



REVIEW

Food-web structure and ecosystem function in the Laurentian Great Lakes—Toward a conceptual model

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Abstract

1. The relationship between food-web structure (i.e., trophic connections, including diet, trophic position, and habitat use, and the strength of these connections) and ecosystem functions (i.e., biological, geochemical, and physical processes in an ecosystem, including decomposition, production, nutrient cycling, and nutrient and energy flows among community members) determines how an ecosystem responds to perturbations, and thus is key to understanding the adaptive capacity of a system (i.e., ability to respond to perturbation without loss of essential functions). Given nearly ubiquitous changing environmental conditions and anthropogenic impacts on global lake ecosystems, understanding the adaptive capacity of food webs supporting important resources, such as commercial, recreational, and subsistence fisheries, is vital to ecological and economic stability.
2. Herein, we describe a conceptual framework that can be used to explore food-web structure and associated ecosystem functions in large lakes. We define three previously recognised broad habitat compartments that constitute large lake food webs (nearshore, pelagic, and profundal). We then consider, at three levels, how energy and nutrients flow: (a) into each basal resource compartment; (b) within each compartment; and (c) among multiple compartments (coupling). Flexible shifts in food-web structures (e.g., via consumers altering their diet or habitat) that sustain these flows in the face of perturbations provide evidence for adaptive capacity.
3. We demonstrate the conceptual framework through a synthesis of food-web structure and ecosystem function in the Laurentian Great Lakes, with emphasis on the upper trophic levels (i.e., fishes). Our synthesis showed evidence of notable adaptive capacity. For example, fishes increased benthic coupling in response to invasion by mussels and round gobies. However, we also found evidence of loss of adaptive capacity through species extirpations (e.g., widespread collapse in the abundance and diversity of ciscoes, *Coregonus* spp., except in Lake Superior).
4. In large freshwater lakes, fishery managers have traditionally taken a top-down approach, focusing on stocking and harvest policy. By contrast, water quality

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managers have focused on nutrient effects on chemical composition and lower trophic levels of the ecosystem. The synthesised conceptual model provides resource managers a tool to more systematically interpret how lower food-web dynamics influence harvestable fish populations, and vice versa, and to act accordingly such that sustainable resource practices can be achieved.

5. We identify key gaps in knowledge that impede a fuller understanding of the adaptive capacities of large lakes. In general, we found a greater uncertainty in our understanding of processes influencing energy and nutrient flow within and among habitats than flows into the system.

KEYWORDS

adaptive capacity, energy, fisheries, nutrients, trophic structure

1 | INTRODUCTION

The majority of the world's lakes are small (<1 km²) and shallow (<10-m depth) (Schindler & Scheuerell, 2002; and references within). However, large lakes (≥500 km²; Herdendorf, 1982), such as Lake Baikal, the African Great Lakes, and the Laurentian Great Lakes, support large human populations and economies (Southwick Associates, 2012) and hold a disproportionate amount of the world's standing freshwater. However, the structure and function of large lake food webs are not well understood compared to small lakes (Schindler & Scheuerell, 2002; Sterner et al., 2017). The large surface area and, in some cases, depth of large lakes makes them subject to biophysical phenomena more common to marine ecosystems than small lakes (Sterner et al., 2017). In addition, trophic and habitat resources are more diverse (i.e., high degree of ecological opportunity), but more geographically distant and patchily distributed in large compared to small lakes. Therefore, the scale of connections among different habitats (i.e., coupling) differs dramatically. Finally, catchment size and human habitation are positively related to the intensity and scale at which anthropogenic modifiers affect structural attributes of the system. For these reasons, extrapolating research results from small to large lakes, large marine ecosystems or inland seas may not describe adequately food-web structure and ecosystem function in large aquatic ecosystems of the world.

Inadequate understanding of large-lake food web structure and ecosystem function is problematic because structure and function appear intricately linked to a system's adaptive capacity, or ability to respond to perturbation without loss of essential functions (McMeans et al., 2016). Exploring how large lakes are structured and how these structures respond to both natural and anthropogenic stressors should lead to a better understanding of the adaptive capacity of large lakes (e.g., Barbiero et al., 2018; Kao, Adlerstein, & Rutherford, 2014; Munawar, Munawar, Dermott, Niblock, & Carou, 2002). Such an understanding has relevance for informing future management efforts aimed at conserving biodiversity, sustaining ecosystem functions, and providing ecosystem services.

Multiple lines of evidence suggest that systems with greater environmental heterogeneity, connectivity among spatial resource or habitat compartments (e.g., inshore, pelagic, profundal), and diversity of species (including populations or morphs within species) capable of flexibly responding to variation, should have greater adaptive capacity compared to more homogenised systems dominated by fewer species or habitats. Environmental variation (i.e., abiotic factors, habitat and resource availability) affects ecosystem processes, such as primary production, but also helps promote and sustain biodiversity by providing consumers, such as fishes, a diverse array of habitats and resources (Truchy, Angeler, Sponseller, Johnson, & McKie, 2015; Woodward & Hildrew, 2002). A high diversity of resources within a community and among different ecosystem components provides greater "insurance" that these resources can compensate for one another in the face of perturbation (Elmqvist et al., 2003; McCann, Rasmussen, & Umbanhowar, 2005; Rooney, McCann, Gellner, & Moore, 2006). Consumer behaviour also plays a role because predators higher in the food web must flexibly respond to variations in prey by altering their foraging behaviour among multiple resource types. Such flexible foraging may be central to adaptive capacity because it can theoretically be a potent stabilising force (McCann et al., 2005; Takimoto, Iwata, & Murakami, 2002) that is empirically documented to drive structural rearrangements of food webs across environmental gradients (McMeans et al., 2016; Thompson et al., 2015; Tunney, McCann, Lester, & Shuter, 2014; Woodward, Perkins, & Brown, 2010). Thus, preserving diverse "portfolios" of species, populations, and habitats is essential to ensuring that ecosystem functions are sustained across a wide array of environmental conditions (Schindler, Armstrong, & Reed, 2015). Any action that causes a loss in variation of, or connection among different habitats, species or functional groups, and that shifts a system towards dominance by any single entity, habitat, or energy flow pathway, can therefore be viewed as a loss in adaptive capacity (McMeans et al., 2016; Truchy et al., 2015).

Although not previously explored for large lakes specifically, the portfolio concept (Schindler et al., 2015) can guide thinking about large-lake adaptive capacity and the management strategies that can



FIGURE 1 Map of Great Lakes basin locations mentioned in text

help preserve such capacity. In particular, large aquatic ecosystems may be buffered from perturbations due to their spatial heterogeneity (e.g., large number of habitats occurring horizontally along complex shorelines and vertically through a deep water column) and a greater diversity of potentially redundant and compensatory species (Vadeboncoeur, McIntyre, & Vander Zanden, 2011). Here, we use the Laurentian Great Lakes of North America (hereafter Great Lakes; Figure 1) as a model system to explore these ideas and to connect food-web structure and function with the potential adaptive capacity of these large lakes. We accomplish this by describing a conceptual framework for food-web structure and function based on three broad habitat compartments (nearshore, pelagic, and profundal), which builds on previous studies that have considered energy and nutrient dynamics within and among these compartments (e.g., Schindler & Scheuerell, 2002; Sierszen et al., 2014; Stewart et al., 2016). As the discrete compartments can be found in smaller lakes and in marine ecosystems, the framework can be broadly applied. We then synthesise current knowledge of how both natural processes and human impacts have altered food-web structure and function in each of the five Great Lakes with emphasis on the upper trophic levels, identify major trends across the lakes, and connect these structural changes with potential effects on adaptive capacity. We end by identifying key gaps in knowledge on the structure and function of these lakes, so as to inform and guide future research, funding priorities, and management agendas in the Great Lakes and globally in other large,

aquatic ecosystems. Although quantitative comparisons of the relationship between structure and function across the Great Lakes are beyond the scope of this paper, previous studies have quantified the food web consequences of human impacts using mass balance models (e.g., in Lake Huron; Kao et al., 2014) and compared changes in lower trophic levels (phytoplankton and zooplankton) between lakes that differ in the timing and extent of human impacts (e.g., Lake Michigan versus Huron; Barbiero et al., 2018). Ideally our synthesis and conceptual framework will inspire future efforts across lakes that differ in their degree of adaptive capacity.

The Great Lakes support fish communities of high economic and ecological value and have faced major anthropogenic perturbations including intensive fish harvest, non-native species invasions, progressive physiochemical alteration, and climate change (Eshenroder & Burnham-Curtis, 1999; Schindler, 2001; Smith, 1972). Individual components of Great Lakes ecosystems are heavily studied (i.e., nutrients, phytoplankton, zooplankton, fishes), but a current synthesis on Great Lakes food web structure and function and its response to human impacts is lacking. Such a synthesis is timely given the rapid advances in ecological tools and tracers (e.g., stable isotopes, fatty acids, contaminants, acoustic telemetry, modelling capabilities; Coll et al., 2015; Donaldson et al., 2014; Layman et al., 2012) that are providing novel insights into food-web structure and ecosystem adaptive capacity (McMeans et al., 2016).

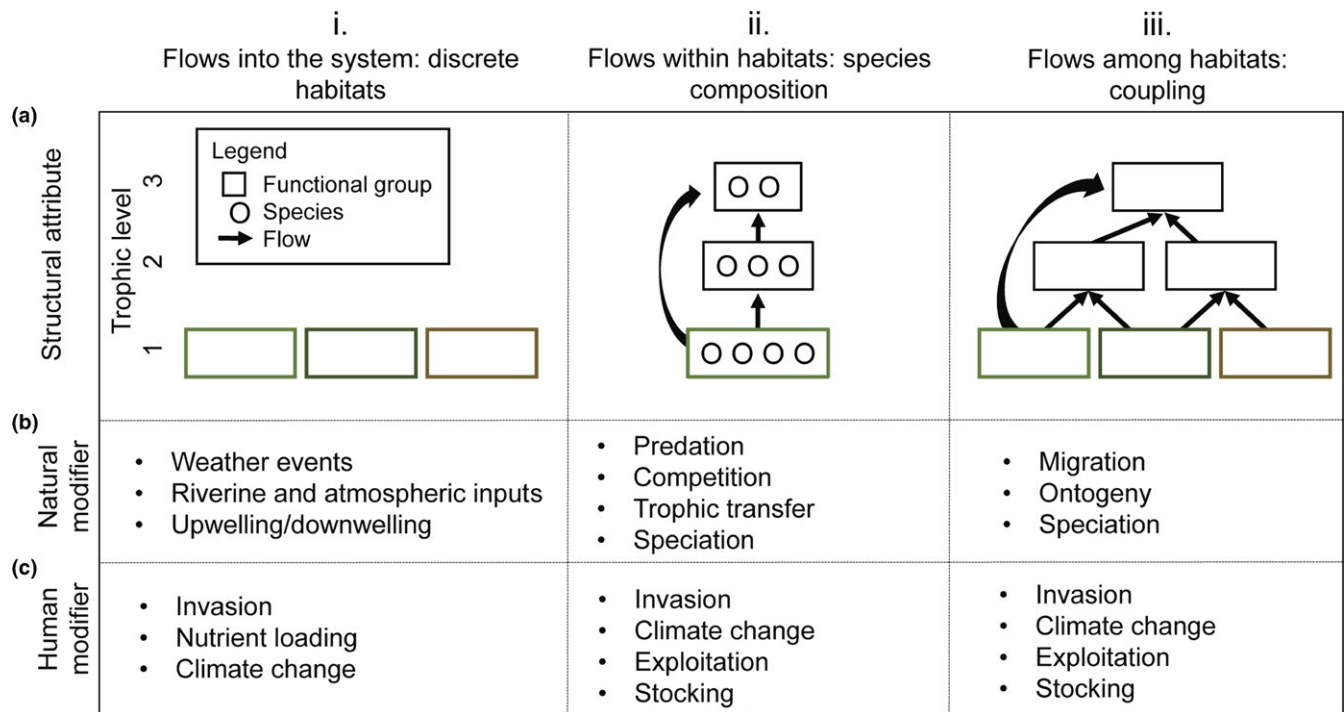


FIGURE 2 Conceptual structural attributes of food webs (a), and both natural (b) and human modifiers (c) of these structural attributes. Structures and their modifiers are considered at three scales: (i) energy and nutrient flows into the system through basal resources in spatially-distinct habitats (e.g., nearshore, pelagic, profundal—represented as different coloured rectangles); (ii) energy and nutrient flows and species composition within a single habitat; and (iii) connections among habitats (e.g., by mobile predators that obtain energy and nutrients from multiple habitats). Natural modifiers include any physical, biological, or ecological process that either defines or influences a species niche space and thus impacts energy or nutrient flow through the system. Human modifiers can directly influence food-web structures or modify natural processes (e.g., water currents, species behaviour) that then (i.e., indirectly) influence food-web structures. Variables given in b and c are examples, and not intended to be exhaustive. Note that energy and nutrient dynamics will vary over time and differentially depend on the spatial scale of coupling [Colour figure can be viewed at wileyonlinelibrary.com]

2 | CONCEPTUAL FRAMEWORK

Our framework categorises food-web structure and resultant ecosystem function through three overarching structural attributes: (a) energy and nutrient flow into the system through basal resources in spatially distinct habitats (Figure 2ai); (b) interactions among species within habitats and functional groups (i.e., species that occupy similar trophic and habitat niches; Figure 2aii); and (c) coupling among habitats (Figure 2aiii). We also consider natural processes (Figure 2b) and human modifiers (Figure 2c) that directly or indirectly alter energy and nutrient flows under each of the three overarching attributes. We build on existing work (e.g., Gorman, Yule, & Stockwell, 2012; Sierszen et al., 2014) to consider trophic links within and among three habitat compartments: nearshore, offshore pelagic (offshore photic waters), and offshore profundal (offshore aphotic waters). We recognise that these zones are non-stationary and are, from a limnological perspective, defined by hydrology linked to thermal water masses and light penetration, but are used herein for convenience to broadly compartmentalise large, deep lakes on the basis of bathymetry and fish communities (Stewart, Todd, & Lapan, 2017). Within other large lake systems, the depth used to define habitats may differ from those used herein.

2.1 | Flow into system

Energy and nutrient flows into the system include phytoplankton in the pelagic zone, both benthic plants (i.e., periphyton and macrophytes) and phytoplankton in the nearshore, and either sedimentation of pelagic phytoplankton or benthic bacterial communities in the profundal. A fundamental driver of food-web structure and ecosystem function is the relative amount of energy and nutrients entering each habitat via autochthonous and allochthonous sources and the availability of such energy and nutrients to higher trophic levels (Polis & Strong, 1996; Vander Zanden & Vadeboncoeur, 2002). The amount of energy and nutrients available to a particular basal resource, and thus its potential production, is mediated both by physical processes, such as currents driving upwelling (Figure 2b), and biotic interactions, such as a consumer shunting energy towards or away from a given habitat. Both types of process have the potential to either support a balance of diverse basal resource types or drive the system towards dominance by a single energy flow pathway. Human modifiers, including introduced species, changes in nutrient loading, and climate change (Figure 2c) may directly affect resource production in each habitat or alter key natural processes that then influence resource production (Kao et al., 2014). Importantly, processes, or modifications of processes, that encourage dominance

of a single basal resource may reduce ecosystem adaptive capacity by limiting subsidies to higher trophic-level consumers, particularly under changing environmental conditions.

2.2 | Flow within habitats

The composition and diversity of individual species that make up functional groups (circles and rectangles, respectively, in Figure 2a) also strongly influence energy and nutrient flows (arrows in Figure 2a) within a given habitat. Although species diversity tends to decline at higher trophic levels (Turney & Buddle, 2016), biotic processes including competition and predation mediate diversity and productivity of individual functional groups (Brooks & Dodson, 1965; Isaac, Hrabik, Stockwell, & Gamble, 2012; O'Malley & Bunnell, 2014), and ultimately determine the amount and quality of energy reaching higher trophic levels from a particular habitat (Brett & Müller-Navarra, 1997). Dominance by a single, low quality or inaccessible species (often non-native), which represents a diversity loss and, thus, reduced adaptive capacity, could act as an energetic bottleneck with the potential to affect diversity and production of predators higher in the food web (Blouzdis et al., 2013; Johnson, Bunnell, & Knight, 2005).

2.3 | Flow among habitats

At the broadest scale within an ecosystem, energy and nutrient flows contribute to ecosystem adaptive capacity through coupling of spatially distinct habitats (Figure 2a-iii). Coupling of habitats can subsidise consumers, allowing them to reach higher densities than possible based on a single resource (Polis & Strong, 1996). Generalist consumers capable of coupling multiple habitats and trophic levels are thought to promote balance and stability within the ecosystem by preventing runaway growth and dominance of any one functional group (Kondoh, 2003; McCann et al., 2005; Rooney et al., 2006; Vander Zanden, Essington, & Vadeboncoeur, 2005). A generalist feeding strategy also releases consumers from dependence on the dynamics of preferred prey (Schindler & Scheuerell, 2002). Mobile generalist consumers are capable of coupling habitats via foraging behaviours (Figure 2b-iii) that respond rapidly to changes in prey availability or via vertical or horizontal migrations (Stockwell, Hrabik, Jensen, Yule, & Balge, 2010; Vander Zanden & Vadeboncoeur, 2002). Species may also act as couplers via ontogenetic diet shifts between habitats and energy sources. In this way, linkages can occur over a range of timescales, from foraging movements on diel or sub-diel scales, to migrations and ontogenetic shifts at seasonal or multiannual scales. Abiotic mechanisms, such as water currents or upwelling events, can also play an important role in spatial coupling. Human activities can influence these linkages, such as through exploitation or stocking of coupling/decoupling species (Figure 2c-iii).

The magnitude and direction of links among habitats will partially determine how a perturbation impacts the whole ecosystem, as organisms in different habitats, or at different trophic levels, may respond differently to stressors (Vadeboncoeur, Vander Zanden, &

Lodge, 2002). Natural processes supporting coupling, particularly flexible foraging behaviour are therefore central to the ability of ecosystems to adaptively respond to perturbations by allowing for rearrangements of food-web structural architecture. Reduced coupling behaviour, either through the loss of available basal resources or habitat types (see section 2.1), loss of mobile or generalist food web members, or via processes that prevent or reduce movement across habitat boundaries, would likely reduce adaptive capacity.

3 | THE LAURENTIAN GREAT LAKES

The Great Lakes are the largest freshwater system in the world, with a surface area of 244,160 km² and a drainage basin of 765,990 km², and support over 47 million people in Canada and the USA (Table 1; Groop, 2013; Herdendorf, 1982). The Great Lakes have been subject to varying degrees of human-induced stress, yet with multiple management interventions (e.g., sea lamprey *Petromyzon marinus* control, widespread fish stocking, nutrient control programmes, fishery regulation) still support high biodiversity compared to historical levels and robust recreational and commercial fisheries (Brenden, Brown, Ebener, Reid, & Newcomb, 2013; Thayer & Loftus, 2013). We first outline major drivers of nutrient and energy flow within each lake and end with a synthesis of major changes in drivers of food-web structure across the Great Lakes. For brevity, the within-lake syntheses are limited here to lakes Superior and Erie with other lake syntheses provided in Data S1. Lakes Superior (oligotrophic) and Erie (western basin eutrophic in 2016, central basin mesotrophic, and east basin oligotrophic; http://www.glf.org/pubs/lake_committees/erie/FTG.htm#pub) were selected as they are the most contrasting in terms of trophic state, ecology, and food-web structure. Note that the material synthesised in each lake section reflects the current state of knowledge, available science, and the expertise of the authors in terms of primary drivers of food-web structure; therefore, information presented may differ in scope and focus among lakes. For all lakes, a threshold depth of 30 m was used to differentiate nearshore and offshore waters (Edsall & Charlton, 1997; Seelbach, Fogarty, Bunnell, Haack, & Rogers, 2013).

3.1 | Lake Superior

Lake Superior's food-web structure is the least altered among the Great Lakes, largely due to the smallest human population within its basin and its furthest upstream location in the catchment. Among the Great Lakes, Superior is the largest by surface area, the last settled by European colonists, experienced the least intensive fisheries (Koelz, 1926; Muir, Krueger, & Hansen, 2012), suffered the least habitat alteration, has been least stocked by hatchery fishes, and has been least colonised by invasive species (Table 1; Mills, Leach, Carlton, & Secor, 1993; Ricciardi, 2001). Despite fish community succession (Smith, 1968), an isotopic analysis of long-term food web change revealed the adaptive capacity of Lake Superior's food web to accommodate non-native species introductions (albeit at lower

TABLE 1 Physical, chemical and biological characteristics of the Laurentian Great Lakes of North America

Lake	Superior	Huron	Michigan	Erie	Ontario
Physical					
Watershed size (km ²)	127,700 ^c	133,400 ^c	118,100 ^c	58,800 ^c	70,000 ^c
Surface area (km ²)	82,100 ^c	59,500 ^c	57,750 ^c	25,657 ^c	19,000 ^c
Volume (km ³)	12,230 ^c	3,537 ^c	4,920 ^c	483 ^c	1,637 ^c
Shoreline (km)	4,795 ^c	5,120 ^c	2,670 ^c	1,377 ^c	1,168 ^c
Average depth (m)	149 ^c	59 ^c	85 ^c	19 ^c	86 ^c
Maximum depth (m)	407 ^c	229 ^c	282 ^c	64 ^c	245 ^c
Retention time (years)	191 ^d	22 ^d	99 ^d	2.6 ^d	6 ^d
Primary inlets	Nipigon, St. Louis, Pigeon, Pic, White, Michipicoten, Bois Brule, Kaministiquia	St. Marys, Straits of Mackinac, Saginaw	Fox, Grand, St. Joseph, Manitowoc, Kalamazoo	Detroit, Sandusky, Maumee	Niagara, Welland Canal
Outlet	St. Marys	St. Clair	Straits of Mackinac	Niagara, Welland Canal, Erie Canal	St. Lawrence
% deep water habitat (>50 m depth)	84 ^e	50 ^e	65 ^e	2 ^e	66 ^e
Watershed land use					
i. agricultural (%)	3 ^d	27 ^d	44 ^d	67 ^d	39 ^d
ii. forest (%)	91 ^d	68 ^d	41 ^d	21 ^d	49 ^d
iii. residential (%)	1 ^d	2 ^d	9 ^d	10 ^d	7 ^d
Chemical					
Surface total oxidised nitrogen (NO ₃ + NO ₂ ; µgN/L)	386.6 (spring 2013) ^f	326.8 (spring 2012) ^f	NA	556.7 (west basin), 100.0 (central basin), 207.5 (east basin) (spring 2013) ^f	400.7 (spring 2013) ^f
TP (µg/L) in April	2.1 ^g	2.5 ^g	3.8 ^g	32.2 (west basin) 13.9 (central basin) 9.7 (east basin) ^g	5.3 ^g
Biological					
Trophic status	Oligotrophic ^h	Primarily oligotrophic except several nearshore areas including Saginaw Bay ^j	Oligotrophic (offshore southern basin) ⁱ	Mesotrophic (west basin), oligotrophic (central and east basin) ^k	Oligotrophic (offshore) ^l
Number non-indigenous species ^a	80 ^m	80 ^m	90 ^m	128 ^m	99 ^m
i. algae	7 ^m	13 ^m	14 ^m	16 ^m	13 ^m
ii. invertebrates	25 ^m	27 ^m	32 ^m	39 ^m	26 ^m
iii. fishes ^b	20 ^m	21 ^m	22 ^m	28 ^m	18 ^m

(Continues)

TABLE 1 (Continued)

Lake	Superior	Huron	Michigan	Erie	Ontario
Five largest commercial fishery exploitation rates in 2015 (thousands of kg) ⁿ	Lake whitefish (2,874); cisco (1,796); lake trout - including siscowet (514); chubs (88); rainbow smelt (34)	Lake whitefish (3,444); lake trout (729); yellow perch (299); walleye (193); Pacific salmon (includes only Chinook in US waters; 69)	Lake whitefish (3,095); lake trout (443); chubs (94); yellow perch (55); suckers (15)	Yellow perch (7,749); smelt (6,881); walleye (6,404); white bass (2,926); white perch (2,780)	Lake whitefish (131); yellow perch (76); sunfish (23); freshwater drum (19); northern pike (19)

Notes. Data were compiled from multiple sources, are not equally current across lakes, and may be highly variable in space and time both within and among lakes; therefore, they should be interpreted within context. Table data are not intended as a comparison among lakes, rather provide a general characterisation of the scale and potential magnitude of lake productivity drivers. NA: no data available.

^aLevels of invasion are not constant. For example, Lake Superior has alewives and *Dreissena* spp., but biomass and distribution are low relative to other lakes. ^bIncludes purposefully introduced species and range expanders. ^cHerdendorf (1982). ^dFuller and Shear (1995). ^eEshenroder and Lantry (2012). ^fDove and Chapra (2015). ^gBunnell et al. (2014). ^hEvans et al. (2011). ⁱRiley (2013). ^jMida et al. (2010). ^kGuildford et al. (2005). ^lDove (2009). ^mGLANSIS. USGS, <https://nas.er.usgs.gov>, accessed September 29, 2016. ⁿBaldwin et al. (2018).

densities and fewer species than the other Great Lakes) while continuing to support native fishes (Schmidt, Vander Zanden, & Kitchell, 2009). The lake continues to sustain essential functions by supporting valuable lake trout *Salvelinus namaycush*, ciscoes *Coregonus* spp., and lake whitefish *Coregonus clupeaformis* harvests (Brenden et al., 2013).

3.1.1 | Flow into system

Lake Superior is oligotrophic, with atmospheric deposition and tributary inflow as the two main nutrient sources to basal resource production. Atmospheric nitrogen (N) sources are important relative to terrestrial sources, particularly to offshore waters, because: (a) the lake receives >50% of its water from precipitation (Bennett, 1978); (b) the geology is primarily igneous rock, resistant to chemical weathering; and (c) tributaries contribute a low nutrient load due in part to high nutrient retention (up to 94%) in the lakes coastal wetlands (Morrice, Kelly, Trebitz, Cotter, & Knuth, 2004). Average total phosphorus (TP) is low (2.3 µg P/L) and stable (Barbiero, Lesht, & Warren, 2012).

Auer and Gatzke (2004) estimated that the spring runoff event (mid-March to late-April) delivers an average of 70% of the annual load of total suspended solids. Waters inshore of the thermal bar become enriched in terrestrial total suspended solids as spring tributary discharges become trapped shoreward of the thermal bar until the onset of vertical stratification (Auer & Gatzke, 2004). Nearshore to offshore gradients in bacteria, phytoplankton, and zooplankton have been associated with nearshore nutrient trapping (see references in Auer & Gatzke, 2004). Pelagic primary production is thought to be limited during most of the year due to a short stratified period and great mixing depth (Guildford & Hecky, 2000). Over the past century, onset of summer stratification has become progressively earlier and the average length of stratification increased by >20 days (Austin & Colman, 2008; Pratt et al., 2016). Changes in stratification may influence onset of the phytoplankton growing season, but water-column primary productivity has remained relatively stable (Pratt et al., 2016; Sterner, 2010). Auer and Powell (2004) suggested bacterioplankton activity in Lake Superior is unlikely to be a major component of autochthonous energy and nutrient cycling, and Munawar, Munawar, Fitzpatrick, Niblock, and Lorimer (2009) found that Lake Superior's summer bacterial biomass was approximately half that in lakes Erie and Ontario in the early 2000s. Nearshore production has not been affected by dreissenid re-engineering or the large *Cladophora* (a nuisance filamentous green algae) blooms to the extent observed in the other Great Lakes (Environment and Climate Change Canada and the US Environmental Protection Agency, 2017; Hecky et al., 2004).

The deep chlorophyll layer (DCL) is probably an important component of Lake Superior's pelagic energy pathway. The DCL is a nutrient-rich phytoplankton concentration in the upper hypolimnion that provides important offshore pelagic habitat and may provide forage for the deepwater community that exists in the

deepest portion of the pelagic zone (Barbiero & Tuchman, 2004a). Changes in the DCL, as have occurred in the lower lakes (Rudstam et al., 2015), are not currently evident in Lake Superior.

3.1.2 | Flow within habitats

Nearshore

Lake Superior is dominated by deepwater habitat (Eshenroder & Lantry, 2012); therefore, nearshore is the least extensive of the habitat zones and, consequently, its trophic structure least studied. Benthic invertebrate populations in Lake Superior are low in comparison to the other Great Lakes, and consist primarily of native amphipods *Diporeia* spp. While insect larvae (e.g., chironomidae) likely play a role in the nearshore food web, data are not readily available. The southeast end of the lake, particularly the shallow Whitefish Bay, historically had a more diverse benthic community including Oligochaeta and Sphaeriidae (12% of biomass) compared to the rest of the lake (Dermott, 1978). Gamble, Hrabik, Yule, and Stockwell (2011) described the nearshore food web of Lake Superior as more complex than that offshore in terms of fish diversity, but the two zones had remarkably similar structure, with fish communities primarily supported by *Mysis diluviana* and *Diporeia*. A direct energetic link between abundant macrophyte biomass in nearshore wetlands and the offshore food web was not evident on the basis of stable isotopes (Keough, Sierszen, & Hagley, 1996). Lean lake trout are the dominant nearshore predator (Bronte et al., 2003) and rely primarily on native coregonines and rainbow smelt *Osmerus mordax* (Gamble, Hrabik, Yule, et al., 2011). Nearshore benthivorous fish biomass is dominated by lake whitefish, which has a varied diet, including non-native *Bythotrephes longimanus* (Gamble, Hrabik, Yule, et al., 2011).

Offshore pelagic

Upper trophic levels in Lake Superior's offshore habitat are dominated by native species (e.g., siscowet lake trout, kiyi *Coregonus kiyi*, and cisco *Coregonus artedii*), but based on long-term bottom trawl surveys native fish biomass appears to be declining (Pratt et al., 2016; Vinson, Evrard, Gorman, & Yule, 2016). Lake Superior has experienced periods of overlapping fishery-induced succession (i.e., changes in organisational structure of fish assemblages in response to ecosystem change; 1900s–1960), non-native invasions (1930–1990), and recovery (1970–present). These successional processes have been the main modifiers of energy, nutrient, and food-web dynamics during the past century, primarily affecting the offshore pelagic habitat through the loss of native fish diversity and abundance. By the 1970s, lake trout and ciscoes were depleted (Smith, 1968), greatly reducing key offshore pelagic functional groups. Data on prey fish abundance from the 2005–2006 and 2011 surveys showed evidence of top-down control on prey fishes by lake trout (Pratt et al., 2016), although sampling bias resulting in underestimates of prey fish biomass may partially explain this result (Yule, Adams, Stockwell, & Gorman, 2007).

Offshore profundal

The trophic structure of Lake Superior's offshore profundal zone is notably less affected by species invasions or loss than other Great Lakes. Lake Superior is the only Great Lake to retain abundant *Diporeia* populations (Barbiero, Lesht, & Warren, 2011), and also the lake with the lowest non-native dreissenid mussel abundance (Grigorovich, Kelly, Darling, & West, 2008). *Diporeia* and *Mysis* are the dominant prey items for slimy *Cottus cognatus*, deepwater *Myoxocephalus thompsonii*, and spoonhead *Cottus ricei* sculpins (Gamble, Hrabik, Stockwell, & Yule, 2011). *Mysis* is also important prey for lake trout and burbot *Lota lota* (Gamble, Hrabik, Stockwell, et al., 2011). Deepwater sculpin, in turn, are a key diet component of siscowet lake trout, particularly smaller (<600 mm) individuals, with larger siscowet also relying heavily on coregonines and burbot (Gamble, Hrabik, Stockwell, et al., 2011; Sitar et al., 2008). The deepwater siscowet lake trout form is the top profundal predator and currently comprises most of the lake trout biomass in this lake (Bronte & Sitar, 2008).

3.1.3 | Flow among habitats

As Lake Superior is the least altered among the Great Lakes, its habitats are well-coupled and serve as a model for the historical food webs of the other Great Lakes. The majority of the offshore Lake Superior community undergoes diel vertical migration (DVM), increasing with depth, from 59% of the community undergoing DVM at 30 m to 95% at >90 m (Gorman et al., 2012), and DVM represents the primary vector of energy and nutrient transport between profundal and pelagic habitats. *Mysis* are the primary planktivorous invertebrate in Lake Superior, and undergo notable DVM (Ahrenstorff, Hrabik, Stockwell, Yulem, & Sass, 2011). The importance of benthos in *Mysis* diets, as well as the importance of *Mysis* in pelagic and profundal fish diets suggests a strong connection between pelagic and profundal habitats (Gamble, Hrabik, Stockwell, et al., 2011; Sierszen et al., 2011). Although the historical deep-water food web of Lake Superior remains largely intact, the extent to which dynamics are affected by non-native planktivores, such as rainbow smelt, remains unknown (Myers, Jones, Stockwell, & Yule, 2009).

Currents and upwelling re-suspend sediments and release and transport nutrients to Lake Superior's offshore, particularly during autumn (Urban, Lu, Chai, & Apul, 2004). Lake whitefish, lean lake trout, and juvenile siscowet lake trout undertake diel horizontal migrations (DHM) from deep profundal to nearshore habitats, linking these Lake Superior habitats (Gorman et al., 2012). Cisco eggs deposited on nearshore shoals during spawning migrations can represent a third (by energy) of lake whitefish annual consumption (Stockwell, Yule, Hrabik, Sierszen, & Isaac, 2014). A bioenergetics-based stable isotope model showed that nearshore prey account for up to 25% of juvenile siscowet production in western Lake Superior (Harvey, Schram, & Kitchell, 2003). Cisco and non-native rainbow smelt occupy both offshore and nearshore pelagia (Johnson et al., 2004), potentially affecting the zooplankton communities of both locations. Rainbow smelt may also consume larval native fishes and could account for up to 52% and 100% of

larval cisco mortality in Thunder and Black Bays, respectively (Myers et al., 2009, 2015).

Several fishes, including burbot, lean and siscowet lake trout, and slimy sculpin, show ontogenetic shifts in habitat and trophic resource use, potentially supporting energetic coupling among habitats (Brandt, 1986; Harvey et al., 2003; Hofmann & Fischer, 2002; Zimmerman, Schmidt, Krueger, Vander Zanden, & Eshenroder, 2009). For example, juvenile (<430 mm) lean and siscowet lake trout co-occur in deepwater and share trophic resources (Zimmerman et al., 2009), whereas adults of these two forms partition resources with leans occupying shallow (<80 m) habitats and siscowet remaining in deep waters (Muir, Hansen, Bronte, & Krueger, 2016; Muir et al., 2012). In addition, siscowet shift from primarily DHM as juveniles to primarily DVM as adults (Gorman et al., 2012).

3.2 | Lake Erie

Lake Erie is the shallowest, warmest, and most productive of the Great Lakes (Table 1). Its three basins, the small, shallow and highly productive western basin; large central basin; and deep, least-productive eastern basin, are distinct in terms of geology, hydrology, trophic status, and food-web dynamics (Morrison, Whittle, & Haffner, 2002). Lake Erie has a diverse fish community (Cudmore-Vokey & Crossman, 2000), which supports valuable commercial and recreational fisheries for walleye *Sander vitreus* and yellow perch *Perca flavescens*. Its food-web structure and dynamics are the most altered among the Great Lakes due to a combination of invasive species, nutrient inputs resulting in regional eutrophication and hypoxic zones, intensive commercial fishing, land-use changes, and industrial pollution. These stressors induced community changes beginning in the late 1800s, and by the mid-1960s, led to extinction of blue pike *Sander vitreus glaucus* and extirpation of cisco and sauger *Sander canadensis* (Eshenroder et al., 2016; Regier & Hartman, 1973) and major population reductions of key species such as lake sturgeon *Acipenser fulvescens*, lake trout and lake whitefish (Leach & Nepszy, 1976). Lake Erie has therefore experienced widespread functional loss.

3.2.1 | Flow into system

Lake Erie receives 95% of its water via the Detroit River, but a large proportion of the nutrient inputs driving basal productivity come from the highly agricultural Maumee River, which enters the western basin (Robertson & Saad, 2011; Stow, Cha, Johnson, Confesor, & Richards, 2015). Nutrient dynamics are poorly understood in Lake Erie, particularly the magnitude of inter-basin transfers and the degree to which phosphorus is recycled from sediments to the water column (but see Maccoux, Dove, Backus, & Dolan, 2016; Watson et al., 2016). High nutrient inputs prior to the 1970s were a major force driving the 1972 and subsequent (1978, 2012) Great Lakes Water Quality Agreements (GLWQA). Phosphorus abatement to reach GLWQA-mandated loads led to declines in phosphorus and chlorophyll-*a* concentrations in all basins until about 1990. However,

starting in the late 1990s and continuing to the present, Lake Erie is experiencing re-eutrophication, particularly in the western basin and nearshore areas of the central and eastern basins (Kane, Conroy, Richards, Baker, & Culver, 2014; Scavia et al., 2014). Recent trends show increases in dissolved phosphorus from 1990 to 2013 from the Maumee River, partially driven by increases in precipitation, while TP has remained stable (Stow et al., 2015). Potential impacts of recent commitments under the 2012 GLWQA to reduce nutrient loads are difficult to predict, but will certainly influence food-web dynamics and productivity of Lake Erie and potentially downstream to Lake Ontario.

Lake Erie is notorious for large harmful algal blooms (HABs) in the western basin, which, beginning in the late 1990s, have occurred sporadically during late summer (Watson et al., 2016). Biovolume of phytoplankton in spring has been dominated by diatoms and potentially influenced by silica inputs from Lake Huron. Spring phytoplankton biovolume is 1.5–6 times larger than summer biovolume, and transported decaying algae is an important driver of summer hypoxia (Reavie et al., 2016). Total phytoplankton biomass has, since the 1990s, been increasing in Lake Erie, driven in part by the soluble reactive phosphorus load in the Maumee River (Kane et al., 2014). Phytoplankton biomass during 2000–2001 exceeded that during the 1970s (Fitzpatrick, Munawar, Leach, & Haffner, 2007). Intermittent erosion and frequent wave-, heat- and ice-induced resuspension, of bottom sediments influence turbidity and productivity in the nearshore habitat (Mortimer, 1987; Schertzer, 1999). The impact of HABs on food webs remains unknown, and merits additional study. Although micro- and mesozooplankton grazing may provide some top-down control of HABs, increased nutrient inputs amplify production exceeding the capacity of this control mechanism (Davis, Koch, Marcoval, Wilhelm, & Gobler, 2012).

3.2.2 | Flow within habitats

Lake Erie has been invaded by 67 fishes and invertebrates (Table 1), some of which have played major roles in altering trophic structure and influencing growth and population dynamics of native species (Crane & Einhouse, 2016; Guzzo, Haffner, Legler, Rush, & Fisk, 2013). In particular, dreissenid mussels, *Bythotrephes*, the amphipod *Echinogammarus ischnus*, and round goby *Neogobius melanostomus* have created a novel Ponto-Caspian food chain, integrated within the larger food web, dramatically reengineering the nearshore zone (Campbell et al., 2009; Hecky et al., 2004; Parker, Rudstam, Mills, & Einhouse, 2001) and thereby altering the delivery of nutrients to offshore habitats.

Nearshore

Lake Erie's coastal wetlands and river mouths have been notably impacted by anthropogenic development. Less than 5% of western basin wetlands remain intact (Churchill, Schummer, Petrie, & Henry, 2016), probably influencing nearshore energy and nutrient flows (Lavrentyev, McCarthy, Klarer, Jochem, & Gardner, 2004). In the 2000s, Lake Erie had the greatest bacterial density of any Great Lake

(Heath, Hwang, & Munawar, 2003), and microbial food webs are most active at the stream-lake confluences (Larson, Frost, Vallazza, Nelson, & Richardson, 2016).

Dreissenid reengineering of Lake Erie's nearshore has been well documented. Dreissenids affect both structure and metabolic function of the benthic bacterial community (Lohner, Sigler, Mayer, & Balogh, 2007). Dreissenids compete with zooplankton for food (Garton, Payne, & Montoya, 2005). Models showed that daily mussel grazing was 1%–2% of combined non-diatom edible algae and diatom biomass in the central and eastern basins, and <10% in the western basin (Zhang, Culver, & Boegman, 2008). Although dreissenid mussel grazing impacts on algal biomass may be limited due to a boundary layer above the mussel bed, indirect effects through nutrient excretion have much greater negative impacts (Zhang et al., 2008). Nitrogen and phosphorus incorporated into mussels themselves, but also into their biodeposits, are sequestered in the nearshore (Hecky et al., 2004), altering the N:P ratio in favour of blue-green algae, and selective filtration by dreissenids may further promote HABs (Vanderploeg et al., 2001). During the 2000s, east basin phytoplankton showed signs of phosphorus deficiency (Guildford et al., 2005), which may have influenced their quality. Smith, Parrish, Depew, and Ghadouani (2007) reported that particulate organic carbon, chlorophyll-*a*, and total lipid concentrations were lower nearshore than offshore, which is reverse the pattern commonly seen in large lakes, but consistent with the hypothesis that filter-feeding dreissenids can cause seston depletion in relatively shallow waters. Round goby amplify the nearshore shunt, accessing the energy in dreissenids and their biodeposits and transferring it to higher trophic levels within the nearshore habitat, via round goby consumption by littoral fishes (Campbell et al., 2009; Johnson et al., 2005; Madenjian et al., 2011). Large benthic invertebrates, such as mayflies *Hexagenia* spp., caddisflies *Trichoptera* spp., and amphipods, have after prolonged absences recolonised the western basin and may facilitate increased growth and production of nearshore fishes (Ludsin, Kershner, Blocksom, Knight, & Stein, 2001; Tyson & Knight, 2001). Observed declines in native amphipod *Gammarus fasciatus* abundance may be due to some interaction with non-native *E. ischnus*, but not due to competitive exclusion for food (Limén, Van Overdijk, & Maclsaac, 2005). In the central and western basins, phytoplankton biomass declined from 1970 to 1986, following the institution of nutrient reductions, but began to increase again sometime between the mid-1990s and 2011 (Scavia et al., 2014). Coinciding with the invasion of *Bythotrephes*, overall species richness of zooplankton communities, as well as abundance of several cladoceran species, declined notably, as seen in lakes Huron and Michigan (Barbiero & Tuchman, 2004b). Hypoxia has recently re-emerged as a prominent feature of the central basin during late summer (Scavia et al., 2014), probably as a byproduct of the nearshore shunt.

Offshore pelagic

Given shallow depths in the western and central basins, the only true offshore pelagic areas in Lake Erie are found in the eastern basin.

The microbial food web is a primary component of Lake Erie's pelagic pathway (Twiss & Campbell, 1998; Twiss, Smith, Cafferty, & Carrick, 2014), but little is known about its contribution to energy and nutrient dynamics. Between 1996 and 2000, the spring phytoplankton bloom in the eastern basin declined to ~20% of pre-dreissenid levels (Barbiero, Rockwell, Warren, & Tuchman, 2006). Compared to the other Great Lakes, Erie does not always establish a DCL, probably due to its shallow depth and deep mixing (Bramburger & Reavie, 2016). The impact of changes in lower trophic-level community composition on the offshore pelagic energy pathway of the eastern basin is largely unstudied.

Offshore profundal

Lake Erie's profundal zone is limited to the deepest portions of the eastern basin. Bottom hypoxia, a prominent feature during the 1950s–1970s, was a major driver in the loss of much of Lake Erie's benthic macroinvertebrate community (Tyson & Knight, 2001; Vanderploeg et al., 2009), but it was mitigated by reductions in nutrient loads following the 1972 GLWQA. Vanderploeg et al. (2009) reported that fishes avoided regions of the hypolimnion with dissolved oxygen concentrations <3 mg/L, a phenomenon that has been implicated as modifying zooplankton-planktivore interactions in Lake Erie (Pothoven, Vanderploeg, Höök, & Ludsin, 2012; Roberts et al., 2012).

3.2.3 | Flow among habitats

Nutrient sequestration by dreissenid mussels has led to enhanced algal (including macrophytes) and benthic invertebrate production in Lake Erie's nearshore and reduced offshore nutrient transport, thus potentially reducing nearshore-offshore coupling. Replacement of native planktivores (*Coregonus* spp.) with the non-native rainbow smelt in the mid-1900s represented another major shift in connections among habitats and possibly a loss of historical profundal-pelagic coupling, as rainbow smelt are known to contribute less to lake-wide DVM than *Coregonus* spp. in other lakes (Ahrenstorff et al., 2011; Gorman et al., 2012).

Walleye are currently the primary coupler among habitats and basins, and through selective piscivory influence fish community structure, a situation unlike that in the other Great Lakes (Knight & Vondracek, 1993). In late spring or early summer, abundant cool-water species, including gizzard shad *Dorosoma cepedianum*, yellow perch and walleye, migrate from spawning grounds in the western basin into the cooler central and eastern basins, following the progression of the thermal bar (Wang et al., 2007; Zhao, Einhouse, & MacDougall, 2011). Movements are both temperature and size-dependent, with larger walleye tending to migrate while juveniles remain in the productive western basin despite temperatures exceeding their optimal growth window (20–23°C; Wang et al., 2007). On average, about 90% of the eastern basin annual harvest comprises walleyes originating from the western basin (Zhao et al., 2011). Even further walleye movement and connectivity is illustrated by the finding that 26% of the walleye harvest in Saginaw Bay,

Lake Huron in 2008–2009 originated from lakes Erie and St. Clair spawning populations (Brenden et al., 2015).

Lake trout, lake whitefish, and burbot are mobile generalist predators, but primarily confined to the eastern basin during stratification. During isothermal conditions, mobile generalist species are likely to be important couplers of profundal, pelagic, and nearshore habitats due to their fall spawning migrations (Cook, Johnson, Locke, & Morrison, 2005). Recent acoustic tagging data support this, showing stocked lake trout move throughout the lake including the western basin and Niagara River (C. Vandergoot, US Geological Survey, personal communication, July 2018). While it appears nutrient inputs in the western basin may subsidise the central and eastern basins, either through physical movement of nutrients or basal resources (e.g., movement of phytoplankton via water currents) or through biological couplers such as mobile fishes, more work is needed to understand the energy and nutrient linkages among basins, and how these connections contribute to Lake Erie's adaptive capacity.

3.3 | Basin-wide synthesis

3.3.1 | Flow into system

Across the Great Lakes, nutrient inputs are an important driver of primary production, especially in the shallowest and smallest regions such as Lake Erie (Table 2; see Data S1 for other lake syntheses). Nutrient loading initially increased with human settlement, but, since the 1970s, TP has declined and remained consistently at or below GLWQA target levels in most locations (Bunnell et al., 2014; Dolan & Chapra, 2012; Dove & Chapra, 2015). Management of nutrient loading following the 1972 GLWQA may have facilitated homogenisation of primary production at a broad spatial scale because, by 2010, lakes Michigan, Huron, and Superior, which in recent history had large differences in primary productivity, showed no significant differences in mean annual phytoplankton production (Fahnenstiel, Sayers, Shuchman, Yousef, & Pothoven, 2016), although this homogenisation may also be related to dreissenid expansion (Evans, Fahnenstiel, & Scavia, 2011).

Dreissenids have acted to modify relative nutrient and energy inputs into basal resource zones across lakes (with minimal effects in Lake Superior) (Barbiero et al., 2018; Hecky et al., 2004; Kao et al., 2014). Dreissenids also change the physical habitat of an invaded site by making unstable bottoms more colonisable by *Cladophora* (Brooks, Grimm, Shuchman, Sayers, & Jessee, 2015). Offshore, dreissenids are reaching their highest biomass densities in the profundal zone in some of the lakes (e.g., lakes Michigan and Ontario), transforming the physical habitat and increasing the biomass of benthic invertebrates relative to the pre-dreissenid community dominated by *Diporeia* (Birkett, Lozano, & Rudstam, 2015; Nalepa, Fanslow, Lang, Mabrey, & Rowe, 2014). This dreissenid filtering activity across the lakes has been implicated in increased water clarity (Higgins & Vander Zanden, 2010), resulting in a deepening photic zone (physically increasing the spatial extent

of the pelagic zone), and increased maximum depth of benthic production. Sequestration of benthic energy by dreissenid mussels could represent a loss in the adaptive capacity of these systems by decreasing the capacity for basal resource functional groups to support consumers (i.e., reduced phytoplankton availability in pelagic and settling into the profundal zones). Indeed, dreissenid-driven benthification has been implicated in declining species diversity, including the loss of *Diporeia* (Stewart et al., 2016). This fundamental shift in energy production to a more benthic-oriented pathway may favour consumers that can adapt and exploit this growing resource. For example, the lake whitefish fishery may have been sustained over the past decade by lake whitefish shifting its diet to consume dreissenid mussels and round gobies (Pothoven, 2005; Rennie, Sprules, & Johnson, 2009).

Peak phytoplankton biomass may be shifting from spring to late summer or fall in lakes Huron, Michigan and Erie, thus affecting biota, dependent on the spring algal bloom, such as spring-hatching larval fishes (Barbiero et al., 2006; Bramburger & Reavie, 2016; Fahnenstiel et al., 2010; Reavie, Barbiero, Allinger, & Warren, 2014). Intriguingly, some evidence exists for increased importance of the DCL in lakes Huron and Ontario (Barbiero, Nalepa, Lesht, & Warren, 2013; Rudstam et al., 2015), which may provide some level of compensation for temporal shifts in plankton blooms. An interesting question is whether the DCL could compensate for lost pelagic phytoplankton production and support consumers affected by benthification.

3.3.2 | Flow within habitats

Throughout the Great Lakes, changing conditions and stressors have resulted in marked shifts in structure within all habitats. Major species losses include the once common *Diporeia* in the offshore profundal, which has undergone a drastic decrease in abundance and is slowly being eliminated from the food web in all Great Lakes other than Superior (Barbiero, Lesht, et al., 2011; Barbiero, Schmude, et al., 2011; Birkett et al., 2015; Lozano, Scharold, & Nalepa, 2001; Nalepa, Fanslow, Pothoven, Foley, & Lang, 2007; Watkins et al., 2007). Zooplankton communities have generally experienced reductions in cladoceran abundance and shifted to being copepod-dominated (Barbiero & Tuchman, 2004b; Rudstam et al., 2015). Shifts in zooplankton community structure and variation in depth of and importance of the DCL may affect energy links between lower and upper trophic levels within the pelagic zone, as forage fishes may differ in their ability to feed below the thermocline (Barbiero et al., 2013). Recent shifts towards a zooplankton community located deeper in the water column in some lakes may favour cold-water planktivores such as native bloater *Coregonus hoyi* and non-native rainbow smelt (Rudstam et al., 2015). These changes may also provide improved ecological conditions for further coregonine restoration (Eshenroder et al., 2016). Concurrent increases in non-native dreissenid, round goby, and copepod abundance may partially compensate for loss of native species, such as *Diporeia*. Some native fishes, such as lake whitefish and cisco, have shifted their diet to exploit these new benthic prey (Madenjian et al., 2015; Randy Claramunt, Michigan

TABLE 2 Subset of key points from synthesis of current knowledge on Great Lakes food webs and energy and nutrient dynamics

	All Great Lakes	Lake Superior	Lake Huron	Lake Michigan	Lake Erie	Lake Ontario
Flow into system: Basal resources	Human-driven nutrient loading may have facilitated homogenised basal resources	Changing stratification timing may impact primary production	Offshore production ↓ by 40% since 1990s, nearshore production high	TP loading declined; Nearshore production may be increasing—lack of time series to test this	Potential re-eutrophication	Inter-lake flows are dominant nutrient sources; Large differences in nearshore and offshore TP levels
Flow within habitats						
Nearshore	Zooplankton communities shift to copepod dominated; Energy shunted to nearshore compartment	Similar food web to offshore, with <i>Mysis</i> and <i>Diporeia</i> key	Fish community shift toward less eutrophic-tolerant species	Heterogeneous and dynamic; Reduced nearshore fish diversity	Phosphorus shunt enhanced by round goby; HAB proliferation	High regional variation in food-web structure
Pelagic	Potential increased importance of the DCL	Zooplankton community shift to copepod dominated	Oligotrophication; Zooplankton community shift to copepod dominated; Alewife collapsed	Oligotrophication; Zooplankton community shift to copepod dominated	True pelagic zone found only in eastern basin; microbial food web key, but not well understood	Alewife dominate; zooplankton community shift to resemble Huron, Michigan, Superior
Profundal	Proliferation of dreissenid mussels Loss of <i>Diporeia</i> ^a	<i>Diporeia</i> remain abundant	Increasing dreissenids; demersal fish community unstable	Dreissenids = significantly reduced bioavailability of energy and nutrients	True profundal zone only found in eastern basin; bottom hypoxia may impact food webs	Unexpected deepwater sculpin recovery; Lake whitefish stable at low levels
Flow among habitats						
Pelagic-profundal coupling	DVM important; Key species: <i>Mysis</i> ; impaired coupling thorough loss of native coregonines	Majority of community undergoes DVM	New and strengthened linkages	DVM	Relatively minor profundal zone; invasive species may have reduced coupling	<i>Mysis</i> are relatively abundant and drive DVM
Nearshore-offshore coupling	Spawning and seasonal migrations; potentially enhanced coupling by non-native species	DHM important	Increased reliance on nearshore energy	Increased reliance on nearshore energy	Western basin probably subsidises other basins; walleyes are primary couplers	Strong linkages dominated by non-native species

Notes. DCL: deep chlorophyll layer; DHM: diel horizontal movement/migration; DVM: diel vertical migration; HAB: harmful algal bloom; TP: total phosphorous. More detail on lakes Huron, Michigan and Ontario can be found in Supplement 1 (Supporting Information).

^aException Lake Superior.

Department of Natural Resources, personal communication, 11 July 2017). However, species replacement in the Great Lakes has, unfortunately, largely occurred with invasive species that may not be energetic or nutrient equivalents to the native forage they replaced (i.e., The Junk Food Hypothesis; Fagan et al., 2017; Rosen & Trites, 2000). For example, in all lakes, to varying degrees, lake whitefish juvenile growth has declined following dreissenid establishment (Fera, Rennie, & Dunlop, 2015). Thus, some adaptive capacity is apparent because shifts in food-web structure occurred and consumers have, in some cases, shifted their diet to exploit these new resources within single habitats. An important conservation and management challenge remains—to preserve and re-establish native species that provide high-quality resources to consumers to sustain trophic structure and maintain ecosystem services.

3.3.3 | Flow among habitats

Studies of invertebrate and fish movement in the Great Lakes have provided evidence of largescale and widespread movements on daily and seasonal timescales that act to couple spatially distinct habitat zones. Offshore pelagic and profundal habitats were historically coupled through DVM at multiple trophic levels, involving zooplankton (e.g., *Daphnia galeata mendotae*), macro-invertebrates (e.g., *Mysis*), their deepwater cisco predators (e.g., bloater), and top predators, such as siscowet lake trout (Ahrenstorff et al., 2011; Gamble, Hrabik, Stockwell, et al., 2011; Isaac et al., 2012). Herbivorous cladoceran zooplankton, such as daphnids, avoid predation by migrating to the hypolimnion during day and returning to warmer epilimnetic waters at night (Pangle, Peacor, & Johannsson, 2007). Likewise, mysids also undergo DVM, but are near the bottom during day and some proportion of the population moves up to shallower water at night (Beeton, 1960; O'Malley, Hansson, & Stockwell, 2017).

Offshore and nearshore zones are primarily coupled by piscivore foraging and by spawning migrations of large, mobile consumers. Several fishes, including lake whitefish and lake trout, may undertake DHM from deep profundal to nearshore habitats (Gorman et al., 2012), whereas alewife *Alosa pseudoharengus*, brown trout *Salmo trutta*, Chinook salmon *Oncorhynchus tshawytscha*, cisco, coho salmon *Oncorhynchus kisutch*, rainbow smelt, rainbow trout *Oncorhynchus mykiss* and sea lamprey, among others, undergo annual or biannual spawning migrations from offshore into nearshore or even tributary habitats (Childress, Allan, & McIntyre, 2014; Childress & McIntyre, 2015; Stockwell et al., 2014). Energy and nutrients can be transferred by excretion or egestion of wastes after foraging and moving to a different habitat or by spawning. In the latter case, fish accumulate somatic and reproductive tissue while feeding in one zone and deposit tissue (i.e., eggs and sperm, and in some cases their carcasses) in another zone. Physical processes and water currents may also drive upwelling events that act to bring offshore nutrients into the nearshore zone (Plattner, Mason, Leshkevich, Schwab, & Rutherford, 2006; Rao, Milne, & Marvin, 2012; Urban et al., 2004; Valipour, León, Depew, Dove, & Rao, 2016).

Ontogeny can result in differential degrees of coupling by a species through its lifecycle. For example, small (<10 mm) mysids rely heavily on pelagic plankton whereas large mysids feed more heavily on benthos (Sierszen et al., 2011). Further, species vary in their lifetime contributions to coupling as some, such as the non-native Pacific salmon and lampreys, are semelparous, while others, such as rainbow trout and lake whitefish, are iteroparous. Sedimentation of phytoplankton is another important one-way coupling of pelagic and profundal habitats that was historically an important basal resource for *Diporeia* (Fitzgerald & Gardner, 1993).

Such connections among ecosystem components play a key role in adaptive capacity by buffering against directional shifts toward a single habitat or energy pathway. Therefore, reduced connectivity translates to lost adaptive capacity. The loss in all lakes, except Superior, of several deepwater coregonine ciscoes and their primary predator, lake trout, during 1900–1950 are evidence of lost capacity and a shift towards pelagic production (Dettmers, Goddard, & Smith, 2012). As the native predator–prey food chain collapsed, non-native alewives were released from competition and predation resulting in a massive population explosion, which sustained for a period before predation and cold winters greatly reduced alewife population numbers (Eck & Wells, 1987; Madenjian et al., 2002; Weidel, Walsh, Holden, & Connerton, 2016). Nearshore–offshore coupling is currently threatened by climate-driven increases in temperatures or turbidity that could prevent cold water stenotherms from accessing nearshore prey (Tunney et al., 2014). Even if a consumer can access nearshore habitats, it may not be able to forage on invasive nearshore prey, such as dreissenids. Pelagic–profundal coupling may be impaired in some lakes by decreased diversity of profundal species that undergo DVM and reduced offshore phytoplankton production limited by the nearshore phosphorus shunt (Hecky et al., 2004). Changes in biomass or abundance of migratory species, such as lake trout or lake whitefish, could also alter offshore to nearshore coupling by altering energy and nutrient subsidies to nearshore spawning locations. Finally, the buffering effect of a predator foraging in multiple habitats and at multiple trophic levels is also lost when any single trophic link becomes dominant, potentially resulting in top-down suppression of prey and trophic cascades. From this perspective, the practice of stocking large, mobile, top predators must be done with caution because their densities can reach such high levels that they contribute to prey collapse, as appears to be the recent case with Chinook salmon and their alewife prey in Lake Huron (He et al., 2015).

3.3.4 | Relevance for management

For the past century, Great Lakes fishery management has undergone a slow evolution from single species towards an ecosystem-level focus (e.g., Guthrie, 2017). Evidence of changes include investment, since 2002, in an international coordinated science and monitoring initiative program (e.g., Richardson, Warren, Nielson, &

TABLE 3 Knowledge gaps in energy and nutrient dynamics of large lake ecosystems. Potential applicable tools are included to inspire future research. Both lists of related citations and potential tools are not intended to be exhaustive

Knowledge gap	Related citations	Potential applicable tools
<i>Flow into system</i>		
<i>Structural attributes</i>		
Importance of macroalgae as a basal resource in the nearshore habitat	Bootsma, Rowe, Brooks, and Vanderploeg (2015)	Remote sensing; trophic markers
Contributions of nutrient inputs to ecosystem and fish production	Bunnell, Johnson, and Knight (2005)	Tributary load monitoring; remote sensing
<i>Natural processes</i>		
Impacts of long-term temporal changes in dietary quality of basal resources	Carrick et al. (2015); Fagan et al. (2017)	Fatty acids; energy density
<i>Human modifiers</i>		
Impacts of land use and climate change on energy and nutrient inputs	Gebremariam et al. (2014)	Tributary load monitoring; sediment cores
<i>Flow within habitats</i>		
<i>Structural attributes</i>		
Drivers of offshore fish community production	He et al. (2015); Kao, Adlerstein, and Rutherford (2016); Riley et al. (2008)	Ecological models
Energy and nutrient dynamics within connecting channels and tributaries, and impacts of these flows on near- and offshore lentic food-web structure	Dove and Chapra (2015); Höök, Rutherford, Mason, and Carter (2007)	Bioenergetics models; movement studies
Role of microbial food-web structure in the dynamics of higher trophic levels	Stewart and Sprules (2011); Hossain, Arhonditsis, Koops, and Minns (2012)	Microcosm studies
Contribution of the deep chlorophyll layer to production, compensation, or both in the pelagic food web	Moll, Brache, and Peterson (1984); Watkins et al. (2007)	Ecological models
Role of the benthic community in nearshore water quality and food web dynamics	Makarewicz and Howell (2012)	Mass balance models or trophic tracers (e.g., fatty acids)
<i>Natural processes</i>		
Implications of density-dependent top-down effects of planktivore grazing and piscivore predation on ecosystem function and adaptive capacity	Negus, Schreiner, and Halpern (2008); Kao et al. (2016)	Ecological models
Drivers of changes in zooplankton community structure and impacts of these changes on food-web structure and adaptive capacity of the system	Barbiero et al. (2012); Barbiero, Lesht, and Warren (2014); Vanderploeg et al. (2012)	Ecological models
Impacts of reduced prey fish diversity and density on the adaptive capacity of the nearshore, pelagic, and profundal habitats	Ludsin et al. (2001)	Ecological models
Impacts of changing seasonal phytoplankton community dynamics (biomass, abundance, species composition) on upper trophic level production	Reavie et al. (2014)	Trophic markers
Applicability of research on nearshore pathway energy and nutrient flows in embayments to areas of open shoreline		
<i>Human modifiers</i>		
Effects of non-native planktivores on trophic structure of pelagic and profundal energy pathways	Myers et al. (2009); Bunnell, Davis, Warner, Chriscinske, and Roseman (2011)	Mass balance or Bioenergetics models
Impacts of harmful algal blooms on food webs	Davis et al. (2012)	Trophic tracers; physiological studies

(Continues)

Horvatin, 2012) to focus on whole food-web sampling of each Great Lake on a rotational cycle, incorporation of fish and fish habitat into the 2012 GLWQA, and the ongoing development by Great Lakes

fishery managers of ecosystem objectives to complement fish community objectives (<http://www.glf.org/joint-strategic-plan-committees.php>). While managers recognise that the lower food web

TABLE 3 (Continued)

Knowledge gap	Related citations	Potential applicable tools
<i>Flow among habitats</i>		
<i>Structural attributes</i>		
Spatial and temporal variation in magnitude and direction of energy and nutrient flows among habitat compartments	Johnson et al. (2005)	Ecological models; linking ecological tracers with telemetry and hydro-dynamics; predator-prey models
Magnitude, mechanisms, and importance of inter-basin coupling	Dolan and Chapra (2012)	
<i>Natural processes</i>		
Changes in coupling among habitat compartments (i.e., magnitude and direction of energetic and nutrient linkages) over time	Barbiero et al. (2012); Bunnell et al. (2014); Hecky et al. (2004)	Among-lake comparative studies; trophic markers
Drivers of carbon cycling between near- and offshore habitats. Do increased nearshore signals represent increased nearshore movement by consumers or increased offshore movement by prey?	Turschak et al. (2014)	Acoustic telemetry; stable isotopes; mass balance models
Role of mussel veligers as prey for larval fishes	Withers, Sesterhenn, Foley, Troy, and Höök (2015)	Laboratory experiments
Contribution of winter energy dynamics, including coupling by mobile consumers, to food-web structure	Stockwell et al. (2014)	Acoustic telemetry with ecological tracers; remote sensing
Mechanisms behind fluctuating abundance of small benthic fishes (e.g., sculpins)	Lantry et al. (2014); Weidel et al. (2016)	Ecological models
Spatiotemporal patterns and rates of transport of particle associated substances from nearshore to offshore	Urban et al. (2004)	Hydrological models
Impacts of changes in abundance of mobile or migratory fishes on nearshore productivity	Stockwell et al. (2014); Vanni (2002)	Acoustic telemetry; Population dynamics models
Changes in phenology of energy subsidies (i.e., climatic influences on spawning run timing)	Quinn and Adams (1996)	Statistical models
<i>Human modifiers</i>		
Impacts of hypoxia on fish movement and coupling among habitats	Ludsin et al. (2001); Scavia et al. (2014); Watson et al. (2016)	Acoustic telemetry; fishery independent surveys
Role of native as compared to non-native benthic fishes as energy vectors between nearshore and offshore profundal habitats	Hondorp, Pothoven, and Brandt (2011); Walsh, Dittman, and O'Gorman (2007)	Stable isotopes; fatty acids; acoustic telemetry

responds more rapidly to environmental and anthropogenic modifiers and precedes—sometimes by a decade—shifts in top predators, there continues to be a need for both a systematic means of interpreting and tools for acting on such food-web changes (e.g., trophic cascades, nutrient loadings, or shifting production among habitats). Several prominent international cases highlight the need for such a systematic approach to understanding how ecosystem health is affected by food-web structure and adaptive capacity of those food webs: (a) eutrophication of Lake Victoria (Hecky, Mugidde, Ramlal, Talbot, & Kling, 2010); (b) regime shifts in the Baltic and Black Seas (Casini et al., 2009; Daskalov, Grishin, Rodionov, & Mihneva, 2007); (c) explosion of HABs in Lake Erie (Michalak et al., 2013; Paerl & Paul, 2012); and (d) oligotrophication and loss of pelagic forage and predatory fishes in Lake Huron (Barbiero, Lesht, et al., 2011; Barbiero, Schmude, et al., 2011; Bunnell et al., 2014; Riley & Adams, 2010). Each of these cases had significant cultural, societal and economic implications. Therefore, an improved understanding of the processes structuring food webs could not only inform management

levers (e.g., land use practices, fish stocking and harvest policies, regulations mitigating effects of invasive species), but also ultimately affect fishery production and its associated economic and cultural consequences. Traditionally, Laurentian Great Lakes fishery management issues and associated levers have often been evaluated and implemented from a top-down perspective, focusing on stocking and harvest policy. By contrast, from a water quality perspective, the reverse is true; water quality managers often focused on nutrient input effects on chemical composition of the lakes. These top-down and bottom-up approaches have yet to merge to form a more holistic view of the health of the Great Lakes ecosystem. We suspect the same to be true of other large lake ecosystems. Our conceptual framework provides managers with a communication tool to more systematically interpret and communicate how lower food-web dynamics influence harvestable fish populations, and to take actions that promote sustainable resource practices. For example, during the early 2000s, the Lake Erie Committee explored establishing a harvest strategy for yellow perch using a suite of ecosystem-state

indicators. This effort ultimately was not adopted by the Committee due to a lack of explicit linkage between lower food-web dynamics, ecosystem state indicators, and fishery production, and difficulties in easily communicating these linkages to stakeholders (J. Tyson, Great Lakes Fishery Commission, personal communication 6 September 2018). Great Lakes fishery managers continue to recognise the need to better understand natural and human modifiers of fishery production and remain committed to developing actionable environmental principles. The framework presented herein could help inform and standardise these efforts. Another potential application of the framework to resource management is that because this approach can track the nutrient flow through complex habitats and across trophic levels, it could facilitate identifying common ground between water quality and fishery managers when phosphorus targets are revised in each lake.

4 | KNOWLEDGE GAPS

Our synthesis revealed 28 knowledge gaps in understanding energy and nutrient dynamics within large lake food webs (Table 3). Knowledge gaps were either explicitly identified in the literature or revealed by the authors through the synthesis of data in the context of our conceptual framework. The list of gaps is not exhaustive and is intended to highlight fertile areas for future research that will lend insights relevant to large aquatic ecosystem ecology and management. A key theme that cut across several knowledge gaps was specifically how components of food-web structure, and processes modifying this structure, influence the system's adaptive capacity. Comprehensive knowledge in this theme will play a critical role in measuring and responding to a system's resilience to perturbations driven by invasive species, human alterations or climate change. The relative roles of bottom-up and top-down processes emerged as a key knowledge gap that could potentially help inform sustainable management practices, including the prosecution of fisheries. Several knowledge gaps revolved around post hoc analysis of human-induced changes including invasive species introductions and dramatic shifts in trophic status of aquatic ecosystems. In general, greater uncertainty was observed in our understanding of processes influencing energy and nutrient flow within and among habitats than flows into the system. This paucity of knowledge, however, probably owes to the reality that many of the questions were untenable without the recent advent of technological capacity to assess questions in the field.

Recent methodological and analytical advances have provided many new tools for redressing questions about energy and nutrient dynamics and are promising to help reduce knowledge gaps in the adaptive capacity of large lake ecosystems. Stable isotopes and fatty acids have permitted tracking of trophic and habitat resource use and assimilation over time scales from months to years (Iverson, 2009; Layman et al., 2012). Acoustic telemetry continues to advance our ability to track fish movements, study behaviours and habitat use in three dimensions, and recently, to evaluate species interactions (Hussey et al., 2015). Linking fish movement and trophic tracers to

resolve energy and nutrient movement across space and time is likely to be the next frontier in the study of trophic dynamics. These types of study are now possible due to acoustic telemetry and advanced powerful computational modelling (Coll et al., 2015). Several mass balance simulation approaches exist and are being employed to describe ecosystem state and model changes in biomass and trophic interactions through time and across space (e.g., Ecopath, Ecosim, and Ecospace; Walters, Christensen, & Pauly, 1997; Walters, Pauly, & Christensen, 1999). Although these models are often data-limited and have other shortcomings, they provide useful insights into ecosystem function. Detailed study of fish, and thereby energy and nutrient spatiotemporal dynamics, will provide a powerful framework to test simulation model assumptions and output. We anticipate that combining new tools and approaches will help resolve some of the knowledge gaps identified herein and provide novel insights into adaptive capacity of food webs.

5 | CONCLUSIONS

The spatial scale of lakes that are either large (>500 km²) or deep (able to thermally stratify) provides potential for a greater diversity of species (and populations and forms within species), habitat (e.g., profundal zone) and basal resource compartments (e.g., DCL) to consumers compared to small lakes. Indeed, small-scale movements via DVM and large-scale movements via DHM and seasonal spawning migrations are important for connecting and coupling discrete habitats in space and time in large lakes. Based on our synthesis, Great Lakes ecosystems have shown adaptive capacity in response to human impacts in cases where: (a) the loss of one resource or habitat is replaced by increased abundance of an alternative species or resource; and (b) consumers respond flexibly by shifting their diet to exploit an alternative resource or habitat and thus sustain production. Examples include increased benthic coupling by fishes in response to invasion by dreissenid mussels and round gobies, and possible increases in the importance of the DCL for zooplankton in the face of reduced epilimnetic production. However, the extirpation or significant reduction of some key species, such as the ciscoes, *Diporeia*, and lake trout, represent a loss of the adaptive capacity in these systems and Great Lakes deep-water food webs remain impaired, or at least considerably altered. In these cases, historical overharvest and the replacement of native species with functionally different, non-native species has clearly influenced the adaptive capacity of lakes Huron, Michigan and Ontario.

Beyond the Laurentian Great Lakes, our conceptual framework presents researchers and resource managers with a tool for investigating and communicating the cumulative effects of natural and anthropogenic stressors on food-web structure and ecosystem function in general. We intend the framework to inspire new ways of considering connections among functional groups and habitats, and anticipate it may help transition management towards more comprehensive ecosystem-based adaptive management. A deeper understanding of the dynamic processes structuring food webs will guide conservation and restoration efforts and potentially allow forecasting of future states of our lakes.

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SUPPORTING INFORMATION

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