

Shoring up the foundations of production to respiration ratios in lakes

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Abstract

The ratio of primary production to ecosystem respiration rates (P:R ratio) is an ostensibly simple calculation that is used to characterize lake function, including trophic status, the incorporation of terrestrial organic carbon into lacustrine food webs, and the direction of carbon dioxide (CO₂) flux between a lake and the atmosphere. However, many predictive links between P:R ratios and lake ecosystem function stem from a historically plankton-centric perspective and the common use of the diel oxygen curve approach. We review the evolution of the use of P:R ratios and examine common assumptions underlying their application to (1) eutrophication, (2) carbon flux through lake food webs, and (3) the role of lakes in the global carbon budget. Foundational P:R studies have been complicated principally by the following: most P:R ratios were calculated from mid-lake measurements and failed to incorporate nonplanktonic dynamics; there has been confusion regarding the food web implications when $P:R \neq 1$; and CO₂ fluxes between lakes and the atmosphere are influenced by nonmetabolic processes. We argue for a re-assessment, or shoring up, of several fundamental assumptions that continue to guide metabolism research in lakes by accounting for mixing, benthic-littoral processes, groundwater fluxes, and abiotic controls on gas dynamics to better understand lake food webs and accurately integrate lake ecosystems into landscape-scale carbon cycling models.

Introduction

The recognition that inland waters are significant players in the global carbon cycle despite their relatively small footprint on the terrestrial landscape (Cole et al. 2007; Tranvik et al. 2009; Raymond et al. 2013; Drake et al. 2017) has increased the focus on carbon cycling in and through lakes. Primary production-to-respiration (P:R) ratios have become a common tool in the effort to define global patterns of carbon flux among terrestrial, aquatic, and atmospheric pools. One of the most widely used and direct methods of calculating P:R ratios in lakes is by comparing water column oxygen concentration dynamics during the day with those at night (here referred to as the diel oxygen technique; Staehr et al. 2010a, 2012b; McNair et al. 2013). After correcting for atmospheric gas exchange, the rates of change in dissolved oxygen concentration (O₂) measured during the daytime (net ecosystem production, NEP) and during the nighttime (ecosystem respiration, R), are used to calculate whole ecosystem gross primary production ($GPP = NEP + R$). GPP is the sum of all aquatic photosynthesis by cyanobacteria, algae, and plants (primary producers), while R includes the autotrophic and heterotrophic respiration of all aquatic organisms in the system. Researchers measure oxygen concentrations on a daily cycle

to assess whether a given body of water is net heterotrophic (oxygen consumption exceeds oxygen evolution through photosynthesis, $R > P$, where P is an established abbreviation of GPP) or autotrophic (oxygen production exceeds oxygen consumption, $R < P$). In a heterotrophic ecosystem, NEP is negative and P:R varies between 0 and 1, while an autotrophic ecosystem is characterized by a positive NEP and $P:R > 1$. Although macrophytes can make substantial contributions in some lakes, benthic and planktonic algae usually dominate GPP (Wetzel 2001) and bacterial and algal respiration dominates R (Wetzel 2001; Andersson and Kumblad 2006; Dodds and Cole 2007; Brothers et al. 2013a). These broad terms, when applied to entire lakes, are widely used to infer whether phytoplankton or bacteria dominate material flows at the base of the food web (Cole et al. 2000; Staehr et al. 2012a; Alfonso et al. 2018).

P:R ratios are used as indices of lake trophic status because production measured mid-lake is likely low in lakes with low phytoplankton biomass and increases with increased nutrient loading to the water column (eutrophication, e.g., Schindler et al. 1997). Because lakes are embedded in terrestrial landscapes, terrestrial organic carbon (OC) loading from the watershed fuels bacterial respiration, making $P:R < 1$ common (del Giorgio and Peters 1994; del Giorgio et al. 1999). Consequently, P:R ratios are used to infer the importance of planktonic primary production (autochthonous production) relative

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to the importance of allochthonous, or terrestrial, OC to higher trophic levels of lacustrine food webs (Cole et al. 2000). Finally, P:R ratios are used to infer the fate of carbon in lakes, including the direction of carbon dioxide (CO₂) exchange between a lake surface and the atmosphere (e.g., Urabe et al. 2005; Urban et al. 2005). Insights into lake ecosystem function have been advanced by the increasing ease of continuously monitoring ecosystem P:R using instrumented buoys. However, the empirical support that has influenced progress in this field of research comes overwhelmingly from data collected from a single monitoring station over the deepest part of the lake during the ice-free season (Staehr et al. 2010a), with the assumption that this approach integrates littoral and off-shore planktonic processes (Cole et al. 2000; Staehr et al. 2012a). We review the role of the open water metabolism technique in this field of work and its contribution to several assumptions underlying the common interpretations of P:R ratios in lakes. We encourage a more inclusive, emergent perspective that accommodates spatial and temporal variation in metabolic, chemical, and physical processes that affect oxygen and carbon dynamics at the whole-lake scale. This perspective stems largely from recent P:R approaches that are both spatially extensive (spanning multiple habitats) and explicit (built on an improved understanding of habitat function and distribution). By improving spatial (littoral, benthic, and groundwater compartments) and temporal coverage (e.g., incorporating under-ice winter dynamics; Hampton et al. 2017), as well as accounting for the physical processes affecting dissolved O₂ dynamics (including gas exchange, stratification, mixing, and advection), studies can more accurately estimate whole-lake metabolism. Clarifying the assumptions underlying metabolism monitoring will refine our understanding of eutrophication, the role of allochthony in food webs, and carbon cycling in lakes.

How well do diel O₂ curves capture whole-lake metabolism?

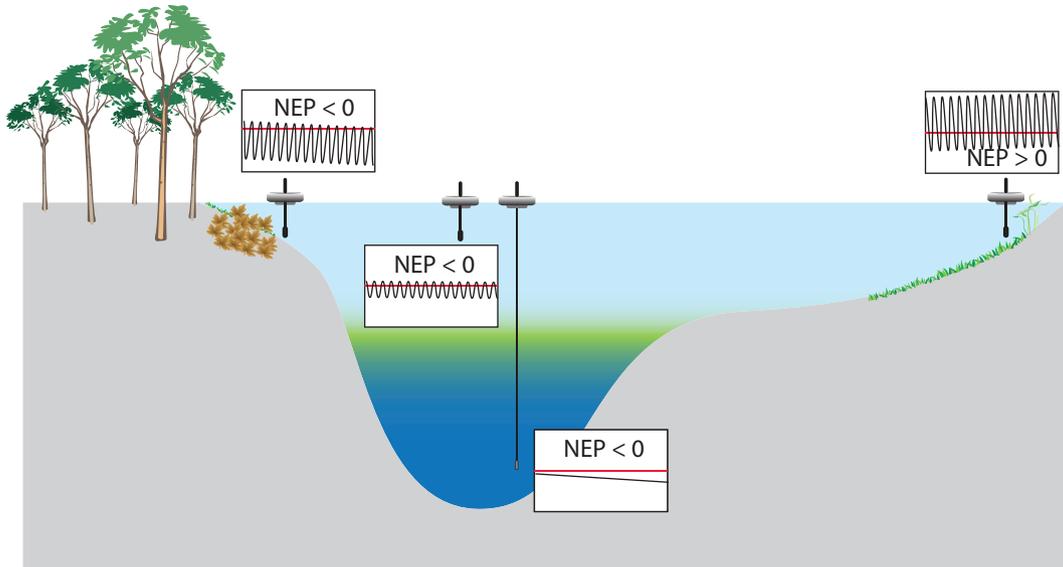
When interpreting P:R ratios, it is necessary to understand and account for the inherent uncertainties associated with adopted methodologies. Uncertainties associated with the widely used diel oxygen technique in lakes have long been recognized (Staehr et al. 2010a). The conclusions of studies that have used this technique, many derived from single off-shore deployments (e.g., Cole et al. 2000; Staehr et al. 2010a; Brentrup et al. 2020) are intertwined with our understanding of the significance of patterns in P:R ratios, and thus whole-lake carbon cycling dynamics. We revisit some of these methodological uncertainties, including the relationship between oxygen and carbon dynamics and the complicating effects of in-lake heterogeneity. We provide guidance on how methodologies may be improved in future studies of P:R ratios in lakes.

Oxygen dynamics are often used as a proxy for carbon dynamics (as discussed by Vachon et al. 2020), but the relationship between these variables is loose. There is a 1:1 M

relationship between O₂ produced and CO₂ assimilated (photosynthetic quotient, PQ = 1) when a carbohydrate is produced and between CO₂ produced per mole of O₂ consumed (respiratory quotient, RQ = 1) when a carbohydrate is respired. In practice, PQ and RQ often diverge from 1 because these quotients are linked to the elemental composition of respired or produced compounds, which are not limited to carbohydrates (Vachon et al. 2020). For instance, one study of 52 lakes in Quebec, Canada identified mean bacterioplankton RQ values of 0.81 in net autotrophic (P:R > 1) lakes vs. 1.35 in net heterotrophic (P:R < 1) lakes (Berggren et al. 2012). Errors are propagated by estimating carbon dynamics using dissolved O₂ measurements, especially in lakes where the saturation of O₂ and CO₂ may be poorly coupled (Laas et al. 2016; Peeters et al. 2016). For instance, in highly alkaline lakes (i.e., >1 meq L⁻¹) calcite precipitation can surpass aquatic metabolism as a dominant driver of lake carbon dynamics (Laas et al. 2016; Khan et al. 2020). This problem is resolved by simultaneously measuring O₂ and CO₂ in lakes (Laas et al. 2016; Vachon et al. 2020).

Mid-lake measurements of dissolved gases cannot be assumed to provide whole-lake metabolism information because vertical and horizontal heterogeneity of metabolism rates in lakes can be high (Fig. 1(a), (b)), while mixing rates can be low or difficult to predict. As photosynthetic rates are driven by light, it is unsurprising that deployment depth has a greater influence on estimates of GPP than it does on R (Coloso et al. 2008; Sadro et al. 2011a; Obrador et al. 2014; Giling et al. 2017). This decoupling of GPP and R with depth means that among-lake comparisons of P:R ratios based on single mid-lake oxygen probes must be made with informed care. Even when multiple probes are deployed at a single depth, there is substantial variation in metabolism (Fig. 1; Lauster et al. 2006; Van de Bogert et al. 2007, 2012). Comparisons of diel O₂ curves measured concurrently in littoral and offshore habitats have found consistent differences in GPP and R among probes deployed at different coordinates on the lake (Lauster et al. 2006; Van de Bogert et al. 2012; Tonetta et al. 2016). Primary production and respiration rates are often higher in littoral habitats compared to the off-shore zones where measurements are typically made (Buesing and Gessner 2006; Lauster et al. 2006; Cavalcanti et al. 2016). Mid-lake measurements can introduce unseen bias because each lake zone can have its own distinct metabolic balance. For instance, benthic and littoral zones may be net autotrophic, but off-shore water columns net heterotrophic (Coveney and Wetzel 1995; Andersson and Kumblad 2006; Vesterinen et al. 2016). “Smoothing” functions may be useful for reducing the high variability (“noisiness”) in metabolism datasets (Batt and Carpenter 2012; Cremona et al. 2014). They do not, however, correct for systematic errors in metabolism rates that may arise from strong habitat gradients in NEP coupled with complex or recurrent physical mixing processes. By failing to account for convective mixing or other physical transport

a. Oligotrophic lake



b. Eutrophic lake

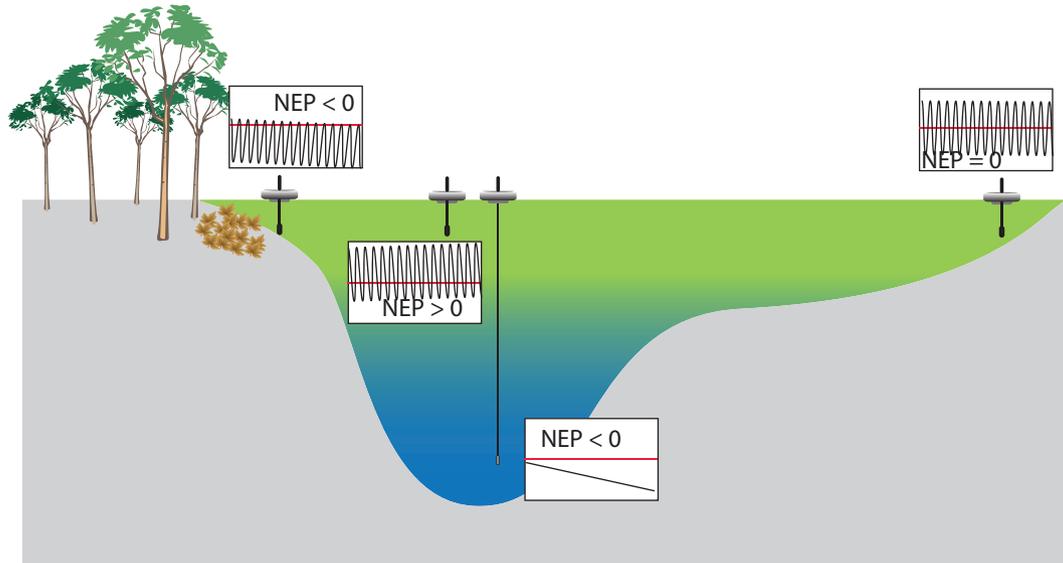


Fig 1. Simplified lake illustrations demonstrating how diel O_2 curves measured in (a) oligotrophic and (b) eutrophic lakes may theoretically differ, depending on sonde placement within each lake. The graphs depict simplified O_2 curves over 15 d. The red lines indicate O_2 saturation at atmospheric equilibrium. Terrestrial OC loads can drive localized near-shore net heterotrophy ($NEP < 0$, $P:R < 1$) and under-saturation of O_2 relative to the atmosphere in either system (left-hand nearshore sondes). High phytoplankton GPP associated with eutrophic conditions can produce net autotrophic conditions and greater diel O_2 fluctuations in the epilimnion, while fueling more rapid hypolimnetic O_2 consumption during stratified periods. Sondes placed in shallow littoral zones (right-hand nearshore sondes) may better capture the oxygen dynamics of periphyton and submerged macrophytes, potentially resulting in higher NEP and net autotrophy ($P:R > 1$) compared to mid-lake measurements. However, in these shallow zones, the positive effect of phytoplankton in the water column on NEP (associated with eutrophication) may be outweighed by the loss of benthic-littoral GPP due to shading, resulting in a slightly diminished NEP (in this case, $NEP = 0$, $P:R = 1$).

processes within a water column, NEP can be either over-estimated (i.e., when NEP is greater in the offshore environment; Antenucci et al. 2013) or underestimated (i.e., when

NEP is greater in the littoral environment; Brothers et al. 2017a). Such heterogeneous O_2 dynamics have highlighted the limitation of using near-surface mid-lake diel

O₂ measurements to accurately describe whole-ecosystem metabolism. Beyond generating a more robust estimate of P:R, consistently incorporating habitat-specific variability and lake mixing dynamics when monitoring lake metabolism will greatly advance our understanding of changes in lake function across trophic, morphometric, and climatic gradients.

Even with multiple sonde deployments spanning lake habitats and depths, it is possible that the diel oxygen technique provides an incomplete picture of lake metabolism. Sediment and hypolimnetic respiration rates are often important drivers of CO₂ and O₂ dynamics in lakes and reservoirs (den Heyer and Kalff 1998; Brothers et al. 2012; Schwefel et al. 2018), but sondes deployed in shallow littoral waters within the photic zone may not fully or reliably capture benthic O₂ dynamics because oxygen gradients are extremely steep (1–2 mm) in periphyton communities located at the sediment–water interface, even under experimentally stirred conditions (Carlton and Wetzel 1987). It is difficult to deploy a sonde within millimeters of a lake’s sediment–water interface in the nearshore zone because factors such as wave action or surge will disrupt its orientation. Deployed sondes may also fail to capture benthic O₂ dynamics due to stratification. Even shallow (<0.6 m mean depth) lakes and ponds can undergo transient daytime stratification (Andersen et al. 2017; MacIntyre et al. 2018), and this effect may be exacerbated by the presence of submerged macrophytes (Madsen et al. 2001).

To address the uncertainties associated with the diel oxygen technique, P:R studies increasingly incorporate multiple parallel methods to assess aquatic metabolism in lakes. Additional aquatic metabolism methods can include the use of oxygen isotopes, compartmental approaches (i.e., habitat-specific approaches that integrate independent quantifications of different primary producer functional groups), chamber incubation experiments (Staehr et al. 2012c), and/or pairing metabolic data with primary production models (Kazanjian et al. 2018; Perga et al. 2018). Pairing multiple diel O₂ curves with sediment incubation experiments (Sadro et al. 2011b) offers a more robust characterization of a lake’s P:R ratio than a single lake-center sonde. Meanwhile, accounting for physical processes such as stratification and mixing dynamics (Antenucci et al. 2013; Brothers et al. 2017a; Andersen et al. 2017b), as well as potential uncertainties in surface gas exchange rates, which may be especially high in small, sheltered ponds (e.g., MacIntyre et al. 2020), allows researchers to better calculate and interpret resulting metabolic data. Such integrated approaches are a welcome and necessary development in the field of aquatic metabolism, and have led to many of the research advances discussed below, allowing us to reassess the meaning and implications of P:R ratios in lakes.

What information do P:R ratios provide about eutrophication?

Cultural eutrophication is a global phenomenon with significant economic and ecological implications, making it a

foremost contemporary water quality issue (Wurtsbaugh et al. 2019). The relationship between nutrients and photo-synthetic production has led to a widely accepted link between metabolic P:R ratios and lake trophic status (e.g., Richardson et al. 2017), allowing us to better understand the effects of eutrophication on aquatic ecosystem function. We define eutrophication as the process whereby nutrient loading increases water column nutrient concentrations, and consequently phytoplankton production (e.g., Wurtsbaugh et al. 2019). Conversely, the term oligotrophic describes lakes with low nutrient concentrations and clear waters due to low phytoplankton productivity. Nutrient-poor (oligotrophic) lakes often have P:R ratios below one (i.e., net heterotrophy) due to low phytoplankton production (del Giorgio et al. 1999; Urban et al. 2005), while eutrophication is expected to increase P:R ratios by promoting phytoplankton production (Dodds and Cole 2007). Within this framework, nutrients (typically phosphorus and/or nitrogen) are the dominant driver of primary production, and thus autochthonous OC supply. Eutrophication increases the value of P in a P:R ratio measured mid-lake because phytoplankton photosynthesis responds positively to increased nutrient availability. In the absence of a change in terrestrial OC loading, eutrophication can increase the P:R ratio of a lake (Fig. 1(b)), often shifting it from net heterotrophic to autotrophic (Schindler et al. 1997; Balmer and Downing 2011). However, as discussed below, this apparently simple relationship becomes more complicated when accounting for multiple primary producer groups, as well as the spatial and temporal dynamics of eutrophication on P:R ratios (i.e., net heterotrophy vs. autotrophy) in lakes.

Many studies continue to view eutrophication through a lens of phytoplankton production alone, despite calls to broaden the concept of lake trophic status to include heterotrophic processes and terrestrial inputs (Dodds and Cole 2007) or to consider a broader range of autotrophs (Canfield et al. 1983). Nutrient enrichment stimulates phytoplankton productivity (reviewed by Elser et al. 1990), but the effects of enrichment on whole-lake primary production across broad trophic gradients is less certain. Benthic primary production can represent a major source of autochthonous OC for fish (Vander Zanden et al. 2011), but benthic primary production often decreases with nutrient enrichment of the surface water (Vadeboncoeur et al. 2003, 2008). Therefore, it is necessary to re-evaluate the phytoplankton-centric conceptual link between eutrophication and net autotrophy (P:R > 1). Studies measuring the response of P:R ratios to nutrient enrichment using off-shore water column measurements are biased towards describing the response of phytoplankton production, and may thus predictably report an increase in P:R with eutrophication. By excluding the littoral zone, compensatory decreases in light-limited benthic primary production associated with increasing phytoplankton biomass (Vadeboncoeur et al. 2003, 2008; Genkai-Kato et al. 2012) are not accounted for. Whole-lake primary productivity may decline with

nutrient enrichment across certain gradients of water clarity and lake morphometry (Blindow et al. 2006; Hagerthey et al. 2010; Brothers et al. 2013b), but declines in benthic GPP are not fully captured by free-water diel O_2 curves (Brothers et al. 2013b). Conversely, groundwater nutrient pollution can cause excessive growth of littoral algae that is not captured by measurements of metabolism and autotrophic biomass made offshore (Timoshkin et al. 2018; Vadeboncoeur et al. 2021). When evaluating the effects of changes in trophic status on food webs or biogeochemical cycling in lakes, it is therefore necessary to account for compensatory dynamics between primary producer groups, and recognize that changes in P:R measured off-shore primarily represent water column processes.

The relationship between eutrophication and P:R ratios is complicated by the spatial and temporal effects of eutrophication on aquatic metabolism. A common negative effect of eutrophication in lakes, especially when coupled with stratification, is the development of anoxia or hypoxia. Given that hypoxia/anoxia is indicative of localized net heterotrophy ($P < R$), an implied link between eutrophication and autotrophy requires careful consideration of whether this designation can or should ever be applied to a whole lake. High rates of phytoplankton production are coupled with elevated rates of respiration by algae and bacteria (Cole et al. 1988). Epilimnetic nutrient enrichment increases phytoplankton biomass; hypolimnetic and sediment oxygen demand subsequently increase owing to the decomposition of settled phytoplankton, leading to anoxia (Hargrave 1973; Nürnberg 1995). Decreases in benthic primary production due to light limitation can also potentially produce or exacerbate hypoxic conditions independent of changing respiration rates (Brothers et al. 2014, 2017b). Alternatively, the likelihood of under-ice anoxia occurring in a given year may be reduced by wintertime primary production oxygenating the water column, as a function of snow cover and light transmission through the ice (Obertegger et al. 2017; Song et al. 2019). If epilimnetic autotrophy often drives hypolimnetic and benthic heterotrophy through increased biological oxygen demand (increased R) or through shading (decreased P) then the causal link between nutrients and $P:R > 1$ may depend strongly on lake morphometry.

The effects of eutrophication on P:R in lakes are complex, temporally sensitive, and modulated by shifts in community structure and food web interactions (Hilt et al. 2017). Thus, studies interpreting the interactions between lake metabolism and eutrophication must account for which lake zones are being measured (e.g., epilimnion vs. hypolimnion), and how different responses of various primary producer groups to nutrients may affect P:R ratios in each of those zones. In small or shallow lakes, the presence of emergent or floating leaved vegetation complicate these estimates because their potentially substantial contributions to primary production are not captured by oxygen dynamics in the water, but their detritus accumulates on the lake bottom and consumes oxygen (Engle et al. 2008).

Do P:R ratios < 1 indicate a dominance of allochthonous OC in metazoan food webs?

P:R ratios < 1 have frequently been interpreted as evidence of consumer reliance on allochthonous organic carbon (Thorpe and Delong 2002). Central to the foundational understanding of the relationship between net heterotrophy ($R > P$) and terrestrial support of aquatic food webs are the ideas that in persistently net autotrophic ecosystems (where $P:R > 1$), food webs are based on phytoplankton OC (e.g., Defore et al. 2016), while in persistently heterotrophic ecosystems (where $P:R < 1$) terrestrial OC is actively incorporated into the food web (e.g., Urabe et al. 2005). We review evidence that mid-lake P:R ratios, despite their appealing simplicity, offer limited insights into metazoan reliance on allochthonous OC owing to (1) the strong effect of microbial production efficiency on R; (2) the strong reliance of metazoan production on autochthonous production irrespective of the rate and amount of allochthonous OC supplied; and (3) the differential effects of external OC supplied in dissolved forms in the water column relative to particulate forms to the benthos.

Allochthonous (terrestrial) OC is incorporated into metazoan food webs through direct consumption (e.g., by detritivores; Marcarelli et al. 2011; Bartels et al. 2012) or by sequestration by bacteria that are subsequently consumed by metazoans (Cole et al. 2006). As mentioned previously, organic carbon processing in lakes is typically dominated by the microbial pathway. In the open-water zone of lakes, about 90% of OC is in dissolved form (DOC; Wetzel 2001; Carpenter et al. 2005) and this DOC is predominantly of terrestrial origin (Hanson et al. 2011; Wilkinson et al. 2013). Open-water R is exceedingly sensitive to microbial respiration of DOC (Hanson et al. 2003; Sadro and Melack 2012). However, the magnitude of the influence of bacteria on R is inversely related to the proportion of metabolized OC that bacteria convert into biomass. Bacterial growth efficiency (BGE) refers to the fraction of assimilated OC that contributes to bacterial biomass. BGE is less than one and is calculated by dividing the rate of production of new bacterial biomass (BP) by the sum of BP and bacterial respiration. BGE can range from < 0.05 to over 0.6, and increases with increasing temperature (del Giorgio and Cole 1998). For instance, with a low BGE of 0.05, 95% of the DOC processed is affecting R and 5% of the DOC is contributing to biomass potentially available to higher trophic levels (Fig. 2). BGE can be as low as 0.01 in nutrient-poor lakes with high ratios of allochthonous to autochthonous OC (del Giorgio and Cole 1998), but BGE increases to around 0.5 in eutrophic lakes where abundant algae provide a labile carbon source for bacteria (Larsson and Hagström 1979; del Giorgio and Cole 1998; Cotner et al. 2001; Kritzberg et al. 2005). Under nutrient-poor conditions or in lakes with high concentrations of refractory OC, bacteria act as a carbon “sink” through respiration, rather than a link between terrestrial OC and metazoans in the food chain (Cole et al. 2002, 2006). A P:R ratio derived from open-water measurements cannot be used

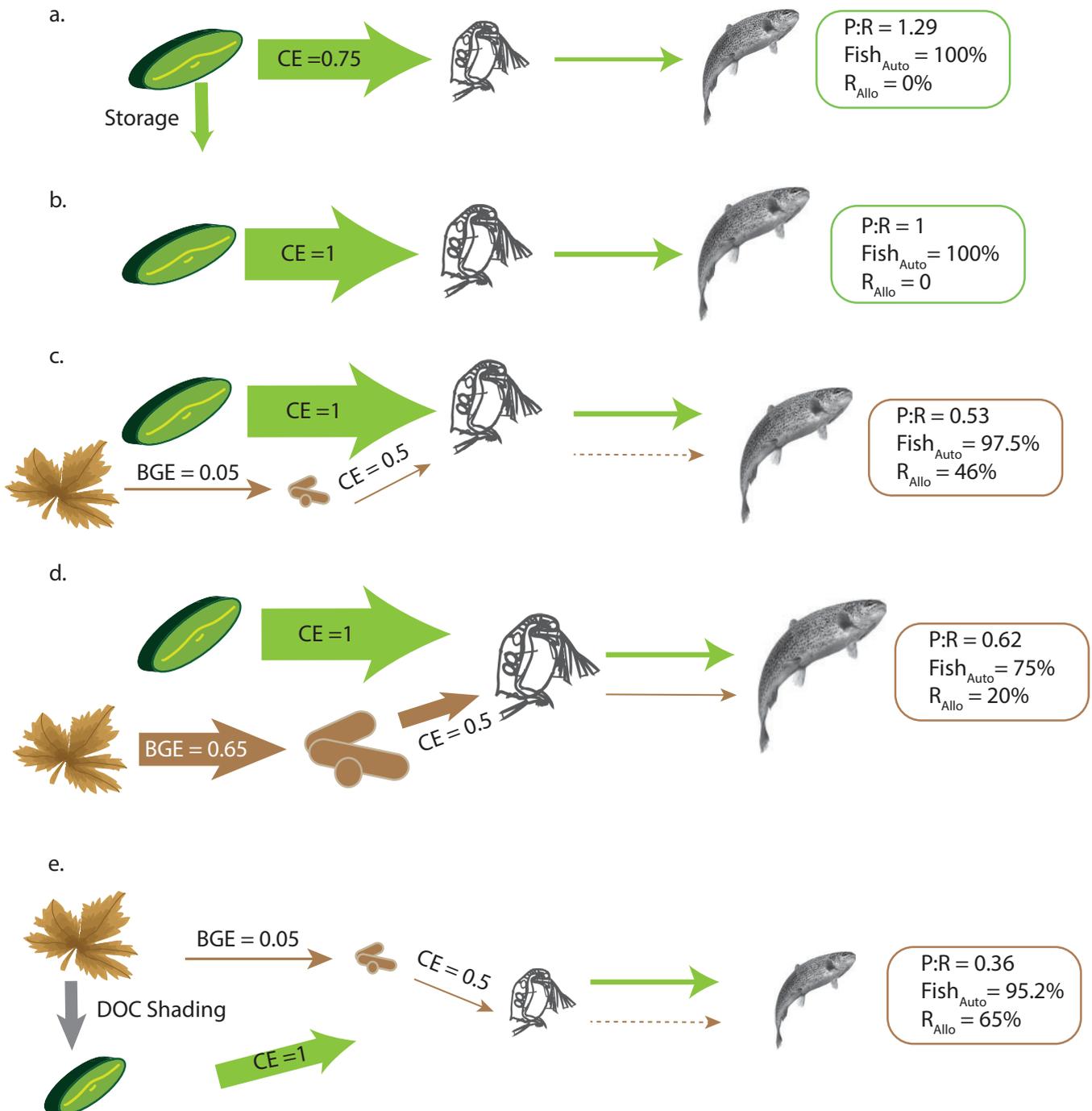


Fig 2. Hypothetical examples, based on simplified models, that demonstrate how uncertainties about the accessibility of food resources and BGE affect our conclusions about entrainment of basal resources into the metazoan food web. **(a)** A lake food web based entirely on algae when the fraction of basal algal resources eaten by primary consumers (consumption efficiency, CE) is 0.75. Unconsumed algae is stored in the lake, resulting in a P:R ratio of 1.29. Autotrophic production supports all animal production (animal %auto = 100) and there is no bacterial respiration of allochthonous carbon (R% Allo = 0). **(b)** When all autotrophic production is consumed by primary consumers, P:R = 1. **(c)** Allochthonous OC is added to the ecosystem in the same mass as autochthonous production. Low BGE (0.05) leads to a very small contribution to metazoan production (2.5%), but respiration of allochthonous OC drives P:R below 1. **(d)** If BGE was higher and consumed by primary consumers, terrestrial OC would boost fish production. However, BGE = 0.65 is typical of bacteria growing on algal, not terrestrial carbon. **(e)** When colored terrestrial DOC shades benthic and planktonic algae (here, reducing autochthonous production by 50%) and it is difficult for bacteria to convert to biomass (BGE = 0.05), DOC suppresses both the P:R ratio and secondary production. Differences in sizes of zooplankton and fish scale to differences in production among scenarios. Differences in arrow size scale to differences in biomass transfer across trophic levels. Consumption efficiency of bacteria by metazoans was set to 0.5. These scenarios together illustrate that P:R ratios are not necessarily correlated with an increase in food web support by terrestrial OC but rather a decrease in overall secondary production. Although zooplankton are depicted, the effect of shading by terrestrial OC would disproportionately impact benthic primary production, and thus benthic grazers.

to infer allochthonous support of the metazoan food web because (1) open-water measurements are biased towards measuring the dynamics of dissolved allochthonous OC (due to the dominance of allochthonous DOC in water columns) and (2) bacterial respiration, rather than biomass production, is often the primary fate of allochthonous DOC (Kankaala et al. 1996; Kritzberg et al. 2005; Cole et al. 2006).

The importance of a resource to the metazoan food web depends upon its contribution to secondary production of animals. Metazoan production cannot be quantified with ecosystem respiration (R), but is correlated with controls of P across lakes (Karlsson et al. 2009) because algae is a high quality resource (Brett et al. 2009). Metazoan growth efficiency (new biomass produced/resource consumed) depends on food quality (Bilby and Bisson 1992; Marcarelli et al. 2011), and consumer growth efficiency is higher on an algal diet compared with a diet of terrestrial OC (Brett et al. 2009, 2017; Wenzel et al. 2012). Thus, terrestrial OC loaded into lakes with high phytoplankton production may lower P:R ratios while making only minor contributions to the metazoan food web, even when the supply rate of allochthonous OC greatly exceeds that of autochthonous OC (Carpenter et al. 2005; Mehner et al. 2016). Zooplankton preferentially consume autochthonous OC (Carpenter et al. 2005; Marcarelli et al. 2011), and incorporation of terrestrial OC may be greatest when phytoplankton OC is unavailable (Taipale et al. 2016).

There is an active debate concerning whether allochthonous OC metabolized by the base of the planktonic food web (lowering lake P:R ratios) necessarily represents a resource subsidy to metazoan consumers because it often reduces the supply of high quality autochthonous OC (Jones et al. 1998, 2012; Pace et al. 2004; Daniel et al. 2005). Most allochthonous OC loaded into lakes is in the form of highly colored DOC that suppresses benthic and planktonic autochthonous OC production by shading (Ask et al. 2009; Jones et al. 2012; Kelly et al. 2018), thereby reducing the absolute amount of autochthonous OC available to consumers (Hessen et al. 2017). Allochthonous OC can only be a subsidy if its use more than offsets the reduction in secondary production caused by depression in primary production. Thus, colored DOC can lower P:R ratios by suppressing primary production by shading, as well as by increasing bacterial respiration. DOC shading of primary production tends to occur above concentrations of ~5 to 15 mg/L (Seekell et al. 2015; Kelly et al. 2018), which is the same concentration range above which temperate lakes tend to be net heterotrophic (Prairie et al. 2002). This makes it difficult to establish whether terrestrial OC is reducing P:R ratios in DOC-rich lakes via decreasing GPP or increasing R.

The insensitivity of mid-lake metabolism monitoring to littoral dynamics (Van de Bogert et al. 2012) is particularly problematic because colored DOC in the water column disproportionately affects benthic algal production (Jones et al. 2012; Batt et al. 2015), and littoral-benthic primary

production makes large contributions to metazoan food webs (Vander Zanden and Vadeboncoeur 2020). Benthic primary production supports zoobenthos, which in turn can be responsible for a substantial fraction of fish biomass production (Vander Zanden et al. 2011; Sierszen et al. 2014). Water column transparency determines the amount of benthic autochthonous OC available to lake food webs (Vadeboncoeur et al. 2008; Doi 2009; Solomon et al. 2011), and allochthonous OC reduces the production of benthic autochthonous OC (Vadeboncoeur et al. 2008; Jones et al. 2012). The suppression of benthic primary production through DOC shading reduces invertebrate and fish reliance on littoral autochthonous OC and reduces fish biomass (Karlsson et al. 2009; Bartels et al. 2016; Mariash et al. 2018; van Dorst et al. 2019). Thus, the indirect negative effects of DOC on benthic primary and secondary production often result in allochthonous DOC suppressing rather than subsidizing resources in lakes. This occurs in the littoral benthic habitat, and plankton P:R ratios alone cannot elucidate these fascinating whole-ecosystem effects.

A less well-studied pathway by which OC is imported into lakes is through particulate detritus loaded to littoral benthic habitats from riparian (Attermeyer et al. 2013; Scharnweber et al. 2014a) and/or emergent vegetation (Waichman 1996; Forsberg et al. 2016). This POC is often less processed (and of higher quality) than the DOC in the water and is directly entrained into the food web by consumption by littoral metazoans (Glaz et al. 2012). We know of no studies that assess P:R responses to these material transfers from terrestrial vegetation to the littoral zone. However, an experimental littoral POC addition caused a short-term stimulation of planktonic, but not benthic, microbial production (Attermeyer et al. 2013), yet stable isotope analyses indicated that the benthic macroinvertebrate community was key in transferring this POC to secondary and tertiary lake consumers (Scharnweber et al. 2014a) and even to the surrounding terrestrial environment (Scharnweber et al. 2014b).

In summary, the differential consumption and growth efficiencies associated with diets of autochthonous vs. allochthonous OC complicates the interpretation of P:R ratios with respect to metazoan food webs, which tend to rely on littoral autochthonous OC (Fig. 2a–d). The sensitivity of P:R ratios to terrestrial DOC and associated bacterial respiration often indicates a sink, not a source of carbon for metazoans, while metazoan respiration contributes little to R at the whole-lake scale (Cole et al. 1988; Andersson and Sobek 2006; Brothers et al. 2013a). A hypothetical lake with no allochthonous OC use but with a 100% efficient incorporation and respiration of autochthonous primary production by a robust metazoan food web would feature a P:R ratio of one (Fig. 2b). Any algae or macrophyte not consumed and respired would result in a P:R ratio > 1 (Fig. 2a), without altering the relative importance of allochthonous OC to this food web. Similarly, any incorporation of allochthonous OC into a food

web characterized by highly efficient utilization of autochthonous resources would shift the P:R ratio below one (Fig. 2c,d). When accounting for the negative effect of terrestrial DOC shading on autochthonous OC, decreased metazoan productivity may be anticipated, and lower P:R ratios, despite a sustained consumer reliance upon autochthonous OC (Fig. 2e). Thus, a P:R < 1 does not necessarily indicate that terrestrial OC is important for its metazoan food web (Thorp and Delong 2002), especially when P:R is measured mid-lake and is tracking respiration of DOC and phytoplankton productivity.

What are the connections between P:R ratios and carbon cycling within lakes at the landscape scale?

P:R ratios have expanded our understanding of the importance of lakes in the global carbon cycle (Cole et al. 2007; Tranvik et al. 2009). Lakes throughout the world tend to be supersaturated in CO₂ relative to the atmosphere, and thus are net CO₂ emitters (Kling et al. 1992; Cole et al. 1994; Raymond et al. 2013). Lakes also typically accumulate organic carbon in their sediments (Mendonça et al. 2017), and the storage of carbon is expected to increase in tandem with increasing autotrophy (Pacheco et al. 2014) because elevated phytoplankton production results in higher rates of accumulation of dead autochthonous production in the sediments (Heathcote and Downing 2012; Brothers et al. 2013a). High supersaturation of pCO₂ in north-temperate lakes has been associated with elevated microbial respiration (Striegl et al. 2001), and the stimulation of phytoplankton production by inorganic nutrient enrichment can shift lakes from net sources to net sinks of atmospheric CO₂ (Schindler et al. 1972; Gelbrecht et al. 1998; Balmer and Downing 2011; Trolle et al. 2012; Pacheco et al. 2014). Conversely, stimulation of bacterial respiration by terrestrial (allochthonous) DOC loading results in increased pCO₂ in lakes, leading to higher CO₂ flux to the atmosphere (Ask et al. 2012; Lapierre et al. 2013). These patterns demonstrate that in-lake metabolic (i.e., algal and bacterial) processes can regulate surface CO₂ emissions. A study of 20 northern temperate oligotrophic lakes similarly concluded that ecosystem oxygen metabolism determined the directionality of lake CO₂ fluxes with the atmosphere (del Giorgio et al. 1999). The net heterotrophy (P:R < 1) of these lakes was attributed to terrestrial OC inputs, establishing a link between heterotrophy, CO₂ emissions, and the uptake of terrestrial OC by aquatic food webs (del Giorgio et al. 1999). These and other studies have led to the transformational understanding that terrestrial OC causes many lakes to be net emitters of CO₂ to the atmosphere (e.g., Cole et al. 2006). Here, we review the recent literature linking carbon cycling dynamics and P:R ratios in lakes. Specifically, we examine (1) whether a terrestrial supply of OC is necessary to support net heterotrophy (P:R < 1), (2) the importance of watershed CO₂ delivery and in-lake non-metabolic CO₂ production in driving CO₂ emissions to the

atmosphere, and (3) the implications of P:R ratios for carbon storage and burial in lakes.

P:R ratios below one indicate a state of net heterotrophy, for which a terrestrial supply of OC would seem necessary. However, net autotrophic zones adjacent to the off-shore water column (either littoral-benthic and/or littoral-planktonic habitats) produce OC that may end up in the off-shore water column. Floating-leaved or emergent macrophytes can dominate OC loading in lakes (Junk 1997; Melack et al. 2009; Brothers et al. 2013a), and their physical placement in lakes sometimes leads to their classification as autochthonous primary producers (e.g., Waichman 1996; Scharnweber et al. 2014a). However, their predominant oxygen exchange is with the atmosphere, and so their production is not captured by aquatic metabolism measurements. Littoral-benthic autochthonous OC (submerged macrophytes and periphyton) may also fuel an apparent state of heterotrophy as measured with diel O₂ curves in the open water (Coveney and Wetzel 1995). In addition to the effect of the physical distance between the site of production and the placement of the oxygen probe, the metabolic exchange of oxygen and carbon by periphyton communities on sediments may be with groundwater instead of the overlying water column (Vadeboncoeur and Lodge 1998; Périllon and Hilt 2016), meaning that even probes placed in the littoral water column may not fully capture periphyton metabolism rates. Their net effect on lake P:R ratios may thus be negative if they are consumed and respired by the aquatic food web. Net heterotrophy can also be a legacy effect from lakes that experienced eutrophication in the past, whereby a surplus of autochthonous OC has accumulated in the sediments and is being slowly respired (Staehr et al. 2010b; Finlay et al. 2019). It is thus possible for past autochthonous OC to fuel current heterotrophy. This effect has produced unexpected relationships between nutrients, DOC, and P:R ratios in studies that incorporate multiple lake habitats. For instance, nutrient-poor DOC-rich lakes are commonly assumed to be net heterotrophic with food webs dominated by allochthonous OC (e.g., Blomqvist et al. 2001), but may instead be net autotrophic due to high rates of benthic primary production (Andersson and Brunberg 2006; Vesterinen et al. 2016). Similarly, a lake might be categorized as autotrophic based on epilimnetic measurements, but be net heterotrophic upon the inclusion of deep-water benthic respiration rates. The complicated role of benthic production, potentially taking up CO₂ from both the water column and groundwater (e.g., Périllon and Hilt 2016), must therefore be assessed before making broad conclusions regarding the implications of water column P:R ratios on lake carbon cycling.

P:R ratios below one are frequently assumed to be associated with a supersaturation of CO₂ relative to the atmosphere (Duarte and Agustí 1998; Laas et al. 2012). By failing to account for imported and/or nonmetabolic sources of dissolved inorganic carbon (DIC), this perspective implies that

CO₂ saturation, and thus CO₂ fluxes, are controlled by in-lake metabolic processes, as has been concluded by many studies (Cole et al. 2000; Duarte and Prairie 2005; Trolle et al. 2012; Pacheco et al. 2014). However, landscape-scale patterns in lake CO₂ saturation often reflect the loading of DIC from the watershed, rather than (Borges et al. 2014; Marcé et al. 2015; Weyhenmeyer et al. 2015; Martinsen et al. 2020) or in addition to (Vachon et al. 2017) CO₂ production within the lake itself. Even hypereutrophic lakes can be net CO₂ sources to the atmosphere (Xiao et al. 2020). This effect should not be surprising, as terrestrial soils are important sites of CO₂ production (Raich et al. 2002; Jassal et al. 2005; Kellman et al. 2015), and groundwater CO₂ concentrations are typically highly saturated (Macpherson 2009). The role of catchment DIC loading (rather than aquatic metabolism) on surface CO₂ emissions has been described in rivers (Johnson et al. 2008; Hotchkiss et al. 2015; Rocher-Ros et al. 2019), and riverine fluxes may likewise play a strong role in river-fed lakes (Chmiel et al. 2019). Terrestrial catchment productivity can be a better predictor of CO₂ concentrations in lakes than in-lake OC mineralization rates (Maberly et al. 2013). As a result of such catchment dynamics, lakes can be both metabolically autotrophic (P:R ratio > 1) and net CO₂ emitters to the atmosphere (Carignan et al. 2000; Stets et al. 2009; Christensen et al. 2013; Borges et al. 2014). To summarize, it is not sufficient to equate net CO₂ emission with lake metabolic heterotrophy in the absence of data on imported or nonmetabolic CO₂ sources.

In addition to considering watershed sources of CO₂ in lake water, we need to account for nonmetabolic transformations of organic carbon in lakes. Abiotic photomineralization of DOC by ultraviolet (UV) radiation (Graneli et al. 1996; Koehler et al. 2014; Ward and Cory 2016) is rarely accounted for in whole-lake estimates of CO₂ flux. UV radiation can also transform DOC into more (Biddanda and Cotner 2003) or less (Benner and Biddanda 1998) labile organic forms. The effect of photodegradation on DOC lability is accounted for in diel O₂ curves via altered respiration rates. However, abiotic CO₂ production by photomineralization suppresses daytime NEP rates via the abiotic consumption of dissolved oxygen (Amon and Benner 1996), but does not affect the nighttime calculated R used to calculate daytime GPP. This results in underestimates of GPP, and thus lower P:R ratios. Although some studies have compared photomineralization and respiration in lakes (Cory et al. 2014; Vachon et al. 2016), photomineralization is frequently overlooked in direct measurements of R, which are typically carried out in the dark to eliminate primary production. By overlooking abiotic light-mediated CO₂ production dynamics, it is possible to misclassify lakes as net heterotrophic (Brothers and Sibley 2018). Precise photomineralization rates are labor-intensive to quantify and complicated by estimations of DOC exposure and reaction times to UV radiation, but should be considered at minimum as a potential source of error when assessing in-lake drivers of P:R ratios.

The link between P:R ratios and carbon storage (the carbon pool contained within a lake) and burial (the sedimented carbon which is not returned to the water column) may seem intuitively clear, but seasonality, lake heterogeneity, and non-metabolic factors complicate this relationship. Fundamentally, carbon burial in lakes is controlled by watershed loading of nutrients and organic carbon (increasing or decreasing P:R ratios), as well as oxygen dynamics (Sobek et al. 2009; Carey et al. 2018). Regional assessments have identified a strong positive effect of agriculture and eutrophication on carbon burial in lakes (Kastowski et al. 2011; Heathcote and Downing 2012; Dietz et al. 2015). As eutrophication is commonly assumed to be linked to net autotrophy (Schindler et al. 1997), this may be taken as indicating that net autotrophy should enhance carbon storage and burial in lakes (Fig. 2a). However, as described previously, the relationship between P:R ratios and eutrophication is not straightforward. Year-round monitoring of low-latitude eutrophic lakes has yielded net heterotrophic (P:R < 1) conditions, whereas spring-to-fall measurements alone implied autotrophy (Alfonso et al. 2018). High respiration rates in a warm, low-latitude tropical reservoir likewise resulted in net heterotrophy and a high efflux of CO₂ and methane (CH₄) even though the lake was eutrophic and highly productive (Almeida et al. 2016). Presumed declines in carbon storage (associated with P:R < 1), for instance a drawdown in the standing DOC pool in the water column, may occur seasonally (Biddanda and Cotner 2002). DOC drawdown may also result from interannual changes in light regime, for instance due to declines in ice cover (Brothers and Sibley 2018). Variation in DOC pool carbon storage may potentially follow long-term (decades to centuries) cycles whose links with measured P:R ratios at a given time may not be straightforward (del Giorgio and Duarte 2002; Cotner et al. 2004). Finally, P:R ratios and carbon fate (whether maintained in the standing carbon pool, stored in the sediments, or exported to the atmosphere) fundamentally reflect the efficiency with which autochthonous OC is integrated into (and respired by) a given lake's metazoan food web (as discussed previously), with lower metazoan consumption and respiration rates producing higher P:R ratios, all else being equal (Schindler et al. 1997). While increases in measured P:R ratios in lakes may intuitively indicate increasing carbon storage and/or burial in lakes, multiple factors must be independently accounted for before establishing this conclusion.

Conclusion

We argue that the tools and approaches that have often been used to quantify P:R ratios in lakes, such as the use of near-surface lake-center diel O₂ curves, have a high likelihood of bias. Even with accurate data, the links between P:R ratios and ecosystem function need shoring up by the inclusion of littoral-benthic habitats and watershed dynamics. Recent studies have recognized and attempted to mitigate the potential

flaws associated with this approach, and are increasingly showing that the foundational groundwork laid by P:R studies on broad limnological themes including trophic status, allochthony, and carbon cycling in lakes, is incomplete and biased by a legacy of a planktonic-centric measurements. In particular, links between P:R ratios and trophic status predominantly describe phytoplankton dynamics, links between P:R ratios and the utilization of terrestrial OC by aquatic organisms cannot be reliably used to identify which resources are most important in sustaining metazoan food webs, and P:R ratios do not provide a complete picture of how lakes interact with terrestrial and atmospheric carbon pools with respect to carbon cycling. While the work in aquatic metabolism using P:R ratios has advanced our understanding of the importance of terrestrial OC to lake food webs, biogeochemical and ecological linkages with watershed groundwater dynamics and the littoral-benthic zone were often excluded from the picture.

Aquatic metabolism studies using P:R ratios have seen major advancements in recent years, and are a powerful tool in helping us understand lakes. New studies continue to demonstrate a more complex reality for lake functioning, where biogeochemical and ecological processes connect off-shore, nearshore, airshed, and above- and below-ground watershed processes. However, new studies may potentially be hampered in their design or interpretation of data if using earlier assumptions of lake functioning in the development of their hypotheses and discussions. We present this synthesis of the evolution and potential shortcomings of prior planktonic-focused P:R studies to demonstrate how new studies may inform and improve these foundational assumptions. We believe that aquatic metabolism studies are on a positive trajectory, providing methodological and conceptual guidance for future research.

P:R ratios can provide valuable information for lake managers, highlighting the effects of changing hydrological inputs on lake metabolism (Idrizaj et al. 2016; Alfonso et al. 2018). Temporal trends in measured P:R ratios may signal browning events such as those caused by storms and high runoff (Sadro and Melack 2012). Measured P:R ratios above one (indicating net autotrophy) should not be used alone as evidence of a lake's CO₂ saturation. However, if coupled with directly measured supersaturation of CO₂, such data might signify that groundwater DIC dynamics are important in that lake. We recommend that P:R ratios be used explicitly to assess water-column, rather than whole-lake integrated metabolism. Apparent patterns in measured P:R linking to trophic status, food web support, or carbon cycling, should be analyzed in a way that explicitly considers littoral-benthic processes, in-lake mixing dynamics, and watershed inorganic carbon loading, rather than only considering phytoplankton PP and terrestrial OC. Ultimately, it is important to understand that lakes are not microcosms (as described by Forbes 1887), or passive pipelines for organic matter, but instead that they are intricately

connected with the terrestrial and atmospheric environments around them (Cole et al. 2007). However, as our understanding of the numerous and heterogeneous processes driving lake metabolism and carbon cycling improves, it is equally important that future research fully accounts for this complexity in their nature.

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Conflict of interest

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