LIMNOLOGY and OCEANOGRAPHY

A review of spatial structure of freshwater food webs: Issues and opportunities modeling within-lake meta-ecosystems

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Abstract

Lakes are currently facing multiple anthropogenic stressors impacting their ecological communities. The best way to understand how these systems will be affected by the changing environment is by modeling community dynamics. Models of lake food webs have tended to focus on pelagic organisms and treat lakes as if they contain single, uniform communities. However, heterogeneity in environmental conditions and resource availability generates within-lake compartmentalization in food web structure. Turnover among species and their interactions resulting from differences in depth and substrate type creates unique food webs in different regions of lakes. Food webs within lakes can therefore be represented as a three-dimensional meta-ecosystem, where food web compartments are connected by flows of nutrients, materials, and consumers with variable degrees of mobility within the lake. We review how food webs are spatially structured within lakes and the processes that connect different parts of the ecosystem. We then discuss how current modeling approaches address the spatial heterogeneity of lake communities, highlighting key methods and some of the constraints preventing more spatially explicit representation of food webs. Finally, we recommend the use of allometric trophic networks to make spatially explicit food web modeling easier. By capitalizing on empirically described allometric relationships to parameterize trophically complex food webs, we can balance generalizable model approaches with system-specific needs. Given the spatially explicit nature of many current threats to freshwater lakes, building an understanding of how space structures the community is imperative to create better approaches for freshwater management and conservation.

Lakes are currently facing threats from multiple anthropogenic stressors, including shoreline development, introduced and invasive species, eutrophication, pollution, and global warming. When considering the impact of stressors on a community, it is imperative to consider the food web because food web structure controls community dynamics (Allesina and Pascual 2008; Gravel et al. 2016; Cenci et al. 2018). Any effects of stressors on individual taxa can cascade through a food web, potentially resulting in even greater indirect impacts (Carpenter et al. 1987). A key tool to determine the impact of a changing environment on lake ecosystems systems is modeling the dynamics of the community.

Many of the stressors commonly impacting lake ecosystems can have variable effects throughout the lake. For instance, by replacing natural forests with residential developments, human alteration of parts of the shoreline can increase detrital accumulation and algal biomass (Rosenberger et al. 2008). Both within and across lakes, eutrophication results in homogenization of

ecological communities (Donohue et al. 2009; Menezes et al. 2015; Salgado et al. 2018). Invasive species can have different effects on food web structure depending on the characteristics of habitat patches within lakes (Kelly and Hawes 2005; Hansen et al. 2017). Global climate change causing warmer water leads to longer and stronger periods of stratification and reduced ice cover at higher latitudes. Reduced ice cover can alter planktonic succession (Adrian et al. 1999), and can cause shifts in food web structure by decoupling littoral and pelagic webs (Tunney et al. 2014; Bartley et al. 2019). We can address the variable spatial impacts of these stressors by considering the food web in the lake as a meta-ecosystem.

Food webs in lakes are large, complex, and heterogeneously distributed in space, posing a particular challenge to our understanding of the effects of anthropogenic influences on lake ecology. Species-specific responses to environmental stressors may be altered by the food web context. Interactions among consumers and their resources play out in an explicit spatial arena, and models accounting for the variability of the environment in space may be better able to make predictions about ecological responses to perturbations (Mougi 2017). This is especially important when attempting to understand processes resulting in spatially isolated or sporadic impacts such as harmful algal blooms, where approaches averaging

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over the whole lake may miss key details (Nijp et al. 2019; Isles and Pomati 2021). Food web model predictions depend largely on the underlying structure of the food web, and the spatial organization of lakes (e.g., littoral, pelagic, and profundal lake zones) may result in distinct food webs by influencing the distribution of species and their interactions.

Within lakes, the focus on understanding and modeling the food web has been centered on pelagic organisms and the approaches used to model these systems have typically assumed that the food web can be considered as a single spatially homogenous entity. The incorporation of spatial information into aquatic food web models has advanced primarily by coupling food webs including nutrients, phytoplankton, and zooplankton to hydrodynamics models (Jørgensen 2010; Mooij et al. 2010; Janssen et al. 2015). The food web component of these models has typically been limited to a few phytoplankton and zooplankton groups, with some models including macrophytes (Berger and Wells 2008; Sachse et al. 2014), mussels (Bocaniov et al. 2014), or fish (Makler-Pick et al. 2011). Of course, freshwater food webs are often much more diverse and structurally complex, with published webs ranging from 35 to as many as 800 trophic groups when including ontogenetic stages and nonphylogenetic categories such as detritus and seeds (Dunne et al. 2002).

In this review, we discuss the spatial structure in lake food webs resulting from heterogeneity in environmental conditions and how such spatial complexity can be interpreted using the framework of meta-ecosystems. We begin by highlighting how food web structure can vary over space and how these spatial compartments are connected. Then we identify common food web models that have been applied to lake ecosystems and how spatial complexity has been accounted for. For these models, we highlight the key constraints limiting them from incorporating additional spatial and trophic complexity. We conclude by proposing a new approach to modeling spatially heterogenous lake food webs using a flexible framework based on within-lake meta-ecosystems.

The lake as a meta-ecosystem

While a metacommunity is a system of patches connected by the dispersal of organisms, a meta-ecosystem includes connections by the flow of nutrients, materials, and organisms (Loreau et al. 2003). Given that a meta-ecosystem requires a set of interconnected ecosystems, it is worth asking: how can a lake, which is often considered a homogenous patch, be represented as a meta-ecosystem? At a coarse scale, the lake can be divided into three distinct zones (the littoral, pelagic epilimnion, and hypolimnion/profundal) that contain unique habitats and food webs yet are connected by the flow of water and movement of organisms (Schindler and Scheuerell 2002; Loreau et al. 2003). At finer scales, particularly within the littoral zone, spatial variation in environmental conditions and habitat characteristics can create a system of patches containing a subset of organisms that prefer those conditions.

Lakes may appear to allow for high dispersal, but there may be cryptic barriers preventing movement across patches. Some fish species with littoral preferences, for example, may be unwilling to venture across open water. Genetic evidence has shown differentiation in fish across multiple sites both within the littoral zone and between the littoral and pelagic zones within multiple lakes (Bergek and Björklund 2007; Faulks et al. 2015). Bacteria, diatoms, macroinvertebrates, and fish have exhibited metacommunity-like dynamics within lake littoral zones (Vilmi et al. 2016*a*,*b*; Langenheder et al. 2017; Tolonen et al. 2017). The relative importance of local environmental conditions (species sorting) and spatial processes (mass effects) on the dynamics of these groups depends on species' traits (Tolonen et al. 2018) and can fluctuate over time (Strecker et al. 2011). For example, while among lake studies suggest that spatial processes become more important for larger species, within lakes environmental filtering is more important for larger-sized and non-flying species (Tolonen et al. 2018). Given that different species experience environmental heterogeneity at different scales, we consider spatial variation at multiple levels and how spatial processes link habitat patches across scales.

A hierarchy of spatial organization

Spatial heterogeneity within lakes drives a hierarchy of spatial organization at multiple scales that can depend on the species. Variation in the horizontal and vertical dimensions in abiotic drivers such as depth, light, chemistry, and temperature generate the three main lake zones (Schindler and Scheuerell 2002). The ecological community in each zone is comprised of a subset of the whole-lake species pool, depending on their habitat preferences and environmental tolerances. Within the littoral zone, habitat patches are generated based on substrate types and biotic variables such as the presence or absence of macrophytes (Stoffels et al. 2005). The differences among the local communities at both the scale of lake zones, and the finer scale of habitat patches, will generate distinct food webs, thereby driving variability in primary and secondary production throughout the lake.

While pelagic food webs are primarily planktonic, littoral food webs include benthic algae, numerous aquatic invertebrates, and fish (Schindler and Scheuerell 2002). Productivity of phytoplankton and periphyton depends on habitat characteristics, with phytoplankton biomass and diversity declining from the littoral into the pelagic and periphyton production having a unimodal relationship with depth (Schweizer 1997; Vadeboncoeur et al. 2014). Some fish species have shown morphological responses to living in the pelagic vs. the littoral resulting from differences in individual specialization (Marklund et al. 2018, 2019). Turnover in both species composition and the interactions among species creates differences in the structure of littoral and pelagic food webs (Fig. 1; Warren 1989; Gamble et al. 2011*a*,*b*; Poisot et al. 2012). In both large lakes and small ponds, littoral food webs are typically
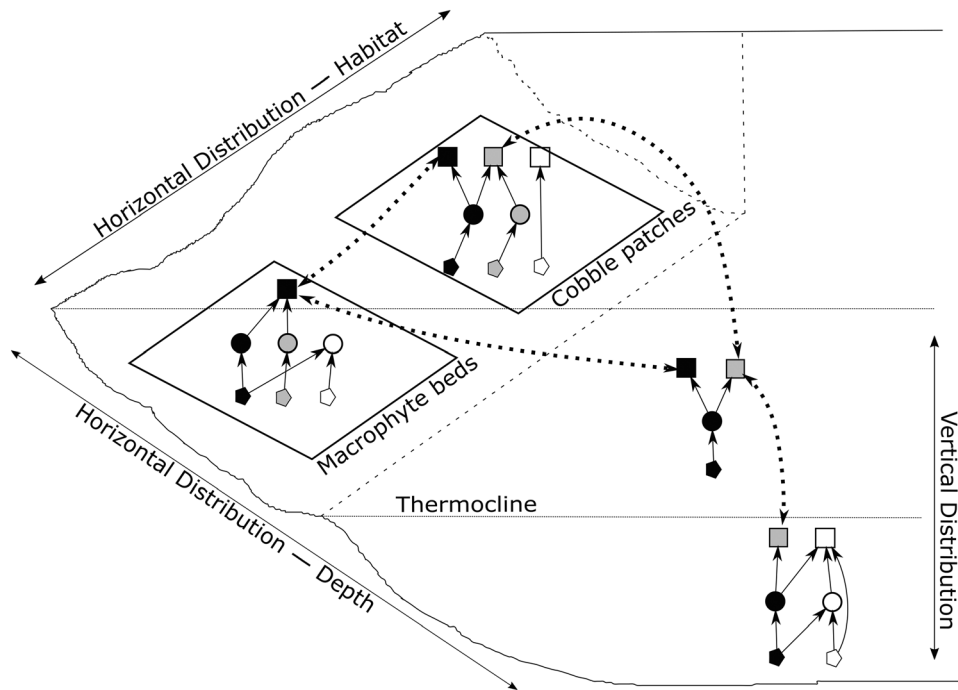
Fig. 1. The combination of environmental heterogeneity, resource distribution, and species turnover creates distinct patches in three dimensions with different food web structure. Along one horizontal dimension, the distribution of habitat types drives food web structure. Along a second horizontal dimension, depth becomes important. In the open water, the vertical distribution of light, temperature, and dissolved oxygen drives changes in community composition. Differently colored symbols represent different species in this meta-ecosystem, with some species able to multiple patches (indicated by the thick dotted lines), and others only a subset of available habitat.

more complex with higher species diversity and more links among them, while the offshore community represents a subset of the littoral community (Warren 1989; Gamble et al. 2011*a*,*b*).

In the vertical dimension of lake heterogeneity, producer species living on the bottom vs. the top of the lake compete along opposing axes of resource availability (Jäger and Diehl 2014). Nutrients tend to be higher near the bottom of the lake because of exchanges from the sediment, and benthic producers such as macrophytes and periphyton are better positioned to use these resources in the littoral zone, when not limited by light availability. In oligotrophic lakes, periphyton can be responsible for greater than 80% of primary productivity, while phytoplankton increasingly dominates productivity as total phosphorus increases (Vadeboncoeur et al. 2003). Shifting producer dominance from the benthos to phytoplankton can impact the structure of the food web in the littoral zone, with more zoobenthos relying on phytoplankton prey over benthic algae (Vadeboncoeur et al. 2003). This variability can drive differences in the ecological community as depth increases (Ali et al. 2002; Hämäläinen et al. 2003). In Iceland's Lake Thingvallavatn, the zoobenthos can be separated into five distinct communities based on depth, with four in the littoral zone, and one found in the profundal zone (Lindegaard 1990). Though the community composition changes with depth along the benthos, they

remain linked by the flow of nutrients and materials, as well as by larger consumers moving through these patches.

In the horizontal dimension, habitat variation within the nearshore environment can generate distinct patches that affect food web structure (Li et al. 2018; Xu et al. 2019). For example, in the littoral zone macrophytes can provide habitat complexity that increases macroinvertebrate density, particularly for detritivores and scrapers (James et al. 2000; Rennie and Jackson 2005). As a result, areas dominated by macrophytes may have longer food chains than areas dominated by algae (Xu et al. 2019). Variable habitat patches drive variability in community composition that we do not often observe in the pelagic zone. Where offshore fish communities tend to be dominated by the same species throughout the lake, nearshore community composition can be more variable across sites (Gamble et al. 2011*b*). Spatially explicit food web structure can also result from variability in intraspecific resource use across different sites even when composition is similar (Hansen et al. 2017; Feiner et al. 2019). In short, the heterogeneity within lake littoral zones produces habitat patches with variable food web structure, further underscoring the need to use a meta-ecosystem approach.

Spatial flows across subsystems

Spatially distinct zones in lakes are linked by movement among the habitat patches, with organisms of different sizes

moving over different spatial scales. Given that the sizes of lake organisms can span 10 orders of magnitude (Brose et al. 2006; Boit et al. 2012), the scale at which these species experience spatial heterogeneity drives their distribution within lakes (Cai et al. 2017). Smaller organisms experience a finer scale of spatial heterogeneity, generating patches of food habitats for larger organisms. Larger organisms are typically more mobile and range over larger areas than smaller organisms (Minns 1995). Thus, larger consumers will connect patchy habitats via foraging, driving both trait and material coupling of patches and impacting the stability of the community (McCann et al. 2005, 2006; Massol et al. 2011).

Fish in particular play an important role linking benthic and pelagic habitats (Vander Zanden and Vadeboncoeur 2002; Vander Zanden et al. 2011). Species that prefer pelagic habitat still have some reliance on littoral-derived carbon, suggesting that while they primarily feed in the pelagic zone they do still forage in the littoral zone (Vander Zanden and Vadeboncoeur 2002). Salmonids, which are often the top predators in lakes, can obtain more than half their carbon from nearshore waters (Hampton et al. 2011). These fish move littoral biomass into the pelagic zone, which can be important for nutrient cycling in deep water (Visconti et al. 2014). This frequent and small-scale foraging behavior generates a shifting mosaic of food web structures across the meta-ecosystem as feeding interactions are altered when consumers move throughout the landscape (Pillai et al. 2009; Massol et al. 2011; Barter and Gross 2017).

The degree of habitat coupling across these lake zones may depend on both the environmental conditions in the lake, such as resource availability or the temperature, and lake morphometry. In many temperate lakes that undergo stratification, there is reduced plankton abundance in pelagic water resulting in a shift in resource use by consumers towards greater reliance on littoral resources (Stewart et al. 2017). Consumers shifting resource use from pelagic to littoral resources results in linkages between the two habitats at the seasonal scale. For some consumers, this link between pelagic and littoral zones is reduced as temperatures rise. Many cold-adapted fish predators, such as lake trout (*Salvelinus namaycush*), prefer to spend their time in the colder metalimnion during summer months, but individuals continue to make excursions into warmer littoral zones for feeding (Bergstedt et al. 2003; Morbey et al. 2006). As temperatures rise, these cold-adapted predators are less likely to make these forays into the warmer nearshore waters because of the metabolic cost resulting in a shift in energy pathways (Tunney et al. 2014). The impact of temperature may also depend on the shape of the lake; more reticulate lakes have less accessible littoral area than more circular lakes because of energetic and thermal restrictions (Dolson et al. 2009). These results indicate that the relative importance of environmental and spatial processes on the meta-ecosystem will depend on the interaction between the abiotic conditions in the lake and its morphometry.

Current models of lake food webs

There are two main methods for modeling freshwater food webs, each with different levels of complexity and approaches to spatial processes. The first modeling approach uses biogeochemical food webs that are often linked to hydrodynamic models in 1–3 spatial dimensions (Fig. 2a; Zhang et al. 2008; Leon et al. 2011; Li et al. 2013). Biogeochemical models typically include relatively small food webs composed of several phytoplankton and zooplankton groups, but also track multiple nutrient cycles (e.g., phosphorus, nitrate, ammonia, etc.; Fig. 2a). Many of these aquatic ecosystem models have been reviewed in detail by Mooij et al. (2010) and Janssen (2015). The second modeling approach uses bioenergetic food webs that are trophically complex and have little to no influence of spatial processes (Fig. 2b; Langseth et al. 2012; Boit et al. 2012). While biogeochemical models follow the flow of nutrients, bioenergetic models follow the flow of energy or biomass through the system. Biogeochemical models have traditionally incorporated spatial processes through coupled hydrodynamics in applied models, but bioenergetic models are typically only spatially explicit in theoretical investigations.

Zero to 3D

In a 0D model, a lake is a spatially homogenous box with some input and output, like the treatment of a chemostat, and is often used in food web models. A 0D box model may be most useful for food webs that include larger fish species that may range over greater distances, as the environmental conditions experienced by these consumers are averaged together. Whereas 0D models average over all spatial dimensions, 1D models incorporate variation in either the vertical dimension (typical for lakes) or one horizontal dimension (e.g., in river systems). Depth is a key driver of environmental variability in lakes, serving as a proxy for both temperature and light, which control primary productivity. As a result, 1D lake models typically assume that the system can be modeled as a single water column, spatially averaging over the horizontal dimension. The 1D approach works best for lakes that stratify where vertical structure is much more important than horizontal structure and offers a means to incorporate key spatial patterns (e.g., the thermocline) into food web models with relatively few computational and data requirements.

In 2D models, space can be represented either as two horizontal dimensions while averaging over depth or as one horizontal dimension and the vertical dimension while averaging over the remaining horizontal dimension. The 2D model approach has been used to represent both horizontal dimensions in pelagic systems to search for early warning signals of critical transitions from a clear water state to an algal bloom state (Serizawa et al. 2008; Buelo et al. 2018). A more common approach to 2D lake modeling is to use the two spatial dimensions to represent depth and the dominant direction of flow in the system (e.g., the CE-QUAL-W2 model; Cole and
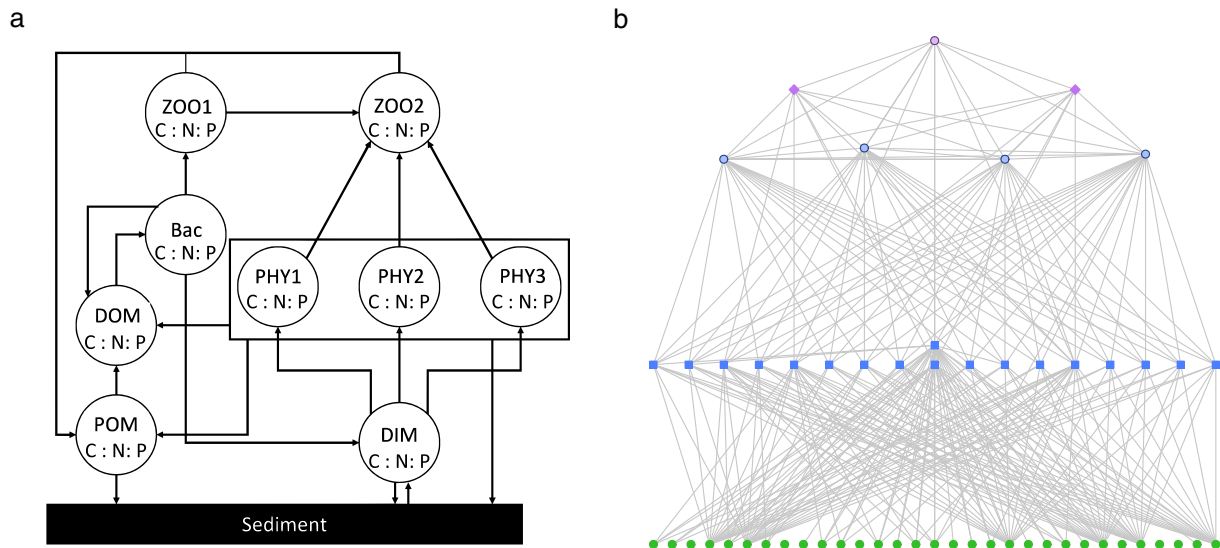
Fig. 2. (**a**) A schematic representation of a biogeochemical food web adapted from the Aquatic Ecodynamics model (Hipsey et al. 2013) includes three phytoplankton groups (PHY), two zooplankton (ZOO), bacteria (Bac), dissolved inorganic materials (DIM), and dissolved and particulate organic matter (DOM, POM). Each group is represented by internal pools of carbon, nitrogen, and phosphorus. (**b**) The food web of Tuesday Lake sampled in 1986 (Cohen et al. 2003) that would be used in a bioenergetic model contains 35 producer groups, 21 invertebrates, and one fish group.

Wells 2006). Fully 3D models represent the system in its entirety, allowing habitat and food web variability in the vertical and both horizontal dimensions and allowing the integration of more complex hydrodynamics. The higher complexity of these 3-D models requires higher resolution lake monitoring to validate spatial processes and greater computational resources to run (Arhonditsis et al. 2018).

Recent efforts to provide a more standardized way of modeling aquatic systems using multiple spatial approaches have resulted in the Framework for Aquatic Biogeochemical Models (FABM; Trolle et al. 2012). FABM facilitates modeling by providing a flexible framework to choose from, using multiple different 0D, 1D, 2D, or 3D hydrodynamic models to link with multiple biogeochemical models. One of the biogeochemical models available through FABM (i.e., PCLake) incorporates a slightly more complex food web than typical biogeochemical models. The PCLake food web includes detritus, macrophytes, three phytoplankton groups (cyanobacteria, green algae, and diatoms), zoobenthos, zooplankton, planktivorous fish, benthivorous fish, and piscivorous fish. It can accommodate more than 100 state variables and was designed to simulate an average shallow lake (Janse and van Liere 1995). More recent iterations of the model, including FABM-PCLake and PCLake+, are more generally applicable and can be applied to deeper lakes with more complex mixing regimes (Hu et al. 2016; Janssen et al. 2019). Coupled with FABM, PCLake allows users to model relatively large food webs and complex spatial processes.

Issues and opportunities

Modeling food webs is inherently difficult because they are complex systems with many interacting biotic and abiotic components. The more species or groups that are included in the food web, the higher the number of parameters required to simulate their dynamics. The number of parameters required for a model increases at a much faster rate than the number of additional species, included in the food web. For each species we need to parameterize functions for growth and loss from consumption and mortality, as well as know how these functions are affected by external drivers like temperature and light. Aquatic biogeochemical models also must identify parameter values for chemical processes for any nutrient cycles included, such as sediment flux, immobilization, and mineralization. Models such as Aquatic Ecosystem Dynamics (AED) and the Computational Aquatic Ecosystem DYnamics Model (CAEDYM) come with some default parameter values, but for most systems these must be tuned to provide good predictions (Hipsey et al. 2005, 2013). A database of parameter values for commonly used groups in aquatic food web models including detritus, phytoplankton, microphytobenthos, and zooplankton has recently been compiled to help address this issue, but there are still data gaps (Robson et al. 2018).

An alternative solution to this "plague of parameters" is that parameter values can be constrained by allometric relationships (Vucic-Pestic et al. 2010; Hudson and Reuman 2013; Kalinkat et al. 2013). For example, freshwater phytoplankton growth and nutrient usage traits are well predicted by cell volume (Edwards et al. 2015). Allometries may also be able to link body size to an individual's ability to move between habitats through relationships with speed, dispersal distance, and home range size (Hirt et al. 2018). Allometrically constrained food web models have been shown to capture a large

percentage of the variability in population dynamics in both terrestrial (Curtsdotter et al. 2019) and aquatic systems (Boit et al. 2012; Shimoda et al. 2016). However, while some argue that allometric relationships enhance predictive power of food web models (Iles and Novak 2016), others have suggested that the predictive power declines as trophic complexity increases (Jonsson et al. 2018). While it is unclear whether allometric parameterization is a complete cure for the plague of parameters, it is a significant first step towards building generalizable food web models from limited data by allowing inferences about consumer-resource interactions to be made from body size information alone.

Including spatial heterogeneity in food web structure will also require increased sampling of lakes to identify how community composition and species interactions change over space. With more spatial dimensions, models need data on temperature and flow as well as other variables of interest (e.g., chlorophyll, phytoplankton, and zooplankton densities) from multiple locations to validate spatial heterogeneity in the lake (Baracchini et al. 2020). Sampling multiple locations often comes with a tradeoff, such as lower temporal or taxonomic resolution. In contrast, monitoring programs using a central location, may be better able to describe changes in abundance of many taxonomic groups (Gaedke et al. 2002; Boit and Gaedke 2014). By sampling a greater number of sites within a lake we will be able to address key data needs of where species are and how their abundance changes across habitat patches, but we will still need to know how often organisms move among the patches.

Part of building spatial complexity into food web models includes modeling the flow of materials in space, which can be derived from physical processes. These physical processes can also drive the passive movement of organisms, particularly plankton, though organisms also can actively move among locations. While many current models use hydrodynamics to drive the flow of materials in space, few include the active movement of individuals among habitat patches which can be an important driver of consumer-resource dynamics (McCann et al. 2005; Brechtel et al. 2019). In theoretical models with patch-based dynamics, movement among patches typically occurs by some fraction of the population in patch i dispersing to patch j based on some set of rules. A common approach is to define a migration strength among patches that may be modified or biased depending on differences in patch conditions (Hamm and Drossel 2017). In some cases the rate may depend on difference in biomass density between patch i and neighboring patches or it may be impacted by resource availability and predator densities (Reynolds et al. 2001; Ristl et al. 2014; Kondoh et al. 2015). Properly parameterizing a migration rate among patches will require increased knowledge of how organisms move within lakes. While there is a rich literature on diel movement of plankton (Bollens and Frost 1991; Burks et al. 2002) and macroinvertebrates (Marklund et al. 2001), less is known about larger scale dispersal patterns within lakes. The

movement ecology of fishes is gaining traction as new technologies like the Great Lakes Acoustic Telemetry Observation System allow large-scale tracking of individuals throughout the lake for several species (Binder et al. 2017; Kessel et al. 2018; Gorman et al. 2019). The movement of organisms among habitat patches remains a significant source of uncertainty for food web models, as the relatively small amount of available data is coupled with potentially large influences on dynamics (McCann et al. 2005).

With increasing spatial complexity, the computational power required to run both the underlying hydrodynamics and food web models also increases. As the spatial resolution of the model increases, a finer scale grid is required to more fully caption the geometry of the lake which means that more computational time will be required to run the model (Arhonditsis et al. 2018). Recent efforts have also shown the benefits of running model ensembles to better capture the uncertainty from model structure (Gal et al. 2014; Trolle et al. 2014; Janssen et al. 2015). Running multiple scenarios or model ensembles for 1D or 2D models is currently not restricted by computational power, but becomes much more difficult for 3D models (Arhonditsis et al. 2018). The question becomes at what spatial scale is most appropriate to address how complex food webs will respond to environmental change. Ideally, the scale will be resolved enough to allow the model to integrate spatially driven anthropogenic impacts while also coarse enough to be applied to systems that do not have large monitoring programs.

To address the issue of spatial complexity we can define the lake as a meta-ecosystem, where environmentally distinct regions of the lake are separated into well-mixed boxes, with material and organismal flows across boundaries. For example, SALMO (Simulation by means of an Analytical Lake MOdel) uses the simplest case for this method, separating the warmer and well-lit epilimnion from the colder, darker hypolimnion. McDermot and Rose (2000) used an individual-based model of the bioenergetics of several fish species and separated a lake into three boxes representing the littoral, epilimnetic, and hypolimnetic zones. In these cases, the lake zones were represented by a single well-mixed compartment with the food web groups able to use each one. The food webs in these models are simplified, with SALMO including only two to three phytoplankton groups and zooplankton, and the individual-based model including only six fish species whose prey are constantly replenished. A multi-compartment approach allows us to capture the key features of within-lake variability without requiring complex spatial models, and this approach could be extended to capture additional spatial and trophic complexity.

Larger or more heterogenous lakes can be represented by linking groups of compartments representing different lake zones in each region of the lake. In a model of Hamilton Harbor on Lake Ontario, Shimoda et al. (2016) used three boxes to represent the epilimnion, metalimnion, and hypolimnion.

To address gradients in the water quality of the system, they separated the eplimnion box into four compartments, three describing areas influenced by inflows and one larger central epilimnetic region. Further extending a spatial box model approach, a model of Lake Simcoe separated the lake into four regions, three represented by a box for the epilimnion and hypolimnion with the fourth shallower region represented with an epilimnion (Gudimov et al. 2015). In these examples, the food web structure was both simplified and constant throughout the spatial compartments; however, given the way species are distributed in a lake it may be more reasonable to allow the structure to vary. The food web within each box will depend on the characteristics of the taxa in the lake (Fig. 3). In the littoral zone box, we expect a relatively complex food web with both planktonic and benthic derived food chains. In the epilimnetic box, a planktonic food web should be represented, and in the hypolimnion a detrital-based food web should be dominant. These box-models can capture variation in both the horizontal and vertical dimensions of the lakes while being considerably less spatially complex than a fully 3D model, which can allow for a better representation of the trophic structure of the system.

A new approach to modeling the meta-ecosystem

We propose that the most effective way to understand and predict lake food web dynamics is by combining the approach of using compartmentalized box models and allometric-scaling relationships to allow both spatial and biological complexity. The in-lake meta-ecosystem can be represented by two to three patch types defined as well-mixed boxes supporting different subsets of the whole-lake food web: the littoral, pelagic epilimnion, and the profundal/hypolimnion if the lake is large enough to stratify (Fig. 3). Additional spatial structure can be incorporated into this approach by adding additional sets of the three boxes, generating a pseudo-3D spatial model of the system potentially representing multiple basins in a large lake (Fig. 4).

Lake size and shape determines how many compartments are required. In small lakes and ponds, we expect to see differences in the littoral and pelagic community, as observed in Skipwith Pond, such that the meta-ecosystem can be comprised of two well-mixed boxes with distinct food webs (Warren 1989). In larger lakes, variability in shoreline use and lake morphometry may drive the need for additional compartments. We expect that larger lakes are more likely to have heterogenous nearshore regions. Human alteration of lake shorelines has been shown to alter littoral macroinvertebrate communities, suggesting that different types of shorelines (e.g., beach, lawn, natural) may require different littoral compartments (Rosenberger et al. 2008; Pätzig et al. 2018). Likewise, larger lakes with complex morphometry may also be more likely to have distinct littoral zones compared to more circular lakes, due to the greater amount of littoral area (Dolson et al. 2009).
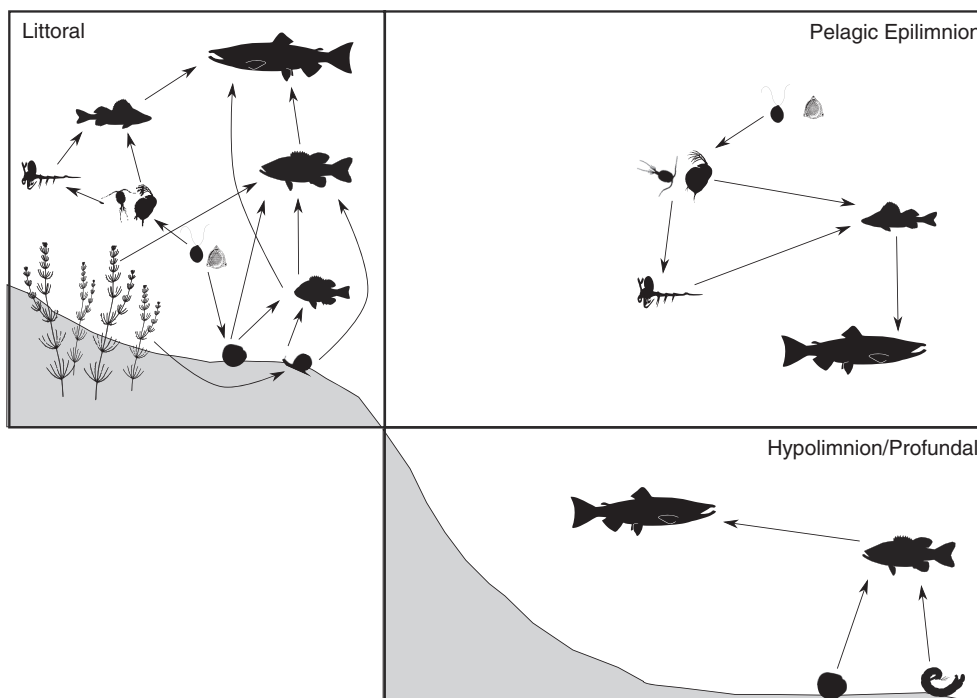

Fig. 3. Food web model contained in three compartments. The littoral zone is home to a complex web made up of both planktonic and benthic pathways. The pelagic epilimnion is host to a planktonic food web, while the hypolimnion has a benthic-derived food web. The top fish predators can move among the three compartments, while smaller consumers are only able to use their preferred habitats (e.g., benthic detritivores are found only along the bottom of the lake).
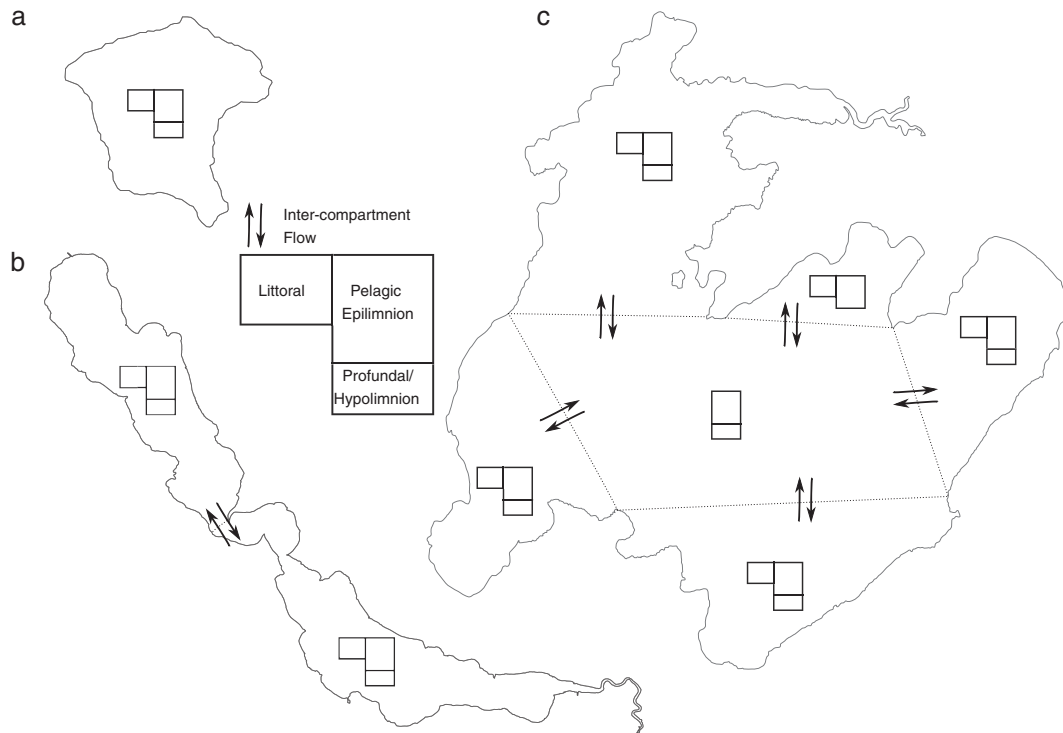
Fig. 4. The meta-ecosystem of a small simple lake (**a**) may be well represented by just a single littoral box, one for the pelagic epilimnion, and, depending on whether it is large enough to stratify, a box for the profundal/hypolimnion. For larger and longer lakes (**b**) multiple set of the three boxes could be linked by the bi-directional flow of water and movement of individuals across the basins. Large lakes with more complex structure (**c**) may be best represented by multiple sets of the three boxes and depending on the bathymetry some basins may only require a subset of patches (e.g., littoral only, littoral and epilimnion, or epilimnion and hypolimnion).

Hydrodynamic models could still be coupled with this approach and used to compute the net fluxes among the different boxes, as well as key abiotic conditions such as temperature and volume of each box (e.g., due to variable thermocline depth). Flow of water from the littoral to epilimnion and hypolimnion and vertical fluxes from the hypolimnion will influence nutrient and detrital resource pools in each compartment. Species traits, such as body size and dispersal mode determine both which boxes they can use and how they move among the boxes. For example, attached producers such as macrophytes and periphyton are only found in the littoral zone as they require light and substrate, benthic species such as bivalves and oligochaetes can only use littoral and hypolimnetic boxes where there is sediment, and many planktonic taxa and fish may be found in all three boxes. Generally, among mobile species larger taxa can move further and movement of these groups may be modeled in one of two ways: (1) as local taxa that can disperse to any patch in the system each time step (Maser et al. 2007) or (2) as global taxa able to consume resources from all or a subset of patches within a time step (McCann et al. 2005; Brechtel et al. 2019). As data on movement within lakes remains relatively sparse, parameterizing the dispersal rates for each group is challenging. Some simplifying assumptions to estimate movement may prove

useful, like scaling dispersal rate to body-mass such that the rate is considered high when it is greater than metabolic losses (Hamm and Drossel 2017).

Many of the food webs that have already been developed for lakes can be readily adapted to this approach. An allometric trophic network (ATN) model would primarily require data on species identities within each box, their body mass, and the interaction structure among species. We can use what we know about the groups that are included in these webs to determine whether they prefer the pelagic or littoral zone, and whether they spend more time in the open water or near the benthos. Other sources of data, such as stable isotopes can be particularly helpful in determining which lake zones consumers prefer to use resources from Vander Zanden and Vadeboncoeur (2002) and Vander Zanden et al. (2011). Species' body mass can be used to parameterize growth and metabolic rates based on the metabolic theory of ecology (Brown et al. 2004; Williams and Martinez 2004). Using this approach will allow for much greater trophic complexity to be incorporated into spatially explicit lake food web models than has previously been used. Combining ATN models for each lake zone and allowing for movement of organisms and materials by coupled hydrodynamics and directed movement can allow us to model the lake meta-ecosystem in a generalized manner,

that can be made more specific depending on the available site-specific data.

Explicitly modeling the food web in each of these boxes would also allow researchers to assess the spatial context of anthropogenic impacts on lake communities. Nutrient pollution, for example, could be included as increased inputs into the littoral zone. These excess nutrients may be taken up by producer groups in the littoral or might be washed into the offshore epilimnetic or hypolimnetic waters. The impacts of warming will result in decreased usage of the littoral zone by some cold-water-adapted species, altering the structure and thus the dynamics of the food web (Bartley et al. 2019). Combining both trophic and spatial complexity into lake food web models will give us a better understanding of the dynamics of the community and allow us to more easily reveal potential ecological surprises caused by multiple stressors (Paine et al. 1998; Christensen et al. 2006).

Conclusion

Natural and anthropogenic factors create spatial heterogeneity in lakes, both vertically and horizontally, and this creates a 3D meta-ecosystem. In the two horizontal dimensions, variability is driven by habitat type and depth, while the vertical structure is determined by depth alone. The distributions of many organisms such as are constrained to patches that provide suitable substrate (e.g., macrophytes or bivalves) or refuge from predation (e.g., gastropods preferring macrophyte beds). Other organisms integrate these patches by ranging over wider regions. Small fish, exhibiting diel movement to forage and hide from predators connect patches at relatively local scales, while far-ranging generalist predators are connecting patches regionally (Brechtel et al. 2019). This inherent spatial structuring of lake food webs contributes to the adaptive capacity of the community by allowing it to quickly respond to varying environmental conditions (McMeans et al. 2016).

There is a growing consensus on the need to apply metacommunity and meta-ecosystem theory to multi-trophic systems (Massol et al. 2011; Guzman et al. 2019). Regional systems of lakes fit well into the metacommunity framework, but when is it important to consider the lake as a meta-ecosystem? Many studies have successfully reproduced broad-scale food web dynamics without this consideration (Makler-Pick et al. 2011; Boit et al. 2012). Over annual timescales, fine-scale variability in the food web may not matter; the dynamics may average out across patches over time. Over shorter timescales, however, such as when trying to predict algal blooms, fine-scale spatial variability likely matters much more. Thus, modeling food webs with explicit spatial context will aid in identifying the impacts of multiple anthropogenic stressors. Because the intensity of these stressors is distributed in space, the effects on the ecological community will be better captured by a meta-ecosystem approach.

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Conflict of Interest

The authors declare no conflict of interest.