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Putting the lake back together 20 years later: what in the benthos have we learned about habitat linkages in lakes?

M. Jake Vander Zanden ^a and Yvonne Vadeboncoeur ^b

^aCenter for Limnology, University of Wisconsin—Madison, Madison, WI, USA; ^bDepartment of Biological Sciences, Wright State University, Dayton, OH, USA

ABSTRACT

Our understanding of lake ecosystems has undergone a paradigm shift over the past few decades. While the classic tradition in limnology has been the study of planktonic, open-water habitats, a shift toward integrative and cross-habitat watershed and whole-lake perspectives has occurred. This change in perspective integrates the role of terrestrial organic matter and littoral/benthic productivity into a general recognition of multiple basal resources and consumer-mediated habitat coupling in lakes. In light of this evolving paradigm, we address 4 broad questions relating to the role of benthic productivity and food web pathways in lakes. Specifically we ask: (1) What is the contribution of attached algae to whole-lake primary production? (2) Are attached algae an important basal resource for consumers? (3) What are the roles of benthic habitats and resources in supporting lake biodiversity? (4) What is the role of lake benthic pathways in aquatic–terrestrial linkages? While this paper focuses on the role of benthic productivity in lake food webs, it reflects a larger movement toward a more integrated and holistic understanding of lake ecosystems. Recognizing the magnitude and implications of aquatic habitat coupling is necessary to understand and conserve these globally important ecosystems in our current era of unprecedented global environmental change.

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Introduction

The field of limnology has a strong tradition of focusing on the dynamics of the open-water zone of lakes (Wetzel 2001, Kalff 2002, Reynolds 2008). Open-water dynamics are well understood and reflect the interaction among physical mixing processes and the resultant vertical gradients in temperature, light, and oxygen. These, in turn, affect the dynamics of dissolved nutrients and free-floating phytoplankton, zooplankton, and predators in the water column, as synthesized by early limnologists (Forel 1892, Birge 1897, 1898). This focus on the open-water zone in lakes closely parallels the open-water emphasis of the field of oceanography (Reynolds 2008).

Fortunately, the past few decades have seen the conceptual boundaries of limnology expand to more fully encompass the surrounding watershed and the entire lake ecosystem (Jones et al. 1998, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Pace et al. 2004). Lakes are embedded in terrestrial landscapes that profoundly affect lake metabolism and ecosystem function. Agricultural nutrient loading accelerates carbon fixation by phytoplankton (Carpenter et al. 1998) while terrestrial detritus and dissolved organic carbon fuels bacterial

respiration (del Giorgio and Peters 1994, Hanson et al. 2003). Terrestrially derived carbon is also a resource for metazoan consumers in lake food webs (Pace et al. 2004). Within the lake itself, the open-water zone is just one of several subhabitats that include littoral, riparian, and profundal zones that can be vitally important to lakewide ecosystem functioning (Scheffer 1998, Wetzel 2001, Schindler and Scheuerell 2002). The recognition that the dynamics of lake habitats are linked, and that these linkages affect the function of the lake as a whole, has fundamentally changed the way we think about lakes (Schindler and Scheuerell 2002, Reynolds 2008).

This synthesis paper is based on a plenary talk authored by Vander Zanden and Vadeboncoeur presented at the 2018 International Society for Limnology (SIL) meeting in Nanjing, China. Within the broader context of the role of habitat linkages in lakes, the talk sought to synthesize our understanding of the role of benthic productivity and littoral food web pathways in lakes. The 2 of us met and began collaborating in the fall of 1998 while we were working with Erik Jeppesen's research group in Silkeborg, Denmark, Jake Vander Zanden as a visiting graduate student (interested mostly

in higher trophic levels) and Yvonne Vadeboncoeur as a postdoctoral fellow (interested mostly in lower trophic levels). We used this talk as an opportunity to reflect upon our 20 years of collaboration and to summarize some of the things we have learned through our cross-habitat and cross-trophic level studies. The approach we adopt here is synthetic; we aim to elucidate broad patterns rather than specific cases. In particular, we focus on how the role of littoral–benthic processes varies along environmental gradients such as lake size, depth, and trophic status. This paper is organized into the following 4 questions relating the role of benthic productivity and food web pathway in lakes: (1) What is the contribution of attached algae to whole-lake primary production? (2) Are attached algae an important basal resource for consumers? (3) What are the roles of littoral–benthic habitats and trophic pathways in supporting biodiversity? (4) What is the role of littoral–benthic pathways in

aquatic–terrestrial linkages? These questions form a scaffolding from which we evaluate the energetic and functional importance of benthic habitats and littoral food web pathways in lakes, as well as the implications of habitat coupling for lake ecosystem function.

We begin with a short orientation to terminology pertaining to lake habitats and zones (Fig. 1). The common terms are derived from oceanography, are ill-suited for lakes, and reflect an earlier time when habitat linkages were of little concern. With respect to habitats, organisms and substrates associated with the lake bottom are benthic, regardless of whether they occur in nearshore waters or in the deepest part of the lake. Unfortunately, no similar, unambiguous term exists for organisms that live in the water. Organisms that float or swim weakly in the water are referred to as planktonic. We use benthic and planktonic to distinguish between whether an organism is primarily associated with surfaces or the water

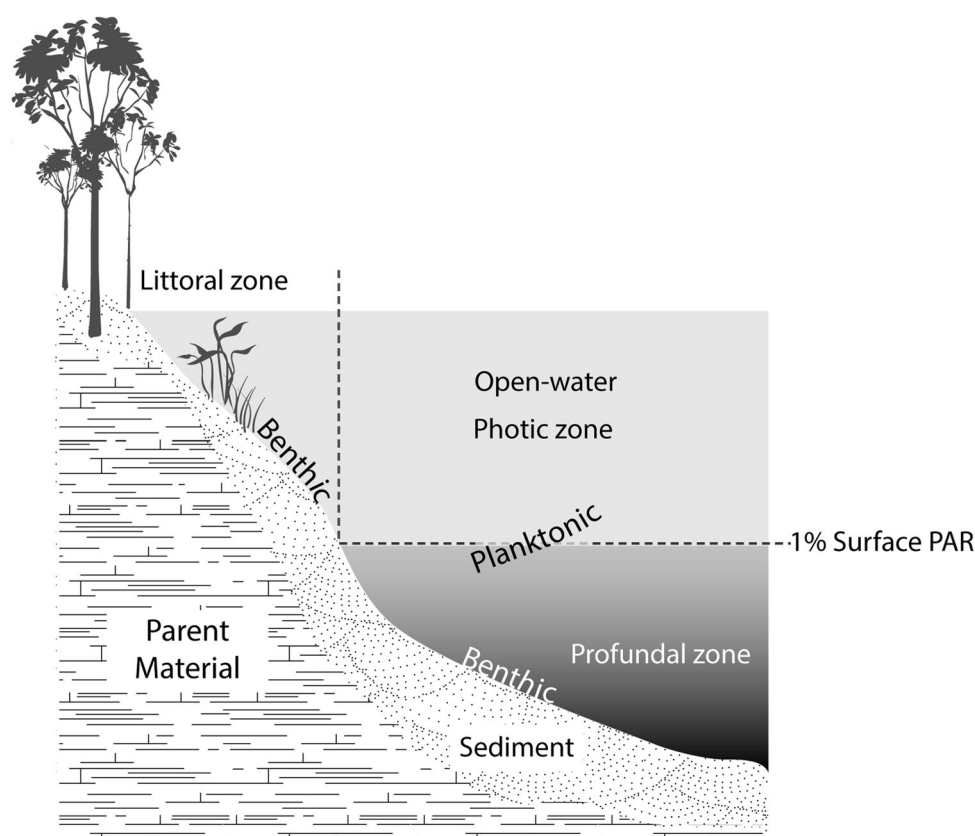


Figure 1. Terminology used in this paper for lake habitats and zones. Habitats: Organisms and substrates associated with the lake bottom are **benthic**, regardless of lake depth (i.e., nearshore to the deepest part of the lake). Organisms that float or swim weakly in the water are described as **planktonic** and are associated with planktonic habitat. Zones: The **open-water** zone receives >1% of surface light (i.e., shallower than compensation depth) and is not in contact with the lake bottom (delineated by dotted lines). The **littoral** zone is nearshore habitat where light hits the lake bottom, allowing for benthic primary producers. Littoral zones are complex structured habitats where periphyton, phytoplankton, and macrophytes contribute to primary production. The **profundal** zone underlies the open-water zone. The absence of light means no photosynthesis. Detrital fallout supports microbial respiration and detritivorous animals. We emphasize that habitats are distinct from zones: planktonic organisms can inhabit littoral, profundal or open-water zones; benthic organisms can inhabit littoral or profundal zones.

column. The benthic–planktonic dichotomy is not easily applied to motile, swimming fish, although it is informative when characterizing their prey.

Stratified lakes can be divided into 3 zones based on whether light penetration is sufficient for photosynthesis (Fig. 1). The size and extent of the open-water, littoral, and profundal zones in lakes are dependent on water clarity. Most limnological research concentrates on the pelagic zone, which refers to the open-water habitat beyond the littoral zone (Kalf 2002). The open-water photic zone receives <1% of surface photosynthetically active radiation (PAR; Wetzel 2001, Kalf 2002) but is not in direct contact with the lake bottom. The open-water zone is bounded by the atmosphere at the surface, the dark profundal zone below, and the waters of the littoral zone on all sides. Phytoplankton, zooplankton, and some fishes are denizens of the open water. The littoral zone is the nearshore habitat where enough light reaches the lake bottom to allow benthic primary producers to grow. Littoral zones are complex, structured habitats where attached algae (periphyton), macrophytes, and phytoplankton contribute to primary production. Periphyton grows on all submerged surfaces that receive sufficient light, including macrophytes (epiphyton), rocks (epilithon), sediments (epipelon), and wood (epixylon). The unlit habitat lying below the open-water zone is called the profundal zone. No photosynthesis occurs in the profundal zone, but detrital fallout from the open-water and littoral zone fuels heterotrophic microbial respiration and supports detritivorous animals. Habitats are distinct from zones; planktonic organisms can inhabit littoral, profundal, or open-water zones, whereas benthic organisms can only occur in littoral or profundal zones. Individual species can inhabit multiple zones or habitats, and motile species often do so.

Question 1—What is the contribution of attached algae to whole-lake primary production?

Foundational papers and classical texts in limnology afforded similar attention to planktonic (phytoplankton) and benthic (periphyton, macrophytes) primary producers in lakes (Forbes 1887, Lindeman 1942, Hutchinson 1957). Nevertheless, the tendency in limnology is to treat phytoplankton as the sole trophic foundation of lake food webs (Reynolds 2008). Indeed, planktonic primary production is synonymous with whole-lake primary production in much of the 20th century literature on lake productivity and metabolism (Vadeboncoeur et al. 2002). But as the boundaries of limnology have expanded beyond the planktonic realm, it has become clear that littoral macrophytes and attached algae can contribute substantially to whole-ecosystem productivity

and metabolism (Vadeboncoeur et al. 2001, 2003, Wetzel 2001, Van de Bogert et al. 2007, Ask et al. 2009, Vesterein et al. 2016, 2017), and attached algae are an important resource for higher trophic levels (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002, Sierszen et al. 2003, Vander Zanden et al. 2011). The recognition that littoral primary production, and attached algae in particular, is fundamental to lake ecosystem function and varies predictably across morphometric and trophic gradients (Vadeboncoeur et al. 2008) led to the concept of “autotrophic structure” to refer to the distribution of primary production between benthic and planktonic habitats (Althouse et al. 2014, Higgins et al. 2014; Fig. 2).

Our earliest collaboration explored the validity of the plankton-centric perspective in a study of shallow lakes in the United States, Greenland, and Denmark (Vadeboncoeur et al. 2003). We used field-based benthic and planktonic primary production measurements to quantify the relative importance of benthic and planktonic algae to whole-lake primary production. This early work demonstrated that attached algae can contribute virtually 100% of whole-lake primary production in shallow, oligotrophic arctic lakes (Vadeboncoeur et al. 2003, 2008). Moreover, autotrophic structure shifted from benthic to planktonic dominance across a broad gradient of water column total phosphorus concentrations (Vadeboncoeur et al. 2003). Another way to look at this is that eutrophication driven by nutrient pollution represented not so much an increase in lake productivity, but rather a shift in autotrophic structure. Clear lakes, which humans typically value, tend to be dominated by littoral primary producers, whereas eutrophic lakes are dominated by phytoplankton. Additionally, littoral primary producers, especially macrophytes, can mitigate the effects of nutrient loading on lake ecosystem structure by maintaining lakes in a clear water state at nutrient concentrations that would otherwise be characterized by high phytoplankton biomass (Jeppesen et al. 1990, Scheffer et al. 1993, Genkai-Kato et al. 2012, Brothers et al. 2013, Kazanjian et al. 2018).

As young researchers, our first publishing efforts met with the criticism that littoral primary production was only important in small or shallow lakes. Although we were tempted to point out that most lakes are small, we instead expanded our research to include a larger range of lake sizes and depths, including the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) lakes in Wisconsin (USA), oligotrophic lakes in the Western United States (Lake Tahoe and Castle Lake), and Lake Tanganyika in east Africa (Vander Zanden et al. 2006, Vadeboncoeur et al. 2014). Expanding the range of study lakes informed the development of

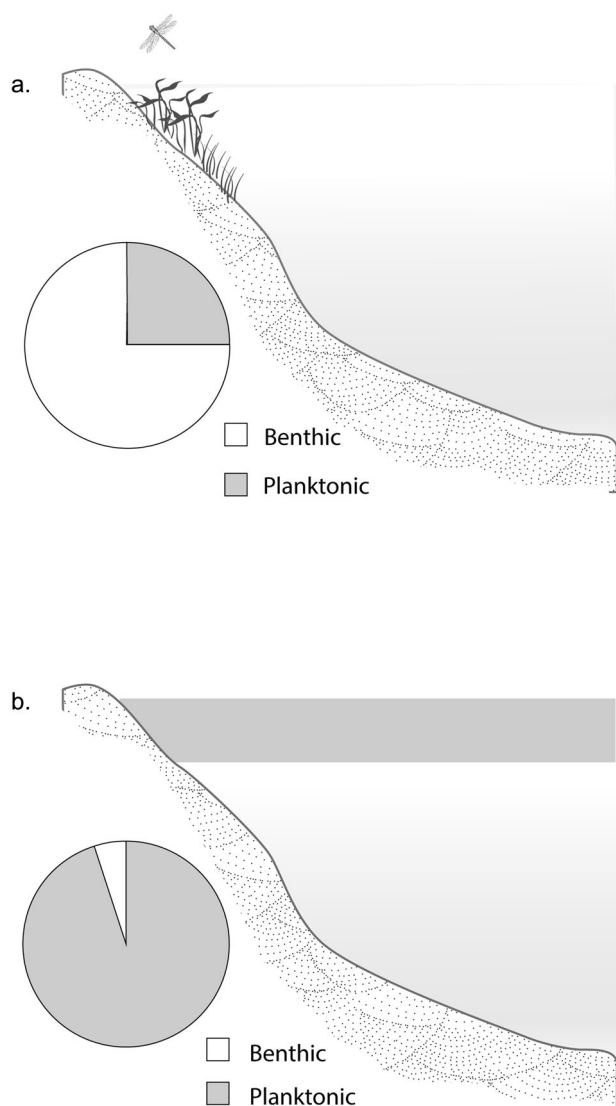


Figure 2. Conceptualization of lake autotrophic structure. (a) Benthic dominance: phytoplankton production and biomass are low. The resultant high water clarity allows high rates of benthic primary production. Lakewide primary production is dominated by periphyton and/or macrophytes. (b) Open-water dominance: high phytoplankton biomass in surface waters reduces light penetration and the lakewide contribution of benthic primary production, such that lakewide primary production is dominated by phytoplankton.

empirically based conceptual models that integrated the multiple factors that influence lake autotrophic structure (Vadeboncoeur et al. 2008). This body of work elucidated how a handful of factors—lake size, morphometry, light, trophic status (Vadeboncoeur et al. 2008), and grazers (Higgins et al. 2011)—interact to determine the benthic contributions to whole-lake primary production. Autotrophic structure tends to shift from benthic to planktonic dominance with increasing lake depth, increasing trophic status, and decreasing water clarity (Vadeboncoeur et al. 2008).

Researchers studying shallow lakes (average depth <5 m) generally recognize the importance of littoral processes because they traverse extensive littoral habitat to find the elusive “deep hole” for plankton sampling. Only shallow lakes, which tend to be small in surface area, exhibit the entire range of autotrophic structures ranging from benthic to planktonic dominance. Small, clear, high-latitude and high-altitude lakes exhibit benthic dominance because scarce nutrients keep phytoplankton biomass low (Vadeboncoeur et al. 2003, Rautio et al. 2011). Lakes in arctic, Antarctic, and alpine landscapes often have undetectable levels of inorganic nutrients in the water, resulting in some of the lowest phytoplankton productivity rates measured in lakes and some of the clearest lake water. However, in these so-called “unproductive” lakes, area-specific production of benthic algal biofilms can be 100 times that of phytoplankton (Rautio et al. 2011). High water clarity combined with relatively high benthic primary productivity produces benthic contributions approaching 100% of whole-lake autotrophic production (Welch and Kalff 1974, Vadeboncoeur et al. 2003). Many boreal lakes contain high concentrations of colored dissolved organic carbon (DOC), which can affect lakes and benthic-pelagic habitat coupling in a multitude of ways (Ask et al. 2009, Karlsson et al. 2009). DOC is often associated with high nutrients and reduced mixing depth (Brothers et al. 2014, Seekell et al. 2015, Vasconcelos et al. 2016). It also reduces light penetration, which could reduce both pelagic and benthic algal productivity. Ask et al. (2009) found that primary production and energy mobilization in benthic habitats were highly sensitive to changing DOC concentrations compared to pelagic habitats. Studies suggest that lake brownification is likely to shift lakes toward greater pelagic dominance (Brothers et al. 2014, Seekell et al. 2015, Vasconcelos et al. 2016). Finally, surprising new evidence shows that epiphytic algal growth on the bog vegetation surrounding humic lakes can dominate ecosystem primary production, far exceeding that of phytoplankton or algae on sediments, both of which are limited by light availability (Vesterinen et al. 2016, 2017).

Primary production in small and shallow lakes in human-dominated landscapes tends to be strongly plankton-dominated (Vadeboncoeur et al. 2003), unless macrophytes are well established (Scheffer 1998). Open-water nutrient availability in these lakes is elevated as a result of anthropogenic nutrient inputs such as agricultural runoff (Carpenter et al. 1998). Again, autotrophic structure is driven by the relative availability of resources for periphyton and phytoplankton. Nutrients accumulate in lake sediments, and unconsolidated sediments are the most extensive surface for attached algae

in most lakes (Vadeboncoeur et al. 2008, Devlin et al. 2016). Attached algae on sediments are not limited by nutrient availability, but by light (Vadeboncoeur and Steinman 2002, Vadeboncoeur et al. 2014). Nutrient-limited phytoplankton respond to nutrient enrichment with large increases in biomass. These phytoplankton blooms reduce water clarity and light penetration to the benthos. The constriction of the littoral zone associated with eutrophication reduces periphyton extent and productivity, such that attached algal contributions to whole-lake primary production in highly eutrophic lakes is negligible (Fig. 2b).

There is extensive literature on the concept of multiple ecosystem states in shallow lakes and the factors and feedbacks that can cause lakes to undergo abrupt shifts between dominance by macrophytes and dominance by phytoplankton (Scheffer et al. 1993, Scheffer 1998). These alternative, stable ecosystem states can be viewed in terms of the autotrophic structure of ecosystems, although this perspective has not been widely applied (but see Brothers et al. 2013). Lakes can exhibit rapid shifts from dominance by macrophytes and attached algae to dominance by phytoplankton in response to a perturbation or food web manipulation. The existence of alternative stable states can be reinforced by attached algae on sediments regulating phosphorus flux between the sediments and the water column (Scheffer et al. 1993, Scheffer 1998, Genkai-Kato et al. 2012). Moreover, autotrophic structure of shallow lakes can vary seasonally (Brothers et al. 2013). For example, attached algal primary production was far greater than that of phytoplankton during winter months in shallow Danish lakes, but this pattern was reversed during the summer (Liboriussen and Jeppesen 2003).

In moderately deep lakes (mean depth = 5–25 m), phytoplankton and attached algae tend to both make substantial contributions to whole-lake primary production due to morphometric surface area:volume relationships alone. Models and empirical data reveal that attached algae can still contribute up to 80% of whole-lake primary production in moderately deep lakes if water clarity is high (Vadeboncoeur et al. 2008). In moderately deep lakes, clarity and nonalgal turbidity are important factors in determining autotrophic structure. Water clarity interacts strongly with lake morphometry (as approximated by the depth ratio) to determine the proportion of whole-lake primary production that is benthic (Vadeboncoeur et al. 2008).

Autotrophic structure of large and deep lakes (mean depth >25 m) tends to be overwhelmingly dominated by planktonic primary production. Even though large lakes tend to be clear (although with notable exceptions),

the large open-water habitat outweighs the illuminated benthic surface area due to ecosystem geometry. The extent of the littoral zone is operationally defined as the area of the lake bottom that receives <1% of surface light. The littoral zone constitutes <10% of total lake area in the world's largest, deepest lakes (e.g., Lake Baikal 4%, Lake Tanganyika 8%, Lake Superior 9.6%; Vadeboncoeur et al. 2011). There are few estimates of benthic primary production for these lakes, but in Lake Tanganyika, littoral primary production accounted for <0.1% of whole-lake primary production (O'Reilly et al. 2003). However, littoral zones comprise 30–40% of lake area in other large lakes (Lakes Erie and Huron, North America; Lake Biwa, Japan; Lake Titicaca, South America; Vadeboncoeur et al. 2011). Historically, attached algae may have contributed as much as 30% of total primary production in the Laurentian Great Lakes, based on measured maximum rates of benthic primary production (Brothers et al. 2016). Regardless of the relative contribution of attached algae to lake metabolism, the littoral zones of large lakes are the most spatially extensive freshwater littoral habitat in the world, and they harbor a rich diversity of species dependent on attached algal production (Hecky and Hesslein 1995, Bootsma et al. 1996, Vadeboncoeur et al. 2011).

Twenty years after our initial benthic and planktonic primary production measurements in shallow lakes across a latitudinal gradient (Vadeboncoeur et al. 2003), we now have a better understanding of how factors such as light and substrate affect benthic primary productivity rates at the local scale. Moreover, understanding of local-level benthic productivity informs a broader, integrative perspective embodied in the concept of lake autotrophic structure, which is, in essence, how whole-lake primary production is distributed between benthic and pelagic primary producers (Althouse et al. 2014, Higgins et al. 2014). Lake ecosystems can range from virtually full benthic to full planktonic dominance of primary production. We understand the handful of factors—lake size, morphometry, trophic status, light, and grazing—that ultimately determine how primary productivity is distributed between these 2 lake habitats (Vadeboncoeur et al. 2008, Higgins et al. 2014). This concept of lake autotrophic structure sets the stage for considering and understanding the broader role of benthic production in lake food webs.

Question 2—Is attached algae an important basal resource for consumers?

For our second question, we shift to an ecosystem energetic perspective rooted in the concept of trophic basis of production (Benke and Wallace 1980). Specifically, we

consider the contribution of attached algae in supporting the production of metazoan consumers and how the importance of attached algae as a resource to consumers varies along environmental gradients. Although macrophytes can be important contributors to lakewide primary production in shallow and productive lakes, there is less evidence that they are directly incorporated into lake food webs (James et al. 2000). Here, we focus on the role of attached algae in lake food webs to facilitate direct comparison with phytoplankton, and as a result we offer a conservative picture of the importance of benthic resources to consumers.

Benthic invertebrates are a diverse and vital component of lake ecosystems (Hutchinson 1957, Covich et al. 1999, Brinkhurst 2002). Studies of benthic metazoans have focused predominantly on macroinvertebrates. Unfortunately, the role of the diverse and abundant benthic micro- and meio-fauna in fueling higher trophic levels remains poorly understood (Strayer 1985). Among the macroinvertebrates, taxa such as snails, mayflies, and caddisflies specialize in consuming attached algae (Lamberti 1996, Merritt and Cummins 1996, Steinman 1996). Generalist taxa, such as larval chironomids, opportunistically consume periphyton, settled phytoplankton, and terrestrial detritus (Merritt and Cummins 1996). Larval dragonflies, damselflies, and megalopterans are efficient predators that feed on zoobenthos and zooplankton (Merritt and Cummins 1996). Benthic macroinvertebrates are a critical food item for fish. During the growth of piscivorous fish, zoobenthos occupy a size gap in a diet that progresses from zooplankton to fish. As we discuss later, the trophic link between zoobenthos and fish in lakes has been reasonably well established through fish gut content studies (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002). However, recognition of the reliance of zoobenthos on attached algae has occurred more slowly. The emphasis has generally been on the importance of phytoplankton and terrestrial detritus as diets for zoobenthos, rather than on attached algae as a food resource (Jónasson 1972, 2003, Rasmussen and Rowan 1997).

Gut content analysis provides insights into consumption of different basal resources but is time consuming and prohibitively difficult to conduct on the diverse benthic fauna of lakes. Stable isotope analysis, especially stable carbon isotopes ($\delta^{13}\text{C}$), revolutionized our ability to establish the importance of littoral primary production to lake food webs by providing a direct index of consumer energetic reliance on attached algae. In lakes, attached algae and phytoplankton often show strong isotopic separation (France 1995, Hecky and Hesslein 1995, Vander Zanden and Rasmussen 1999). Attached algae have a less negative $\delta^{13}\text{C}$ signal than phytoplankton

because algae growing in biofilms discriminate less against ^{13}C than do algae suspended in water because of boundary layer effects (Hecky and Hesslein 1995). These isotopic differences at the base of the food web are subsequently passed to higher consumers, such that consumer carbon isotope values provide a strong basis for inferring carbon sources, especially phytoplankton versus attached algae, supporting higher trophic levels in lakes.

The carbon isotopic signal of periphyton is also directly correlated with light availability because light often limits productivity, and attached algae discriminate against ^{13}C less as productivity increases (Hill et al. 2008, Devlin et al. 2013). In 5 NTL-LTER lakes in Wisconsin, periphyton $\delta^{13}\text{C}$ was directly correlated with periphyton productivity and was maximal in the well-lit upper littoral zone of the lakes (Devlin et al. 2013). Infaunal primary consumers (chironomids) and predators closely tracked this depth-specific pattern of periphyton $\delta^{13}\text{C}$, with a nearly 1:1 relationship between $\delta^{13}\text{C}$ of these consumers and that of attached algae in all 5 lakes (Devlin et al. 2013). The $\delta^{13}\text{C}$ values of infaunal filter feeders (native mussels) did not vary with depth and were similar to those of zooplankton, indicating that the benthic mussels fed on phytoplankton. Interestingly, highly motile epifaunal primary consumers such as mayflies, snails, and amphipods were also directly correlated with the $\delta^{13}\text{C}$ of periphyton but were more enriched than the bulk attached algal biofilm. Based on these patterns, we inferred that these motile grazers feed selectively on the most productive, surficial layers of the biofilm (Devlin et al. 2013). Thus, coexisting functional feeding groups partitioned periphyton basal resources, and only filter feeding unionid mussels demonstrated reliance on phytoplankton.

Studies in large, deep lakes have attributed a decline in primary consumer $\delta^{13}\text{C}$ with depth to a shift in resource use from periphyton (isotopically enriched) to phytoplankton fallout (isotopically depleted; Chandra et al. 2005, Sierszen et al. 2006). However, periphyton itself becomes more isotopically negative with depth owing to the decline in primary productivity with depth (Devlin et al. 2013, Vadeboncoeur et al. 2014). With increasing water column depth, the productivity of light-limited periphyton decreases while at the same time the contribution of phytoplankton detritus increases. Thus the decline in benthic invertebrate $\delta^{13}\text{C}$ in large lakes may reflect either a strong reliance on attached algae (Devlin et al. 2013) or a progressively increasing reliance on phytoplankton detritus (Chandra et al. 2005). Although the importance of phytoplankton detritus as a resource necessarily increases with depth, the overall decrease in zoobenthic production as a function of depth (Butkas et al.

2011) suggests that the increased availability of phytodetritus does not offset the loss of attached algae as a resource.

Area-specific zoobenthic production is usually highest in the eulittoral zone and subsequently decreases with depth (Brinkhurst 2002, Butkas et al. 2011, Pätzig et al. 2018). As noted earlier, the relative importance of phytodetritus as a food resource for zoobenthos increases with water column depth (Chandra et al. 2005) over the same gradients that zoobenthic production declines. Terrestrial detritus is another possible carbon source for zoobenthos in lakes (Solomon et al. 2011). The availability of terrestrial detritus might be expected to decline with depth owing to the increasing distance between the riparian source of terrestrial detritus and the middle of the lake. However, wave action and sediment focusing generally prevent detrital accumulation in shallow areas (Rowan et al. 1992), making depth a poor proxy for availability of terrestrial detritus. Despite the lack of emphasis on attached algae as a basal resource in lake food webs, littoral zoobenthic production is closely correlated with attached algal production, peaking in shallow well-lit waters below the influence of waves and subsequently declining with depth (Butkas et al. 2011). This correlation between benthic primary and secondary production along the depth gradient thus reinforces the isotopic evidence that littoral zoobenthos tend to be strongly reliant on attached algal production.

Fish are more mobile than most zoobenthic taxa and generally move easily between littoral and open-water zones. Many fish species are flexible feeders and adapted to foraging in diverse habitats, and as such, there is growing awareness of fishes as couplers of these habitats (Stein et al. 1995, Schindler et al. 1996, Vanni 1996, Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005). Synthetic analyses of gut content and stable isotope data have provided key insights into the importance of various resources and carbon sources to this key group of higher consumers.

A seminal study describing the important role of benthic algal pathways to higher consumers was Hecky and Hesslein (1995), who presented stable carbon isotope data for benthic and planktonic primary producers, invertebrates, and fishes from lakes spanning tropical, temperate, and arctic zones. They found that higher consumers tended to exhibit near-equal dependence on benthic and planktonic algal carbon and concluded that “this equal dependence would not be predicted from the relative magnitude of planktonic and benthic algal photosynthesis as currently estimated in these systems” (p. 631; Hecky and Hesslein 1995).

Subsequent stable isotope food web studies focusing on one or a few lakes have confirmed the overall importance of carbon fixed by attached algae to lentic fishes (Sierszen et al. 2003, Karlsson and Byström 2005, Vander Zanden et al. 2006, Hampton et al. 2011). A similar conclusion has emerged in literature synthesis studies (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2011). A synthesis of gut content data from 470 individual fish populations of 15 common North American fish species found that on average, >60% of their overall diet was composed of or traced back to zoobenthic prey (Vander Zanden and Vadeboncoeur 2002). A synthesis of stable carbon isotope data for largely the same set of species provided a similar picture of ~60% benthic algal reliance (Vander Zanden and Vadeboncoeur 2002). These broad averages mask a high degree of species-specific and among-lake variation, but the key point is that benthic basal resources are a nontrivial resource for consumers. For example, a multi-lake comparison of lake trout (*Salvelinus namaycush*) diets revealed that this species tends to consume benthic prey in small lakes, but not large lakes (Vander Zanden and Vadeboncoeur 2002). Moreover, studies have demonstrated how benthic reliance on the part of consumers can shift abruptly in response to ecological perturbations. Several studies have documented dramatic shifts toward increased fish benthic reliance following zebra mussel invasion (Rennie et al. 2009, Turschak et al. 2014).

Overall, lake food web diagrams show that small (i.e., forage) fishes exhibit strong niche separation along a benthic–planktonic resource axis and are bimodal in their resource use, whereas predatory or piscivorous fishes exhibit unimodal distributions of resource use and an intermediate degree of benthic reliance. Such studies reveal the role of predatory fishes in coupling or integrating benthic and pelagic trophic pathways (Fig. 3; Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002).

The qualitative observation of unexpectedly high reliance of fishes on benthic algal sources relative to their perceived importance at the base of the food web (Hecky and Hesslein 1995) raises several intriguing questions. One potential explanation is that the importance of benthic algal photosynthesis has simply been underestimated. While this explanation is probable, it does not explain what often seems to be extreme overrepresentation of attached algal carbon to higher trophic levels. For example, in deep, oligotrophic Lake Crescent in Washington (USA), 50% of the carbon in apex salmonid predators was derived from nearshore benthic habitats, even though the nearshore zone only

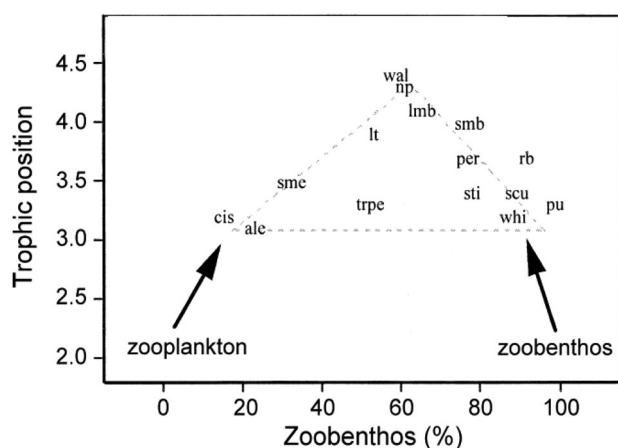


Figure 3. Energy flow pathways for higher trophic levels in lake food webs, where the x-axis represents the degree of benthic reliance and the y-axis represents trophic position. Each symbol represents the trophic niche of a different fish taxa common in north-temperate lakes of North America. Forage fishes show strong niche partitioning and a bimodal pattern along the benthic–pelagic gradient, with most taxa exhibiting benthic reliance. Predatory (piscivorous) fishes exhibit intermediate benthic reliance, reflective of their tendency to forage across benthic and pelagic trophic pathways. This food web configuration is thus described as triangular. Based on Vander Zanden and Vadeboncoeur (2002); cis = cisco; ale = alewife; sme = rainbow smelt; trpe = trout-perch; lt = lake trout; wal = walleye; np = northern pike; lmb = largemouth bass; smb = smallmouth bass; per = yellow perch; rb = rock bass; sti = stickleback; scu = sculpin; whi = lake whitefish; pu = pumpkinseed.

accounted for ~2.5% of lake volume (Hampton et al. 2011). The magnitude of this mismatch suggests highly selective fish foraging in the littoral zone. Such observations also suggest that trophic transfer efficiency of benthic productivity to higher trophic levels is higher than its planktonic counterpart. This hypothesis was tested in a small alpine lake, Castle Lake, California (Vander Zanden et al. 2006). In this study, a combination of stable isotope data and production estimates revealed that benthic algal production was much more efficiently passed up the food chain to fish than was planktonic algal production, which made a surprisingly minor contributor to supporting fish production. In contrast to Castle Lake, a recent study of 2 shallow eutrophic lakes in Germany revealed notably lower ecological efficiency along benthic pathways (Lischke et al. 2017). While most broad syntheses indicate that fish show surprisingly high benthic reliance (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Vander Zanden et al. 2011), the issue of differential ecological efficiencies for benthic and planktonic pathways remains unresolved and may depend on habitat type and other environmental and taxa-specific factors.

Question 3—What is the role of benthic habitats and productivity in supporting aquatic biodiversity?

Isotopic evidence overwhelmingly suggests that most fish species are strongly reliant on littoral pathways, even in lakes where phytoplankton dominate autotrophic structure. We found this pattern puzzling within a framework of production dynamics. But perhaps the strong consumer reliance on attached algae-based trophic pathways was indicative of the distribution of species diversity in lakes. Freshwater ecosystems occupy far less than 1% of the earth's surface, yet they support a disproportionate fraction of the earth's biodiversity, including ~10% of all described animal species and ~33% of all vertebrate species (Dudgeon et al. 2006, Strayer and Dudgeon 2010). Here we explore whether this diversity is disproportionately associated with littoral zones, and why this might be so.

Although many thorough assessments of lentic zooplanktonic assemblages have been conducted, reflecting the traditional research focus on the open-water zone, surprisingly few have comprehensively assessed zoobenthic diversity. Moreover, rarely do studies of zoobenthic communities go beyond cursory assessments of the macro-zoobenthos (>200 μ m mesh size) to include the meio- and micro-zoobenthic fauna. A notable exception is a detailed monograph documenting the zoobenthic metazoans of Mirror Lake, New Hampshire, USA (Strayer 1985). This study documented 322 benthic-dwelling animal species spanning 12 different phyla. Considering that certain benthic taxa were not sampled or evaluated in great detail, Strayer (1985) used species counts for specific taxa from other well-studied lakes and estimated total zoobenthic species richness of Mirror Lake to be ~600 species, which is consistent with the few other detailed zoobenthic community studies (Monard 1918, Muckle 1942). By contrast, only 29 zooplankton species have been documented in Mirror Lake (Likens 1985). In other well-studied lakes, zoobenthic species richness also vastly exceeds zooplanktonic species richness, although we again note that the species lists for benthic fauna in these lakes are woefully incomplete. Furthermore, in stratified lakes, the vast majority of the zoobenthic species diversity is concentrated in the structurally complex littoral zone. Zoobenthic species richness tends to decline sharply with lake depth (Strayer 1985, Brinkhurst 2002), but benthic sampling equipment (e.g., Eckman and Ponar grabs) are specialized for sampling the soft sediments that accumulate in deep, relatively species-poor habitats.

Most of the world's lakes are small and dominated by benthic and littoral habitats (Strayer 1985, Wetzel 2001).

By contrast, littoral zones are a relatively small proportion of total lake area in large lakes. Nevertheless, the most extensive, contiguous freshwater littoral habitat in the world occurs in large lakes, and ecosystem size has a profound effect on biodiversity. Furthermore, the world's largest lakes (e.g., Lake Baikal and the African rift lakes) are also the world's oldest lakes (Martens 1997, Vadeboncoeur et al. 2011, Salzburger et al. 2014). The littoral zones of these isolated, ancient lakes are cradles of endemism and home to globally significant adaptive radiations for numerous aquatic taxa (Martens 1997, Vadeboncoeur et al. 2011, Salzburger et al. 2014). We explored the role of large lakes in supporting aquatic biodiversity by synthesizing published data from 14 of the world's best-studied large lakes (Vadeboncoeur et al. 2011), which alone contain ~5% of global species diversity for the taxa we catalogued. Notably, these lakes alone contained 10–25% of global non-insect invertebrate diversity (excluding most meio- and micro-faunal taxa) and ~15% of global freshwater fish diversity. The concentration of such a sizeable portion of global freshwater biodiversity in such a small number of waterbodies is striking, but we were particularly interested in how much of this diversity was associated with the narrow rind of littoral zone that bordered the vast expanses of open water.

As ecosystems, large lakes are dominated by the vast open-water zones that dwarf the narrow, if often deep, littoral zones. Of the 14 lakes included in Vadeboncoeur et al. (2011), on average ~18% of lake surface area is littoral (water depth shallower than depth of 1% light level). Yet despite the relatively minor contribution of littoral habitats at the whole-lake scale, fish and invertebrate biodiversity is overwhelmingly concentrated in the littoral zone. In our 14 study lakes, on average 80% of invertebrate species occurred exclusively in the littoral zone, and 94% of invertebrate species were in habitats that include the littoral zone. Even for taxonomic groups widely associated with the open-water zone such as Copepods and Cladocerans, species diversity was predominantly littoral (Vadeboncoeur et al. 2011). Species–area relationships across the 14 lakes differed substantially among the littoral, open-water, and profundal zones (Fig. 4). Species richness was positively correlated with habitat area, but average species density (species per unit area) in the littoral zone was 10 times higher for fishes and 50 times higher for invertebrates compared to species density in the open-water zone. Profundal species richness was intermediate between open-water and littoral zones.

The complex physical structure of littoral zones, and to a lesser extent profundal zones, probably fosters high diversity by allowing niche partitioning among species. Littoral habitats are complex; diverse substrates

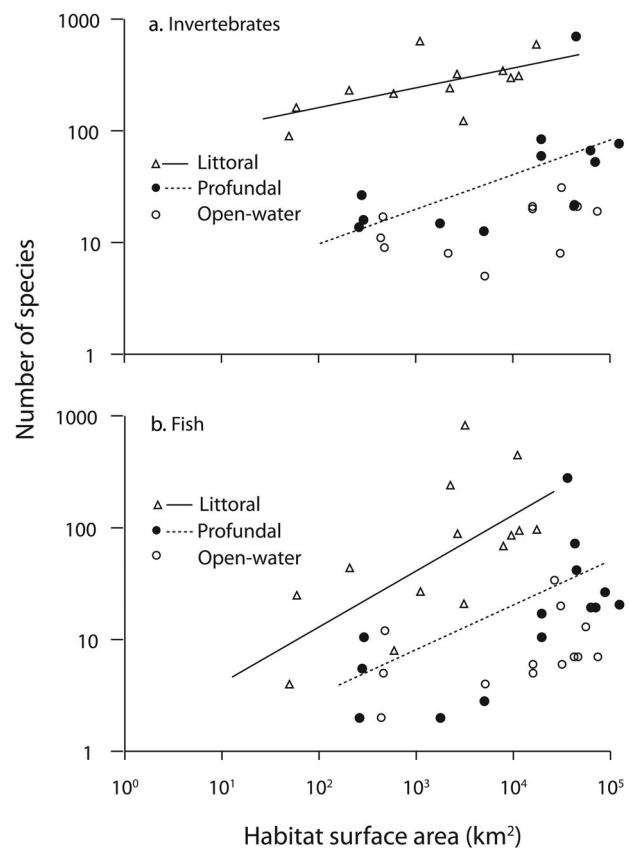


Figure 4. Habitat-specific species–area relationships for (a) invertebrates and (b) fish from 14 of the world's largest lakes. In the case of fish, for a given habitat area, the littoral zone supports ~10 times more species than the open-water zone. For invertebrates, the littoral zone supports ~50 times more species than the open-water zone. From Vadeboncoeur et al. (2011).

including sand, mud, rocks, wood, and various aquatic plant forms provide spatial heterogeneity across gradients of depth and disturbance. Profundal zones are more physically complex than the open-water zone because in addition to water, profundal regions incorporate the lake bottom. However, the profundal benthic habitat is relatively homogeneous (i.e., mud) compared to the more varied benthic habitat in the littoral zone. Moreover, the profundal is dark, cold, and can be seasonally anoxic. As a result, invertebrate species diversity in the profundal zone is lower than in the littoral. The open-water zone generally has the lowest metazoan species diversity. Although light is available and the habitat supports autotrophic (phytoplankton) production, relatively few taxa of fish and invertebrates are adapted to inhabiting and thriving in this mixed and unstructured habitat. Not only do species strongly associate with physically structured habitats, structured habitats also generate potential for ecological niche partitioning and evolutionary divergence that ultimately lead to high species richness (Vadeboncoeur et al. 2011).

Classifying the primary habitat of invertebrates as either benthic or planktonic is relatively easy. By contrast, fishes are highly motile and tend to defy a simple benthic–planktonic habitat classification. For example, a benthic-feeding fish may spend much of its time swimming through the water column in search of feeding patches. Fishes often act as couplers of benthic and planktonic habitats (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002). Moreover, fish species can be quite broad in their resource and habitat use and may be reliant on benthic and planktonic habitats or prey at different times throughout their life, or for different aspects of their life history. Fish species tend to be planktonic during early life-history stages, but they undergo ontogenetic diet and habitat shifts to benthic invertebrate and fish with increasing body size (Olson 1996). While studies of lake food webs have traditionally adopted a planktonic focus (Carpenter and Kitchell 1993), fishes are increasingly recognized as mobile consumers whose lives span benthic and planktonic habitat boundaries, thereby linking these 2 lake habitats (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002). Recognizing the role that fishes play in these cross-habitat linkages is critical for understanding ecological function of lakes (Schindler et al. 1996, Vanni 1996, Schindler and Scheuerell 2002, Vanni et al. 2005).

One might expect fishes in the world's largest lakes to rely predominantly on planktonic food chains and resources. However, assessment of fish diets revealed that the vast majority of fish species in these lakes consume benthic resources, either exclusively or in conjunction with planktonic resources (Vadeboncoeur et al. 2011). In fact, <10% of fish species in these large lakes rely solely on planktonic food items (Vadeboncoeur et al. 2011). More broadly, gut content data for many common fish species from hundreds of lakes reveal that most fish species consume predominantly benthic-derived prey (Vander Zanden and Vadeboncoeur 2002, Vadeboncoeur et al. 2011), and stable isotope analysis confirms this finding. While some are certainly obligate planktonic specialists, most fish species forage on littoral zoobenthos and, as a result, exhibit strong reliance on carbon fixed by benthic primary producers (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002, Sierszen et al. 2003, Karlsson and Byström 2005).

Our exploration of patterns of diversity in large lakes helped us understand this somewhat counterintuitive result: although phytoplankton often dominates autotrophic structure of lakes, particularly in large lakes, most fish species are reliant on littoral resources, irrespective of lake size (Vander Zanden et al. 2011). We argue that the persistent and widespread reliance of fish species on littoral resources reflects patterns in fish species

distribution and diversity, not patterns in whole-lake secondary production. Complex littoral habitats foster and support more species of higher consumers and finer ecological niche partitioning. Even in large lakes, which are dominated by pelagic primary production, we find that the majority of fish species are supported by benthic habitats and benthic production (Vander Zanden et al. 2011). In such lakes, total primary production and ecosystem-wide energy flows tend to be predominantly pelagic. Yet this largely planktonic primary production base supports relatively few fish species, even though the secondary production of these relatively few fish species is high. One way to think about this contradiction of few fish but high secondary production is that the large amount of planktonic primary production is “coarsely partitioned” into relatively few fish species. By contrast, the limited benthic primary production is much more “finely partitioned” into many species. The result is that fish species diversity per unit primary production is higher for the benthic than the open water. Either way, littoral habitats and benthic production pathways clearly support a disproportional amount of lentic biodiversity (Vadeboncoeur et al. 2011, Vander Zanden et al. 2011). The relevance of lentic systems is especially evident when we consider that freshwater ecosystems are global biodiversity hotspots. Freshwater biota are also highly imperiled (Strayer and Dudgeon 2010), primarily as a result of rapidly intensifying physical, chemical, and biological alterations (Carpenter et al. 2011). The effect of not only water extraction and pollution, but also dam construction, invasive species, habitat loss, overharvest, and climate change, pose serious threats to freshwater ecosystems and biodiversity (Dudgeon et al. 2006, Carpenter et al. 2011). Given these threats and the concentration of biodiversity in littoral zones, the protection of littoral zones is a seemingly essential focus of global biodiversity conservation, particularly because they are the most impacted by habitat disturbance and other human activities (Brauns et al. 2007, Strayer and Findlay 2010, Brauns et al. 2011).

Question 4—What is the role of lake benthic pathways in aquatic–terrestrial linkages?

The rich ecological history of studying linkages between aquatic habitats and their surrounding watersheds has predominantly emphasized the flux of materials and nutrients from terrestrial to aquatic habitats. This emphasis is understandable given that freshwater ecosystems are embedded in much larger terrestrial landscapes, and gravity transports terrestrial-derived nutrients and materials downhill to lakes and rivers. Agriculture and urbanization have dramatically increased nutrient inputs

to aquatic systems, resulting in cultural eutrophication (Carpenter et al. 1998), and the terrestrial environment is a source of both dissolved and particulate matter for aquatic systems (Gasith and Hasler 1976, Dillon and Molot 1997).

Interest is growing in the inputs or subsidies of aquatic productivity to nearby terrestrial ecosystems (Schindler and Smits 2017) as part of a larger movement toward more integrated study of terrestrial and aquatic systems (Soininen et al. 2015). Emergence of aquatic insects is the most well-known example of the biologically mediated aquatic-to-terrestrial linkages (Nakano et al. 1999, Gratton and Vander Zanden 2009, Schindler and Smits 2017). Many aquatic insect taxa emerge from the water and move to adjacent terrestrial habitats to complete their life cycle (Merritt and Cummins 1996). As a result, adult stages of aquatic insects can serve as an organic matter and nutrient source for adjacent terrestrial ecosystems (Schindler and Smits 2017). They can also serve as important prey for consumers in terrestrial food webs and are of particular interest because of their high food quality and concentration of essential fatty acids (Martin-Creuzburg et al. 2017). Because aquatic insects may themselves be partially reliant on terrestrially derived organic matter, any sort of rigid distinction between allochthonous and autochthonous carbon sources is blurred (Scharnweber et al. 2014).

Notably, most studies examining inputs of aquatic insects to terrestrial systems have been conducted on streams (Nakano et al. 1999, Power et al. 2004, Baxter et al. 2005, Ballinger and Lake 2006) and comparatively few on lakes. Gratton and Vander Zanden (2009) compiled and used stream and lake aquatic insect emergence data from the literature to simulate how the flux of aquatic insect to land varies across a gradient of aquatic ecosystem size for both lakes and streams. The overall result was that, while per-unit-area insect emergence from aquatic systems tends to be lower for lakes than for streams, lakes also tend to have much larger surface areas than streams; in other words, the total flux of aquatic insects to land tends to be higher for the average lake compared to the average stream (Gratton and Vander Zanden 2009). This result highlights the important role of aquatic ecosystem geometry (in this case, the ratio of surface area to edge) in governing the magnitude of aquatic-to-terrestrial linkages and suggests the need for a better understanding of the importance of these linkages for lakes, given they have been rarely studied.

Lake Mývatn in northeastern Iceland was the subject of a series of intense observational and experimental studies focusing on aquatic-to-terrestrial linkages during the 1970s and 1990s, and we have been involved in research on this lake during the 2000s. Mývatn may be

the most extreme example of lake-to-terrestrial trophic linkages resulting from the sheer magnitude of the aquatic-to-terrestrial flux. Mývatn is a large (50 km²), shallow (4 m depth), highly productive subarctic lake. Around 80% of whole-lake primary productivity is benthic, with a notable contribution of the benthic diatom *Fragilaria*. The lake supports exceptionally high densities of midges (largely *Tanytarsus* and *Chironomus*), on the order of 100 000 individuals per m² (Lindegaard 1979, Lindegaard and Jonasson 1979). Midge populations in Mývatn undergo dramatic population fluctuations on a roughly 5–7 year cycle (Einarsson et al. 2002, Ives et al. 2008).

This body of research revealed that the flux of the lake's benthic productivity to land via midge emergence has had a profound and transformative impact on the structure and function of the nearby terrestrial ecosystems. Studies have demonstrated effects on soil nutrients, plant communities, terrestrial arthropods, and birds (Gardarsson and Einarsson 1997, Gratton et al. 2008, Hoekman et al. 2011, Dreyer et al. 2012, 2015, Hoekman et al. 2012). Dreyer et al. (2015) measured midge emergence from Mývatn and estimated fluxes to adjacent terrestrial systems using terrestrial infall traps. Insect deposition to the nearshore terrestrial habitat was estimated to be on the order of 100 kg ha⁻¹ per year. These input rates greatly exceeded background aerial nutrient input rates and highlight the role of lentic aquatic insects as a substantial source of nutrients to terrestrial systems. In addition, stable carbon isotopes revealed that many terrestrial arthropod taxa adjacent to Mývatn were highly reliant on aquatic (midge)-derived carbon (Gratton et al. 2008). Moreover, terrestrial predatory and detritivorous arthropod densities were elevated adjacent to high midge lakes (Dreyer et al. 2012). Consistent with this, experimental addition of midge carcasses adjacent to a non-midge lake increased arthropod abundances (Hoekman et al. 2011, Gratton et al. 2017), increased soil organic nitrogen, and strongly affected terrestrial plant community composition. Stable isotopes further revealed that experimental midge additions were rapidly incorporated into terrestrial food webs, with effects spanning multiple trophic levels (Hoekman et al. 2012).

The high magnitude of aquatic insect emergence makes Mývatn an exemplary system for studying the local impacts of lake–terrestrial linkages. Yet Mývatn is clearly an extreme example of this cross-habitat linkage. To consider aquatic-to-terrestrial inputs for less extreme situations and at regional spatial scales, Bartrons et al. (2013) combined GIS hydrological datasets and models estimating lake and stream insect production to estimate aquatic insect emergence from lakes and streams for the

entire state of Wisconsin. For this landscape, 79% of the region-wide aquatic insect emergence was estimated to be of lake origin, due largely to the greater surface area of lakes relative to streams. Lake-derived inputs to land were more spatially concentrated than stream inputs, while stream inputs covered a larger spatial extent. This study suggested the importance of lakes and large rivers as a driver of regional level aquatic-to-terrestrial inputs.

In summary, lake benthic productivity is exported to the terrestrial environment in the form of aquatic insect emergence (Gratton and Vander Zanden 2009, Dreyer et al. 2015, Schindler and Smits 2017). These inputs are of particular interest because of their high quality and nutritional value to terrestrial consumers (Martin-Creuzburg et al. 2017). As a result, their ecological importance is large relative to their magnitude. Depending on ecosystem geometry, insect productivity, and emergence rates, aquatic insect emergence can be an important prey source for a variety of terrestrial consumers, and in many cases can represent an important overall flux of nutrients to terrestrial systems, particularly where terrestrial primary productivity is low (e.g., high latitude, high altitude, deserts). Studies have found that aquatic inputs have important dynamic implications for food web interactions in the recipient terrestrial system in the form of a spatial food web subsidy (Polis et al. 1997, 2004, Baxter et al. 2005). More work and a stronger cross-ecosystem approach (Soininen et al. 2015) are needed to understand the magnitude and importance of aquatic-terrestrial linkages beyond the handful of well-studied lakes.

Synthesis and summary

We hope our collaboration over the last 20 years has contributed to the “reintegration” of the role of benthic production and food web pathways into a more holistic understanding of lakes (Vadeboncoeur et al. 2002, Soininen et al. 2015). We use the term reintegration because many of the ideas and findings are not at all new, but rather were described and recognized quite early in the history of limnology and ecology (Forbes 1887, Lindeman 1942). In this review, we provided evidence that benthic habitats are a surprisingly large contributor to whole-lake primary production; we quantified how the benthic contribution to whole-lake primary production varies across environmental gradients such as lake size, lake morphometry, and water clarity; and we showed that benthic primary and secondary production are an important energy source supporting higher trophic levels and plays a particularly important role in supporting fish production. The littoral zone supports a high

concentration and a disproportionate fraction of lake biodiversity, even in the world’s largest lakes dominated by planktonic habitats as a result of their low edge to volume ratio. And finally, benthic productivity plays a critical role in linking aquatic and terrestrial habitats through phenomena such as aquatic insect emergences, with implications for terrestrial plants, consumers, and ecosystems. An overarching conclusion of our synthesis is that nearshore littoral zones and their associated benthic production pathways are hotspots of productivity and species diversity within lakes. Moreover, the vast majority of lentic animal species live and feed on or around surfaces rather than in open water, and lentic species tend to be energetically dependent on benthic production pathways. Given that most of the world’s lakes are also small and shallow (Wetzel 2001, Downing et al. 2006), it is fair to say that benthic habitats and production pathways support the majority of lentic species diversity at the global scale.

Lakes as coupled ecosystems

While we aim to shed light upon the contribution of littoral-benthic production, food web pathways, and habitats to lake ecosystems, we also aim to dispel any preconception that benthic and planktonic food chains are isolated from each other. Lakes are complex ecosystems in which the dynamics of benthic and planktonic organisms and habitats are linked through resource competition, cross-habitat food web linkages, and nutrient cycling (Schindler and Scheuerell 2002). Thus, as primary production is transferred to primary consumers and on up the food chain, the boundaries between planktonic and benthic food chains are quickly obscured (Vander Zanden and Vadeboncoeur 2002). Here we mention just a few examples: phytoplankton and periphyton compete for light and nutrients; phytoplankton detritus or “fallout” is a resource for benthic primary consumers, particularly in the profundal zone; and filter-feeding invertebrates such as dreissenid mussels live in the benthos, consume planktonic seston, and excrete pseudo-feces and nutrients that enrich the benthos with an open-water resource. And finally, mobile consumers such as fishes tend to have broad diets and forage across benthic and planktonic habitats and food chains. In this way, fishes play a critical role in the energetic coupling of littoral and open-water zones and food chains (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002).

This concept of fishes as couplers of benthic and planktonic food chains may at first seem incongruous with classically described food chain dynamics. The classic lake food chain model is composed of phytoplankton,

zooplankton grazers, zooplanktivorous fishes, and piscivorous fishes (Carpenter et al. 1985, Persson et al. 1992, Carpenter and Kitchell 1993). Fishes exert strong top-down control in the planktonic food chain, with effects often cascading from piscivorous fishes all the way to phytoplankton in a classic illustration of the concept of trophic cascades (Carpenter et al. 1985, Terborgh and Estes 2010). A small body of literature has linked the stability of the planktonic trophic cascade itself to the existence of spatial food web subsidies from benthic trophic pathways (Schindler et al. 1996, Vanni 1996, Post et al. 2000, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2005, Vander Zanden et al. 2005). Piscivorous fishes show strong diet selectivity for their preferred prey, zooplanktivorous fishes. Piscivorous fishes readily consume zooplanktivorous fish when available but switch to alternative prey such as zoobenthos when zooplanktivorous fishes are not available or occur at low abundance (notably, the reason for low prey zooplanktivorous abundance may be predation by piscivorous fishes). In effect, consumption of zoobenthos bolsters and stabilizes the piscivorous fish population (Schindler and Scheuerell 2002, Vander Zanden et al. 2005). Piscivores suppress populations of zooplanktivorous fishes, and piscivorous fish populations remain high and prevent zooplanktivore populations from rebounding, specifically because piscivore populations are subsidized via consumption of alternate resources such as zoobenthos.

With increasing recognition in ecology of the ubiquity of trophic flows across habitat boundaries (Polis et al. 2004), numerous studies have examined what these more complex, lateral food web configurations mean for food web stability. Work with a well-described food web model (McCann et al. 1998) generally suggests that trophic complexity such as allochthonous inputs tends to stabilize food webs, especially in cases where consumer prey preference is for the autochthonous resource (Huxel and McCann 1998, Post et al. 2000). These types of consumer-resource models have been adapted specifically for exploring the dynamics of linked aquatic food chains. In lakes, studies demonstrate that higher trophic level fishes forage across benthic and planktonic food chains (Vander Zanden and Vadeboncoeur 2002). Several studies have assessed the implications of this habitat coupling for food web dynamics and stability. Vadeboncoeur et al. (2005) used a food web model to examine the strength and stability of top-down trophic control and found that the stabilizing effect of linked food chains was strongest when both pathways contributed substantially to production of higher trophic levels, resulting in strong and stable top-down control in the phytoplankton-based food chain. Post et al.

(2000) similarly found that predator-linked food chains generally dampened oscillations and imparted stability to food webs, and that prey preference determines the stabilizing effect of linked food chains. The above examples can be thought of as extensions of classical trophic cascade theory that include more complex and lateral food web configurations.

Changing paradigm of lake ecosystem function

Perhaps the major paradigm shift in limnology in recent decades has been expanding beyond the simple pelagic-centric worldview that derives from the historical influence of open-ocean oceanography in limnology (Reynolds 2008). For example, we now know that terrestrial carbon fuels lake metabolism in many lakes (del Giorgio and Peters 1994, Hanson et al. 2003), and that terrestrial carbon can play a role in supporting higher trophic levels, especially in small lakes (Pace et al. 2004). With regard to littoral habitats, we have a much fuller appreciation of the important contributions of benthic primary production to whole-lake primary production, and we recognize that these food web pathways can be surprisingly important in supporting higher trophic levels. These food web pathways are also the basis for cross-habitat linkages and have important dynamic implications for top-down control and stability of food webs (Post et al. 2000, McCann et al. 2005, Vadeboncoeur et al. 2005). These and other recent findings profoundly challenge the traditional pelagic-centric view of lake ecosystem function (Lodge et al. 1988, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Reynolds 2008).

Unfortunately, this paradigm shift has not greatly changed or transformed the way we study and manage lakes. Despite conceptual advances, it is fair to say that our monitoring programs and our limnology classes still trudge out to the “deep hole” sampling station for routine limnological sampling, although one promising development has been the inclusion of benthic and littoral sampling under the European Water Framework Directive (Birk et al. 2012). By sampling the deep hole, the unspoken intent is to minimize the effects of the littoral zone and nearshore processes in our data in an effort to detect a “pure” offshore signal. But in doing so, are we intentionally overlooking critically important aspects of the lake ecosystem? While littoral processes and ecological coupling among habitats are perhaps increasingly recognized, the field is still grappling with how to operationalize and incorporate this process into how we sample and study lakes. This problem is particularly vexing because littoral zones are complex and

highly heterogeneous, although our experience has been that they are not so complex and variable as to be unmanageable (Devlin et al. 2016). Moreover, with littoral zones serving as the nexus of interaction between humans and lakes, these nearshore and riparian habitats are often the first to be impacted by human activities such as lakeshore development, eutrophication, water level manipulation, habitat alteration, invasive species, and climate change (Jennings et al. 2003, Winfield 2004, Strayer and Findlay 2010). Our hope is that in the next 20 years the field of limnology experiences true integration of benthic production and littoral zone function into not only conceptual models of lakes, but also our understanding of anthropogenic impacts and management of our vital lake ecosystems.

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ORCID

M. Jake Vander Zanden  <http://orcid.org/0000-0002-8122-1416>

Yvonne Vadeboncoeur  <http://orcid.org/0000-0002-1026-5390>

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