Got *Daphnia*? Why it Matters to Lake Managers

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A description of the zooplankton community of a lake or reservoir can provide managers with considerable information about the characteristics of the fish population and algal composition. Because of their pivotal position in the planktonic food web, they are critical to packaging photosynthetic energy into biomass. Zooplankton are animals suspended in the water column with limited powers of locomotion and include protozoa, rotifers, and two subclasses of microcrustaceans – cladocerans and copepods. The smallest zooplankton (microzooplankton), protozoa and rotifers, are generally less than 0.2 mm (microbial food web, see Havens and Beaver 2010). The larger zooplankton (macrozooplankton) include copepods and cladocerans (the subject of this paper) differentiated on the basis of body structure, length of antennae, and legs.

Most cladoceran zooplankton in North American lakes and reservoirs are small (0.2 to 3.0 mm), possess a distinct head, and the body is covered by a bivalve carapace (Figure 1). Locomotion is accomplished mainly by means of the large second antennae. The cladoceran *Daphnia* (water flea, named after the Greek virgin nymph, Daphne, who also thrived without males) is distributed globally and is the keystone zooplankton species in both lakes and reservoirs. Filter-feeding *Daphnia* are often the principal grazers of algae as well as the other components of the microbial food web. *Daphnia* are the primary food for many larval and forage fish and thus higher trophic levels. The intermediary position of cladocerans should be of special interest to lake managers because they are essential to efficient energy transfer from phytoplankton to higher trophic levels. Robust populations of large cladocerans such as *Daphnia* are associated with clear lakes supporting healthy sport fish populations. They are widely utilized as an indicator species to assess the response of ecosystems to environmental change because of their well-described genome and genetic plasticity.

Cladoceran Zooplankton Feeding/ Distribution

Most non-predatory cladocerans use suspension-feeding of particles (i.e., algae, bacteria, detritus) to collect food. The effectiveness of this grazing varies seasonally and among lakes and reservoirs. Generally, the potential filtering rates of cladoceran zooplankters are proportional to body size and increased temperatures (Table 1). All types of phytoplankton are grazed, but cyanobacteria are the least preferred, as they are capable of producing toxins that may reduce the fitness of cladocerans. Cladoceran feeding rates usually stabilize or decrease as concentrations of food particles increase. Herbivorous zooplankton communities only filter a small portion of the water column each day, but if the algal food quality is high they can graze enough particles to cause marked increases in water clarity and alter algal species composition. Assimilation efficiency is variable, but is usually less than 50 percent, and even less efficient when the plankton is dominated by detritus. A positive correlation usually exists between the rates of production of phytoplankton and of zooplankton in an individual lake or reservoir.

The structure and composition of temperate zooplankton communities are significantly altered with high trophic state and is accompanied by less efficient energy transfer to higher trophic levels. Although the total abundance of all zooplankton groups increases with increasing trophic state, simultaneously there is a shift in dominance from large-bodied cladocerans such as *Daphnia* (more efficient, high per capita filtering rates, Figure 1) to small-bodied cladocerans such as *Bosmina, Chydorus,* and *Ceriodaphnia* (less efficient, lower per capita filtering rates, Figure 2). A greater proportion of the phytoplankton biomass in oligotrophic and mesotrophic lakes and reservoirs is composed of smaller, more edible and nutritious algae while higher productivity systems have larger (colonial or filamentous), less edible and less nutritious forms of phytoplankton such as cyanobacteria. Larger particles reduce food collection efficiency by increasing the time needed to manipulate the food. This can result in reduced growth and fecundity disproportionately for large-bodied cladocerans. Increased cyanobacterial populations associated with warmer temperatures would be an additional pressure for *Daphnia*. In addition, the larger cyanobacteria may clog the feeding apparatus of large-bodied zooplankton such as *Daphnia* and toxic strains negatively affect early survival and population growth (Sarnelle et al. 2010).

Predation by Fish and Size Selectivity

Planktivorous fish are often important in regulating the composition, abundance, and size structure of cladoceran zooplankton populations. Vertebrate planktivores (e.g., bass, bluegill, perch, threadfin shad) visually locate their prey based on size or may collect cladoceran zooplankton less discriminately on gill rakers by pump-filter feeding (e.g., gizzard shad). Similarly, invertebrate

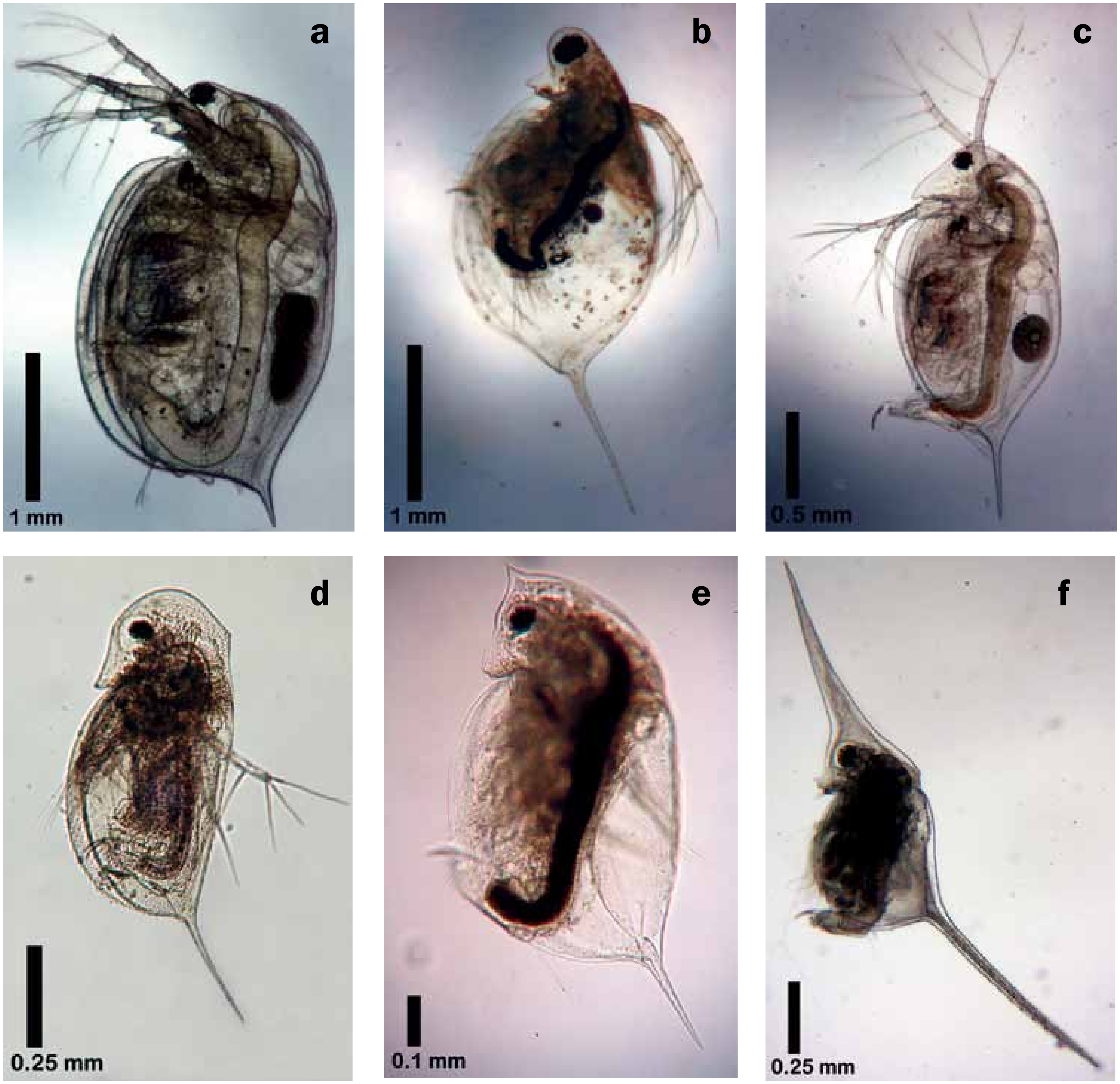

Figure 1. Photomicrographs of representative Daphnia *from lakes or reservoirs of varying latitudes displaying a positive correlation of latitude and* Daphnia *body length: (a)* Daphnia magna *from Shaker Lake, OH photographed at 35X, (b)* Daphnia middendorffiana *from British Columbia, Canada photographed at 35X, (c)* Daphnia pulex *from Lake Mead, NV photographed at 35X, (d)* Daphnia catawba *from Branch Lake, VT photographed at 40X, (e)* Daphnia ambigua *from Lake Okeechobee, FL photographed at 100X. (f) Photomicrograph of the invasive species* Daphnia lumholtzi *from Lake Okeechobee, FL photographed at 50X.* Photographed by Teodoro Rosati, Thomas Renicker, Kyle Scotese, and John Beaver.

predators (e.g., predaceous cladocerans and copepods, phantom midge larvae) use size-selective predation on smaller zooplankton including *Daphnia*. Organism size and swimming patterns are major factors in prey selection by planktivorous fish. Cladocerans are the most vulnerable zooplankton to predation because of their slower and steady swimming movements. Because zooplankton communities are structured by both top-down (fish predation) and bottom-up (food quality and quantity) trophic interactions, they are valuable for characterizing lakes and reservoirs. Brooks and Dodson (1965) in their seminal publication described the size efficiency hypothesis that states that large-bodied cladocerans are better competitors for food than small-bodied species, however, large-bodied cladocerans will

Table 1. Body Size and Filtering Rates of Common Cladocerans in North American Lakes and Reservoirs.

Species	*Size (mm)*	*Filtering Rate (ml animal^{-1} day^{-1})*
Daphnia magna	2.5-3.0	76.8
Daphnia pulex	1.3-2.9	20.4-26.9
Daphnia galeata	1.5-1.7	3.7-6.4
Daphnia parvula	0.7-1.2	3.8
Ceriodaphnia quadrangula	0.7-0.9	4.6
Bosmina longirostris	0.4-0.6	0.44
Chydorus sphaericus	0.1-0.2	0.18

Modified from Wetzel 2001 and McCullough and Reat 1991.

suffer higher predation losses than small-bodied species due to size-selective predation by planktivorous fish. When top-down factors in a plankton food web are strong, the cladoceran community is likely to be reduced in overall numbers and body size.

Vertical and Horizontal Migration

Survival for cladoceran zooplankton in the water column often necessitates avoiding predation by daily vertical and/or horizontal migrations. Some zooplankton, particularly cladocerans, exhibit marked diurnal vertical migrations as refugia from predation by size-selective fish predators. The migration patterns typically follow an upward movement from deeper strata to higher in the water column during darkness when sight-feeding fish are not active and the subsequent return to deeper areas at dawn. Some cladocerans are known to migrate up and down 20 meters or more nightly, the equivalent of a human running a nightly marathon. Rates of grazing are often greater during dark conditions. Vertical migration in deeper lakes may also provide cooler, thermal refugia during summer months allowing modest populations to persist when water temperatures are not optimal. The bottom range of vertical migration is often defined by decreased oxygen concentrations in the hypolimnion. Vertical migration may also reduce competition among filter-feeding zooplankton taxa, allowing multiple species to use food resources located in different levels of the water column. The spatial distribution of zooplankton is notoriously uneven and patchy within a lake or reservoir, and water currents, avoidance of light, Langmuir circulations, and planktivorous fish avoidance have all been implicated.

Cyclomorphosis and Predation

Cyclomorphosis (seasonal polymorphism) is an adaptive feature that many species of cladocerans use to reduce predation and includes significant elongation in some dimension of the organism (Figure 3). Enlargement of the peripheral features decreases capture success of both invertebrate and vertebrate predators. Cyclomorphosis by cladocerans is well described and has been shown in temperate systems to be induced by increased temperature, turbulence, photoperiod, and food availability. Typically in the spring with increasing water temperatures in North American lakes and reservoirs, there is an extension of the head to form a helmet and/or elongation of the tail spine (Figure

Figure 2. Photomicrographs of representative small-bodied cladocerans from North American lakes and reservoirs: (a) Eubosmina tubicen *from Branch Lake, VT photographed at 100X, (b)* Chydorus sphaericus *from Orman Lake, WY photographed at 200X, (c)* Ceriodaphnia spp. *from Shaker Lake, OH photographed at 100X.* Photographed by Teodoro Rosati, Thomas Renicker, Kyle Scotese, and John Beaver.

Figure 3. Photomicrographs of representative Daphnia *displaying helmet cyclomorphosis: (a)* Daphnia retrocurva *from Cheney Reservoir, KS photographed at 50X, (b)* Daphnia retrocurva *from Orman Lake, WY photographed at 40X, (c-d)* Daphnia galeata *from Lake Mead, NV photographed at 100X.* Photographed by Teodoro Rosati, Thomas Renicker, Kyle Scotese, and John Beaver.

3). Cyclomorphosis is less common with decreasing latitude. Enlargement of peripheral features has an energetic cost to the organism since the energy used to produce the additional appendage is no longer available for reproduction but is essential for survival during periods of high predation (Figure 1f).

Latitude and Temperature

A well-described seasonality for *Daphnia* in the temperate zone includes rapid increase in the spring, declines in summer, followed by increase again in fall. Temperature is important for *Daphnia* growth and reproduction. Peak populations have been shown to occur at approximately 18ºC and to decline rapidly at water temperatures greater than 20ºC, indicating that regardless of latitude, water column temperatures and individual thermal regimes of particular lakes and reservoirs are the important determinants for *Daphnia* seasonality. There is a decline in the mean size of cladocerans in the temperate zone with decreasing latitude such that the average size of cladocerans is considerably smaller in subtropical areas such as Florida (Figure 1a-e). Although physiological constraints (higher water column temperatures) in lower latitude lakes have been suggested as a major factor (Gillooly and Dodson 2000), more intense fish predation and an increased proportion of small planktivorous fish in warmer lakes and reservoirs are likely the key factor in the absence or very modest populations of large-bodied cladocerans (Iglesias et al. 2011).

Climate Change

Potential impacts of climate change on plankton trophic interactions may include disruption (decoupling) of established food web relationships. *Daphnia* life history traits include a strong relationship between body-size, fecundity and feeding efficiency, with optimal temperatures approximately at 18ºC (winter, fall in temperate systems) and decreasing population and metabolic status at lower and higher temperatures. Acceleration of the timing of elevated temperatures in the spring may alter thermal regimes and the timing of peak high quality food (e.g., cryptomonads, diatoms) in lakes and reservoirs. Because of *Daphnia*'s reliance on appropriate thermal conditions for population expansion in the spring, their seasonal success may be reduced if their principle food is not synchronized with their populations. The timing, extent, and taxonomic composition of phytoplankton spring blooms are often synchronized with *Daphnia* community dynamics. Winder and Schindler (2004) demonstrated the unique and differing responses of *Daphnia* and diatoms to the timing of a warmer spring water column in Lake Washington, where thermal stratification and the spring diatom bloom were accelerated while *Daphnia* population peaks were delayed and reduced. Potential impacts of climate change on planktonic cladoceran communities would be expected to result in an increased importance of small-bodied forms such as *Bosmina, Chydorus,* and *Ceriodaphnia* which are more tolerant of elevated temperatures but less efficient in transferring energy to higher trophic levels, resulting in less desirable fish populations (Figure 2).

Conclusions

Planktonic crustaceans, particularly cladocerans, are highly sensitive to local and changing environmental conditions. The composition of the cladoceran zooplankton communities of North American lakes and reservoirs has clear implications for the perceived desirable uses of these resources. Robust populations of *Daphnia* suggest a more balanced aquatic ecosystem in the traditional sense. Eutrophication, whether natural or manmade, typically produces a less desirable zooplankton community from a food web or managerial standpoint. Additional, multiple stressors such as climate change and associated alterations to individual lake and reservoir thermal regimes and/or anthropogenic impacts to watersheds suggest that large-bodied zooplankton communities in North American lakes and reservoirs will be less common in the future.

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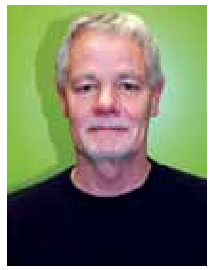

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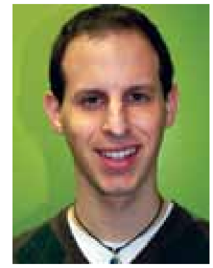

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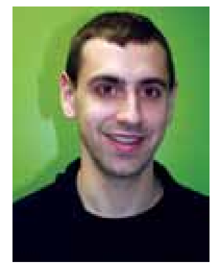

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