The Complexity of **Aquatic Food Webs**

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Aquatic Food Webs – The Intricate Gears of a Functioning Ecosystem

Lakes and ponds are mosaics of natural habitats occupied by aquatic plants and animals. Like other realms of nature, the forces of life and death are constantly at work within these habitats. An aquatic plant leaf is grazed down by an insect that, in turn, is taken by a minnow, which ends up as lunch for a passing pickerel. These links, which control or modify patterns of energy production and transformation, are often conceptually portrayed as diagrammatic food web relationships (Figure 1). These food webs are typically portrayed as pyramids, mimicking the relative reductions in biomass between each ascending food chain step or *trophic level*, as higher organisms need to consume large numbers of prey to sustain growth and reproduction. In reality, aquatic food web relationships tend to be much more extensive and complex, as many organisms are both omnivorous and opportunistic, feeding on whatever the environment offers that day, be it plant, animal, or *detritus* (the polite term for dead and rotting organic material).

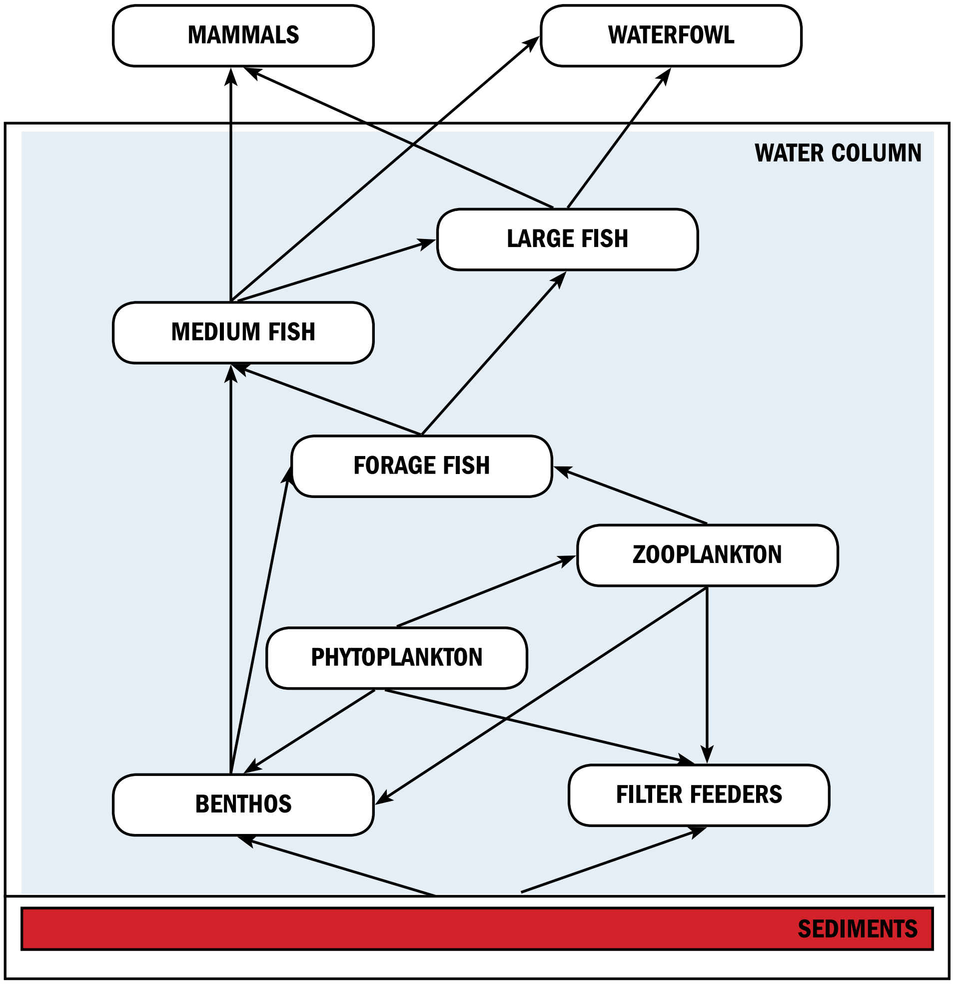

Figure 1. Typical aquatic food web. Source: USEPA 2009. Users Guide and Technical Documentation. KABAM. Version 1.0 (K_{ow} (based) Aquatic BioAccumulation Model). Environmental Fate and Effects Division; Office of Pesticide Programs. Electronically accessible at: http://www.epa.gov/oppefed1/models/water/kabam/kabam_user_guide.html#Section1_3.

Why are Food Webs of Interest?

For ecologists, these food webs are convenient conceptual tools to summarize the principal means by which energy (in the form of carbon) and nutrients are exchanged, altered, or exported in the aquatic ecosystem. The exact form and components of food webs can differ with lake type, geographic region, and season, and comparative limnology often finds insight in these differences. Looking at the propagation and interaction of direct and indirect population effects up and down the food chain, a process that is termed "trophic cascades," provides lake managers with interesting biological options for ecosystem restoration (Carpenter et al. 1985). For anglers, food webs supply useful advice for selecting the best fly or lure to tempt a crafty bass out of the weed beds. For the local lakeside resident, knowledge of food webs provides greater appreciation of the natural drama occurring just offshore and better understanding of the importance of maintaining local shoreline habitats.

While aquatic food webs are often portrayed in cartoons as a succession of bigger and bigger fish madly snapping each other up, reality is much more mundane. The aquatic food web that is the most studied is that found in open waters, which includes four trophic levels: *phytoplankton* (primary producer), *zooplankton* (primary consumer), young-of-the-year or forage fish (secondary consumer), large piscivores, such as lake trout or eagle (tertiary consumer). In shallow waters, analogous trophic levels may include rooted aquatic plants (*macrophytes*), snails, crayfish, and smallmouth bass. Research tracking food sources via isotopic markers has indicated that in many lakes the benthic food chains may be more important to fish diets than the open water (Vander Zanden and Vadeboncouer 2002).

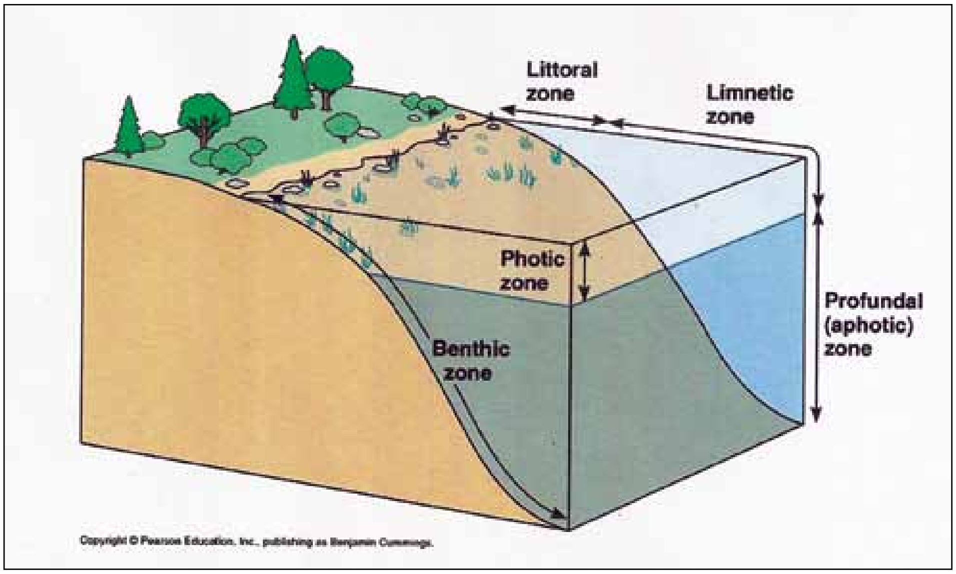

Figure 2. Zonation of lake habitat. Source: Pearson Education, Inc.

Ecological Zonation Within a Lake

In understanding lake food webs, it is important to recognize that most of the action is located relatively near the shoreline, in the shallow, well-lit waters that are termed the *littoral zone* (Figure 2). The role of this structured edge habitat is critical to lake-wide energy and nutrient dynamics. The littoral zone is more physically complex than the homogeneous *limnetic zone* that constitutes the main open waters of a lake. Continuing outward and downward from the shore, the waters get colder and darker in the *profundal zone*, which is beyond the reach of light and which receives a steady rain of detritus from the productive upper waters. Found near, upon, or within the bottom substrates of the littoral and profundal zones in lakes and ponds is a community of aquatic invertebrate life forms that are collectively known as the *benthos*.

The benthos is comprised of a diverse collection of creatures, including many familiar creatures such as dragonflies, mayflies, mosquitoes, midges, backswimmers, snails, crayfish, freshwater mussels, and leeches – benthic aquatic macroinvertebrates inhabiting numerous substrates including rocks, sand, sediment, woody debris, and aquatic vegetation. Aquatic macroinvertebrates are important as the trophic or feeding links between the energy and nutrients released through the consumption of algae, plant material, and decomposition of organic material and the nutrition of higher organisms. As the mid-level connection in the aquatic food web, macroinvertebrates are often the principal prey for juvenile and adult stages of fishes, but may also be utilized by reptiles, amphibians, waterfowl (ducks, shorebirds) and wildlife (muskrat, otter). Since describing the vast array of aquatic macroinvertebrates and their food web roles would be a challenge for a textbook, we offer instead a glimpse of some representative macroinvertebrates found in distinctive habitats on or within the lake and which have unusually important role in structuring the aquatic community.

Life at the Top and Within the Weeds

At the very top, we encounter insects that are specialized for life at the air-water interface, which use the surface tension of the water as a stable platform for support as well as a source of sustenance. The surface is the playground of the gyrinids or whirligig beetles that can occur in aggregations of thousands (Figure 3). Whirligig beetles earned their common name from the adult's wildly sporadic swimming behavior. While their rapid circular movement may attract inquisitive fish, they secrete distasteful chemicals that deter predators from feeding on them. Whirligig beetles have other interesting adaptations for "life at the top." For example, they possess a specialized organ at the base of the antennae that enables them to echolocate using surface wave vibrations. In addition, their compound eyes are split into two pairs, one for watching above and one below the water surface, enabling them to detect both aerial and aquatic predators. Gyrinds scour the surface film of the water, feeding on the small animals and materials displaced from terrestrial habitats by wind or runoff, forming an important energy transfer between the earthly and watery worlds.

Going deeper into the littoral zone, beds of macrophytes are common lair for damselfly nymphs. Damselflies are close taxonomic cousins to the swifter, larger dragonfly, but their larval or nymph form can be distinguished by their delicate narrow body form with three gills extending in a tripod formation at the posterior end. Their brown and green coloration provides a measure of camouflage, allowing the nymph to blend within the habitat of plants and pond bottoms (Figure 4). Damselfly nymphs are voracious predators and feed on snails, other insects, crustaceans, worms, and even small fish. They are classic ambush predators, lying in wait for prey to get within range and then explosively shooting their extensible jaw out to grab and reel back their victim, in a mode that served as the model for the *Alien* movie predator's deadly attacks.

Life in the Bottom and Deeper Still

Leaving the weeds beds, we may happen upon a sandy or gravelly patch

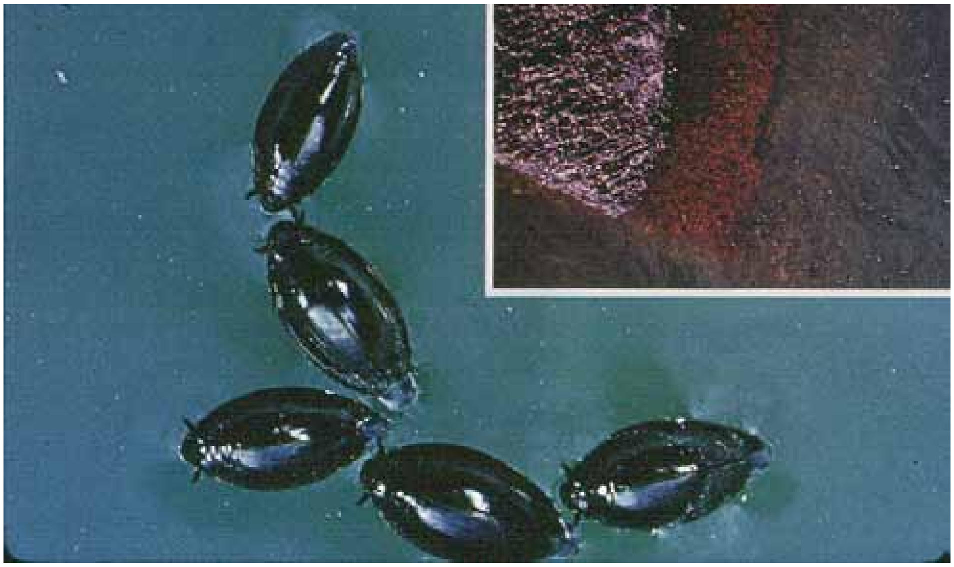

Figure 3. Adult gyrinds (whirligig beetles). Credit: Bobbi Peckarsky.

Figure 4. Damselfly nymph. Credit: Lars Hedin.

of bottom, especially along well-washed pond margins, where populations of freshwater mussels can be found. Like their better known saltwater brethren, these filter-feeding freshwater "clams" spend most of their lives partially buried, pulling water into their bodies, filtering it to remove food particles, and pumping the rest back into the environment. Mussels play a pivotal role in aquatic ecosystems, consuming large portion of phytoplankton and zooplankton, and, in turn, providing food for many fish and mammals species. Freshwater mussels often comprise the largest proportion of benthic biomass (i.e., weight) since they can sequester significant amounts of minerals and nutrients in their shells. As described below, when large numbers of mussels are present, they can significantly shift the balance of energy flow from the open water to the nearshore environment.

In shallow, productive lakes with soft, organically rich bottom sediments, burrowing mayflies may be found in profusion (Figure 5). Burrowing mayflies are a favored food of bottom-eating fish such as yellow perch, freshwater drum, and various catfish species. Where abundant, the flying swarms of hatching adults can cause temporary nuisances for local residents due to their prolific numbers (and messy remains) mobbing backyard porch lights, splattering auto windshields, and piling up in windrows on local beaches. Since burrowing mayflies are very susceptible to low oxygen and/or sediment contamination, they are useful ecological indicators of good water quality or ecosystem recovery.

Venturing into deeper northern lakes, we may encounter opossum shrimp (mysids), a so-called "relict" species whose present geographical distribution reflects the extent of ancient glacial ice advances. These crustaceans are relatively small, omnivorous, and are a major food source for fishes (Figure 6). To avoid fish predation, mysids seek refuge in deep, unlit waters during daytime, feeding on benthic prey and detritus in the sediments. As dusk approaches, they rise upwards in long vertical migrations (e.g., >300 ft) to feed on zooplankton and algae in the mid-waters, returning to the protective bottom waters at dawn. Due to this lifestyle, this species forms an important link in the transfer of energy between the benthic and pelagic food webs. Their role in the food web is further complicated because mysids can affect the size, structure, and abundance of zooplankton, which has secondary impacts on zooplankton-eating fish, with potential effects up the trophic levels to top wildlife predators such as bears and eagles.

In the depths of the profundal zone, we encounter a cold, dark habitat with little or no plant cover and sparse physical structure. These fine, silty sediments are home to chironomid or midge larvae. Midge larvae are small, wormlike creatures that are ubiquitously distributed throughout aquatic ecosystems, even in highly polluted or oxygen-poor waters. Larvae of some midge species have bright red coloration due to the abundance of hemoglobin in their bodies earning the nickname of "bloodworms." Chironomids feed on algae, bacteria and organic matter in the water and sediment. In most lakes, midge larvae constitute the most numerically abundant aquatic insects and are a steady source of food for many bottom-feeding fish.

Critical Linkages of Energy and Nutrients

While these are but a few of the species within a food web, what links all these species to each other is the transfer of energy, nutrients, and unfortunately, pollutants. Energy transfers are typically

Figure 5. Burrowing mayfly nymphs. Credit: Bobbi Peckarsky.

Figure 6. Mysid shrimp. Credit: unknown.

measured by ecologists by the amount of organic carbon that flows between trophic levels. Each successively higher trophic level requires more energy and biomass to sustain its population. While this might suggest that all potential prey must go the way of tooth and claw, the fact is most of the organic biomass is not directly consumed by predators. The majority of aquatic plants and animals simply peacefully expire and their decaying remains become the feast for bacteria, fungi, and detritivores (those animals and fish that specialize in the recycling business). Some of this material is rapidly recycled to the water column, while a large amount is buried in the bottom sediments.

Food webs are very important in recycling nutrients, nitrogen, and phosphorus between waters, sediments and the tissues of living organisms. Zooplankton grazing on phytoplankton leads to significant release of nutrients during the summer. When other phytoplankton pass through these enriched patches of water, they readily take up these nutrients, which sponsor new growth and biomass. Similarly, as bits of decaying macrophyte hit the bottom, scavenging insects and bacteria can recycle nutrients to the water column. Nutrients in the sediment can be released by the activities of burrowing mayflies that can re-suspend previously buried nutrients into the water column, increasing local productivity. Alternatively, nutrients can be exported from a lake system when a mink makes a meal of a crayfish or insect larvae hatch and take wing.

What Food Webs Tell Us About Lakes Gone Bad

Scientists can also use food webs diagnostically to identify types of stresses (e.g., eutrophication, toxics, invasive species, etc.) that are altering expected patterns of community organization since imbalances in the expected numbers or diversity of a trophic level may be a clue to causal factors. The over-fertilization of lakes from nutrients (also called cultural eutrophication) leads to overabundance of phytoplankton, shading out and reducing rooted plant growth and leading to a shift in resources away from benthic areas. Our knowledge of food webs has also been enhanced by the study of trophic transfers of bioaccumulative chemicals (e.g., DDT, mercury, PCBs) that trace the increase in concentrations of body burdens of these chemicals up the food chain, often with disastrous results for the top predators. This process is also the reason for the posting of fish advisories for lakes in many regions of the country.

Invasive species can alter the patterns of energy flow in food webs. For example, lakes colonized by non-native nuisance, macrophyte species (e.g., Eurasian watermilfoil, fanwort) may increase numbers of macroinvertebrate species sheltering in the stems and leaves that reduce access to fish predators. Perhaps the most dramatic example of trophic alteration in our lifetime has been the invasion of the Great Lakes drainage system by the non-native zebra mussel (Figure 7). Due to its rapid colonization and prolific numbers, the cumulative high filtration capacity of zebra mussel beds has profoundly altered the aquatic food web in afflicted lakes. Since zebra mussels became established in Lake Erie, the combined filtration of these invasives has purged the water of so much phytoplankton that water clarity has increased from 6 inches to 30 feet in some areas (USGS 2008). Reduction of the phytoplankton that supply food for larval fish and other invertebrates has resulted in the reduction of populations of some pelagic fish species. On the other hand, benthic-feeding fish species (yellow perch, freshwater drum, catfish, and lake sturgeon) have adapted to feed on the zebra mussels. It has been reported that some species of migratory ducks have changed their annual flight patterns in response to the locations of zebra mussel colonies.

Using Food Webs to Help Make Lakes Right Again

Our increased awareness of food web interactions has found practical application in lake management. For lake managers, altering patterns of predation pressure by, for example, stocking large numbers of a predator gamefish is a well-

Figure 7. Zebra mussel colonies. Credit: David Strayer.

recognized lake management technique called *biomanipulation.* Briefly, for this "top-down" biomanipulation example, a rise in large piscivore biomass brings decreased numbers of planktivorous fish, increases biomass of grazing zooplankton, and decreased phytoplankton biomass, to meet the objective improving lake conditions (e.g., increased clarity). Biomanipulation has proved successful in some lakes and less so in others, suggesting that factors such as depth or nutrient supply can confound the success of the technique (Benndorf et al. 2002).

While most shoreline residents rarely get to practice lake management on the large scale, there is a portion of the lake where they hold sole domain and can positively influence local aquatic food webs. The recent comprehensive lake survey, the National Lake Assessment (NLA), was conducted in 1,048 lakes over the nation (USEPA 2010). In the NLA survey, lakeshore habitat was rated poor in 36 percent of the lakes. Poor ecological community health was three times more likely in lakes with poor lakeshore habitat relative to lakes with good habitat. These findings reinforce the need for today's shoreline residents to (1) retain native bordering vegetation, (2) conserve valuable littoral zone habitat such as submerged logs and branches at the water's edge, and (3) not disturb existing bottom substrates submerged aquatic vegetation (i.e., do not import sand to make a beach). These lake stewardship actions will link you to maintaining the integrity and biodiversity of the interacting species found just off your shore.

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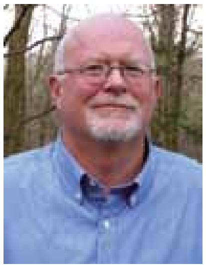

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