Food Webs 37 (2023) e00315

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.elsevier.com/locate/fooweb

Putting a lake together: Integrating synthetic data and field observations to build a better food web

Jonathan J. Borrelli [a,*], Matthew S. Schuler [b], William D. Hintz [c], Mary Alldred [d], Brian Mattes [a], Candace Schermerhorn [a], Erika Yates [a], Lawrence W. Eichler [a], Mark A. Lucius [a], Rick A. Relyea [a]

[a] *Rensselaer Polytechnic Institute, Troy, NY, USA*
[b] *Montclair State University, Montclair, NJ, USA*
[c] *Department of Environmental Sciences and Lake Erie Center, University of Toledo, Oregon, OH, USA*
[d] *SUNY Plattsburgh, Plattsburgh, NY, USA*

ARTICLE INFO

Keywords:
Trophic interactions
Lake food web
Network topology
Aquatic systems
Data integration

ABSTRACT

Food webs provide context to understand how ecological communities will respond to environmental change, but revealing their structure typically relies upon time-intensive sampling and analysis of species' diets. As a result, all food web models require some unavoidable simplifications because of limited data availability, whether temporally, spatially, or taxonomically. Large databases of published trophic interactions have made this process somewhat easier, but knowledge gaps persist. We combine the use of databases with extensive field surveys, including gut-content analysis, to generate a food web for Lake George, NY. Including aquatic plants, phytoplankton, zooplankton, macroinvertebrates, and fish, our analysis identified 279 genera in the lake involved in 1910 interactions. After removing genera with no identified interactions or improbable interactions and grouping some genera into higher categories, the food web included 49 nodes with 484 interactions among them. The network structure of the inferred Lake George food web exhibits several common patterns such as relatively few trophic levels and the prevalence of tritrophic chains. Our results suggest that constructing food webs from databases provides a useful first step to determine topology. However, in situ sampling allowed us to account for additional interactions, as only 50 of the 106 directly observed interactions between fish and their prey were also found in published databases. Finally, we highlight the need to focus on developing a better understanding of herbivory in lakes, as species interactions among the diverse plankton and macroinvertebrate populations are not well known.

1. Introduction

Food webs are networks of consumer-resource interactions and offer a useful model for understanding community structure, ecosystem processes, and population dynamics. Despite their importance, identifying food web structure is empirically difficult and requires a substantial amount of time-intensive sampling and possible experimental feeding trials. Various methods exist to determine the structure of food webs, including expert opinion (Martinez, 1991), literature surveys (Patonai and Jordán, 2021), phylogenetic relationships (Naisbit et al., 2011; Eklöf et al., 2012), stable isotope analysis (Vander Zanden et al., 1997), and gut-contents analysis. Because guts can be empty and highly variable in individual diet snapshots, many samples are required to identify all feeding interactions between consumers and resources (Baker et al., 2014). Moreover, proper identification of soft-bodied organisms without sequencing analysis remains difficult, and this method may not work for some small-bodied zooplankton. Ultimately, in situ data must almost always be supplemented with alternative data sources or methods to properly estimate or quantify species and trophic interactions. Constructing reliable food web networks is critical for developing models to simulate population dynamics, forecast how biomass will change over time, and estimate the effects of anthropogenic change.

Literature surveys of food webs are becoming easier with new computational methods and the recent development of large databases of empirically derived trophic interactions (Brose et al., 2005; Poelen et al., 2014; Gray et al., 2015), but the data are often not standardized or may not include species of interest. Data from these published compilations have shown great promise for large-scale qualitative predictions

---

[*] Corresponding author at: 110 8th St, Troy, NY 12180, USA.
E-mail address: borrej4@rpi.edu (J.J. Borrelli).

https://doi.org/10.1016/j.fooweb.2023.e00315
Received 21 February 2022; Received in revised form 21 July 2023; Accepted 14 September 2023
Available online 22 September 2023
2352-2496/© 2023 Elsevier Inc. All rights reserved.

and to help identify knowledge gaps for biological systems (Poisot et al., 2016). However, the value, as well as the costs and benefits, of using synthetic data to inform small scale predictions remains unclear.

Food web models frequently include taxonomic aggregation, which may be exacerbated when synthetic data are used. The level of aggregation (i.e., resolution) directly impacts the structure of the network (Martinez, 1991). Because topology and dynamics are linked, misleading topology can result in incorrect inference about the resilience of the system. However, we may still be able to glean useful knowledge about the system when constructing a food web, as multiple network characteristics can be robust to varying levels of aggregation (Gauzens et al., 2013). For example, many lake food web models have included age- or stage-based fish taxa, while simultaneously grouping zooplankton into multi-species groups, such as cladocerans (Kao et al., 2014; Colvin et al., 2015). These models have guided understanding of how impacts such as eutrophication and invasion have altered the flow of energy through the food web. Similarly, using a functional-group approach often results in differing aggregation levels, but this approach is useful to construct generalized food web models that replicate observed dynamics like the seasonal trends in the pelagic food web of Lake Constance (Boit et al., 2012). Thus, we must balance the need for accurate food web topology with the availability of data.

In this study, we combined published interaction data with recent and past biological field surveys to construct a food web for Lake George, NY (USA). Using this approach, we sought to address three main questions: (1) what are the costs and benefits of applying database-centered approaches to construct food webs, (2) how much can database-centered food webs be improved by incorporating field observations, and (3) once the food web structure is determined, how does it compare to our expectations based on other published food webs? We identified the limitations of the database approach and the gaps in our knowledge of species interactions in the lake by comparing inferred interactions against direct observations. We further identified the structural properties of the aggregated Lake George food web and interpret how they compare to other published food webs.

2. Methods

2.1. Study system

Lake George is a large, temperate, dimictic, oligotrophic lake located in upstate New York, U.S.A. The average lake depth is 18 m, with the deepest point at 58 m. The surface area of the lake is 11,400 ha, with 210 km of shoreline. The total volume is 2.1 km^3. Lake George has been the subject of numerous biological surveys, and an offshore chemistry and phytoplankton monitoring program since 1980 (Hintz et al., 2020).

2.2. Field surveys

We developed a list of taxa for Lake George based on extensive field surveys. We also obtained a list of phytoplankton taxa based on past studies of the lake (Howard, 1973; Siegfried, 1981). The Offshore Chemistry Program on Lake George has included zooplankton collection at 11 sites throughout the lake since 2013, using depth-integrated sampling to the 1% light level. For each zooplankton sample, 10 L of water were filtered through a 64-μm mesh net and preserved using Lugol's iodine. Zooplankton were identified using an Olympus SZ-16 microscope with a 1× objective and assigned to one of four groups: cladocerans, cyclopoid copepods, calanoid copepods, or rotifers. Predatory cladocerans and copepod nauplii were counted separately.

We sampled the nearshore regions of the lake (<5 m depth) in summer and fall from 2015 to 2019 for zooplankton and macroinvertebrates. Zooplankton were sampled at 28 sites around the lake using a 64-μm mesh net dragged from approximately 1 m off-bottom to the surface of the lake. The zooplankton were identified using the same protocol as the offshore survey. We sampled macroinvertebrate communities from 38 different sites throughout the lake using a petite Ponar grab sampler. We filtered each sample through a 1-mm sieve and preserved the organisms in 70% ethanol for future enumeration and identification using an Olympus SZ51 microscope. We supplemented the nearshore surveys with haphazard sampling of the fish community using a variety of gear types (Fyke nets, gill nets, dipnets, seines, and electrofishing) throughout the lake from 2015 to 2019.

2.3. Food web construction

As part of the fisheries survey, 504 specimens of 20 different fish species were preserved and dissected to identify their gut contents in 2015, 2016, and 2017. We preserved fish by storing them in a freezer; individual guts were dissected under an Olympus SZ-16 microscope with a 1× objective, and prey were identified to the lowest taxonomic level possible. For each individual fish, we also measured length and mass. Most guts were from pumpkinseed (*Lepomis gibbosus*, $n = 112$) and yellow perch (*Perca flavescens*, $n = 109$). We had at least 20 individuals for redbreast sunfish (*Lepomis auritis*), yellow bullhead (*Ameiurus natalis*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), and rock bass (*Ambloplites rupestris*). The one specimen of brown bullhead (*Ameiurus nebulosus*), and two northern pike (*Esox lucius*) had empty guts and were not considered further in the gut-content analysis. Across the 504 guts, 88 different prey groups were counted. The 88 prey-item types were subsequently aggregated into 30 groups, by lumping more specific groups into more general (e.g., *Daphnia* were included in the cladoceran category; Table A1).

In addition to gut-content analysis, we included interactions among taxa derived from the literature. We searched several trophic databases including the Global Biotic Interactions Database (GLOBI; Poelen et al., 2014), and data compilations from Brose et al. (2005), and Gray et al. (2015). We obtained estimates of average body mass from published databases, though many fish taxa were measured directly in our field surveys (Brose et al., 2005; Gray et al., 2015).

To construct a food web that more easily matched observed data and reduced the number of errors, we aggregated the food web derived from interaction databases. We chose to group taxa primarily to match the level to which organisms could be commonly identified, and the scale at which they are reliably monitored (Table A2). We lacked sufficient data for most macrophytes, so we grouped all genera into a single macrophyte node. Phytoplankton abundance is typically measured indirectly as chlorophyll concentrations, but we lumped genera to the class level to better match with observations using a fluoroprobe, which can detect multiple pigment groups. Zooplankton from the databases were grouped the same as in our survey data (i.e., cladocerans, cyclopoid copepods, calanoid copepods, or rotifers). We aggregated macroinvertebrates to order. We have reliable data on presence and diet for most large fish, so we aggregated them at the genus level; however, we grouped the smaller Cyprinidae genera to a single node at the family level.

We also explored the impact of aggregation on the structure of the Lake George food by continuing to lump taxa into larger groups. We assessed 11 additional food webs with varying levels of aggregation into functional groups from 8 to 36 nodes with 18 to 322 links among them (Table A3).

2.4. Analysis

We examined the food web structure using multiple whole-web and node-based metrics including connectance, trophic position, generality, and vulnerability. All analyses were conducted using R version 4.0.4 (Appendix B; R Core Team, 2021). Connectance is defined as the proportion of realized links in the food web (L/(S*(S-1))), where L is the number of links and S is the number of nodes. Trophic position was calculated as 1 plus the average trophic position of a species' prey, where all producers have a trophic position of 1, using the *NetIndices* R package (Kones et al., 2009). For each trophic group, we computed the trophic generality (number of prey) and vulnerability (number of predators), normalized by the link density (L/S) using the *cheddar* package (Hudson et al., 2013). Finally, we calculated the importance of species in the network defined as the betweenness (i.e., the average number of paths connected to a node).

We characterized the meso-scale structure of the network based on three-species motifs. The standardized frequencies of three-species motifs tend to be similar across many food webs (Milo et al., 2002; Stouffer et al., 2007). The degree to which each motif is over- or under-represented in the food web, relative to what is expected by chance, has been linked to the dynamic properties of the community, and over-represented motifs constitute the basic building blocks of the food web (Milo et al., 2002; Prill et al., 2005; Borrelli, 2015). There are 13 possible connected three-species motifs in food webs, 5 that contain only single-directional links (A - > B) and 8 that also include double links (A < -> B). Single-directional link motifs include the commonly studied tritrophic chains (s1), intraguild predation (s2), trophic loops (s3), direct competition (s4), and apparent competition (s5). Motifs with bi-directional motifs do not have named analogues like the single-directional motifs. The d1 motif is apparent competition, where the competitors consume each other. The d2 motif is direct competition with the competitors consuming each other, the d3 motif is direct competition with the consumed group also consuming one of the competitors, and d8 is the same but with the prey also consuming both consumers. The d5 motif is a trophic loop with one reciprocal interaction. To identify patterns of over- and under-representation, we computed the motif profile of the Lake George food web using the *triad.census* function from the *igraph* package and compared the count to a null distribution (Csárdi and Nepusz, 2006). Each count was normalized by computing the mean and standard deviation of a null distribution of food webs (Stouffer et al., 2007; Borrelli, 2015). The null distribution was constructed by permuting the observed network using the Curveball algorithm (Strona et al., 2014). Permutations preserved the number of predators and prey each species has. We permuted the Lake George food web 1000 times to generate the null distribution.

We also computed the fluxes of energy among different groups using the *fluxweb* package (Gauzens et al., 2019). Computing the flux requires species' metabolic rates, feeding efficiencies, and biomasses (Table B1). Metabolic rates were estimated according to the allometric equation $X_i = x_0 M_i^b$, where x_0 and b are constants, and M_i is body mass (Brown et al., 2004). The allometric constants were assumed to be $x_0 = 0.71$ and $b = -0.25$ (Brown et al., 2004; Gauzens et al., 2019). We used feeding efficiencies derived from the literature according to the type of prey, with detritus = 0.158, plants = 0.545, and animals = 0.906 (Lang et al., 2017; Gauzens et al., 2019). We lack estimates for biomass of most organisms in the food web, so we made the simplifying assumption that biomass scales to the quarter power with body mass, following the metabolic theory of ecology (Brown and Gillooly, 2003; Cohen et al., 2003).

3. Results

3.1. Gut contents

The number of prey items in the guts of our fish samples ranged from 0 to 20. As expected, we found that fish species represented by more individuals contained more unique prey items (Fig. 1).

The most common prey items were trichopterans, amphipods, and ephemeropterans, with each appearing in 16, 14, and 11 out of 18 species' guts, respectively (Fig. 2). No single prey species dominated the diets of any fish species, with each prey item appearing in fewer than 20% of samples for each consumer species. Yellow perch most frequently contained amphipods (17% of guts) followed by cladocerans and isopods (10% each). Pumpkinseed most often contained amphipods, which appeared in 15% of guts. Redbreast sunfish contained trichopterans (22% of guts) and ephemeropterans (10% of guts). At least 12% of rock bass guts contained trichopterans, crayfish, amphipods, and

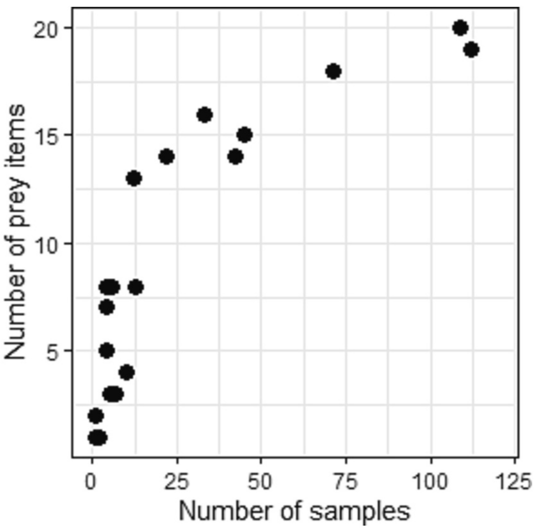

Fig. 1. The number of unique prey items found in each fish species' gut increases with the sample size across fish species.

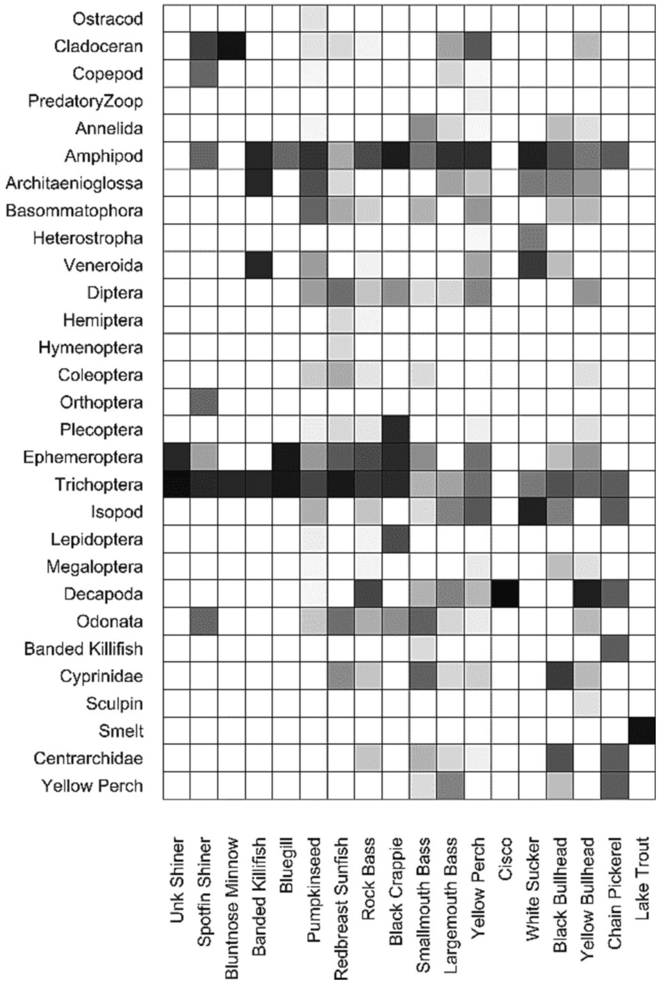

Fig. 2. Proportion of fish species' guts (columns) containing each prey item (rows). Filled squares indicate the presence of the prey in at least 1 individual's gut, darker shading indicates a higher proportion.

ephemeropterans. Just under 10% of smallmouth bass guts contained cyprinid prey and odonates, while 16% of largemouth bass guts contained amphipods. Yellow bullhead preferred crayfish (22% of guts), with the next most frequent prey, trichopterans, in 9% of guts.

3.2. Food web structure

Based on our survey of Lake George biota, we identified 279 genera in the lake, plus detritus. Our genus list included 20 aquatic plants, 108 phytoplankton, 2 protozoa, 24 zooplankton, 97 macroinvertebrates, and 28 fish. The initial food web construction based on the GLOBI Database included 1910 interactions among the 280 genera (including a detritus group). We found that the interaction matrix derived from the database contained numerous errors, possibly due to mismatches or partial matches between names in the database and genus names supplied to the API, as well as missing data. For example, several macrophytes (*Sagittaria*, *Elodea*, and *Bidens*) and phytoplankton (*Navicula*, *Ochromonas*, *Gymnodinium*, and *Peridinium*) were listed as consuming various fish, diatoms, and detritus. We removed these impossible or improbable interactions manually. In contrast, many consumers—3 zooplankton, 38 macroinvertebrates, and 1 fish—did not have any identified prey. Many genera in the list had no identified interactions at all, including 25 phytoplankton, 12 macrophytes, 1 protozoa, 1 zooplankton, and 31 macroinvertebrates. To better match synthetic data to observed data, we aggregated genera into higher-order taxonomic groups and removed disconnected nodes.

After grouping genera into broader groups (Table A2) we were left with a food web for the lake consisting of 49 nodes (Table A4; Fig. 3) with 484 interactions among them. The connectance was 0.21, which is within the expected range of food web connectance (0.05 to 0.25), though on the higher end (Dunne et al., 2002; Vermaat et al., 2009). Increased aggregation generally increased connectance, with a 14-node web having a connectance of 0.32 and webs of 16–30 nodes having connectance values of 0.26–0.29 (Table A5).

The aggregated food web included 7 producers, 2 protozoa, 4 zooplankton, 17 macroinvertebrates, 18 fish, and detritus. Of the 484 interactions, 434 were derived from the databases and 106 (22%) were observed in the fish diets of Lake George. Of the 106 interactions based on fish diets, 56 (53%) overlapped with those found in the databases. Comparing diet proportion as a measure of interaction strength, we found no difference between those interactions derived from the databases and those that were not, suggesting that the database is not biased toward strong interactions.

Mean trophic position in the food web was 2.6 (standard deviation = 0.97). The top predators with the highest trophic positions include pickerel and pike (*Esox*), black crappie (*Pomoxis*), yellow perch (*Perca*), and largemouth and smallmouth bass (*Micropterus*). Increasing aggregation of the food web resulted in reduced mean trophic position, to a minimum of 1.7 with only 8 nodes (Table A5). No genera were free from consumption, with even those in the top trophic positions having 2 to 9 consumers. The most generalist consumers were Atlantic salmon and brown trout (*Salmo*), lake trout (*Salvelinus*), yellow perch, largemouth bass, and smallmouth bass. The most vulnerable prey groups (those with the most consumers) were amphipods, dipterans, diatoms, and detritus. Trophic position was strongly positively correlated with the species' generality ($r = 0.84$, 95% CI = [0.73, 0.90]), but a negative correlation with vulnerability was much weaker ($r = -0.35$, 95% CI = [−0.58, −0.08]). The most important groups to the food web (i.e., those with the highest betweenness) were dipterans, yellow perch, and cyclopoid copepods.

The motif distribution of the food web showed patterns of strong over- and under-representation. Motif names (Fig. 4a) indicate that they either include single-directional links (s), or double links (d), following Stouffer et al. (2007). The network was characterized by over-representation of the s1, d2, and d6 motifs (Fig. 4b). The s2, s3, s4, d3, d5, and d8 motifs were all under-represented in the network. Increased aggregation (reducing the number of nodes in the network) resulted in changes to the representation of different motifs when the number of nodes was reduced to 25 or fewer (Fig. B1). With >25 nodes the pattern of motif representation was largely consistent. When the food web was less aggregated the s1, d2, and d6 motifs tended to be over-represented, while the s3, s4, d4, d5, and d8 motifs became more

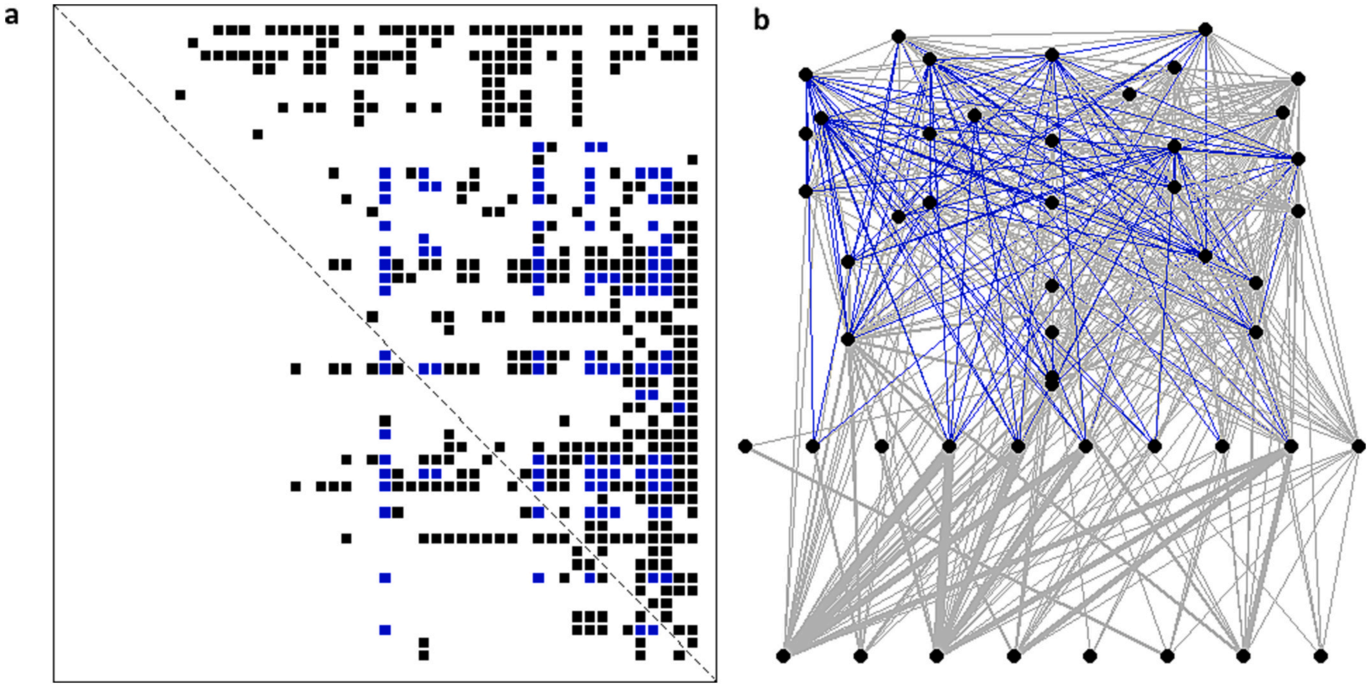

Fig. 3. Adjacency matrix for the Lake George food web (a) and the network structure (b). Blue boxes and links represent interactions that have been validated by gut content analysis. Other interactions are represented by black boxes (a) and gray lines (b). Link weights in b show flux from resource to consumer, increasing in trophic level from bottom to top. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

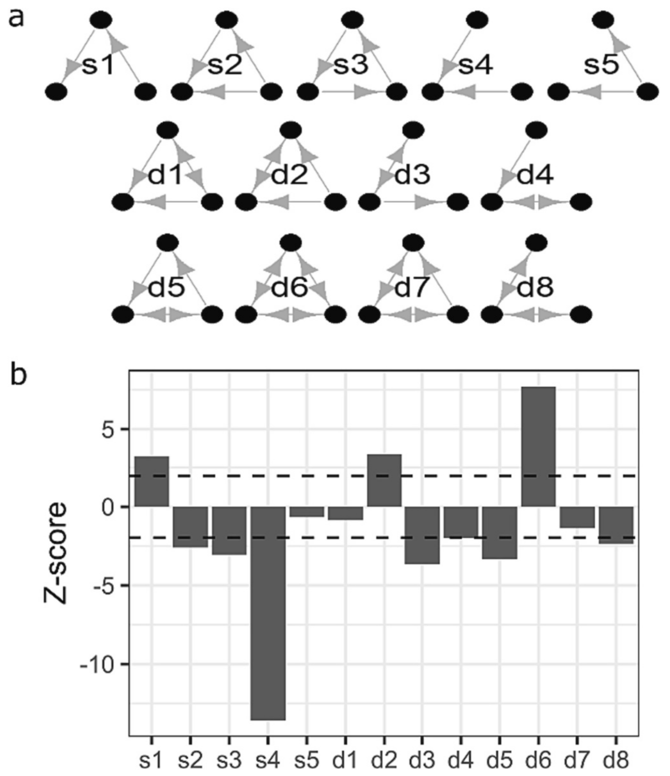

Fig. 4. The 13 distinct three-species motifs (a) and the motif z-score profile of the Lake George food web (b). *Z*-scores were computed by subtracting each motif count from the mean of a null distribution (generated by permuting the food web 1000 times) and dividing by the standard deviation of the distribution. The two dotted lines indicate +/− 1.96, and z-scores above/below the lines indicate significant over- or under-representation.

under-represented.

To get an idea of how energy flows through the food web and quantify key ecosystem functions, we computed the fluxes between trophic groups. Most energy in the food web comes through consumption of diatoms and detritus as these had the two highest total fluxes. We further used flux calculations to determine ecosystem functions including detritivory, herbivory, and carnivory. Relative to the total energy flux through the system, detritivory accounted for 16%, herbivory for 38%, and carnivory for 46%. These ratios were not sensitive to 10% variation in species' biomasses or body masses (i.e., altering metabolic rates).

4. Discussion

Approaches to food web construction that rely on field surveys will always be limited by the amount of data that can be collected. We assessed whether databases provide a useful supplement to observed data and to what extent they can be used to build a food web model. We linked interactions that were inferred from trophic databases to those that we observed directly in the guts of Lake George fishes. Our results indicated a broad validation of the top of the food web, with 22% of interactions directly observed. Including database-derived information was clearly necessary to construct the Lake George food web, as nearly 90% of the interactions included were derived from the literature. Only 13% of the 434 interactions from the food web database were also found by direct observation. Yet the database approach had substantial limitations, with nearly half of our observed interactions not included in the databases. Missing interactions in databases may be caused by mismatches in taxonomic resolution of observations both in our study and in previous ones.

Interactions among larger-sized components of the food web, such as fish, were generally easier to establish than interactions among plankton or other invertebrates. Measured interactions with primary producers are rare, even using databases that include thousands of published interactions across hundreds of food webs. In our aggregated food web, direct herbivory accounted for 16% of interactions, yet validation of herbivorous links with observations remains difficult. Given that relatively few food web studies have explored the planktonic food web with high taxonomic resolution and the high diversity of planktonic organisms, it is not surprising that knowledge gaps remain in our understanding of open-water herbivory (Boit and Gaedke, 2014; Sarno et al., 2016; Jordán et al., 2018). We also found substantial gaps in our knowledge of interactions among macroinvertebrate genera and their resources. Nearly 40% of the genera in our list of macroinvertebrates lacked any identified interaction data in the database (both as consumer and prey). Trophic lumping in food web studies may be the cause of missing interactions, with many macroinvertebrates grouped into nodes such as “benthic insects” (Fayram et al., 2006) or “meiobenthos” (Liu et al., 2007). In the future, additional benthic sampling and interaction detection using new technologies such as eDNA may help provide further validation of links at the bottom of the food web (Pringle and Hutchinson, 2020). These knowledge gaps highlight our need for a greater understanding of herbivory in aquatic food webs.

A great deal of effort is often expended to measure productivity in lake ecosystems, yet we lack sufficient understanding of community dynamics that contribute to rates of herbivory. Our estimates suggest that herbivory accounts for 38% of the total energy flux through the food web. More generally, herbivory can play a large role in driving dynamics within the phytoplankton community (Carpenter et al., 1987). Fluctuating stability in the interactions among *Daphnia*, pelagic diatoms, and pelagic detritus in a model freshwater ecosystem can drive shifts between clear-water and algal-dominated states during eutrophication (Kuiper et al., 2015). Estimates of taxa-specific herbivory pressure may also improve our ability to predict dominance of phytoplankton species, including blooms. Pelagic and benthic algal blooms are becoming an increasing nuisance in freshwater systems (Ho et al., 2019; Vadeboncoeur et al., 2021). It is imperative that we improve taxonomic resolution in our understanding of how energy moves through the lake food web to determine the causes and consequences of blooms. To determine the diets of herbivorous consumers reliably in situ will likely require DNA-based methods, though such approaches are still in development (Sheppard and Harwood, 2005).

Characteristics of the structure of the Lake George food web broadly conform to what we would expect for an oligotrophic lake. The Lake George food web had a similar level of connectance and size (number of taxa) as other published food webs (Dunne et al., 2002). Previously published high resolution lake food webs had connectance values ranging from 0.118 to 0.171 with 25 to 172 trophic groups (Dunne et al., 2002). The food web we constructed is more similar to those used in Ecopath models, such as those of Lake Huron (47 groups, 434 links; Kao et al., 2014) and Lake Erie (47 groups, 377 links; Zhang et al., 2016), rather than the more complex web of Little Rock Lake (181 taxa, 2431 interactions; Martinez, 1991). Because connectance and network size are the two most important parameters driving food web structure, we would expect other structural properties to be similar as well (Vermaat et al., 2009).

Average food chain length in Lake George was relatively short (mean trophic position = 2.6) and the highest trophic position was 4. The average food chain length remained similar for webs with additional aggregation down to 34 nodes, and maximum trophic position remained similar down to 28 nodes. The presence of relatively short food chains matches what we would expect based on published high resolution webs from multiple ecosystem types, which typically have fewer than 5 trophic levels (Williams and Martinez, 2004; Borrelli and Ginzburg, 2014). The trophic position of fish taxa estimated in the Lake George food web were generally within the range found in the literature and by stable isotope analysis (Vander Zanden et al., 1997).

In addition to trophic structure, we also explored the basic building blocks of the Lake George food web by examining the motif distribution. Motifs characterize distinct types of networks, with food webs typically sharing similar patterns of motif representation (Milo et al., 2002). Notably, the over-representation of the tri-trophic chain is common in multiple food webs across ecosystem types (Stouffer et al., 2007; Borrelli, 2015). Tri-trophic chains are expected to be stable structures (Borrelli, 2015), with species participating in them tending to be less susceptible to perturbations (Cirtwill and Wootton, 2022). Omnivory, apparent competition, and direct competition are also considered to result in increased stability (Borrelli, 2015; Cirtwill and Wootton, 2022), but were not over-represented in our network as we would expect. It is possible that their under-representation and the over-representation of tri-trophic chain are related, as increased aggregation lumps competitors into a single-node. The over-representation of competition with competitors consuming each other (d2) and the fully connected motif (d6) are also predicted by structural models (e.g., the niche model; Williams and Martinez, 2000), and can be common in food webs (Stouffer et al., 2007). However, species participating in the d2 and d6 motifs are unlikely to persist over time, and therefore the pattern should be somewhat under-represented (Borrelli, 2015).

One explanation for the over-representation of motifs with reciprocal links is that stage-structured interactions are important in the Lake George food web, and in aquatic food webs more generally. Over their lifetimes, fish body size can range over several orders of magnitude and many may undergo ontogenetic shifts in diet preferences as they grow (Mittelbach and Persson, 1998). As an example, a lake trout may be consumed by smaller fish like perch when trout are still juveniles, but when trout reaches adulthood the interaction switches. If we consider the interaction without age-structure, eventually one species would outcompete the other and one would go extinct. Including explicit age-structure in double-link interactions may result in increased stability by creating size-based refuges for each species (Nilsson et al., 2018). Data on trophic interactions occasionally include information on resource or consumer age class, but not often. Our network does not account for age-structured shifts in interactions, though they could easily generate three-species patterns wherein each species eats the other or two competitors eat each other.

Over-representation of motifs that include reciprocal links may, alternatively, be the result of over-aggregation of the nodes, with some species within the coarser taxonomic groups interacting and others not. It would require a higher resolution food web to disentangle the impact of aggregation on motif representation, as motif profiles are largely consistent across more aggregated webs.

The aggregated version of the web we analyzed is likely a maximally connected food web, including all possible interactions among groups. Trophic aggregation is, for now, an intrinsic limitation of the approach to using databases to inform food web models. However, food web structure is preserved over a large range of aggregation in food webs, suggesting that with enough taxa many limitations can be overcome (Gauzens et al., 2013). In that sense, because the database approach allows us to incorporate known interactions among more taxa than would otherwise be available by direct observation, the benefits likely exceed the costs.

Building a preliminary food web for a lake is a key first step toward improving research on the long-term dynamics of the system and building understanding of how it will respond to environmental change. The Lake George food web is complex, with nearly 300 interacting genera that we can detect and measure within the lake itself. The food web we created for Lake George, as well as the multiple aggregated versions of the food web, could also be used as part of a dynamic food web model. By comparing model output against observations of population densities we can determine optimal food web structural complexity for understanding the lake. Multiple modelling frameworks are available to build inference about complex network effects of perturbations and external factors (Patonai and Fábián, 2022). We could also identify the importance of different food web links to replicate the observed changes in population densities.

We have not considered cross-ecosystem interactions driven by birds and insects, and we lack data on amphibians and aquatic mammals. However, we have shown that including interactions derived from databases shows promise for bridging gaps in our field data. Supplementing observations with occurrence data using the Global Biodiversity Information Facility (GBIF) database and determining their interactions with GLOBI may be a fruitful way to expand the current food web for Lake George (Poisot et al., 2016). We could then quickly begin to generate quantitative testable predictions about cross-ecosystem interactions within the Lake George watershed. Using interactions derived from the literature is a common practice when constructing food webs for analysis, but the limitations and benefits are not always explicit (Sánchez-Hernández et al., 2015; Peralta-Maraver et al., 2017; Olivier et al., 2019). Despite the potential drawbacks, we suggest that the benefits of combining database-derived interactions with field observations outweigh the costs. Our preliminary food web for Lake George exhibits many structural patterns that are commonly observed in food webs, such as short food chains and three-species motifs. We have also shown that using the database alone yields a network that captures about half of the interactions we directly observed among fish consumers and their prey. Given the low cost (both in time and effort) of obtaining database-derived interactions, generating food webs using this approach is highly valuable even for lakes with limited to no data. The derived food webs can be used as a starting point for simulations of population dynamics, forecasting how biomass will change over time and estimating the effects of anthropogenic change.

Declaration of Competing Interest

None.

Acknowledgements

Funding was provided by The Jefferson Project at Lake George, which is a collaboration of Rensselaer Polytechnic Institute, IBM Research, and the Lake George Association. We would additionally like to thank the many undergraduate assistants who aided in the sampling of the lake.

Appendix A. Appendix

Table A1
Fish gut content grouping.

Original_ID	Group_ID
Un-ID aquatic insect	Other
Un-ID terrestrial insect	Other
Trichoptera	Trichoptera
Trichoptera House	Trichoptera
Ephemeroptera	Ephemeroptera

(continued on next page)

Table A1 (*continued*)

Original_ID	Group_ID
Fish Eggs	Other
Blunt Nosed Minnow	Cyprinidae
PUS	Centrarchidae
Cyprinidae	Cyprinidae
YEP	Yellow Perch
ROB	Centrarchidae
BKF	Banded Killifish
Centrarchidae	Centrarchidae
Smelt	Smelt
Un-ID Fish	OtherFish
Minnow	Cyprinidae
Scales	Other
Sculpin	Sculpin
LMB	Centrarchidae
Un-ID Sunfish	Centrarchidae
Gammarus	Amphipod
Hyallela	Amphipod
Isopod	Isopod
Amphipod	Amphipod
Snail Eggs	Other
Helisoma	Basommatophora
Ramshorn	Basommatophora
Physa	Basommatophora
Gyraulus	Basommatophora
Chinese Mystery Snail	Architaenioglossa
Valvata piscinalis	Heterostropha
Operculum	Other
Un-ID Snail	OtherSnail
Banded Mystery Snail	Architaenioglossa
Campeloma	Architaenioglossa
Daphnia dubia	Cladoceran
Daphnia spp.	Cladoceran
Bosmina longirostris	Cladoceran
Chydoridae	Cladoceran
Daphnia pulex	Cladoceran
Cladoceran	Cladoceran
Bosmina longirostrus	Cladoceran
Eurycerus spp.	Cladoceran
Simocephalus serrulatus	Cladoceran
Copepod	Copepod
Ostracod	Ostracod
Limnadia	OtherZoop
Bythotrephes longimanus	PredatoryZoop
Holopedium gibberum	Cladoceran
Crayfish	Decapoda
Zygoptera	Odonata
Dragonfly larvae	Odonata
Anisoptera	Odonata
Plecoptera	Plecoptera
Sceliphron Caementarium	Hymenoptera
Megaloptera	Megaloptera
Diptera	Diptera
Midge Larvae	Diptera
Moth/Butterfly	Lepidoptera
Midge	Diptera
Lepidoptera	Lepidoptera
Haliplus (Haliplidae)	Coleoptera
Coleoptera	Coleoptera
Hemiptera	Hemiptera
Belostoma testaceum (Belostomatidae)	Hemiptera
Hylecoetus (Lymexyloidea)	Coleoptera
Phyllotreta	Coleoptera
Mosquito (*Aedes albopictus*)	Diptera
Chironomid	Diptera
Tipulidae	Diptera
orthoptera	Orthoptera
Pisidium	Veneroida
Fingernail Clam	Veneroida
Sphaeridae	Veneroida
Naididae	Annelida
Nematoda	Other
Horse Hair Worm	Other
Annelida	Annelida
Cestoda	Other
Leech	Other
Nematomorpha	Other

(*continued on next page*)

Table A1 (*continued*)

Original_ID	Group_ID
Water Mite	Other
Macrophyte seed	Other
Plant material	Other
Garbage	Inorganic
Pebbles	Inorganic
un-ID fish guts	Other
un-ID item	Other

Table A2

Food web grouping – 290 genera are aggregated to the 49 groups listed in the DietGrp column.

Type	Common	Genus	DietGrp
Submerged Aquatic Veg	Grassy arrowhead	*Sagittaria*	Macrophyte
Submerged Aquatic Veg	Water marigold	*Bidens*	Macrophyte
Submerged Aquatic Veg	Lake cress	*Rorippa*	Macrophyte
Submerged Aquatic Veg	Awlwort	*Subularia*	Macrophyte
Submerged Aquatic Veg	Water lobelia	*Lobelia*	Macrophyte
Submerged Aquatic Veg	Chara	*Chara*	Macrophyte
Submerged Aquatic Veg	Smooth stonewort	*Nitella*	Macrophyte
Submerged Aquatic Veg	Small waterwort	*Elatine*	Macrophyte
Submerged Aquatic Veg	Pipeworts	*Eriocaulon*	Macrophyte
Submerged Aquatic Veg	Alternateflower watermilfoil	*Myriophyllum*	Macrophyte
Submerged Aquatic Veg	Eurasian watermilfoil	*Myriophyllum*	Macrophyte
Submerged Aquatic Veg	Slender watermilfoil	*Myriophyllum*	Macrophyte
Submerged Aquatic Veg	American waterweed	*Elodea*	Macrophyte
Submerged Aquatic Veg	Slender naiad	*Najas*	Macrophyte
Submerged Aquatic Veg	Duck celery	*Valisneria*	Macrophyte
Submerged Aquatic Veg	Quillwort	*Isoetes*	Macrophyte
Submerged Aquatic Veg	Lake quillwort	*Isoetes*	Macrophyte
Submerged Aquatic Veg	Large-spored quillwort	*Isoetes*	Macrophyte
Submerged Aquatic Veg	rushes	*Juncus*	Macrophyte
Submerged Aquatic Veg	Bladderwort	*Utricularia*	Macrophyte
Submerged Aquatic Veg	Water star grass	*Heteranthera*	Macrophyte
Submerged Aquatic Veg	Largeleaf pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Curly-leaf pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Grassy pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Claspingleaf pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Whitestem pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Small pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Robbins pondweed	*Potamogeton*	Macrophyte
Submerged Aquatic Veg	Horned pondweed	*Zannichellia*	Macrophyte
Submerged Aquatic Veg	Water buttercup	*Ranunculus*	Macrophyte
Phytoplankton	Diatoms	*Achnanthes*	Diatoms
Phytoplankton	Diatoms	*Amphiprora*	Diatoms
Phytoplankton	Diatoms	*Asterionella*	Diatoms
Phytoplankton	Diatoms	*Cyclotella*	Diatoms
Phytoplankton	Diatoms	*Cymbella*	Diatoms
Phytoplankton	Diatoms	*Epithemia*	Diatoms
Phytoplankton	Diatoms	*Eunotia*	Diatoms
Phytoplankton	Diatoms	*Fragilaria*	Diatoms
Phytoplankton	Diatoms	*Frustulia*	Diatoms
Phytoplankton	Diatoms	*Gyrosigma*	Diatoms
Phytoplankton	Diatoms	*Meridion*	Diatoms
Phytoplankton	Diatoms	*Navicula*	Diatoms
Phytoplankton	Diatoms	*Nitzschia*	Diatoms
Phytoplankton	Diatoms	*Pinnularia*	Diatoms
Phytoplankton	Diatoms	*Pyrrhophyta*	Diatoms
Phytoplankton	Diatoms	*Stauroneis*	Diatoms
Phytoplankton	Diatoms	*Stephanodiscus*	Diatoms
Phytoplankton	Diatoms	*Suirirella*	Diatoms
Phytoplankton	Diatoms	*Synedra*	Diatoms
Phytoplankton	Diatoms	*Tabellaria*	Diatoms
Phytoplankton	Diatoms	*Amphipleura*	Diatoms
Phytoplankton	Diatoms	*Amphora*	Diatoms
Phytoplankton	Diatoms	*Aulacoseira*	Diatoms
Phytoplankton	Diatoms	*Chlamydodiscus*	Diatoms
Phytoplankton	Diatoms	*Diatoma*	Diatoms
Phytoplankton	Diatoms	*Gomphonema*	Diatoms
Phytoplankton	Diatoms	*Monoraphidium*	Diatoms
Phytoplankton	Diatoms	*Cocconeis*	Diatoms
Phytoplankton	Diatoms	*Diatomella*	Diatoms
Phytoplankton	Green-algae	*Ankistrodesmus*	Green-algae

(*continued on next page*)

Table A2 (*continued*)

Type	Common	Genus	DietGrp
Phytoplankton	Green-algae	*Asterococcus*	Green-algae
Phytoplankton	Green-algae	*Carteria*	Green-algae
Phytoplankton	Green-algae	*Chlamydomonas*	Green-algae
Phytoplankton	Green-algae	*Chlorella*	Green-algae
Phytoplankton	Green-algae	*Chlorococcum*	Green-algae
Phytoplankton	Green-algae	*Closteriopsis*	Green-algae
Phytoplankton	Green-algae	*Closterium*	Green-algae
Phytoplankton	Green-algae	*Cosmarium*	Green-algae
Phytoplankton	Green-algae	*Crucigenia*	Green-algae
Phytoplankton	Green-algae	*Elakatothrix*	Green-algae
Phytoplankton	Green-algae	*Gloeocystis*	Green-algae
Phytoplankton	Green-algae	*Golenkinia*	Green-algae
Phytoplankton	Green-algae	*Gonyostomum*	Green-algae
Phytoplankton	Green-algae	*Kirchneriella*	Green-algae
Phytoplankton	Green-algae	*Micractinium*	Green-algae
Phytoplankton	Green-algae	*Oocystis*	Green-algae
Phytoplankton	Green-algae	*Oocystis*	Green-algae
Phytoplankton	Green-algae	*Quadrigula*	Green-algae
Phytoplankton	Green-algae	*Scenedesmus*	Green-algae
Phytoplankton	Green-algae	*Schroederia*	Green-algae
Phytoplankton	Green-algae	*Sphaerocystis*	Green-algae
Phytoplankton	Green-algae	*Spirogyra*	Green-algae
Phytoplankton	Green-algae	*Tetraedron*	Green-algae
Phytoplankton	Green-algae	*Volvox*	Green-algae
Phytoplankton	Green-algae	*Chlamydocapsa*	Green-algae
Phytoplankton	Green-algae	*Desmidium*	Green-algae
Phytoplankton	Green-algae	*Pediastrum*	Green-algae
Phytoplankton	Green-algae	*Staurastrum*	Green-algae
Phytoplankton	Green-algae	*Ulothrix*	Green-algae
Phytoplankton	Green-algae	*Coelastrum*	Green-algae
Phytoplankton	Green-algae	*Mougeotia*	Green-algae
Phytoplankton	Green-algae	*Nephrocytium*	Green-algae
Phytoplankton	Green-algae	*Ophiocytium*	Green-algae
Phytoplankton	Green-algae	*Protococcus*	Green-algae
Phytoplankton	Green-algae	*Oocystis*	Green-algae
Phytoplankton	Green-algae	*Hyalotheca*	Green-algae
Phytoplankton	Green-algae	*Eudorina*	Green-algae
Phytoplankton	Golden-algae	*Dictyosphaerium*	Golden-algae
Phytoplankton	Golden-algae	*Dinobryon*	Golden-algae
Phytoplankton	Golden-algae	*Mallomonas*	Golden-algae
Phytoplankton	Golden-algae	*Synura*	Golden-algae
Phytoplankton	Golden-algae	*Botryococcus*	Golden-algae
Phytoplankton	Golden-algae	*Chrysocapsa*	Golden-algae
Phytoplankton	Golden-algae	*Chrysosphaerella*	Golden-algae
Phytoplankton	Golden-algae	*Ochromonas*	Golden-algae
Phytoplankton	Cryptomonad	*Cryptomonas*	Cryptomonad
Phytoplankton	Cryptomonad	*Cryptomonad*	Cryptomonad
Phytoplankton	Cyanobactera	*Anabaena*	Cyanobacteria
Phytoplankton	Cyanobactera	*Aphanocapsa*	Cyanobacteria
Phytoplankton	Cyanobactera	*Aphanothece*	Cyanobacteria
Phytoplankton	Cyanobactera	*Chroococcus*	Cyanobacteria
Phytoplankton	Cyanobactera	*Chroococcus*	Cyanobacteria
Phytoplankton	Cyanobactera	*Coelosphaerium*	Cyanobacteria
Phytoplankton	Cyanobactera	*Gloeocapsa*	Cyanobacteria
Phytoplankton	Cyanobactera	*Gloeothece*	Cyanobacteria
Phytoplankton	Cyanobactera	*Gomphosphaeria*	Cyanobacteria
Phytoplankton	Cyanobactera	*Lyngbya*	Cyanobacteria
Phytoplankton	Cyanobactera	*Merismopedia*	Cyanobacteria
Phytoplankton	Cyanobactera	*Microcystis*	Cyanobacteria
Phytoplankton	Cyanobactera	*Oscillatoria*	Cyanobacteria
Phytoplankton	Cyanobactera	*Synechococcus*	Cyanobacteria
Phytoplankton	Cyanobactera	*Synechocystis*	Cyanobacteria
Phytoplankton	Cyanobactera	*Aphanizomenon*	Cyanobacteria
Phytoplankton	Cyanobactera	*Gloeotrichia*	Cyanobacteria
Phytoplankton	Cyanobactera	*Glaucocystis*	Cyanobacteria
Phytoplankton	Cyanobactera	*Nostoc*	Cyanobacteria
Phytoplankton	Cyanobactera	*Dactylococcopsis*	Cyanobacteria
Phytoplankton	Flagellates	*Euglena*	Flagellates
Phytoplankton	Flagellates	*Phacus*	Flagellates
Phytoplankton	Flagellates	*Trachelomonas*	Flagellates
Phytoplankton	Dinoflagellate	*Glenodinium*	Dinoflagellate
Phytoplankton	Dinoflagellate	*Gymnodinium*	Dinoflagellate
Phytoplankton	Dinoflagellate	*Peridinium*	Dinoflagellate
Phytoplankton	Dinoflagellate	*Ceratium*	Dinoflagellate
Phytoplankton	Green-algae	*Euastrum*	Green-algae
Phytoplankton	Green-algae	*Pandorina*	Green-algae

(*continued on next page*)

Table A2 (*continued*)

Type	Common	Genus	DietGrp
Phytoplankton	Green-algae	*Selenastrum*	Green-algae
Phytoplankton	Green-algae	*Xanthidium*	Green-algae
Phytoplankton	Cyanobactera	*Rhabdoderma*	Cyanobacteria
Phytoplankton	Diatoms	*Rhoicosphenia*	Diatoms
Phytoplankton	Diatoms	*Rhopalodia*	Diatoms
Protozoa	Protozoa	*Acanthocystis*	Protozoa
Protozoa	Protozoa	*Strobilidium*	Protozoa
Zooplankton	Copepod	Unk Diaptomidae	Calanoid
Zooplankton	Copepod	*Leptodiaptomus*	Calanoid
Zooplankton	Copepod	*Leptodiaptomus*	Calanoid
Zooplankton	Copepod	*Skistodiaptomus*	Calanoid
Zooplankton	Copepod	*Epischura*	Calanoid
Zooplankton	Copepod	*Limnocalanus*	Calanoid
Zooplankton	Copepod	*Senecella*	Calanoid
Zooplankton	Cladoceran	*Bosmina*	Cladoceran
Zooplankton	Cladoceran	*Daphnia*	Cladoceran
Zooplankton	Cladoceran	*Daphnia*	Cladoceran
Zooplankton	Cladoceran	*Daphnia*	Cladoceran
Zooplankton	Cladoceran	*Diaphanosoma*	Cladoceran
Zooplankton	Cladoceran	*Holopedium*	Cladoceran
Zooplankton	Cladoceran	*Polyphemus*	Cladoceran
Zooplankton	Cladoceran	*Leptodora*	Cladoceran
Zooplankton	Cladoceran	*Bythotrephes*	Cladoceran
Zooplankton	Copepod	*Cyclops*	Cyclopoid
Zooplankton	Copepod	*Diacyclops*	Cyclopoid
Zooplankton	Copepod	*Mesocyclops*	Cyclopoid
Zooplankton	Copepod	*Tropocyclops*	Cyclopoid
Zooplankton	Copepod	Unknown Copepod	Copepod
Zooplankton	Rotifer	*Kellicottia*	Rotifer
Zooplankton	Rotifer	*Keratella*	Rotifer
Zooplankton	Rotifer	*Polyarthra*	Rotifer
Zooplankton	Rotifer	*Conochilus*	Rotifer
Zooplankton	Rotifer	*Gastropus*	Rotifer
Zooplankton	Rotifer	*Synchaeta*	Rotifer
Zooplankton	Rotifer	*Trichocerca*	Rotifer
Invert	Worms	*Clitellata*	Annelida
Invert	Leeches	*Clitellata*	Annelida
Invert	Riffle Beetles	*Dubiraphia*	Coleoptera
Invert	Riffle Beetles	*Microcylloepus*	Coleoptera
Invert	Riffle Beetles	*Promoresia*	Coleoptera
Invert	Riffle Beetles	*Macronychus*	Coleoptera
Invert	Riffle Beetles	*Neoelmis*	Coleoptera
Invert	Riffle Beetles	*Rhizelmis*	Coleoptera
Invert	Beetles	*Haliplus*	Coleoptera
Invert	Beetles	*Psephenus*	Coleoptera
Invert	Beetles	*Dicranopselaphus*	Coleoptera
Invert	Flies	*Chironomidae*	Diptera
Invert	Flies	*Culicidae*	Diptera
Invert	Flies	*Ceratopogonidae*	Diptera
Invert	Flies	*Empididae*	Diptera
Invert	Flies	*Tipulidae*	Diptera
Invert	Mayflies	*Fallceon*	Ephemeroptera
Invert	Mayflies	*Caenis*	Ephemeroptera
Invert	Mayflies	*Attenella*	Ephemeroptera
Invert	Mayflies	*Ephemera*	Ephemeroptera
Invert	Mayflies	*Ephemerella*	Ephemeroptera
Invert	Mayflies	*Eurylophella*	Ephemeroptera
Invert	Mayflies	*Hexagenia*	Ephemeroptera
Invert	Mayflies	*Drunella*	Ephemeroptera
Invert	Mayflies	*Litobrancha*	Ephemeroptera
Invert	Mayflies	*Serratella*	Ephemeroptera
Invert	Mayflies	*Stenacron*	Ephemeroptera
Invert	Mayflies	*Maccaffertium*	Ephemeroptera
Invert	Mayflies	*Neoephemera*	Ephemeroptera
Invert	Mayflies	*Tricorythodes*	Ephemeroptera
Invert	Mayflies	*Ableptemetes*	Ephemeroptera
Invert	Moths and Butterflies	*Petrophila*	Lepidoptera
Invert	Moths and Butterflies	*Oxylophila*	Lepidoptera
Invert	Moths and Butterflies	*Synclita*	Lepidoptera
Invert	Alderflies and Dobsonflies and Fishflies	*Sialis*	Megaloptera
Invert	Alderflies and Dobsonflies and Fishflies	Unknown Corydalidae	Megaloptera
Invert	Dragonflies	*Enallagma*	Odonata
Invert	Dragonflies	*Amphiagrion*	Odonata
Invert	Dragonflies	*Argia*	Odonata
Invert	Dragonflies	*Coenagrion*	Odonata
Invert	Dragonflies	*Boyeria*	Odonata

(*continued on next page*)

Table A2 (*continued*)

Type	Common	Genus	DietGrp
Invert	Dragonflies	*Cordulegaster*	Odonata
Invert	Dragonflies	*Epitheca*	Odonata
Invert	Dragonflies	*Arigomphus*	Odonata
Invert	Dragonflies	*Gomphus*	Odonata
Invert	Dragonflies	*Progomphus*	Odonata
Invert	Dragonflies	*Dromogomphus*	Odonata
Invert	Dragonflies	*Hagenius*	Odonata
Invert	Dragonflies	*Archlestes*	Odonata
Invert	Dragonflies	*Libellula*	Odonata
Invert	Dragonflies	*Macrothemis*	Odonata
Invert	Dragonflies	*Lestes*	Odonata
Invert	Dragonflies	*Didymops*	Odonata
Invert	Dragonflies	*Epicordulia*	Odonata
Invert	Caddisflies	*Helicopsyche*	Trichoptera
Invert	Caddisflies	*Molanna*	Trichoptera
Invert	Caddisflies	*Dolophilodes*	Trichoptera
Invert	Caddisflies	*Beraea*	Trichoptera
Invert	Caddisflies	Psycomiiadae	Trichoptera
Invert	Caddisflies	Limnephilidae	Trichoptera
Invert	Caddisflies	Phryganeidae	Trichoptera
Invert	Caddisflies	Polycentropodidae	Trichoptera
Invert	Caddisflies	Polycentropodidae	Trichoptera
Invert	Caddisflies	Polycentropodidae	Trichoptera
Invert	Caddisflies	Brachycentridae	Trichoptera
Invert	Caddisflies	Dipseudopsidae	Trichoptera
Invert	Caddisflies	Hydroptilidae	Trichoptera
Invert	Caddisflies	Lepidostomatidae	Trichoptera
Invert	Caddisflies	Leptoceridae	Trichoptera
Invert	Caddisflies	Odontoceridae	Trichoptera
Invert	True Bugs	*Hemiptera*	
Invert	Stoneflies	*Plecoptera*	
Invert	Amphipods	*Hyalella*	Amphipod
Invert	Amphipods	*Gammarus*	Amphipod
Invert	Amphipods	*Diporeia*	Amphipod
Invert	Crayfish	*Cambarus*	Decapoda
Invert	Crayfish	*Orconectes*	Decapoda
Invert	Isopods	*Caecidotea*	Isopod
Invert	Shrimp	*Mysis*	Mysis
Invert	Pea clams	*Pisidium*	Veneroida
Invert	Mussels	*Elliptio*	Unionoida
Invert	Asian Clam	*Corbicula*	Veneroida
Invert	Pond Snails	*Acella*	Basommatophora
Invert	Bladder Snails	*Physella*	Basommatophora
Invert	Ramshorn Snails	*Gyraulus*	Basommatophora
Invert	Ramshorn Snails	*Planorbella*	Basommatophora
Invert	Ramshorn Snails	*Promenetus*	Basommatophora
Invert	Valve Snails	*Valvata*	Heterostropha
Invert	Snail	*Amnicola*	Neotaenioglossa
Invert	Faucet Snail	*Bithynia*	Neotaenioglossa
Invert	Banded Mystery Snail	*Viviparus*	Architaenioglossa
Invert	Pointed Campeloma	*Campeloma*	Architaenioglossa
Invert	Caddisflies	*Brachycentrus*	Trichoptera
Invert	Dragonflies	*Brechmorhoga*	Odonata
Invert	Caddisflies	*Cernotina*	Trichoptera
Invert	Dragonflies	*Cordulia*	Odonata
Invert	Caddisflies	*Cyrnellus*	Trichoptera
Invert	Ramshorn Snails	*Helisoma*	Basommatophora
Invert	Mussels	*Lampsilis*	Unionoida
Invert	Caddisflies	*Limnephilus*	Trichoptera
Invert	Caddisflies	*Mystacides*	Trichoptera
Invert	Caddisflies	*Nectopsyche*	Trichoptera
Invert	Caddisflies	*Nyctiophylax*	Trichoptera
Invert	Caddisflies	*Oecetis*	Trichoptera
Invert	Riffle Beetles	*Optioservus*	Coleoptera
Invert	Caddisflies	*Palaeagapetus*	Trichoptera
Invert	Caddisflies	*Phylocentropus*	Trichoptera
Invert	Flatworms	*Planaria*	Flatworm
Invert	Caddisflies	*Polycentropus*	Trichoptera
Invert	Caddisflies	*Psilotreta*	Trichoptera
Invert	Mussels	*Pyganodon*	Unionoida
Invert	Caddisflies	*Setodes*	Trichoptera
Invert	Pond Snails	*Stagnicola*	Basommatophora
Fish	White Sucker	*Catostomus*	Catostomus
Fish	Lake Chub	*Couesius*	Cyprinid
Fish	Spotfin Shiner	*Cyprinella*	Cyprinid
Fish	Silvery Minnow	*Hybognathus*	Cyprinid

(*continued on next page*)

Table A2 (*continued*)

Type	Common	Genus	DietGrp
Fish	Common Shiner	*Luxilus*	Cyprinid
Fish	Golden Shiner	*Notemigonus*	Cyprinid
Fish	Bridle Shiner	*Notropis*	Cyprinid
Fish	Bluntnose Minnow	*Pimephales*	Cyprinid
Fish	Longnose Dace	*Rhinichthys*	Cyprinid
Fish	Blacknose Dace	*Rhinichthys*	Cyprinid
Fish	Creek Chub	*Semotilus*	Cyprinid
Fish	Banded Killifish	*Fundulus*	*Fundulus*
Fish	Northern Pike	*Esox*	*Esox*
Fish	Chain Pickerel	*Esox*	*Esox*
Fish	Central Mudminnow	*Umbra*	*Umbra*
Fish	Brook Stickleback	*Culaea*	*Culaea*
Fish	Rainbow Smelt	*Osmerus*	*Osmerus*
Fish	Rock Bass	*Ambloplites*	*Ambloplites*
Fish	Redbreast Sunfish	*Lepomis*	*Lepomis*
Fish	Pumpkinseed	*Lepomis*	*Lepomis*
Fish	Largemouth Bass	*Micropterus*	*Micropterus*
Fish	Smallmouth Bass	*Micropterus*	*Micropterus*
Fish	Black Crappie	*Pomoxis*	*Pomoxis*
Fish	Johnny Darter	*Etheostoma*	*Etheostoma*
Fish	Yellow Perch	*Perca*	*Perca*
Fish	Cisco	*Coregonus*	*Coregonus*
Fish	Rainbow Trout	*Oncorhynchus*	*Oncorhynchus*
Fish	Atlantic Salmon	*Salmo*	*Salmo*
Fish	Brown Trout	*Salmo*	*Salmo*
Fish	Lake Trout	*Salvelinus*	*Salvelinus*
Fish	Brook Trout	*Salvelinus*	*Salvelinus*
Fish	Slimy Sculpin	*Cottus*	*Cottus*
Fish	Yellow Bullhead	*Ameiurus*	*Ameiurus*
Fish	Brown Bullhead	*Ameiurus*	*Ameiurus*
Fish	Tadpole Madtom	*Noturus*	*Noturus*
Fish	Bluegill	*Lepomis*	*Lepomis*
Fish	Black Bullhead	*Ameiurus*	*Ameiurus*

Table A3
Food web grouping for higher levels of aggregation.

nodeid	grpA	grpB	grpC	grpD	grpE	grpF	grpG	grpH	grpI	grpJ	grpK
detritus	detritus	detritus	detritus	detritus	detritus	detritus	detritus	detritus	detritus	detritus	detritus
Macrophyte	plant	plant	plant	plant	plant	plant	plant	plant	plant	plant	plant
Diatoms	phyto	phyto	brown	brown	brown	brown	brown	brown	brown	brown	brown
Green-algae	phyto	phyto	green	green	green	green	green	green	green	green	green
Golden-algae	phyto	phyto	brown	brown	brown	brown	brown	brown	brown	brown	brown
Cryptomonad	phyto	phyto	red	red	red	red	red	red	red	red	red
Cyanobacteria	phyto	phyto	blue	blue	blue	blue	blue	blue	blue	blue	blue
Flagellates	flag	flag	flag	flag	flag	flag	flag	flag	flag	flag	flag
Protozoa	prot	prot	prot	prot	prot	prot	prot	prot	prot	prot	prot
Lepidoptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	aqIns	aqIns	aqIns	aqIns	aqIns
Neotaenioglossa	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	snail	snail	snail	snail	snail
Isopod	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	iso	iso	iso	iso	iso
Veneroida	macroinv	benthFilt	macroinv	benthFilt	benthFilt	benthFilt	clam	clam	clam	clam	clam
Basommatophora	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	snail	snail	snail	snail	snail
Dinoflagellate	prot	prot	prot	prot	prot	prot	prot	prot	prot	prot	prot
Coleoptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	aqIns	aqIns	aqIns	aqIns	aqIns
Heterostropha	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	snail	snail	snail	snail	snail
Architaenioglossa	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	snail	snail	snail	snail	snail
Annelida	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	worm	worm	worm	worm	worm
Ephemeroptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	aqIns	aqIns	ephem	aqIns	ephem
Decapoda	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	cray	cray	cray	cray	cray
Culaea	fish	fish	fish	fish	smFish	smFish	smFish	smFish	smFish	gasterostid	gasterostid
Rotifer	zoop	zoop	rot	rot	rot	rot	rot	rot	rot	rot	rot
Mysis	macroinv	benthPred	macroinv	benthPred	benthPred	benthPred	mys	mys	mys	mys	mys
Ameiurus	fish	fish	fish	fish	fish	fish	fish	benthFish	detFish	ictalurid	ictalurid
Megaloptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	aqIns	aqIns	aqIns	aqIns	aqIns
Amphipod	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	amph	amph	amph	amph	amph
Catostomus	fish	fish	fish	fish	fish	fish	fish	benthFish	detFish	catostomid	catostomid
Fundulus	fish	fish	fish	fish	smFish	smFish	smFish	smFish	smFish	fundulid	fundulid
Osmerus	fish	fish	fish	fish	fish	fish	fish	plnkfish	plnkfish	osemerid	osemerid
Etheostoma	fish	fish	fish	fish	smFish	smFish	smFish	smFish	smFish	percid	percid
Cottus	fish	fish	fish	fish	smFish	smFish	smFish	benthFish	detFish	cottid	cottid
Calanoid	zoop	zoop	cal	cal	cal	cal	cal	cal	cal	cal	cal
Cladoceran	zoop	zoop	clad	clad	clad	clad	clad	clad	clad	clad	clad

(*continued on next page*)

Table A3 (*continued*)

nodeid	grpA	grpB	grpC	grpD	grpE	grpF	grpG	grpH	grpI	grpJ	grpK
Trichoptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	aqIns	aqIns	trich	aqIns	trich
Diptera	macroinv	benthDep	macroinv	benthDep	benthDep	benthDep	dip	dip	dip	dip	dip
Lepomis	fish	fish	fish	fish	fish	fish	fish	bforfish	bforfish	centrarchid	centrarchid
Odonata	macroinv	benthPred	macroinv	benthPred	benthPred	benthPred	odo	odo	odo	odo	odo
Umbra	fish	fish	fish	fish	smFish	smFish	smFish	smFish	smFish	umbrid	umbrid
Cyclopoid	zoop	zoop	cyc	cyc	cyc	cyc	cyc	cyc	cyc	cyc	cyc
Ambloplites	fish	fish	fish	fish	fish	fish	fish	bforfish	bforfish	centrarchid	centrarchid
Pomoxis	fish	fish	fish	fish	fish	fish	fish	bforfish	bforfish	centrarchid	centrarchid
Cyprinid	fish	fish	fish	fish	smFish	smFish	smFish	smFish	smFish	cyprinid	cyprinid
Coregonus	fish	fish	fish	fish	fish	fish	fish	plnkfish	plnkfish	salmonid	salmonid
Esox	fish	fish	fish	fish	fish	lrgFish	lrgFish	nspfish	nspfish	esocid	esocid
Micropterus	fish	fish	fish	fish	fish	fish	fish	bforfish	bforfish	centrarchid	centrarchid
Perca	fish	fish	fish	fish	fish	fish	fish	bforfish	bforfish	percid	percid
Salvelinus	fish	fish	fish	fish	fish	lrgFish	lrgFish	ospfish	ospfish	salmonid	salmonid
Salmo	fish	fish	fish	fish	fish	lrgFish	lrgFish	ospfish	ospfish	salmonid	salmonid

Table A4
Trophic interactions in the Lake George food web with observed diet proportions.

	prey	predator	prop
1	detritus	Isopod	
2	detritus	Veneroida	
3	detritus	Basommatophora	
4	detritus	Coleoptera	
5	detritus	Heterostropha	
6	detritus	Architaenioglossa	
7	detritus	Annelida	
8	detritus	Ephemeroptera	
9	detritus	Decapoda	
10	detritus	Rotifer	
11	detritus	Ameiurus	
12	detritus	Megaloptera	
13	detritus	Amphipod	
14	detritus	Catostomus	
15	detritus	Fundulus	
16	detritus	Osmerus	
17	detritus	Cottus	
18	detritus	Calanoid	
19	detritus	Cladoceran	
20	detritus	Trichoptera	
21	detritus	Diptera	
22	detritus	Lepomis	
23	detritus	Odonata	
24	detritus	Umbra	
25	detritus	Cyclopoid	
26	detritus	Cyprinid	
27	detritus	Coregonus	
28	detritus	Micropterus	
29	detritus	Salvelinus	
30	detritus	Salmo	
31	Macrophyte	Lepidoptera	
32	Macrophyte	Ephemeroptera	
33	Macrophyte	Decapoda	
34	Macrophyte	Amphipod	
35	Macrophyte	Fundulus	
36	Macrophyte	Trichoptera	
37	Macrophyte	Diptera	
38	Macrophyte	Micropterus	
39	Macrophyte	Salmo	
40	Diatoms	Neotaenioglossa	
41	Diatoms	Isopod	
42	Diatoms	Veneroida	
43	Diatoms	Basommatophora	
44	Diatoms	Dinoflagellate	
45	Diatoms	Coleoptera	
46	Diatoms	Heterostropha	
47	Diatoms	Annelida	
48	Diatoms	Ephemeroptera	
49	Diatoms	Rotifer	
50	Diatoms	Mysis	
51	Diatoms	Ameiurus	
52	Diatoms	Megaloptera	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
53	Diatoms	Amphipod	
54	Diatoms	Cottus	
55	Diatoms	Calanoid	
56	Diatoms	Cladoceran	
57	Diatoms	Trichoptera	
58	Diatoms	Diptera	
59	Diatoms	Odonata	
60	Diatoms	Cyclopoid	
61	Diatoms	Cyprinid	
62	Diatoms	Coregonus	
63	Diatoms	Esox	
64	Diatoms	Perca	
65	Diatoms	Salvelinus	
66	Diatoms	Salmo	
67	Green-algae	Dinoflagellate	
68	Green-algae	Coleoptera	
69	Green-algae	Annelida	
70	Green-algae	Ephemeroptera	
71	Green-algae	Rotifer	
72	Green-algae	Mysis	
73	Green-algae	Amphipod	
74	Green-algae	Calanoid	
75	Green-algae	Cladoceran	
76	Green-algae	Trichoptera	
77	Green-algae	Diptera	
78	Green-algae	Cyclopoid	
79	Green-algae	Cyprinid	
80	Golden-algae	Calanoid	
81	Golden-algae	Cladoceran	
82	Golden-algae	Cyclopoid	
83	Cryptomonad	Protozoa	
84	Cryptomonad	Rotifer	
85	Cryptomonad	Calanoid	
86	Cryptomonad	Cladoceran	
87	Cryptomonad	Diptera	
88	Cryptomonad	Cyclopoid	
89	Cyanobacteria	Heterostropha	
90	Cyanobacteria	Annelida	
91	Cyanobacteria	Ephemeroptera	
92	Cyanobacteria	Rotifer	
93	Cyanobacteria	Mysis	
94	Cyanobacteria	Amphipod	
95	Cyanobacteria	Fundulus	
96	Cyanobacteria	Calanoid	
97	Cyanobacteria	Cladoceran	
98	Cyanobacteria	Trichoptera	
99	Cyanobacteria	Diptera	
100	Cyanobacteria	Cyclopoid	
101	Flagellates	Rotifer	
102	Flagellates	Calanoid	
103	Flagellates	Cladoceran	
104	Flagellates	Diptera	
105	Flagellates	Cyclopoid	
106	Protozoa	Dinoflagellate	
107	Lepidoptera	Odonata	
108	Neotaenioglossa	Lepomis	
109	Neotaenioglossa	Salmo	
110	Isopod	Decapoda	
111	Isopod	Amphipod	
112	Isopod	Cottus	
113	Isopod	Cyprinid	
114	Veneroida	Etheostoma	
115	Veneroida	Cottus	
116	Veneroida	Lepomis	0.05
117	Veneroida	Coregonus	
118	Veneroida	Esox	
119	Veneroida	Perca	0.04
120	Veneroida	Salvelinus	
121	Veneroida	Salmo	
122	Basommatophora	Culaea	
123	Basommatophora	Etheostoma	
124	Basommatophora	Trichoptera	
125	Basommatophora	Lepomis	0.07
126	Basommatophora	Odonata	
127	Basommatophora	Coregonus	
128	Basommatophora	Salvelinus	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
129	Basommatophora	Salmo	
130	Dinoflagellate	Mysis	
131	Dinoflagellate	Calanoid	
132	Dinoflagellate	Cladoceran	
133	Dinoflagellate	Cyclopoid	
134	Dinoflagellate	Cyprinid	
135	Coleoptera	Odonata	
136	Coleoptera	Cyprinid	
137	Coleoptera	Salvelinus	
138	Coleoptera	Salmo	
139	Heterostropha	Lepomis	
140	Heterostropha	Coregonus	
141	Heterostropha	Salvelinus	
142	Heterostropha	Salmo	
143	Architaenioglossa	Umbra	
144	Architaenioglossa	Ambloplites	
145	Architaenioglossa	Pomoxis	
146	Architaenioglossa	Coregonus	
147	Architaenioglossa	Esox	
148	Architaenioglossa	Micropterus	0.04
149	Architaenioglossa	Perca	0.03
150	Architaenioglossa	Salmo	
151	Annelida	Decapoda	
152	Annelida	Culaea	
153	Annelida	Ameiurus	0.03
154	Annelida	Megaloptera	
155	Annelida	Catostomus	
156	Annelida	Fundulus	
157	Annelida	Etheostoma	
158	Annelida	Cottus	
159	Annelida	Trichoptera	
160	Annelida	Diptera	
161	Annelida	Lepomis	
162	Annelida	Odonata	
163	Annelida	Umbra	
164	Annelida	Ambloplites	
165	Annelida	Pomoxis	
166	Annelida	Cyprinid	
167	Annelida	Coregonus	
168	Annelida	Esox	
169	Annelida	Micropterus	0.04
170	Annelida	Perca	
171	Annelida	Salvelinus	
172	Annelida	Salmo	
173	Ephemeroptera	Megaloptera	
174	Ephemeroptera	Amphipod	
175	Ephemeroptera	Etheostoma	
176	Ephemeroptera	Cottus	
177	Ephemeroptera	Trichoptera	
178	Ephemeroptera	Diptera	
179	Ephemeroptera	Odonata	
180	Ephemeroptera	Umbra	
181	Ephemeroptera	Ambloplites	0.12
182	Ephemeroptera	Pomoxis	0.17
183	Ephemeroptera	Cyprinid	0.12
184	Ephemeroptera	Coregonus	
185	Ephemeroptera	Esox	
186	Ephemeroptera	Micropterus	0.06
187	Ephemeroptera	Perca	0.08
188	Ephemeroptera	Salvelinus	
189	Ephemeroptera	Salmo	
190	Decapoda	Cyprinid	
191	Decapoda	Micropterus	0.05
192	Decapoda	Salvelinus	
193	Decapoda	Salmo	
194	Culaea	Cyprinid	
195	Culaea	Salvelinus	
196	Culaea	Salmo	
197	Rotifer	Mysis	
198	Rotifer	Fundulus	
199	Rotifer	Osmerus	
200	Rotifer	Calanoid	
201	Rotifer	Cladoceran	
202	Rotifer	Lepomis	
203	Rotifer	Odonata	
204	Rotifer	Umbra	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
205	Rotifer	Cyclopoid	
206	Rotifer	Ambloplites	
207	Rotifer	Pomoxis	
208	Rotifer	Cyprinid	
209	Rotifer	Esox	
210	Rotifer	Micropterus	
211	Rotifer	Perca	
212	Mysis	Osmerus	
213	Mysis	Coregonus	
214	Mysis	Perca	
215	Mysis	Salvelinus	
216	Mysis	Salmo	
217	Ameiurus	Esox	
218	Ameiurus	Salvelinus	
219	Ameiurus	Salmo	
220	Megaloptera	Ameiurus	0.03
221	Megaloptera	Trichoptera	
222	Megaloptera	Diptera	
223	Megaloptera	Odonata	
224	Megaloptera	Umbra	
225	Megaloptera	Ambloplites	0.01
226	Megaloptera	Pomoxis	
227	Megaloptera	Coregonus	
228	Megaloptera	Micropterus	
229	Megaloptera	Perca	0.01
230	Megaloptera	Salvelinus	
231	Megaloptera	Salmo	
232	Amphipod	Architaenioglossa	
233	Amphipod	Decapoda	
234	Amphipod	Culaea	
235	Amphipod	Mysis	
236	Amphipod	Ameiurus	0.09
237	Amphipod	Megaloptera	
238	Amphipod	Catostomus	0.21
239	Amphipod	Fundulus	0.20
240	Amphipod	Osmerus	
241	Amphipod	Etheostoma	
242	Amphipod	Cottus	
243	Amphipod	Trichoptera	
244	Amphipod	Diptera	
245	Amphipod	Lepomis	0.09
246	Amphipod	Odonata	
247	Amphipod	Ambloplites	0.12
248	Amphipod	Cyprinid	0.09
249	Amphipod	Coregonus	
250	Amphipod	Esox	0.10
251	Amphipod	Micropterus	0.12
252	Amphipod	Perca	0.16
253	Amphipod	Salvelinus	
254	Amphipod	Salmo	
255	Catostomus	Coregonus	
256	Catostomus	Esox	
257	Catostomus	Micropterus	
258	Catostomus	Salvelinus	
259	Catostomus	Salmo	
260	Fundulus	Salvelinus	
261	Fundulus	Salmo	
262	Osmerus	Coregonus	
263	Osmerus	Esox	
264	Osmerus	Perca	
265	Osmerus	Salvelinus	0.50
266	Osmerus	Salmo	
267	Etheostoma	Ameiurus	
268	Etheostoma	Umbra	
269	Etheostoma	Cyprinid	
270	Etheostoma	Micropterus	
271	Etheostoma	Salvelinus	
272	Etheostoma	Salmo	
273	Cottus	Osmerus	
274	Cottus	Coregonus	
275	Cottus	Esox	
276	Cottus	Micropterus	
277	Cottus	Perca	
278	Cottus	Salvelinus	
279	Cottus	Salmo	
280	Calanoid	Osmerus	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
281	Calanoid	Etheostoma	
282	Calanoid	Cladoceran	
283	Calanoid	Lepomis	
284	Calanoid	Umbra	
285	Calanoid	Cyclopoid	
286	Calanoid	Ambloplites	
287	Calanoid	Pomoxis	
288	Calanoid	Cyprinid	
289	Calanoid	Coregonus	
290	Calanoid	Micropterus	
291	Calanoid	Perca	
292	Calanoid	Salvelinus	
293	Calanoid	Salmo	
294	Cladoceran	Culaea	
295	Cladoceran	Mysis	
296	Cladoceran	Catostomus	
297	Cladoceran	Fundulus	
298	Cladoceran	Osmerus	
299	Cladoceran	Calanoid	
300	Cladoceran	Lepomis	0.02
301	Cladoceran	Odonata	
302	Cladoceran	Umbra	
303	Cladoceran	Cyclopoid	
304	Cladoceran	Ambloplites	0.01
305	Cladoceran	Pomoxis	
306	Cladoceran	Cyprinid	0.27
307	Cladoceran	Coregonus	
308	Cladoceran	Esox	
309	Cladoceran	Micropterus	0.04
310	Cladoceran	Perca	0.10
311	Cladoceran	Salvelinus	
312	Cladoceran	Salmo	
313	Trichoptera	Megaloptera	
314	Trichoptera	Etheostoma	
315	Trichoptera	Cottus	
316	Trichoptera	Diptera	
317	Trichoptera	Odonata	
318	Trichoptera	Umbra	
319	Trichoptera	Ambloplites	0.15
320	Trichoptera	Pomoxis	0.17
321	Trichoptera	Cyprinid	0.33
322	Trichoptera	Esox	0.10
323	Trichoptera	Micropterus	0.04
324	Trichoptera	Perca	0.08
325	Trichoptera	Salvelinus	
326	Trichoptera	Salmo	
327	Diptera	Architaenioglossa	
328	Diptera	Ephemeroptera	
329	Diptera	Decapoda	
330	Diptera	Culaea	
331	Diptera	Ameiurus	0.05
332	Diptera	Megaloptera	
333	Diptera	Amphipod	
334	Diptera	Catostomus	
335	Diptera	Fundulus	
336	Diptera	Osmerus	
337	Diptera	Etheostoma	
338	Diptera	Cottus	
339	Diptera	Trichoptera	
340	Diptera	Lepomis	0.06
341	Diptera	Odonata	
342	Diptera	Umbra	
343	Diptera	Ambloplites	0.03
344	Diptera	Pomoxis	0.06
345	Diptera	Cyprinid	
346	Diptera	Coregonus	
347	Diptera	Esox	
348	Diptera	Micropterus	0.02
349	Diptera	Perca	0.06
350	Diptera	Salvelinus	
351	Diptera	Salmo	
352	Lepomis	Pomoxis	
353	Lepomis	Esox	
354	Lepomis	Micropterus	
355	Lepomis	Perca	
356	Lepomis	Salvelinus	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
357	Lepomis	Salmo	
358	Odonata	Megaloptera	
359	Odonata	Diptera	
360	Odonata	Umbra	
361	Odonata	Ambloplites	0.04
362	Odonata	Pomoxis	0.06
363	Odonata	Cyprinid	0.09
364	Odonata	Micropterus	0.06
365	Odonata	Perca	0.01
366	Odonata	Salmo	
367	Umbra	Ambloplites	
368	Umbra	Pomoxis	
369	Umbra	Micropterus	
370	Umbra	Perca	
371	Cyclopoid	Culaea	
372	Cyclopoid	Catostomus	
373	Cyclopoid	Fundulus	
374	Cyclopoid	Osmerus	
375	Cyclopoid	Etheostoma	
376	Cyclopoid	Cottus	
377	Cyclopoid	Calanoid	
378	Cyclopoid	Cladoceran	
379	Cyclopoid	Trichoptera	
380	Cyclopoid	Lepomis	
381	Cyclopoid	Odonata	
382	Cyclopoid	Umbra	
383	Cyclopoid	Ambloplites	
384	Cyclopoid	Pomoxis	
385	Cyclopoid	Cyprinid	
386	Cyclopoid	Coregonus	
387	Cyclopoid	Esox	
388	Cyclopoid	Micropterus	
389	Cyclopoid	Perca	
390	Cyclopoid	Salvelinus	
391	Cyclopoid	Salmo	
392	Ambloplites	Cyclopoid	
393	Ambloplites	Pomoxis	
394	Ambloplites	Micropterus	
395	Ambloplites	Perca	
396	Pomoxis	Cyclopoid	
397	Pomoxis	Ambloplites	
398	Pomoxis	Esox	
399	Pomoxis	Micropterus	
400	Pomoxis	Perca	
401	Cyprinid	Lepomis	0.06
402	Cyprinid	Umbra	
403	Cyprinid	Ambloplites	0.03
404	Cyprinid	Pomoxis	
405	Cyprinid	Esox	
406	Cyprinid	Micropterus	0.06
407	Cyprinid	Perca	0.02
408	Cyprinid	Salvelinus	
409	Cyprinid	Salmo	
410	Coregonus	Esox	
411	Coregonus	Perca	
412	Coregonus	Salvelinus	
413	Coregonus	Salmo	
414	Esox	Micropterus	
415	Esox	Perca	
416	Micropterus	Cyclopoid	
417	Micropterus	Ambloplites	
418	Micropterus	Pomoxis	
419	Micropterus	Esox	
420	Micropterus	Perca	
421	Perca	Cyclopoid	
422	Perca	Ambloplites	
423	Perca	Pomoxis	
424	Perca	Coregonus	
425	Perca	Esox	0.10
426	Perca	Micropterus	0.04
427	Perca	Salvelinus	
428	Perca	Salmo	
429	Salvelinus	Catostomus	
430	Salvelinus	Esox	
431	Salvelinus	Salmo	
432	Salmo	Catostomus	

(*continued on next page*)

Table A4 (*continued*)

	prey	predator	prop
433	Salmo	Esox	
434	Salmo	Salvelinus	
435	Amphipod	Pomoxis	0.22
436	Architaenioglossa	Ameiurus	0.06
437	Architaenioglossa	Catostomus	0.07
438	Architaenioglossa	Fundulus	0.20
439	Architaenioglossa	Lepomis	0.07
440	Fundulus	Esox	0.10
441	Fundulus	Micropterus	0.02
442	Basommatophora	Ambloplites	0.02
443	Basommatophora	Ameiurus	0.04
444	Basommatophora	Micropterus	0.04
445	Basommatophora	Perca	0.05
446	Cladoceran	Ameiurus	0.04
447	Coleoptera	Ambloplites	0.02
448	Coleoptera	Ameiurus	0.02
449	Coleoptera	Lepomis	0.03
450	Coleoptera	Micropterus	0.02
451	Cyprinid	Ameiurus	0.09
452	Decapoda	Ambloplites	0.13
453	Decapoda	Ameiurus	0.22
454	Decapoda	Coregonus	1.00
455	Decapoda	Esox	0.10
456	Decapoda	Lepomis	
457	Decapoda	Perca	0.04
458	Ephemeroptera	Ameiurus	0.04
459	Ephemeroptera	Lepomis	0.13
460	Heterostropha	Catostomus	0.07
461	Heterostropha	Perca	
462	Isopod	Ambloplites	0.03
463	Isopod	Ameiurus	0.07
464	Isopod	Catostomus	0.21
465	Isopod	Esox	0.10
466	Isopod	Lepomis	0.04
467	Isopod	Micropterus	0.04
468	Isopod	Perca	0.10
469	Lepidoptera	Ambloplites	0.01
470	Lepidoptera	Lepomis	0.01
471	Lepidoptera	Pomoxis	0.11
472	Megaloptera	Lepomis	
473	Odonata	Ameiurus	0.04
474	Odonata	Lepomis	0.06
475	Cottus	Ameiurus	0.02
476	Trichoptera	Ameiurus	0.10
477	Trichoptera	Catostomus	0.07
478	Trichoptera	Fundulus	0.20
479	Trichoptera	Lepomis	0.23
480	Veneroida	Ambloplites	0.01
481	Veneroida	Ameiurus	0.03
482	Veneroida	Catostomus	0.14
483	Veneroida	Fundulus	0.20
484	Perca	Ameiurus	0.03

Table A5
Properties of the full and aggregated webs including group name, prey averaged trophic level (mean and standard deviation), mean generality, number of nodes, number links, and connectance.

Grouping	PreyAvTL	PreyAvTLSD	MaxTL	Gen	N	L	Conn
A	1.70	0.77	2.66	2.00	8	18	0.28
B	1.88	0.81	2.87	1.67	10	27	0.27
C	1.70	0.76	2.74	2.00	14	62	0.32
D	1.79	0.75	2.83	1.78	16	73	0.29
E	1.86	0.79	3.06	1.70	17	84	0.29
F	1.94	0.84	3.15	1.64	18	97	0.30
G	2.16	0.83	3.35	1.39	25	163	0.26
H	2.31	0.91	3.63	1.33	28	214	0.27
I	2.35	0.90	3.63	1.30	30	245	0.27
J	2.55	0.97	3.82	1.26	34	287	0.25
K	2.57	0.95	3.81	1.24	36	322	0.25
full	2.64	0.97	3.99	1.20	49	484	0.20

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00315.

References

Baker, R., Buckland, A., Sheaves, M., 2014. Fish gut content analysis: robust measures of diet composition. Fish Fish. 15, 170–177. https://doi.org/10.1111/faf.12026.

Boit, A., Gaedke, U., 2014. Benchmarking successional progress in a quantitative food web. PLoS One 9. https://doi.org/10.1371/journal.pone.0090404.

Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. Ecol. Lett. 15, 594–602. https://doi.org/10.1111/j.1461-0248.2012.01777.x.

Borrelli, J.J., 2015. Selection against instability: stable subgraphs are most frequent in empirical food webs. Oikos 124, 1583–1588. https://doi.org/10.1111/oik.02176.

Borrelli, J.J., Ginzburg, L.R., 2014. Why there are so few trophic levels: selection against instability explains the pattern. Food Webs 1, 10–17. https://doi.org/10.1016/j.fooweb.2014.11.002.

Brose, U., Cushing, L., Berlow, E.L., others, 2005. Body sizes of consumers and their resources. Ecology 86, 2545.

Brown, J.H., Gillooly, J.F., 2003. Ecological food webs: high-quality data facilitate theoretical unification. Proc. Natl. Acad. Sci. U. S. A. 100, 1467–1468. https://doi.org/10.1073/pnas.0630310100.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., Geoffrey, B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Carpenter, S., Kitchell, J., Hodgson, J., others, 1987. Regulation of Lake primary productivity by food web structure. Ecology 68, 1863–1876.

Cirtwill, A.R., Wootton, K.L., 2022. Stable motifs delay species loss in simulated food webs. Oikos, e09436. https://doi.org/10.1111/oik.09436.

Cohen, J.E., Jonsson, T., Carpenter, S.R., 2003. Ecological community description using the food web, species abundance, and body size. Proc. Natl. Acad. Sci. 100, 1781–1786. https://doi.org/10.1073/pnas.232715699.

Colvin, M.E., Pierce, C.L., Stewart, T.W., 2015. A food web modeling analysis of a Midwestern, USA eutrophic lake dominated by non-native common carp and Zebra mussels. Ecol. Model. 312, 26–40. https://doi.org/10.1016/j.ecolmodel.2015.05.016.

Csárdi, G., Nepusz, T., 2006. The igraph software package for complex network research. InterJ. Complex Syst. 1695, 1–9.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Food-web structure and network theory: the role of connectance and size. Proc. Natl. Acad. Sci. 99, 12917–12922. https://doi.org/10.1073/pnas.192407699.

Eklöf, A., Helmus, M.R., Moore, M., Allesina, S., 2012. Relevance of evolutionary history for food web structure. Proc. R. Soc. B 279, 1588–1596. https://doi.org/10.1098/rspb.2011.2149.

Fayram, A.H., Hansen, M.J., Ehlinger, T.J., 2006. Characterizing changes in maturity of lakes resulting from supplementation of walleye populations, 7, pp. 103–115. https://doi.org/10.1016/j.ecolmodel.2006.02.038.

Gauzens, B., Legendre, S., Lazzaro, X., Lacroix, G., 2013. Food-web aggregation, methodological and functional issues. Oikos. https://doi.org/10.1111/j.1600-0706.2013.00266.x.

Gauzens, B., Barnes, A., Giling, D.P., others, 2019. Fluxweb: an R package to easily estimate energy fluxes in food webs. Methods Ecol. Evol. 10, 270–279. https://doi.org/10.1111/2041-210X.13109.

Gray, C., Ma, A., Perkins, D., Hudson, L., Figueroa, D., Woodward, G., 2015. Database of Trophic Interactions. https://doi.org/10.5281/ZENODO.13751.

Hintz, W.D., Schuler, M.S., Borrelli, J.J., others, 2020. Concurrent improvement and deterioration of epilimnetic water quality in an oligotrophic lake over 37 years. Limnol. Oceanogr. 65, 927–938. https://doi.org/10.1002/lno.11359.

Ho, J.C., Michalak, A.M., Pahlevan, N., 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. Nature 574, 667–670. https://doi.org/10.1038/s41586-019-1648-7.

Howard, H.H., 1973. Phytoplankton in the Lake George Ecosystem.

Hudson, L.N., Emerson, R., Jenkins, G.B., others, 2013. Cheddar: analysis and visualisation of ecological communities in R M. Spencer [ed.]. Methods Ecol. Evol. 4, 99–104. https://doi.org/10.1111/2041-210X.12005.

Jordán, F., Endrédi, A., Liu, W., D'Alelio, D., 2018. Aggregating a plankton food web: mathematical versus biological approaches. Mathematics 6, 336. https://doi.org/10.3390/math6120336.

Kao, Y.C., Adlerstein, S., Rutherford, E., 2014. The relative impacts of nutrient loads and invasive species on a Great Lakes food web: an Ecopath with Ecosim analysis. J. Great Lakes Res. 40, 35–52. https://doi.org/10.1016/j.jglr.2014.01.010.

Kones, J.K., Soetaert, K., van Oevelen, D., Owino, J., 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. Ecol. Model. 220, 370–382. https://doi.org/10.1016/j.ecolmodel.2008.10.012.

Kuiper, J.J., Van Altena, C., De Ruiter, P.C., Van Gerven, L.P.A., Janse, J.H., Mooij, W.M., 2015. Food-web stability signals critical transitions in temperate shallow lakes. Nat. Commun. 6, 1–7. https://doi.org/10.1038/ncomms8727.

Lang, B., Ehnes, R.B., Brose, U., Rall, B.C., 2017. Temperature and consumer type dependencies of energy flows in natural communities. Oikos 126, 1717–1725. https://doi.org/10.1111/oik.04419.

Liu, Q.G., Chen, Y., Le Li, J., Chen, L.Q., 2007. The food web structure and ecosystem properties of a filter-feeding carps dominated deep reservoir ecosystem. Ecol. Model. 203, 279–289. https://doi.org/10.1016/j.ecolmodel.2006.11.028.

Martinez, N.D., 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecol. Monogr. 61, 367–392.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., Alon, U., 2002. Network motifs: simple building blocks of complex networks. Science 298, 824–827. https://doi.org/10.1126/science.298.5594.824.

Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. Can. J. Fish. Aquat. Sci. 55, 1454–1465. https://doi.org/10.1139/cjfas-55-6-1454.

Naisbit, R.E., Kehrli, P., Rohr, R.P., Bersier, L.-F., 2011. Phylogenetic signal in predator – prey body-size relationships. Ecology 92, 2183–2189.

Nilsson, K.A., McCann, K.S., Caskenette, A.L., 2018. Interaction strength and stability in stage-structured food web modules. Oikos 1–12. https://doi.org/10.1111/oik.05029.

Olivier, P., Frelat, R., Bonsdorff, E., others, 2019. Exploring the temporal variability of a food web using long-term biomonitoring data, pp. 1–15. https://doi.org/10.1111/ecog.04461.

Patonai, K., Fábián, V.A., 2022. Comparison of three modelling frameworks for aquatic ecosystems : practical aspects and applicability. Commun. Ecol. 23, 439–451. https://doi.org/10.1007/s42974-022-00117-3.

Patonai, K., Jordán, F., 2021. Integrating trophic data from the literature: the Danube River food web. Food Webs 28, e00203. https://doi.org/10.1016/j.fooweb.2021.e00203.

Peralta-Maraver, I., Robertson, A.L., Rezende, E.L., others, 2017. Winter is coming: food web structure and seasonality in a subtropical freshwater coastal lake. Ecol. Evol. 7, 4534–4542. https://doi.org/10.1002/ece3.3031.

Poelen, J.H., Simons, J.D., Mungall, C.J., 2014. Global biotic interactions: an open infrastructure to share and analyze species-interaction datasets. Ecol. Inform. 24, 148–159. https://doi.org/10.1016/j.ecoinf.2014.08.005.

Poisot, T., Gravel, D., Leroux, S., others, 2016. Synthetic datasets and community tools for the rapid testing of ecological hypotheses. Ecography (Cop.) 39, 402–408. https://doi.org/10.1111/ecog.01941.

Prill, R.J., Iglesias, P.A., Levchenko, A., 2005. Dynamic properties of network motifs contribute to biological network organization. PLoS Biol. 3, 1881–1892. https://doi.org/10.1371/journal.pbio.0030343.

Pringle, R.M., Hutchinson, M.C., 2020. Resolving food-web structure. Annu. Rev. Ecol. Evol. Syst. 51, 55–80.

R Core Team, 2021. R: a language and environment for statistical computing. R Found. Stat. Comput. https://doi.org/10.1007/978-3-540-74686-7.

Sánchez-Hernández, J., Cobo, F., Amundsen, P.A., 2015. Food web topology in high mountain lakes. PLoS One 10, 1–17. https://doi.org/10.1371/journal.pone.0143016.

Sarno, D., Margiotta, F., D'Alelio, D., Mazzocchi, M.G., Ribeira d'Alcalà, M., Montresor, M., 2016. Plankton food-webs: to what extent can they be simplified? Adv. Oceanogr. Limnol. 7, 67–92. https://doi.org/10.4081/aiol.2016.5646.

Sheppard, S.K., Harwood, J.D., 2005. Advances in molecular ecology: tracking trophic links through predator-prey food-webs. Funct. Ecol. 19, 751–762. https://doi.org/10.1111/j.1365-2435.2005.01041.x.

Siegfried, C.A., 1981. Phytoplankton of Lake George: Seasonal and geographic patterns. In: The Lake George Ecosystem: Proceedings of the Lake George Research Symposium, vol. III.

Stouffer, D.B., Camacho, J., Jiang, W., Amaral, L.A.N., 2007. Evidence for the existence of a robust pattern of prey selection in food webs. Proc. R. Soc. B 274, 1931–1940. https://doi.org/10.1098/rspb.2007.0571.

Strona, G., Nappo, D., Boccacci, F., Fattorini, S., San-Miguel-Ayanz, J., 2014. A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. Nat. Commun. 5, 4114. https://doi.org/10.1038/ncomms5114.

Vadeboncoeur, Y., Moore, M.V., Stewart, S.D., others, 2021. Blue waters, green bottoms: benthic filamentous algal blooms are an emerging threat to Clear Lakes worldwide. Bioscience 71, 1011–1027. https://doi.org/10.1093/biosci/biab049.

Vander Zanden, M.J., Cabana, G., Rasmussen, J.B., 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ^{15}N) and literature dietary data. Can. J. Fish. Aquat. Sci. 54, 1142–1158. https://doi.org/10.1139/f97-016.

Vermaat, J.E., Dunne, J.A., Gilbert, A.J., 2009. Major dimensions in food-web structure properties. Ecology 90, 278–282.

Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. Nature 404, 180–183. https://doi.org/10.1038/35004572.

Williams, R.J., Martinez, N.D., 2004. Limits to trophic levels and omnivory in complex food webs: theory and data. Am. Nat. 163, 458–468. https://doi.org/10.1086/381964.

Zhang, H., Rutherford, E.S., Mason, D.M., others, 2016. Forecasting the impacts of silver and bighead carp on the Lake Erie food web. Trans. Am. Fish. Soc. 145, 136–162. https://doi.org/10.1080/00028487.2015.1069211.