Microbial Food Webs & Lake Management

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Scientists and managers dealing with the open water (pelagic) region of lakes and reservoirs often focus on two components when considering water quality or fisheries – the suspended algae (phytoplankton) and the suspended animals (zooplankton). This is for good reason. Phytoplankton is the component responsible for noxious algal blooms and it often is the target of nutrient reduction strategies or other in-lake management solutions such as the application of algaecide. Zooplankton is the component that provides the food resource for most larval fish and for adults of many pelagic species. Lake management that explicitly considers the pelagic food web uses approaches generally referred to as biomanipulation – where the goal is to reduce the biomass of phytoplankton by creating a situation that favors the dominance of large efficient zooplankton such as *Daphnia* that can graze the noxious algae.

That these food web manipulations often are not successful (DeMelo et al. 1992), is due in part to additional food web complexity beyond just algae, zooplankton and fish. In particular, a large portion of the biomass, nutrient cycling, and energy transfer in the pelagic food web involves plankton components in a different pathway than the aforementioned grazing food chain, including bacteria and a variety of different protozoa.

The aim of this paper is to describe this microbial food web (MFW), identify its major components and their role in the lake ecosystem, and discuss how knowledge about the MFW can be helpful in guiding lake management.

Trophic Levels and Trophic States

In this paper the term trophic *level* is used in a context that considers an organism's position in the food web. Organisms occurring at lower trophic levels (e.g., bacteria and flagellates) are near the "bottom" of the food web, where energy and nutrients first enter the ecosystem. Organisms occurring at higher trophic levels (e.g., zooplankton and fish) are closer to the top of the food web, i.e., near the biological destination of the energy and nutrients. We also use the more familiar term trophic *state*, however only in the context of degree of nutrient enrichment.

Who Discovered the Microbial Food Web?

Although the concept of the MFW may be new to lake managers, its potentially important role in the plankton was recognized as early as the 1940s, when Lindeman (1942) hypothesized that bacteria transfer energy to higher trophic levels in the pelagic zone of lakes and ponds. A Polish ecologist, Z.M. Gliwicz, further elaborated on pathways of carbon and energy flow, postulating that the link between bacteria and zooplankton becomes predominant, vs. algae to zooplankton, in lakes as they become more heavily enriched with nutrients (Gliwicz 1969). The full scope of the MFW, as we know it today, was described by a marine scientist (Pomeroy 1974). In the late 1980s, the MFW was widely studied in lakes and linkages made with fisheries management, food web efficiency, and water quality.

Who are the Major Players in the Microbial Food Web?

The MFW is comprised of three major components – bacteria, flagellates, and ciliates. Bacteria (Figure 1a-b), ranging in size from about 0.5 to 2 µm (a µm is one millionth of a meter and cells of this size are visible only at about 1,000 X magnification under a microscope) are prokaryotic cells that represent one of the first and simplest forms of life on the earth. Most are heterotrophic, meaning that they require organic sources of carbon, however, some can synthesize carbon by photosynthesis or chemosynthesis. The blue-green algae (cyanobacteria) actually are bacteria, but for the purpose of this discussion, are not considered part of the MFW because they function more like phytoplankton in the grazing food chain. Flagellates (Figure 1c), larger in size (typically 5 to 10 µm) than bacteria but still very small compared to zooplankton, are eukaryotes that similarly include species that are heterotrophs – however, some are "myxotrophs," meaning that they can carry out photosynthesis and make use of organic sources of carbon.

Flagellates are named for their organelle of locomotion – the flagellum – which may occur individually, as a pair, or in some atypical cases as three units. The flagellum is a complex structure largely comprised of tubes of protein that is able to synchronously beat in order to move the cell through the water. Ciliates (Figure 1d-f), the largest members of the MFW (typically 20 to 50 µm), also are eukaryotic, and for the most part are heterotrophs. Their name comes from the fact that the cell surface is covered with fine cilia (each structurally similar to a flagellum) that beat in synchrony to propel the animal through the water and/or to generate feeding currents to capture smaller food particles.

How Do They Interact as a Web?

The components of the MFW are interconnected as part of a complex network (Figure 2), in which organic carbon and energy are captured and transferred to higher trophic levels

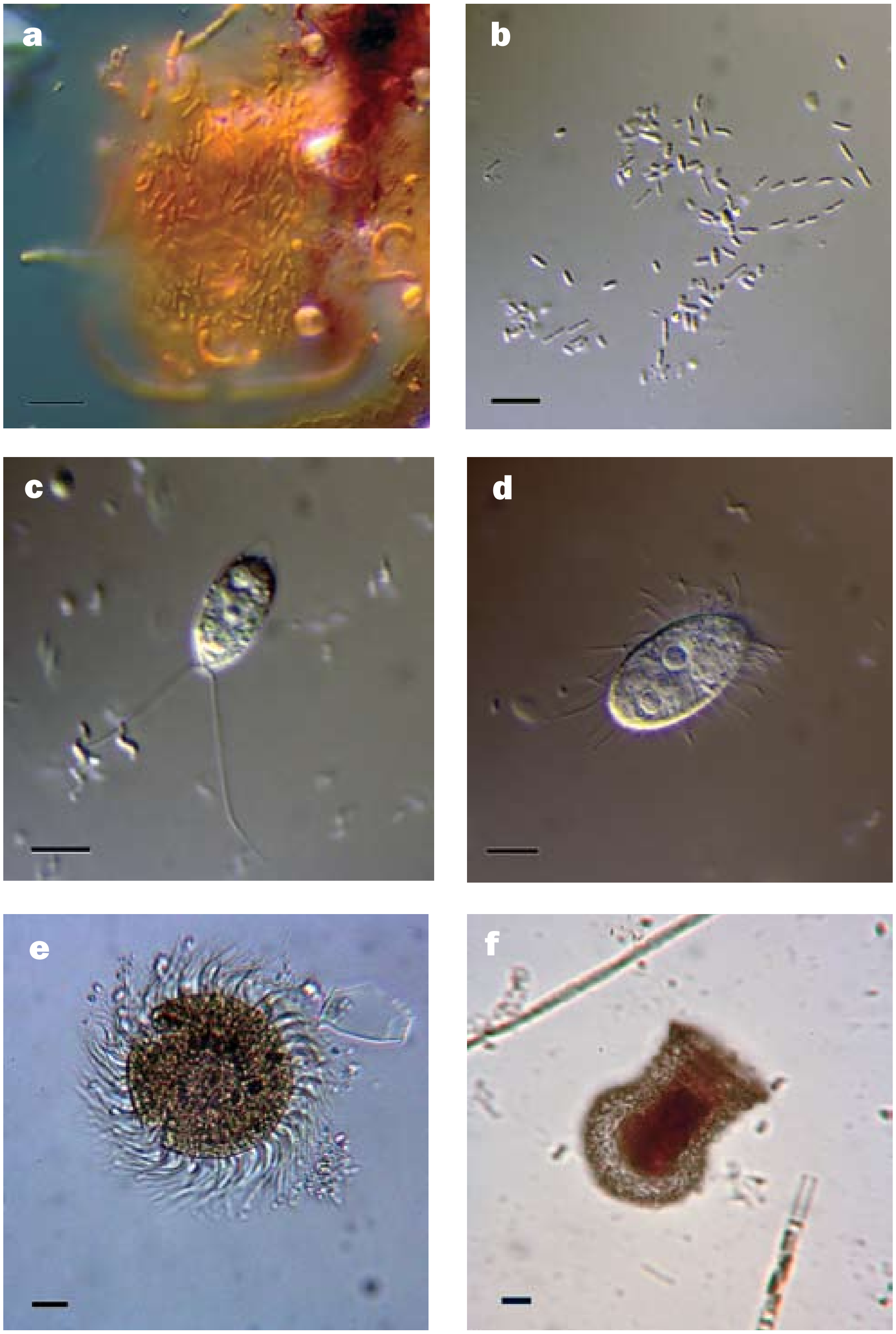

Figure 1. Photomicrographs of representative components of the microbial food web of a lake or reservoir: (a-b) rod-shaped bacteria from Lake Erie photographed at 2000X, (c) flagellate from Lake Erie photographed at 2000X, (d) the ciliate Cyclidium sp. *from Lake Erie photographed at 2000X, (e) the ciliate* Strombidium sp. *from Lake Powell photographed at 630X, (f) the ciliate* Codonella cratera *from Lake Okeechobee photographed at 400X. Scale bar is 10 µm.* Photographed by Kyle Scotese, Teodoro Rosati, Jeff Johansen, and John Beaver.

(zooplankton and fish) in the lake ecosystem. When phytoplankton carry out photosynthesis, they fix dissolved CO_2 from the water into organic carbon (glucose and subsequently other molecules), and during their metabolism and death, much of this fixed carbon is released into the lake water. Bacteria can incorporate some of this carbon into their own biomass, thereby recapturing carbon into the food web that otherwise would have been lost. Subsequently, the bacteria may be directly grazed by zooplankton that has the ability to filter very fine particles (e.g., rotifers and certain cladocerans including *Daphnia*), or they can be grazed by flagellates and/or ciliates in the MFW. Flagellates in turn are a food source for ciliates, rotifers, and many of the larger zooplankton. Ciliates are consumed by larger zooplankton, such as calanoid copepods, that can graze large food particles.

Ultimately, the MFW transfers carbon and energy from the base of the food web (bacteria) to the top (zooplankton and fish). Early in the investigation of the marine MFW a controversy developed as to whether it functioned as a "link or sink" for carbon – the rationale for the sink argument being that much of the recaptured carbon is lost through respiration in the many steps in the longer chains (Ducklow et al. 1986). However, it was soon identified that the grazing food chain has a similarly low efficiency (Sherr et al. 1987). Thus, a reasonable way to look at the MFW is that like the grazing food chain, it is inefficient, however, it serves an important function of recapturing what otherwise would be lost carbon and energy. A considerable amount of the nutrient recycling that occurs in the pelagic zone also happens within the MFW, as phosphorus and nitrogen excreted by algae and zooplankton are picked up by bacteria and transferred upward in this web.

Does the Importance of the MFW Change with Lake Trophic State?

In general, the importance of the MFW, whether measured as the percent of plankton biomass associated with bacteria, flagellates, and ciliates, or the percent of carbon and energy flow, has a unimodal relationship with lake trophic state – with greatest importance in ultra-oligotrophic lakes and hypereutrophic lakes, and lowest importance in mesotrophic lakes (Stockner et al. 1989; Weisse and Stockner 1992). There are, however, exceptions. Lakes in the mesotrophic range that receive water with a high organic (humic) content will tend to support high rates of bacterial productivity and may have a food web that is predominantly microbial (Tranvik 1992). Ultra-oligotrophic lakes, which largely have been investigated in Boreal regions, typically have much of their primary productivity associated with bacteria-sized phytoplankton called pico-plankton and

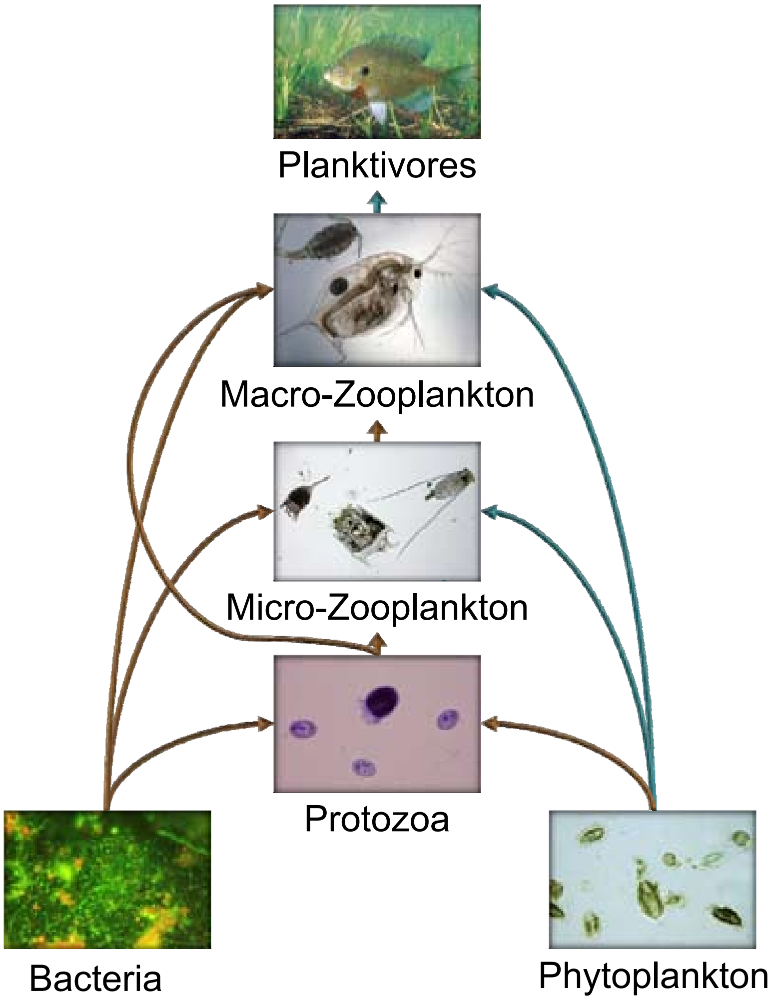

Figure 2. Food web diagram showing trophic links between the various components of the traditional grazing food chain (green arrows) and the microbial food web (brown arrows), and subsequent links to fish. Carbon can enter this food web in two ways – by photosynthesis carried out by phytoplankton and certain flagellates, and by uptake of dissolved organic carbon by bacteria.

their dominant crustacean zooplankton is copepods that cannot graze such small food particles. In those lakes the MFW plays a critical role where flagellates and ciliates "package" the energy of the picoplankton into particles large enough to be available to the copepods. In mesotrophic lakes, a typical situation is dominance of the phytoplankton by moderate sized diatoms, greens and cryptophytes, and cladocerans such as *Daphnia* that can directly graze them. Under these circumstances, the MFW is present but plays a lesser role in carbon and energy transfer than the grazing food chain. As lakes undergo eutrophication and proceed along the gradient from mesotrophic to eutrophic to hypereutrophic, two things occur, leading to a plankton food web in which the MFW is predominant. First, there is a tendency for fish densities and the associated predation pressure on zooplankton to increase as species like threadfin and gizzard shad become increasingly dominant. This reduces the biomass of large effective zooplankton grazers such as *Daphnia*, leaving a community dominated by smaller taxa including rotifers, small cladocerans (e.g., *Bosmina*, *Chydorus*), and copepods that have escape maneuvers. At the same time, the phytoplankton community shifts toward increasing dominance by large filamentous and colonial blue-greens that are too large for the small zooplankton to directly consume. This situation sets up the MFW as the main route for carbon and energy flow, as bacteria sequester carbon excreted by the algae and transfer it upward to the zooplankton via flagellate and ciliate grazers.

How is this Information Important for Lake Management?

The importance of plankton food web structure to fisheries productivity was identified in the late 1980s and subsequently that information was widely applied in fisheries management. This work predominantly occurred in Canada, where John Stockner and his colleagues (Stockner and Shortreed 1989) documented that ultra-oligotrophic lakes in British Columbia, with MFW dominance and associated long food chains, had low efficiency in energy transfer (as noted above, because of many steps in the chains), and supported low fish productivity compared with oligotrophic lakes were the grazing food chain was predominant and fish productivity was higher.

This information was part of the scientific foundation (the other part being a net loss of nutrients due to over-fishing that reduced return of fish to spawning grounds) for large-scale fertilization of ultra-oligotrophic lakes, aimed at increasing algal productivity and enhancing the relative biomass of larger algae that could be directly grazed by zooplankton. From the standpoint of increased fisheries productivity and the associated socio-economic benefits this program was a great success (Stockner and MacIsaac 1998).

Lake managers more often are concerned with an excess of nutrients rather than a lack thereof, and are engaged in projects to reduce nutrient inputs in order to reduce algal blooms, and/or conduct in-lake measures to enhance water quality and fisheries quality. Because of the inefficient plankton food web and loss of summer refuges from warm surface waters, hyper-eutrophic lakes often lose their piscivorous fish (e.g., pike), which in turn releases smaller omnivorous fish from predation leading to greater grazing pressure on zooplankton (Persson et al. 1988). The coincidence of high fish predation and large blue-green algae results in small grazers that cannot eat the algae and therefore must rely on the inefficient MFW. One strategy that may be helpful to make such foods more efficient, under certain circumstances and in combination with nutrient reduction, is biomanipulation – for example, stocking lakes with piscivores and/or removing plantivores and omnivores to reduce grazing pressure on zooplankton and allow large species such as *Daphnia* to become abundant (Figure 3).

When biomanipulation is successful (and admittedly it does not always work), a part of that success is associated with an increase in the relative importance of the grazing food chain vs. the MFW. This reflects the fact that *Daphnia* can graze a wide range of plankton particles, from the smallest bacteria up to relatively large ciliates and phytoplankton. This "short-circuits" the MFW and results in a much more efficient food web in regard to supporting continued productivity of fish. The trick, of course, is maintaining the enhanced piscivores/planktivore ratio, which might be an ongoing process in temperate lakes if continued high nutrient inputs and algal blooms lead to anoxic or hypoxia hypolimnetic waters and lack of a summer refuge from high epilimnetic water temperatures. It is not an effective process in the subtropics where large *Daphnia* do not occur, cyanobacteria are abundant, and the MFW is quite important (Crisman and Beaver 1990).

Summary

In addition to the traditionally recognized algal-zooplankton "grazing food chain," the plankton of lakes and reservoirs includes a more complex microbial food web where bacteria take up dissolved organic carbon from the water (carbon released from algae excretion or carbon entering from outside the lake) and transfer some of it upwards to fish via protozoa and small zooplankton. An understanding of this food web and how it can be manipulated has been used to successfully address low productivity of fisheries in ultra-oligotrophic lakes and can potentially help lake managers achieve a successful enhancement of fisheries and water quality in eutrophic lakes where biomanipulation methods are under consideration.

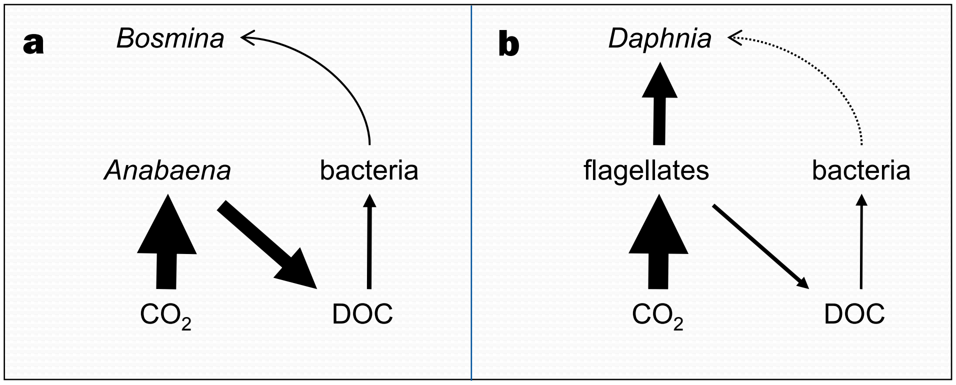

Figure 3. Two simple food web diagrams, showing cases of (a) low efficiency of carbon and energy transfer when small zooplankton co-occur with large inedible algae; and (b) high efficiency of carbon and energy transfer when large Daphnia *co-occur with edible algae. From a fisheries or water quality standpoint, condition (b) is usually desired.* CO_2 *represents the inorganic carbon taken up by algal photosynthesis and DOC is dissolved organic carbon excreted by algae. This is a highly simplified diagram and neither respiratory carbon losses nor release of DOC from zooplankton during feeding and excretion are shown.*

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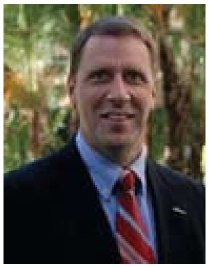

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