

Ecologists have long been fascinated by the biological, chemical, and physical processes that regulate the flow of carbon, or energy, within ecosystems (Odum 1968). Carbon resources govern the structure of ecological communities and influence many other ecological processes. Therefore, understanding patterns in the spatial and temporal variation of the biological availability and quantity of organic resources moving within and through systems is an essential component in the study of stream ecology.

Energy sources in streams fall into two broad categories: autochthonous inputs derived from aquatic primary producers, and allochthonous inputs of organic matter from terrestrial ecosystems (Fig. 14.1). Heterotrophs—microorganisms, meiofauna, and macrofauna—decompose and consume supplies of organic carbon, ultimately mineralizing some fraction of the total as CO₂. Variable amounts of carbon may be stored within sediments, the riparian zone, and the floodplain (Fig. 14.2; Sutfin et al. 2016), and substantial quantities of allochthonous and autochthonous energy are exported downstream. This whole-ecosystem view brings into focus a series of topics that comprise the study of riverine carbon dynamics.

Lotic ecosystems are open, meaning that they receive energy from and supply energy to upstream and downstream habitats. Lateral energy exchanges between terrestrial and aquatic habitats are often substantial, especially when rivers are connected to a floodplain. Allochthonous organic matter is comprised of material derived from the tissues of plants and animals; it is a mixture of molecules that includes carbon and other elements. Allochthonous inputs of coarse, fine, and dissolved organic matter are substantial sources of carbon in many stream settings, especially in small streams shaded by a forested riparian zone, and in streams with high sediment load where algal primary production tends to be light-limited. In contrast, autochthonous production by algae and other primary producers is expected to make a greater contribution to the carbon pool in wider streams and rivers with reduced canopy cover, but less so in deeper and more

turbid rivers when light becomes limiting. Shifts between autochthony and allochthony represent a conversion from reliance on internal to external energy sources, and the relative contribution of internal versus external sources is expected to vary through space and time with landscape setting and along the river continuum (e.g., Vannote et al. 1980; Minshall et al. 1985; Thorp et al. 2006; Winemiller et al. 2010).

In this chapter, we focus on the biological processes that influence carbon fluxes as revealed by tracing the sources and fates of allochthonous organic matter, quantified from carbon budgets and transport estimates, and by measuring primary production (carbon fixed through photosynthesis) and respiration (carbon released through cellular respiration), collectively referred to as stream metabolism. Comparison of primary production and respiration across streams and seasons provides the basis to explore how environmental setting influences stream metabolism, and to gain insight into the relative contributions of autochthonous and allochthonous carbon sources. Quantification of the inputs, rates of utilization, transport, and storage of carbon, including particulate and dissolved organic matter originating from terrestrial and upstream sources, makes it possible to construct carbon budgets and estimate carbon utilization, providing additional insight into ecosystem processing of energy supplies. Together these approaches provide a powerful foundation allowing stream ecologists to measure and model carbon dynamics, and better understand some of the biological, chemical, and physical factors that influence carbon cycling in rivers and streams.

14.1 Energy Flow in Lotic Systems

It is apparent that energy flow in lotic ecosystems is spatially and temporally complex, and is dominated by a longitudinal gradient that is frequently interrupted by lakes, dams, stepped changes due to tributary inputs, and discrete habitat

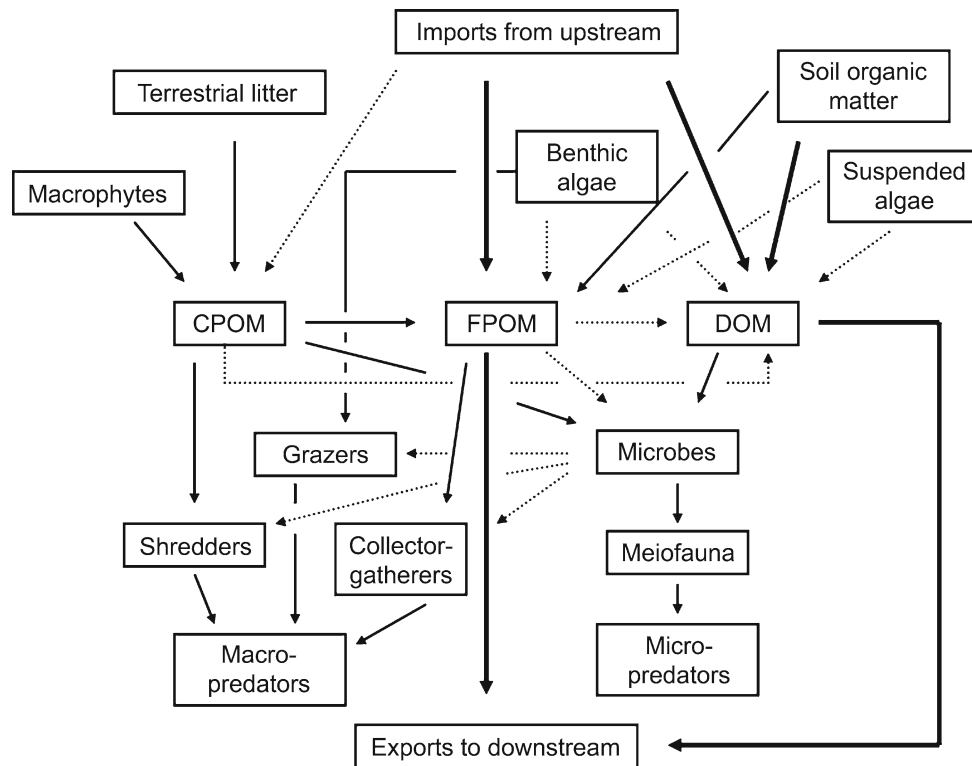


Fig. 14.1 Simplified model of principal carbon fluxes within a stream ecosystem (CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter; DOM, dissolved organic matter). Heavier lines indicate dominant pathways of transport or metabolism of organic

matter in a temperate woodland stream. Note that mineralization of organic carbon to CO_2 by respiration and storage are omitted. (Reproduced from Wetzel 1983)

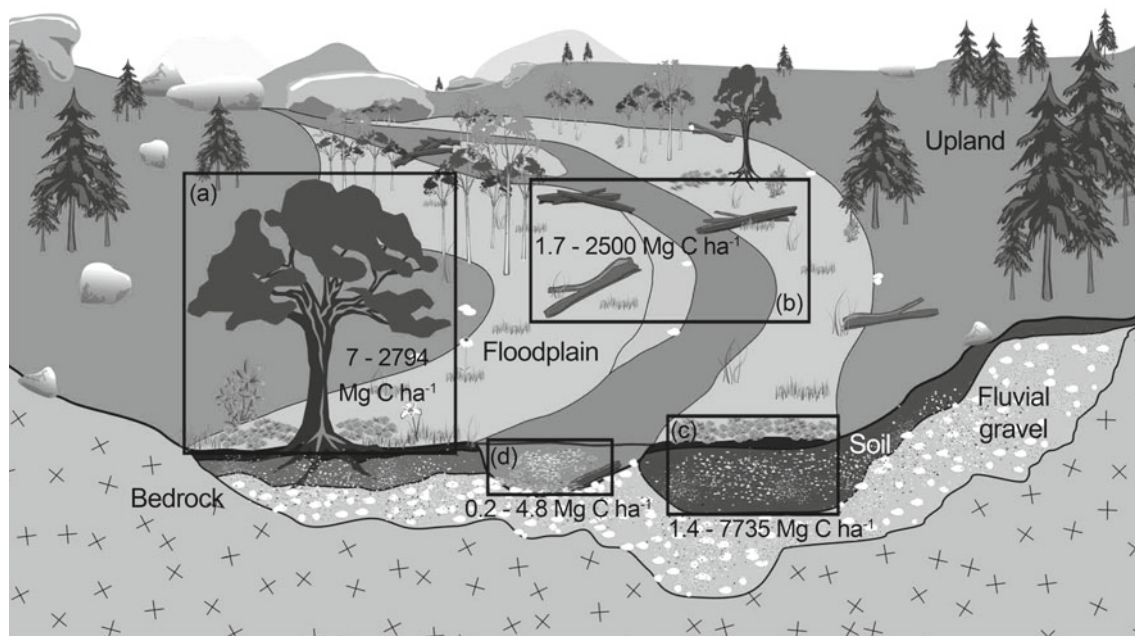


Fig. 14.2 Organic carbon is stored within four primary reservoirs in river systems: (a) above- and below-ground standing biomass as riparian vegetation, (b) large in-stream and downed wood on the floodplain, (c) sediment on the floodplain surface and in the shallow subsurface, including soil organic carbon, litter, and humus, and (d) in-stream biomass including filamentous algae, periphyton, benthic

invertebrates, fish, and particulate organic matter. Values indicate the estimated range of organic carbon per area (Mg C ha^{-1}). Note that in-stream biomass (d) accounts for a relatively small portion of carbon stored in river systems per area when compared to the other three reservoirs. (Reproduced from Sutfin et al. 2016)

types (Poole 2002; Webster 2007). The food webs of streams and rivers are fueled by a complex mixture of autochthonous and allochthonous energy sources, such that unraveling their relative contributions to higher trophic levels is a considerable challenge that stream ecologists have been studying for decades (Cummins and Klug 1979; Cummins et al. 1973; Minshall 1978).

Unlike terrestrial systems where large plants visible to the naked eye dominate autotrophic biomass, the primary producers of greatest significance in streams are the mostly microscopic benthic algae. These are found on stones, wood, and other surfaces and occur where light, nutrients, and other conditions are suitable for their growth. Organic matter that enters the stream from the surrounding land, such as leaf fall and other plant and animal detritus, is a significant energy source in most streams. Bacteria and fungi are the immediate consumers of organic substrates and in doing so create a microbe-rich and nutritious food supply for consumers, including biofilms on both inorganic and organic surfaces, and autumn-shed leaves riddled with fungal mycelia. These were the topics of Chaps. 6, 7 and 8.

The sources, processing, and fate of organic carbon are the determinants of energy flow in rivers and streams. Landscape constraints on the physical structure of a stream ecosystem determine which processes have local preeminence. For example, when lateral connectivity is high, the stream system will be strongly influenced by floodplain interactions; when vertical connectivity is high, the stream system will be strongly influenced by interactions with the hyporheos; and when both lateral and vertical connectivity are constrained, the stream will be most strongly impacted by upstream processes and by interruptions due to lakes and dams. Measuring the fluxes of primary production and respiration, and quantifying the flow of carbon through aquatic communities, are some of the principal methods to help researchers unravel the magnitude, range of variation, and response of carbon dynamics to both natural and anthropogenic factors.

Scientists have developed many conceptual frameworks to predict energy flow in rivers and streams. Collectively, these concepts provide a foundation for research in aquatic biogeochemistry and food web ecology. They also highlight some of the important, site-specific aspects of rivers to consider when examining carbon dynamics, including network connectivity and the ease of assimilation of diverse carbon sources. Some of the most important concepts pertain to changes along a river's length, the river's interactions with its floodplain, and the relative importance of different energy sources in supporting higher consumers in the food web.

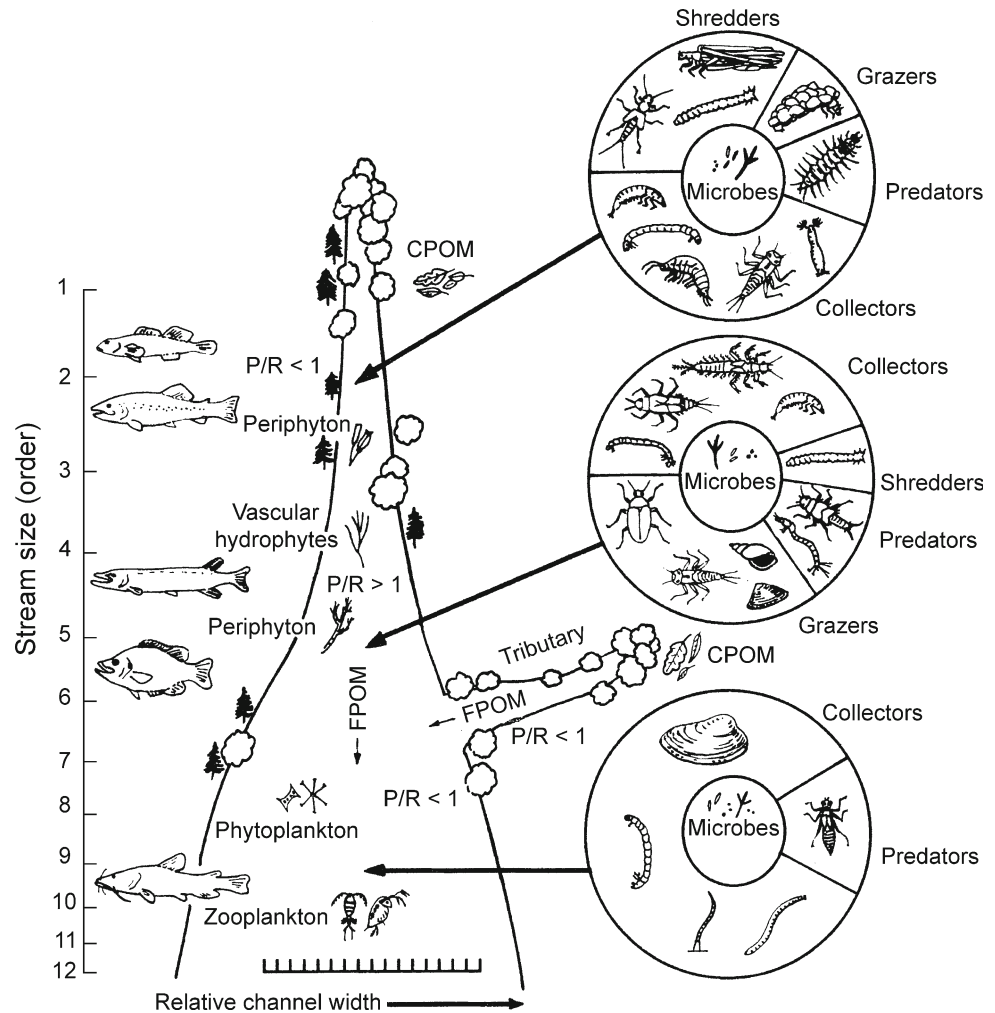
The river continuum concept (RCC) has been widely applied to examine trophic interactions, productivity, and respiration in rivers and streams throughout the globe

(Vannote et al. 1980). First introduced in Chap. 1, we include this figure again here to portray the integration of stream order, energy sources, food webs, and to a lesser degree nutrients, into a longitudinal model of energy flow in streams (Fig. 14.3). Originally conceived for river systems flowing through forested regions in the temperate zone, the RCC asserts that headwaters (stream order 1–3) should be heavily shaded and receive abundant leaf litter, but algal growth often will be light-limited. Streams of order four through six are expected to support more algae and aquatic plant life because they are wider and less shaded, and also should be fueled by organic particles from upstream. According to the RCC, headwaters should have relatively more allochthonous inputs, indicated by a ratio of primary production to respiration well below one, whereas the mid reaches should have more autochthonous production and a higher ratio of primary production to respiration. Higher-order rivers are thought to be too wide to have energy supplies dominated by riparian leaf fall, and too deep for energy to be primarily derived from algal production on the bed. Instead, organic inputs from upstream and the floodplain, along with river plankton, should play a greater role.

The river continuum concept has proven to be a resilient summary of the relative roles played by different basal resources along an idealized river system. Furthermore, as previously described (Sect. 9.1.5), the longitudinal distribution of functional feeding groups often, although not invariably, can be shown to be at least approximately in accord with expectations from the RCC. Nonetheless, the applicability of this model to running waters worldwide has been questioned (e.g., Winterbourn et al. 1981; Lake et al. 1985), and research has demonstrated that factors including climate, dominant land cover, and altitude also are known to influence resource gradients and the functional groups of aquatic consumers in streams (Tomanova et al. 2007).

To re-examine the predicted changes in dominant carbon resources along a river continuum, researchers compared gut contents from macroinvertebrate specimens archived from the original RCC study in 1976 with specimens collected from the same study sites in 2009 (Rosi-Marshall et al. 2016). Macroinvertebrate diets remained similar through time, and as predicted by the RCC, there was a longitudinal pattern in the dominance of allochthonous resources in macroinvertebrate diets. However, in contrast to expectations, autochthonous resources were exceptionally important (~35–75% of diets) at all of the sites (Rosi-Marshall et al. 2016), suggesting that the hypothesized pattern of changing energy pathways from headwaters to river mouth idealized in the RCC is only a first approximation of a more complete understanding of how energy is acquired within lotic ecosystems.

Fig. 14.3 The river continuum concept summarizes expected longitudinal changes in energy inputs and consumers as one proceeds from a first-order stream to a large river. A low ratio of primary production to respiration (P/R) indicates that the majority of the energy supplied to the food web derives from organic matter and microbial activity, and mostly originates as terrestrial production outside the stream channel. A P/R approaching one indicates that much more energy to the food web is supplied by primary production within the stream channel. An important upstream-downstream linkage is the export of fine particulate organic matter (FPOM) from the headwaters to locations downstream. (Reproduced from Vannote et al. 1980)



Though rivers are often conceptualized as continua of flowing waters, in many regions rivers are periodically interrupted by naturally occurring or anthropogenically-derived lentic waters. Lake Tonlé Sap in the Mekong basin in Cambodia and Lake Saint-Pierre in the Saint Lawrence basin in Canada are good examples of large, natural lentic habitats within river networks. In contrast, the impoundments caused by damming of rivers and streams have well-documented impacts on upstream-downstream linkages, including habitat fragmentation, changes to flow and thermal regimes, and altered transport of sediments, nutrients, and organic matter. The effects of a dam eventually dissipate, although often not for many tens of kilometers. Because many rivers have multiple dams, they can experience repeated breaks in the river continuum, referred to as serial discontinuity (Ward and Stanford 1983). Recovery of the river downstream of each dam depends on dam size, its position on the river network, tributary inputs, and other factors. In the case of rivers that historically were connected to extensive floodplains, dams and levees may permanently

sever lateral connectivity (Ward and Stanford 1995), resulting in the loss of critical ecosystem functions.

For many lowland rivers, energy inputs derive primarily from upstream sources, including tributaries and any production that occurs within the main channel, but lateral inputs can be substantial in rivers that inundate their floodplains (Junk et al. 1989). Often, larger rivers in both temperate and tropical regions are characterized by seasonal floods that redefine both terrestrial and aquatic habitats, and shift conditions from lotic to lentic predictably on an annual basis (Fig. 14.4). During the annual flood pulse, organic matter from the floodplain as well as algae and organic matter from fringing channels and floodplain lakes make substantial contributions to the secondary production of the river-floodplain biota (Tockner et al. 2000). These ideas form the basis of the flood-pulse concept (FPC; Junk et al. 1989; Junk and Wantzen 2004).

Authors of the FPC assert that in large, undammed rivers, riverine animal biomass is primarily supported by organic matter inputs from the floodplain, rather than by carbon sources transported from upstream (Fig. 14.5). Indeed, the

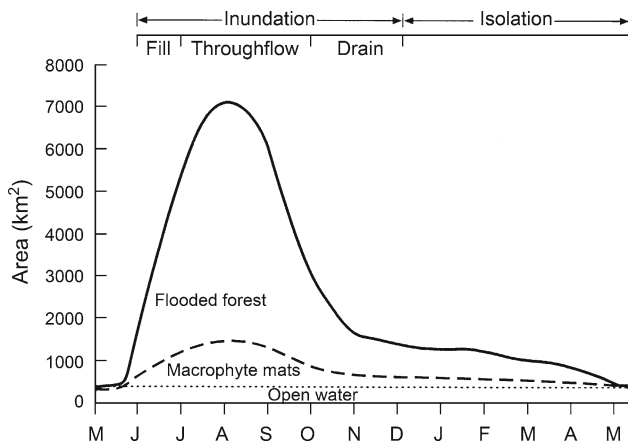


Fig. 14.4 Contributions of flooded forest, macrophyte mat, and open water to the Orinoco floodplain area throughout the hydrological cycle (Reproduced from Lewis et al. 2001)

most productive freshwater fisheries are located in large rivers with extensive floodplains, where the recruitment of young fishes correlates with interannual variation in the strength of flooding and thus determines the size of the catch when those juveniles mature into harvested size classes (Welcomme 1979). In the Rio Solimões, the growth of omnivore fishes was clearly linked to hydrological seasonality (Bayley 1988), as was also true in the lower Mississippi river provided that flooding coincided with temperatures above 15 °C (Schramm and Eggleton 2006).

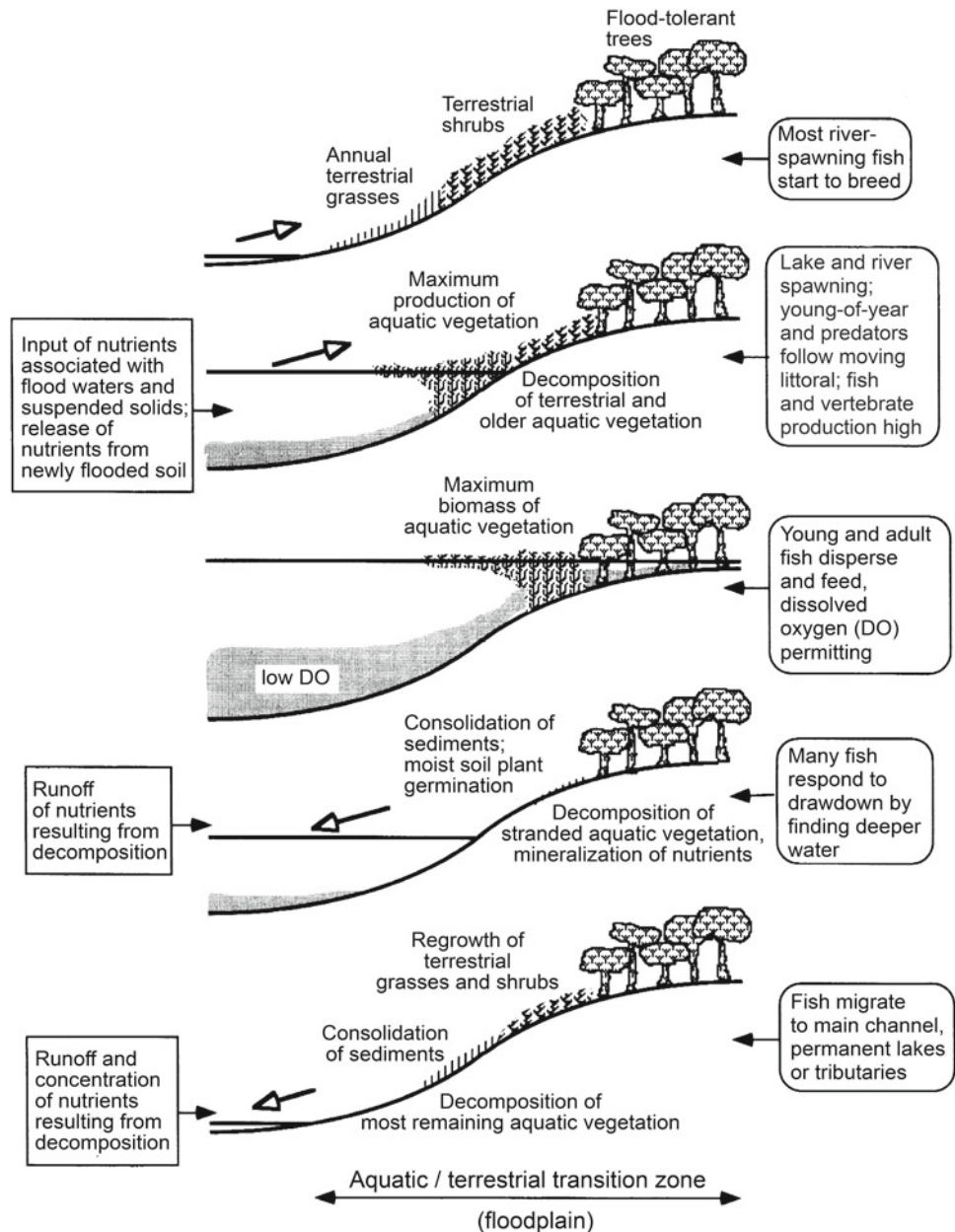
Recent work has documented nuanced responses of fish populations and communities to the flood-pulse, suggesting that behavior, ontogeny, and species identity are important factors mediating consumer response to the flood-pulse. In a study examining the influence of degree of flooding on fish abundance, Castello and others (2019) documented a positive relationship between flooding and the abundance of pacu (*Colossoma macropomum*), a long-lived, over-harvested fish in the Brazilian Amazon, but these effects were only realized by fishes during their early stages of development. Tropical floodplain fishes in Tonlé Sap Lake in the Mekong River network are subject to annual flooding that increases freshwater habitat by approximately 500%. Research by McMeans et al. (2019) suggests that fishes in this system have diverse trophic responses to rising waters. Some species—especially small piscivores—shifted their trophic position by increasing their consumption of invertebrates and plant material during flooding. In Lake Saint-Pierre in the St. Lawrence River of North America, researchers used stable isotope techniques to demonstrate that fishes using floodplain habitat in the early portion of the growing season benefitted most from resources associated with flooding. Notably, the contribution of floodplain resources to fish diets declined through time, indicating that the quality and quantity of resources associated with the

flood-pulse may change throughout the period of inundation (Farly et al. 2019). Similar to findings from tropical systems in the Amazon and Mekong basins, the fish community in the St. Lawrence also demonstrated ontogenetic and species-specific responses to the flood pulse (Farly et al. 2019), underscoring the point that flood-pulse dynamics are not limited to tropical river networks. Understanding how aquatic communities respond physiologically, behaviorally, and trophically to seasonal changes in resource availability is an emerging frontier in stream ecology (McMeans et al. 2019).

The effects of the flood pulse are not realized in all rivers. As important as the floodplain may be to secondary production in large rivers, at least one-fourth of the fish species from a number of large temperate rivers can complete their life cycle in the main channel (Galat and Zweimüller 2001). Fishes including larvae and juveniles were abundant in the main channel of the Illinois and Mississippi Rivers and appeared to be supported by in-channel production based on the presence of zooplankton and invertebrates in their diet (Dettmers et al. 2001). These apparently contrasting findings may reflect differences in the role of floodplain inundation in tropical versus temperate settings, or between more pristine rivers versus rivers with more developed floodplains. In rivers characterized by high rates of primary production, regulated flows, or where the floodplain is not as productive as the main channel due the timing of the flood, fish production may be more dependent on in-channel production (Junk and Wantzen 2004). In rivers with extensive flooding driven by an annual flood pulse, the original model may apply.

There is no question that detrital energy inputs are important sources of organic carbon in virtually all lotic ecosystems; however, budgetary accounts of inputs and exports may fail to provide an accurate view of the energy supplies that fuel higher trophic levels. Even in larger rivers, there is evidence that instream productivity and energy contributions from instream carbon dynamics can be important in supporting secondary production (Rosi-Marshall et al. 2016; Brett et al. 2017). By analyzing the signature of certain isotopes in animal consumers, it is possible to identify their primary food supplies, and in a number of instances where the energy sources were assumed to be allochthonous, a surprising dependency on autochthonous production was revealed. Isotopic signatures of fishes and invertebrates indicated that transported organic matter, including living and detrital algal components, was the main source of carbon for primary consumers in both constricted and floodplain reaches of the Ohio River (Thorpe et al. 1998). In the Orinoco floodplain, macrophytes and leaf litter from the flooded forest represented 98% of the total carbon available, but isotope analysis showed that phytoplankton and periphyton were the major carbon sources for fish and macroinvertebrates. In addition, isotope data did not

Fig. 14.5 Depiction of the flood-pulse concept. During the annual hydrological cycle in a floodplain river, the littoral boundary of the river moves laterally with the rise and fall of the flood pulse, influencing fish recruitment and exchanges of nutrients and organic matter. The right-hand column indicates typical life-history traits of fish. DO refers to dissolved oxygen. (Reproduced from Bayley 1995)



indicate that vascular plant carbon reached invertebrates through the microbial loop, suggesting instead that virtually all detrital carbon entered a “microbial dead end” and thus did not contribute to animal secondary production in the Orinoco floodplain (Lewis et al. 2001).

From the perspective of ecosystem metabolism, large lowland rivers are highly heterotrophic, reflecting high microbial respiration supported by high concentrations of dissolved and particulate organic matter. Secondary production by macroconsumers, however, may be based to a much greater extent on autochthonous production that occurs within the channel or in side-channels and floodplain lakes (Fig. 14.6). The riverine productivity model (RPM;

Thorp and Delong 1994) emphasizes that carbon resources derived from autochthonous production may be important because they can be assimilated easily and are stored for longer periods of time near the bank where benthic macroinvertebrates tend to aggregate. According to the RPM, autochthonous carbon fuels much of secondary production in rivers, especially those with constricted channels, and can be an important energy supply to macroconsumers in rivers with floodplains (Thorp and Delong 1994, 2002).

Vertical connectivity is the third important spatial dimension of rivers that may influence energy flow. Groundwater enters stream channels along multiple flow paths, both deep and shallow, which vary with rainfall, soil

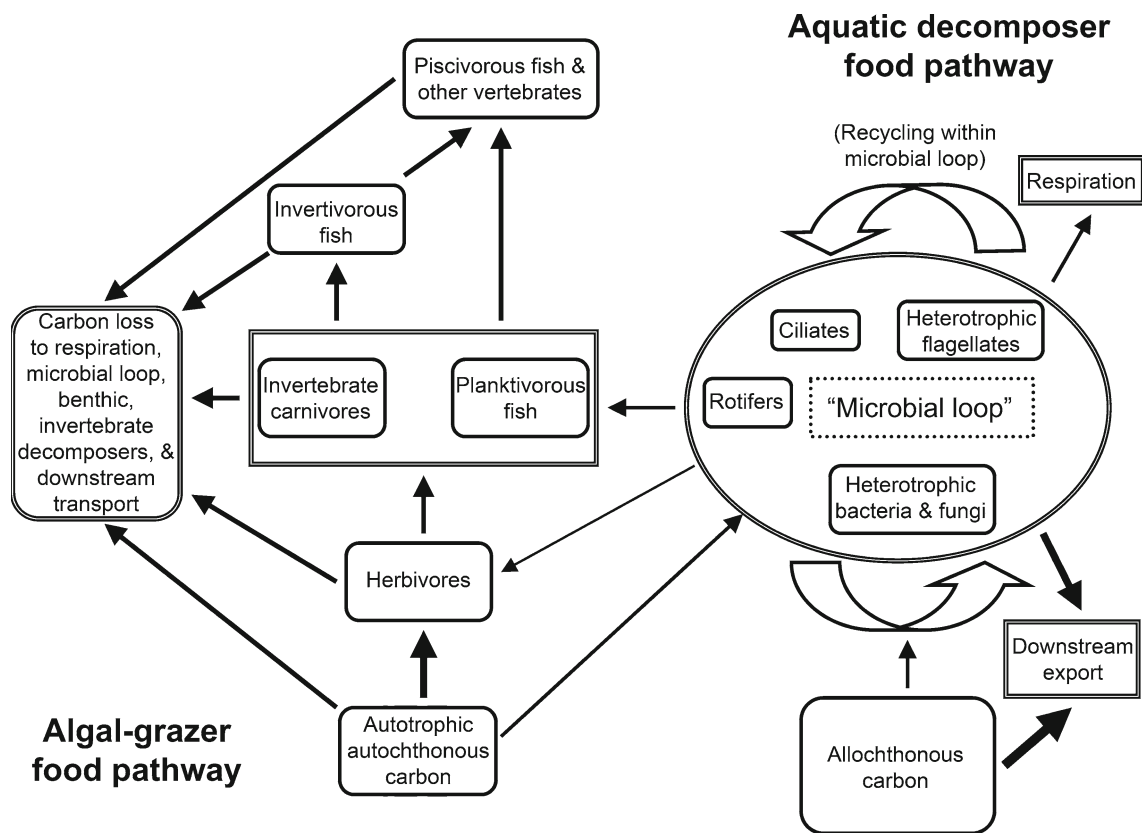


Fig. 14.6 The riverine productivity model proposes that secondary production by macroinvertebrates and fishes depends on autochthonous organic matter produced in the river channel and in the riparian zone, which are more labile but less abundant than organic matter of

allochthonous origin transported from upstream reaches. The latter dominates the total amount of organic matter transported by rivers and contributes to high rates of microbial respiration but contributes little to the higher food web. (Reproduced from Thorp and Delong 2002)

moisture, and season, and result in distinctive signatures in their chemical constituents, including nutrients, dissolved organic carbon, and carbon dioxide. Conditions within the sediments can be particularly important to nutrient and carbon cycling because sediment characteristics affect abiotic uptake and storage, and because patches that differ in the availability of oxygen and organic matter strongly influence other biogeochemical cycles (Stegen et al. 2018). Connectivity between the water column and hyporheic zone can be mediated by discharge; therefore, changes in flow may alter carbon dynamics in the hyporheic zone (Fasching et al. 2016). For example, Romeijn et al. (2019) used an incubation experiment to demonstrate that the quality and quantity of organic matter in stream sediments can significantly influence CO_2 production from the hyporheic zone. They estimated that, under certain conditions, stream sediments can account for 35% of total stream evasion documented in other studies, a rate of CO_2 production that is much greater than typically reported.

Until relatively recently, rivers were often considered to be pipes, transporting carbon from terrestrial to marine systems. While still a research frontier, the incorporation of

river systems into global carbon models generates a macro-scale view of the relative contribution of rivers as storage sites, active processors, or exporters of carbon downstream. Recent work has shown that the quantity of terrestrially derived carbon entering streams and rivers substantially exceeds the amount of riverine carbon delivered to the oceans, indicating that streams may play important but understudied roles in carbon storage and processing via respiration and subsequent release of CO_2 to the atmosphere (Cole et al. 2007; Wohl et al. 2017; Battin et al. 2008; Battin et al. 2009). This idea is borne out by recent estimates by Raymond et al. (2013) that indicate the amount of carbon emitted from rivers by outgassing of CO_2 exceeds the amount of carbon exported by rivers to oceans.

Estimates of global CO_2 evasion from inland waters are much higher for rivers than for lakes and reservoirs, but these numbers are constantly updated as technology improves and measurements are collected in more and more systems (Rocher-Ros et al. 2019). Though the assessments are tentative due to lack of data from some regions, it appears that a great majority of stream CO_2 evasion ($\sim 70\%$) originates from tropical and sub-tropical waters—systems

that comprise a relatively small proportion of the Earth's surface (Raymond et al. 2013; Allen and Pavelsky 2018). The primary source of CO₂ emitted from inland waters is not known with certainty, but lateral inputs of CO₂ from groundwater that are derived from carbon fixation in forested systems, and the decomposition of organic matter within streams and rivers, undoubtedly play large roles in the generation of CO₂ and changes along a stream network (Hotchkiss et al. 2015; Campeau et al. 2019; Horgby et al. 2019). In lower order streams, the contribution of CO₂ derived from decomposition of material from the terrestrial environment is much greater than the contribution of CO₂ from in-stream metabolism, a ratio that changes moving downstream as the connectivity of the stream to the terrestrial systems declines with increasing water volume.

14.2 Stream Ecosystem Metabolism

The energy that supports the majority of Earth's ecosystems ultimately is derived from the sun. Photosynthetic organisms convert CO₂, water, and solar energy into reduced forms of carbon that can be consumed by heterotrophic organisms. This conversion process is termed gross primary production (GPP), and the rate of GPP often is measured from the amount of oxygen generated as a by-product of photosynthesis. Both autotrophic and heterotrophic organisms consume oxygen to use the energy contained in organic carbon compounds through the process of cellular respiration. Net primary production (NPP) is the difference between carbon fixed by autotrophs through GPP and autotrophic respiration (R_A), or the fraction of carbon used to meet their own metabolic demands. Net primary production is represented by Eq. 14.1, where R_A is a negative term as it is often measured as the amount of oxygen consumed:

$$\text{NPP} = \text{GPP} + R_A \quad (14.1)$$

Ecosystem respiration (ER) is an aggregate estimate of R_A and heterotrophic respiration (R_H) in a system. Net ecosystem productivity (NEP), also referred to as net ecosystem metabolism, is the sum of GPP and ER, where ER is a negative term, and is described by the following relationship:

$$\text{NEP} = \text{GPP} + \text{ER} \quad (14.2)$$

Estimating the contribution of respiration by autotrophs to ER is essential to describe carbon dynamics. In terrestrial ecosystems, estimates of metabolism may include estimates of both NEP and NPP, as scientists can obtain relatively robust estimates of R_A . In contrast, estimates of net production in rivers are typically restricted to NEP because the turnover of autotrophic biomass is very high and the

standing stock of autotrophic biomass is comparatively low; hence, it is very challenging to quantify R_A . Additionally, stream autotrophs form complex communities with heterotrophs in biofilms, making it infeasible to measure R_A separately from R_H (Hall and Hotchkiss 2017). Autotrophic respiration is influenced by many factors, including the physiological activity of the algae, self-shading by algal communities, and the respiration of closely associated heterotrophic organisms; thus, variation in R_A is expected among systems (Hall and Beaulieu 2013).

To address the problem of estimating the fraction of GPP consumed by R_A , Hall and Beaulieu (2013) developed a modeling approach based on observations of GPP and ER from more than 20 streams. In systems where GPP and ER did not covary (i.e., sites where productivity was not driving patterns in respiration) and that were characterized by large temporal variation in GPP, average R_A was approximately 44% of ER. Though the authors emphasize that their method did not address the challenge of separating R_A from the R_H of closely associated heterotrophs, and acknowledge that estimates of R_A varied substantially among streams, this approach can be applied to estimate R_A in other systems.

Net ecosystem production represents the contribution of autochthonous production in supporting heterotrophic production, and hence to whole system metabolism. Thus, NEP can be used to evaluate internal versus external organic carbon inputs to a stream reach—estimates that can be scaled up empirically or through modelling to examine metabolic transitions along the length of a river through time. At one extreme, NEP can be much less than zero, indicating that GPP contributes relatively little energy to the system. At the other extreme, NEP values greater than zero implies that primary production contributions to total heterotrophic respiration exceed the reliance on allochthonous materials, producing excess carbon that may be exported downstream.

Stream metabolism is a metric that integrates physico-chemical characteristics of a stream (i.e., estimates of gas exchange with the environment) with estimates of biological activity (i.e., photosynthetic activity and aerobic respiration). Metabolism is measured in a river as a function of oxygen concentrations (Odum 1956) using the following equation:

$$\frac{dO}{dt} = \text{GPP} + \text{ER} + K(O_{def}) \quad (14.3)$$

where $\frac{dO}{dt}$ is the change in oxygen concentration through time. In this relationship, GPP is the rate of O₂ produced through photosynthesis and is a positive flux; ER is the rate of O₂ consumed through respiration, and is a negative flux. The net exchange of O₂ between water and air is the product of a gas exchange rate K and the oxygen deficit (O_{def}). The O_{def} is the difference between the O₂ concentration at saturation in water at a given temperature and atmospheric

pressure, and the measured O_2 concentration in the water. Carbon production can be estimated from metabolism estimates using the formula $g\ C = 0.286 \times g\ O_2$ and reported in $g\ C\ m^{-2}\ day^{-1}$.

14.2.1 Factors Controlling Autochthonous Production

The photosynthetic activities of benthic algae, macrophytes, and phytoplankton constitute the principal autochthonous inputs to lotic ecosystems. Compared to terrestrial systems where vascular plants dominate autotrophic biomass, the periphyton, consisting mainly of benthic algae and cyanobacteria, are the most important autotrophs in most rivers and streams. As discussed in detail in Chap. 6, patterns in benthic primary production are governed by many factors including, but not limited to, light and nutrient availability, grazing, discharge, and disturbance.

Productivity in streams is very heterogeneous, with highly productive systems producing an average of approximately $13\ g\ O_2\ m^{-2}\ d^{-1}$ (Hoellein et al. 2013). Low rates of GPP are often found in turbid systems, in streams characterized by high levels of hydrologic disturbance, and in streams with dense riparian shading. In contrast, streams and rivers with exceptionally high rates of GPP often have elevated concentrations of nutrients, higher temperatures, and greater light availability when compared to relatively undisturbed systems (Hall 2016).

Instream productivity and metabolism are strongly related to light availability. For instance, daily and seasonal variation in GPP were strongly related to light availability in a small stream in Tennessee, US, with peaks during early spring prior to leaf out (Fig. 14.7; Roberts et al. 2007). In a study of streams from various biomes across North America, Mulholland and others (2001) highlighted the strong relationship between GPP and light availability. Similarly, in their review of over 60 estimates from stream sites in eastern North America, Webster et al. (1995) found that primary production in forested streams was about half that of open streams, although results were highly variable. Predictions of in-stream light availability are complex, as in-stream light regimes are strongly influenced by channel features such as canyon walls (Hall et al. 2015) or incised channels (Blaszczak et al. 2018), sediment and organic matter load affecting turbidity, and the phenology and timing of leaf-out of riparian plants.

Estimates of the contribution of macrophytes to ecosystem primary production are too few to generalize, but at least in some circumstances they can be significant. In the New River, Virginia, US, short-term production by *Podostemum ceratophyllum* was about equivalent to periphyton production (Hill and Webster 1982, 1983). Short-term estimates

also suggested that macrophytes contributed about 9% of the annual primary production in the Fort River, Massachusetts (Fisher and Carpenter 1976), and about 15% in the Red River, Michigan (King and Ball 1967). In a study of Brazilian streams, Tromboni and others (2017) documented that where present, macrophytes can generate a large fraction of reach-scale GPP.

14.2.2 Factors Controlling Ecosystem Respiration

Ecosystem respiration is the integrative measure of the utilization of organic carbon from all sources and by all organisms within the stream channel. It includes respiration by primary producers, microbial heterotrophs, and animals, which conceptually can be separated into the R_A of autotrophs and R_H of heterotrophs. As previously mentioned, it is very challenging to quantify R_A in flowing waters, as the turnover of autotrophic biomass is very high, and the standing stock of autotrophic biomass is relatively low. Therefore, respiration estimates in streams are often limited to ER (Hall and Hotchkiss 2017).

Though direct contributions by microorganisms have yet to be measured and compared within streams, we assume their respiration is the largest component of R_H , reflecting the roles of bacteria and fungi in the breakdown of organic matter and their ability to use labile DOM from stream water. Because metabolic processes can be strongly temperature dependent (Demars et al. 2011), respiration is expected to vary with temperature and season. Total respiration should also increase with increasing amounts of benthic organic matter (BOM), but its biological availability is at least as important as its quantity (Findlay et al. 1986). In the woodland stream mentioned earlier (Fig. 14.7), respiration was highest in early spring due to high GPP, and again in autumn after leaf fall, which are periods of moderate temperature, and respiration was low during the warmer mid-summer period because of low organic matter supplies. A downstream increase in benthic respiration might be expected if total carbon inputs increase, because warmer temperatures stimulate higher rates, or because larger rivers receive greater inputs from domestic sewage or agricultural runoff. Due to the relative scarcity of data for large rivers, relationships between ER and longitudinal position are still poorly documented. However, downstream increases in ER have been reported in systems as disparate as the highly autotrophic Salmon River (Minshall et al. 1992) and highly heterotrophic blackwater rivers in Georgia (Meyer and Edwards 1990).

Respiration rates within a site can also vary with discharge. In a study of two streams within the Glensauigh Research Station in north-east Scotland, Demars (2019) demonstrated that rates of ER following peak flows can be exceptionally

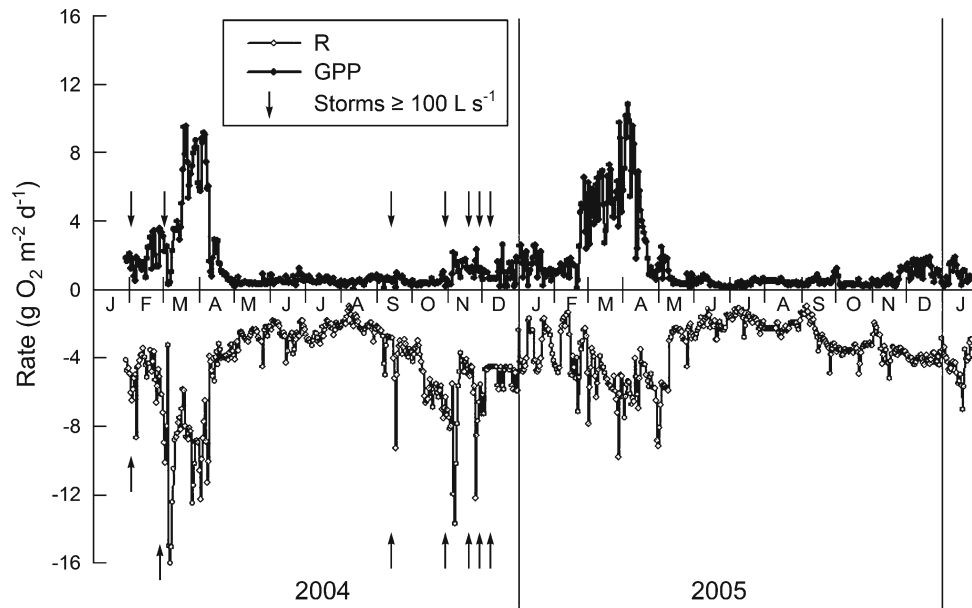


Fig. 14.7 Daily rates of gross primary production (GPP: positive values, black line) and ecosystem respiration (R: negative values, gray line) measured in Walker Branch in Tennessee in the eastern US from 28 January 2004 through 31 January 2006. Vertical lines separate years. Arrows indicate storms during which maximum instantaneous

discharge was greater than or equal to 100 L s^{-1} . Variance in GPP correlates with seasonal and day-to-day variation in light levels. Variance in ecosystem R correlates with seasonal and day-to-day variation in GPP and autumn leaf inputs. (Reproduced from Roberts et al. 2007)

high. Storm-associated pulses of respiration have been observed previously, but this was one of the first investigations to document how hydrological connectivity between riparian and stream habitats during storm events can enhance the instream supply of DOC and stimulate respiration.

In a cross-biome comparison of 22 streams, Sinsabaugh (1997) summarized stream benthic respiration rates in relation to benthic organic matter, temperature, primary production, and other system variables (Fig. 14.8). Benthic respiration was directly proportional to stream temperature and, presumably due to high rates of utilization, the standing stock of benthic organic matter was inversely related to stream temperature. Owing to these offsetting trends, respiration per gram of benthic organic carbon was strongly related to temperature. Because the coefficient of this relationship was too high for a simple metabolic response, Sinsabaugh inferred that other factors also must be operating, such as higher quality BOM or greater nutrient availability in streams of warmer climates.

14.2.3 Factors Controlling Gas Exchange

Stream metabolism relies on the exchange of oxygen between the atmosphere and water to maintain adequate amounts of oxygen in solution. This flux is a function of the transfer velocity of the gas at the air-water interface, the solubility coefficient of the gas, and the difference in gas

concentrations between the air and the water. In streams, the turbulence generated by water flowing over benthic substrates is the dominant driver of oxygen exchange, producing spatial and temporal heterogeneity within and among systems (Fig. 14.9; Ulseth et al. 2019). Unlike lacustrine systems, in some streams, gas exchange rates rather than biological processes can effectively control oxygen concentrations and make it difficult to estimate gas exchange (Hall 2016). An analysis by Ulseth et al. (2019) suggests that gas exchange in streams exists in two different states. In low-energy streams that are characterized by channels with shallow slopes, turbulent diffusion of gasses—the transfer of gasses at the air-water interface due to irregular or chaotic motion—is the primary factor influencing the exchange of gas with the atmosphere. In contrast, in high-energy systems characterized by steep slopes, turbulence generates air bubbles in the water column that dominate gas exchange processes. The ability to accurately estimate the factors mediating gas-exchange in streams is essential in estimating stream metabolism and in quantifying the global contribution of streams to fluxes of greenhouse gases.

14.2.4 Methods to Estimate Stream Metabolism

Until recently, advances in our knowledge of stream metabolism were limited mainly by technological capabilities and expense. Initial estimates of metabolism were made by

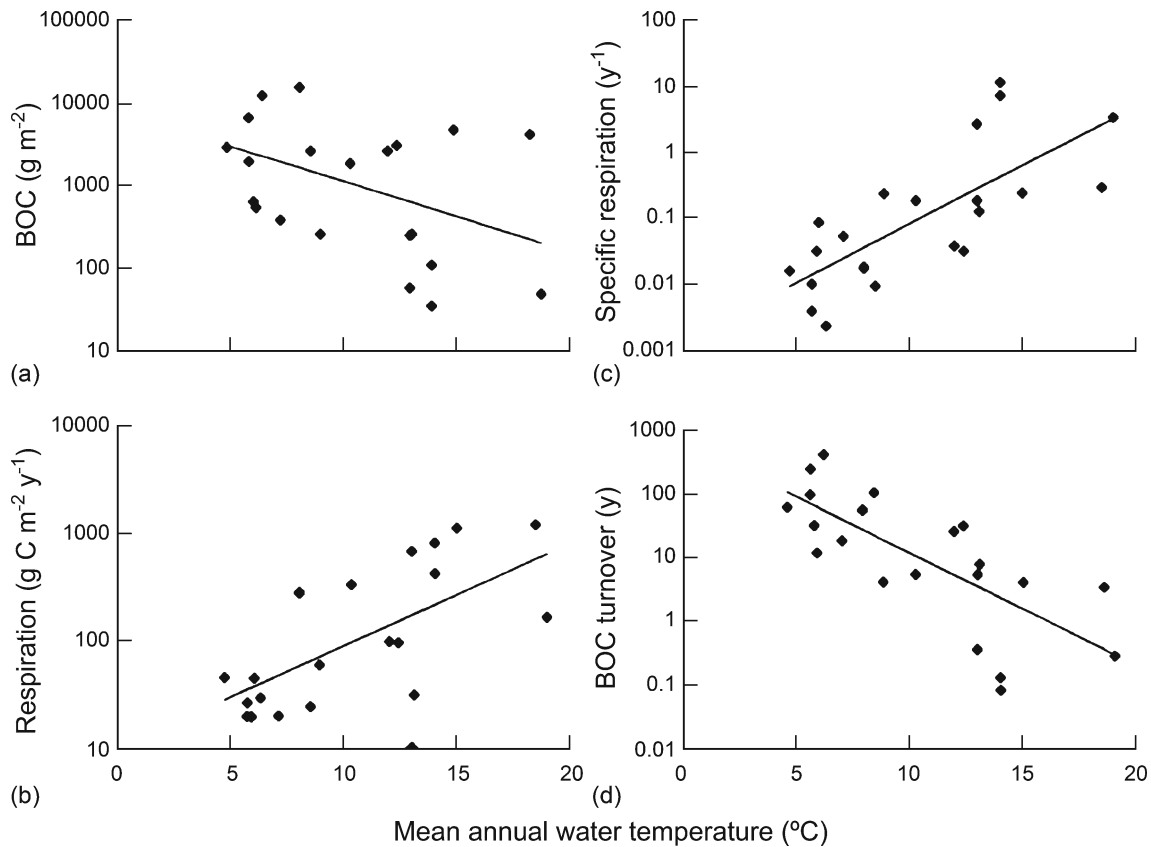


Fig. 14.8 Relationships of respiration rate and standing stock of benthic organic carbon (BOC) with stream temperature for 22 streams. (a) BOC decreases and (b) respiration rate increases with mean annual

water temperature. (c) Specific respiration increases and (d) the turnover rate of BOC decreases with temperature. See text for further explanation. (Reproduced from Sinsabaugh 1997)

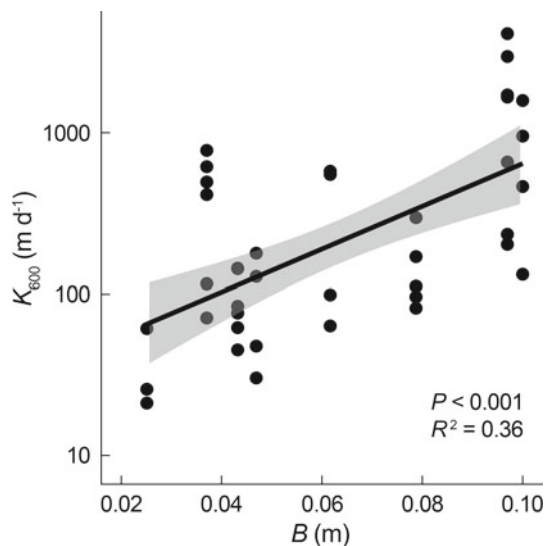


Fig. 14.9 Gas exchange (k_{600}) increased with median streambed roughness (B) across eight of the Swiss alpine stream reaches studied. The black line is the fit from log linear regression and the grey band represents 95% CI of the predicted k_{600} . (Reproduced from Ulseth et al. 2019)

collecting water samples every few hours throughout the day and laboriously titrating each sample to determine fluctuations in dissolved oxygen levels (e.g., Odum 1956). Subsequently, large, expensive, and finicky sensors were developed at the end of the last century to generate continuous oxygen and temperature data; however, the size, cost, and maintenance of these sensors prevented most researchers from deploying them in all but the most easily monitored systems during periods of stable in-stream conditions. Therefore, our initial understanding of within-stream variation in metabolism was primarily limited to smaller streams in the temperate zone during low flows on sunny days. In the past decade, the arrival of smaller, cost-effective sensors has allowed ecologists to collect large amounts of data from a wide range of rivers and streams throughout the world. These sensors can be deployed continuously (collecting data in intervals of seconds or minutes) and for longer periods of time (months or years), documenting diel patterns in oxygen concentrations. Local habitat heterogeneity can strongly influence estimates of stream metabolism and should be considered when deploying sensors (Siders et al. 2017; Dodds et al. 2018). Coupled with new computational tools,

data generated by these sensors are providing insights into the metabolic regimes of rivers (Hall 2016), and an improved understanding of human influence on diel and seasonal patterns in stream ecosystem function (Arroita et al. 2019).

In addition to open water measurement of oxygen flux to estimate whole stream metabolism, increasingly by continuous monitoring using sensors, researchers have employed closed chambers to estimate metabolism. Many of the initial estimates of stream metabolism were made using enclosed benthic chambers, where oxygen change in the light measures NEP, and oxygen change at night or in darkened chambers provides an estimate of ecosystem respiration (Bott et al. 2006). At least in small streams, all primary production and virtually all respiration can reasonably be assumed to occur at the streambed. Using benthic chambers, GPP is estimated by adding respiration measured during the night to net oxygen change in the light, and NEP is calculated as the difference between GPP and 24-hour ecosystem respiration. Benthic chambers are especially useful for measuring local-scale heterogeneity and testing of environmental variables, but are difficult to scale up to the entire ecosystem, unless extensively replicated. It is important also to note that in larger systems, metabolism can be dominated by planktonic photosynthesis and respiration, which would require suspended bottles containing the biota of the water column to estimate planktonic contributions to system-wide metabolism (e.g., Reisinger et al. 2015), as is also done in lakes.

Gas exchange rates often are measured by injecting tracer gases, such as sulfur hexafluoride, propane, or argon, into streams and measuring the decline in tracer concentration over the study reach (Raymond et al. 2012; Hall and Ulseth 2020). Velocities can also be estimated using equations derived from channel geomorphology and hydraulics or ecosystem metabolism models. In large, slow-moving systems, floating chambers may also be an effective way to estimate gas exchange (Beaulieu et al. 2012). Methods to estimate gas exchange present challenges to stream ecologists. First, with gas injection, the sampling effort and cost of analysis can be significant hurdles to overcome if researchers are working on limited budgets, in remote sites, or are comparing numerous sites. Additionally, if the stream bed is relatively uniform or the flow is low, gas exchange rates can be exceptionally low and decreases in tracer concentrations difficult to measure within a given reach (Hall 2016). There is also some uncertainty in scaling gas exchange rates across systems with empirical equations, because they cannot be generalized for all streams and rivers. This is especially true in streams with steep slopes and great hydrologic energy, such as many streams in mountainous regions (Ulseth et al. 2019). Global efforts to collect more DO and gas exchange data are constantly enhancing the power of the models needed to successfully estimate reaeration, and future work will be improved by this effort.

The power of whole stream metabolism estimation using near-continuous water column monitoring is the integration of all GPP and ER for a stream reach, which can be expanded to a much greater temporal and spatial coverage by deploying multiple sensors. In addition, production and respiration in the benthic and hyporheic zones can influence system-wide metabolism in rivers, processes that are not robustly estimated using benthic chambers (Mulholland et al. 2001; Webster et al. 1995). Thus, many recent estimates of metabolism have been made using open-water methods. Spatial and temporal variability remain as challenges, however. Large, within-system variability in metabolism is most likely one of the reasons why researchers have had difficulty identifying the factors governing metabolic rates within and among river networks (Rodríguez-Castillo et al. 2019; Koenig et al. 2019).

Readers interested in learning more about the specific methods associated with measuring, modeling, and interpreting metabolism data should consider contributing to, and reading work by researchers associated with the Stream-PULSE Project (<http://streampulse.org/>; e.g., Appling et al. 2018b; Hall 2016; Hall and Hotchkiss 2017; Hall et al. 2016; Appling et al. 2018a). Tradeoffs associated with specific methods used to measure metabolism have been discussed by many authors, including Hall et al. (2007), Staehr et al. (2012), Song et al. (2016), and Dodds et al. (2018).

14.2.5 Interpretation of Relationships Between Productivity and Respiration

The ratio of GPP to ER (often referred to as the P/R ratio), has long been used as a simple index of the relative importance of energy fixed by primary producers within the stream, versus allochthonous organic matter derived from terrestrial plant production. However, continuous sensor measurement has documented great variation in within- and among-stream metabolism estimates due to spatial and temporal fluctuations in productivity and respiration, suggesting that short-term and/or spatially-restricted measurements may not be appropriate metrics to compare metabolic activity among streams (Bernhardt et al. 2018; Hall 2016). Therefore, conclusions about metabolic regimes that were supported using short-term measurements, including many studies estimating P/R, should be interpreted with caution.

To better understand the difficulties of interpreting P/R ratios, recall that R is the sum of respiration by autotrophs (R_A) and by heterotrophs (R_H). Heterotrophic respiration can be further broken down into respiration supported by autotrophic production and respiration supported by allochthonous sources. Whichever is the larger fraction of R_H , is the true measure of autotrophy versus heterotrophy. As a further caveat, predicting the fraction of ecosystem respiration that

is supported by autochthonous versus allochthonous sources, and estimating how much respiration is generated by microorganisms, as compared to other organisms, remains a substantial challenge. For example, microorganisms may derive their energy from both autochthonous and allochthonous sources, and metazoans primarily from autochthonous sources (Thorp and DeLong 1994, 2002).

This sort of reasoning may help to explain a striking discrepancy between Bayley's (1989a) analysis of carbon flux in the Rio Solimões, the whitewater branch of the Amazon River, which showed most carbon originating as detritus from aquatic and floodplain macrophytes, and other investigations that focused their studies on carbon flow within the food web of the river. For instance, an analysis of the stable isotope of carbon, ^{13}C , in fish tissue and in various plants found that the food chain supporting an abundant group of detritivorous fishes, the Characiformes, begins with phytoplankton and not macrophyte detritus as might be expected (Araujo-Lima et al. 1986). More recent work has reached similar conclusions. Mortillaro et al. (2015) demonstrated that detritivores were positioned at the base of the food chain as expected, but fatty acid analysis pointed to inclusion of autochthonous food sources, such as microalgae, in their diets. In the Orinoco floodplain, phytoplankton and attached microalgae again are the main source of carbon for fishes and aquatic invertebrates, despite the greater abundance of macrophytes and terrestrial litter (Hamilton et al. 1992; Lewis et al. 2001).

14.2.6 Patterns in Stream Metabolism

With the advent of continuous monitoring of oxygen flux at multiple sites, it is now feasible to search for broad patterns in the net ecosystem productivity of streams and rivers (Bernhardt et al. 2018). Studies of terrestrial and lake ecosystems have documented predictable patterns related to seasonal variation in environmental variables such as light, temperature, and nutrients; however, the same cannot be said for river ecosystem metabolism. In flowing waters, the seasonality of light and temperature often are not synchronous, and autotrophic biomass can be quickly reduced or eliminated by scouring flows associated with seasonal or aseasonal patterns in precipitation. Pulses of allochthonous resources, such as leaf-litter in the fall in the temperate zone, can decouple relationships between GPP and ER. Allochthonous inputs of carbon can exceed autochthonous production, differentially influencing productivity and respiration. Increased sediment load, due to surface runoff, reduces the amount of light reaching the benthos and influences GPP. Fluctuating discharge throughout the year can also produce scouring, burial,

and drying events that influence autotrophic biomass and community composition, and subsequently alter patterns in productivity (Bernhardt et al. 2018).

The two years of daily measurement of GPP and ER from a small stream in the southeastern United States clearly shows how factors controlling stream metabolism change seasonally (Fig. 14.7). This first-order, deciduous forest stream was heterotrophic throughout the year except during the open-canopy spring, when GPP and ER were equal. Leaf phenology was the main control of seasonal variation, day-to-day weather variation influenced light availability and GPP, and storms suppressed GPP in spring by scouring algae but stimulated GPP in fall by removing leaf litter and increasing light availability. Daily ER was controlled by autotrophic activity in the spring and allochthonous organic matter inputs from leaf litter in autumn. After an initial decrease following storms, labile organic matter inputs from the surrounding terrestrial system led to a multi-day stimulation of ER. Thus, variability in ecosystem metabolism was evident on all time scales, and attributable to daily and seasonal influence of light interacting with vegetation, and episodic high flows.

The decoupling of GPP and ER is frequently driven by large fluctuations in ER in streams characterized by relatively low GPP. However, in streams characterized by high GPP, algae and their associated bacteria generate a large proportion of system-wide ER. Under these circumstances GPP and ER do frequently covary. An excellent example of such covariation was documented in a study of NEP by Huryn et al. (2014) in a spring-fed stream in Alaska in the northern United States (Fig. 14.10). Peak summer rates of GPP and ER were comparable to those of productive streams at temperate latitudes. In contrast, winter rates were low. They suggested that light availability was responsible for patterns in GPP, whereas carbon limitation of heterotrophs, due to low GPP, limited ER.

In both temperate and tropical rivers, seasonal changes in allochthonous inputs can dominate energy flow and influence metabolic regimes, but the factors controlling leaf senescence differ between regions. In the temperate zone, the phenology of deciduous vegetation is largely controlled by temperature and photoperiod (Piao et al. 2019). In autumn, as temperatures cool and day length shortens, leaf fall provides a pulse of allochthonous matter entering streams. In contrast, precipitation, rather than temperature, plays a dominant role in leaf senescence in the tropics. Shedding of leaves during the driest months may help tropical plants reduce water stress (Reich and Borchert 1984), and generate seasonal inputs of riparian leaf litter in some tropical biomes (Tonin et al. 2017). Because anthropogenic climate change is expected to both increase temperatures and alter

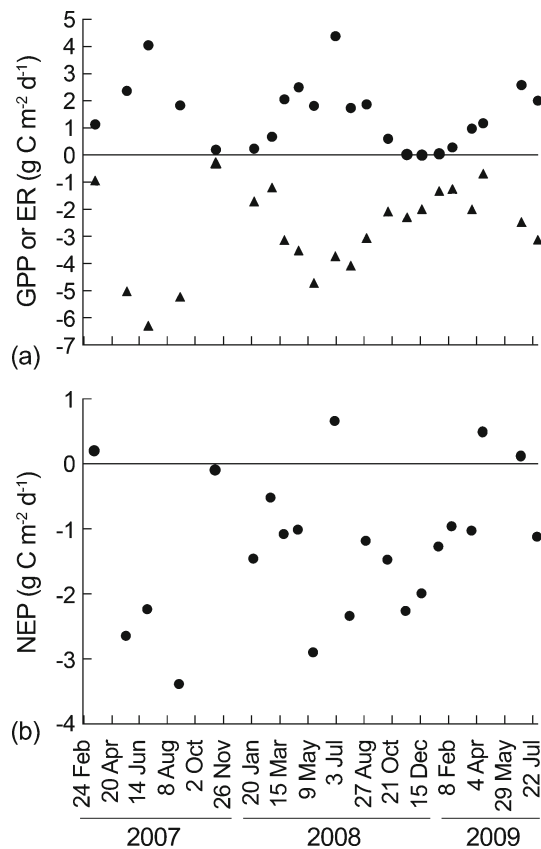


Fig. 14.10 Seasonal patterns of (a) gross primary production (GPP, circles) and ecosystem respiration (ER triangles, top panel) and (b) net ecosystem production (NEP) for Ivishak Spring, Alaska, US. All values were estimated semi-monthly from March 2007 to August 2009. (Reproduced from Huryn et al. 2014)

precipitation regimes, climate change has the potential to influence the quantity, biological availability, and timing of allochthonous inputs, and alter the metabolic regimes of rivers throughout the world (Larsen et al. 2016).

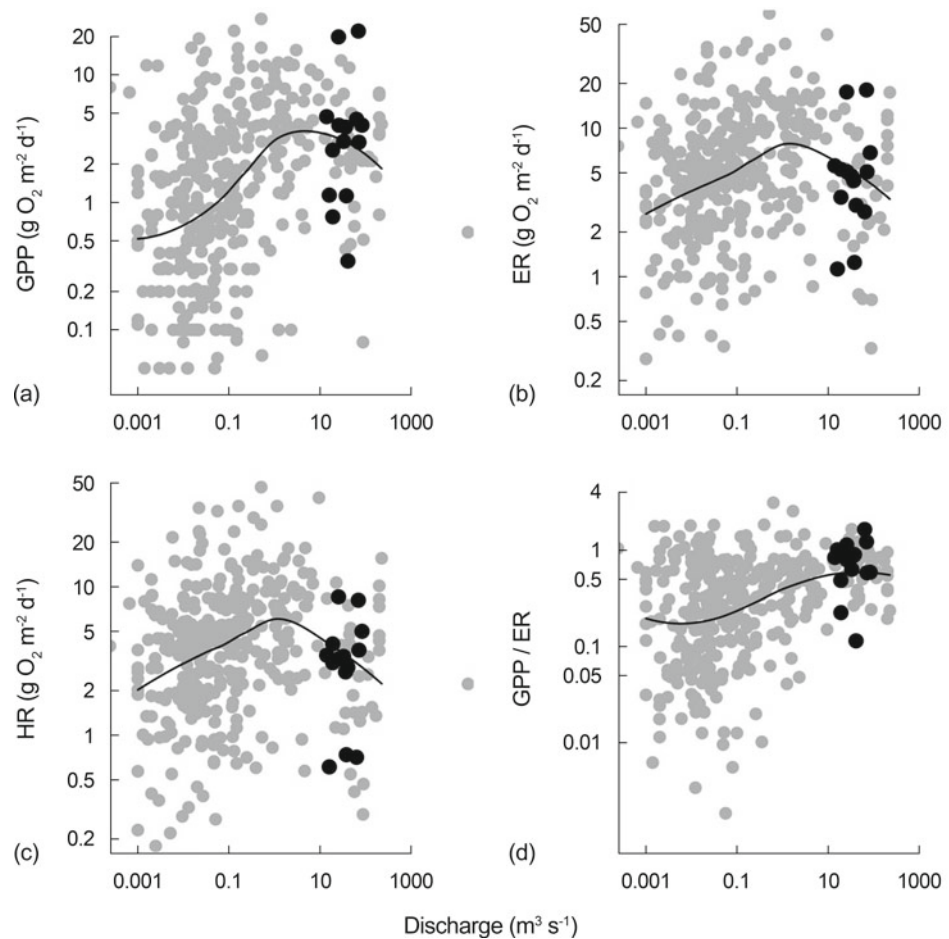
Stream size may also affect patterns in GPP and ER. Reach-scale metabolism measurements have only recently been collected in larger systems, now providing insights into how the size and position of a river within a watershed influence patterns in metabolism. In a study of 14 mid-sized rivers in the western and midwestern United States, variation in GPP among rivers spanned much of the range of GPP that has been documented in smaller streams (Hall et al. 2016). However, the rivers included in the study had lower rates of heterotrophic respiration relative to GPP, and both GPP and ER peaked in rivers of medium size (Fig. 14.11). In a study of Spanish rivers by Rodríguez-Castillo et al. (2019), NEP was lowest and the difference between GPP and ER was the greatest in the smallest tributaries; however, there was no distinct pattern in NEP that was associated with stream size.

Much of what we have learned about patterns in river energy dynamics has been gleaned from studies conducted

in systems with highly predictable flow regimes (e.g., regulated or spring fed systems; Bernhardt et al. 2018). Yet, stream metabolism is likely to vary with hydrologic disturbance and stream channel retentiveness because these factors directly influence organic matter storage, and thus may alter patterns in benthic respiration (Demars 2019). Even when exposed to intense light, streams with relatively frequent bed-moving flows have relatively low productivity. Frequent hydrologic disturbance can influence stream metabolism by scouring periphyton and biofilms from stone surfaces, and in more extreme cases, through bed transport and up-ending of stones. Measurement of ecosystem metabolism in a sixth-order, gravel-bed Swiss River for 447 days showed strong effects due to bed-moving spates (Uehlinger and Naegeli 1998). Immediately after spates, primary production and ecosystem respiration both declined. Primary production recovered more rapidly in summer than in winter, whereas recovery of respiration showed less seasonal dependency. Spates may have less effect on respiration than primary production because heterotrophic processing of organic matter within the streambed is likely to be less affected by disturbance than autotrophic activity on the bed surface. Thus, depth of scouring, amount of organic matter storage within the streambed, and magnitude of the disturbance will determine the extent to which ecosystem metabolism is altered.

Recent work offers preliminary evidence that it may be possible to classify river systems by their rates of total and net productivity and by the seasonal patterns of photosynthesis and respiration. In an analysis of long-term metabolism datasets from 47 rivers in the United States, Savoy et al. (2019) documented two dominant riverine productivity regimes characterized by the timing of peak productivity. Summer-peak rivers had the mean date of peak productivity in midsummer and an extended period of high GPP. In contrast, spring-peak rivers were characterized by a discrete peak in GPP earlier in the year, followed by very unproductive summer months. A set of environmental variables, including watershed area, water temperature, and discharge, placed most rivers into one of these two productivity regimes. The analysis also hinted at the existence of two additional productivity clusters: aseasonal systems with relatively constant, low rates of GPP year-round, and summer decline rivers with early productivity peaks that declined gradually throughout the summer. This work suggests that a classification system for streams based on patterns in net productivity may be an additional tool to estimate the impact of human activities on stream ecosystem function. Figure 14.12 depicts a conceptualization of the different patterns in climate, light, and hydrology that may occur along the river continuum. Acting together, these drivers of metabolic rates can produce a wide range of values for both GPP and ER, and their sum, NEP. However, additional

Fig. 14.11 (a) Gross primary production (GPP), (b) ecosystem respiration (ER), (c) heterotrophic respiration (HR), and (d) GPP/ER as a function of river discharge. All ER values are absolute values. Black points are the 14 rivers from this study; gray points are data from other studies. Axes are log scaled. The point far to the right is from the Mississippi River and represents the largest possible size for a North American river. Because of the zero density in points between the Mississippi River and the second largest river in the dataset, the regression line was not fit to include the Mississippi River. (Reproduced from Hall et al. 2016)



long-term, continuous data are needed from a greater number and greater diversity of rivers and streams to create a robust classification system.

Predicting how energy flows from headwaters to a river delta is made even more complicated because streams and rivers are often part of complex freshwater networks made up of both lentic and lotic habitats that are impacted by human activities (Hotchkiss et al. 2018). Because water residence times differ markedly between rivers and lakes, the opportunity for metabolic processing and for export along the river system vary as well; this may be especially true in river systems that have been dammed. Modelling carbon dynamics in complex river networks is an emerging challenge for stream ecologists, and essential for developing global carbon budgets.

14.2.7 Additional Factors Influencing Metabolic Processes

The distribution of plants and animals may also influence metabolic processes in streams and rivers. An evaluation of substrate-specific GPP and ER in Atlantic Rainforest streams

in Brazil by Tromboni et al. (2017) documented strong contributions to GPP from substrate covered by epilithon and macrophytes, and large contributions to system-wide respiration estimates from substrate covered by leaf litter (Fig. 14.13). Animals may also influence patterns in GPP and ER, as demonstrated for aggregations of mussels. Though significant effects were not observed for ER or NEP, reaches with mussel beds had much greater rates of GPP than reaches without beds (Atkinson et al. 2018). Plants and animals that enter rivers and streams from other habitats also have the potential to influence stream metabolism. Though not often considered, respiring roots from riparian tree species may influence in-stream oxygen dynamics, especially in smaller systems (Dodds et al. 2017). Migrating and senescing salmon can have substantial effects on instream GPP and ER (Levi et al. 2013). In the cobble-bottom streams of southeast Alaska, US, GPP doubled during the salmon run (Fig. 14.14). However, GPP responded inconsistently to the presence of salmon in sand-bottom streams in Michigan in the north-central US, possibly because salmon-derived nutrients enriched autotrophic and heterotrophic communities in all streams, but the changes in nitrogen and phosphorus in Michigan were not as dramatic as were the changes in Alaskan streams (Levi et al. 2013).

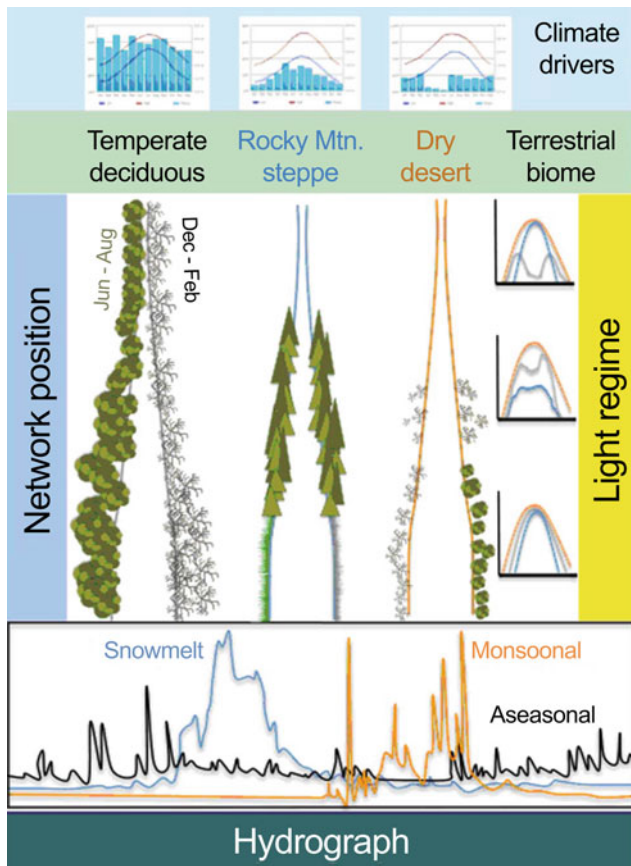


Fig. 14.12 A conceptual model depicting how differences in climate, light, and hydrologic regimes vary along the river continuum and between three terrestrial biomes. The climate diagrams across the top show average monthly precipitation in blue bars with daily air temperatures shown as blue (minimum) and red (maximum) lines. (Reproduced from Bernhardt et al. 2018)

Land use change can alter metabolic processes in rivers and streams, often by increases in light and nutrient concentrations associated with land conversion (Masese et al. 2017; Griffiths et al. 2013; Tank et al. 2010). Pooling data from periodic daily measurements of whole-stream metabolism from six nutrient-rich streams draining row-crop agriculture in the midwestern United States, Griffiths et al. (2013) documented the influence of variation in light, water temperature, and nutrient concentrations associated with agricultural development (Fig. 14.15). Primary production varied with light level, which was influenced by stream incision and aspect despite the lack of riparian canopy (Fig. 14.15a). Higher water temperatures and greater concentrations of soluble reactive phosphorus were linked with greater rates of respiration (Fig. 14.15b). Measured only during baseflow, both productivity and respiration were high relative to more pristine systems, and one-fourth of all daily measurements had a $P/R > 1$. Interestingly, the range of metabolic rates was similar across the six streams, possibly because of imposed homogeneity due to agriculture.

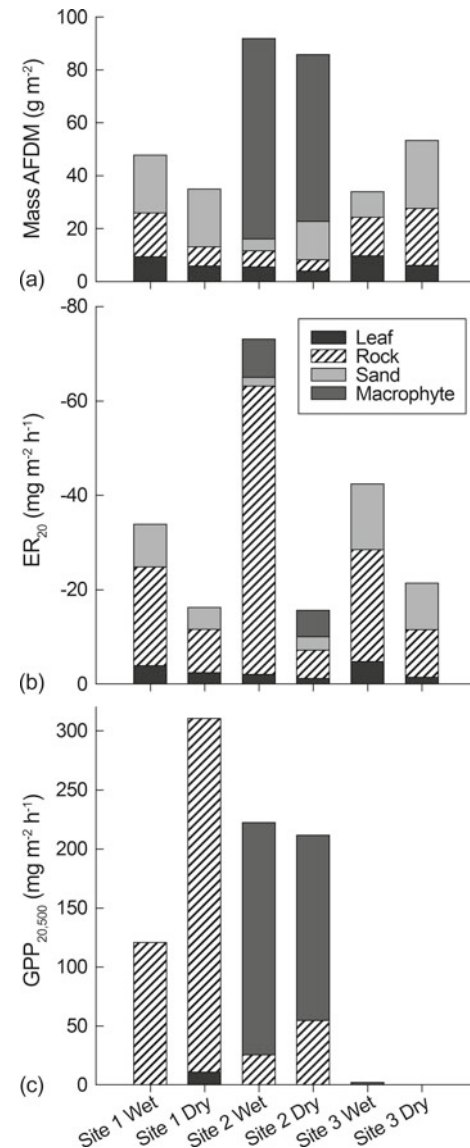


Fig. 14.13 (a) Standing stock of ash-free mass per unit stream area by stream and by season, (b) ecosystem respiration (ER), and (c) gross primary production (GPP) rates per unit area for three streams in wet and dry seasons and on different substrates. (Reproduced from Tromboni et al. 2017)

At the global scale, access to wastewater treatment can be quite limited. Even in regions with wastewater infrastructure, large volumes of untreated waste may be discharged into surrounding rivers and streams (Connor et al. 2017), influencing stream metabolism. Using a 20-year dissolved oxygen record following the construction of a wastewater treatment plant on the Oria River in northern Spain, Arroita et al. (2019) demonstrated that respiration considerably exceeded GPP in the sewage-impacted river. Wastewater treatment reduced the summer peaks of productivity (Fig. 14.16a) and had an even greater dampening effect on annual rates of respiration (annual rates of respiration by

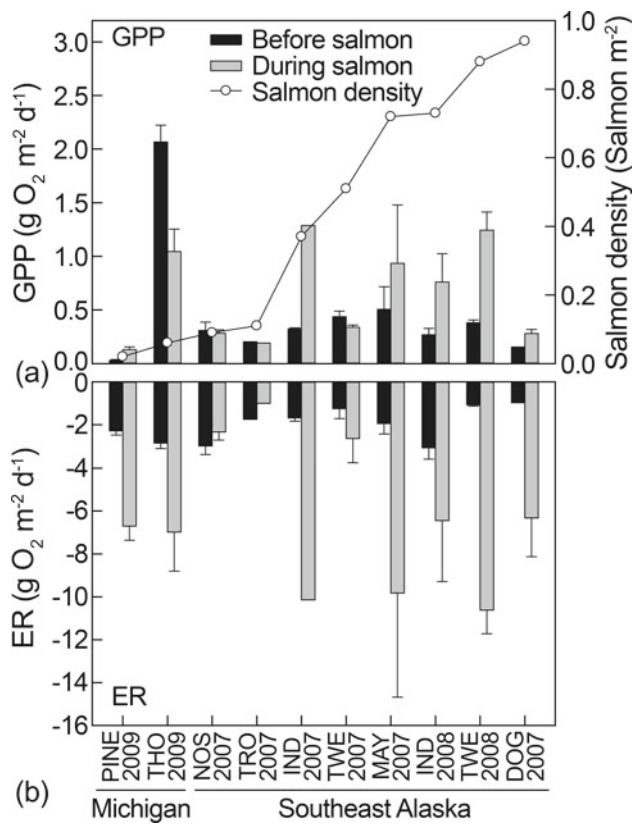


Fig. 14.14 Estimates (mean \pm SE) of daily (a) gross primary production (GPP) and (b) ecosystem respiration (ER) before and during the salmon run for streams in Alaska and Michigan. ER, representing the consumption of oxygen, is displayed as negative values to provide contrast with concurrent GPP. Streams are ordered from left to right according to increasing peak salmon density (line connecting open circles) along the horizontal axis. (Reproduced from Levi et al. 2014)

autotrophs and heterotrophs combined, Fig. 14.16b), resulting in an increase in net ecosystem productivity in the river (Fig. 14.16c). Consequently, river metabolism shifted from strongly heterotrophic to near equilibrium between primary production and ecosystem respiration, indicating that autotrophs were the main drivers of metabolism, and resulting in conditions that facilitated the recovery of aquatic macroinvertebrates and fishes.

Climate change may also induce changes in the processes underpinning stream metabolism (Harjung et al. 2019; Song et al. 2018), and alpine systems may be especially at risk. In 12 study reaches of the Ybbs River network in Austria, researchers documented peaks in productivity in ten of the sites during spring snowmelt that were linked to patterns in light reaching the stream surface and catchment area. As winter precipitation shifted from snow to rain in the spring of a low-snow year, the streams experienced increases in respiration, which converted net ecosystem production in the spring from autotrophy to heterotrophy (Ulseth et al. 2018).

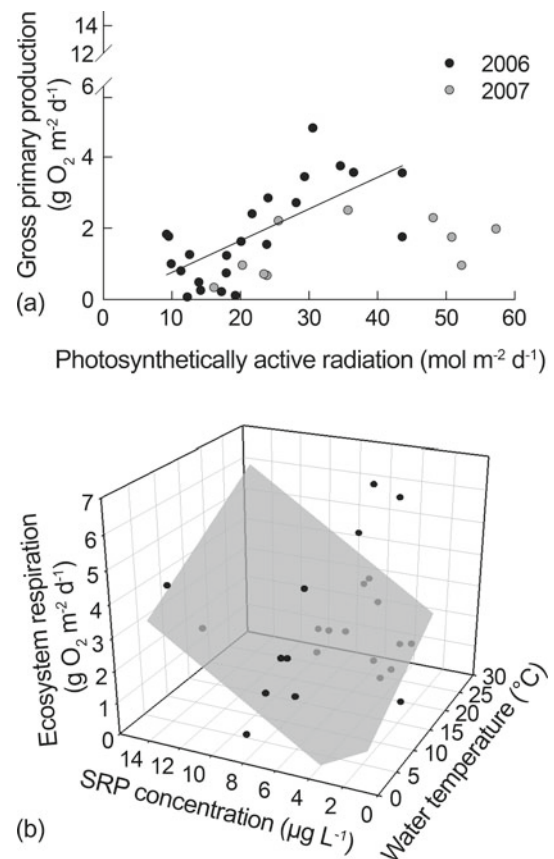


Fig. 14.15 Relationships between (a) gross primary production (GPP) and photosynthetically active radiation (PAR), and (b) ecosystem respiration (ER) with streamwater temperature and soluble reactive phosphorus concentration (SRP). (Reproduced from Griffiths et al. 2014)

These findings suggest that climate-induced changes in temperature and precipitation regimes may also transform the source-sink dynamics of carbon in streams and rivers. Warming temperatures and reduced snow pack may influence food web structure and ecosystem processes throughout river networks if streams in alpine regions begin emitting more within-stream respiratory CO_2 and supplying less autochthonous energy to reaches downstream. Research in other cold regions of the globe also has demonstrated that increasing water temperatures can influence patterns in instream productivity. In an experimental manipulation of streams in Iceland, Hood et al. (2018) artificially increased water temperatures but retained seasonal changes in light. Irrespective of light seasonality, primary production was greater under warmer temperatures. This change was linked to a shift in the autotroph community, suggesting that altered thermal regimes associated with climate change may influence aquatic community structure in ways that change important ecosystem processes in streams (Fig. 14.17).

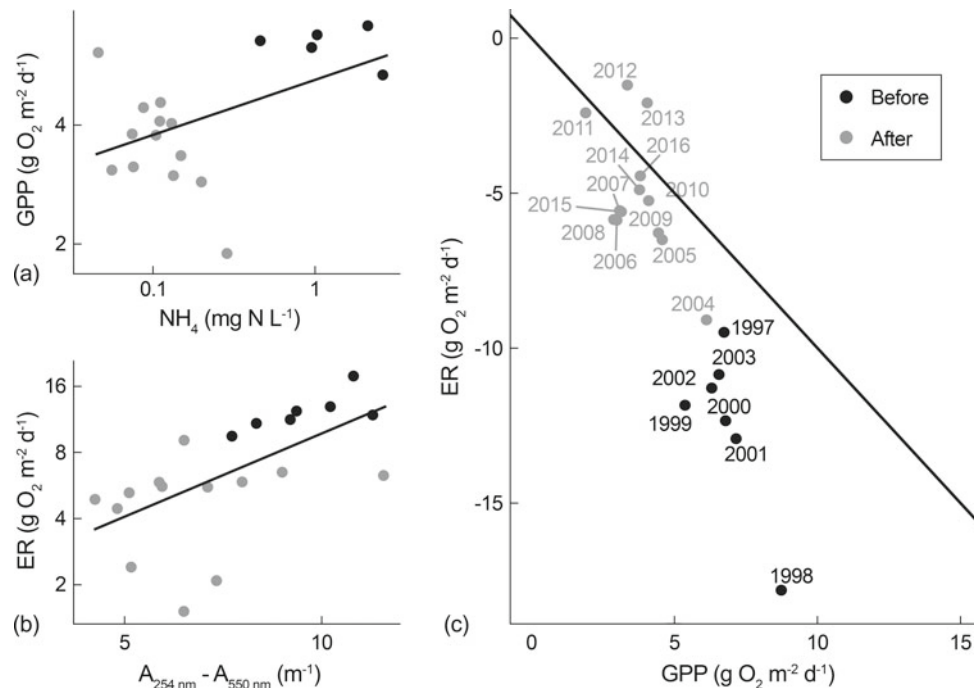


Fig. 14.16 Relationships between (a) the annual peak of gross primary production (GPP) and ammonium concentration and (b) the annual peak in ecosystem respiration (ER) and the absorbance of dissolved organic matter (a proxy for the concentration of dissolved organic matter) before and after wastewater treatment plant installation

in the Oria River in the northern Iberian peninsula. (c) The decrease in ER exceeded that for GPP, and the river went from heterotrophy to equilibrium between GPP and ER (i.e., closer to the 1:1 line represented by the black line). All values correspond to summer means. (Reproduced from Arroita et al. 2019)

The intensification of extreme weather events, such as drought and hurricanes, is associated with anthropogenic climate change (Stott 2016; Ornes 2018). Though work is relatively limited, studies have begun to reveal some of the implications of these events on stream metabolism. In an investigation of the response of urban streams to Superstorm Sandy on the east coast of the United States, Reisinger et al. (2017) found that both productivity and respiration declined precipitously following floods associated with storm events; however, the impact was greater on primary production. Both processes recovered quickly (4–18 days) after the disturbance event, and did not differ significantly in recovery rate. This suggests that metabolic processes in urban streams may be more susceptible to change in response to an event, but may recover more quickly after intense storms compared to streams in less disturbed watersheds, because urban streams are often characterized by a flashy hydrograph (Reisinger et al. 2017).

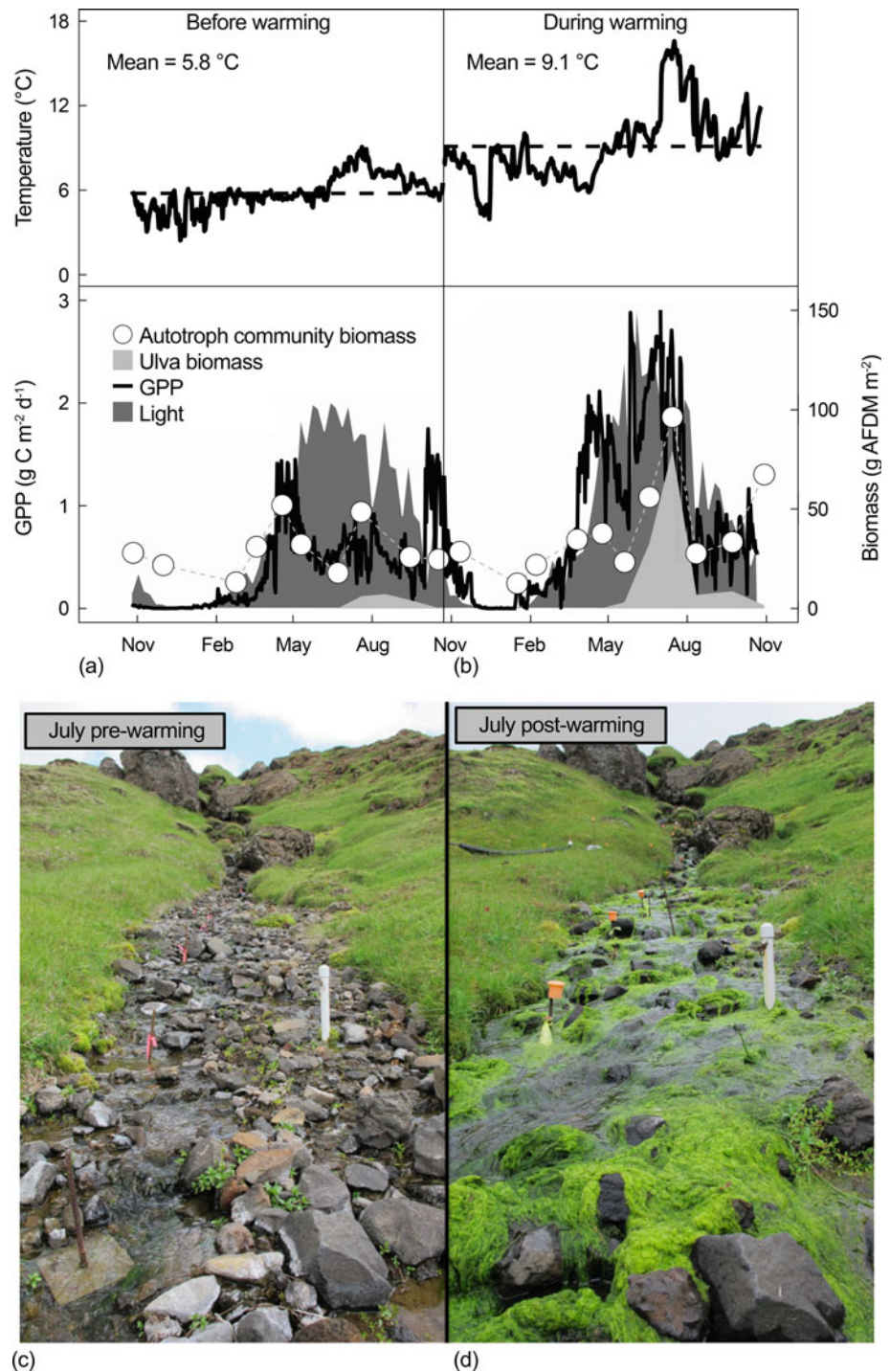
Extreme weather can create conditions that catalyze other environmental events that subsequently influence ecosystem process in rivers and streams. For example, a drought-induced defoliation event by larval gypsy moths (*Lymantria dispar*) in Rhode Island in the northeastern US reduced canopy cover by over 50%. Relative to the prior year of data, water temperatures were warmer, light availability was greater, and autotrophic activity was enhanced following defoliation (Addy et al. 2018). In addition, both

caterpillar frass (feces) and leaf detritus associated with the event added particulate carbon and organic nutrients to the stream that may have enhanced respiration. During the defoliation event, the stream experienced lower mean daily levels and wider diel cycles of dissolved oxygen. Though both instream productivity and respiration were significantly higher during the defoliation event, the impact on respiration was greater.

Although flow extremes are initially disruptive, organic matter may be deposited within the sediments as the flood subsides, and so any decline ecosystem respiration may be short-lived. Light, nutrients, and other factors favoring algal growth will of course influence how rapidly the autotrophic community recovers. In comparison to sites with frequent disturbance events, rates of GPP often are maximized in clear streams with high light availability and low flows. In these systems, productivity rates can be as high as those recorded for temperate forests (Bernhardt et al. 2018). Globally, the pressure on freshwater resources is increasing, and more and more streams are subject to low flows and drying events. Desiccation, like flooding, can influence the timing and magnitude of riverine productivity. Hence, changes in flow are predicted to alter patterns in stream metabolism.

As our understanding of patterns in stream metabolism expands, it is likely that rivers and streams will be characterized by their “metabolic regimes” and serve as the basis

Fig. 14.17 An ecosystem-level temperature manipulation undertaken to quantify how coupling of stream ecosystem metabolism and nutrient uptake responded to a realistic warming scenario. Water temperature and gross primary production (GPP) are shown before (a) and after (b) warming. Water temperatures were higher during the warming manipulation, but retained the same seasonality. Gross primary production (GPP) was higher during the warming manipulation, and the autotroph community shifted toward dominance of *Ulva*, a macroscopic green alga, during June and July. During the warming manipulation, GPP peaked in April–May and June–July. The second peak in production was associated with an *Ulva* bloom as shown in the photographs of the experimental stream in July before (c, 2011) and during (d, 2013) the warming manipulation. (Reproduced from Hood et al 2018)



for a new functional classification system for rivers and streams (Ulseth et al. 2019; Bernhardt et al. 2018). Anthropogenic activities, including but not limited to, land use change, water infrastructure, and increasing temperatures and altered precipitation regimes associated with climate change, are all expected to influence spatial and temporal

variation in metabolic processes. Systems characterized by short periods of peak metabolism are expected to experience the most severe effects of human disturbance, as small shifts in the magnitude and timing of productivity could result in large changes in energy dynamics in the system (Bernhardt et al. 2018).

14.3 Organic Matter Budgets

Organic carbon is the common currency that can be used to quantify all inputs, transfers, and exports of energy flowing through an ecosystem. The previous section explored internal energy production measured as GPP, and energy consumption by autotrophs and heterotrophs measured as ER. As was discussed, the importance of allochthonous carbon sources is indirectly captured by comparing GPP to ER; when the latter is large relative to the former, external energy sources must be fueling ecosystem metabolism. Organic carbon (OC) budgets provide a more detailed accounting of all carbon sources, especially allochthonous inputs. Organic carbon budgets are also referred to as organic matter (OM) budgets because researchers often quantify organic matter, and subsequently estimate carbon content to be approximately 50% of total OM. Organic matter budgets, including energy inputs and losses, can provide insightful cross-system comparisons of the overall efficiency with which ecosystems use available energy (Webster and Meyer 1997).

Instream primary production and terrestrial production that enters streams as allochthonous material will either be used by stream heterotrophs or exported from the system, either as CO₂ that is respired and outgasses to the atmosphere, or via downstream transport, potentially to the oceans. Organic matter can accumulate over relatively short periods, on the timescale of weeks to months, and storage on or within the streambed and on banks and floodplains can occur on the timescale of years to decades, and perhaps even longer. Storage of organic matter depends on flow variation, as material tends to accumulate during low flows and be exported by high flows. Averaged over long periods, storage was originally thought to be negligible, at least for streams of low order. However, more recent work suggests that mountain streams can store large amounts of carbon (Wohl et al. 2017). Thus, factors that influence the relative rates of conversion of organic carbon to CO₂ versus transport largely determine what fraction of organic matter is mineralized within stream ecosystems, and this is expected to differ among OM compartments. A high rate of utilization relative to transport indicates that OM is contributing to stream metabolism and the stream ecosystem is efficient in its processing of organic carbon inputs. The opposite result indicates that most OM is stored or exported downstream and the stream ecosystem is relatively inefficient in processing carbon resources.

It should be noted that dissolved inorganic carbon (DIC) can comprise a large amount of the total carbon budget in streams (Argerich et al. 2016; Campeau et al. 2017). In-stream DIC is derived from biological and geological sources, originating in both terrestrial and aquatic

environments. Soil respiration is often a primary source of DIC entering streams, but its relative importance to carbon dynamics is often regulated by underlying geology (e.g., the weathering of carbonate minerals). Evasion of CO₂ from streams, stream metabolism, and anaerobic processes are also often key components in DIC cycling (Campeau et al. 2018). As our focus is on organic matter budgets we will not explore DIC dynamics in depth, but this is an important aspect of carbon biogeochemistry.

Organic matter budgets are constructed for some delimited area of an ecosystem. This can be a stream or river reach, or in the case of small headwater streams, the entire catchment. Organic matter budgets attempt to measure all inputs, including primary production, POM from leaf litter and other sources, and DOM from upstream and groundwater; all standing stocks of CBOM, FBOM, and wood; and ecosystem outputs as respiration and export. Budgets can reveal transformations that occur within the study system (for example, CPOM might dominate inputs while FPOM dominates outputs), thereby lending insight into the physical and biological processes that alter the quantity and quality of material within the stream. Coupled with measurement of internal fluxes and the processes that are responsible, the budget approach can provide considerable insight into the flow of material through ecosystems.

In their landmark study of a 1,700 m reach of Bear Brook, a small woodland stream in New Hampshire, Fisher and Likens (1973) pioneered the use of organic matter budgets in running waters. OM inputs from litter, throughfall, and surface and subsurface water were quantified. Because impermeable bedrock underlies this drainage basin, all hydrologic outputs could be estimated from streamflow and organic matter concentrations measured at a weir. The amount of stored material in Bear Brook was assumed to be constant, and on this basis, respiration was estimated from the excess of imports over exports. From the annual energy budget for Bear Brook (Table 14.1), it appears that greater than 99% of the energy inputs were due to allochthonous material (with particulates contributing more than dissolved matter), and about 65% of this was exported downstream (Webster and Meyer 1997). More POM was exported from the study segment than entered it from upstream, and this difference was made up by inputs of litter fall. Virtually all internal processing was attributed to microorganisms.

Organic matter budgets have since been constructed for a number of river ecosystems spanning a range of conditions. A predominance of allochthonous inputs seems to be the rule wherever there is ample riparian vegetation. In a first-order blackwater stream in Virginia with a tree canopy along its entire length, litterfall represented 100% of total inputs (Smock 1997). Similarly, the carbon budget of the Kuparuk

Table 14.1 Organic matter budget for Bear Brook, New Hampshire, in the Hubbard Brook Experimental Forest. Bear Brook is a second order stream, with a catchment area of 132 ha and a streambed area of 6,377 m². Based on a compilation of studies by Findlay et al. (1997)

Organic matter parameters	
Inputs (g AFDM m ⁻² y ⁻¹)	
Gross primary production	3.5
Litterfall and lateral movement	594
Groundwater DOM	95
Standing crops (g m ⁻²)	
Wood > 1 mm	530
CBOM > 1 mm (not including wood)	610
FPOM < 1 mm	53
Outputs	
Autotrophic respiration (g m ⁻² y ⁻¹)	1.75
Heterotrophic respiration (g m ⁻² y ⁻¹)	101
Particulate transport (kg y ⁻¹)	1700
Dissolved transport (kg y ⁻¹)	514

River, originating in the Brooks Range of Alaska, US, and flowing northwards into the Arctic Ocean, is almost totally dominated by allochthonous inputs (Peterson et al. 1986). In this tundra stream meandering through peatland, allochthonous inputs of peat and tundra plant litter exceeded benthic algae primary production by almost an order of magnitude. Although the Kuparuk River is unshaded, cold temperatures and low phosphorus concentrations limit periphyton production. Subsequent estimates showed that net primary production by mosses is similar in magnitude to benthic algal production, increasing the total contribution of autochthonous carbon to this river but not altering the main finding that primary production is modest (Harvey et al. 1997).

The autochthonous component of organic matter budgets is expected to increase downstream as rivers increase in width and the effects of shading and allochthonous inputs from riparian vegetation diminish. In subarctic streams in Quebec, Canada, allochthonous material contributed over 75% of total inputs in streams of low order (Naiman and Link 1997). In contrast, allochthonous inputs contributed only 6–18% the total in larger streams of order five and six. The contribution of autochthonous organic matter to total inputs was positively related to stream order in a synthesis of organic matter budgets from 35 streams located in North America, the Caribbean, Europe, and Antarctica (Webster and Meyer 1997). Arid-land streams were an exception because they are open to the sun and receive few litter inputs.

Instream primary production typically dominates desert stream organic matter budgets (Bunn et al. 2006; Fisher et al.

1982) and high latitude streams (McKnight and Tate 1997; Huryn and Benstead 2019). Primary production in Sycamore Creek, Arizona, was sufficiently high that it substantially exceeded community respiration (Table 14.2); the excess was accounted for by accrual of algal biomass and by downstream export (Grimm 1988). In a meltwater stream in the McMurdo Dry Valleys of Antarctica, primary production by algal mats, composed primarily of filamentous cyanobacteria, was the only carbon source; unsurprisingly, in a land without terrestrial vegetation, allochthonous inputs were zero. Although autochthonous production may be low in many stream types, many researchers have argued that the role of instream primary production has been under-appreciated (Brett et al. 2017). Primary production exceeds litter inputs in a number of examples (Table 14.3), and there is a fairly obvious alternation in their relative importance depending upon forest canopy development.

Seasonality and land use can also drive organic matter dynamics in lotic systems (Tank et al. 2010). In temperate forested streams, peak litterfall occurs in the autumn. Large litter inputs also can result from water stress, as seen in many tropical systems during the dry season (Tonin et al. 2017). In streams draining landscapes with limited riparian vegetation, such as desert streams, seasonal pulses can be less pronounced or nonexistent (Schade and Fisher 1997). Streams in forested watersheds have significantly higher POM inputs when compared to streams draining non-forested watersheds (Golladay 1997). Furthermore, in the temperate zone, streams draining undisturbed watersheds typically have greater leaf litter inputs than do streams draining watersheds that have been logged (Webster et al. 1990).

Fewer organic matter budgets have been constructed for segments of large rivers. Bayley (1989b) approximated a carbon budget for a 187 km stretch with a maximum inundated area of 5,330 km² of the Solimões River (the Amazon above Manaus, Brazil). Only a small fraction of the total carbon supply originated with transport of material from upstream (<1%), or as primary production by river phytoplankton (5.4%) and periphyton attached to macrophytes (1.5%). Production by aquatic and terrestrial macrophytes in the littoral regions and floodplain, and litter inputs from the flooded forest, collectively accounted for approximately 90% of carbon production, and so river-floodplain interactions were of far greater consequence than events within the channel. Findings from the Orinoco floodplain of Venezuela were similar: forest litter represented 27% and macrophytes 68% of total carbon sources, and inputs from phytoplankton and periphyton production together contributed only 2% (Lewis et al. 2001). In a sixth-order blackwater river in Georgia, river channel gross primary production accounted for only about one-fifth of total inputs, which were dominated by floodplain organic matter originating in extensive riparian swamps of up to 1–2 km in width (Meyer and

Table 14.2 Organic matter budget for Sycamore Creek, Arizona. Sycamore Creek is a 5th-order stream with a catchment area of 50,500 ha and a streambed area of 33.1 m². Budget is based on a compilation of studies by Jones et al. (1997)

Organic matter parameters	
Inputs (g AFDM m ⁻² y ⁻¹)	
Gross primary production	1,888
Litterfall	16.5
Lateral movement	3.1
Standing crops (g m ⁻²)	
CBOM > 1 mm (not including wood)	5.2
BOM (not including leaves and wood)	104
Hyporheic FPOM	39
Outputs	
Autotrophic respiration (g m ⁻² y ⁻¹)	944
Heterotrophic respiration (g m ⁻² y ⁻¹)	372
Hyporheic respiration (g m ⁻² y ⁻¹)	3259
Particulate transport-baseflow (kg y ⁻¹)	11,900
Dissolved transport (kg y ⁻¹)	506,000

A synthesis of 36 organic matter budgets from six different biomes reveals distinct trends related to landscape controls of inputs to streams (Webster and Meyer 1997). A principal components analysis of major budget components categorized streams along a first axis that was positively correlated with litterfall and BOM, and negatively correlated with primary production; and a second axis that was strongly correlated with POM and DOM concentrations in transport (Fig. 14.18). Small mountain streams cluster in the lower right of Fig. 14.18, sharing the characteristics of high litterfall and BOM, and low GPP. Lowland streams have much higher organic matter concentrations and thus greater transport, and arid-land streams fall at the opposite end of the first axis with high GPP and low litterfall and BOM. Thus climate, terrestrial biome, and position along the elevational gradient can be seen to be important underlying controls on stream organic matter budgets.

The budget approach to organic matter dynamics has been highly informative, but its limitations must be acknowledged. Missing terms are common, particularly DOM sources, POM inputs from floodplains, and storm

Table 14.3 Comparison of energy inputs from net primary production (NPP) versus litter fall for a number of spring and running water studies. Additional inputs (e.g., groundwater, transport from upstream) are not considered here. From Peterson et al. (1986) after Minshall (1978). See Petersen (1986) for citations to individual studies

River	Energy input (g C m ⁻² y ⁻¹)		
	Autochthonous NPP	Allochthonous litter inputs	Reference
Bear Brook, NH	0.6	251	Fisher and Likens (1973)
Kuparuk River, AK	13	100–300	Peterson et al. (1986)
Root Spring, MA	73	261	Teal (1957)
New Hope Creek, NC	73	238	Hall (1972)
Fort River, MA	169	213	Fisher (1977)
Cone Spring, IA	119	70	Tilly (1968)
Deep Creek, ID 1	206	0.2	Minshall (1978)
Deep Creek, ID 2	368	7	Minshall (1978)
Deep Creek, ID 3	761	1.1	Minshall (1978)
Thames River, U.K.	667	16	Mann et al. (1970)
Silver Springs, FL	981	54	Odum (1957)
Tecopa Bore, CA ^a	1229	0	Naiman (1976)

^aThermal spring

Edwards 1990). However, as discussed earlier in the chapter, food webs can be fueled largely by autochthonous sources even in systems dominated by allochthonous inputs. Hence, when considered in conjunction with data indicating that many aquatic organisms derive their energy from autochthonous resources, these studies collectively highlight that OM budgets can be used to track carbon through ecosystems, but do not necessarily identify the carbon sources that support secondary production.

transport of POM. Dissolved organic matter inputs are influenced by stream size, precipitation, dominant land use, the presence of wetlands in a watershed, hydraulic conductivity, and hydrologic flow paths (Tank et al. 2010). Stream DOM is predominantly derived from riparian soils and terrestrial leaf litter and accounts for a large percentage of total organic matter inputs (Tank et al. 2018). Additionally, DOM can be derived from instream primary production, suggesting that some DOM is a byproduct of

photosynthesis. Lower concentrations of DOM tend to be found in watersheds where soils have high adsorption capacities (e.g., soils rich in clay; Tank et al. 2010).

Inputs, outputs, and storage can vary substantially among years, but because of the effort involved, organic matter budgets often are estimated for just one year, or pieced together with data from multiple years. In a comparison of 23 organic matter budgets from rivers of various sizes, located in different biomes, only one was in steady state (Cummins et al. 1983). Substantial accrual of stored organic matter occurred in 14 budgets, while exports exceeded imports in the remaining eight. The input-output balance for 17 streams reported by Webster and Meyer (1997) included several cases where outputs exceeded inputs by a large margin. These authors argue that it is unlikely that exports will be higher than inputs in annual budgets, and suggest that underestimation of inputs from groundwater and floodplains may be responsible for the imbalance. However, interannual variation in disturbances such as fire, storms, and logging that occur infrequently are important to ecosystem dynamics,

and they are unlikely to be incorporated in a one-year “snap-shot”. For example, FPOM export varied fourfold over a seven-year study in a stream in the southeastern United States (Wallace et al. 1997). Ideally, any ecosystem budget should be placed in a historical context in order to capture among-year variation in processing, storage and export.

A more recent effort to document multi-year variation in the carbon budget of a headwater stream by Argerich et al. (2016) estimated that $159 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ was exported from the system. This was notable because the stream comprised only 0.4% of the watershed area, but was exporting carbon at a rate similar to published estimates for much larger systems. Through time, carbon export was dominated by the transport of DIC downstream ($\sim 40\%$ of the total) and by the evasion of CO_2 to the atmosphere ($\sim 26\%$ of the total). Dissolved ($\sim 11\%$) and particulate ($\sim 21\%$) organic carbon comprised a much smaller fraction of the total carbon exported from the system. Carbon export was seasonally variable, as 90% of total carbon export occurred between November and April,

Fig. 14.18 A principal components analysis of 25 stream energy budgets from six biomes shows that arid streams, small mountain streams, and lowland streams separate along axes determined by energy inputs, benthic organic matter, and transport rates of organic matter. See text for further explanation. (Reproduced from Webster and Meyer 1997)

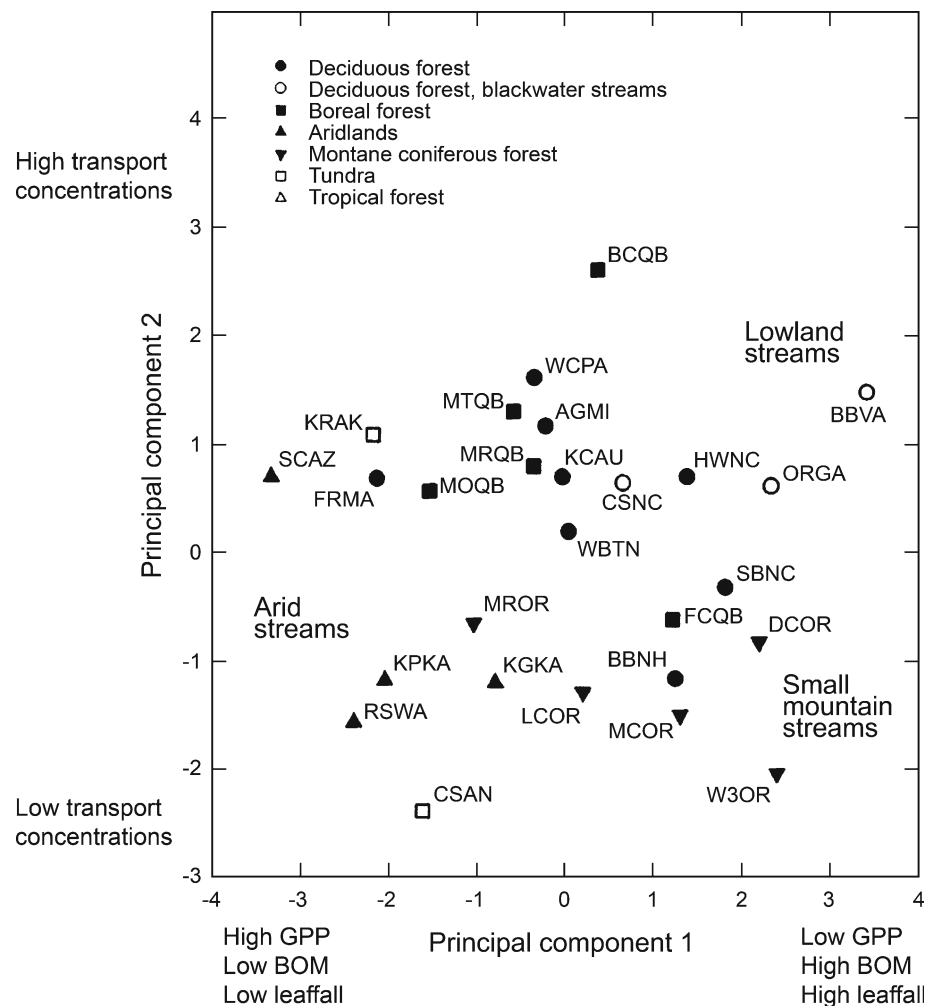
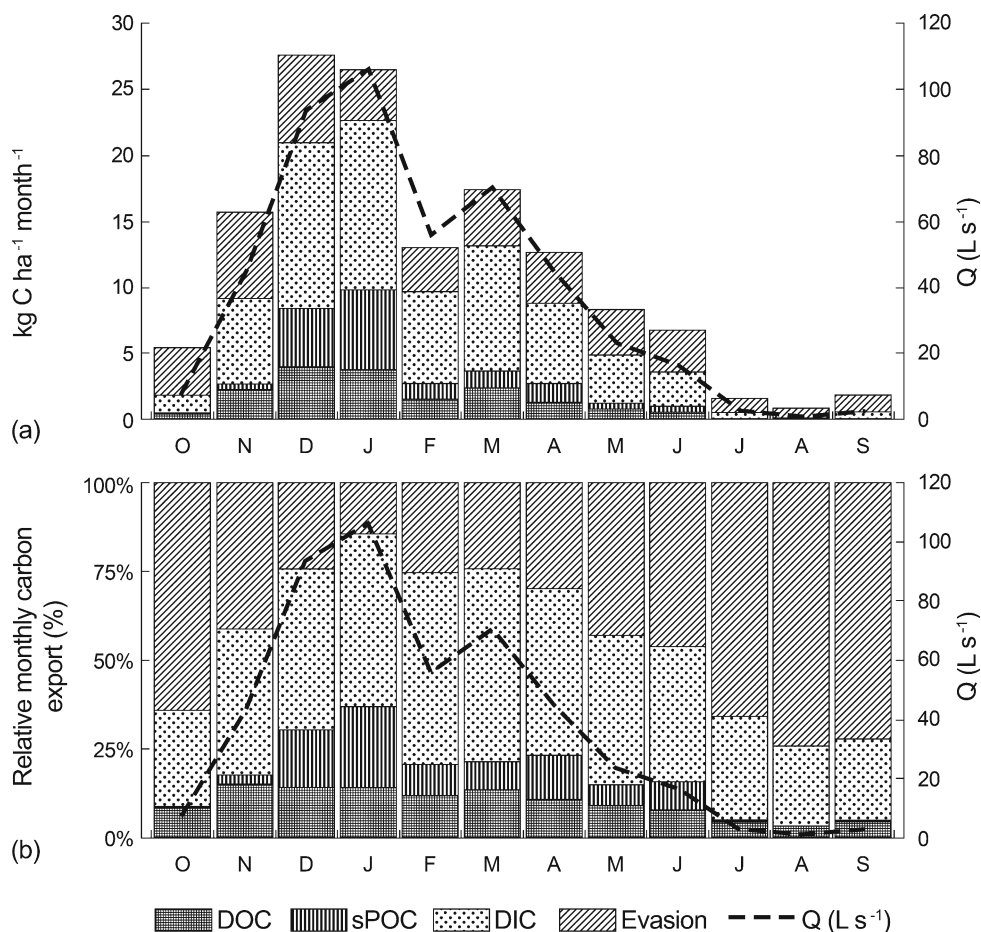


Fig. 14.19 The total (a) and relative monthly (b) contribution of different sources of carbon to stream carbon export. Mean monthly discharge (Q) is represented by the dotted line in both figures. The carbon values were calculated from weekly composite samples ($n = 3$) that were collected between 2004–2013. (Reproduced from Argerich et al. 2016)



the period of the year associated with the greatest flows (Fig. 14.19). Interannual variation was also observed, but the drivers of variation differed among the different forms of carbon. Flow was a good predictor of the export of DIC and DOC, but not POC. In contrast, annual variation in stream metabolism was related to in-stream temperatures and photosynthetic active radiation.

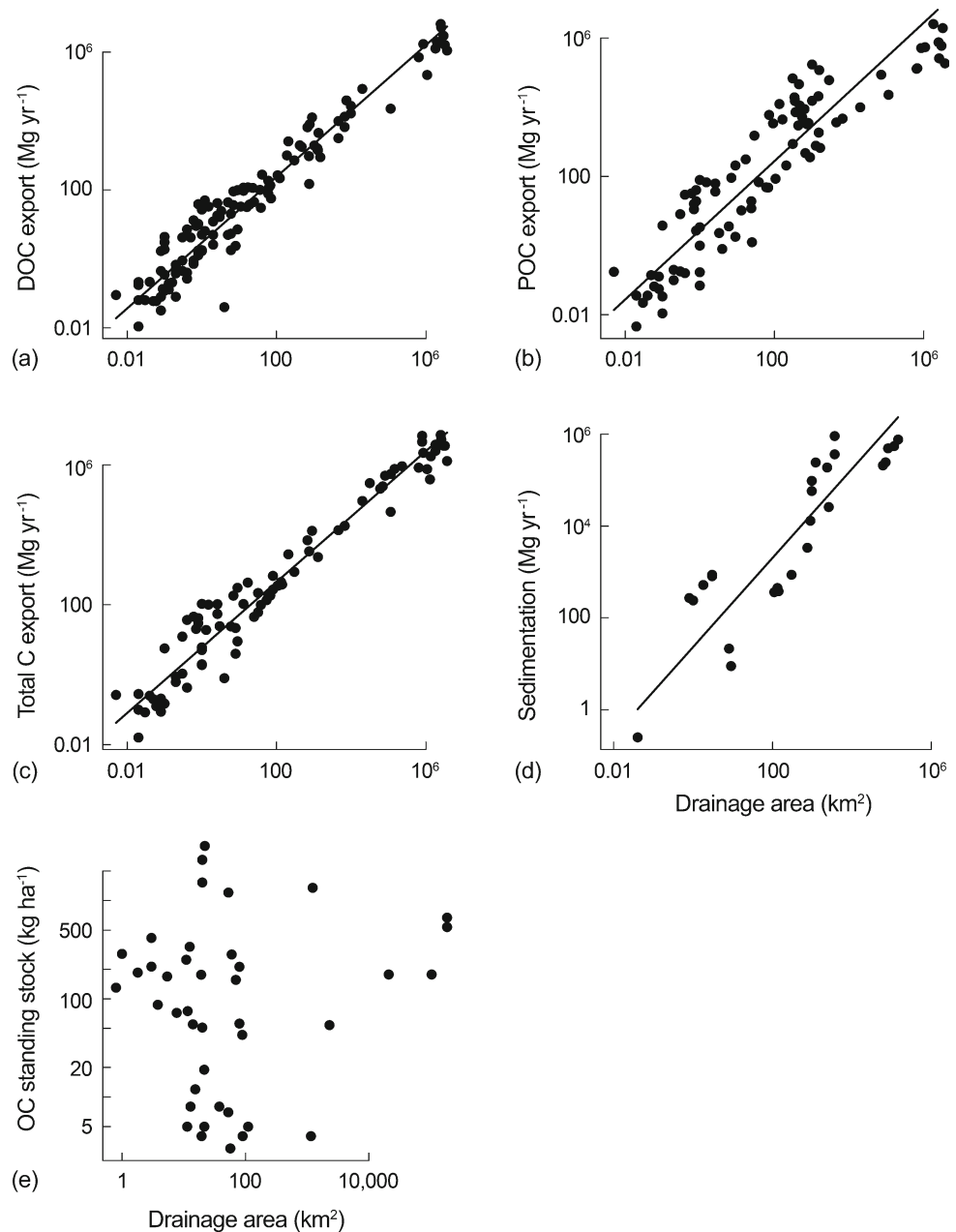
Quantification of the amount of organic carbon stored within river systems makes clear that vastly more carbon is stored within riparian vegetation, downed wood, and sediments than is contained within all of the instream biotic compartments (Fig. 14.2). Organic matter in riparian systems is primarily stored in above-ground standing biomass, large woody debris, and sediment on and beneath the floodplain surface (Sutfin et al. 2016). The residence time of retained organic material ranges from days (e.g., labile sugars) to hundreds of years (e.g., woody debris; Tank et al. 2010). The mechanisms promoting retention differ among the fractions of organic matter because of their varying physical and chemical characteristics. For example, DOM is biologically retained, whereas POM is first physically retained and then processed biologically (Tank et al. 2010). Though many components of the carbon budget are

positively correlated with increasing drainage area, carbon standing stocks are not, indicating that other factors must account for variability in this term (Fig. 14.20; Wohl et al. 2017). For instance, the size of carbon pools varies with environmental variables, such as riparian vegetation, soil type, and microbial activity that are influenced by climate, flow regime, valley geometry and underlying geology, making it difficult to generalize about patterns in OC standing crop. However, rivers in cool, wet regions with complex channel geometry within unconfined valleys are optimal conditions for the retention and storage of organic matter in riparian habitats (Fig. 14.21; Sutfin et al. 2016).

Human activities likely have increased riverine carbon flux, especially since the mid-20th Century. From the world's longest record of DOC concentrations, some 130 years for the Thames Basin, UK, Noacco et al. (2017) found that 90% of the long-term rise in fluvial DOC is explained by increased urbanization and is linked to rising population and increased sewage effluent. Land disturbance also has increased carbon export, related to the conversion of grasslands to agriculture and the mobilization of carbon stored in soils. Recent studies analyzing the ^{14}C content of transported organic matter have found that a major

Fig. 14.20 Scaling of organic carbon fluxes and standing stock with river drainage area. If the slope of the line is significantly less than 1, the flux or stock decreases more slowly relative to the increase in drainage area. If slope of the line is significantly greater than 1, the flux or stock decreases at a faster rate than drainage area. A slope of 0 indicates no relationship between flux or stock and drainage area.

(a) The regression between dissolved organic carbon (DOC) flux and drainage area. (b) The regression between particulate organic carbon (POC) flux and drainage area. (c) The regression between total organic carbon (TOC = DOC + POC) and drainage area. (d) The regression between sedimentation rate of OC within the riparian zone and drainage area. (e) No relationship was seen between the stock of OC and the drainage area. (Reproduced from Wohl et al. 2017)



component in most rivers is highly aged material >1,000 years in age, further evidence of the mobilization of stored carbon by human disturbance. Analysis of a global data set of radiocarbon ages of riverine dissolved organic carbon found that the age of dissolved organic carbon in rivers increases with population density and the proportion of human-dominated landscapes within a watershed, and decreases with annual precipitation (Butman et al. 2015). Although one might expect that organic material that has withstood decomposition for thousands of years would be a poor food source compared to recently produced material, studies have found surprisingly significant incorporation of

aged carbon into planktonic food webs in the Hudson River, New York, US (Caraco et al. 2010).

14.4 Carbon Spiraling

Carbon spiraling, a measure of the distance traveled by an atom of carbon in organic form until it is mineralized to CO₂, serves as a comparative measure of an ecosystem's efficiency in processing organic material (Newbold et al. 1982). Because organic matter transport is such a dominant process in streams, estimates of the travel time or distance of

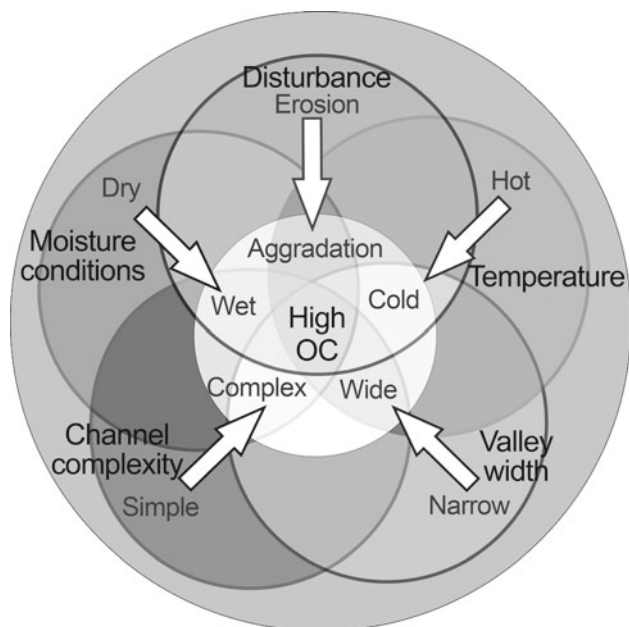


Fig. 14.21 Some of the regional and local controls on organic carbon storage in river corridors. White arrows indicate the gradient toward optimal conditions. (Modified from Sutfin et al. 2016)

a carbon atom is a useful comparative measure. Carbon spiraling length includes two components: uptake length, which is the distance traveled in dissolved inorganic form before being immobilized by the biota; and turnover length, which is the distance traveled by an atom of carbon in organic form before being completely converted to CO_2 by metabolic processes. These terms are also used for nutrient uptake and subsequent mineralization or release. Uptake length for dissolved organic carbon (DOC) can be estimated based on whole-stream releases of organic compounds or leaf leachates. In some cases, the material released is labeled with ^{13}C and researchers can trace changes in isotopic signatures, providing insight into how DOC is incorporated into aquatic food webs (Mineau et al. 2016).

Turnover length, a measure of ecosystem efficiency, can be estimated from downstream carbon flux divided by ecosystem respiration (Newbold et al. 1982). The turnover length (S_p) of different types of POM is estimated from the average particle velocity (V_p) divided by breakdown rate (k):

$$S_p = \frac{V_p}{k} \quad (14.3)$$

This represents the distance a particle travels before entering the next pool of organic matter (for CPOM to become FPOM, or for FPOM to become DOM). The breakdown rate k for FPOM is estimated from its respiration rate in the laboratory. V_p can be calculated as:

$$V_p = \frac{S_w}{T_t + \frac{S_w}{V_w}} \quad (14.4)$$

where S_w is the distance traveled by the particle in the water, T_t is the turnover time or the time that the particle remains on the stream bed, and V_w is water velocity.

Carbon spiraling rates vary among rivers and streams, influenced by organic matter inputs, retention capacity, and metabolic processes such as GPP and ER. In a study comparing carbon turnover length and turnover times in impounded and free-flowing sections of the Spree River in Germany, Wanner et al. (2002) documented that free-flowing sections of the river recycled approximately 50% of the standing stock of particulate organic carbon, but impoundment reduced recycling rates to just 25%. The impounded section had larger standing stocks of carbon, shorter carbon turnover lengths, and longer turnover times compared to the free-flowing reach (Fig. 14.22), suggesting that impoundments can alter multiple stocks and flows of the carbon budget.

In their synthesis of many studies of breakdown and transport in forested small streams in the southeastern United States, Webster et al. (1999) compared biological turnover time (a term that also includes physical and chemical breakdown) and transport distance for the four main categories of OM. Breakdown rates ranged from nearly six years for sticks to a few months for leaves, and exceeded a year for FPOM. Although these estimates are provisional for many reasons, the outcome is reasonable: transport rates were higher than breakdown rates for sticks in comparison with leaves and FPOM. Particle turnover lengths were estimated to be 0.15, 0.11 and 42 km for sticks, leaves, and FPOM. Webster and Meyer (1997) reported a significant correlation between discharge and turnover length, implying that small streams are more efficient in the use of organic matter. In the Taieri River, New Zealand, organic carbon turnover length ranged between 10 and 98 km, with higher values downstream where discharge also was higher (Young and Huryn 1997). In the Snake River, Idaho, turnover lengths were between 11 and 108 km and were related to patterns in current velocity (Thomas et al. 2005).

Spiraling length also varies over time and is influenced by land use (Lisboa et al. 2016). In small streams draining agricultural landscapes in Indiana in the central US, spiraling length changed seasonally, from 7.7–54.4 km in winter to 0.2–9.0 km in summer (Griffiths et al. 2012). Unsurprisingly, the authors suggested seasonality was primarily driven by differences in discharge, suggesting that hydrology tightly controls the fate of organic carbon in these streams. This work also provided evidence that relative to forested streams, agricultural streams tended to be less retentive of

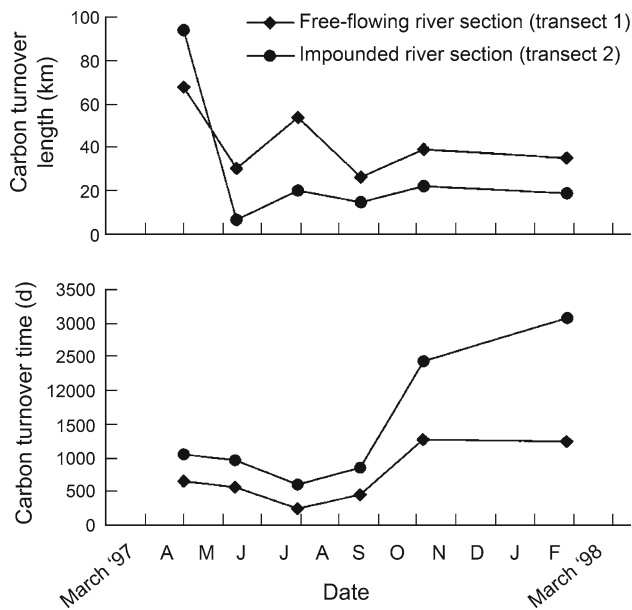


Fig. 14.22 Temporal variation in turnover lengths (a) and turnover times (b) of organic carbon for free-flowing and impounded sections of the River Spree, Germany. (Reproduced from Wanner et al. 2002)

organic carbon. Griffiths et al. (2012) inferred that small streams draining agricultural areas primarily function as conduits transporting organic carbon downstream, except during low, stable-flow periods when they can be as retentive of organic carbon as forested headwaters (Fig. 14.23).

14.5 Summary

In a prescient essay published in 1975, Noel Hynes wrote that “in every respect the valley rules the stream”. Geology determines the availability of ions and the supply of sediments, topography determines slope and degree of containment, climate and soils determine vegetation and hence the availability of autochthonous and allochthonous organic matter, and so on. Decades of research support this view. The river continuum concept describes how basal resources and thus consumer assemblages and stream metabolism change along a river’s length owing to changes in river size and terrestrial influences. The flood pulse model reminds us that carbon dynamics in rivers is strongly influenced by hydrology and connectivity with the surrounding terrestrial environment. In addition, our perspective on rivers within landscapes has expanded to encompass more explicit consideration of the physical template and spatial hierarchy provided by the river network. Intriguingly, Hynes (1975) also opined that every stream “is likely to be individual and

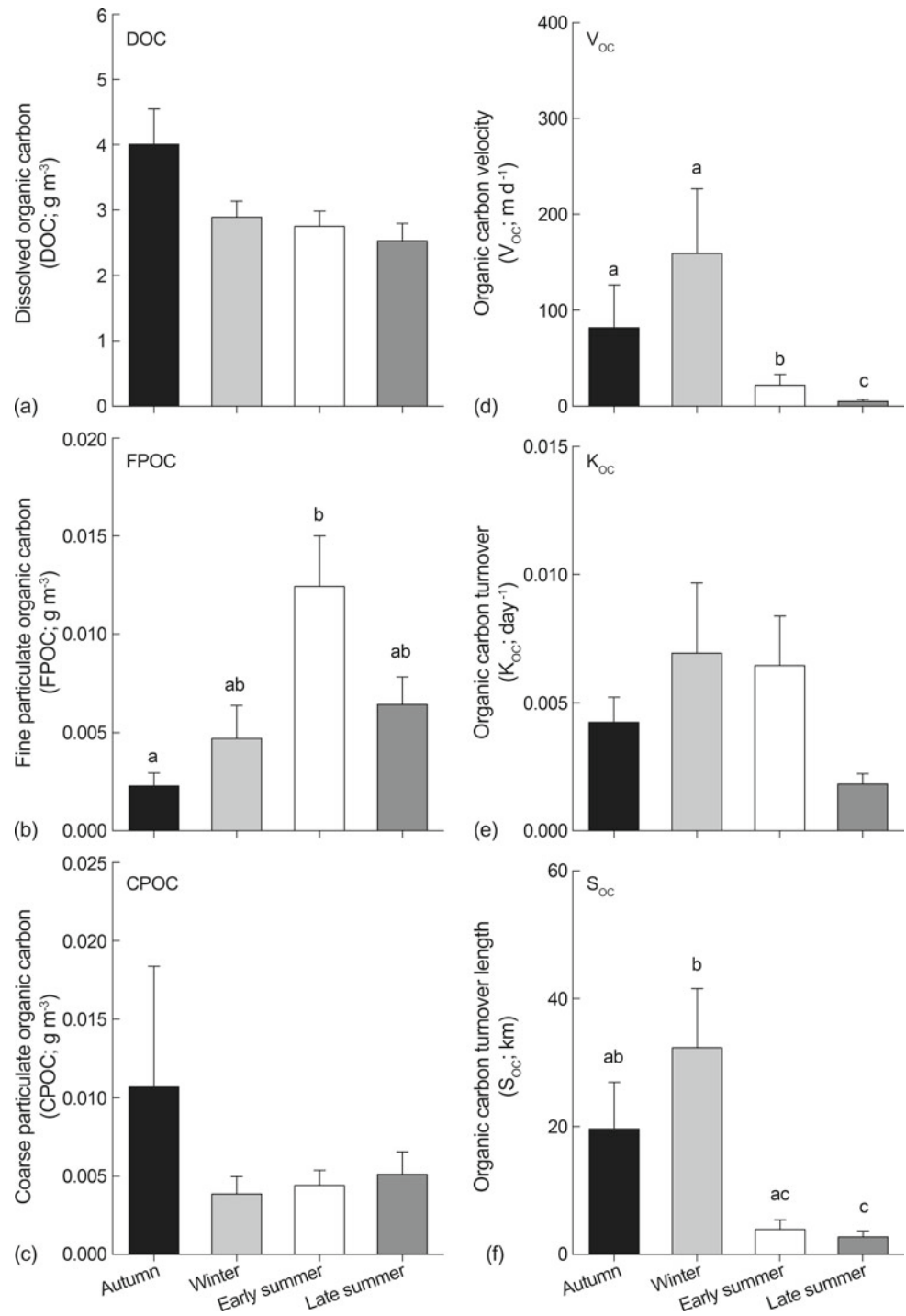
thus not really very easily classifiable”. Yet, decades of effort to place the individuality of streams within the frameworks of scale and landscape have significantly advanced our understanding of the causes of that individuality. New advances, supported by the increasing availability of sensors, adoption of open-water methods to measure whole stream metabolism, and new statistical tools will support emerging efforts to classify streams by their metabolic processes.

Sources of organic carbon in lotic ecosystems include autochthonous production by algae and aquatic plants, and allochthonous inputs of dead organic matter from terrestrial primary production. Studies of stream ecosystem metabolism address two central questions: the relative magnitude of internal versus external energy sources, including their variation along a river’s length and with landscape setting; and the efficiency of the stream ecosystem in metabolizing those energy supplies versus loss of carbon to downstream ecosystems, the atmosphere, and the oceans. Principal approaches include the comparison of gross primary production to ecosystem respiration, mass balance estimation of all inputs and exports, and measures of the efficiency with which organic carbon is utilized.

Stream metabolism is measured by accounting for the oxygen produced through primary production, lost through ecosystem respiration, and exchanged with the atmosphere. The relationship between gross primary production and ecosystem respiration can indicate whether an ecosystem is reliant mainly on internal production, or requires organic matter subsidies to sustain respiration. The net flux of oxygen, measured as the sum of gross primary productivity (a positive value) and ecosystem respiration (a negative value) is called net ecosystem productivity. Macroscale patterns in stream metabolism and the biological, physical, and chemical factors that regulate productivity, respiration, and riverine gas exchange are becoming better understood as longer-term data are collected in a broader diversity of lotic systems. Ecologists and water resource managers may soon be able to use the metabolic regimes of streams to assess the influence of anthropogenic activities on the function of flowing waters.

Organic carbon budgets are based on the estimation of all inputs, standing stocks, and losses within a stream reach or, ideally, a catchment, although the latter is practical only for headwater streams. Budget studies demonstrate how the climate and the terrestrial biome influence the relative magnitude of allochthonous versus autochthonous inputs. Inputs of coarse, fine, and dissolved organic matter from terrestrial primary production typically dominate the energy supply in small, forested streams where algal primary production tends

Fig. 14.23 Left Panel: Carbon transported as (a) dissolved organic carbon (DOC), (b) fine particulate organic carbon (FPOC), and (c) coarse particulate organic carbon (CPOC). Right Panel: Organic carbon spiraling metrics: (d) organic carbon velocity (V_{oc}), (e) biotic turnover rate of organic carbon (K_{oc}), and (f) organic carbon turnover length (S_{oc}). Mean values are reported (\pm standard error) for each biologically important time period (autumn, winter, early summer, and late summer). Letters represent significant differences between seasons based on results from Tukey's HSD post-hoc tests (Reproduced from Griffiths et al. 2012)



to be light-limited, but primary production is of greater importance in open locations that receive sufficient light. Thus, longitudinal position and landscape setting determine the relative magnitude of sources of organic carbon to stream ecosystems. In general, arid-land, meadow, and prairie streams have high primary production relative to detrital

inputs, temperate forested streams are the opposite and highly dependent upon external energy inputs, and lowland streams have large quantities of DOC and POC in transport.

Organic matter that enters the channels of streams and rivers can be stored for some time on streambanks and by burial within the channel, but ultimately it is exported to downstream

ecosystems or mineralized to CO₂ by the biota and lost from the system by outgassing. Export is the fate of a great deal of organic matter. Organic matter export is determined by the interaction of material available on the stream bottom, retentive capacity of the system, and hydrologic variability.

Globally, rivers respire significant quantities of carbon to the atmosphere and export significant quantities of organic carbon from terrestrial primary production to downstream locations and the oceans. Streams of low order are frequently inefficient, exporting large quantities of FPOM and DOM to downstream reaches. Our understanding of the role of smaller systems in watershed-level CO₂ evasion is just emerging. Large rivers transport substantial amounts of POM and DOM, but declines in DOC concentrations in lower reaches of large rivers and their super-saturation with CO₂ provide evidence of substantial metabolic activity, indicating that significant mineralization takes place near the lower terminus of rivers.

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