

The metabolism of aquatic ecosystems: history, applications, and future challenges

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Abstract Measurements of the production and consumption of organic material have been a focus of aquatic science for more than 80 years. Over the last century, a variety of approaches have been developed and employed for measuring rates of gross primary production (P_g), respiration (R), and net ecosystem production ($P_n = P_g - R$) within aquatic ecosystems. Here, we reconsider the range of approaches and applications for ecosystem metabolism measurements, and suggest ways by which such studies can continue to contribute to aquatic ecology. This paper reviews past and contemporary studies of aquatic ecosystem-level metabolism to identify their role in understanding

and managing aquatic systems. We identify four broad research objectives that have motivated ecosystem metabolism studies: (1) quantifying magnitude and variability of metabolic rates for cross-system comparison, (2) estimating organic matter transfer between adjacent systems or sub-systems, (3) measuring ecosystem-scale responses to perturbation, both natural and anthropogenic, and (4) quantifying and calibrating models of biogeochemical processes and trophic networks. The magnitudes of whole-system gross primary production, respiration and net ecosystem production rates vary among aquatic environments and are partly constrained by the chosen methodology. We argue that measurements of ecosystem metabolism should be a vital component of routine monitoring at larger scales in the aquatic environment using existing flexible, precise, and durable sensor technologies. Current and future aquatic ecosystem studies will benefit from application of new methods for metabolism measurements, which facilitate integration of process measurements and calibration of models for addressing fundamental questions involving ecosystem-scale processes.

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Introduction

The dynamic nature of food webs and biogeochemical cycles in aquatic ecosystems is tied to metabolic processes that involve the formation and/or utilization of organic matter (O'Neill 1986; De Angelis 1992). The combined anabolism and catabolism of all organisms within an ecosystem can be summed to quantify the metabolism of that ecosystem. This metabolism represents an integrated

measure of a system in terms of its overall rates of production and consumption of organic matter (Odum 1971). Efforts to quantify metabolism initially developed in parallel to ecosystem science, and as a result, have been highly influential in the development of aquatic ecology (Juday 1940; Lindeman 1942; Dineen 1953; Odum and Odum 1955; Woodwell and Whittaker 1968). Such measurements should continue to be an essential component of aquatic ecology in understanding large and complex changes to the biosphere.

Aquatic ecosystem metabolism has been determined with an increasingly diverse collection of methods, all of which have their limitations and strengths (Gazeau et al. 2005a; Kemp and Testa 2011). The methods vary widely in precision and temporal/spatial scale, and differ in their utility to measure gross or net processes. While no single method is perfect, the diversity and flexibility of the various methods allow for their application in studies of streams, rivers, lakes, estuaries, and the open ocean. Given the long research history of these measurements, it is useful to reconsider the range of successful applications, and their role in aquatic ecological research.

Although much has been learned during this long history, many questions remain regarding the influences of widespread anthropogenic perturbations on aquatic ecosystems, especially in poorly studied regions (Dodds and Cole 2007; Williamson et al. 2008). We describe here the rich and diverse contributions of ecosystem metabolism studies to the field of aquatic science, with an emphasis on methodological development and lessons learned from past research. We also identify future challenges for ecosystem metabolic studies including: (1) development of robust and flexible tools to quantify error associated with scaling and extrapolation, (2) matching methods with appropriate applications, and (3) understanding the role of climate change in aquatic metabolic balances.

Literature survey

The quantitative basis for this paper is a thorough review of text books and 350 published papers about aquatic ecosystem metabolism during the past century. Peer reviewed journal articles were initially collected in *ISI web of knowledge* using a search profile with “metabolism”, “production” and, “respiration” in combination with lakes, rivers, streams, estuaries, and oceans. Then, a backward search strategy was applied providing articles citing older central articles on aquatic ecosystem metabolism. Finally, articles were found via citations in textbook chapters on aquatic ecosystem metabolism. Although the list of papers reviewed is not exhaustive, as there have been published several thousands of articles on this subject, it is

representative and sufficiently large to provide a broad overview of methods and applications of aquatic metabolism.

Essential terms used in ecosystem metabolism studies

Many terms have been widely used in the literature to describe rates of ecosystem-level primary production and respiration. Gross primary production (P_g) is defined as the total autotrophic conversion of inorganic carbon to organic forms, independent of its fate. Ecosystem respiration (R) is the total oxidation of organic C to inorganic C by both heterotrophic and autotrophic organisms, with alternative notations including R_e , ecosystem R, ER, or where a method measures only a subset of the ecosystem components, community R or CR. Net ecosystem production (P_n) is the difference between P_g and R , and reflects the balance between all anabolic and catabolic processes. From a conceptual viewpoint it is useful to partition R_e into the respiration of the autotrophs themselves (R_a) and that of the heterotrophic organisms (R_h) (Lovett et al. 2006; Dodds and Cole 2007). Methodological constraints have, however, limited the ability to distinguish autotrophic from heterotrophic respiration (del Giorgio and Williams 2005). Assuming that R_a can be determined, it is possible to quantify the portion of primary production available for consumption, referred to as net primary production ($NPP = P_g - R_a$, Fig. 1, Woodwell and Whittaker 1968; Lovett et al. 2006; Cole et al. 2006). New terms for ecosystem metabolism have also appeared with the development of novel techniques, including gross oxygen production (GOP), which is the anabolic rate derived for the triple oxygen isotope technique (e.g. Luz and Barkan 2000).

Usually, different terms have been used for describing aquatic versus terrestrial ecosystem metabolism (Lovett et al. 2006; Chapin et al. 2006). In aquatic science, GOP and net community production (NCP) are comparable to P_g and P_n , respectively. GOP is used when O_2 is measured instead of carbon (Luz and Barkan 2000), and NCP is often used when just the pelagic aquatic community is being measured (e.g. Sweeney et al. 2000). Although P_n has been measured from the summation of container incubations or water column changes in dissolved inorganic carbon or O_2 , in most cases it can also be computed from import–export budgets (e.g. Kemp et al. 1997; Dillon and Molot 1997). Thus, P_n becomes equivalent to the carbon export (C_{export}) minus carbon import (C_{import}) plus the change in storage of organic material ($\text{del}C_{\text{org}}$ or just $\Delta C_{\text{storage}}$, Fig. 1):

$$P_n = \Delta C_{\text{storage}} + C_{\text{export}} - C_{\text{import}} \quad (1)$$

When considering long time frames, $\Delta C_{\text{storage}}$ is usually equated with the organic C that is buried in soils or

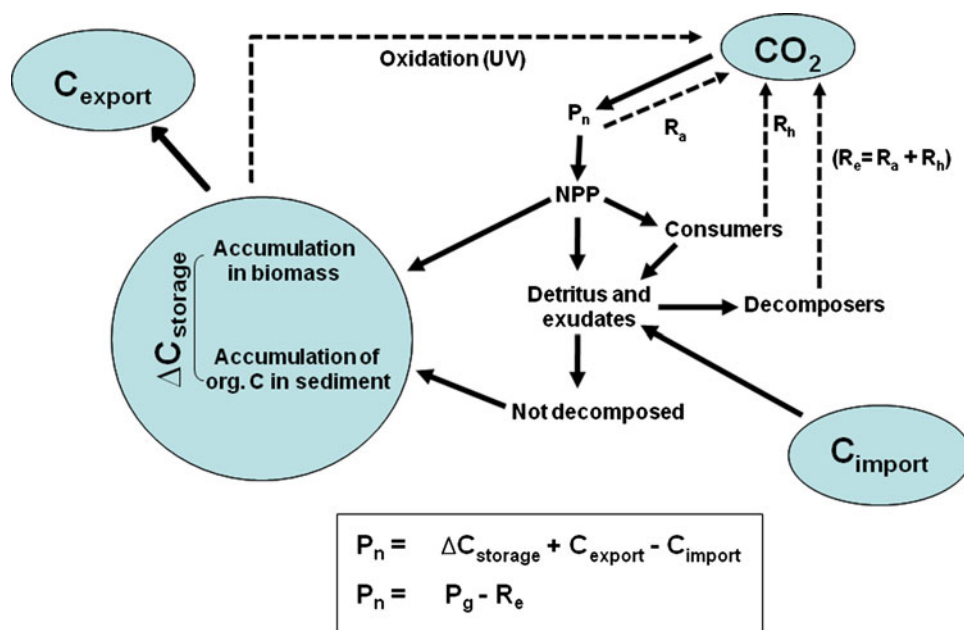


Fig. 1 Fates of organic carbon (C) fixed in or imported into an aquatic ecosystem. Total ecosystem respiration (R_e) is the sum of autotrophic respiration (R_a) and heterotrophic respiration (R_h). *Accumulation in biomass* represents all biomass (plant, animal, or microbial); the *arrow* is drawn from NPP in this diagram because plant biomass accumulation is generally the largest biomass term. NPP, net primary production; P_n , net ecosystem production; P_g , gross

primary production; CO_2 , carbon dioxide; UV, ultraviolet. *Dashed lines* represent degradation of C, *solid lines* production and/or transfer of C. Net autotrophic ecosystems ($P_n > 0$) have a net accumulation and/or net export organic matter, contrary to net heterotrophic ecosystems ($P_n < 0$) which depend on imported organic substances (After Lovett et al. 2006)

sediments and often notated as B (burial) or S (storage; Cole et al. 2007). The rationale for this terminology is that we do not expect to see significant changes in refractory organic carbon over time. Such P_n estimates are based on computed or measured physical fluxes.

History of methods development

The diversity of methods employed to measure or calculate P_g , R and P_n are characterized by a wide range of inherent scales (litres to km^3 , hours to years) and precisions, as well as particular differences in the processes that are actually being estimated. The scope and direction of ecosystem metabolism studies have often been constrained by the available techniques. Consequently, methodological developments have evolved over the last 80 years in parallel to growth in understanding of controls and variations in metabolic rates, which have followed an exponential increase in publications (Fig. 2). An analysis of 350 published studies of aquatic ecosystem metabolism reveals that this research has been done predominantly in North America (68%, USA and Canada), with fewer in Europe (27%), and very few in Asia and Africa (6%). The majority of studies have been conducted in temperate waters (79%), with far fewer in subtropical (10%), tropical (8%) and

arctic (3%) ecosystems. Although several novel techniques have been developed and applied during the last decade (Table 1), there is no apparent trend toward widespread application of a single type of method (Kemp and Testa 2011). Detailed descriptions of each method we outline below and their associated advantages and disadvantages can be found in the electronic supplementary material.

Direct measurements: bottle and chamber incubations

The pioneering work on coastal plankton metabolism in the 1920s included measurements of changes in dissolved O_2 concentrations during incubations of small bottles in light and darkness to estimate rates of primary production and respiration, respectively (Gaarder and Gran 1927). In fact, of all the methods used to measure aquatic ecosystem metabolism, the popularity of using incubations of water in bottles and chambers has persisted over time (Fig. 3), with subsequent developments using ^{14}C additions or tracing changes in dissolved inorganic carbon ($DIC = CO_2 + HCO_3^- + CO_3^{2-}$). Similar incubations of sediment chambers have been used to measure benthic photosynthesis and respiration, and when these rates are combined with bottle incubations of the water, they provide estimates of integrated ecosystem metabolism (e.g. Barko et al. 1977; Kemp et al. 1997; Gazeau et al. 2005a).

Fig. 2 Frequency in different methods used to investigate aquatic ecosystem metabolism during the last 80 years. The majority of studies have been devoted to understanding the carbon balance of the ecosystem. Many descriptive studies of annual, seasonal or daily changes in production and respiration have also been performed. A considerable amount of work has concerned the development of new techniques to measure ecosystem net production. In recent years, many studies have compared the carbon balance of different types of aquatic ecosystem and modeling has eventually become an important topic

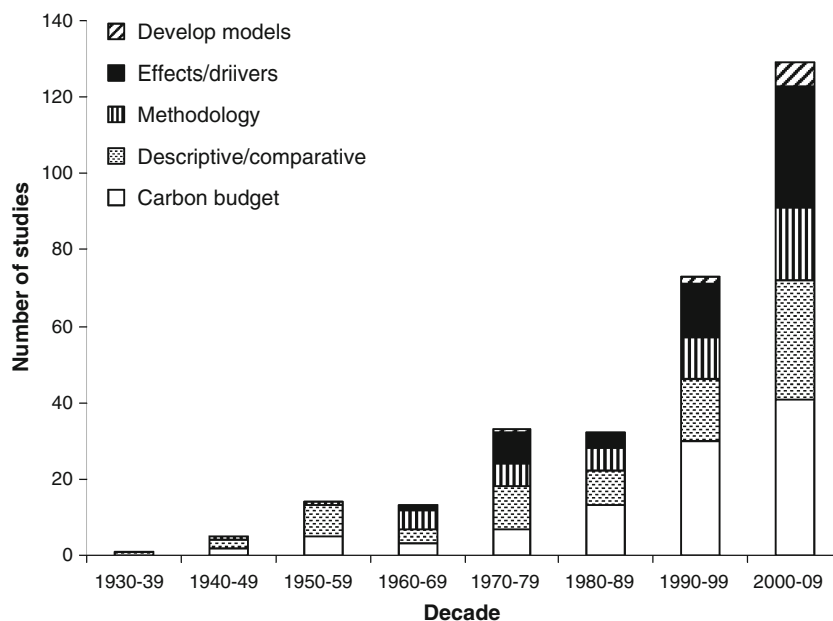


Table 1 A comparison of aspects of the most popular methods used to estimate P_g , R , P_n , and $P_g:R$ in aquatic ecosystems

Method	System	Temporal scale	Advantages	Disadvantages
Diel O_2 , TCO_2 (Including the response surface method)	Estuary, lake, river, ocean	Daily, seasonal, annual	Measures all system components Remote data collection Straightforward computation Precise measurements High frequency rates Multi-variable sensors	Air–water flux difficult to quantify $O_2:C$ conversion problems Physics may obscure biology O_2 method misses anaerobic R Horizontal and vertical heterogeneity Stratification causes problems No component rates Import of water with gas super- or sub-saturated
Oxygen isotopes	Estuary, lake, river, ocean	Daily, seasonal	Measures all system components Rates can be long- and short-term Sensitive method	Air–water flux needed (TI) $O_2:C$ conversion problems (TI, ^{18}O) Sampling is work intensive (TI, ^{18}O) Traces diurnal P_g and R (^{18}O) Known fractionations limited (TI)
Ecosystem budgets	Estuary, lake, river, ocean	Seasonal, annual	Measures all system components Straightforward computation Data widely available Formal error estimates	Air–water flux difficult to quantify $O_2:C:DIP$ conversion problems Abiotic effects on PO_4^{3-} Large aggregation error Net rates (P_n) only
Incubations	Estuary, lake, river, ocean	Hourly, daily	Direct process measurement Highly controlled Precise measurements Can separate ecosystem components	$O_2:C$ conversion problems Containment artifacts Labor intensive Difficult to upscale to ecosystem

For isotope methods comments specific to the triple oxygen approach (TI) and the ^{18}O approach (^{18}O) are noted

Open water methods: O₂ or DIC concentration changes

It was not until the development of the diel curve technique (Sargent and Austin 1949, 1954) on a coral reef that ecosystem metabolism measurements became readily available for aquatic ecosystem studies. The method has been used extensively over the past three decades in all aquatic systems (Smith and Marsh 1973; Cole and Fisher 1978; Kemp and Boynton 1980; Barnes 1983; Gattuso et al. 1993; D'Avanzo et al. 1996; Caffrey 2003; Staehr and Sand-Jensen 2007; Coloso et al. 2008). The diel open-water technique provided a powerful alternative to bottle and chamber incubations, as it avoided the container artifacts and error propagation associated with incubations. This method allows measurement of aquatic ecosystem metabolism as changes in water column concentrations of O₂ or DIC in situ associated with photosynthesis during daylight and respiration at night (Odum 1956; Kenney et al. 1988). Although the open-water diel O₂/DIC technique has not changed fundamentally since the late 1950s, the advent of new, relatively inexpensive and robust sensors (especially for O₂) has made it possible to radically increase the range of temporal and spatial scales of observations (e.g. Van de Bogert et al. 2007; Coloso et al. 2008; Hanson et al. 2008; Staehr et al. 2010a). New statistical and modelling approaches based on this approach have been used to account for advection and mixing of O₂ due to tides, wind, and flow (Swaney et al. 1999) and to estimate

reaeration coefficients and metabolic properties, including better estimates of uncertainty (Aristegi et al. 2009; Holtgrieve et al. 2010; Tobias et al. 2009).

Open water methods: oxygen isotopes

Oxygen isotopes can be used as alternatives or enhancements to conventional measurements of O₂ changes for estimating P_g, P_n, R, and P_g:R (Quay et al. 1995; Bender et al. 2000; Luz and Barkan 2000; Russ et al. 2004; Tobias et al. 2007; Ostrom et al. 2005; Sarma et al. 2005; Venkiteswaran et al. 2008). Rates of P_g integrated across broad spatial and temporal scales can be estimated from measurements of the relative isotopic composition of atmospheric and dissolved O₂ (¹⁶O₂, ¹⁷O₂ and ¹⁸O₂) and the rate of exchange of O₂ between air and water (Luz et al. 1999; Sarma et al. 2005). Measurements of δ¹⁸O have also been used to estimate P_g, R, and P_g:R separately over diel cycles in open waters (Tobias et al. 2007), in enclosed bottle experiments (e.g. Bender et al. 2000; Luz et al. 2002), and the P:R ratio can also be estimated using the ratio of ¹⁸O₂ to ¹⁶O₂ (Quay et al. 1995; Russ et al. 2004). Isotope methods, although relatively new, are promising due to their high precision (Bender et al. 1987), their ability to estimate rates integrated over larger spatial scales (Sarma et al. 2005), and their ability to provide short-term estimates (diel changes) of P_g, R and P_g:R (Tobias et al. 2007).

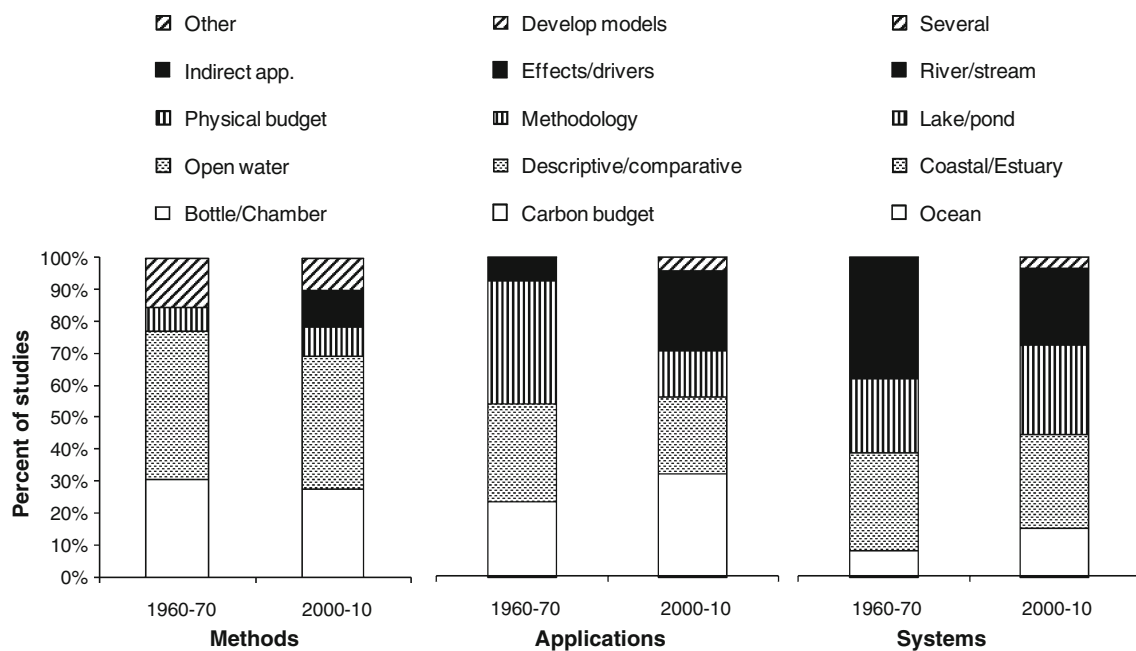


Fig. 3 Comparisons between the periods 1960–1970 and 2000–2010 of the proportion of publications where (left) methodology used to compute ecosystem metabolism, (middle) the application of different methods used to determine net ecosystem metabolism or a related term of metabolism, and (right) the type of aquatic ecosystem where

metabolic measurements were made. See text for details on the different methods. The data suggest a general trend toward more diverse methods in more ecosystem types, while the balance of applications has shifted away from descriptive and methodological studies toward more studies concerning drivers and budgets

Ecosystem budgets

Although ecosystem metabolism was historically estimated directly from tracing metabolites over short time in containers or open waters (Beyers and Odum 1959; Smith 1973; Smith and Key 1975), the advent of large-scale, high-quality water quality monitoring programs allowed for estimates of net metabolism to be made indirectly from mass balances of physical inputs and outputs for marine ecosystems (Smith and Hollibaugh 1993; Gordon et al. 1996; Crossland et al. 2005; Gazeau et al. 2005a; Testa and Kemp 2008). Ecosystem budget approaches allow determinations of mean P_n integrated over larger time and space scales than bottle incubations and open water methods. With this approach, P_n is estimated as the residual flux for inputs and outputs across discrete volumes (i.e. the remaining net flux after all other physical fluxes are taken into account for fluxes of carbon (TOC or DIC), dissolved inorganic phosphorus (DIP), or O_2). The physical transport terms (advective flow and diffusive mixing) in such budgets are computed from water- and salt-balance equations where salinity distribution and freshwater inputs are known (e.g. Smith and Hollibaugh 1993; Gazeau et al. 2005a; Testa and Kemp 2008) or from numerical models (e.g. Kremer et al. 2010). This approach can be widely applied to different aquatic ecosystems world-wide over multiple seasons and years, thus allowing a uniform standardized methodology for comparative analysis of diverse ecosystems, and represents a powerful approach for analyzing P_n responses to changes in climate and nutrient loading and other perturbations. Despite the limitations of this approach (Table 1, Smith et al. 1991; Gazeau et al. 2005a; Testa and Kemp 2008), the scales of estimates it provides are difficult to obtain otherwise. Efforts that combine mass balance computations (estimates of import, export and whole-system productivity) with internal, short-term rate measurements (e.g. container incubations) are perhaps the most comprehensive efforts (Kemp et al. 1997; Gazeau et al. 2005a), but are difficult to achieve.

Other approaches

Several other approaches have been applied to aquatic ecosystems to estimate P_n . For example, investigators have evaluated P_n by measuring partial pressures of O_2 and DIC in surface water and the atmosphere, and multiplying the difference between the measured concentration by the solubility saturation concentration (or gas partial pressure, pO_2 , pCO_2) by an air–water exchange coefficient (“piston velocity”) estimated from empirical relationships with wind speed (Cole et al. 1994; Frankignoulle et al. 1998; del Giorgio et al. 1999; Cole et al. 2000; Najjar and Keeling 2000; Borges et al. 2004; Sobek et al. 2005) and/or with

water current velocity (Sand-Jensen and Staehr 2011). Estimates of global net community production can also been determined from the decrease in salinity normalized total DIC inventory in the surface mixed layer corrected for changes due to net air-sea CO_2 , exchange and diffusive carbon flux from the upper thermocline (Lee 2001). Monitoring of the uptake and distribution of isotopically labelled inorganic C (^{14}C or ^{13}C) following addition to whole ecosystems offers an alternative approach to measuring primary production (Kelly et al. 1978; Hesslein et al. 1980; Schindler 1998). Recent reports have exploited the contrasting distributions of O_2 and N_2 gas to estimate system metabolism at various depths (McNiell et al. 2006). Finally, continuous measurements of air–water exchange of CO_2 (or O_2) at fixed stations or station arrays represent a direct approach for measuring P_n (e.g. Borges et al. 2005; Frankignoulle et al. 1998; Gattuso et al. 1993; Kemp and Testa 2011).

Application of ecosystem metabolism measurements

The application of metabolic measurements in aquatic science varied widely over the past 80 years, without a consistent objective. Many efforts were descriptive (aiming to understand the magnitude and variability in metabolic rates), while others tested new methods, examined external controls, or quantified contributions to large-scale budgets (Fig. 2). Here, we highlight selected applications of metabolic measurements that illustrate insights gained regarding ecosystem function.

Quantifying rates and trophic status

Rates of primary production as well as respiration can be used to evaluate what has been called the “trophic state” of an aquatic ecosystem (Dodds and Cole 2007). Many early studies also focused on describing the status of aquatic ecosystems with respect to the balance between organic matter production and consumption (e.g. Odum 1956). Generally, these measurements indicated that most aquatic ecosystems are net heterotrophic ($P_g < R$) indicating that they receive significant inputs of organic carbon from adjacent ecosystems (del Giorgio et al. 1999; Duarte and Prairie 2005; Dodds and Cole 2007). But over longer durations and for larger spatial scales, ecosystem production and respiration tend to move toward a balanced condition where $P_g = R$ and $P_n = 0$ if burial is minimal (Odum 1956). Theoretically, this balance arises because any increases in primary production yield organic matter, which in a relatively closed system, will eventually be respired proportionally. Alternatively, any increases in respiration will release inorganic nutrients that

proportionally stimulate primary production. Deviations from P_g :R balance are interesting because they reveal metabolic responses to recent or nearby perturbations (e.g. Yvon-Durocher et al. 2010). An important proportion of metabolic studies have investigated the time scales under which changes in rates and drivers of regulation occur (e.g. Smith and Hollibaugh 1997; Uehlinger 2006; Roberts et al. 2007; Staehr and Sand-Jensen 2007). Regions where carbon production or consumption dominates may be separated such that the carbon balance of streams, rivers, and estuaries varies along the continuum from headwaters to the sea (e.g. Heath 1995; Garnier and Billen 2007). Comparisons of metabolic rates across different systems may also enhance our theoretical understanding of functional differences and similarities among systems (e.g. Odum 1956; Gordon et al. 1996; Smith et al. 2005b; Dodds and Cole 2007; Staehr et al. 2010b). These comparisons are useful because P_n is a fundamental property of all ecosystems that provides a unique, integrated measure of many physiological and ecological processes. Such studies have clearly described how metabolism varies (1) over seasons and among regional subsystems (e.g. Kemp et al. 1997), (2) with system size and location (e.g. Dodds and Cole 2007; Sand-Jensen and Staehr 2007), and (3) over inter-annual or decadal scales (e.g. Smith and Hollibaugh 1997).

Metabolic balance and exchanges with adjacent systems

Metabolic balance in ecosystems open to exchange (especially streams and estuaries) is sensitive to inputs and outputs of organic matter (Fisher and Likens 1973; Tank et al. 2010), where watershed disturbance may cause metabolic imbalances in receiving aquatic ecosystems (Odum 1971). Past studies have highlighted the role of external carbon imports (e.g., via riverine inflows) in fueling net heterotrophy (e.g. Howarth et al. 1996; Ram et al. 2003; Cole et al. 2006), while others have revealed how carbon produced in one region of an aquatic system may cause heterotrophy in adjacent regions following horizontal or vertical transport (e.g. Kemp et al. 1999; Cole et al. 2007; Williamson et al. 2008; Lamberti et al. 2010). Although few studies have quantified carbon flows and transformations across entire ecosystems (e.g. Algesten et al. 2004; Caraco and Cole 2004), such information will allow more specific predictions for how major changes in land use and global climate will influence metabolic balance (Blenckner 2005; Benoy et al. 2007; Jonsson et al. 2007).

Measured rates of P_n in upper layers of the water column have been shown to correlate with net vertical transport (sinking) of particulate organic carbon (POC) and to subsequent bottom-layer respiration supported by this sinking organic matter (e.g. Oviatt et al. 1993; Kemp et al. 1994,

1999; Bozec et al. 2006; Staehr et al. 2011). In addition to vertical exchanges, lateral and longitudinal carbon exchanges occur and can be supported by external inputs of nutrients or organic carbon (e.g. Vadeboncoeur et al. 2001, 2003; Testa and Kemp 2008). Stimulation of P_g by nutrient enrichment generally enhances P_n , leading to elevated POC transport to bottom waters, which has been associated with expanding low- O_2 areas in lakes and coastal waters (Diaz and Rosenberg 2008; Kemp et al. 2009). Shallow regions of aquatic ecosystems tend to be net autotrophic, often exporting particulate and dissolved organic matter to support respiration in adjacent deeper regions of a water body (e.g. Kemp et al. 1997; Caffrey et al. 1998; Van de Bogert et al. 2007). Carbon exchanges are also longitudinal, where carbon produced in nutrient enriched estuaries is transported seaward to fuel net heterotrophy downstream or on the adjacent shelf (Ram et al. 2003), or landward transport of organic matter from coastal upwelling areas can drive heterotrophy in adjacent estuarine ecosystems (e.g. Smith and Hollibaugh 1997).

Responses of metabolism to natural and human activity

Aquatic ecosystem metabolism represents a unique, convenient and integrative process that reflects system-level responses to external perturbations. Although P and R are expected approximately to balance over yearly to decadal time spans (Odum 1956), metabolic responses over shorter periods (seasonal and daily) reveal characteristic effects of disturbance and external inputs of inorganic or organic nutrients or contaminants (Odum 1971). The dynamics of ecosystem metabolism vary in response to normal seasonal changes in climatic conditions, as well as to unpredictable extreme disturbances (e.g. floods and storms). Many studies have examined effects of episodic events on metabolism in freshwater ecosystems (Aoki et al. 1996; Uehlinger et al. 2003; Acuña et al. 2004; Hanson et al. 2006; Tsai et al. 2008) and less in marine systems (Guadayol et al. 2009; Sarma et al. 2005). Episodic increases in stream flow, wind-driven mixing and sediment resuspension elicit clear responses in magnitude and balance of ecosystem P_g and R (e.g. Flöder and Sommer 1999). High flow events are often accompanied by pulsed inputs of inorganic nutrients, dissolved organic carbon (DOC) and suspended sediments, which can induce both positive and negative effects on primary production and respiration (e.g. Hanson et al. 2008; Tsai et al. 2008; Staehr et al. 2010b). Fundamental understanding of these responses to such episodic and intermittent events could be improved by deploying automated sensor systems in diverse aquatic ecosystems.

Aquatic ecosystems also receive inputs of inorganic and organic pollutants from agricultural, industrial, and urbanized land-uses and can be viewed as sentinels to

measure changes occurring in their catchments (Sanders et al. 2007; Williamson et al. 2008). Inputs of nutrients, labile organics, toxins and turbidity will elicit a range of metabolic responses in aquatic ecosystems. Ecosystem metabolism responses to eutrophication of lakes and estuaries are well documented worldwide (Oviatt et al. 1986; Smith et al. 2005b; Matthews and Effler 2006; Kemp et al. 2009), and to some extent in rivers (e.g., Gucker et al. 2009). In general, mesocosms studies on ecosystem metabolism responses to toxic contaminants (e.g., heavy metals, PCB's, pesticides) on ecosystem metabolism have reported that toxins reduce P_g and P_n , with mixed effects on R (e.g. Giddings and Eddlemon 1978; Laursen et al. 2002; Wiegner et al. 2003). However, since toxins primarily accumulate in sediments, effects are most obvious on benthic production with potential impacts on pelagic production through feedback mechanisms (Laursen et al. 2002). In nature, the effects of a single stressor (e.g. herbicide) are difficult to separate from that of other stressors (e.g. nutrients), as most ecosystems experience inputs of multiple stressors and nutrients may compete successfully with toxins (e.g. Reuther 1992; Wiegner et al. 2003). Further studies measuring P_g and R in polluted environments will help unravel the interacting effects of nutrients and toxins on aquatic metabolism.

Metabolism and global carbon balance

Observations of rising global temperatures and its association with anthropogenic net generation of CO_2 (Parry et al. 2007) have stimulated research into understanding whether aquatic ecosystems function as sinks or sources of CO_2 to the atmosphere through net autotrophic or heterotrophic annual balances (e.g., Smith and Hollibaugh 1993; del Giorgio and Williams 2005; Duarte and Prairie 2005; Cole et al. 2007; Bates and Mathis 2009). Various synthesis papers have combined numerous ecosystem metabolism measurements and biogeochemical models to estimate contributions of particular biomes or regions to the global carbon cycle (e.g. Lee 2001; Jin et al. 2006; Tranvik et al. 2009). Initial budgets of the global carbon balance suggested that the world's oceans represent a major sink for atmospheric CO_2 , and subsequent measurements indicated that autotrophic surface water (positive P_n) could be an important mechanism driving this sink (e.g. Broecker et al. 1979). This has later been supported by model studies suggesting that phytoplankton, diatoms and coccolithophorids in particular, provide a global carbon export to the ocean seafloor in the order of $1.1 \text{ PgC year}^{-1}$ (Jin et al. 2006). This is similar to recent estimates ($0.9 \text{ PgC year}^{-1}$) of total carbon export from land to sea (Tranvik et al. 2009). In recent studies, analyses of oceanic plankton community production and respiration indicated that large regions of

surface water in the ocean could be net heterotrophic (Duarte and Agusti 1998) and/or net autotrophic (e.g. Williams 1998; Laws et al. 2000), depending on the duration and spatial scale of integration (Karl et al. 2003). More recent analyses of surface pCO_2 and pO_2 distributions in the open ocean revealed strong seasonal cycles and regional trends in oceanic P_n and air–sea gas exchange (Najjar and Keeling 2000; Lee 2001, Takahashi et al. 2002). Additionally, the combined P_n for all shallow vegetated habitats in the coastal ocean (mangroves, salt marshes, seagrass, macroalgae) is estimated to exceed that of the pelagic ocean, serving as an important sink for atmospheric CO_2 (Duarte et al. 2005). Thus, these shallow vegetated habitats play a critical role in maintaining the oceanic sink for atmospheric CO_2 . Other researchers suggest that net heterotrophy in estuaries and coastal bays are counterbalanced by net autotrophy in marginal seas (Smith and Hollibaugh 1993; Borges et al. 2005; Chen and Borges 2009). A growing appreciation for the contributions of chemoautotrophy to C-fixation in the “dark ocean” (e.g. Reinthaler et al. 2010) and eutrophic systems (Gazeau et al. 2005c) should lead to further investigations, especially considering the fact that unlike all other metabolic processes described here, chemoautotrophic nitrification consumes both O_2 and DIC. Recent investigations of metabolism in arctic and subarctic latitudes should lead to better understanding of the contributions of these ecosystems to the global carbon balance (Ask et al. 2009; Bates and Mathis 2009; Squires et al. 2009).

Estimates of carbon uptake, release and storage in aquatic ecosystems are of growing importance as we seek to quantify the major sources and sinks of carbon in the biosphere to establish global carbon budgets in the face of climate change (Houghton 2007). The current limited sampling of metabolic estimates, and the inherent fine-scale variations in these processes have made calculations of net production for ocean basins (as well as for lakes and estuaries) extremely challenging (e.g. Kettle and Merchant 2005). The dynamic nature of aquatic ecosystems demands that estimates of contribution to global CO_2 balance be based on frequent, spatially distributed measurements of P_n over longer time periods. Continued development of new tools will be required to expand our understanding of contributions of aquatic ecosystems to the global carbon balance (e.g. Jenkins 1977; Smith and Hollibaugh 1993; Duarte and Agusti 1998; Gattuso et al. 1999; Laws et al. 2000; Lee 2001; Duarte and Regaudie-de-Gioux 2009).

Partitioning metabolism among habitats

Direct measurements of integrated metabolism can be combined with container incubations to quantify contributions by each biotic component to total metabolic rates

(e.g. Odum 1957; Hopkinson et al. 1999). Such rate partitioning allows a focus on one particular metabolic group or to address questions related to methodology or response to perturbation (e.g. Kemp et al. 1986; Smith and Hollibaugh 1997; Gazeau et al. 2005b, c). This application is often motivated by an interest in improving knowledge about interactions among ecosystem subunits or habitats or in investigating loss of ecosystem function with a decline in one component (e.g. Twilley et al. 1985). Metabolic partitioning studies also provide a check on the relative agreement between contrasting methods for estimating annual P_n , and recent studies suggest good agreement between budget approaches and the summation of plankton and benthic rates measured from container incubations (Kemp et al. 1997; Gazeau et al. 2005a).

In shallow estuaries and lakes, it is sometimes useful to partition the relative contributions to total ecosystem metabolism by *planktonic* versus *benthic* components, which have different turnover times within the ecosystem and support fundamentally different food-chains. For example, comparative studies of contemporaneously measured planktonic and benthic metabolism conclude that relative benthic contributions to total ecosystem respiration are inversely related to water column depth (e.g. Kemp et al. 1992; Heip et al. 1995). In addition, shallow aquatic systems are often co-inhabited by large-rooted vascular plants and by single-cell algae (planktonic and epiphytic), all of which compete for light and nutrients. Several studies partitioning P and R among these autotrophic groups have demonstrated that relative contributions of phytoplankton to total ecosystem metabolism tend to increase with nutrient enrichment (e.g. Twilley et al. 1985; Borum and Sand-Jensen 1996; Kaldy et al. 2002; Gazeau et al. 2005b, c).

Integration with ecosystem models

Ecological theory suggests that simple allometric scaling laws describe metabolic and bioenergetic rates for organism as a function of body size (e.g. Peters 1983). Similar relationships also appear to hold for metabolic processes and related ecological properties at larger scales of organization (Brown et al. 2004; Harris et al. 2006). The metabolic theory of ecology proposed by Brown et al. (2004) which integrates individual organisms into carbon cycle models at the ecosystem level, has recently been further developed for the open ocean (Lopez-Urrutia et al. 2006) and applied for lake mesocosms (Yvon-Durocher et al. 2010). These studies show that the balance between key biogeochemical fluxes at the ecosystem level can be predicted by the mass and temperature dependence of the metabolism of individual organisms.

Most ecological models are designed to portray trophic flux networks and/or simulate dynamic bioenergetics for

ensembles of organisms, populations, and functional groups. Because of their robust nature, these allometric relationships are often incorporated directly in the model structures or used to compute bioenergetic rate coefficients (e.g. Moloney and Fields 1991; Christensen and Walters 2004). Mass-balance constraints require that sum of metabolic rates (photosynthesis and respiration) for all model organisms and functional groups must equal the integrated metabolism of the model ecosystem. Recent studies have used trophic network models to calculate variations in ecosystem metabolism and organic carbon transport in relation to hypoxia development for different seasons near the Mississippi River plume in the northern Gulf of Mexico shelf (Breed et al. 2004; Green et al. 2006). Although this analysis represents an effective use of mass-balance models to compute ecosystem metabolism, this linkage of models with estimates of ecosystem metabolism would be more rigorous in reverse, where independent measurements of metabolism were used to constrain the trophic network model. With this mass-balance constraint imposed, the model could be used with greater confidence to compute, for example, changes in organic matter transport and consumption in relation to variations in hypoxia intensity and extent (e.g. Kemp and Testa 2011). Similarly, comparison of simulated patterns of ecosystem metabolism at different time and space scales with direct rate measurements represents a rigorous, but rarely used, test of skill for ecosystem process models (Prowse et al. 2009; Quinones-Rivera et al. 2009; Kemp and Testa 2011).

Future challenges and frontiers

Metabolic responses to climate variability

Climatic change and variability will alter both respiration and primary production (and thus the balance between the two) through a variety of mechanisms and pathways. Previous studies have documented effects of climate variability on aquatic metabolism (Smith and Hollibaugh 1997; Howarth et al. 2000; Roberts et al. 2007; Doney et al. 2009). Most analyses of global climate change predict regional increases in ambient temperature (Parry et al. 2007), shifts in precipitation and storm frequency (e.g. Arnell 1999; Rabalais and Gilbert 2009), and increased acidity of the ocean (e.g. Hoegh-Guldberg et al. 2007).

Although it is clear that decadal cycles and long-term changes in climatic and associated biogeochemical processes will have significant impacts on organic matter production and consumption, the magnitudes, trajectories, and geographic distributions of these changes are poorly understood. Climate induced increases in precipitation would tend to increase ecosystem production due to

increased stream-flow and associated nutrient delivery (e.g. Justic et al. 1996, 2003; Arnell 1999), as well as reduced estuarine residence time (e.g. Hagy et al. 2000; Smith et al. 2005a). Elevated loads of organic material under high flow will, however, also enhance respiration (Howarth et al. 1996) and reduce light availability for photosynthesis. These responses will be modulated by potentially increasing enrichment with inorganic nutrients, which generally tend to increase P_g more than R (Oviatt et al. 1986; Borum and Sand-Jensen 1996; D'Avanzo et al. 1996; Caffrey 2004; Rabalais et al. 2009). Changes in atmospheric pressure fields and associated wind patterns could decrease the intensity of upwelling-induced ecosystem production along many coastal shelf areas (e.g. Barth et al. 2007), while changing winds could also contribute to changes in stratification strength, as well as bottom O_2 pools and respiration rates in lakes and estuaries. Loss of coral reefs associated with ocean acidification would greatly diminish metabolic rates in these important ecosystems (Kleypas and Yates 2009). Although global temperature increases are likely to enhance both primary production and respiration (Smith and Kemp 1995; Caffrey 2003; Allen et al. 2005; Staehr and Sand-Jensen 2006), metabolic theory suggests that stronger effects on respiration will lead to lower P_n in the coastal ocean (Lopez-Urrutia et al. 2006). Future empirical and modeling studies should focus on improving knowledge about how ecosystem metabolism will respond to changing environmental conditions and alter the nature of productivity in aquatic environments.

Uncertainty analysis and error propagation

Each method used to measure ecosystem metabolism (Table 1) relies on a set of assumptions and each is constrained to particular temporal and spatial scales. There are surprisingly few studies comparing rates estimated using multiple methodologies (Bender et al. 1987; Kemp et al. 1997; Gazeau et al. 2005a) and even fewer studies have examined which methods are best suited to address which scientific questions. Statistical comparisons among methods and use of these methods to address scientific questions require quantification of errors and uncertainties associated with metabolic rate computations. Improved confidence in these rate measurements will result from rigorous methodological comparisons, and from efforts to scale up from short-term incubation measurements to rates integrated over larger space and time scales.

A way to address issues of scaling in methodological comparisons is to develop statistical protocols for quantifying uncertainty and error propagation. Uncertainty is inherent in all current methods (e.g. attributable to under-sampling, natural variability) and errors are propagated when the uncertainty associated with individual rates from

compartment incubations and budget terms are added to quantify metabolic rates at larger scales. Past comparisons have included very limited estimation of error propagation in their computations (e.g. Kemp et al. 1997; Smith and Hollibaugh 1997), while others have included estimates for a subset of the methods in the comparison (Gazeau et al. 2005a). Recent developments of novel approaches for quantifying errors and uncertainty (e.g. Holtgrieve et al. 2010; Lehrter and Cebrian 2010) need to be broadly utilized and applied consistently for metabolic rates derived from chamber incubations, open-water measurements, and mass-balance calculations.

New instrumentation

Improved and increasingly affordable instrumentation will allow for more temporally and spatially resolved estimates of metabolism along land-sea gradients. Improved instrumentation will also allow us to evaluate spatial and temporal variability within ecosystems by performing simultaneous high frequency time-series measurements at many positions. For example, recent oceanic and lacustrine deployments of spatially distributed arrays of sensor systems with continuous vertical profiling of O_2 and/or DIC, temperature and salinity, and chlorophyll-a provided unprecedented basin scale estimates of P_n and controlling factors (Van de Bogert et al. 2007; Martz et al. 2008). Automated Underwater Vehicle systems with similar instrumental capabilities provide an exciting alternative approach for measuring metabolic rates of larger oceanic, estuarine or lacustrine ecosystems (e.g. Nicholson et al. 2008). Deployment of these instruments will substantially improve the temporal and spatial frequency of rate estimates (both vertically and horizontally), allowing for evaluations of the effects of habitat gradients, physical transport regimes, phytoplankton patchiness, and other processes on metabolism (e.g. Kemp et al. 1997; Staehr et al. 2011).

Increasing data availability will continue to set the stage for expanded analyses of existing monitoring data for two approaches to estimating ecosystem metabolism: (1) the diel O_2 method and (2) biogeochemical budgets. Increasing availability of hydrologic and hydrographic monitoring will allow greater applicability of biogeochemical budgets in coastal ecosystems worldwide. Such analyses have the advantage of applying a consistent approach to all systems that can easily be computed with standardized computations, as has already been achieved (Smith et al. 2005b). With new data sets and continued analyses of such time series, a better understanding of external controls (e.g. management actions, climatic changes) will be allowed. Recent studies have already begun efforts to perform cross-system analyses to explore the effects of habitat, nutrient loading, and physical forcing (e.g. Caffrey 2004; Smith

et al. 2005b), while others have examined multi-decadal time-series for particular systems (e.g. Matthews and Effler 2006; Testa and Kemp 2008).

Conclusions

Eighty years of measurements of aquatic ecosystem metabolism have led to vastly improved understanding of metabolic processes, including their variability in many types of aquatic ecosystems, their response to external perturbations, and their influence in food web dynamics. Future ecological research in this field would benefit from a unified and coordinated approach that applies ecosystem metabolism measurements to address complex research questions and integrate modeling and empirical analyses. A unified research effort is particularly needed to improve our understanding of consequences of climate change on potential positive and negative metabolic feedbacks that could reinforce or stabilize climatic changes. Enhanced ability to compute error and estimate uncertainty in ecosystem metabolism measurements will improve their applicability for addressing resource management questions. Most of our contemporary understanding of aquatic ecosystem metabolism derives from studies in temperate and subtropical regions, and future investigations should focus more on metabolism of ecosystems at high and low latitudes. To facilitate cross-system analysis, there is a pressing need to compare different ecosystem metabolism methodologies, while utilizing improved sensor instrumentation to enhance our understanding of variability and controls on production and respiration processes throughout the globe.

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