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Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism

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Abstract

H. T. Odum's influential *Limnology and Oceanography* 1956 publication compared gross primary production (GPP) and ecosystem respiration (ER) among aquatic ecosystems. Few syntheses of aquatic ecosystem metabolism have been completed since. We used Odum's conceptual framework to compare GPP and ER from open-water diel oxygen curves in lakes, wetlands, estuaries, and streams (n = 350). We also documented environmental drivers of metabolism among ecosystems. GPP and ER were strongly related in lakes and estuaries, but weakly related in streams and wetlands. GPP and ER were highest in estuaries, and GPP : ER was lowest in streams. Differences in the magnitude and variability of metabolism among ecosystems were attributable to landscape and water-column factors. Watershed size and phosphorus (P) concentrations were positively related to GPP and ER across all ecosystems. Considered independently, lake and estuary GPP were driven by P concentrations. In contrast, land-use and canopy cover drove stream metabolism, not nutrient concentrations. Results confirmed the classic paradigm that estuaries are the most productive aquatic ecosystem; however, our synthesis showed that relative to streams and estuaries, there was higher variation in lake GPP and ER than previously documented. Results will be valuable for management, restoration, and carbon budgets, which incorporate metabolism measurements at both the catchment and landscape scales. As metabolism datasets grow, future syntheses will address challenges including seasonality, sensor deployment time and location, hydrology, and variation in analytical conventions by discipline. Ongoing technological and computational advancements, combined with increased communication among subdisciplines, should also expand insights generated by subsequent metabolism syntheses.

Gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) are fundamental metrics of an ecosystem (Odum 1956; Marcarelli et al. 2011; Staehr et al. 2012*b*). GPP is the rate of organic matter production within an ecosystem by photosynthesis, whereas ER (also referred to as community respiration) represents the total consumption of organic matter in an ecosystem via aerobic respiration. NEP, also referred to as net ecosystem metabolism, is the balance between GPP and ER. Because metabolism metrics integrate the activity of all organisms carrying out photosynthesis and aerobic respiration, they can be compared across locations and through time to infer how entire ecosystems respond to environmental change (Odum 1956; Mulholland et al. 2001; Caffrey 2004). Models of global carbon (C) sinks and sources are based upon syntheses of empirical studies that measure metabolism across a diversity of ecosystem types and conditions including aquatic (Aufdenkampe et al. 2011) and terrestrial environments (Yvon-Durocher et al. 2012). Therefore, it is critical to document the balance between autotrophy and heterotrophy, as well as compare controls of GPP and ER across ecosystems.

Ecosystem metabolism is commonly measured in all aquatic ecosystems, including streams (Young et al. 2008; Bernot et al. 2010), lakes (Cole et al. 2000; Staehr and Sand-Jensen 2007), wetlands (Hagerthey et al. 2010), and estuaries (Howarth et al. 1991; Caffrey 2004; Russell et al. 2006). However, in half a century of research on aquatic ecosystem metabolism, empirical analyses among disparate ecosystem types have rarely extended beyond comparing within each ecosystem type across a geographic space (Caffrey 2004; Bernot et al. 2010), through time (Roberts et al. 2007), or among varied trophic states (Staehr et al. 2010). A recent meta-analysis of research foci for publications that included aquatic ecosystem metabolism showed that although an equal proportion of studies were conducted in rivers, lakes, estuaries, or the coastal ocean between 2000 and 2010, only ~ 3% of studies considered more than one type of ecosystem (Staehr et al. 2012*b*). Past data syntheses have assessed a combination of terrestrial and aquatic environments (Whittaker and Likens 1973; Begon et al. 1986; Yvon-Durocher et al. 2012), but none have focused specifically on aquatic ecosystems. Expanding metabolism analyses to include multiple ecosystem types could illustrate patterns in the relative ranges of GPP and ER among ecosystems and reveal environmental drivers of metabolism that may be obscured when ecosystem types are considered independently.

Partitioning aquatic metabolism research by ecosystem is contrary to a foundational paper on the subject. Odum (1956) used diel oxygen (O_2) curves to compare rates and environmental drivers of GPP and ER in flowing waters relative to other aquatic ecosystems. This paper provided an analysis that summarized both the absolute and relative values for GPP and ER across aquatic ecosystems in a single figure (Fig. 1A). Odum (1956) showed that the magnitude and the relative values of GPP and ER varied between standing and flowing waters, in rivers receiving terrestrial or anthropogenic organic C inputs, and in

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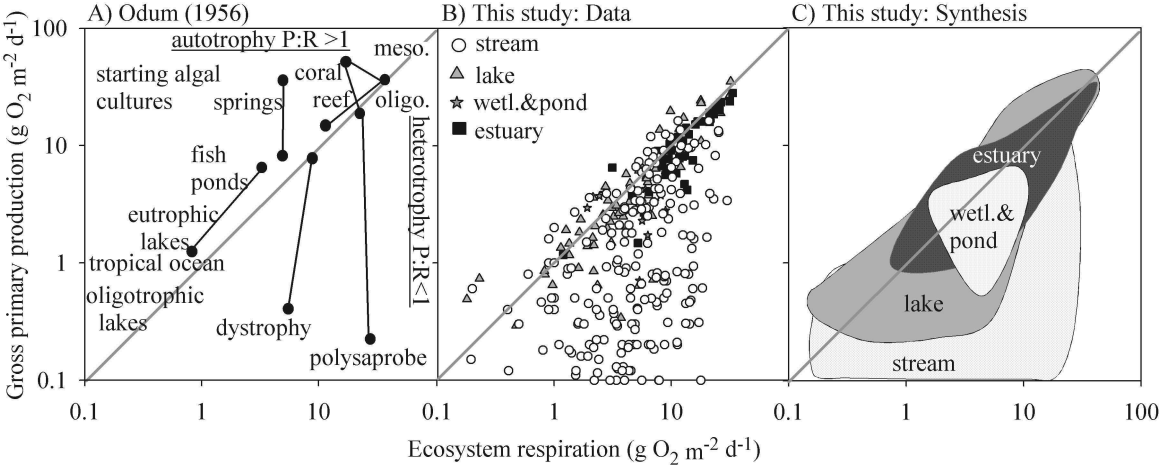

Fig. 1. (A) Odum's (1956) synthesis of metabolism measurements across aquatic ecosystems. Points connected by lines were taken within the same site; meso = mesosaprobe; oligo = oligosaprobe. (B) Our synthesis of data from open-water measurements of metabolism in streams, lakes, wetlands and ponds, and estuaries using identical graphical framework and axes to those in Odum (1956), and (C) a plot of the two-dimensional area that encompasses all data points for each of the four ecosystem types. The gray line indicates 1 : 1 value of GPP : ER on each panel (Odum 1956).

ecosystems with high nutrient loads. Overall, Odum (1956) asserted there was considerable variability in NEP among ecosystems, but that most aquatic ecosystems will balance between autotrophy and heterotrophy when measurements are repeated over large spatial and temporal scales.

Recent developments in ecosystem metabolism research suggest that a new compilation of metabolism data, generated across aquatic environments and compared using the graphical summary from Odum (1956), will provide new insights into the scales of variation in metabolism and its environmental drivers across aquatic ecosystems. Improved dissolved oxygen (DO) sensor technology has led to widespread replacement of Clark cell sensors with luminescent DO (LDO) sensors. The LDO probes require less maintenance, are easier to calibrate, and have greater precision (Tengberg et al. 2006). In addition, a number of organizations are collecting or are planning to collect the data needed to calculate metabolism via long-term sensor networks with wide geographic distributions, including the Global Lake Ecological Observatory Network (GLEON; http://www.gleon.org; Hanson 2007), the National Estuarine Research Reserve System (NERRS; http://cdmo.baruch.sc.edu), and the National Ecological Observatory Network (http://www.neoninc.org). Models used to estimate components of metabolism and abiotic DO dynamics have been refined (Hanson et al. 2008; Holtgrieve et al. 2010; Staehr et al. 2010). Finally, a major synthesis of temperature dependence of ER in terrestrial and aquatic ecosystems recently showed that subsidies of terrestrial C in aquatic ecosystems relax constraints on ER by autochthonous production and affect the relationship between temperature and ER (Yvon-Durocher et al. 2012). However, the analysis did not analyze other metabolism drivers or address comparisons among aquatic ecosystems.

Our goal was to use the graphical summary of Odum (1956) to compare newly assembled datasets of metabolism across aquatic ecosystem types. We present the findings of Odum (1956) in Fig. 1A alongside our results (Fig. 1B) and synthesis (Fig. 1C). Our overarching hypothesis was that the differences in the magnitude and variation of GPP and ER among aquatic ecosystems would reveal either shared or unique environmental drivers of metabolism across ecosystem types.

We predicted that all ecosystems would be heterotrophic, but that estuaries would have the highest GPP and ER of all ecosystems we considered. Shallow coastal estuaries exhibit many characteristics that would suggest high productivity. Estuaries are interfaces between terrestrial, freshwater, and marine environments, and receive organic matter and nutrients from riparian zones, rivers, and the ocean (Howarth et al. 1991). Many estuaries exhibit rapid internal nutrient cycling (Gardner et al. 2006; Russell et al. 2006) and high biodiversity (Norse 1995), suggesting the highest rates of biological production are most likely in estuaries.

In streams, wetlands, and lakes, we predicted terrestrial subsidies of organic matter would induce heterotrophic conditions to a greater degree than estuaries (Yvon-Durocher et al. 2012). We predicted that streams would be most variable in GPP and ER, as they can alternate between autotrophy and heterotrophy with changes in land use and seasonal canopy cover (Roberts et al. 2007; Young et al. 2008; Bernot et al. 2010). We also expected high variation in GPP and ER in lakes, but that this variation would be lower than in streams. GPP in lakes is less likely to approach zero because of greater pelagic production than that in streams (Van De Bogert et al. 2012). Finally, we predicted that GPP would be driven by phosphorus (P) concentrations in freshwaters and nitrogen (N) concentrations in estuaries (Howarth and Marino 2006; Paerl 2009).

Methods

We created an ecosystem metabolism database from a survey of primary literature and direct communication with researchers. In late 2011 and early 2012, primary literature

databases, including Google Scholar, Science Direct, and Web of Science, were searched using key words "metabolism" and "lake," "stream," "river," "pond," "estuary," or "wetland." From these literature results, we selected papers with open-water, diel O_2, metabolism measurements that had GPP and ER measurements for at least 1–90 d during the summer months, which we defined as June through August in the Northern Hemisphere. We focused only on summer to facilitate our cross-ecosystem synthesis because that is by far when most data were available (*see* "Challenges" below). Also, our goal was to analyze variation among ecosystem types, which could be obscured by seasonality within sites (Roberts et al. 2007; Yvon-Durocher et al. 2012).

In addition to literature searches, we directly contacted scientists to request metabolism data. Some of our primary sources were the GLEON for lakes (Solomon et al. 2013); the Lotic Intersite Nitrogen Experiment I and II (Mulholland et al. 2001; Bernot et al. 2010) and the large woody debris addition project for streams (Hoellein et al. 2007, 2009, 2012); Caffrey (2004) data from NERRS for estuaries; and Hagerthey et al. (2010) and the South Florida Water Management District for wetlands. Our database had information from 350 sites with 296 locations in the U.S. and 54 international sites with measurements from lakes (n = 72), wetlands (n = 13), estuaries (n = 47), and streams (n = 218; *see* Web Appendix www.aslo.org/lo/toc/vol_58/issue_6/2089a.html for citations and data).

This synthesis does not represent all available metabolism literature from all ecosystem types, as some studies were excluded based on methodology or data presentation. Metabolism studies employ many alternate methods including free-water C dioxide (CO_2) changes (Souza et al. 2009; Mead and Wiegner 2010), mass balance of dissolved inorganic C, N, and P (Kemp et al. 1997), oxygen isotopes (Holtgrieve et al. 2010), and DO modeling in partially mixed (Swaney et al. 1999) or well-mixed estuaries (Vallino et al. 2005). We focused on shallow, well-mixed estuarine ecosystems that are amenable to free-water diel DO methods (Caffrey 2004), which facilitated our comparisons across aquatic ecosystems. Deeper estuaries, those that are not well mixed, or those with complex hydrology are not represented in our cross-ecosystem comparison. Finally, we excluded studies in estuaries, lakes, and streams that did not distinguish summer results in text or tables, or presented data in figures as continuous lines rather than data points.

In general, the model for diel O_2 change over time (Eq. 1) is a summation of both biological fluxes (NEP = GPP − ER) and air–water exchange (reaeration; D).

$$dO_2\ dt^{-1} = GPP - ER + D \quad (1)$$

The same model, with some variations noted below, was originally described in Odum (1956) and was used consistently for all metabolism rates in this synthesis. ER was measured as nighttime NEP, extrapolated to the entire 24 h period, and represents only aerobic respiration. NEP was measured as change in DO during the day, and GPP calculated as NEP + ER. Reaeration was estimated using a variety of techniques that varied by ecosystem, including sulfur hexafluoride or propane tracers (Marzolf et al. 1994), nighttime regression models (Hornberger and Kelly 1975), models using constant gas exchange coefficients (Kemp and Boynton 1980), or models for gas exchange based on wind speed (Cole and Caraco 1998). We used the daily or average depth (unstratified habitats) or depth of the thermocline (stratified habitats) to convert between rates expressed in terms of water volume (g O_2 m^{-3} d^{-1}) to areal rates (g O_2 m^{-2} d^{-1}). Wetland data were from open-water measurements, and we note this approach does not integrate the metabolism of emergent macrophytes.

Daily metabolism was calculated over each 24 h period (Cole et al. 2000; Caffrey 2004; Marcarelli et al. 2011). For each site, we collected the average GPP and ER for all days reported, or averaged across dates when each day was reported separately. We calculated mean NEP and GPP : ER ratios from the average values of GPP and ER over the available time period. The other possibility for estimating mean NEP and GPP : ER was to calculate each metric on each day, and average across the entire time period reported. However, this was not possible because some sources did not report separate daily measurements of NEP and GPP : ER and we wanted to be consistent across study locations. We note that streams tended to have fewer days for the measurements (1–30 d), whereas the other ecosystems had more permanent buoys and sensors, allowing for longer time periods (> 1 month).

Where reported, we added all available ancillary data to our database, including longitude, latitude, mean and maximum depth, elevation, temperature, water residence time, watershed size, and land use or land cover (e.g., % forest, agriculture, wetland, and urban). We also included water chemistry values for N, P, dissolved organic C (DOC), and chlorophyll *a* (Chl *a*). The measurements for water chemistry differed across ecosystem type. For example, N was measured as total N (TN), ammonium (NH_4^+), nitrate (NO_3^-), nitrite + nitrate (NO_x), or dissolved inorganic N (DIN; $NH_4^+ + NO_x$). P was measured as total P (TP) or soluble reactive P (SRP). Few sites recorded both dissolved inorganic and total nutrient concentrations. To compare across ecosystems, we used TN or TP when available and DIN or SRP when TN or TP was not reported. We acknowledge that comparing these TN and DIN or TP and SRP data could obscure differences in N or P composition and concentrations, but when comparing across ecosystems and orders of magnitude of N and P concentrations, they are likely reasonable estimates for comparisons. Finally, water chemistry data were not available for the NERRS system to complement the data of Caffrey (2004). Instead, we compiled a 5 yr average of water chemistry from each site in the NERRS system 2002–2007. NERRS land cover data were provided by the National Oceanic and Atmospheric Administration Coastal Change Analysis Program, downloaded from the NERRS website (http://cdmo.baruch.sc.edu).

To determine differences among streams, estuaries, lakes, and wetlands, we used one-way analysis of variance (ANOVA) for GPP, ER, NEP, and GPP : ER ratios followed by Tukey's multiple comparison test. We used

simple linear regression between GPP and ER within each ecosystem type to measure coupling between GPP and ER. To determine environmental drivers of metabolism, we used simple linear regression of watershed attributes and water chemistry variables with GPP and ER. We completed regressions with all ecosystems combined and for each individually. Because of low numbers of open-water wetland measurements, wetlands were not included in the regressions for environmental drivers. For all regressions, we $\log_{10}$ transformed data to achieve normal distribution as it spanned several orders of magnitude. We were unable to use multivariate or multilevel analyses because of the highly unbalanced nature of the dataset (i.e., few of the same ancillary variables were reported in all studies). ANOVA and *t*-tests were completed with SYSTAT 13 (SYSTAT Software, Inc.), and regressions were done using R statistical packages (R Development Core Team 2009).

Results

Ecosystem metabolism among aquatic ecosystems—GPP and ER were strongly related in lakes and estuaries (r^2 = 0.84 and 0.87, respectively), and less strongly related in streams (r^2 = 0.23) and wetlands (r^2 = 0.02; Table 1). The slope of the relationship between GPP and ER for estuaries was 1.04 and for the other ecosystems the slope was < 1 (Fig. 1B,C; Table 1). Most sites were heterotrophic, including 87–89% of estuaries and streams, 77% of wetlands, and 61% of lakes (Fig. 2C; Table 1).

Variation in GPP and ER was different for each ecosystem. Streams and lakes had the highest variability (i.e., coefficient of variation) in GPP and ER (Table 2). Estuaries had intermediate variability in GPP and ER, and variation in wetlands was lowest. However, we note the number of wetlands in our analysis was lower than the numbers of the other ecosystem types. Stream GPP was the most variable metabolism metric we examined. Relative to other aquatic ecosystems, the stream dataset contained many more sites where ER was relatively high but GPP remained low or zero (Fig. 1B,C).

GPP, ER, NEP, and GPP : ER were each significantly different among the four ecosystem types. Overall, estuaries had significantly higher rates for GPP (ANOVA, $F_{3,349}$ = 39.23, $p < 0.001$) and ER (ANOVA, $F_{3,349}$ = 18.28, $p <$ 0.001) relative to other ecosystems (Fig. 2A; Table 2). Lakes had intermediate GPP, streams the lowest, and wetlands were not different between streams and lakes (Fig. 2A). There was no difference in ER among lakes, wetlands, and streams (Fig. 2B). Finally, there was no difference in GPP : ER between estuaries and lakes, but streams had significantly lower GPP : ER (ANOVA $F_{3,349}$ = 13.68, $p < 0.001$; Fig. 2D).

Drivers of ecosystem metabolism among and within ecosystem types—When all ecosystem types were considered together, only two factors explained variation in GPP and ER. Watershed size was positively related to GPP (r^2 = 0.344, $p < 0.001$) and ER (r^2 = 0.230, $p < 0.001$; Table 2; Fig. 3). Data points within each regression were distributed by ecosystem type: estuaries had the largest watershed size and highest rates of GPP and ER, lakes were intermediate, and streams had the lowest metabolism rates and watershed sizes (Fig. 3). P concentration, as TP or SRP, was positively related to GPP across ecosystem types (r^2 = 0.216, $p <$ 0.001; Table 2). Potential drivers that did not explain variation in GPP and ER with all ecosystems combined include DIN, TN, N : P, land use, temperature, and DOC. We note our explanatory power for land use and DOC was low because few studies presented these values.

When data from each ecosystem were considered independently, different environmental factors drove variation in GPP and ER within each ecosystem type. In general, drivers of GPP in streams were landscape factors (i.e., land use and riparian canopy cover), whereas water-column nutrient concentrations were strongly related to metabolism metrics in lake and estuaries. Open-canopy streams had higher GPP (*t*-test t = 8.70, degrees of freedom [df] = 111, $p < 0.001$) and ER (*t*-test t = 2.38, df = 111, p = 0.019) relative to closed-canopy streams (Table 2). Streams with dominant agricultural, grassland, and urban land use had higher GPP (ANOVA $F_{4,190}$ = 20.07, $p <$ 0.001) and GPP : ER (ANOVA $F_{4,190}$ = 10.28, $p < 0.001$) relative to streams with forested or desert land use (Table 2). However, there was no difference in stream ER among land-use types (ANOVA $F_{4,190}$ = 1.177, p = 0.322). Across lakes, TP was positively related to GPP (r^2 = 0.261, $p < 0.001$) and ER (r^2 = 0.239, $p < 0.001$) and chlorophyll *a* was positively related to GPP (r^2 = 0.204, p = 0.001) and ER (r^2 = 0.162, p = 0.001; Table 2). Also, GPP : ER in lakes was negatively related to DOC ($F_{1,48}$ = 12.48, $\log(\text{GPP}:\text{ER}) = -0.422 \times \log(\text{DOC}) + 0.253$, r^2 = 0.177, p = 0.001). Finally, SRP concentration was positively related to both ER (r^2 = 0.230, p = 0.004) and GPP in estuaries, and N : P ratio was negatively related to ER and GPP (r^2 = 0.170, p = 0.016; Table 2).

Discussion

Stronger coupling of ER and GPP in lakes and estuaries relative to rates in streams and wetlands is consistent with general paradigms for the relative importance of heterotrophy within each ecosystem type (Caffrey 2004; Young et al. 2008; Solomon et al. 2013), though few studies have incorporated this range of ecosystems in recent decades. Much of the ER in estuaries and lakes appears to be respiration of pelagic material because of the strong coupling of ER and GPP. However, a majority of sites were heterotrophic for all ecosystems (Table 1), so respiration of stored or allochthonous organic matter must also be contributing to ER in most cases. In addition, pelagic measurements of metabolism in lakes and estuaries underestimate rates of benthic heterotrophy, as the DO signal from sediment respiration or littoral areas may not be detected by the sensor in the water column (*see* "Challenges" below; Van De Bogert et al. 2012). In general, our results are consistent with recent studies illustrating the importance of allochthonous resources to food webs in lakes (Marcarelli et al. 2011; Wilkinson et al. 2013) and estuaries (Chanton and Lewis 2002), especially in ecosystems with high DOC. Although the data show clear

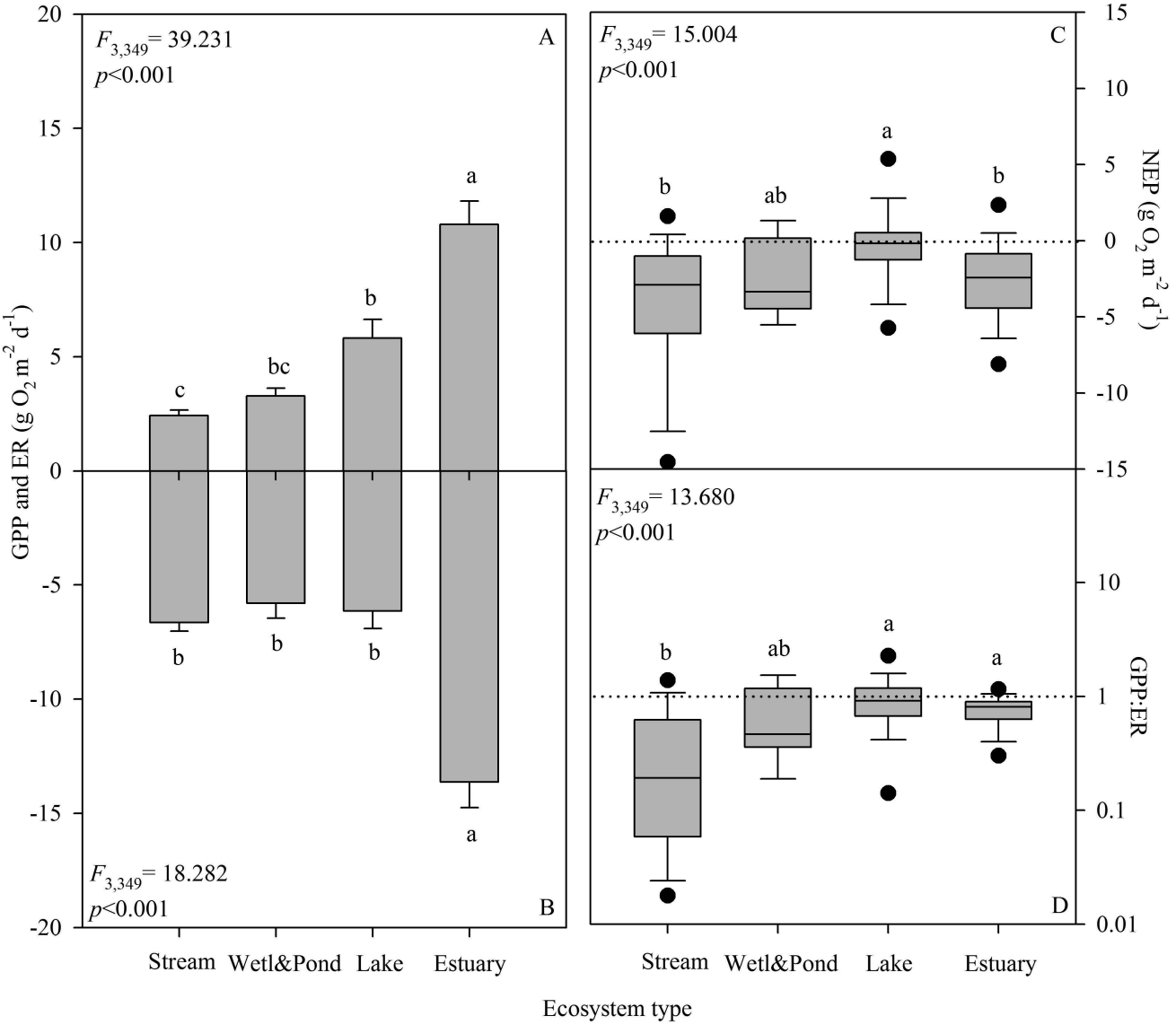

Fig. 2. Mean (± standard error) for (A) GPP and (B) ER across ecosystem types. Box and whisker plots of (C) NEP and (D) GPP : ER across aquatic ecosystems showing median (center line), 25th–75th percentiles (boxes) and 10th–90th percentiles (error bars). F and p values are from one-way ANOVA across ecosystem types for each metabolism metric. Dashed lines indicate NEP = 0 (C) and GPP : ER = 1 (D). Wetl&Pond = wetlands and ponds.

differences among ecosystem types, mean metabolism values suggest each aquatic ecosystem is more likely a CO_2 source rather than a sink, despite the potential for the open-water method to underestimate benthic heterotrophy in lakes and estuaries.

Both Odum (1956) and Whittaker (1975) considered lakes to be less productive than estuaries or other shallow marine environments. In contrast, our synthesis showed the most productive lakes had GPP and ER values that were nearly identical to metabolism in estuaries (Fig. 1B). Metabolism in estuaries was less variable than in lakes, however, so some lakes had much lower GPP and ER than any of the estuaries. High rates of GPP in lakes are logical given that many of the same factors credited with driving high GPP and ER in estuaries could also occur in some lakes. These include rapid nutrient cycling, long water residence time, the influence of vegetation, and watershed size. The potential for some lakes to have rates of GPP and ER comparable to those of estuaries was not included in previous conceptual models and C budgets (Whittaker 1975). Our analysis supports the concept that productive lakes have the capacity for C storage on the landscape (Cole et al. 2007), even though the majority of sites in our analyses were heterotrophic as measured by NEP.

Increasing DOC concentrations in lakes drove metabolism rates perpendicular to the 1 : 1 line from autotrophic to heterotrophic (Fig. 1B,C), mainly affecting ER. DOC has been shown to increase heterotrophic respiration and microbial productivity (Hanson et al. 2003; Maranger et al. 2005) and limit productivity via shading of autotrophic organisms (Carpenter et al. 1998; Karlsson et al. 2009) across ecosystem types. DOC quantity,

Table 1. Results of linear regressions between GPP (independent variable) and ER and for each ecosystem (units for GPP and ER: g O_2 m^{-2} d^{-1}) and the proportion of NEP measurements < 0. Wetl&Pond = wetlands and ponds.

	Linear regression					NEP<0	
Ecosystem	Equation	F	p	r^2	n	No.	%
Stream	ER=0.78×GPP+4.8	63.9	<0.001	0.23	215	186	87
Wetl&Pond	ER=0.25×GPP+5.0	0.19	0.671	0.02	13	10	77
Lake	ER=0.86×GPP+1.1	364.0	<0.001	0.84	72	44	61
Estuary	ER=1.04×GPP+2.5	273.3	<0.001	0.87	43	42	89

composition, and lability can control how DOC affects metabolism before C is exported or stored (Kaplan et al. 2008). This relationship is likely not unique to lakes; however, we were unable to evaluate the connection in the other ecosystem types because our dataset included DOC measurements for only 33% of the stream and 4% of the estuary metabolism measurements.

High rates of ecosystem metabolism in estuaries relative to other ecosystem types are consistent with classic literature (Lieth 1978; Whittaker 1975; Whittaker and Likens 1973). This has been attributed to effective turnover of nutrients in shallow marine environments (Gardner et al. 2006), water residence time (Russell et al. 2006), the influence of macrophytes and rooted vegetation (An and Joye 2001), and the movement of nutrients into estuaries from both marine and terrestrial environments. Our study adds new information to these drivers of high metabolism rates in estuaries, as we showed that the largest watersheds had the greatest rates of GPP and ER across all ecosystem types (Fig. 3). Estuaries had the highest and least variable watershed size in our synthesis, and the highest rates of GPP and ER. Large watersheds could drive higher metabolism rates because of the size of the landscape relative to the aquatic ecosystem, which would likely drain more nutrients, including N, P, silica, and C, into receiving bodies of water, stimulating GPP and ER (Howarth et al. 1991).

Metabolism measurements from open-water techniques indicate that wetlands and shallow ponds are heterotrophic (Fig. 2). This technique excludes the contribution of emergent macrophytes from estimates of open-water primary production (Hagerthey et al. 2010). Macrophytes with biomass production above the water surface produce atmospheric O_2, which is not recorded by DO sensors in the water. However, senescence of emergent macrophyte production builds organic matter pools at the wetland benthos, which can generate high rates of ER that *is* measured in open-water DO measurements (Hagerthey et al. 2010). In this way, open-water measurements reflect artificially low GPP : ER, and wetlands and ponds are autotrophic when macrophyte production is included with open-water estimates of metabolism (McKenna 2003; Thebault et al. 2008). We found a limited number (n = 13) of open-water estimates for wetlands and ponds (Table 2), and the NEP data in our synthesis do not include metabolism estimates for above-water GPP and ER that may be obtained through other metrics such as eddy covariance towers.

In contrast to lakes and estuaries, streams had greater instances of heterotrophy (Table 1) and the highest variation in GPP (Fig. 1B,C). To a greater extent than typically considered for estuaries and lakes, much of GPP and ER in streams occurs at the benthic surface rather than in the water column, and in some instances, the subsurface and parafluvial zones contribute significantly to stream ER (Gregory et al. 1991; Fellows et al. 2001). Therefore, ecosystem metabolism in streams may be more sensitive to changes in terrestrial riparian conditions (i.e., shading), and alterations to geomorphology (i.e., organic matter retention) than rates in lake or estuarine habitats. The dynamic nature of stream channels, benthic conditions, and riparian zones likely contributes to the high variation in GPP and ER among streams, and offers explanations for differences in environmental drivers of metabolism in streams relative to other aquatic habitats.

Drivers of ecosystem metabolism among and within ecosystem types—Our results contribute to the ongoing, vigorous debate on the relative importance of N and P in controlling rates of production in freshwater and marine ecosystems (Howarth and Paerl 2008; Schindler et al. 2008; Paerl 2009). Classic literature favored P limitation across all aquatic environments, but the importance of N limitation or N and P co-limitation is also recognized (Howarth and Marino 2006; Lewis et al. 2011). Our results support the paradigm with positive relationships among TP, chlorophyll *a*, and GPP in lakes. However, we did not find a relationship between N concentrations and GPP in estuaries as expected. Instead, the influence of P on GPP and ER was strong across estuaries. The relationship between P and GPP has been documented for estuaries elsewhere (Malone et al. 1996; Tyrrell 1999). However, we acknowledge that our results could also be due to the artifacts in data collection for our meta-analysis. The NERRS sites that make up most of our estuarine metabolism data are shallow and have high variation in salinity, nutrients, and hydrology. Therefore, these sites may not show N limitation commonly encountered at estuary locations with dominant marine influences. In addition, our NERRS water chemistry data were assembled from 5 yr averages of water chemistry from each site as a reasonable estimate of estuarine nutrients for a comparison across ecosystem types. Alternatively, the inclusion of many shallow, nearshore estuarine environments in our analysis could help illustrate a range in estuarine nutrient limitation patterns within the continuum of habitats from coastal to marine-influenced systems.

A notable difference in environmental drivers of ecosystem metabolism in streams relative to other ecosystem

Table 2. Mean, range, coefficient of variation (CV), and environmental drivers for GPP, ER, and NEP across ecosystem types (g O_2 m^{-2} d^{-1}). ag = agricultural; ns = no significant drivers; na = not applicable; Wetl&Pond = wetlands and ponds; SLR = simple linear regression; Chl *a* = chlorophyll *a*; wshed = watershed.

Ecosystem	Rate	Mean	Range	CV	Driver	Test	*F* or *t* value	*p* value	Equation or multiple comparison test
Stream (n=215)	GPP	2.4	0.0–16.3	144	Canopy	*t*-test	t_{111}=8.7	<0.001	Open>closed
	—	—	—	—	Land use	ANOVA	$F_{4,190}$=20.1	<0.001	Urban, ag., grassland>forest, desert
	ER	6.7	0.0–30.0	85	Canopy	*t*-test	t_{111}=2.4	<0.001	Open>closed
	NEP	−4.2	−27.0–7.3	—	ns	—	—	—	—
Wetl&Pond (n=13)	GPP	3.3	0.7–5.7	38	na	—	—	—	—
	ER	5.8	1.9–8.9	40	na	—	—	—	—
	NEP	−2.5	−6.0–1.3	—	na	—	—	—	—
Lake (n=72)	GPP	5.8	0.1–35.2	120	Chl *a*	SLR	$F_{1,64}$=16.4	<0.001	log(GPP)=0.454×log(Chl *a*)+0.016
	—	—	—	—	TP	SLR	$F_{1,47}$=16.6	<0.001	log(GPP)=0.651×log(Chl *a*)−0.468
	ER	6.1	0.1–32.1	107	Chl *a*	SLR	$F_{1,64}$=12.4	<0.001	log(ER)=0.412×log(Chl *a*)+0.121
	—	—	—	—	TP	SLR	$F_{1,47}$=14.8	<0.001	log(ER)=0.502×log(TP)−0.122
	NEP	−0.3	−7.0–9.9	—	ns	—	—	—	—
Estuary (n=47)	GPP	10.8	1.2–28.1	62	SRP	SLR	$F_{1,32}$=10.9	0.013	log(GPP)=0.388×log(SRP)+0.392
	—	—	—	—	N:P	SLR	$F_{1,32}$=7.5	0.010	log(GPP)=−0.310×log(N:P)+1.173
	ER	13.6	1.2–33.4	54	SRP	SLR	$F_{1,32}$=9.5	0.004	log(ER)=0.282×log(SRP)+0.689
	—	—	—	—	N:P	SLR	$F_{1,32}$=7.6	0.016	log(ER)=−0.238×log(N:P)+1.165
	NEP	−2.7	−9.0–5.2	—	ns	—	—	—	—
All (n=350)	GPP	4.2	0–35.2	132	TP or SRP	SLR	$F_{1,302}$=7.9	0.006	log(GPP)=0.046×log(P)+0.107
	—	—	—	—	wshed size	SLR	$F_{1,171}$=89.7	<0.001	log(GPP)=0.256×log(size)−0.036
	ER	7.4	0–33.4	87	wshed size	SLR	$F_{1,170}$=80.9	<0.001	log(ER)=0.127×log(size)+0.584
	NEP	−3.1	−26.6–9.9	—	ns	—	—	—	—

Fig. 3. Simple linear regressions between watershed size and (A) GPP and (B) ER across aquatic ecosystems. The number of replicates and r^2 indicated in each panel are results of significant regressions ($p < 0.001$ in both cases). Dotted lines represent 95% confidence intervals.

types is the lack of a clear relationship with nutrient concentrations. Previous studies of stream metabolism also showed the strongest drivers for GPP or NEP were landscape factors (i.e., canopy cover and land use), whereas stream water N or P concentrations were secondary drivers or unrelated to metabolism (Dodds and Cole 2007; Young et al. 2008; Bernot et al. 2010). Although our results confirm patterns from the stream literature, the contrast that terrestrial factors drive stream metabolism whereas water-column factors are more important to other aquatic habitats is rarely made explicit and warrants explanation.

Potential explanations for the lack of relationship between water-column nutrients and metabolism in streams relative to lakes and estuaries could be differences in hydrology or the metabolic demands of stream heterotrophs. In lakes and estuaries, much of GPP occurs in the epilimnion or surface waters, where phytoplankton are the

dominant primary producers, light penetration is at a maximum, water residence time is long, and nutrients are turbulently mixed throughout the epilimnion. However, ecosystem metabolism in streams predominantly occurs in benthic biofilms and hyporheic zones. This requires continuous exchange of nutrients between the water column and benthic zone across flow boundaries (Battin et al. 2003). As a result of the hydrologic disconnect, water-column concentrations may not accurately reflect nutrients available for stream biofilm metabolism. In addition, for heterotrophic stream ecosystems, nutrients may be obtained through pathways other than uptake of inorganic N and P from the water column. Heterotrophs that use dissolved organic nutrients (Brookshire et al. 2005) or obtain nutrients from the decomposing substrata on which they live (Dodds et al. 2004) may disconnect water-column nutrient concentrations and ER.

Using the framework of a highly balanced dataset for ecosystem metabolism and ancillary variables among 72 North American streams, Bernot et al. (2010) used structural equation modeling to quantify the strength of direct and indirect drivers of stream GPP and ER (fig. 7 in that paper). We were unable to use this quantitative approach, as our meta-dataset was unbalanced across all ecosystem types; however, results in Table 2 indicate that the strengths of direct (e.g., nutrients) and indirect (e.g., land-use) drivers to metabolism vary across all aquatic ecosystems. For example, light is a direct driver of GPP. For streams, the presence of riparian forest canopy cover dictates when light limits GPP (Table 2; Roberts et al. 2007). In lakes, DOC concentration can affect whether GPP is light limited (Solomon et al. 2013). Turbidity in estuaries is controlled by catchment conditions, the hydrograph of inflowing rivers and tides, internal geomorphology, and hydrodynamics, which together affect light levels that drive GPP (Caffrey 2004). As more comprehensive, long-term metabolism datasets emerge, structural equation models quantifying the relative importance of these interactions on GPP and ER across ecosystem types will strengthen our understanding of aquatic ecosystem function.

Temperature is an important driver of variation in ecosystem metabolism across terrestrial and aquatic ecosystems (Caffrey 2004; Hanson et al. 2006; Yvon-Durocher et al. 2012). Our use of only summer data may have obscured the importance of temperature in this synthesis. However, we note that other factors that drive GPP and ER can be greater than the influence of temperature under some conditions. For example, spring blooms of algae follow water-column mixing or sediment nutrient releases in coastal and pelagic marine ecosystems and in some lakes, despite relatively low temperatures (Siegel et al. 2002). In temperate forested streams, springtime algal blooms produce the highest rates of GPP during the year because light limitation is alleviated, whereas autumn leaf fall generates the highest ER (Roberts et al. 2007). Future studies that incorporate seasonality in aquatic ecosystem syntheses will be positioned to address the complexity of relationships among metabolism and seasonal variation in light, temperature, and nutrients across different aquatic ecosystems.

A comparison of the highest values of GPP and ER in this synthesis can help to delineate the range over which metabolism might be expected using the open-water diel O_2 method and to identify potential drivers of metabolism. The top 5% of GPP was similar in lakes and estuaries at 27.1 and 25.1 g O_2 m^{-2} d^{-1} respectively, whereas for streams the top 5% was 13.2 g O_2 m^{-2} d^{-1}. The highest 5% of ER in lakes, estuaries, and streams was relatively uniform at 26.8, 30.4, and 22.7 g O_2 m^{-2} d^{-1}, respectively. Using chamber approaches with individual organisms and communities of algae and macrophytes exposed to a gradient of irradiance, Binzer et al. (2006) and Sand-Jensen and Krause-Jensen (1997) estimated the maximum potential O_2 production of aquatic primary producers at 61–72 g O_2 m^{-2} d^{-1} (22–26 μmol O_2 m^{-2} s^{-1}). Our highest results are approximately 50% of this potential. GPP in natural ecosystems is reduced from maximum potential by many factors, including ambient temperature, shading, turbidity, and competition from heterotrophs. These comparisons, in addition to future syntheses, can help establish ranges of expected metabolism values for aquatic ecosystem types, which will be useful for protocols incorporating metabolism into ecosystem monitoring or management plans.

Rates of ecosystem metabolism and nutrient cycling—Functional measurements (e.g., rates of ecosystem metabolism and nutrient cycling) are advantageous in ecosystem assessment because they integrate the action of multiple organisms and trophic levels, and therefore are indicators of biological activity at the time of measurement (Lake et al. 2007; Williamson et al. 2009; Woodward et al. 2012). Although structural measurements (e.g., nutrient concentrations, Chl *a*, and invertebrate community composition) are successfully used to monitor water quality, they result from activity occurring over unknown periods of time, and may be less indicative of ecological processes occurring at the exact time the samples were collected (Palmer and Febria 2012). Therefore, delineation of environmental drivers of metabolism among ecosystem types may benefit from comparing them to rates of nutrient cycling rather than nutrient concentrations alone. For example, rapid NH_4^+ cycling rates can be masked by low and steady NH_4^+ concentrations (Gardner et al. 2006), and nutrient loading rates can be more strongly related to GPP than nutrient concentrations (Caffrey et al. 2007). In addition, nutrient uptake rates, rather than concentrations, explain variation in stream metabolism among sites and dates (Hoellein et al. 2007). Linking nutrient transformation rates with ecosystem metabolism metrics across ecosystem types is challenging, but it is a worthwhile goal as it may inform best practices for management and monitoring (Russell et al. 2006; Woodward et al. 2012).

Challenges for cross-ecosystem data syntheses—The comparison of ecosystem metabolism among aquatic environments is a powerful tool for analyzing controls on GPP and ER within and among ecosystems; however, there are important considerations for data interpretation related to disciplinary conventions, hydrology, and methodology. For example, in lakes and wetlands, N and P are typically

reported as TN and TP, whereas in streams and estuaries, we found DIN and SRP were more commonly measured. This convention inhibits data interpretation via statistical applications more sophisticated than simple linear regression (e.g., multivariate statistics). The absence of a common measurement may help explain why inorganic N concentration was unrelated to ecosystem metabolism in estuaries or when all ecosystem types were combined. In a similar fashion, the lack of concurrent DOC and metabolism measurements in streams and estuaries inhibited our analyses. Finally, the deployment times for sondes in lakes, estuaries, and wetlands were typically longer than in streams (but *see* Roberts et al. 2007; Izagirre et al. 2008). The data reported for the latter were often integrated over one or several days, whereas measurements from the former three groups represented weeks or months. The reason for shorter deployment times in lotic ecosystems could be a greater focus on spatial variation in studies from streams, or flooding may represent a danger for damage or loss of equipment in streams that is not as commonly encountered in wetlands, lakes, or estuaries, where water velocity changes are less rapid and buoys or engineered docks reduce flooding risk.

A persistent challenge for open-water measurements of metabolism is determining the three-dimensional boundaries of the area included in the measurement. A sensor in a lake or estuary measures DO changes that are influenced by epipelagic NEP, whereas the relative contribution of benthic NEP to DO patterns is variable (Van De Bogert et al. 2012). For example, during periods of stratification by DO or salinity, we assume DO measurements were influenced only by biological activity in surface waters and atmospheric exchange. However, in unstratified or very shallow waters, the contribution of benthic organisms to the DO signal may be much higher. The dynamic hydrology of estuaries from flooding and tides can shift stratification depth on short time scales, further complicating the relative influence of benthic metabolism. It is also important to consider that in shallow water, DO can be influenced by benthic NEP and the influence of the littoral zone's submerged vegetation. Stream measurements of DO have similar unknown spatial boundaries. If using the one-station method, it is unclear how far upstream organisms are influencing the DO measurement (Chapra and DiToro 1991), and the influence of the hyporheic zone, parafluvial flows, or riparian vegetation can be highly variable (Gregory et al. 1991). Studies that examine variation in metabolism over small spatial scales are required to resolve the relative contribution of different habitat types to open-water measurements (Van De Bogert et al. 2012). These challenges affect data interpretation when comparing metabolism rates among sites and are opportunities for exploring new dimensions in metabolism within each environment.

Future syntheses and applications—Recent and ongoing technological developments will facilitate advances in aquatic metabolism research. Sensor networks that link data from a diversity of ecosystem types are rapidly expanding, and will enable syntheses of metabolism estimates from aquatic ecosystems at a global scale (Solomon et al. 2013). Further developments in robotics, wireless networks, and microchip sensors will enable spatially explicit analyses within an ecosystem type as well (Rundel et al. 2009). Data management among global networks represents a significant challenge for future metabolism data syntheses (Hanson 2007). Coordination with programmers and information technologists will enable more rapid syntheses of this growing data stream. Computationally intensive methods for metabolism parameter estimation, like inverse modeling (Solomon et al. 2013) and Bayesian Markov chain Monte Carlo modeling (Holtgrieve et al. 2010), will allow researchers to estimate daily metabolism metrics and establish uncertainty. Spatially explicit metabolism models will allow more comprehensive estimation of metabolism within each ecosystem and the connection between stratified layers; lotic and lentic areas; or littoral, pelagic, and benthic zones (Staehr et al. 2012*a*). Finally, R or Python computing environments could enable tools for metabolism calculation from live, streaming sensor data.

There is strong interest in using ecosystem metabolism as a management tool to indicate overall ecosystem health, response to restoration, and role in climate change (Lake et al. 2007; Williamson et al. 2009). Relative to single or average DO measurements, metabolism rates are integrative and dynamic (Odum 1956; Palmer and Febria 2012). In addition, the expensive infrastructures for high-resolution monitoring of DO, temperature, and weather are in place at many sites, and the data are frequently available on the Internet. Our synthesis shows clear patterns in the magnitude and variation of metabolism among ecosystem types, as well as environmental drivers of metabolism, which can inform ecosystem management and restoration, which use measurements of GPP and ER. However, our results also show that nutrient data reporting can be increased and standardized (e.g., DOC, DIN), more data integration is needed to consider seasonality, the spatial boundaries of open-water measurements require greater resolution, and analyzing how short-term changes in hydrology influence GPP and ER will help further understand their environmental drivers. These opportunities for continued syntheses will represent meaningful contributions towards basic and applied research in ecosystem metabolism across aquatic environments.

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