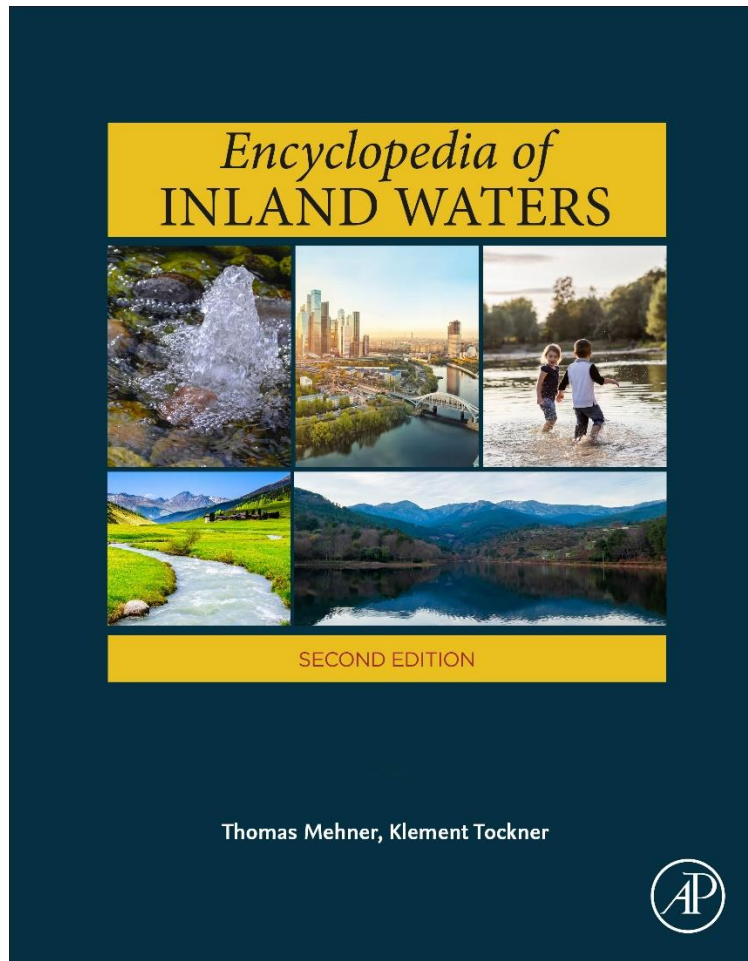


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Lake Food Webs

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Glossary

Food web A description of the feeding relationships among organisms in an ecosystem.

Trophospecies A group of species that use the same resources and/or occupy the same trophic level (sometimes referred to as a “trophic guild”).

Omnivory A feeding preference wherein an organism feeds on multiple prey or trophic levels.

Benthic energy pathway Resources originating from the bottom substrates of a lake.

Pelagic energy pathway Resources originating from the open-water area of a lake.

Bottom-up control The case in which nutrients regulate the biomass and community of primary producers, with effects that propagate to higher trophic levels to structure the ecosystem.

Top-down control The case in which predators regulate the abundance and/or size structure of their prey, with subsequent effects on the abundance and/or size structure of lower trophic levels to structure the ecosystem.

Trophic cascade The propagation of predation-driven, indirect changes in the abundance and/or community composition of trophic levels in a food chain, sometimes driven by the addition or removal of a top predator.

Bio-manipulation Deliberate modification of an ecosystem by adding or removing species, usually predators.

Microbial loop Food web pathway in which dissolved organic matter is returned to the classical metazoan food web via food web linkages involving bacteria, protists, and crustaceans.

Biomagnification The process of the accumulation of contaminants in consumers at successively higher trophic levels.

Benthification A shift in energy production from the pelagic to benthic habitat.

Introduction

The study of food webs is the study of feeding or trophic relationships among species in an ecosystem. Interest in studying food webs stems from the fact that no species exists on its own. Rather, each species is embedded in a network of predator-prey interactions. These predator-prey interactions are of interest themselves and food web studies often provide a description of the feeding relationships among species within an ecosystem. Yet it has become clear that food webs have far-reaching consequences for ecosystems. Food web interactions greatly affect the abundance and dynamics of species. Food webs also have implications for ecosystem-level processes such as nutrient cycling and energy flux. Thus the study of food webs bridges population, community, and ecosystem ecology. At a foundational level, food webs provide a powerful framework for evaluating a collection of organisms as an ecological system.

It is critical to recognize that food web studies can encompass an exceptionally broad range of approaches and types of studies. Here, we identify three major approaches to studying food web study. A *connectance* (also known as topological or structural) food web is the binary (presence/absence) of predator-prey links among species in a community (Fig. 1A; Martinez, 1993, Dunne et al., 2002). *Energetic* food webs aim to represent the pathways and flows of energy through the food web, where links are weighted according to their energetic importance (Fig. 1B). Finally, *dynamic* (also known as functional) food webs focus on the factors that structure the abundance of different organisms and trophic levels, with emphasis on how the effect of predation cascades throughout food webs (Fig. 1C).

Food webs in nature are exceptionally complex. Studies of food webs inevitably involve simplifying this vast complexity into something more manageable. Examples include lumping similar species into ‘trophospecies’ (e.g., trophic guild), simplifying the ecosystem into discrete trophic levels or steps in a food chain, and ignoring taxa and habitats that are not considered important.

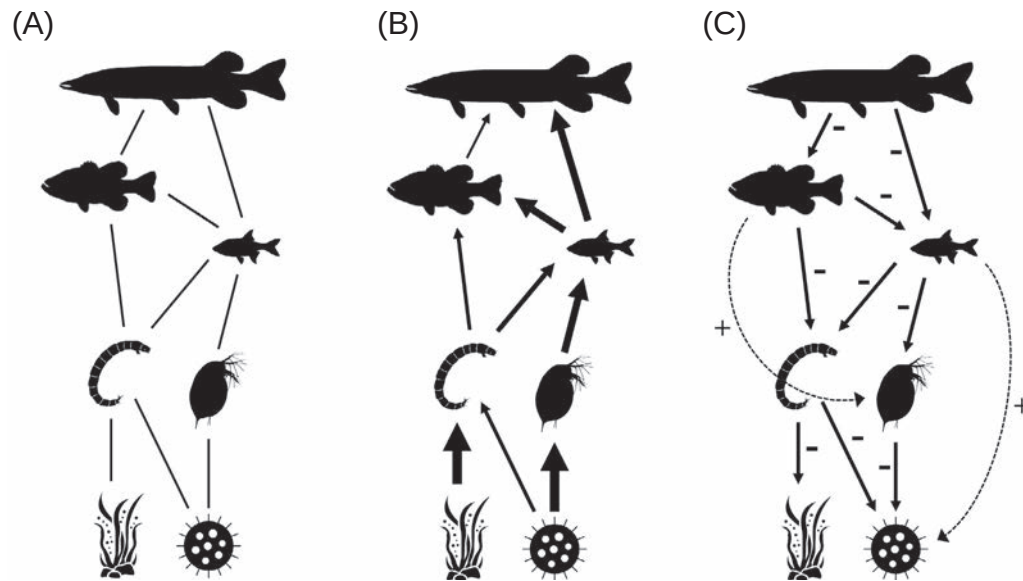


Fig. 1 Conceptual illustration of three approaches to the study of food webs: (A) connectance webs represent predator-prey links in an ecosystem, (B) energetic webs include information about the energetic importance (fluxes and flows) of food web links, (C) dynamic webs represent the linkages important for regulating abundance, including indirect and direct effects. In panel B, the size of the arrow indicates the magnitude of energy flow between trophic levels. In panel C, dashed arrows represent indirect interactions. Sign (– or +) represents the effect of the interaction.

Given the complexity of food webs, it is important to think carefully about what information is being described in a food web diagram or study.

The goal of this chapter is to provide a broad overview of lake food webs and highlight current areas of research interest. Lakes occupy a small portion (<2%) of the earth's surface, but are a vital source of freshwater to humanity, and provide a diversity of exceptionally valuable ecosystem services (Wilson and Carpenter, 1999). Studies have demonstrated that shifting food webs can have important implications for lakes and the ecosystem services they provide (Walsh et al., 2016). Moreover, several foundational advances in ecology emerged from studying lake food webs, including Lindeman's tropho-dynamic concept (Lindeman, 1942) and the concept of trophic cascades (Carpenter et al., 1985). One reason that the study of lake food webs has made broad contributions may be that lakes have well-defined boundaries, making them amenable to ecosystem study. While early ecologists viewed lakes as self-contained microcosms, researchers now recognize that there are strong inter-connections between lakes and their surrounding watersheds.

We divide this chapter into four sections. The first briefly addresses *connectance food webs*. While we do not expand broadly on this perspective, we offer multiple references for further reading. The second section focuses on food web studies taken from an energetic approach (*energetic food webs*). These studies tend to be 'bottom-up' in nature and emphasize how resources or energy at the base of the food web are transferred to higher trophic levels, as well as identifying the resources and energy pathways supporting higher trophic levels. The third focuses on *dynamic food webs*. These studies emphasize the effects of predators on their prey, and the interaction between 'bottom-up' and 'top-down' controls in structuring lake food webs. The fourth and final section highlights *integrative and applied perspectives* on food web studies including areas of emerging research interest in the study of lake food webs.

Connectance food webs

Connectance food web studies examine broad-scale patterns across collections of empirical food webs. These food webs are based on information about the presence/absence of trophic linkages. Connectance food webs are essentially network diagrams (Martinez, 1993; Dunne et al., 2002). Broad patterns can be examined - for example the number of observed trophic links can be related to the number of species, leading to a measure of food web connectance (Cohen and Briand, 1984; Paine, 1988). Connectance studies have also evaluated the relationship between the number of links in a food web and how many predators and prey occur (Cohen and Briand, 1984). Although connectance food webs can provide information about a system, many have critiqued this approach based on the arbitrary and poor quality of the data, as it fails to go beyond simple presence/absence of food web linkages (Paine, 1988).

Energetic food webs

Food chain concept—While natural food webs are characterized by vast complexity, many food web studies simplify matters by grouping functionally similar organisms. When considered in energetic terms, organisms are often combined into trophic levels – groups of species that are thought of as comprising a single step in ecosystem energy transfer. Photosynthetic organisms are considered primary producers (Λ_1) and are the foundation of the food web. They are consumed by herbivores or primary consumers (Λ_2), which are in turn consumed by secondary consumers (Λ_3), and in many cases, tertiary consumers (Λ_4). At each step, energy is lost, ultimately limiting the number of trophic levels in the food chain (Fig. 2). This fundamental concept of energy flow through successive trophic levels and concurrent energetic loss at each trophic level was presented by Elton (1927) and later Lindeman (1942) in his study of Cedar Bog Lake, Minnesota. While the transfer of energy from one discrete trophic level to the next is undoubtedly an oversimplified depiction of real food webs, the food chain concept has proven to be an exceptionally useful heuristic for conceptualizing energy flow in ecosystems.

Embracing complexity – the food web concept—Observational studies of feeding relationships generally reveal that the food chain concept with its simple trophic levels is a gross oversimplification of nature. Many species are ‘omnivorous,’ feeding on multiple

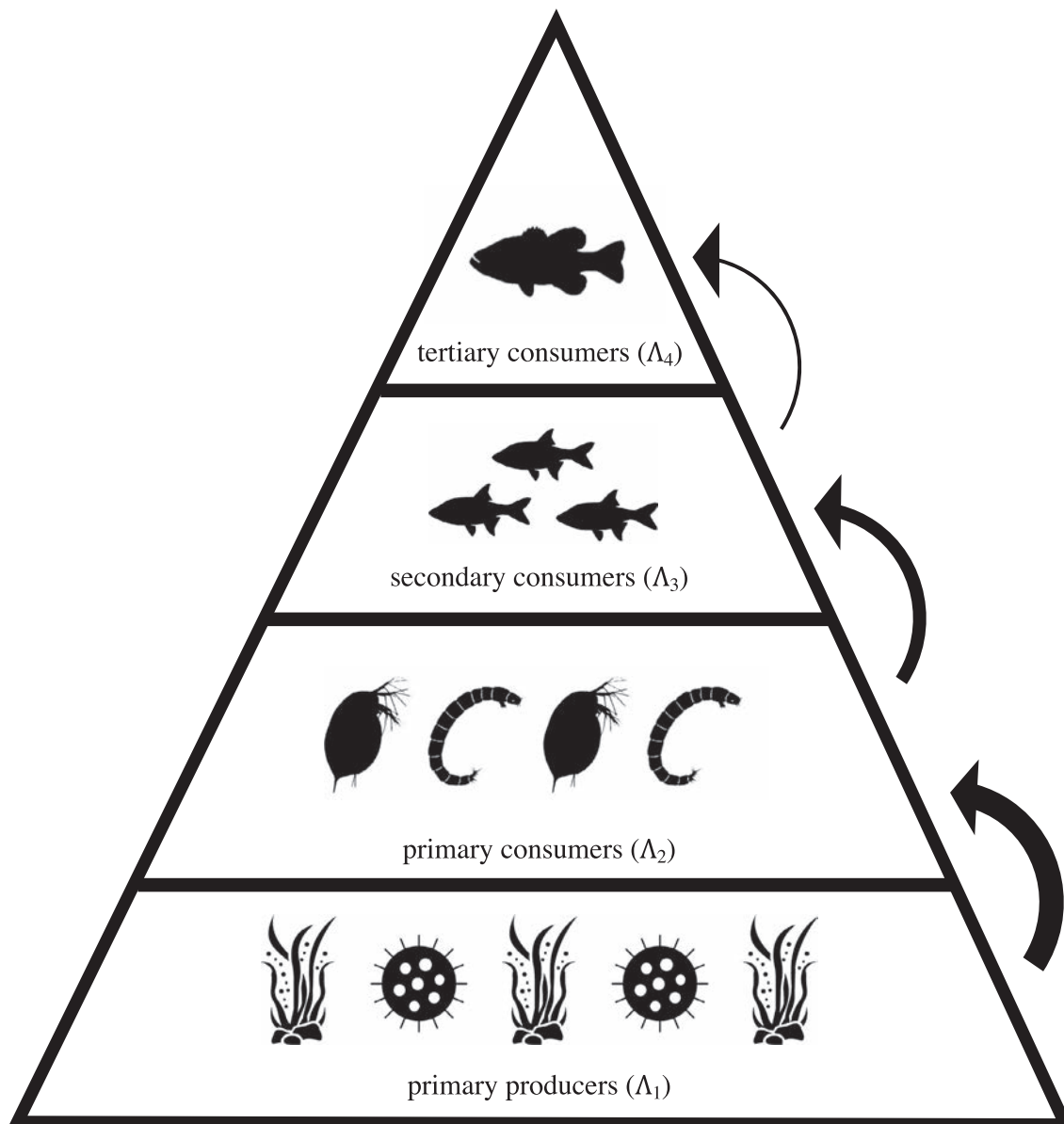


Fig. 2 Trophic pyramid showing energy flow across four trophic levels (Λ_1 , Λ_2 , Λ_3 , Λ_4). Pyramid highlights the decrease in production at successive trophic levels. Arrow width indicates the magnitude of energy flow.

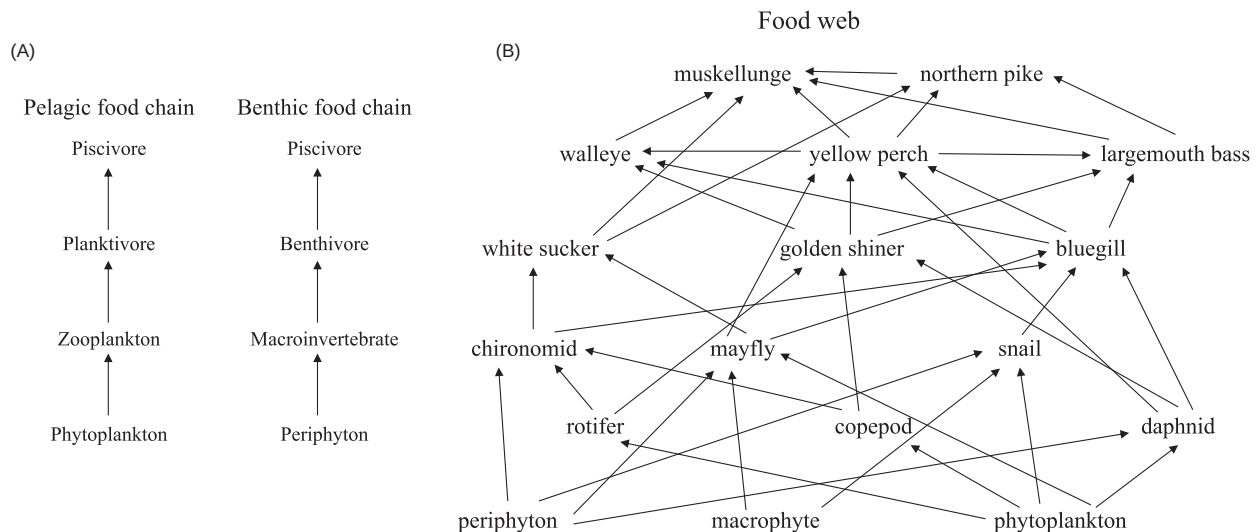


Fig. 3 Two idealized, linear food chains from pelagic and benthic habitats (panel A), as well as a simplified reticulate food web of a north temperate lake (panel B). Adapted from Rudstam LG, Allen Y, Johnson BM, Luecke C, Post JR, and Vanni MJ (1992) Food web structure of Lake Mendota. In: *Food Web Management*, pp. 233–242. New York, NY: Springer.

prey or trophic levels. Diets can vary among individuals of a trophic level, and shift during the ontogeny of a species, adding further complexity. Food web diagrams, sometimes comprised of numerous food chains (Fig. 3A), can be used to represent these more reticulate and complex food web relationships (Fig. 3B). But even these still tend to be an oversimplification of actual feeding relationships. The concept of trophic position incorporates some of this complexity. Though conceptually analogous to trophic level, trophic position is non-integer in nature and reflects the weighted average of the various feeding pathways supporting a consumer. Trophic position can be estimated from diet data. In recent decades trophic position has been estimated using stable nitrogen isotope ratios sampled from organismal tissues. Stable nitrogen isotope ratios become enriched between prey and predator tissues, thus providing a measure of consumer trophic position (Cabana and Rasmussen, 1996; Fry, 2006).

What basal energy sources support lake food webs?—Lake food web studies in the past decades have focused on identifying the trophic basis of support for higher consumers. These studies have revealed new insights into energy flow pathways in lakes. One important area of research has examined the energy (carbon) sources supporting higher trophic level production. Studies examining organisms' diets and stable carbon isotopes have found benthic (bottom) algae-based production pathways to be especially important in supporting higher consumers such as fish (Vander Zanden and Vadeboncoeur, 2002). This was surprising, as benthic production and trophic pathways have traditionally received little attention in limnology. An important implication is that fish play a central role in coupling benthic and pelagic production pathways in lakes.

Studies have also reported an important role of terrestrial-derived carbon in supporting higher trophic levels in lakes (Pace et al., 2004). This is especially the case in small lakes with high levels of terrestrially-derived dissolved organic carbon (DOC). This work reveals the potentially important role of heterotrophic bacterial food web pathways in supporting the production of metazoan consumers. Heterotrophic bacteria are known for their role in decomposition of organic matter. More recent work reveals that microbial food chains involving flagellates, protozoans, and rotifers funnel bacterial production (albeit with varying efficiency) back into classical metazoan food webs, ultimately supporting higher consumers such as fish. The presence of terrestrially-derived DOC plays a critical role. It reduces light penetration, and thus limits lake primary production. It also fuels heterotrophic bacterial production, and the microbial food web pathways described above (Karlsson et al., 2009).

Cross-habitat linkages—It has long been recognized that the structure and function of lakes is strongly influenced by their surrounding landscape. Due to their low-lying position in the landscape, organic matter and nutrient runoff from the land readily make their way into waterways and ultimately into lakes. Expanding agricultural and urban land use have dramatically accelerated nutrient inputs. Land use is the dominant driver of lake and coastal eutrophication (i.e., nutrient enrichment of a waterbody), a global problem that has led to the degradation of lakes worldwide.

More recently, studies have identified the importance of lake-to-land linkages wherein lake-derived productivity fuels or influences adjacent terrestrial ecosystems (Gratton et al., 2008). Lakes support the early life stages of many invertebrates, which then emerge and continue their lives in terrestrial environments. Emergent insects transport nutrients from lake-to-land, sometimes resulting in a significant flux of nutrients and prey to terrestrial systems. Riparian predators rely on emergent aquatic insects as a food source. The export of aquatic production to terrestrial ecosystems is common and can alter the functioning of terrestrial food webs through a nutrient fertilization effect, and by providing prey subsidies to terrestrial consumers.

Dynamic food webs

Drivers of food web structure—What ultimately controls the abundance of organisms at different trophic levels in an ecosystem? This is a central question of dynamic food web studies. Energy flow in ecosystems is unidirectional, moving from lower to higher trophic levels. So it is perhaps obvious that lower trophic levels influence higher trophic levels as a result of this direct energetic reliance. But predators also influence their prey, and the implications can be far-reaching. Dynamic food web studies attempt to understand the controls that structure organismal abundance across different trophic levels. Two predominant paradigms arose: bottom-up and top-down, leading to a debate over the relative importance of these controls. For decades, scientists emphasized the importance of bottom-up factors. In lakes, this was supported by that fact that there is a strong relationship between nutrient loading or nutrient concentration and algal biomass (Schindler, 1974). More recently, the structuring role of consumers, or top-down controls have been investigated in lake food web studies. Today it is well recognized that both bottom-up (nutrients) and top-down (consumers) forces interact to structure lake food webs, and that complex interactions yield a much richer range of dynamics than would be the case with simple linear food chains (Zaret and Paine, 1973; Carpenter et al., 1987; Knight et al., 2005; Koel et al., 2019).

Trophic cascade concept—The influential role of predators in structuring prey communities in lakes has been known for many decades. In response to variability in phytoplankton biomass that could not be explained by nutrients, it was proposed that changes in top predators could propagate to lower trophic levels through what is now known as a trophic cascade (Carpenter et al., 1985). Through whole-lake manipulations, it was established that while potential phytoplankton biomass is set by nutrients, realized biomass is influenced by the reciprocal effects of predators on prey transmitted through the food web. In these experiments, the removal of top predators (piscivores) resulted in the increased abundance of zooplanktivores, decreased grazer abundance, and higher algal biomass (Fig. 4).

Behaviorally mediated effects—Many studies emphasize the effects of direct, lethal predation in creating cascades in lake food webs, but predators also greatly influence prey behavior, which indirectly alters community interactions. In the presence of predators, prey may reduce activity or change their use of habitat, thereby altering prey diets and interactions in food webs. For example, the presence of piscivorous largemouth bass (*Micropterus salmoides*) altered the habitat use of juvenile sunfish (*Lepomis* spp.), leading to behaviorally-mediated cascading effects on benthic macroinvertebrates (Werner et al., 1983). Without largemouth bass, juvenile sunfish prefer the pelagic zone, but in the presence of largemouth bass, sunfish change habitat to the vegetated littoral zone where

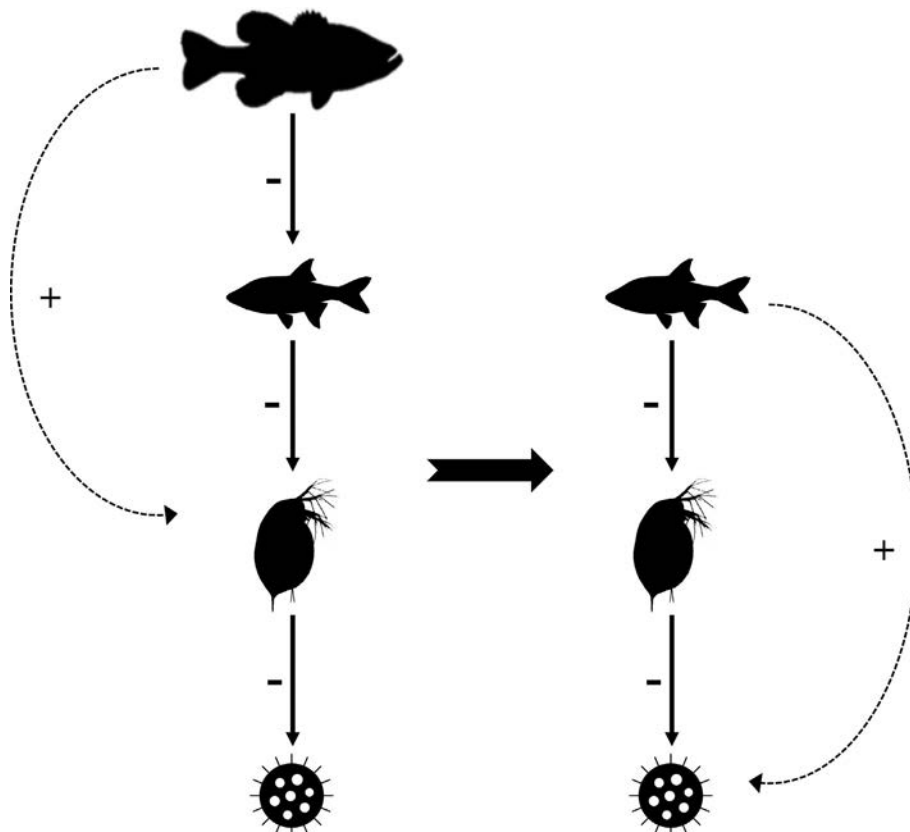


Fig. 4 A simplified dynamic pelagic food web consisting of four trophic levels. Solid arrows indicate direct interactions. Dashed arrows represent indirect interactions. Sign (– or +) represents the effect of the interaction. The horizontal arrow indicates an ecosystem shift wherein the top piscivore predator is removed.

they increase feeding on benthic macroinvertebrates, leading to reduced macroinvertebrate densities. It is clear that predators can have significant indirect effects on lake food webs by causing behavioral shifts in intermediate consumers.

The importance of indirect food web interactions is now well documented in a variety of contexts. This includes responses to the introduction of invasive species, situations involving cross-habitat linkages, and dynamics that play out over long time scales. In addition to providing a useful framework for assessing the role of top-down and bottom-up factors in structuring food webs, the trophic cascade concept also informs efforts to improve water quality in lakes (Hansson et al., 1998). Food web manipulations ('biomanipulations') such as stocking piscivores or removing coarse fish, are commonly employed to improve lake water quality, particularly where further nutrient reductions are not possible.

Structuring role of macrophytes—Macrophytes (i.e., aquatic plants) are an important group of primary producers in lakes that can play a role in regulating food webs. Beyond serving as a food source for certain lower level consumers, they also play an important structuring role in food webs. Macrophytes provide habitat for many species, serve as a predation refuge for invertebrates and fish, and greatly influence animal communities in a variety of ways (e.g., spawning, feeding habitat). By shaping predator-prey interactions, their effects can propagate through food webs. In this way macrophytes play a central role in the coupling of pelagic and littoral zones (Jeppesen et al., 1998).

Alternative stable states—Ecosystems exposed to changing environmental conditions, such as climate change or nutrient loading, may respond in different ways. Some systems change gradually, while others may abruptly shift between alternative states over a range of environmental conditions. An ecosystem exhibits 'alternative stable states' when the system response is not continuous given gradual changes in an environmental variable but instead shifts abruptly between two alternative equilibria (Scheffer et al., 1993). This theory was established from the study of shallow lakes in response to varying nutrient loading. Researchers observed that lakes displayed two equilibria: a clear state dominated by aquatic vegetation and a turbid state characterized by high phytoplankton biomass. Characteristic of alternative stable states, the lakes remained in their respective regime and a change in nutrient loading was insufficient to reverse states. Instead, considerable effort or a severe perturbation, such as intensive removal of zooplanktivorous fishes (biomanipulation) was needed to "push" the system back to the alternative state.

Food web stability—A topic of long-time interest to food web ecologists centers on how food web structure and complexity influences ecosystem stability. Stability can have different meanings, but often refers to susceptibility to runaway variation in species' abundances. Historically it was argued that complex food webs were buffered against strong dynamics and thus likely to be more stable. But theoretical analyses by May (1972) found that complexity tended to destabilize food webs. The most recent work reveals that if most food web linkages are weak, complexity tends to confer stability to food webs (McCann et al., 1998). Weak links serve to reduce fluctuations between consumers and producers, thereby maintaining populations further away from collapse. Studies of natural lake communities reveal that food webs are largely composed of weak interactions and few strong interactions. Today, food web stability and interaction strength in lakes continues to be a topic of great interest.

Integrative and applied perspectives

Lake food webs are characterized by complex biotic interactions. Food web interactions in lakes can also be influenced by external physical, chemical, and biological drivers. While the primary paradigms for how organisms interact and regulate one another are well established, the study of lake food webs is interdisciplinary and draws upon multiple realms of knowledge. As a result, there are many other approaches used to further our understanding of lake ecosystems that ultimately inform the use and management of lakes. Here we highlight several integrative and applied perspectives that demonstrate the cross-disciplinary approaches taken in the study of lake food webs.

Incorporation of microbial components—Historically studies of lake food webs largely overlooked microbial components of the ecosystem. But even with traditional food web approaches, many observed that the energy produced by phytoplankton was not enough to explain the productivity of higher trophic levels, prompting recognition of the importance of the 'microbial loop'. Heterotrophic bacteria are well known for their role in the decomposition of organic matter in lakes. There is a more recent recognition that bacteria form the basis of a pelagic microbial food web involving organisms such as heterotrophic flagellates, ciliates, and rotifers that ultimately links to the traditional metazoan food web (crustacean zooplankton, fish). The degree to which this microbial loop is an energetic 'link' or 'sink' in lakes is highly context dependent. Incorporation of the microbial loop provided new insights into energy flow in lakes.

Stoichiometric approach — "you are what you eat"—Everything in ecosystems is made up of chemical elements, such as carbon (C), nitrogen (N), and phosphorus (P). The study of the ratios among these chemical elements is called stoichiometry, which has become particularly influential in aquatic ecology with the field of ecological stoichiometry. Ecological stoichiometry considers the relative contribution of nutrients (e.g., C, N, P) as structuring agents of food webs (Sterner and Elser, 2002). This approach stems from the finding that a consumer's chemical composition reflects the chemical composition of its food, or in other words, "you are what you eat." Although ecological stoichiometry is applicable to any element, most studies focus on C, N, and P as they are the dominant components of organisms and often growth limiting (especially N and P). In aquatic systems, the ratio between C, N, and P (C:N:P) in the water is used to assess which of these nutrients is limiting for primary producers and thus higher trophic levels. In this view, relative nutrient concentrations provide the fuel for potential ecosystem productivity and animals represent large pools of nutrients that interact to structure lake communities (Sterner and Elser, 2002).

In addition to storing nutrients in their bodies that may be made available as they die and decompose, animals also have important indirect effects on lake stoichiometry. Higher level consumers, such as fishes, excrete and translocate nutrients within ecosystems, providing a substantial portion of phytoplankton nutrient demand (Vanni, 2002). For example, when zooplanktivorous fish become abundant they reduce grazing pressure by zooplankton (top-down effect), but they also promote phytoplankton growth by increasing available phosphorus through excretion (indirect bottom-up effect). Through direct and indirect impacts on ecosystems, consumers act as sources and sinks of nutrients and can impact lake community interactions.

Contaminants—The study of food webs has also made contributions to our understanding of contaminants in lakes. For contaminants such as methyl mercury, Polychlorinated biphenyls (PCBs), and dichloro-diphenyl-trichloroethane (DDT) that are transferred up food chains from prey to predator, the trophic position of a consumer is a strong determinant of contaminant levels (Cabana and Rasmussen, 1994). For these toxins, higher contaminant concentrations are found in progressively higher trophic levels, accumulating as they move up the food chain in a process known as ‘biomagnification.’ Food chain biomagnification can have noteworthy impacts, especially when highly contaminated prey are eaten by fish-eating birds and mammals, and toxins are passed on to adjacent ecosystems (Blais et al., 2007). Recent work has also identified concern over neonicotinoid insecticides. These chemicals are widely used in agriculture and have toxic impacts on planktonic and benthic invertebrates. The decimation of the food base due to neonicotinoids has led to fishery declines and is an emerging area of research (Yamamoto et al., 2019).

Bio-manipulations with unintended consequences—Natural resource managers have often intentionally introduced species to achieve management objectives. Such efforts have involved the introduction of predatory fish to elicit a trophic cascade to increase water clarity (Hansson et al., 1998). Others have aimed at supplementing the forage base. These species introductions can have unintended consequences that ripple throughout the food web. One example involves the opossum shrimp (*Mysis relicta*), a predatory zooplankton that has been introduced into lakes of western North America and elsewhere to augment the food base for salmonids. Opossum shrimp introductions have led to sharp declines in large zooplankton species (e.g., *Daphnia*) and a shift to smaller zooplankton taxa, often leading to fishery declines. Specifically, in Lake Tahoe (CA-NV, USA), opossum shrimp were introduced in the 1960s, which led to significant declines in large zooplankton, reduced water clarity, and declines in Kokanee salmon. In Flathead Lake (MT, USA) the effect of introduced *Mysis* was similar in that zooplankton declined. In addition, this introduction bolstered populations of the non-native piscivore, Lake Trout. This increased predation on Kokanee salmon, thereby leading to their collapse. Further, these shifts redirected ecosystem energy flow, limiting resources available to nearby ecosystems and causing declines in terrestrial top predators (e.g., bald eagles; Ellis et al., 2011).

Fish species are commonly introduced to lakes to satisfy fishery management objectives but can have unexpected food web consequences. In some instances, the introduction of non-native species can have effects that cascade through the food web and adjacent ecosystems. For example, following the stocking of non-native lake trout (*Salvelinus namaycush*) in Yellowstone Lake (WY, USA), highly valuable endemic Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) declined significantly (Koel et al., 2019). But it is not only non-native species that cause concern. Stocking of native fishes has also resulted in unintentional effects. In many lakes in North America and Europe, fishes of recreational interest are stocked annually. This practice can homogenize fish faunas, reduce genetic variation, and alter community composition as a result of higher predator populations than may occur naturally (Eby et al., 2006). In summary, intentional efforts to manipulate biotic composition in lakes often has unexpected effects that can ripple through multiple trophic levels and even into adjacent ecosystems (Koel et al., 2019).

Invasive species impacts on food webs—The introduction of non-native species can have profound effects on lake food webs. The Laurentian Great Lakes, with >180 introduced non-native species, have experienced so many food web disruptions that it can be difficult to interpret. One exception has been the invasion of Dreissenid mussels (*Dreissena* sp.). In 1988, Dreissenid mussels were discovered and quickly spread throughout much of the Great Lakes. Dreissenids are effective filter feeders and excrete organic material to the benthic substrate they inhabit. Given the rapid expansion and population growth of Dreissenid mussels in the Great Lakes, water clarity increased. This resulted in widespread ‘benthification’ wherein energy production shifted from pelagic to benthic regions, leading to an ecosystem-wide shunt from pelagic to benthic food web pathways (Mayer et al., 2013). The invasion of Dreissenid mussels greatly modified physical habitat with far-reaching effects on lake food webs.

Climate change impacts on food webs—As climate changes, food webs may experience strong perturbations resulting in unexpected consequences if interacting species respond differently to shifting environmental conditions. In Lake Washington (WA, USA), it was shown that increasingly warmer springs over the past 40 years have led to the uncoupled timing of phytoplankton and zooplankton blooms (Winder and Schindler, 2004). The spring diatom bloom no longer synchronized with the keystone herbivore (*Daphnia*) hatching period due to climate warming, resulting in long-term declines in *Daphnia*. Beyond the effects of climate change on the phenological coupling of trophic levels, climate change is expected to dramatically alter species interactions in lakes, though there is still much uncertainty regarding what the future will look like given the potential for unexpected results.

Social and economic change as a result of food web shifts—Food webs can change as a result of many drivers including bio-manipulations, invasive species, and climate change. Structural food web changes can have drastic impacts on lake ecology itself, but these shifts can also ripple throughout human communities reliant on these ecosystems for nourishment, suitable water quality, as well as employment/tourism opportunities causing dramatic social and economic changes. One of the most pronounced examples of this occurred in Lake Victoria, Africa when a large-bodied piscivore, Nile perch (*Lates niloticus*), was introduced in the 1950s. Nile perch have transformed the lake food web as they rapidly consumed native fishes, specifically causing the extinction/near-extinction of numerous endemic cichlids (Bairwa et al., 2003). As a result of the disrupted native ecosystem, many locals were displaced from traditional occupations in the fishing trade or bought into the cash economy to purchase nets capable of catching adult Nile perch. The introduction of Nile perch ushered in a robust commercial fishery, leading to a novel international trade economy that has

further impacted social dynamics in the region. Beyond drastically altering the lake food web, the Nile perch fishery has led to further deforestation in the region, increased conflicts over fish exportation, and has rippled into the illegal trade of wildlife (e.g., bushmeat) as fishery catches fluctuate. Given the demand and reliance on Nile perch, this species has been overfished, which in combination with other ecosystem changes (e.g., water quality declines, nearshore human population growth) has led to further food web shifts and socio-economic changes (Balirwa et al., 2003). People are highly reliant on lakes for numerous services, including nutrition, employment, and recreation. Perhaps it should not come as a surprise that changing food webs can have dramatic consequences for human societies and well-being.

Conclusion

Food webs are a way of representing predator-prey relationships, energy flow, and multi-trophic level interactions in ecosystems. While food webs show the pathways of energy flow in ecosystems, predator-prey interactions simultaneously influence this flow of energy and cycling of nutrients, thereby shaping the productivity and abundance of organisms across multiple trophic levels. The structure of food webs is influenced by both internal and external drivers. Despite their relatively small global coverage, lakes provide disproportionately valuable ecosystem services to humans, which are highly influenced by food web interactions. Many different approaches and perspectives are used to understand lake food webs, including connectance, energetic, and dynamic approaches. In combination with other disciplines, these approaches highlight how food web structure affects community and ecosystem properties of lakes, including the ecosystem services that benefit humans.

Knowledge Gaps

- How can we simplify the vast complexity of natural food webs into something more manageable to inform our understanding and management of these ecosystems?
- How does food web structure and food web complexity in particular influence ecosystem stability and resilience?
- What are the causes and consequences of abrupt shifts in lake ecosystem states?
- What are the consequences of invasive species for lake food webs?
- How do shifting external drivers such as climate interact with changing food webs?
- What are the implications of changing lake food web for the multitude of ecosystem services provided by lakes?
- What is the role of adaptation and evolution in species interactions, and what are the broader food web consequences?
- How do parasitic interactions affect lake food webs?

Case Studies.

<i>Site name</i>	<i>Country</i>	<i>Coordinates</i>	<i>Topic/concept</i>	<i>Key reference</i>
Cedar Bog Lake	USA	45.4105, –93.1991	Tropho-Dynamic Concept	Lindeman (1942)
Peter, Paul and Tuesday Lakes	USA	46.2522, –89.5040	Trophic cascade	Carpenter et al. (1987)
Peter and Paul Lakes	USA	46.2522, –89.5040	Terrestrial support	Pace et al. (2004)
Lake Mývatn and 7 nearby lakes	Iceland	65.5975, –17.0029	Cross-habitat linkages	Gratton et al. (2008)
Great Linford Pits and Ponds	UK	52.0698, –0.7571	Alternative stable states	Scheffer et al. (1993)
Flathead Lake	USA	47.8999, –114.1165	Biomanipulation	Ellis et al. (2011)
Laurentian Great Lakes	USA	42.1159, –81.4271	Invasive species effects (benthification)	Mayer et al. (2013)
Lake Victoria	Kenya, Uganda, Tanzania	–0.595261, 33.462087	Socio-economic effects	Balirwa et al. (2003)

See Also: Fundamental concepts and theories: Parasites in Aquatic Food Webs: How and Why Environmental Gradients Influence Epidemics and Their Implications; Trophic Dynamics and Food Webs in Aquatic Ecosystems; Structures and functions of Inland Waters - Groundwater: Trophic Interactions in Subterranean Environments; Structures and functions of Inland Waters - Lakes: Predation on Zooplankton; Structures and functions of Inland Waters - Rivers: Aquatic Food Webs In Rivers; Ecological and Evolutionary Consequences of Disturbance in Freshwater Ecosystems; Energetics and Food Webs in Large Rivers; Secondary Production in Streams

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