How Algae Fit into Lake Food Webs

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WYSIWYG (What you see is the result of a whole bunch of different processes going on at the same time!)

Welcome to the wild and wacky world of algal population dynamics! Many of you may remember the term, WYSIWYG, coined in the '80s as word processors became more sophisticated and companies started advertising that what you actually saw on the computer screen was what you were going to get when you printed. Programming that series of commands to make the text print in bold, indented, and capitalized is somewhat like the many processes that determine what algal species or communities will dominate under different environmental scenarios. We often observe what would appear to be similar lakes with totally different dominant communities and our inclination is to figure out why, so we can predict what might bloom in the next few weeks or months (Figure 1). Unless you understand the system functionally, you can't effectively manage it.

Not only is the entire aquatic food web based on the algal composition at any given time (okay, and maybe the bacteria, too), but the ultimate community affects how much carbon enters the lake system, the trophic status, how much stress the system is under from too much or too little algal biomass, the perceived water quality (which in turn affects property values), and ultimately how safe the water is for human and animal contact. The question becomes: What population dynamics are responsible for the taxa that are present? Amazingly, it's all about the relatively simple proportions of growing versus dying. Many algal taxa have evolved very ingenious survival strategies to tip the scales toward growing. There are some great references on general algal ecology available and just a few of my favorites are listed at the end of this article.

Growth Processes . . . Or What Grows Up . . .

So let's start with the growth part of the equation. It all initiates with primary productivity, the process of adding carbon via photosynthesis. In order to photosynthesize, you have to have pigment. The pigment common to all of the different algal groups is chlorophyll-*a* (as a reminder, algae are an evolutionary trash can, so the only thing they have in common is that they photosynthesize). Chlorophyll-*a* does not absorb green, instead it reflects green, so that's exactly what the most common algal color is, just like land plants (Figure 2). Epi-fluorescence is a special enhancement on a microscope that allows us to shine a specific wavelength of light on the algae (excitation), and

Figure 1. (Left): Green algae dominated bloom (Cladophora)*; (right): Blue-green algae dominated bloom* (Microcystis).

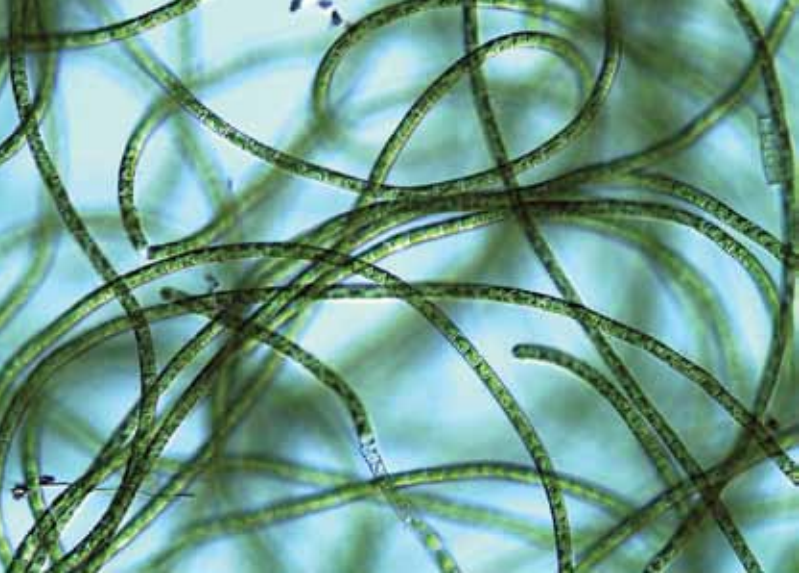



Figure 2. Examples of green algae. (Left): Ulothrix*; (right):* Pediastrum.

it shines back a different wavelength of light (emission). A taxon like *Chara* or stonewort has a lot of pigment, which is really obvious when you put it under blue light epi-fluorescence (Figure 3). No matter what the pigment (there are also accessory pigments called carotinoids, and phycobilins in addition to other chlorophylls), primary productivity potential will be modified by light and nutrient availability, temperature (sometimes many weeks prior to a bloom), algal physiology, and competition.

Some algae do well under low light, low temperature conditions such as *Plantothrix* (Figure 4), forming pink blooms under the cracked ice or at depth during the summer and fall. Others have developed specialized structures called heterocysts to fix nitrogen when it's in short supply in the water column such as *Cylindrospermopsis* (Figure 5). But beating the nutrient and temperature game is only part of the equation. Algae must maintain their position in the water column so that they can be at optimum light, be near the nutrients they need, and hopefully avoid grazers (more about that below).

There are some amazing adaptations for staying where they need to be. Some algae have solved the problem with motility, like *Pyramichlamys* and *Cryptomonas* (Figure 6). Others have developed buoyancy mechanisms by either adding oils to their colonial structure (*Botryococcocus*, Figure 7) or air vesicles to their cells or filaments like *Microcystis* (Figure 8). Yet others have spines or extensions that increase their surface area and slow their sinking (*Stephanodiscus* and *Micratinium*, Figure 9).

Staying near the light for photosynthesis may be a problem in winter, at depth or under intense competition, so many algae have evolved additional routes for nutrition. On the spectrum of nutrition, there are pure autotrophs where algae can only photosynthesize, and then the facultative heterotrophs, which can augment with or completely switch to heterotrophy (clever little cells!). Heterotrophy can take the form of osmotrophy (uptake of organic compounds in the water) and phagotrophy (ingestion of organic material or even bacteria and other algae). Diatoms exhibit classic osmotrophy (*Nitzschia*, Figure

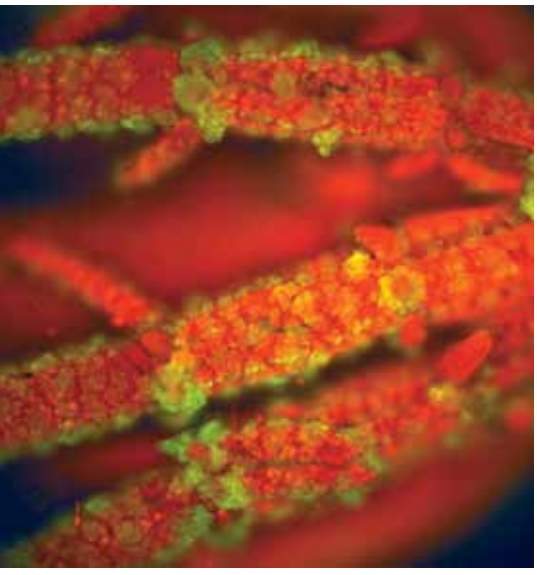
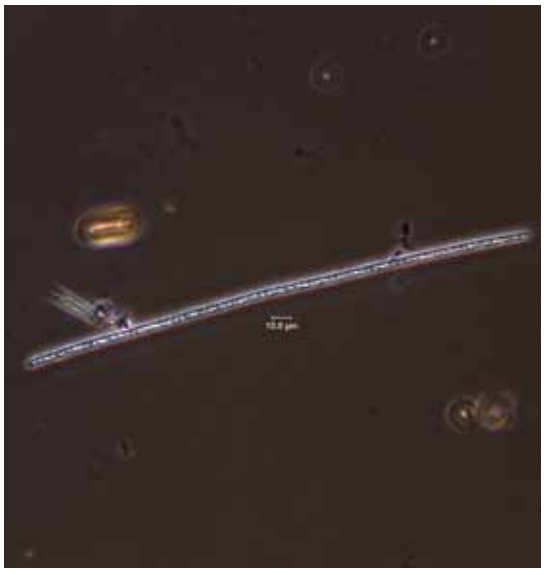
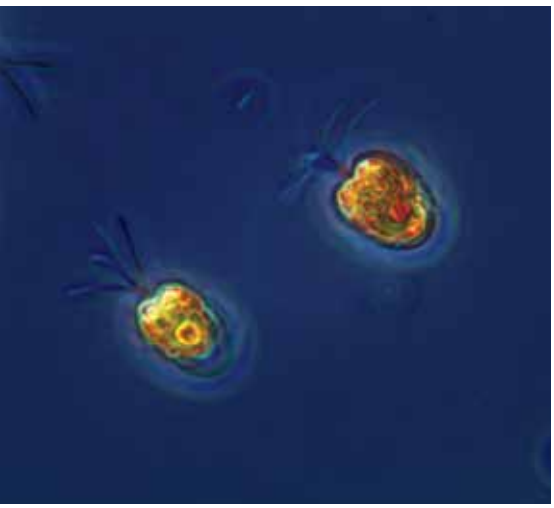




Figure 3. Chara *(stonewort). Chlorophyll-*a *fluoresces red while the calcium carbonate glows green on the filament surface.*

Figure 4. Planktothrix *from an under ice bloom.*

Figure 5. Cylindrospermopsi *with terminal heterocysts.*



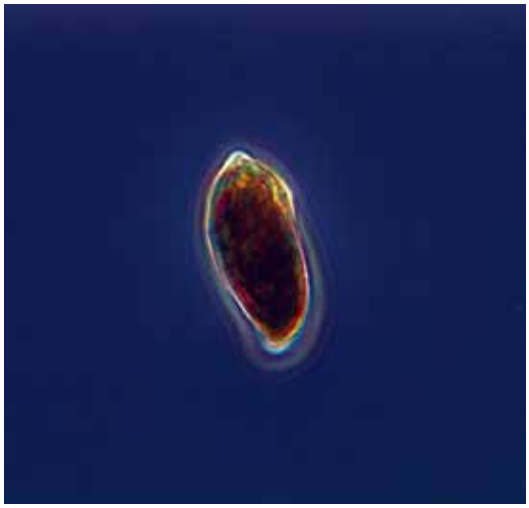


Figure 6. Examples of motile algae. (Left): Pyramychlamys*; (right):* Cryptomonas.

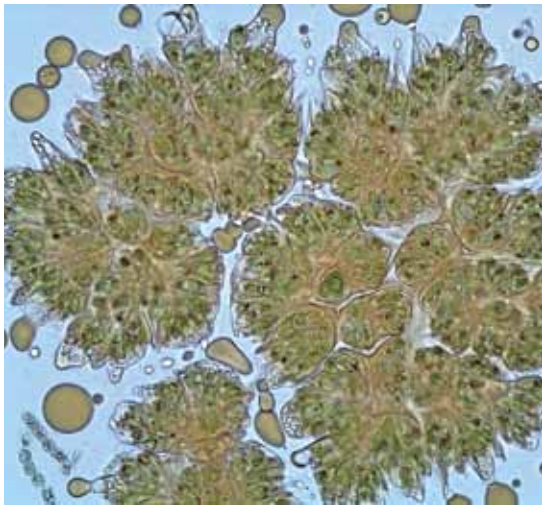


Figure 7. Botryococcus *with oil droplets.*

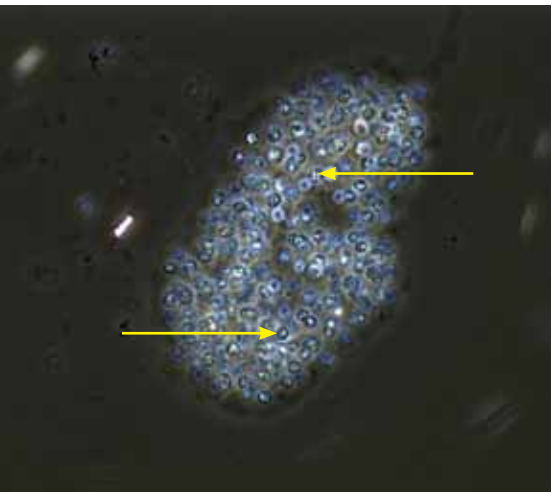
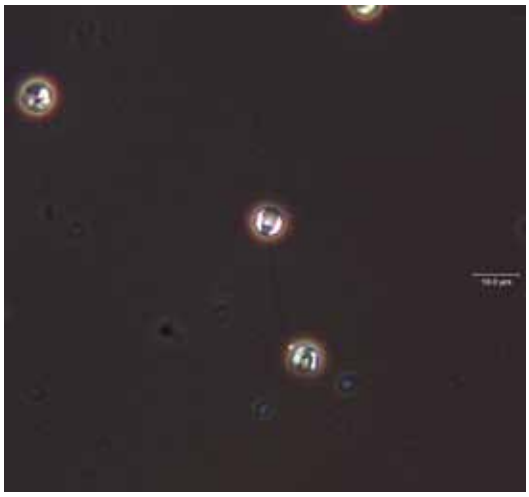


Figure 8. Microcystis *with clear air vesicles (arrows).*



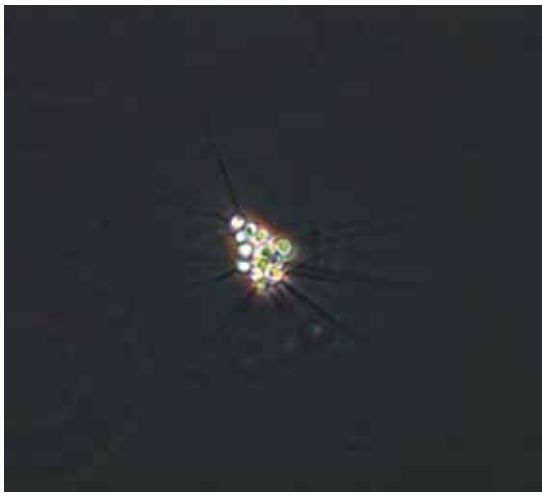


Figure 9. Examples of cell extensions. (Left): Stephanodiscus*; (right):* Micractinium.

10). There are also algae, like many euglenoids (*Euglena*, Figure 11), which has members who either uptake compounds or phagasotize. Then there are those that supplement nutrition only through phagotrophy (*Cryptomonas* and *Dinobryon*, Figure 12). In fact, *Dinobryon* cannot be cultured without bacteria present! That brings us to the coolest strategy of all: dinoflagellates. These ingenious algae, like *Ceratium* (Figure 13), exude something called a "pallium" that engulfs other algal colonies. The algal cell then swims around with the pallium attached, digesting the algae inside, and when they're done sucking up the nutrients, the pallium is jettisoned and the dinoflagellate goes in search of another algal colony to digest.

Continuing on our quest to add cells or biomass to the water column

Figure 10. Nitzschia*, capable of absorbing organic compounds.*

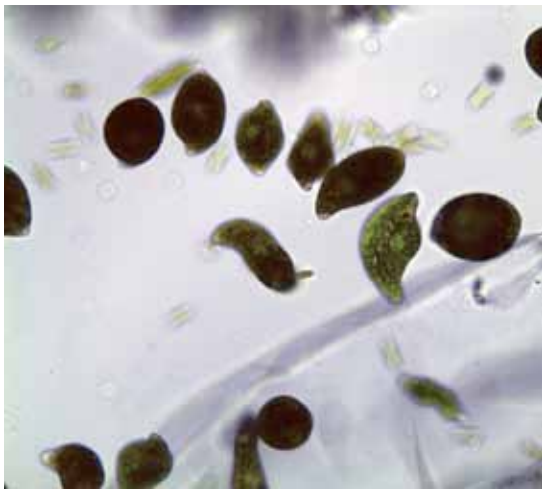
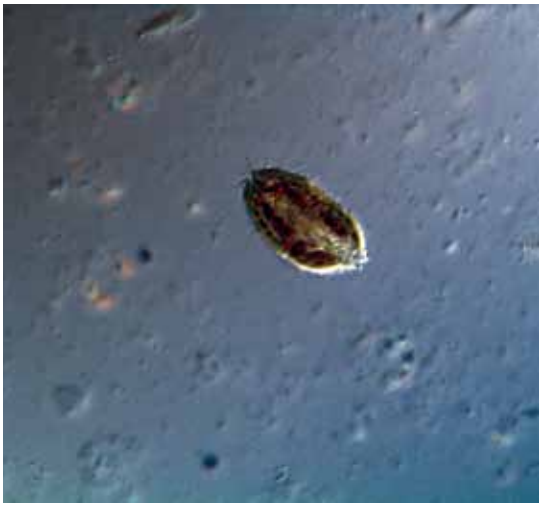


Figure 11. Facultative heterotroph – Euglena.



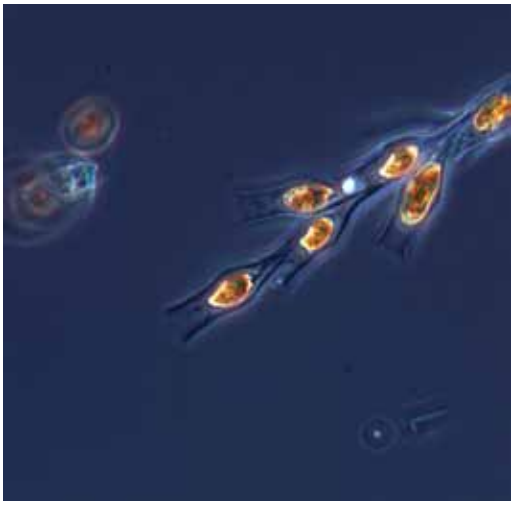


Figure 12. Facultative heterotrophs. (Left): Cryptomona*; (right):* Dinobryon.

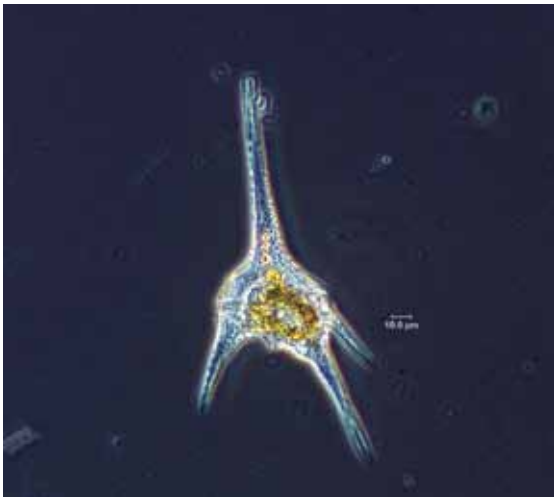


Figure 13. Ceratium.

is recruitment from the sediments. This one is tricky only because it's both a loss and growth process depending on where you hit the cycle. There are really only two options at the end of the growing season: Either a small inoculum remains up in the water column so that next season the growth cycle can start again, or cysts or resting stages are produced that settle down to the bottom and wait for either the right conditions or turbulence to bring them up again. Many different groups of algae take advantage of cyst or resting cell formation. Chrysophytes, like *Dinobryon*, and dinoflagellates like *Ceratium* (Figure 14), produce cysts that float down to the bottom and wait for the right environmental conditions (increasing light and nutrients, and increased turbulence at turnover) to bring them back up into the water column to begin the life cycle again. Others, like many members of the blue-green algae, produce either condensed filaments of a few cells called hormogonia (*Plectonema*, Figure 15) or resting cells called akinetes (*Aphanizomenon* and *Anabaena*, Figure 16). Akinetes in particular are extremely robust and can sit in the sediments for decades (or even centuries!), waiting for a turnover event to bring them back up into the light. Additionally, akinetes often sit on the sediment surface, waiting for the proper increases in light and temperature, and then start growing on the bottom without needing turbulence to re-suspend them. After a certain amount of growth, the colonies start to produce gas vesicles (remember buoyancy described above) and they rise on their own up through the

Figure 14. Cyst forming algae. (Left): Dinobryon*; (right):* Ceratium.

water column. Many of these blue-greens are good at luxury uptake of phosphorus as well, so that by the time they get to the surface, nutrient availability is not an issue and they can continue blooming with relatively low surface nutrient concentrations.

That brings us to the non-growing part of the conversation, but still a process that adds cells to the water column, and that is colonization. Although many of us have to deal with invasive species regularly, let's ignore the human-induced sources here like ballast water. That leaves the few natural ways that algal cells can be moved from system to system. Although floods and drift from upstream are key mechanisms, and actually well documented, don't forget the seemingly less obvious sources either. Aerialization is one mechanism that is

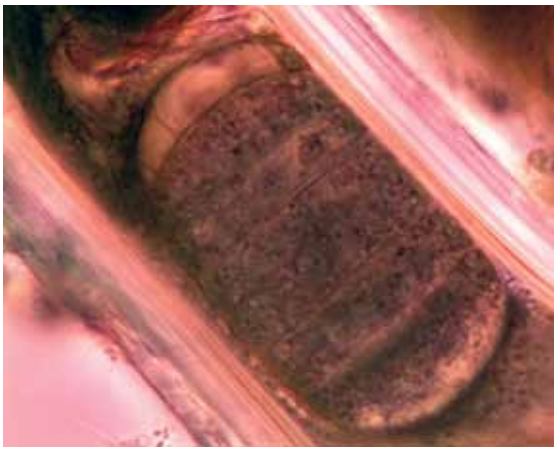


Figure 15. Plectonema *hormogonia.*

often under-quantified. We know that algal toxins and cells in lake spray and updraft from lakes during wind and storm events can be measureable. The other often overlooked and under-appreciated

source is movement by wildlife, and more specifically, waterfowl. We honestly can't overlook the ubiquitous "duck feet and feathers" as a common source of recruitment to new systems (Figure 17).

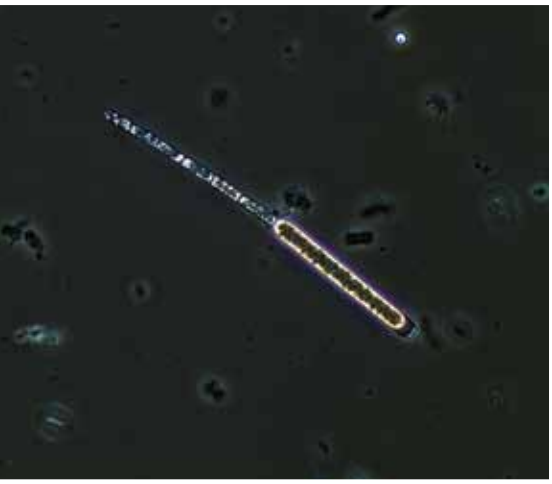
Loss Processes . . .
Or What Must Eventually Senesce . . .

Loss processes are equally important and are often operating simultaneously with the growth processes (kind of like photosynthesis and metabolism). The most obvious is physiological mortality. All cells have to die sometime, and whether they are single cells or colonial, often an entire population will senesce within a week or two. Although limiting resources or the inability to stay up in the water column during stratification are often the driving force behind physiological death, infections and parasites like chitrids are also important. This is very common in *Asterionella* and other colonial diatoms (Figure 18).

When naked flagellates (cells with no particularly hardy outer cell wall or casing) like *Cryptomonas* or *Chlamydomonas* die, they are very labile in the water column and often leave no lasting evidence. Other algae with more robust cell walls or tests (cases that enclose the cell made of silica or cellulose) often leave empty cells around as evidence for several days to weeks (*Dinobryon* and *Pediastrum*, Figure 19). As discussed above, many of these algae will produce cysts (*Peridinium* and *Cosmarium*, Figure 20) or akinetes before the end of the season as light, nutrients and temperature become limiting (see above).

Other loss processes that need to be considered include sedimentation and/or burial. Strategies to survive include cyst or resting cell formation (see above), or in an added twist, the ability to migrate back to the surface. This includes several motile genera of diatoms. Remember too, that physiological health greatly affects sinking rates, so the healthier the cell or colony is, the less likely it is to sink. Hydraulic washout can be a factor, especially in reservoirs or during a flood (not much the algae can do about that one!). Desiccation can happen during normal hydrologic cycles or following large geologic events. The blue-green algae handle desiccation the best, often growing well after being dried for long time periods.

Grazing is perhaps the most complicated loss process because although it often results in death, sometimes it results in growth if you happen to be one of the lucky ones that benefits from grazing, directly or



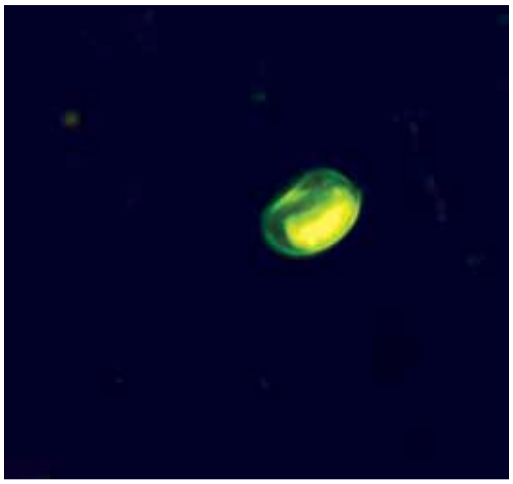
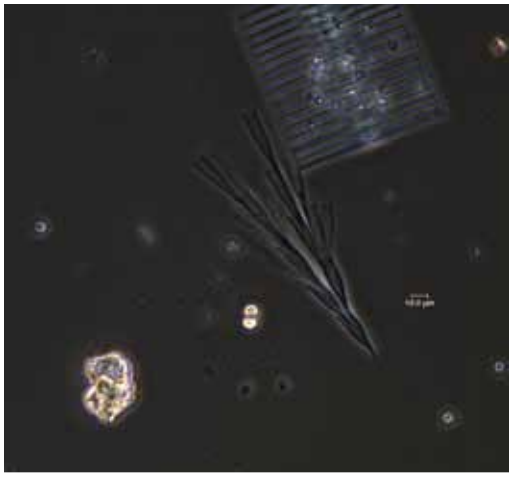


Figure 16. Examples of blue-green akinetes. (Left): Aphanizomenon*; (right):* Anabaena.

Figure 17. Migratory waterfowl.

Figure 18. Asterionella *infected with a parasite.*



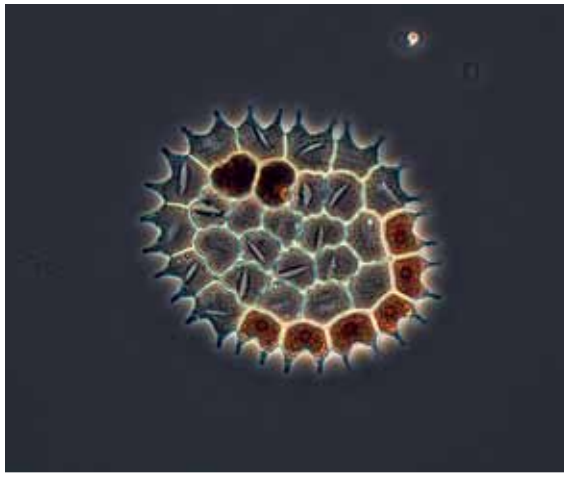


Figure 19. Examples of remnants of dead cells. (Left): Dinobryon*; (right):* Pediastrum.

indirectly. Top down control (grazing) is always competing with bottom up control (resource availability like light and nutrients). If algae avoid being grazed, it's very possible that they may benefit when competitors are grazed. Grazer size is one of the main determinants in how much grazing pressure the algal community experiences. Copepods (Figure 21) can be predatory (cyclopoids) or herbivorous (calanoids), but as a group are selective and not very large (less than 1 mm for the most part, with a small threshold on food items). Rotifers are much smaller (grazers generally less than 0.3 mm), but they can exert consistent grazing pressure on smaller algae, especially single cells flagellates like *Pyramichlamys* (Figure 22).

This brings us to the workhorses of the grazer world, cladocerans. The smaller cladocerans like *Bosmina* are too small to be very effective grazers (0.4-0.5 mm, Figure 23), so although they eat their fair share, they can only do so much damage to the algal community. *Daphnia* (0.5-3.5 mm), however, are considered to be generalist grazers (pretty much anything that can pass through the feeding apparatus or up to about 30 µm, Figure 24). Any *Daphnia* above 1 mm is considered to be an effective grazer (kind of like teenage boys). Interestingly, although very large colonies such as the *Aphanizomenon* above and large Anabaena colonies (Figure 25) are out of bounds, *Daphnia* have good success grazing the periphery of *Gloeotrichia* colonies (Figure 26). They actually make good use of picoplankton when present as well (Figure 27). *Cryptomonas* avoids grazing by migrating down in the water column at night, away from the grazing *Daphnia*. *Micractinium* spines keep it up in the water column, but they also make it hard to eat. It's unclear whether the algal toxins produced by blue-green algae are a defense mechanism against grazing or secondary metabolites, but when they are producing toxins in high concentrations, there tend to be fewer zooplankton in the water column. Food preference goes as follows:

Cryptomonads > Diatoms/Chrysophytes > Greens > Blue-greens

Indirect effects within the grazer world can be significant as well. *Sphaerocystis* is one of the algae (gulp) that can successfully travel the zooplankton gut, absorbing nutrients along the way (Figure 28). Other algae benefit from differential grazing. *Microcystis* (Figure 29), for example, is not a preferred food of zebra/quagga

Figure 20. Examples of encysting algae. (Left): Peridinium*; (right):* Cosmarium.

Figure 21. Cyclopoid Copepod.

Figure 22. Brachionus *(rotifer) grazing on* Pyramichlamys.

Figure 23. Bosmina *(Cladoceran).*

Figure 24. Daphnia *(Cladoceran).*

Figure 25. Anabaena *colony.*

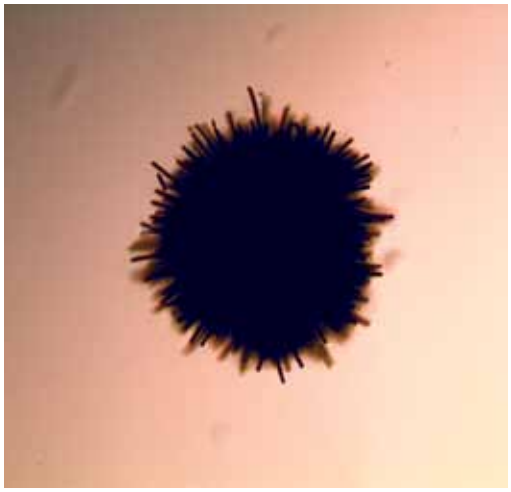


Figure 26. Gloeotrichia *colony that has been grazed by* Daphnia.

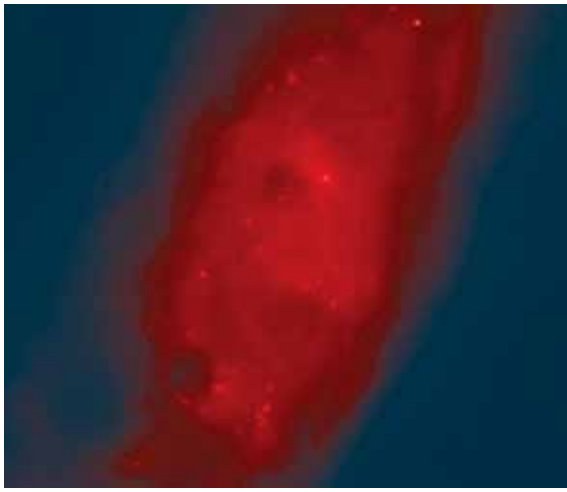


Figure 27. Moina *with picoplankton (the bright red rods and spheres are picoplankton in the 1-2 µm range) in the gut.*

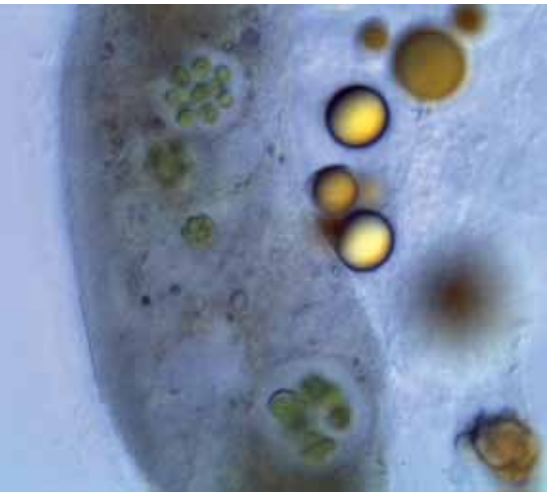
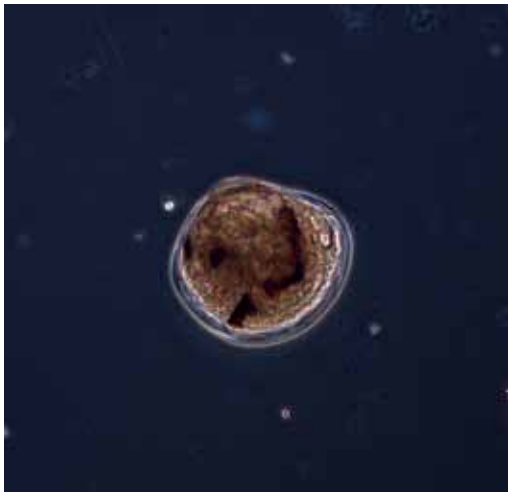


Figure 28. Moina *with* Sphaerocystis *(green algae) in the gut.*



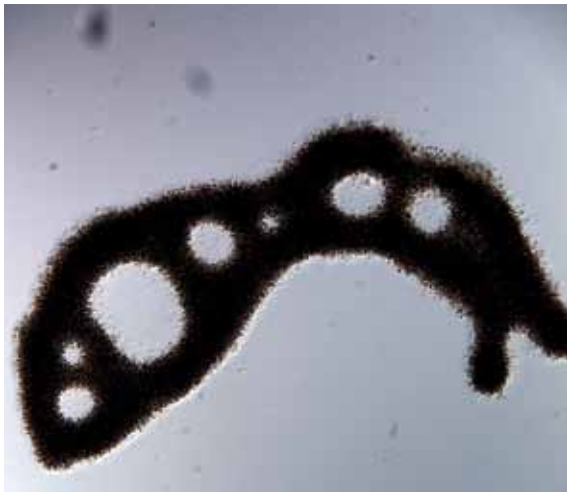


Figure 29. (Left): Dreissena *before settling; (right):* Microcystis *colony.*

mussels, but benefits from the release from competition that occurs when these mussels filter everything else out of the water column and then excrete in a nutrient ratio favorable to *Microcystis*.

So the next time you are passing by an interesting lake, before you ask yourself how best to manage it, perhaps you should ask yourself who's physiologically healthy and who is eating whom?

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