

Fish Reliance on Littoral–Benthic Resources and the Distribution of Primary Production in Lakes

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ABSTRACT

Pelagic, littoral, and terrestrial resources can all play a role in supporting consumers in lakes. The role of benthic algal-derived food web pathways in lakes is perhaps the least understood because limnologists have historically focused on pelagic (open-water) production and processes. We compiled carbon stable isotope data from 546 fish populations (75 lakes), and used a two end-member mixing model to calculate littoral–benthic reliance for each fish species in each lake. Fish littoral–benthic reliance values were averaged by lake to assess overall fish species benthic reliance for each lake. Lake-specific mean littoral reliance (BR_L ; fish species not weighted according to production or biomass) averaged 57% and was independent of lake morphological and limnological attributes. For these same lakes, water column nutrients, light, and morphometry data were used to estimate whole-lake benthic algal and phytoplankton primary production. On average, benthic algae com-

prised 36% of whole-lake primary production ($BP_f = 0.36$). BP_f and BR_L were weakly correlated: BR_L tends to be high even in large/deep lakes in which benthic algae is a minor contributor to whole-lake primary production. The high littoral–benthic contribution to individual fish species appears to reflect the high concentration of fish species diversity in the littoral zone. Our work cannot be extrapolated to whole-lake fish production. However, the result is consistent with other work indicating that most fish species inhabit the littoral zone, whereas relatively few exclusively inhabit the pelagic. Our results suggest that it takes less primary production to support a single fish species in the littoral zone than is required to support a species in the pelagic.

Key words: benthic; periphyton; phytoplankton; trophic pathways; energy flow; primary production.

Received 7 March 2011; accepted 5 May 2011;
published online 28 May 2011

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-011-9454-6) contains supplementary material, which is available to authorized users.

Author Contributions: JVZ designed the study, performed the research, analyzed data, contributed new methods or models, and wrote the paper, YV performed the research, analyzed data, contributed new methods or models, and wrote the paper, SC performed the research and wrote the paper.

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INTRODUCTION

Ecosystems often have multiple carbon sources at their base. For example, higher trophic level production in small streams is supported by terrestrial carbon inputs and in-stream benthic algal (periphyton) production (Vannote and others 1980; Wallace and others 1997; Finlay 2001), lake food webs are supported by phytoplankton, benthic

algae, and terrestrial inputs (Vadeboncoeur and others 2002; Cole and others 2006), and terrestrial food webs are supported by both aboveground plant and soil/detrital carbon sources (Wardle and others 2004). Ecosystem geometry and physiochemical attributes can often determine the relative importance and availability of carbon sources (Gratton and others 2008). For example, forested streams tend to have little benthic algae production and are dominated by litterfall inputs, whereas grassland streams have lower rates of carbon input and higher rates of autochthonous production. In lakes, water chemistry, lake size, and morphometry are thought to set the relative contributions of benthic algae and phytoplankton to whole-lake primary production (Vadeboncoeur and others 2008).

Characterizing the contributions of carbon sources to species at higher trophic levels has proven to be difficult, in part due to the vast complexity of natural food webs. Lakes are useful study systems for linking carbon sources and higher trophic levels because they have clear boundaries and are amenable to ecosystem-scale studies (Carpenter and others 1995). The study of lakes has historically been dominated by the study of pelagic (phytoplankton-based) production and processes. A central tenet of modern limnology has been that nutrients limit the rate of pelagic primary production, and that this pelagic production is the basis for higher trophic levels in lakes (Vadeboncoeur and others 2002; Reynolds 2008). Yet recent work indicates that benthic algae can dominate whole-lake primary production in oligotrophic and shallow lakes (Vadeboncoeur and others 2003; Ask and others 2009a, b), and that littoral–benthic resources can play a surprisingly large role in supporting lacustrine fishes (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002; Karlsson and Bystrom 2005).

Though recent findings point to the potentially important role of littoral–benthic food webs pathways in lakes, individual studies have generally focused on a single lake or a small numbers of lakes within a confined geographic region. A sizeable number of individual studies have now accumulated, such that a comparative synthesis that includes a broad range of lake types would provide general insights into the relative importance of benthic primary production and food web pathways in lakes. Here, we present a synthesis of littoral–benthic contributions to lake food webs using two distinct measures of benthic ‘importance’ in lakes: one quantifies the reliance of fish species on benthic food webs, whereas the second estimates

the benthic algal contribution to whole-lake primary production. We use original and literature-derived carbon stable isotope data to quantify littoral contributions to fish body carbon for 546 lentic fish populations, originating from 75 separate lakes. For each study lake we also used the model of Vadeboncoeur and others (2008) to estimate the benthic algal contribution to whole-lake primary production, which is a measure of relative benthic resource *availability*. Our direct comparison of littoral–benthic contribution to fish body carbon and benthic algal contribution to whole-lake primary production for a large number of lakes reveals some notable differences in the role of littoral and pelagic food web pathways in lake ecosystems.

METHODS

Fish Reliance on Littoral–Benthic Resources

We conducted a literature search for lake food web studies that reported stable carbon isotope data, and supplemented this with published and unpublished data from our own research. Lake-specific data are presented in Appendix 1 (Supplementary material); variables and abbreviations are shown in Table 1.

It is widely established that the base of the littoral food web is enriched in ^{13}C relative to that of the pelagic and most terrestrial carbon sources (France 1995a; Hecky and Hesslein 1995; Post 2002; Vander Zanden and Vadeboncoeur 2002). This isotopic difference occurs because periphyton undergo incomplete isotopic fractionation during photosynthesis, as a result of boundary layer carbon depletion in benthic habitats (Hecky and Hesslein 1995). This isotopic separation provides the basis for use of simple linear mixing models to estimate the importance of littoral–benthic resources to fish populations (Post 2002; Vander Zanden and Vadeboncoeur 2002). For each fish species within each lake (hereafter referred to as fish population), littoral–benthic reliance (BR_S) was estimated as:

$$\text{BR}_S = \frac{(\delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{nl}})}{(\delta^{13}\text{C}_{\text{lit}} - \delta^{13}\text{C}_{\text{nl}})} \quad (1)$$

$\delta^{13}\text{C}_{\text{nl}}$ and $\delta^{13}\text{C}_{\text{lit}}$ are non-littoral–benthic (that is, pelagic + terrestrial) and littoral–benthic end-members, respectively. Note that BR_S values range from 0 to 1, and that $1 - \text{BR}_S$ represents non-littoral–benthic reliance. This model assumes no $\delta^{13}\text{C}$ trophic enrichment. Trophic fractionation for $\delta^{13}\text{C}$ sometimes deviates from 0.0‰, and synthesis studies have been mixed as to whether trophic

Table 1. Variables Included or Estimated in This Study

Variable	Description	Units/expressed as
Fish littoral–benthic reliance variables		
BR _S	Littoral–benthic contribution to fish body carbon, species-level	Fraction (0–1)
BR _L	Littoral–benthic contribution to fish body carbon, lake-level (mean of all species from a lake)	Fraction (0–1)
Primary production variables		
TPP _B	Whole-lake benthic primary production	mg C day ⁻¹
TPP _P	Whole-lake pelagic primary production	mg C day ⁻¹
BP _f	Benthic fraction of whole-lake primary production	Fraction (0–1)
Fish diversity variables		
N _B	Number of fish species supported by littoral–benthic resources	
N _P	Number of fish species supported by non-littoral–benthic resources	

fractionation differs significantly from 0.0‰ (Vander Zanden and Rasmussen 2001; Post 2002; McCutchan and others 2003). We also ran the mixing model to include a +0.4‰ per trophic level fractionation (Appendix 2 in Supplementary material).

Use of equation (1) requires determination of lake-specific littoral–benthic ($\delta^{13}\text{C}_{\text{lit}}$) and non-littoral–benthic ($\delta^{13}\text{C}_{\text{nl}}$) end-members. Though primary producers comprise the base of the food web, they exhibit high temporal variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Cabana and Rasmussen 1996). Primary consumers such as unionid mussels and snails are effective integrators of spatial and temporal isotopic variation at the base of pelagic and littoral food webs (Post 2002). For the pelagic end-member, we used the average $\delta^{13}\text{C}$ of all pelagic-feeding primary consumer taxa (zooplankton and unionid mussels). For the littoral end-member, many data sources reported $\delta^{13}\text{C}$ values for several littoral zoobenthic primary consumer taxa. They often spanned a range of $\delta^{13}\text{C}$ values, depending on the mix of periphyton (which is highly enriched in ^{13}C) and other more ^{13}C depleted sources such as macrophytes, phytoplankton detritus, and allochthonous material. Where multiple littoral zoobenthic taxa were reported, we used the most isotopically enriched taxa as the littoral–benthic end-member. In many lakes the most enriched taxa were gastropods, which are known to be periphyton grazers, and reliable indicators of the underlying periphyton isotopic value (Post 2002; Devlin 2011). Though it is possible that even the most isotopically enriched littoral zoobenthic taxa could still incorporate small contributions of allochthonous or pelagic-derived carbon, our approach offers the best possible approximation of a lake's overall littoral–benthic isotopic signal. In a handful of lakes, seston and periphyton were used as model end-members; these lakes are indicated in Appendix 1 (Supplementary material).

The mixing model (equation 1) generated some (less than 10%) BR_S values that were either greater than 1.0 or less than 0.0. These values were set to 1 or 0, respectively. For each lake, we calculated the mean of all BR_S (species-specific) values, which we denote as BR_L (lake-specific). BR_L reflects the degree to which fish species from a lake rely on littoral–benthic resources—note that fish species are not weighted according to their abundance or production.

Lakes were excluded from the analysis for the following reasons: (a) end-members could not be estimated, or differed by less than 5‰, thus precluding our ability to resolve littoral and non-littoral production sources (Vander Zanden and Rasmussen 2001), (b) fish sampling was focused on specific habitats, such that it would not characterize the overall lake fish community, (c) limnological variables used to estimate benthic algal contribution to whole-lake primary production were not presented in the primary study, and could not be obtained. Our final dataset consisted of 75 lakes located on 5 continents. The lakes ranged in size from 0.02 to greater than 82,000 km², and spanned a wide range of trophic conditions (Table 2).

Table 2. Summary (Median, Minimum, Maximum) of Basic Limnological Attributes for the 75 Lakes Included in This Study

Attribute	Median value (minimum, maximum)
Lake area (km ²)	2.1 (0.02–82,367)
Mean depth (m)	10.1 (0.6–740)
Max depth (m)	23.0 (1.3–1,637)
TP (µg l ⁻¹)	8.2 (2–241)
Chl a (µg l ⁻¹)	2.3 (0.3–44.1)
Secchi depth (m)	5.3 (0.4–24)

Benthic Algal Contribution to Whole-Lake Primary Production

We used the model of Vadeboncoeur and others (2008) to estimate total (whole-lake) primary production for benthic (TPP_B) and pelagic (TPP_P) habitats for each of the 75 lakes. This model is built upon established, empirical relationships between nutrients, light, morphometry, and primary production for benthic and pelagic habitats. The model is intended to characterize the algal contribution to whole-lake primary production, and does not explicitly include macrophytes, which can be important contributors to benthic primary production in some lakes. For this reason, the model provides a minimum estimate of benthic contribution to whole-lake primary production.

For each lake, we collected key morphological (lake area, mean depth, maximum depth) and limnological (mean annual secchi depth, total phosphorus, chlorophyll a, light attenuation coefficient, dissolved organic carbon) parameters. These values were taken from the original stable isotope data sources and other published and online sources (that is, world lakes database, <http://www.ilec.or.jp/database/database.html>).

As described in Vadeboncoeur and others (2008), the model used pelagic chlorophyll a data to estimate pelagic primary production. If chl a data were unavailable, total phosphorus was used to estimate chl a concentrations; $\text{chl a} = 0.41 * \text{TP}^{0.87}$, Prairie and others (1989). Pelagic primary production was summed over the depth of the photic zone (>1% incident light) to yield total pelagic primary production per square meter of lake surface area. Benthic algal primary production was calculated at discrete depth intervals, and area-specific benthic primary production was a function of light availability at depth. We set the maximum, light-saturated rate of primary production (BP_{max}) to 30 mg C m⁻² h⁻¹. This value is typical of benthic primary production in oligotrophic to moderately productive lakes. However, literature values range from 3 to 300 mg C m⁻² h⁻¹, so this parameterization can generate substantial variation in our estimates of the fractional contribution of benthic algae to whole-lake primary production, particularly in small lakes. The model generates a decline in primary production with depth as a result of declining light availability. Secchi depth measurements, and where available, light attenuation coefficients (k_d) were used to characterize light attenuation for individual lakes (Kalf 2002). Lake area, mean depth, and maximum depth were used to scale these relationships to the whole-lake level

(Vadeboncoeur and others 2008), thereby allowing estimation of the relative contribution of benthic algae to whole-lake primary production (BP_f) for each lake. Because of our simplifying assumptions (for example, BP_{max} constant for all lakes), our reported BP_f estimates should be viewed as an index of the benthic contribution to whole-lake primary production.

RESULTS

$\delta^{13}\text{C}$ values of individual fish populations and lake-specific littoral–benthic and non-littoral–benthic end-members ($\delta^{13}\text{C}_{\text{lit}}$ and $\delta^{13}\text{C}_{\text{nl}}$) are shown for each of the 75 study lakes (Figure 1). $\delta^{13}\text{C}_{\text{lit}}$ was consistently enriched relative to $\delta^{13}\text{C}_{\text{nl}}$ (mean values: -21.1‰ vs. -30.3‰). Fish $\delta^{13}\text{C}$ values generally fall between the two end-members, and often vary widely for a given lake (Figure 1). For each fish population, littoral–benthic reliance (BR_S) was calculated using equation (1). BR_S varied widely among the 546 fish populations—the overall mean BR_S was 0.50 (that is, average littoral–benthic reliance was 50% ± 0.28%, 1 SD, Figure 2A). Use of ‘lake’ as a categorical predictor explained 38% of the variation in BR_S (ANOVA; $P < 0.0001$, $F = 3.82$, $df = 82,507$).

Lake-specific mean fish littoral–benthic reliance (BR_L) was less variable than for individual fish populations. Mean BR_L was 0.57 ± 0.20 (1 SD, Figure 2B). There were no significant relationships between BR_L and any limnological, morphometric, or geographical variables examined (mean depth, maximum depth, lake area, TP, secchi, chl a, latitude).

On average, benthic algae constituted 36% of whole-lake primary production in our 75 study lakes (BP_f = 0.36 ± 0.24 , range 0.01–0.87, Figure 2C). There was a significant, but weak correlation between BP_f and BR_L (Pearson product-moment correlation coefficient = 0.29, $P = 0.013$; Figure 2), indicating that BR_L was not highly dependent on lakewide benthic resource availability. BR_L was higher than the benthic contribution to whole-lake primary production (BP_f) in 80% of lakes (60 of 75 lakes, Figure 3), and was significantly higher than BP_f overall (paired t test, $t = 6.56$, $P < 0.0001$, $df = 74$).

The uncoupling of BP_f and BR_L is partially driven by the results for large, deep lakes (note: mean depth and lake area are closely correlated in our dataset: $\log(\text{mean depth}) = 0.30 * \log(\text{area}) + 0.83$, $F = 108.2$, $P < 0.0001$, $r^2 = 0.59$). BR_L did not vary significantly as a function of mean depth (BR_L = $-0.05 * \log(\text{mean depth}) + 0.62$, $P = 0.17$,

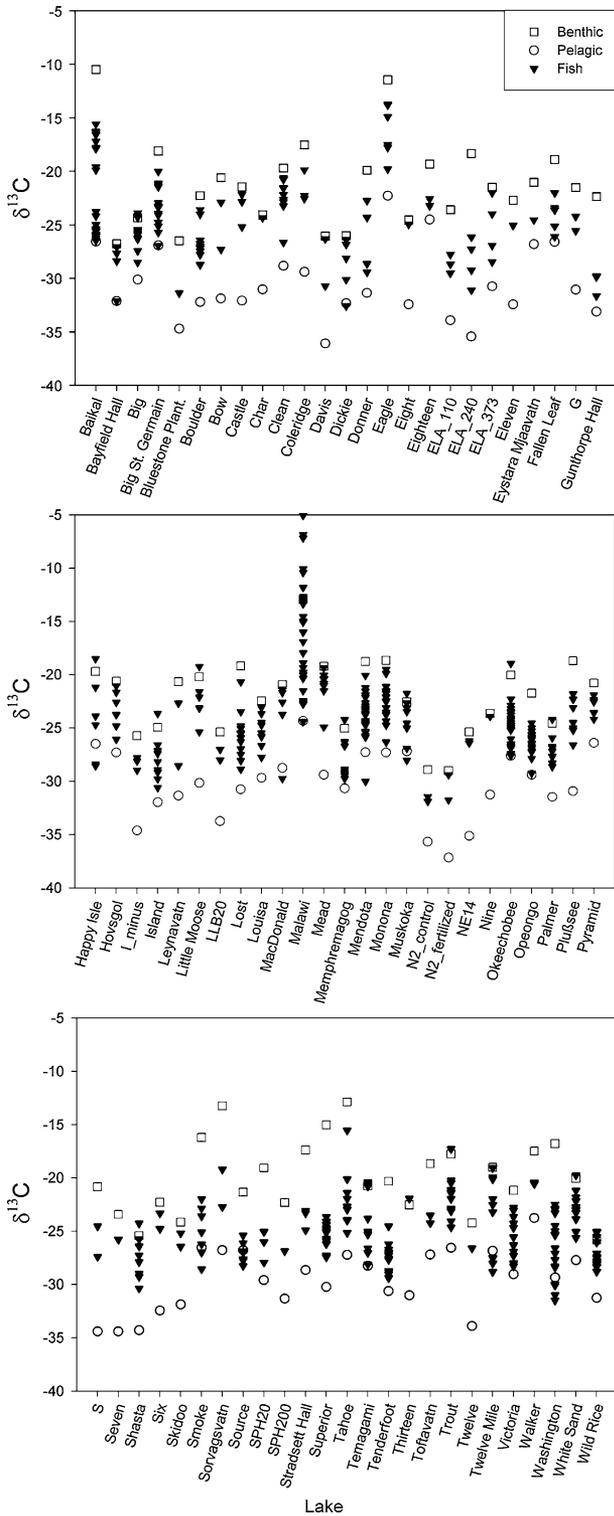


Figure 1. Carbon isotope data for each of the 75 lakes included in this study. *Symbols* are as follows: $\delta^{13}\text{C}$ of individual fish populations (*black triangles*), lake-specific littoral-benthic end-member ($\delta^{13}\text{C}_{\text{lit}}$, *open squares*), lake-specific non-littoral-benthic end-member ($\delta^{13}\text{C}_{\text{nl}}$, *open circles*).

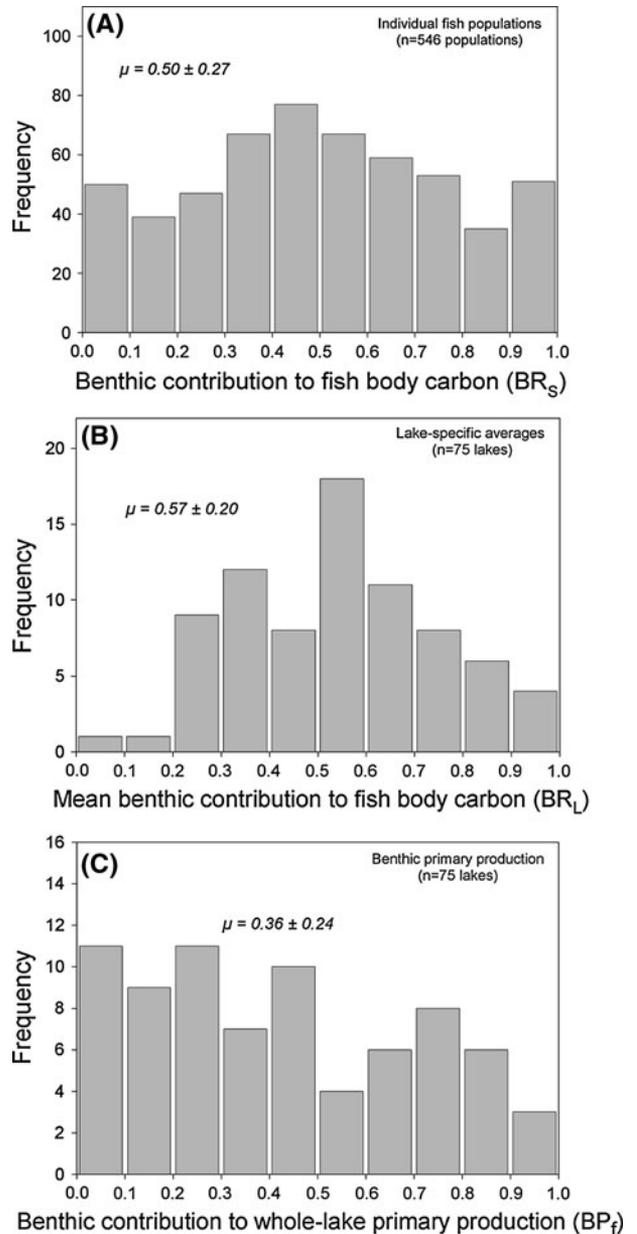


Figure 2. Frequency distributions of the benthic variables estimated in this study: **A** littoral-benthic reliance of individual fish populations (BR_{f}), **B** littoral-benthic reliance, lake-specific means (BR_{L}), **C** estimated benthic algal contribution to whole-lake primary production (BP_{f}).

$F = 1.89$, Figure 4A). BP_{f} tended to be high, though quite variable, in shallow lakes, and was consistently low in lakes deeper than 25 m. In lakes less than 25 m, BP_{f} is very sensitive to water clarity; BP_{f} in shallow lakes can vary between nearly 1.0 in clear lakes where the majority of lake surface area is littoral, to close to 0.0 in eutrophic lakes. In large, deep lakes water clarity is often optimal for benthic

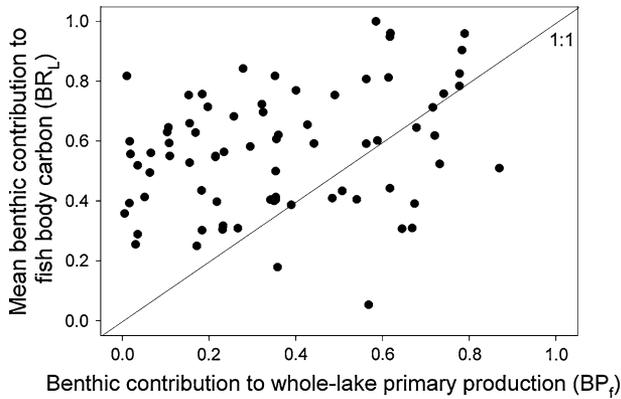


Figure 3. The relationship between benthic algal contribution to whole-lake primary production (BP_f) and the mean littoral–benthic contribution to fish (BR_L) for our 75 study lakes. BR_L is the mean of all individual fish species in a lake; species are not weighted according to biomass or production. 1:1 line is shown.

algae, but low littoral surface area relative to pelagic volume limits littoral–benthic contributions to whole-lake primary production. Overall, BP_f was negatively correlated with mean depth ($BP_f = -0.21 * \log(\text{mean depth}) + 0.57$, $P < 0.0001$, $F = 26.3$, Figure 4B). Overall, our results indicate that many more fish species are dependent on littoral–benthic trophic pathways compared to the pelagic. This is the case even in large deep lakes, in which benthic algae are a minor contributor to whole-lake primary production.

DISCUSSION

We evaluate and compare two distinct measures of benthic importance in lake ecosystems: (1) littoral–benthic reliance by fish, expressed as the mean of all fish species from a lake, BR_L , and (2) the contribution of benthic primary production to whole-lake primary production, BP_f . Among our 75 study lakes, BR_L and BP_f were weakly correlated (Figure 2). These two measures were uncoupled in large/deep lakes—specifically, benthic algae are a minor contributor to whole-lake primary production, yet littoral–benthic food web pathways still support many fish populations (Figure 3). Overall, the littoral–benthic contribution to fish populations, BR_L was significantly higher than benthic contribution to whole-lake primary production, BP_f .

One possible explanation for the greater representation of littoral–benthic resources to fish relative to primary production is that benthic primary production is more efficiently passed to higher trophic levels. The hypothesis that benthic trophic pathways have relatively higher ecological

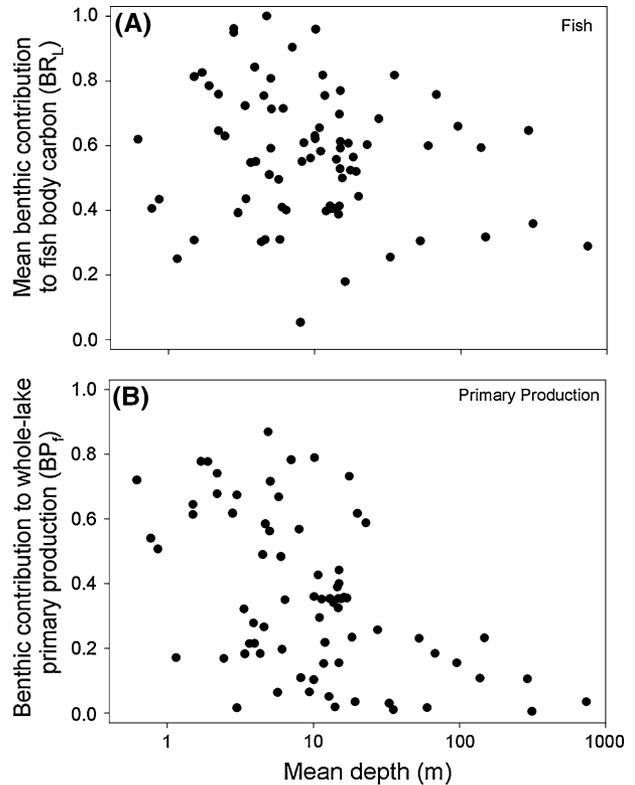


Figure 4. Relationship between benthic variables and lake mean depth for our 75 study lakes: **A** littoral–benthic contribution to fish body carbon (BR_L) and **B** benthic algal contribution to whole-lake primary production (BP_f).

efficiencies (defined as production at trophic level $_x$ /production at trophic level $_{x-1}$) was forwarded by Hecky and Hesslein (1995). The few studies that have explicitly considered this hypothesis tend to be supportive (Lindgaard 1994; Hecky and Hesslein 1995; Vander Zanden and others 2006). We cannot directly evaluate this explanation using the data included here because fish production is not known. Even where complete production data are available, comparisons of ecological efficiencies are difficult due to high uncertainty in production estimates.

A number of previous studies have concluded that benthic pathways are important to fish at the ecosystem level (Hecky and Hesslein 1995; Sierszen and others 2003; Vander Zanden and Vadeboncoeur 2002). Notably, these studies have not considered the possibility that benthic habitats simply support more fish species than pelagic habitats. As with these previous studies, our lakewide measure of fish littoral–benthic reliance, BR_L , is simply the mean of all individual fish species inhabiting a given lake; each fish species is weighted equally,

regardless of its abundance or contribution to whole-lake fish production. A measure of littoral–benthic reliance that weighted fish species according to their contribution to whole-lake fish production would provide a useful contrast with the unweighted measure, BR_L , used here and elsewhere. Unfortunately, data on fish production are not available for our study lakes, thereby precluding a direct comparison.

In light of the above issue of species weighting, it is interesting to further consider the role of benthic and pelagic habitats in supporting fish species diversity. The concept is somewhat analogous to niche partitioning—a resource (in this case, primary production in either pelagic or benthic habitat) may be finely or coarsely partitioned among consumer (fish) species. For example, consider a lake in which a large pelagic zone supported a relatively small number of highly abundant fish species, and a comparatively small littoral zone supported a large number of rare species. In such a case, benthic primary production is finely partitioned among fish species, whereas pelagic primary production is coarsely partitioned. In the absence of any species weighting, the above situation would produce the results reported in this study—that the littoral–benthic contribution to fish would be higher than the benthic algal contribution to whole-lake primary production.

Our data can be used to quantify fish species partitioning of benthic and pelagic resources. We have estimates of total daily benthic and total pelagic primary production for each lake (TPP_B and TPP_P , mg C day^{-1} , values were used to calculate BP_f), and we can estimate how many fish species are supported by each unit of benthic and pelagic primary production. Using these data, we can estimate the amount of primary production per fish species (separately for pelagic and benthic primary production) for each lake (mg C species^{-1}). Each individual fish species was partitioned into benthic (BR_S) and pelagic ($PR_S = 1 - BR_S$) fractions based on the isotope mixing model outputs. Because we do not have information on terrestrial carbon inputs, we assume non-benthic reliance to be completely pelagic in origin. N_B (the number of fish species supported by benthic sources) is the sum of BR_S values. N_P (the number of fish species supported by pelagic sources) is the sum of PR_S values, or $n - \sum BR_S$ where n = total fish species richness. Finally, for each lake, the amount of primary production per fish species was estimated for each pathway: TPP_B/N_B (benthic) and TPP_P/N_P (pelagic).

The amount of primary production per fish species was, on average, three times lower for benthic

production compared to pelagic production (paired t test, $t = -4.98$, $P < 0.0001$, $df = 72$). In other words, a unit of benthic primary production supports a greater number of fish species compared to a unit of pelagic primary production. The contrast is particularly strong in large/deep lakes, in which BP_f is small, but BR_L is high (Figure 3). Conversely, the available pelagic primary production is partitioned among fewer fish species, hence individual pelagic fish species tend to be more productive at the lake-level.

The above calculations indicate that benthic production pathways, on a per unit primary production basis, support greater fish species diversity compared to pelagic production. Is this result consistent with previous studies? Notably, no studies have examined how productivity in benthic and pelagic lake habitats relates to diversity of higher consumers. Surprisingly few studies have explicitly compared species diversity among benthic and pelagic habitats in lakes. The few studies that have addressed this indicate greater fish and invertebrate diversity in the littoral zone (Likens 1985; Alimov 2001; Karatayev and others 2005; Tolonen and others 2005). Vadeboncoeur and others (in press) found that approximately 90% of fish and invertebrate species in the world's large lakes inhabited littoral or profundal habitats to some extent, and that only a small fraction of fish and invertebrate species were exclusively pelagic, even though these large lakes are dominated by pelagic production. The situation is analogous to that of marine ecosystems, where nearshore habitats support a disproportionate fraction of fish and invertebrate species diversity (Sale 1977; Roberts and others 2002). The underlying explanations for species diversity differences among diverse marine habitats are poorly understood. Recent empirical studies have identified habitat complexity as a predictor of fish species diversity at local and regional scales (Gratwicke and Speight 2005a, b).

Methodological Considerations

Our goal was to broadly assess littoral–benthic contributions to lake food webs. Including a large number of lakes spanning the broadest possible range of conditions maximizes contrasts, and permits broad generalization about lake ecosystems. On the other hand, use of literature-derived stable isotope data also introduces a potential source of variability. Among studies, there was a range of sampling intensity and duration. Many studies may not have included all of the fish species present, particularly because lakes often contain fish species

that are rare or difficult to catch. With this in mind, we only included primary studies that attempted to sample the whole fish community (that is, targeting multiple habitats and sampling methods). Because not all fish species were collected in all lakes, there is a possibility of bias if fish from either benthic or pelagic habitats were targeted or were more effectively sampled. Incomplete sampling of the fish community also affects estimates of the role of benthic and pelagic production in supporting fish species diversity. For example, if only 50% of the fish species from a lake were sampled, primary production/fish species would be overestimated by a factor of 2. For this reason, we considered only the relative differences between benthic and pelagic pathways, rather than the absolute magnitude of primary production/fish species.

Our estimates of BP_f involve several assumptions, and are meant to serve as an index of benthic algal contribution to whole-lake primary production. First, the model does not explicitly include macrophytes, hence our focus on ‘algal’ contributions. Macrophytes can be an important contributor to whole-lake primary production in some lakes, and our estimates are thus conservative estimates of overall (algal and non-algal) benthic primary production. In addition, we assumed maximum (that is, light-saturated) benthic primary production (BP_{max}) to be $30 \text{ mg C m}^{-2} \text{ h}^{-1}$ for all lakes. This is a typical value for lake periphyton from the literature, though actual estimates range from 3 to greater than $300 \text{ mg C m}^{-2} \text{ h}^{-1}$, depending on substrate and lake type (Vadeboncoeur and others 2008). The sensitivity of BP_f to changes in BP_{max} was explored in detail in Vadeboncoeur and others (2008; Figure 4). Fortunately, lakes included in our analysis span more than six orders of magnitude in lake area. At this level, lake area and morphometry are the dominant factors in determining benthic and pelagic contributions to whole-lake primary production (Vadeboncoeur and others 2008). In addition, we recently compared whole littoral zone primary production estimates derived from highly resolved periphyton production measurements in five north-temperate lakes with estimates generated by the model as parameterized here. Whole littoral zone production generated by the model varied from the more spatially explicit estimates by up to 10% (Devlin 2011). Though we note that BP_f are estimates, we feel confident that our model provides reasonable approximations of benthic and pelagic algal contributions to whole-lake primary production at this broad spatial scale.

Our methods are not intended to detect allochthonous (terrestrial) carbon inputs to lakes. A

growing body of work indicates that terrestrial-derived carbon can be incorporated into metazoan food webs in a wide range of aquatic ecosystems (Zeug and Winemiller 2008; Caraco and others 2010; Cole and others 2011). Terrestrial and pelagic carbon sources tend to show a high degree of overlap in $\delta^{13}\text{C}$, often centered around -28‰ (Pace and others 2004). As a result, we are not able to differentiate between terrestrial and pelagic carbon. Instead, pelagic and terrestrial carbon sources were simply lumped as ‘non-benthic’ in our measure of fish resource use. This isotopic overlap between terrestrial and pelagic carbon was the rationale for recent whole-lake ^{13}C addition experiments aimed at resolving the relative contributions of allochthonous and autochthonous carbon sources (Pace and others 2004; Cole and others 2006).

For isotopic end-members, we used the most ^{13}C -enriched and the mean $\delta^{13}\text{C}$ values of benthic and pelagic primary consumers, respectively. Use of primary consumers as indicators of littoral–benthic and pelagic isotopic signals is a widely advocated and well established approach (Cabana and Rasmussen 1996; Vander Zanden and Rasmussen 1999; Post 2002). Periphyton are consistently enriched in $\delta^{13}\text{C}$ relative to phytoplankton (France 1995b; Hecky and Hesslein 1995), which provides the basis for assessing fish littoral–benthic reliance using $\delta^{13}\text{C}$. Primary producers exhibit a high degree of temporal and taxon-specific variability (Vuorio and others 2006; Cabana and Rasmussen 1996), and many food web studies did not report primary producer $\delta^{13}\text{C}$ values, or lack temporal sampling that would allow estimation of a temporally averaged primary producer $\delta^{13}\text{C}$. In contrast, primary consumers are widely reported in food web studies, and are less temporally variable compared to primary producers (Cabana and Rasmussen 1996). Primary consumers, particularly snails and unionids, reflect the average isotopic values of periphyton and phytoplankton, respectively (Post 2002; Devlin 2011). Nevertheless, even the most isotopically enriched littoral primary consumers still could have consumed resources other than periphyton, such as phytoplankton detritus, allochthonous matter, and macrophytes. This would make littoral primary consumers more isotopically negative (depleted) than the underlying periphyton signal. To the extent to which this occurs, our estimate of littoral–benthic reliance would tend to over-estimate benthic algal contribution to fish. Fortunately, the difference between littoral–benthic and pelagic $\delta^{13}\text{C}$ end-members tends to be large; on average the difference is 9.2‰ (-21.1‰ vs. -30.3‰). Our end-member isotopic values are

typical for periphyton and phytoplankton found in most lakes (France 1995a; Post 2002). Nevertheless, we note that our measure of littoral–benthic reliance could reflect some allochthonous and pelagic detrital carbon. Our measure of littoral–benthic reliance is a direct measure of consumption of littoral–benthic invertebrates, and is an index of periphyton reliance. These methodological issues noted here highlight some of the challenges of natural abundance stable isotope studies.

Our findings emphasize the need to focus more explicitly on benthic and littoral zones, not only as habitat for aquatic organisms, but as a potential contributor to the productivity and species diversity of higher trophic levels. The role of different primary production sources in supporting species at higher trophic levels, and how this varies along key gradients such as lake size, has not been previously assessed. An important strength of our analysis is that it includes a large number of lakes from around the world, spanning a wide range of lake types and sizes. Additional insights will arise from more detailed analyses that include direct estimates of production at multiple trophic levels.

Littoral habitats, the source of benthic primary production, are located near the land–water interface, and are particularly susceptible to anthropogenic impacts such as nutrient loading, invasive species, and direct habitat modification (Rosenberger and others 2008; Strayer and Findlay 2010). In particular, lake eutrophication and zebra mussel invasion have the potential to dramatically shift the distribution of autochthonous primary production between benthic and pelagic habitats (Vadeboncoeur and others 2003; Hecky and others 2004). Not only might such changes affect the fundamental structuring of the ecosystem (that is, the distribution of primary production among lake habitats), but may also have unexpected implications for fish communities and diversity.

All lakes contain both benthic and pelagic habitats. Though closely juxtaposed in space, and tightly coupled in many ways (Schindler and Scheuerell 2002), the two habitats are also profoundly different. Benthic and pelagic habitats are likely to require very different adaptations and life-history strategies for the species that inhabit them, and our findings may derive from there being a greater number of fish species inhabiting littoral habitats. The greater complexity and heterogeneity of littoral habitats may result in greater fish species richness, with the result being a finer partitioning of littoral production among fish species. Our results suggest that benthic production pathways play a disproportionately important role in supporting

fish species diversity, though not necessarily overall fish production, in lakes. Interestingly, this is the case even in large lakes, in which littoral habitats comprise a small fraction of total habitat area, and are a minor contributor to whole-lake primary production.

ACKNOWLEDGMENTS

Thanks to Kira Langree, Scott Higgins, Chris Solomon, Claudio Gratton and Eric Moody for comments and assistance with the manuscript. This work was funded by the U.S. National Science Foundation (DEB-0449076 to M. J. Vander Zanden and DEB-0448682 to Y. Vadeboncoeur). Special thanks are extended to the GRIL group at Université du Québec à Montréal for providing sabbatical leave support to JVZ.

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