grass-blade morphology (J. Hrbáček pers. comm.). When *D. pulicaria* was removed by fish, *Aphanizomenon* was replaced by *Microcystis* (a colonial, gelatinous blue-green). Similar findings have been noted by Losos and Heteša (1973).

It appears that *Aphanizomenon* only maintains grass-blade morphology in the face of intense grazing pressure from large *Daphnia*. Many eutrophic lakes throughout North America have *Aphanizomenon*

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blooms in the absence of large *Daphnia*, but under these conditions the alga usually exists as single or small groups of filaments.

I here pose a hypothesis to explain the distribution and morphology of *A. flos-aquae* based on the abundance of large *Daphnia*. The data I present are drawn from studies conducted in Pleasant Pond (about 0.25 hectares, maximum depth = 2.5 m, and located about 10 km north of St. Paul, Minnesota) (Lynch and Shapiro in prep.). In 1975 the pond was without vertebrate predators and contained a large population of *D. pulex*. However, after the pond was divided by a polyethylene curtain in early 1976, a dense population of the zooplanktivorous fathead minnow (*Pim-*

ephales promelas) developed in the southern half and removed all of the *Daphnia*; the north half remained without fish (Lynch 1979). Grass-blade blooms occurred in the pond at different times each year. While these blooms attained high densities even when *Daphnia* was abundant, they only commenced when *Daphnia* was scarce and the bottom waters were well oxygenated (Fig. 1).

The growth of an *Aphanizomenon* bloom in the presence of dense *Daphnia* populations may simply result from an expansion of individual colonies. It is unlikely that new colonies can develop from small cells or filaments when exposed to such intense grazing. However, a tempor-

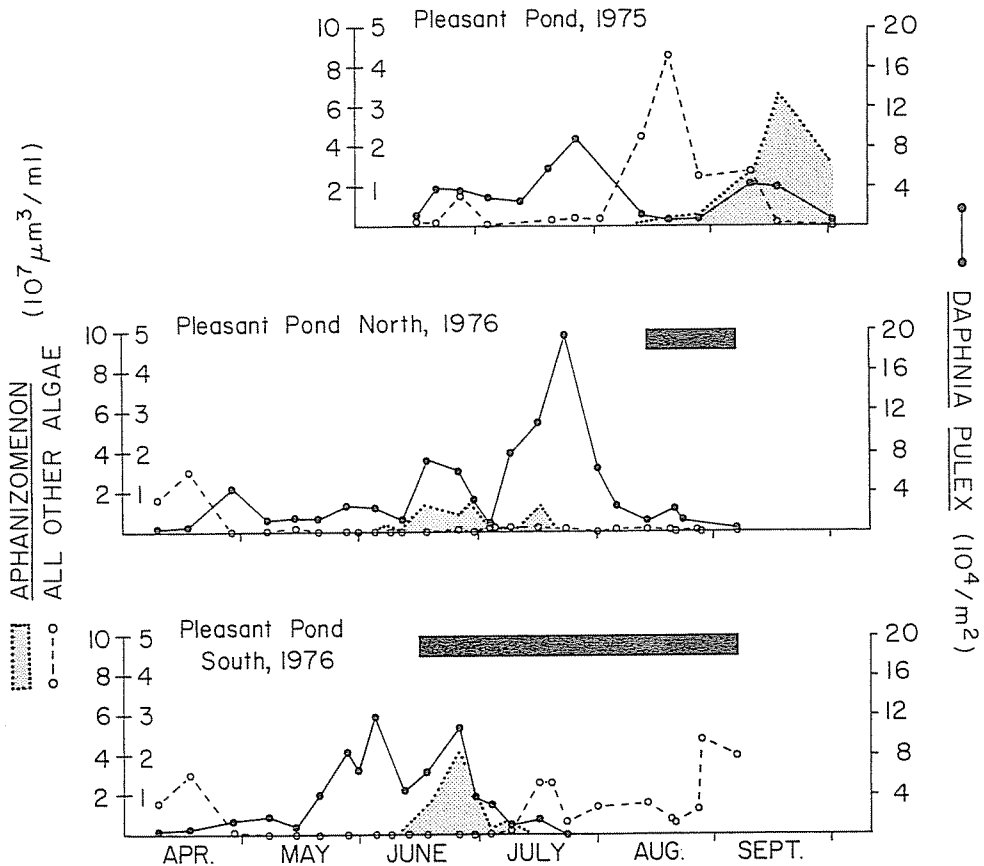


Fig. 1. Seasonal variation in abundance of *Aphanizomenon* "grass-blades" (stippled area), all other algae (dashed line), and *Daphnia pulex* (solid line). Solid bars indicate periods during which bottom waters were anoxic.

ary, spatial segregation from *Daphnia* could allow new *Aphanizomenon* colonies to reach a large enough size to avoid grazing upon exposure to *Daphnia*. The sediments may provide such a refuge. Since grass-blade blooms only commenced when the surface sediments were well oxygenated, it is possible that the blooms are initiated by an influx of new colonies which develop from akinetes deposited in the sediments.

Estimations of growth and loss rates for *Aphanizomenon* further implicate the importance of oxygenated bottom waters for the maintenance and development of a grass-blade bloom. Uptake of inorganic carbon was determined for samples incubated at a depth of 0.5 m for 24 h using track autoradiographic techniques (Knoechel and Kalff 1976). All incubations were done on cloudless days. Specific growth rates were calculated as

$$k = \ln \frac{\bar{x} \text{ cell C} + \bar{x} \text{ C fixed cell}^{-1} \text{ day}^{-1}}{\bar{x} \text{ cell C}}, \quad (1)$$

cell carbon being estimated from the cell carbon: cell volume regressions in Strathmann (1967). Specific loss rates (d) were calculated as the difference between the predicted growth rate (k) and the observed growth rate (r), where

$$r = \frac{\ln N_t - \ln N_0}{t}. \quad (2)$$

This analysis assumes that 24-h incubations give measurements close to net incorporation of carbon, i. e. growth; recent support for this contention can be found in Eppley and Sharp (1975) and Paerl and Mackenzie (1977). It also assumes that most cells are similar in size and composition.

Except for early May, estimates of *Aphanizomenon* loss rates were consistently negative in Pleasant Pond North (Table 1) indicating that the population was expanding at a higher rate than could be accounted for by its growth in the surface water. The bottom waters of Pleasant Pond North were well oxygenated throughout this period (Fig. 1). Loss rates

were also negative in Pleasant Pond South early in the summer; however, when the bottom became anoxic in mid-June, the loss rates increased dramatically, becoming strongly positive. The regular appearance of these negative death rates, especially in Pleasant Pond North, suggests that they were not artifacts of horizontal or vertical transport of colonies. Rather, the results imply that a significant growth of *Aphanizomenon* occurs in the bottom waters when these are well oxygenated.

Consistent with this observation is the fact that artificial isolation of the water column from the sediments prevents the development and/or maintenance of a grass-blade bloom. Over a period of 2 years several experiments were done in Pleasant Pond in 1-m-diameter polyethylene bags suspended from the pond's surface and closed at the bottom (Lynch 1979). Grass-blade blooms never developed in any of these enclosures. Even when grass-blades were present at the outset of an experiment, they never persisted within an enclosure for more than 2 weeks. It is possible that in the absence of a suitable refuge *Aphanizomenon* was not capable of developing into large enough colonies to avoid grazing by the dense *Daphnia* (and *Ceriodaphnia*) populations present in many of these enclosures.

Aphanizomenon did become abundant as single filaments in several enclosures stocked with planktivorous fish (*Lepomis*) in 1975 (Lynch 1979). These fish altered the herbivore community from one dominated by *Daphnia* and *Ceriodaphnia* to one consisting primarily of *Bosmina* and rotifers. Analysis of the phytoplankton and zooplankton data suggests that the success of *Aphanizomenon* in fish enclosures may have resulted from the absence of large herbivores. There was a clear negative relation between the density of filamentous blue-greens (*Aphanizomenon* and *Anabaena*) and the abundance of *Daphnia* and *Ceriodaphnia* (Fig. 2). Furthermore, there appeared to be a threshold density of these herbivores below which filamentous blue-greens could escape predation.

Table 1. Specific growth (k) and loss (d) rates for *Aphanizomenon* (day^{-1}) in Pleasant Pond, 1976. Estimates derived from autoradiographic determinations (Knoechel and Kalff 1976).

		13 May	26 May	11 Jun	26 Jun	8 Jul	22 Jul	19 Aug
Pleasant Pond North	k	0.11	0.10	0.14	0.10	0.10	0.17	0.01
	d	0.33	-0.31	-0.12	-0.06	-0.26	-0.21	-
Pleasant Pond South	k	0.14	0.13	0.21	0.04	0.15		
	d	2.02	-1.59	-0.51	0.19*	0.73*		

* Anoxic bottom waters.

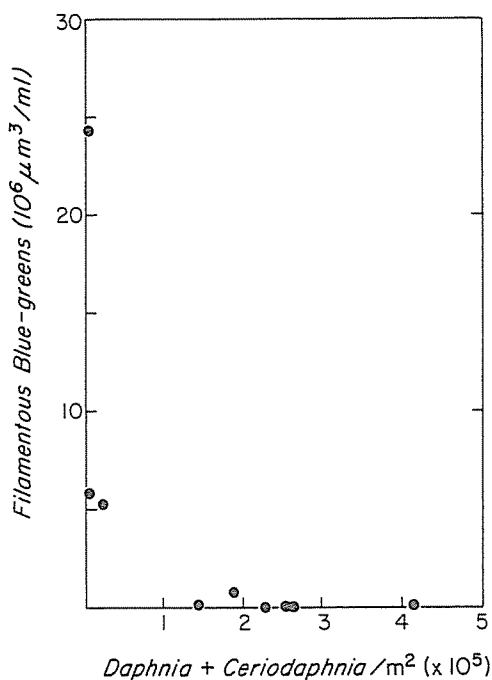


Fig. 2. Relation of abundance of filamentous blue-green algae to density of *Daphnia* + *Ceriodaphnia* in an enclosure experiment in Pleasant Pond (Lynch and Shapiro in prep.). Enclosures were stocked with different densities of a zooplanktivorous fish which selectively removed these herbivores. ●—Mean densities for last three sampling dates for different enclosures.

In terms of nutrient uptake, the formation of a large aggregation of filaments is probably detrimental—a tremendous amount of surface area is given up, particularly by filaments in the center of the colony. Since small filter-feeders are incapable of handling

particles as large as those taken by large *Daphnia* (Burns 1968), there would be less selective pressure for *Aphanizomenon* to maintain large grass-blades in the absence of large *Daphnia*. This may explain the tendency for *Aphanizomenon* to form smaller colonies in communities dominated by small herbivores. However, even when “forced” to maintain grass-blade morphology, *Aphanizomenon* has a behavioral attribute which may offset the “cost of coloniality.” The grass-blades are not constant with respect to size or shape. The individual filaments are constantly in motion, sliding past each other (Dodd 1954). Such behavior may serve to increase the exposed surface area of the individual filaments and may also increase the availability of nutrients by diminishing nutrient depletion in the immediate vicinity of the cells (Pasciak and Gavis 1974).

Finally, despite the fact that *Daphnia* may prevent the development of a grass-blade bloom under some circumstances, once a bloom is initiated it may actually provide a service to *Aphanizomenon* by removing potential algal competitors. At the peak of a bloom the water is always extremely transparent with the exception of the abundant grass-blades (Fig. 1). The grass-blades, being much larger than *Daphnia*, are not grazed.

From these observations, a hypothesis concerning the distribution of grass-blades can be made—

1. A grass-blade bloom will not develop when *Daphnia* is very abundant and the

bottom waters are anoxic; grass-blade development requires a temporary refuge from *Daphnia* grazing.

2. Once a grass-blade bloom is established, it will be maintained in the presence of dense *Daphnia* populations as long as there is a refuge for new *Aphanizomenon* colonies to develop in.

3. An established grass-blade bloom will not be maintained when *Daphnia* is reduced to low numbers.

This hypothesis is in accord with all aspects of the distribution of *Aphanizomenon* in Pleasant Pond except for the late June declines in 1976 when the bloom crashed in both sides of the pond after reaching high densities (Fig. 1). This crash did not appear to be a result of a shortage of phosphorus or nitrogen (Lynch and Shapiro in prep.). Since other algae did not increase during this decline, it is possible that some other micronutrient was limiting the growth of phytoplankton in the pond at that time. Soon after this crash, however, another grass-blade bloom developed in Pleasant Pond North. It commenced when *Daphnia* was rare and the bottom waters were well oxygenated, and continued to expand as *Daphnia* became very abundant. When *Daphnia* attained very high densities, the bloom crashed. A second bloom did not appear in Pleasant Pond South; instead, since the *Daphnia* was removed by fathead minnows, many other small species of algae increased dramatically. Since the curtain was removed in spring 1977, fathead minnows have continued to inhabit the pond at extremely high densities. Not only have *Daphnia* been completely eradicated, but grass-blades have not reappeared.

Further support for the hypothesis comes from a study I have done on a small enriched pond north of Minneapolis called Loch Loso. From late 1974 to mid-July 1975, the pond had a substantial population of *D. pulex* and the phytoplankton community was dominated by grass-blade *Aphanizomenon*. However, planktivorous fish, which were added to the pond in 1975, reproduced early that summer. Consequently all *Daphnia* was removed by mid-July; at that same

time the *Aphanizomenon* bloom crashed and was replaced by other species of phytoplankton. In 1976 extremely dense populations of planktivorous fish developed; no *Daphnia* was noted, and grass-blades did not reappear. A complete fish-kill occurred during winter 1977, and in the summer large numbers of *D. pulex* reappeared. Once again a very dense bloom of grass-blades developed in the pond.

While my hypothesis is predictive in nature, it leaves several questions about the *Daphnia*-*Aphanizomenon* interaction unanswered. The mechanism regulating the clonal morphology of *Aphanizomenon* is not known. Grass-blades may be genetically distinct from their non-grass-blade counterparts. Alternatively, there might be a chemical or physical cue elicited by *Daphnia* which triggers the formation of grass-blades. In the absence of *Daphnia*, grass-blade colonies dissociate within 48 hours (B. Monson, V. Smith, and J. Shapiro, pers. comm.) Also in this regard, J. Almenninger and D. Tilman recently discovered that when exposed to grazing by *Daphnia*, *Nostoc*—a filamentous blue-green alga—forms dense aggregates of filaments.

The size which grass-blades must attain to acquire invulnerability to grazers is unclear, as is the mechanism of formation of new colonies within the water column. Dodd (1954) suggested that new colonies may be produced by the mechanical fragmentation of existing grass-blades. If this is true, then it is unclear why grass-blade blooms cannot establish when the sediments are anoxic; a grass-blade bloom could conceivably maintain itself in the absence of a refuge, if newly produced fragments were large enough to avoid grazers. Rose (1934) suggested that such fragmentation is not the usual method of reproduction.

Since other blue-green algae (*Oscillatoria*, *Gloeotrichia*, *Microcystis*) are known to develop into colonies on the sediment surface before entering the water column (Gerloff and Skoog 1954; Roelofs and Oglesby 1970; Gahler and Sanville 1971), this life-history strategy may be a common adaptation of blue-green algae against

intense grazing by *Daphnia*. Thus, any efforts to "biologically control" the quantity of phytoplankton in lakes will have to consider the defensive mechanisms of these nuisance algae.

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