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# A review of allochthonous organic matter dynamics and metabolism in streams

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**Abstract.** The role of allochthonous organic matter in lotic ecosystems has been an important research topic among aquatic ecologists since the seminal work by Lindeman was published in 1942. Since 1986, studies on organic matter budgets, ecosystem metabolism, and decomposition published in *J-NABS* have made significant contributions to the overall understanding of organic matter dynamics in streams. In this review, we summarize the utility of organic matter budgets, cover the major advances in research on ecosystem metabolism, and describe the intrinsic and extrinsic factors influencing organic matter decomposition. We also discuss future directions and current applications of research and highlight the need for additional studies on the role of land use and climate change, as well as continued use of organic matter processing as a functional metric in biomonitoring studies. We emphasize the need for continued data synthesis into comprehensive organic matter budgets. Such comparative studies can elucidate important drivers of organic matter dynamics and can assist in the understanding of large continental/global changes that might be occurring now and in the near future. In general, continued emphasis on synthesizing information into a larger framework for streams and rivers will improve our overall understanding of the importance of organic matter in lotic ecosystems.

**Key words:** organic matter dynamics, streams, litter breakdown, carbon cycling, decomposition, organic matter budgets, metabolism.

Allochthonous organic matter has long been known to fuel stream food webs; this early understanding of the importance of allochthony is a classic and well studied example of ecological subsidies. Beginning with Lindeman (1942; Fig. 1), multiple studies have confirmed that the linkages across terrestrial–aquatic boundaries and among aquatic ecosystems (e.g., stream–lake connections) are fundamental to understanding organic matter dynamics. In particular, papers published in *J-NABS* have made significant contributions to our understanding of organic matter dynamics in lotic systems (158 publications since its inception in 1986; Fig. 2).

We have divided the topic of organic matter dynamics in lotic ecosystems into 3 broad categories: organic matter budgets, ecosystem metabolism, and decomposition. In each section, we have included information on the unique contributions of *J-NABS* papers. We begin with a summary of the utility of the organic matter budget approach, and we detail the general understanding of the particular compartments and fluxes that represent the factors that control organic matter budgets, i.e., inputs, transport and export, and retention. Next, we cover major advances in our current understanding of ecosystem metabolism. The section on organic matter decomposition includes: 1) intrinsic and extrinsic factors affecting decomposition, 2) decomposition in 'other' systems (moving forward from temperate forested headwaters), 3) decomposition of different forms of organic matter besides leaf litter (e.g., wood and fine particulate organic matter [FPOM]), and 4) the influence of macroinvertebrates on decomposition

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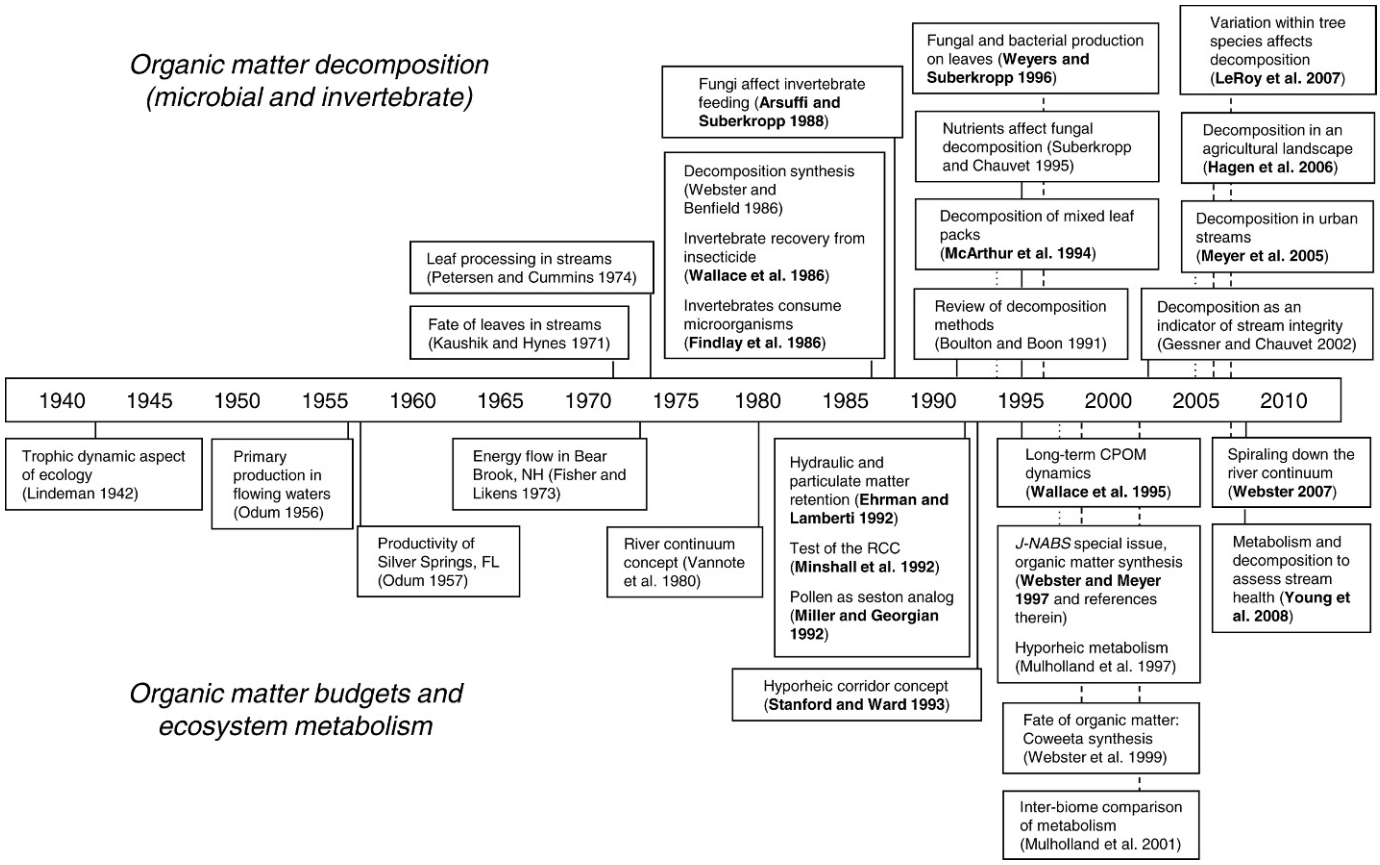



FIG. 1. Timeline illustrating major contributions to the understanding of organic matter processing in lotic ecosystems. FL = Florida, NH = New Hampshire, CPOM = coarse particulate organic matter, RCC = River Continuum Concept. Dashed lines are used for clarity when a connecting line passes behind a box. Boldface indicates paper was published in *J-NABS*.

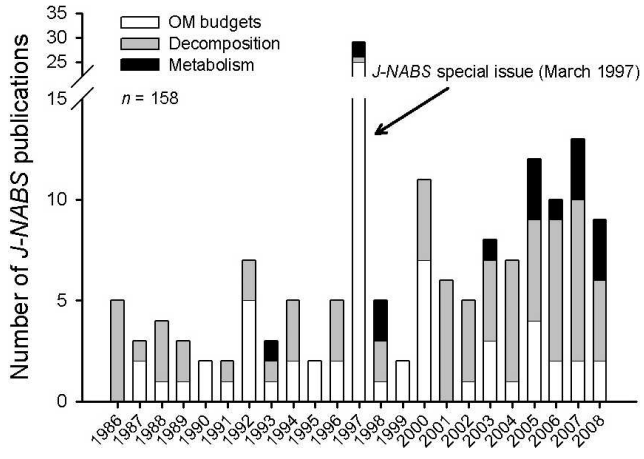



FIG. 2. The number of *J-NABS* publications focused primarily on organic matter dynamics from *J-NABS*' inception in 1986. For the purpose of this review, the topic of organic matter dynamics has been divided into 3 areas: organic matter budgets, ecosystem metabolism, and decomposition.

rates as a function of invertebrate diversity, geographic distribution, and organic matter quality. Last, we explore some future directions and current applications of the understanding of organic matter dynamics.

## Organic Matter Budgets

Organic matter budgets (quantification of energy inputs and outputs) provide insight into the relative importance of various resources that support stream ecosystems and are a useful tool for evaluating and comparing stream ecosystems. For any given stream, energy inputs can take the form of instream primary production, litterfall and lateral contributions from riparian vegetation, dissolved organic matter (DOM) in ground water, and inputs from upstream. Stream ecologists traditionally have classified organic matter by size: coarse particulate organic matter (CPOM; >1 mm) including wood and leaves, FPOM (~0.45 μm–1 mm), and dissolved organic matter (DOM;

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<~0.45 μm). Inputs of these size classes of organic matter are either retained within the system or output via physical export or respiration, and the difference between inputs and outputs represents instream processing through energy transformations and storage. Detailed budget data can be simplified to indices that express organic matter processes in aggregate (e.g., ecosystem efficiency, Fisher and Likens 1973 [Fig. 1]; stream metabolism index, Fisher 1977; or organic matter turnover length, Newbold et al. 1982).

*Historical perspective to 1986: from calories to C, using the common currency of organic matter*

Aquatic ecologists were leaders in developing ecosystem energy budgets. As early as 1926, Birge and Juday indicated that detritus standing stocks far exceeded living organic material in lakes and suggested that this allochthonous organic matter might be used as a food resource. Lindeman (1942) first quantified the energy flows among trophic levels in Cedar Bog Lake, Minnesota (USA), and his study emphasized the significant role of detritus in energy transfers. However, *actual* energy flows were not documented until 1957, in Howard T. Odum's study of a spring stream in Florida (USA) (Fig. 1). His seminal paper provided a baseline for comparison to other systems, conceptualized an ecosystem using a static compartment model, and quantified the role of detritus in supporting the Silver Springs food web. The Fisher and Likens (1973) study of Hubbard Brook, New Hampshire (USA), was one of the first budgets constructed for a forested headwater stream and provided a comprehensive account of inputs, standing stocks, and outputs of organic matter, and demonstrated the overwhelming contribution of allochthonous material to stream energy budgets (>99% of total inputs). In general, these early budget studies indicated that streams were detritus-based and heterotrophic in nature, and therefore, were highly dependent on organic matter derived from their adjacent watersheds. However, this conclusion was biased because most early study sites were headwater streams draining deciduous forests. Teal (1957), Fisher (1977), and Minshall (1978) demonstrated that autochthonous production also could be a substantial source of organic matter to headwater streams.

*1986 to present: a breakdown of budgets*

*Overarching contribution of* J-NABS *to organic matter budgets.*—Since 1986, the number of publications focusing on organic matter budgets (e.g., inputs, standing stocks, transport, and export) has varied among the major aquatic journals. *J-NABS* has published the greatest number (~70), followed by *Freshwater Biology* (~50), *Limnology and Oceanography* (~40), and *Canadian Journal of Fisheries and Aquatic Sciences* (~20).

*J-NABS*' most notable contribution to the study of organic matter budgets was the 1997 special issue edited by Jack Webster and Judy Meyer (volume 16, issue 1). This issue presented an intersite comparison of organic matter budgets for 35 streams across 7 biomes. The papers in that issue constitute ~35% of the total number of organic matter budgets published in *J-NABS* through 2008 (Fig. 2). The major conclusion of this synthesis was that climate, through its effect on vegetation, was the strongest controller of organic matter dynamics. Because of the overriding influence of climate, Webster and Meyer (**1997a**[1]; Fig. 1) stressed that a global comparison of patterns of stream function did not reveal much about specific mechanisms influencing stream function. With hopes of providing "generalities that might guide more specific studies", Webster and Meyer (**1997a**) synthesized the organic matter compartments and fluxes from these studies and pointed to new avenues of investigation, including the overwhelming influence of terrestrial vegetation on instream C resources, the episodic nature of organic matter transport, quantification of organic matter reservoirs in deep hyporheic storage, and the need to consider DOM as a significant and biologically available energy resource. Just as Odum's seminal study served as a reference point for early ecosystem energy budgets, the *J-NABS* organic matter issue provided a new baseline for comparative organic matter studies in lotic systems.

In the early 1980s, Cummins et al. (1983) reflected on the future directions of research on organic matter budgets and suggested that budgets covering longer time scales would improve understanding of storage dynamics (i.e., long-term decomposition, flood effects, and internal processing dynamics of each storage pool). Despite this call to generate interannual organic matter budgets for stream ecosystems, even construction of annual budgets has fallen out of favor. Few such studies have been published in *J-NABS* since the 1997 special issue (but see **Larned 2000**). The number of organic matter budgets published through time has not changed (Fig. 2), but the focus has shifted from construction of complete budgets to study of specific budgetary components.

*Organic matter inputs: particulate organic matter.*—The quantity and type of particulate organic matter (POM) inputs, and the spatial and temporal delivery

[1] Boldface indicates paper was published in *J-NABS*

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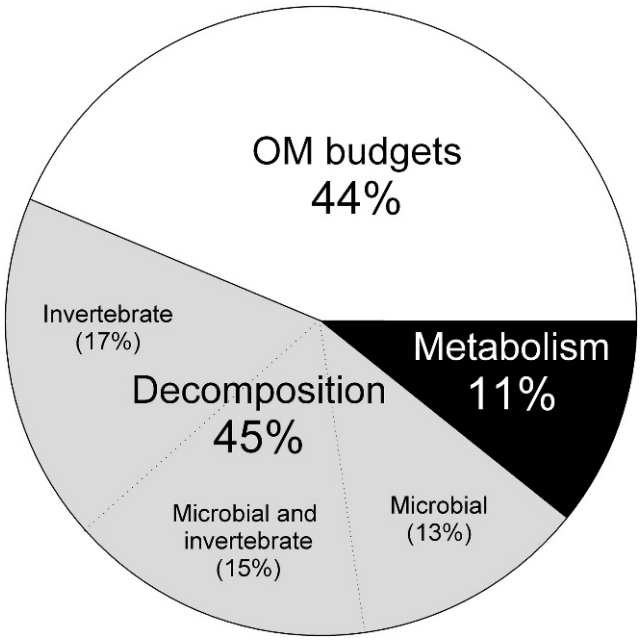



FIG. 3. The proportion of organic matter papers published in *J-NABS* ($n = 158$) by topic. For the purpose of this review, the topic of organic matter dynamics has been divided into 3 areas: organic matter budgets, ecosystem metabolism, and decomposition. Decomposition is divided into 3 categories: decomposition by invertebrates, microbial decomposition, and combined invertebrate and microbial decomposition.

of those inputs to streams, are highly variable. Particulate inputs, such as litterfall, are influenced primarily by the character of riparian vegetation and seasonality. Streams draining forested watersheds have significantly higher POM inputs than do streams draining nonforested areas (**Golladay 1997**), and streams draining undisturbed systems have higher litter inputs than do streams draining disturbed (i.e., logged) watersheds (**Webster et al. 1990**). In temperate forested streams, peak litterfall occurs in the autumn because of leaf abscission (Fisher and Likens 1972, Conners and Naiman 1984, **Benfield 1997**). Afforestation with nondeciduous species (e.g., eucalyptus, conifers) can alter the timing of peak inputs or eliminate seasonal peaks altogether (**Pozo et al. 1997**). Peaks in litterfall also can result from increased abscission in response to water stress (Spain 1984, **Larned 2000**). In streams draining landscapes with naturally sparse riparian vegetation (e.g., desert or tundra), seasonal pulses can be less pronounced or nonexistent (**Schade and Fisher 1997**).

The importance of lateral exchange of POM between lotic ecosystems and their floodplains has long been stressed (Minshall et al. 1985, Junk et al. 1989) and has been quantified for low-gradient, large rivers and coastal-plain streams with extensive floodplains (Mulholland 1981, Grubaugh and Anderson 1989, **Jones and Smock 1991**). Less is known about floodplain dynamics in smaller, high-gradient systems. Neatrour et al. (**2004**) investigated floodplain inputs in smaller, high-gradient sites in the Little Tennessee drainage basin in North Carolina (USA) and concluded that floodplain inputs to the stream channel made up a smaller fraction of particulate inputs than did direct litterfall and were smaller in magnitude than their large-river counterparts. Langhans et al. (2006) developed a conceptual model for large river–floodplain ecosystems (based on the Tagliamento River in northeastern Italy) that incorporated leaf decomposition, organic matter inputs, storage and quality, and their relationships to flow and inundation regimes. This contribution was a step toward a more systematic understanding of floodplain inputs, but the field would benefit from a more complete assessment of the relative importance of floodplain inputs from a wider range of stream systems with a diversity of inundation regimes. Current progress is hampered by a need to develop better methods that quantify POM inputs through time.

*Organic matter inputs: DOM.*—DOM is one of the largest organic matter fluxes from watersheds (**Jones and Smock 1991**, **Meyer et al. 1997**, **Mulholland 1997**, Johnson et al. 2006) and is the largest pool of organic matter in running waters (Fisher and Likens 1973, Karlsson et al. 2005). Evidence suggests that DOM accounts for a significant portion of total organic matter inputs (**Marxsen et al. 1997**, **Treadwell et al. 1997**, **Webster and Meyer 1997a**) and is predominantly derived from riparian soils (Fiebig et al. 1990) and terrestrial leaf litter (Kaplan and Newbold 1993). DOM can be linked to instream primary production, indicating that some dissolved C might be a leaky byproduct of photosynthesis (Kaplan and Bott 1989). DOM inputs are influenced by hydrologic flow paths (Mulholland et al. 1990, Kaplan and Newbold 1993, Hornberger et al. 1994), hydraulic conductivity (**Chestnut and McDowell 2000**), precipitation (Hemond 1990), the presence of wetlands in the watershed (Eckhardt and Moore 1990, Hinton et al. 1998), stream size (**Mulholland 1997**), and landuse type (**Kaplan et al. 2006**). Greatest DOM concentrations are found in streams draining wetlands and areas with organic soils (**Mulholland 1997**), and lower DOM concentrations tend to occur in watersheds where soils have high adsorption capacities (e.g., high clay content; Nelson et al. 1993).

The general understanding is that most DOM is recalcitrant, and thus, contributes little to annual respiration (Battin et al. 2003). However, even in

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recalcitrant forms (e.g., humic compounds), DOM is susceptible to microbial processing (Bano et al. 1997). DOM quality varies depending on its origin (Thorp and Delong 2002), riparian flow path (**Datry et al. 2005**), watershed land use (**Harbott and Grace 2005**), and photoreactivity (**Larson et al. 2007**). In some systems, readily labile DOM might support >50% of the community respiration near the point of input, whereas intermediately labile DOM might be an important subsidy to downstream systems (**Wiegner et al. 2005**). Study of DOM was long limited by available methods, but techniques now exist to trace organic matter origins (e.g., fluorescence signature; **Roelke et al. 2006**) and to assess its bioavailability (e.g., quantification of extracellular enzymatic activity; **Harbot and Grace 2005**). These and other new techniques should be used to quantify fully the role of DOM as a relevant energy resource to stream systems and to evaluate the common assumption that DOM simply flows through stream ecosystems with little instream processing.

As suggested in the 1997 *J-NABS* special issue (**Webster and Meyer 1997b**), a common shortcoming of organic matter budgets was underestimation of groundwater DOM inputs and the contribution of storms to DOM inputs and transport. Webster (**2007**; Fig. 1) revisited the issue of fully accounting for organic matter inputs by modeling the organic matter dynamics in the Little Tennessee River watershed based on a 26-y data set. He concluded that DOM and floodplain contributions were inadequately quantified, and that their exclusion caused an imbalance of inputs and outputs in the organic matter budget of the Little Tennessee River watershed.

*Organic matter transport and export.*—Unidirectional transport of materials from upstream to downstream is a unique spatial linkage that integrates ecosystem processes throughout entire stream networks. Early researchers concluded that most stream reaches are net exporters of organic matter (Meyer and Likens 1979). It follows that a given organic particle is more likely to be transported than broken down in situ by biological processes (Webster et al. 1999; Fig. 1). Organic matter export is determined by the interaction of material available on the stream bottom (i.e., benthos), hydrologic variability, and retention mechanisms (Naiman 1982, **Golladay et al. 1987**, Jacobson et al. 2000). In general, the smaller the particle size, the more closely its transport is related to hydrology (Thomas et al. 2001). Reported contributions of POM to total organic export range from 4% in a blackwater river in Georgia (USA) (**Golladay 1997**) to 97% in a large ephemeral river in Africa (Jacobson et al. 2000). On an annual basis, the major fraction of particulate material in transport is FPOM (**Jones and Smock 1991**, **Minshall et al. 1992** [Fig. 1]). However, seasonal differences occur. Jones and Smock (**1991**) found that particulate export was dominated by CPOM in autumn and FPOM in spring and summer. Mean POM size decreases in the downstream direction (Webster et al. 1995), probably because of metabolic processing during transport. Most measurements of transport continue to be limited to those made at baseflow conditions, despite the long recognition that high discharge events (e.g., flooding from storms) dominate organic matter transport in streams (Fisher and Likens 1973, Webster et al. 1987, **Wallace et al. 1995** [Fig. 1], Clark et al. 2007). For example, in a 3$^{rd}$-order stream, 33% of the annual water export occurred at storm flow, which carried 97% of the POM (**Newbold et al. 1997**). In lieu of intensive storm sampling, some researchers have constructed organic matter rating curves to capture the effects of these brief but ecologically relevant events. We reiterate the call made by Cummins et al. (1983) and Webster and Meyer (**1997a**) to include the rare, but important, high-discharge events in measurements of organic matter transport.

*Organic matter retention.*—Retention of organic matter is of particular interest because most biological processing occurs on material stored in the stream channel (Webster et al. 1999, Lamberti and Gregory 2006). The benthic residence time of retained material ranges from days (e.g., labile sugars) to hundreds of years (e.g., large wood) depending on substrate type (Aumen et al. 1983). Retention mechanisms differ because of the different physical and chemical characteristics of particulate vs dissolved fractions of organic matter. For example, DOM is biologically retained, whereas POM is first physically retained and then processed biologically.

Numerous methods have been developed to assess instream POM retention. These methods include use of marked or tracked natural particles, such as deciduous leaves, sticks, and logs (Young et al. 1978, **Ehrman and Lamberti 1992** [Fig. 1], Webster et al. 1999), or particle analogs, such as those made from waterproof paper (**Webster et al. 1994**), plastic strips (Speaker et al. 1988, Muotka and Laasonen 2002), and wooden dowels (**Ehrman and Lamberti 1992**, **Webster et al. 1994**). Benthic retention of POM can occur because of a decrease in stream velocity (Speaker et al. 1984, **Brookshire and Dwire 2003**) or an interaction with an obstacle (Young et al. 1978). Mechanisms of retention include channel morphological features (Speaker et al. 1984, **Ehrman and Lamberti 1992**, James and Henderson 2005), debris dams (Bilby and Likens 1980), snags (James and Henderson 2005),

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macrophyte beds (**Koetsier and McArthur 2000**), hyporheic exchange (Brookshire et al. 2005), floodplains (Cuffney 1988, **Jones and Smock 1991**), riparian vegetation (Speaker et al. 1988), and filter-feeding invertebrates (Monaghan et al. 2001). CPOM (e.g., leaves and twigs) tends to be retained near its point of entry (**Webster et al. 1994**, 1999), particularly in small streams that can act as collecting zones (**Golladay 1997**). CPOM in transport is likely to be retained by logs, tree roots, debris dams, and rocks (**Golladay et al. 1987**, **Ehrman and Lamberti 1992**, **Cordova et al. 2008**). The presence of instream wood generally increases POM retention and benthic standing stocks, and reduces organic matter export (Bilby and Likens 1980, Wallace et al. 1996, **Jones 1997**). As a retention structure, wood can act directly by holding back organic matter and indirectly by influencing flow and channel heterogeneity (**Trotter 1990**). Organic matter retention can serve as an indicator of anthropogenic effects, such as climate change (Sabater et al. 2008), water withdrawal (Dewson et al. 2007), channelization associated with agricultural drainage (Rosi-Marshall et al. 2007), and restoration success (Millington and Sear 2007, Quinn et al. 2007).

The study of FPOM retention has been influenced by the challenge of identifying and tracking tiny particles. A range of FPOM tracers have been used, including bacteria (Hall et al. 1996), corn pollen (**Miller and Georgian 1992**; Fig. 1), fluorescent *Lycopodium* spores (**Wanner and Pusch 2000**), brewers yeast (**Paul and Hall 2002**), $^{14}$C-labeled leaf particles (**Jones and Smock 1991**), and $^{14}$C-labeled natural seston (**Minshall et al. 2000**). Tracking particle analogues generally measures instantaneous retention, whereas tracking $^{14}$C-labeled material allows partitioning of the simultaneous processes of particle generation, deposition, resuspension, and biological use. FPOM retention occurs via mechanisms similar to those for CPOM (**Miller and Georgian 1992**, **Wanner and Pusch 2000**, **Paul and Hall 2002**, Rosi-Marshall et al. 2007), but the transport distance of FPOM exceeds that of leaves or wood because of its smaller particle size (**Jones and Smock 1991**).

The study of FPOM transport has been advanced by adoption of metrics analogous to those used to measure nutrient spiraling (Newbold et al. 1981), which have facilitated identification of the controls on FPOM deposition, such as velocity, depth, uptake length of water, and transient storage (as in Cushing et al. 1993, **Minshall et al. 2000**, Thomas et al. 2001). Hyporheic interstitial filtration (Metzler and Smock 1990, **Brunke and Gonser 1999**), invertebrate feeding (Monaghan et al. 2001), adhesion to substrates (Hall et al. 1996), and biofilm adhesion (Bouwer 1987) are important drivers of patterns of FPOM deposition and transport (**Minshall et al. 2000**, Thomas et al. 2001, Hunken and Mutz 2007). This area of research is biased toward moderate- to high-gradient streams with coarse sediments, but Hunken and Mutz (2007) determined that particle deposition dynamics in low-gradient sand-bed streams did not significantly differ from dynamics in mountain systems. Much work remains to be done to identify patterns and controls on FPOM retention, including the influence of transient storage, variation in benthic turnover time, and the role of biologically mediated processes.

DOM is removed from the water column via biotic and abiotic processes (Fiebig 1992, **Findlay and Sobczak 1996**). Biotic uptake typically is a slower process than abiotic sorption, but accounts for most DOM removal from the water column (Dahm 1981). Factors that increase hydrologic retention can promote DOM retention. However, in general, rates of removal from the water column are more related to water-column DOM concentration and benthic metabolism than to hydrologic factors, such as dilution or residence time (**Findlay and Sobczak 1996**, Sobczak and Findlay 2002). DOM retention also can be a function of DOM quality. Labile DOM is taken up near its point of entry to the stream, whereas less labile DOM is exported to downstream reaches (**Wiegner et al. 2005**). Abiotic immobilization can occur when DOM is adsorbed to sediment particles or the polysaccharide matrix of biofilms (McDowell 1985, Fiebig 1992, Freeman and Lock 1995). Mechanisms of adsorption to inorganic substrates have been studied extensively and are dependent on pH and concentration (Day et al. 1994, Evanko and Dzombak 1998). The process of adsorption to organic substrates is less understood, but might be subject to similar pH and concentration controls (Campbell et al. 1997).

### Ecosystem Metabolism

Ecosystem metabolism is a measure of the production (P) and respiration (R) of organic matter within a stream reach and can determine the relative contribution of allochthonous and autochthonous C sources to the stream food web (with some uncertainty described below). Ecosystem metabolism is defined as a functional metric of ecosystem activity because it is an integrative measure of the processes controlling organic matter dynamics and nutrient cycling in streams. As such, ecosystem metabolism can be used to assess stream health (e.g., Fellows et al. 2006, **Young et al. 2008**, see Future Directions and Applications below).

The 2 common methods used to measure ecosystem metabolism are the open-water exchange method

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introduced by Odum (1956; Fig. 1) and the recirculating chamber method introduced by McIntire et al. (1964). Despite undergoing major refinements since their introduction >50 y ago, each technique measures ecosystem metabolism with some inherent uncertainty. Chambers allow controlled, substrate-specific measurements of P and R, and do not require an estimate of reaeration. However, enclosure artifacts (e.g., nutrient depletion), unnatural conditions (e.g., benthic disturbance, altered temperature and flow), problems with scaling rates of P and R to the whole stream, and failure to include hyporheic respiration generally result in rates of metabolism that are lower than those measured using whole-stream methods (Bott et al. 1978, Marzolf et al. 1994). In contrast, the open-water exchange method uses natural diel changes in streamwater $O_2$ concentration to determine P and R rates from either a parcel of water flowing downstream (2-station) or from a reach upstream of a certain point (1-station). The open-water exchange method integrates metabolism over a large spatial scale, and thus, to minimize uncertainty in P and R estimates, requires accurate measurements of $O_2$ concentrations, reaeration rates (Wanninkhof et al. 1990, Marzolf et al. 1994, Young and Huryn 1999), and groundwater inflows (McCutchan et al. 2002, Hall and Tank 2005). Turbulent streams with high reaeration and low metabolic rates have the greatest uncertainty in P and R when determined from the whole-stream method (**McCutchan et al. 1998**). Reaeration rates are notoriously difficult to measure accurately, and numerous methods including tracer gas injections (Rathbun et al. 1978), use of the $O_2$ profile (Kosinski 1984), and empirical depth–velocity equations (Wilcock 1982), have been devised to determine reaeration rates. Despite being labor-intensive, tracer gas methods tend to be the most accurate (Wanninkhof et al. 1990, Marzolf et al. 1994, Young and Huryn 1999). However, novel methods, such as use of sound pressure measurements (**Morse et al. 2007**) might be promising, especially for continuous monitoring of ecosystem metabolism (e.g., **Uehlinger and Naegeli 1998**, Roberts et al. 2007, **Izagirre et al. 2008**). Despite these difficulties, recent improvements in the whole-stream method to minimize uncertainty associated with reaeration and groundwater inflows (e.g., Marzolf et al. 1994, Young and Huryn 1998, McCutchan et al. 2002, Hall and Tank 2005) and the availability of automated data-logging $O_2$ probes have made whole-stream metabolism measurements more accurate and easier to use. Thus, the frequency of papers using whole-stream methods to quantify metabolism has increased in recent years (Figs 2, 4).

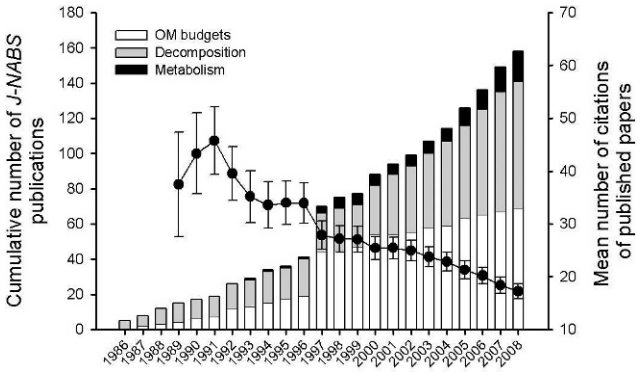



FIG. 4. Cumulative number of *J-NABS* publications from 1986 through 2008 (bars) in comparison to the mean number of citations per paper (line). Citation data is reported from 1989 to present because Institute for Scientific Information (ISI) Web of Knowledge began publishing these data in December 1988.

### *Historical perspective to 1986: the River Continuum Concept stimulates studies of ecosystem metabolism*

Studies before 1986 addressed a disparate range of topics, such as use of whole-stream metabolism to assess eutrophic conditions in streams (Hornberger et al. 1977), how stream metabolism impacts fish migration (Hall 1972), and assessing the contribution of macrophytes to whole-stream metabolism rates (Fisher and Carpenter 1976). In 1980, the River Continuum Concept (RCC; Vannote et al. 1980; Fig. 1) provided a framework of testable hypotheses regarding stream ecosystem dynamics that created a directed focus for subsequent metabolism studies. Streams are intimately linked with the surrounding terrestrial environment (e.g., Fisher and Likens 1973), so a major tenet of the RCC was that changes in the physical properties along a stream network would, in turn, influence the dominant basal food resources of the stream. Initially, the balance of production and respiration (P/R ratio) was used to determine the dominant organic matter supply to streams. However, problems equating the P/R ratio to the relative supplies of allochthonous vs autochthonous organic matter soon were acknowledged (discussed below). One prediction of the RCC was that allochthonous inputs would be predominant in forested headwater streams ($1^{st}$–$3^{rd}$-order), and these inputs, in turn, would fuel heterotrophic metabolism ($P/R < 1$). Autotrophic production would be predominant in mid-order ($4^{th}$–$6^{th}$-order) streams without significant riparian canopy cover ($P/R > 1$). Heterotrophic metabolism ($P/R < 1$) would be the most important energy source in large rivers (>$7^{th}$-order) because primary production would be limited by light

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availability (increased turbidity). Soon after the RCC was introduced, several studies used ecosystem metabolism measurements to test and confirm the hypotheses suggested by the RCC (Naiman and Sedell 1980, Minshall et al. 1983, 1992, Naiman 1983, Bott et al. 1985).

*1986 to present: use of ecosystem metabolism as response metric is increasing*

Publications focusing on ecosystem metabolism have been fairly equally distributed among the major aquatic journals since 1986: *Freshwater Biology* (~30), *Canadian Journal of Fisheries and Aquatic Sciences* (~10), *Limnology and Oceanography* (~30), and *J-NABS* (~20). Nevertheless, in *J-NABS*, publications on ecosystem metabolism comprise only 11% of the total publications on organic matter (Fig. 3). Here, we review 3 areas of stream metabolism research in which *J-NABS* has made a significant contribution: 1) assessing the RCC across multiple catchment types, 2) factors controlling ecosystem metabolism, and 3) use of stream metabolism to assess ecosystem-level responses to natural (e.g., floods) and human-induced (e.g., land use) disturbance.

*Further assessments of the RCC.*—The RCC was developed originally for streams within temperate forested catchments (Vannote et al. 1980), but subsequent elaborations of the RCC accounted for streams with different riparian character (e.g., xeric catchments) and allowed streams to enter the continuum at different points (Cummins et al. 1984, Minshall et al. 1985). Multiple studies evaluated the RCC in the context of streams draining different biomes and land uses. For example, in the blackwater Ogeechee River in Georgia (USA), the entire continuum was heterotrophic ($P/R < 1$) because of ongoing inputs of organic matter from riparian swamps, in spite of longitudinal increases in production (Meyer and Edwards 1990). Similarly, an undisturbed tropical stream continuum in Puerto Rico was heterotrophic despite high light availability and increased P longitudinally, a result that the authors attributed to significant herbivore grazing (**Ortiz-Zayas et al. 2005**). An open-canopy grassland stream continuum in New Zealand tended to be autotrophic; however, trophic status appeared to be driven by variation in discharge because the stream became heterotrophic during periods of high flow (Young and Huryn 1996). Further, an agricultural prairie system in the midwestern US was autotrophic in the headwaters ($<3^{rd}$ order) and heterotrophic downstream as turbidity increased and light inputs declined from the encroaching canopy. However, this downstream shift in trophic status was most frequently observed during the summer months (Wiley et al. 1990). Headwater desert streams are regarded as fueled by autochthony (Fisher et al. 1982, Mulholland et al. 2001 [Fig. 1]). However, even in these high-light, open-canopy systems, respiration from the hyporheic zone can contribute up to 50% of total ecosystem respiration (Grimm and Fisher 1984). The contribution of hyporheic respiration to total ecosystem respiration can be extensive (Fuss and Smock 1996, Mulholland et al. 1997 [Fig. 1], **Naegeli and Uehlinger 1997**, Fellows et al. 2001), especially in alluvial rivers. Thus, the RCC has been extended to include hyporheic contributions (**Stanford and Ward 1993**; Fig. 1).

P/R ratios have been used to define the trophic status of streams as heterotrophic ($<1$) or autotrophic ($>1$) and to assess the dominant organic matter supply (allochthonous and autochthonous, respectively) fueling respiration and secondary production (e.g., Vannote et al. 1980). However, caution must be used when relating the P/R ratio to the dominant organic matter supply because the transition between the dominance of allochthony to dominance of autochthony tends to occur at a P/R ratio between 0.5 and 1 (Rosenfeld and Mackay 1987, Meyer 1989). Recently, McTammany et al. (**2003**) tested the RCC along a 37-km segment encompassing $4^{th}$- to $6^{th}$-order reaches of the Little Tennessee River, North Carolina (USA). They used a combination of ecosystem metabolism and budget (autochthonous and allochthonous inputs) measurements to compare the locations of the shifts from heterotrophy to autotrophy and from allochthonous to autochthonous C. They concluded that the switch from allochthonous to autochthonous C occurred further upstream than the point at which $P/R = 1$.

*Factors driving ecosystem metabolism.*—The primary factors that influence stream ecosystem metabolism include light availability, temperature, nutrients, and organic matter supply (Elwood et al. 1981, Hill et al. 1995, **Lamberti and Steinman 1997**, **Sinsabaugh 1997**, Mulholland et al. 2001), and these factors are influenced by local (riparian zone and geomorphology) and regional (hydrologic and climatic) factors. Most metabolism studies found correlations between P and R rates and biotic and abiotic factors, but factors controlling metabolic rates appear to be stream-specific. A few studies have examined broad patterns driving whole-stream metabolism, and 2 of these studies were published as part of the *J-NABS* special issue in 1997. In an analysis of large-scale respiration trends in 22 streams, respiration was positively correlated with stream temperature, negatively correlated with latitude, and was not influenced by stream

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order (**Sinsabaugh 1997**). Lamberti and Steinman (**1997**) found that watershed area, discharge, and soluble reactive phosphorus concentration predicted primary production across a large spatial scale. More recently, authors of an interbiome comparison of 1st to 3rd-order streams across North America found that P was driven primarily by photosynthetically active radiation and streamwater phosphorus concentrations, whereas R was positively influenced by phosphorus and size of the transient storage zone (indicative of the hyporheic zone) (Mulholland et al. 2001). Nutrient concentrations might be correlated with metabolism metrics in some cases, but concentration does not always indicate demand, and authors of several recent studies reported significant correlations between metabolism and nutrient uptake velocity (Hall and Tank 2003, Webster et al. 2003, **Meyer et al. 2005** [Fig. 1], Hoellein et al. 2007).

*Use of metabolism to examine the ecosystem-level response to disturbance.*—Metabolism is an integrative metric of ecosystem function, and thus, provides an integrated response of a system to disturbance (**Young et al. 2008**; Fig. 1). Papers published in *J-NABS* have made a significant contribution toward understanding ecosystem response to disturbance. Authors of 2 papers examined recovery of metabolism after floods, and authors of 5 papers examined the effects of land use on ecosystem metabolism. The response of metabolism to natural disturbance, such as floods, appears to vary by stream. In some streams, P or R decrease in response to floods (Fisher et al. 1982, **Uehlinger and Naegeli 1998**, Uehlinger 2000, 2006, **Izagirre et al. 2008**) because of increased turbidity and scouring of the benthos. Uehlinger and Naegeli (**1998**) suggested that R might be more resistant than P to flooding in gravel-bottomed systems because the hyporheic zone was less influenced by floods, although multiple, continuous bed-moving spates eventually depressed R significantly. In other systems, R was enhanced after floods because of entrainment of organic matter from floodplains or resuspension of sediments (Roberts et al. 2007). Acuña et al. (**2007**) found seasonal recovery of metabolism in a 3rd-order forested Mediterranean stream following floods because of seasonal variation in benthic organic matter and light availability. P recovered quickly during the spring when light availability was high, whereas R recovered quickly after autumnal floods because of replenishment of benthic organic matter.

The response of stream metabolism to human-induced disturbances also appears to vary by stream. Houser et al. (**2005**) examined the effect of intense, localized upland disturbance from military training on metabolism metrics. R was negatively correlated with disturbance, potentially because of increased sedimentation and burial of organic matter. However, P was not negatively influenced by disturbance but instead was driven by differences in light availability. Studies of the effect of urbanization on whole-stream metabolism also have yielded contrasting results. Meyer et al. (**2005**) found no effect of urbanization on metabolism metrics, whereas Bott et al. (**2006**) found negative correlations between P and urban land use, although drivers were masked by the confounding factors, stream size and canopy cover. An assessment of 19 streams in northern Spain classified by trophic level (oligotrophic, mesotrophic, eutrophic, and polluted) showed that polluted sites had the highest R, potentially because of high sewage inputs (**Izagirre et al. 2008**). Few studies have examined the impact of agriculture on stream ecosystem metabolism, but McTammany et al. (**2007**) examined how regrowth of the riparian zone after agricultural abandonment affects metabolism. Some agricultural influences disappear quickly, e.g., light availability and stream water temperature decrease with canopy reformation, but some agricultural effects are long-lasting, e.g., elevated nutrient concentrations and increased suspended solids. McTammany et al. (**2007**) found that P was similar in streams with historically forested riparian zones compared to streams that had recovered from agriculture, a result suggesting that shading caused by reforestation might be an important recovery mechanism from agricultural land use. Overall, these studies suggest that metabolism might be a sensitive metric that reflects human-induced disturbances, but drivers and responses probably are stream-specific.

## Organic Matter Decomposition

Examining the rate at which organic matter is processed and its incorporation into the food web via consumers has been an important focus of stream ecology research for the past ~40 y. Decomposition is defined as the catabolism of organic matter into its inorganic constituents (e.g., $CO_2$, inorganic N and phosphorus) from leaching of soluble compounds, physical fractionation, microbial (fungal and bacterial) conditioning, and invertebrate feeding (Hanlon 1982, Boulton and Boon 1991 [Fig. 1]). The rate at which organic matter is processed in streams is influenced by the chemical and physical properties of organic matter, the biota, and environmental factors (e.g., temperature and nutrients; reviewed by Webster and Benfield 1986; Fig. 1). Organic matter decomposition is considered an integrative measure of the biotic and abiotic components of stream

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ecosystems, and its use as an indicator of stream integrity has been proposed (Gessner and Chauvet 2002 [Fig. 1], **Young et al. 2008**).

Numerous approaches have been used to delineate and quantify relative biotic and abiotic contributions to decomposition. The methods used in decomposition studies have been reviewed elsewhere (Boulton and Boon 1991, Graça et al. 2005), but we describe them briefly here. Leaf breakdown, measured as mass loss over time (Hanlon 1982), is commonly assessed with litter packs (leaves tethered to the benthos) or litter bags, and breakdown rates usually are determined by fitting mass-loss data to an exponential decay model (Benfield 2006, but see Boulton and Boon 1991 for discussion of alternate decay models). Leaf species, life stage, and preparation for incubation differ with the project objectives and often have large effects on decomposition rates. Either green or senesced leaves are used in decomposition studies depending on the question and location of the study (e.g., tropics vs temperate forest). Pretreatment of leaves (e.g., leaching in water, freezing, oven drying) before incubation in the stream also affects decomposition rate (see Boulton and Boon 1991 for more in-depth discussion).

The role of microorganisms in the decomposition process can be assessed through measurements of microbial biomass, production, and activity (see **Findlay 2010**). Bacterial and fungal biomass are commonly measured via epifluorescence microscopy (**McNamara and Leff 2004**) and ergosterol assays (Newell et al. 1988, Young 1995, Gessner and Schmitt 1996, Graça et al. 2005), respectively, whereas measurements of ATP can assess the biomass of the entire active microbial community (Suberkropp et al. 1993, **Gonçalves et al. 2006b**, 2007). Bacterial and fungal production can be quantified by measuring uptake rates of radioactive isotopes, such as $^{3}$H-leucine into proteins and $^{14}$C-acetate into ergosterol (**Weyers and Suberkropp 1996**; Fig. 1). Microbial activity is measured as the change in $CO_2$ or $O_2$ concentration (Bott et al. 1978, Cuffney et al. 1990, **Tank and Musson 1993**), $^{14}$C glucose mineralization (**Peters et al. 1989**), or extracellular enzyme activity (**Sinsabaugh et al. 1994**). More recently, molecular approaches, such as terminal restriction fragment length polymorphism and denaturing gradient gel electrophoresis, have been used to estimate microbial diversity on decomposing organic matter (Nikolcheva et al. 2003, 2005, Das et al. 2007).

In the field, the relative influence of invertebrate and physical processing vs microbial processing of organic matter is commonly differentiated by pairing measurements in coarse-mesh bags that allow invertebrate feeding and abrasion with measurements in fine-mesh bags that restrict macroinvertebrate access (Benfield et al. 1979, **Robinson et al. 2000**, **Graça et al. 2001**). Additional methods used to distinguish microbial vs invertebrate processing include electric exclosure fences that reduce densities of large macroinvertebrates (e.g., crayfish and large shredders, Pringle and Hamazaki 1997), pesticide application (**Wallace et al. 1986** [Fig. 1], Cuffney et al. 1990), and manipulation of species identity, guild diversity, and biomass of invertebrate communities in the field or laboratory (**Jonsson and Malmqvist 2005**).

*Historical perspective to 1986: decomposition studies have been a cornerstone of stream ecology research*

The study of organic matter decomposition has its roots in the early ecosystem approaches of the 1950s and 1960s when interest in quantifying energy sources and flows through ecosystems was high (Lindeman 1942, Odum 1957). Stream ecologists working in temperate forested systems observed that aquatic organisms were consuming leaves that had originated in terrestrial environments. These observations led to the hypothesis that terrestrial detritus provided an important energy source to headwater streams (Ross 1963, Minshall 1967), which in turn spurred numerous studies that quantified organic matter budgets (e.g., Fisher and Likens 1973) and detailed studies of organic matter decomposition. Authors of early decomposition studies adapted leaf-pack methods from soil ecologists and designed studies aimed at understanding the general patterns and processes of leaf decomposition. For example, in one of the most cited aquatic decomposition studies, Petersen and Cummins (1974; Fig. 1) quantified the breakdown of 15 leaf species in a forested headwater stream in Michigan. Recognition that decomposition rates varied by an order of magnitude among some leaf species (0.005/d–0.02/d) in their study led Petersen and Cummins to describe a ''hierarchy of leaf species along a processing continuum,'' along which leaves decomposed at a range of rates from slow to fast and, thus, provided a constant resource to stream macroinvertebrates. By 1986, decomposition studies in freshwater ecosystems were so commonplace that Webster and Benfield (1986) published a review that tabulated breakdown rates from 117 studies, published between 1967 to 1985, that summarized the intrinsic (e.g., organic matter quality) and extrinsic (e.g., stream water temperature, pH, nutrient concentrations) factors influencing organic matter decomposition rates. Since 1986, the use of unique approaches, such as comparative studies, novel questions, and

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large-scale experimental manipulations has continued to elucidate the intrinsic and extrinsic drivers of decomposition rates.

*The role of macroinvertebrates in organic matter processing.*—Early studies of organic matter processing by invertebrates were focused on answering how and at what rate invertebrates are able to process organic matter. Most early studies were done in small forested streams in North America (e.g., Kaushik and Hynes 1971 [Fig. 1], Fisher and Likens 1973, Cummins 1974, Benfield et al. 1977) and publications reported how invertebrate species traits influenced organic matter processing (e.g., Slack 1936, Nykvist 1962, Wallace et al. 1970, Anderson and Sedell 1979). For example, researchers found that shredding invertebrate taxa were physiologically adapted to assimilate leaves or wood through specialized gut fauna (Slack 1936, Nykvist 1962, Wallace et al. 1970, Anderson and Sedell 1979). Other studies quantified how leaf quality (e.g., nutrient content and structure) and chemical composition (e.g., phenolics and tannins) affected consumption and assimilation rates (Slack 1936, Daubenmire 1953, Kaushik and Hynes 1971, Cummins 1974). A few studies also linked shredding invertebrate life histories to the timing of leaf litter inputs from the surrounding watershed (Chapman and Demory 1963, Minshall 1967, Benfield et al. 1977). Before 1986, the importance of macroinvertebrate consumption and assimilation of organic matter had been established both experimentally and under natural field conditions, but the influence of macroinvertebrates on organic matter processing rates had not been examined.

### *1986 to present: organic matter decomposition*

Since 1986, more research articles with a focus on organic matter decomposition have appeared in *J-NABS* (~70) and *Freshwater Biology* (~100) than in other major aquatic journals, such as *Canadian Journal of Fisheries and Aquatic Sciences* (~25) and *Limnology and Oceanography* (~40). The number of *J-NABS* publications on organic matter decomposition has increased since the journal's inception (Fig. 4), and these decomposition studies comprise almost ½ of the 158 publications on organic matter dynamics (Fig. 3). After 1986, research shifted to examining the influence of macroinvertebrates on decomposition with foci on changes in processing rates following natural (**Robinson et al. 2000**) and anthropogenic (**Mulholland et al. 1987**, **Sponseller and Benfield 2001**, **Chaffin et al. 2005**) disturbances and on the primary factors driving rate changes across a wider geographic area (**Mathuriau and Chauvet 2002**, **Gonçalves et al. 2006b**, **Wantzen and Wagner 2006**). In general, proportionally fewer studies on decomposition in lentic systems (e.g., lake and wetlands) have been published in *J-NABS* than in the other aquatic journals listed above. For the purposes of this review, we selected 4 areas of decomposition research in which *J-NABS* papers have made especially important contributions: 1) intrinsic and extrinsic factors affecting decomposition, 2) decomposition in other systems (moving forward from temperate forested headwaters), 3) decomposition of different forms of organic matter besides leaf litter (e.g., wood and FPOM), and 4) the influence of macroinvertebrates on decomposition rates as a function of invertebrate diversity, geographic distribution, and organic matter quality.

*Intrinsic and extrinsic factors affecting decomposition.*—The intrinsic factors that influence decomposition of various organic matter types include N content (Kaushik and Hynes 1971, Richardson et al. 2004), lignin (Melillo et al. 1984, Gessner and Chauvet 1994, Royer and Minshall 2001), tannins (Mathuriau and Chauvet 2002, but see Ostrofsky 1993), and leaf structure (Bärlocher et al. 1978). In a large study with standardized methods and uniform site conditions, Ostrofsky (**1997**) found that ~50% of the variation in decomposition rates of 48 leaf species was explained by total phenolics, N content, and % lignin. However, recent studies showed that variation in organic matter quality within a single tree species also could affect the rate at which material is processed. For example, LeRoy et al. (**2007**; Fig. 1) found that 4 cottonwood hybrids differed in organic matter quality (tannins and lignin) and, thus, had hybrid-specific breakdown rates, a result supporting the hypothesis that genetic-scale differences within and across species can affect decomposition. Further, Lecerf and Chauvet (2008b) found that decomposition rates of senescent alder leaves (*Alnus glutinosa*) collected from 5 countries across Europe and incubated in a single stream differed because of variation in phosphorus (0.034–0.187%) and lignin (3.9–18.7%) contents.

Naturally occurring leaf packs generally are composed of numerous leaf species, and authors of recent studies have examined whether the presence of multiple species influences decomposition rates. Studies of the effects of multiple leaf species on decomposition dynamics are commonplace in the terrestrial literature, but comparable studies have been published only recently in the aquatic literature. In one of the first mixed-species studies, McArthur et al. (**1994**; Fig. 1) found that leaf packs containing sweetgum (*Liquidambar styraciflua*) and water oak (*Quercus nigra*) leaves had lower bacterial densities and broke down at a slower rate than sweetgum

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alone, perhaps because oak leaf leachate inhibited microbial processing of sweetgum leaves. Swan and Palmer (**2004**) found that mixed-species breakdown differed seasonally because decomposition was nonadditive in summer but predictable in autumn. Several recent studies showed that the diversity of mixed-species leaf packs influences decomposition rates in aquatic environments (LeRoy and Marks 2006, Kominoski et al. 2007b, Lecerf et al. 2007b, Taylor et al. 2007); however, some of these studies also stress that organic matter quality and environmental conditions can have overriding influences on decomposition rates. Examining the decomposition of mixed-species leaf packs is an important and novel approach to decomposition research because mixed packs more realistically represent the heterogeneity of organic matter sources in streams. Furthermore, these studies have important implications in human-influenced watersheds that have experienced riparian zone alteration and species replacement, which change the diversity of organic matter entering streams.

Human activities also influence the intrinsic quality of leaf litter entering streams by altering the environmental conditions under which trees are grown (e.g., increasing atmospheric $CO_2$, ground-level $O_3$, ultraviolet radiation, water stress, and aerial N deposition). Studies of these anthropogenic effects on leaf litter decomposition are common in terrestrial environments, and reviews and meta-analyses are now available (Penuelas and Estiarte 1998, Norby et al. 2001, Caldwell et al. 2007). Considerably fewer such studies have been done in aquatic ecosystems, and more research is needed to clarify the effects of global climate change on aquatic organic matter decomposition. The effect of increasing atmospheric $CO_2$ on organic matter decomposition in aquatic environments is a growing area of research (**Rier et al. 2002**, 2005, Tuchman et al. 2002, 2003, **Kominoski et al. 2007a**; see Future Directions and Applications below), and *J-NABS* publications have made notable contributions. For example, quaking aspen (*Populus tremuloides*) leaves grown under elevated $CO_2$ concentrations had higher phenolics, lignin, and C:N ratios, and thus increased resistance to microbial breakdown, compared to quaking aspen grown under ambient $CO_2$ concentrations (**Rier et al. 2002**). Recent data show that increased $CO_2$ concentration can increase the amount of refractory dissolved organic matter leached from leaves, with consequences for instream algal productivity and potential cascading effects on algal consumers (**Kominoski et al. 2007a**). Several *J-NABS* publications also have furthered our understanding of the effects of atmospheric N deposition on organic matter decomposition. Chadwick and Huryn (**2003**) proposed that N deposition might alter organic matter decomposition via 2 pathways: 1) elevated $NO_3^-$ concentrations in stream water, and 2) increased N content of foliar detritus. They used data from the long-term N-deposition experiment at Bear Brook Watershed in Maine (USA) and found that elevated foliar N significantly increased processing rates of organic matter, whereas elevated streamwater $NO_3^-$ concentrations had minimal influence on processing rates, perhaps because other nutrients (e.g., phosphorus) were limiting microbial decomposers (**Chadwick and Huryn 2003**).

Several extrinsic factors, including streamwater nutrient concentrations, temperature, $O_2$ concentration, and physical abrasion, influence organic matter decomposition. Naturally decaying leaves (**Methvin and Suberkropp 2003**) and yellow poplar (*Liriodendron tulipifera*) leaves (**Weyers and Suberkropp 1996**) had greater fungal or bacterial production in a high-nutrient hardwater stream than in a low-nutrient softwater stream. However, experimental manipulations are needed to determine cause and effect. Nutrient additions generally increase microbial activity and biomass on organic matter (Tank and Webster 1998, **Grattan and Suberkropp 2001**, Gulis and Suberkropp 2003, Stelzer et al. 2003, Gulis et al. 2004, Ferreira et al. 2006b), a result implying that microorganisms assimilate nutrients from the water column when needed (Suberkropp and Chauvet 1995; Fig. 1). Stream water temperature also can influence decomposition rates, primarily through its effect on metabolism. Tank et al. (**1993**) found that the breakdown rates of naturally decaying sticks and rhododendron (*Rhododendron maximum*) leaves were positively correlated with water temperature. Microbial breakdown dominates organic matter decomposition in the tropics, where fast processing rates are attributed to consistently high water temperatures (**Mathuriau and Chauvet 2002**, Abelho et al. 2005). Organic matter decomposition also occurs at a slow, but detectable rate even under very cold conditions (Short et al. 1980), such as in glacial streams in the Swiss Alps (**Robinson and Jolidon 2005**). At larger spatial scales, organic matter decomposition varies along latitudinal (Irons et al. 1994) and altitudinal (Fabre and Chauvet 1998) gradients. Decreases in decomposition rates with increasing latitude and altitude are hypothesized to be the result of differences in temperature that, in turn, influence microbial activity. Medeiros et al. (2009) examined the diversity and activity of aquatic fungi under various $O_2$ concentrations (4–94% saturation) and found that fungal biomass, sporulation, and diversity all de-

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creased with decreasing $O_2$ saturation. Physical abrasion of organic matter also tends to increase decomposition rates (Chergui and Pattee 1988, Canton and Martinson 1990). Rader et al. (1994) used chemical inhibitors to isolate the effects of physical abrasion and invertebrate feeding on sweet gum leaf decomposition, and found that microbial activity was the primary factor influencing decomposition rates. Ferreira et al. (2006a) found that stream water velocity (up to 2.35 m/s) alone did not affect breakdown of alder leaves, except when fine sediments were entrained in the water column.

Human activities influence organic matter processing rates by altering extrinsic factors (e.g., pollution, nutrient inputs, pH) that influence decomposition. Mulholland et al. (**1987**) found that a pH $< 5.7$ slowed leaf decomposition because of decreased microbial activity associated with aluminum (Al) toxicity, and similar effects of acidic conditions on breakdown have been found in other studies (**Thompson and Bärlocher 1989**, Dangles and Guerold 1998). In a stream reach directly downstream of an arsenic (As) mine, breakdown rates of red maple (*Acer rubrum*) and white oak (*Quercus alba*) leaves were much slower than in an upstream reference reach, primarily because of decreased invertebrate densities (**Chaffin et al. 2005**). Eutrophic polluted sites in Portugal supported higher fungal biomass and production on organic matter, and thus, faster decomposition rates than at a reference site (**Pascoal et al. 2005**). However, the influence of anthropogenic degradation can cause confounded effects on decomposition. For example, high nutrient concentrations in agricultural streams stimulate microbial decomposition, but a concurrent lack of shredding invertebrates can suppress breakdown rates (Huryn et al. 2002, **Hagen et al. 2006** [Fig. 1]).

*Decomposition in other systems (moving forward from temperate forested headwaters).*—Before 1986, most decomposition studies were done in temperate forested headwater streams. For many years, this bias influenced stream ecologists' understanding of decomposition dynamics. More recently, decomposition studies have expanded from forested headwaters to address organic matter dynamics 1) outside the stream channel, 2) in different biomes, and 3) in different landuse types.

Organic matter processing in lotic systems occurs in all areas physically associated with the stream channel, including the hyporheic and parafluvial zones and floodplains associated with larger streams, but few decomposition studies have been conducted in these environments. Crenshaw et al. (**2002**) found that fungal biofilms and invertebrates colonized wood veneers in the hyporheic and parafluvial zones of a mountain stream in New Mexico, a result suggesting that organic matter and associated biofilms are important food resources for invertebrates in these subsurface areas. However, decomposition tends to be slow in hyporheic sediments (Rulik et al. 2001, Tillman et al. 2003). Larger streams and rivers receive organic matter from the surrounding floodplains, and these sites also are important zones for litter processing (e.g., **Tiegs et al. 2007**), especially when inundated (**Neatrour et al. 2004**, **Rueda-Delgado et al. 2006**). In a recent study in the Tagliamento River in Italy, Langhans et al. (2008) found that decomposition rates were fastest in the river channels, slowest in the terrestrial habitat, and intermediate in the ponds associated with the floodplain. The effect of drought on decomposition rates in intermittent streams also has received attention in recent years. Most studies found decreased decomposition rates during periods of drought (Tate and Gurtz 1986, Gurtz and Tate 1988, Richardson 1990, Maamri et al. 2001, Pinna and Basset 2004, Fritz et al. 2006, Sangiorgio et al. 2006, 2007, **Gaudes et al. 2009**).

Since 1986, stream ecologists have increasingly examined organic matter decomposition in streams flowing through biomes other than temperate forested environments. Decomposition dynamics have been well studied in tropical streams across the globe, including in Hawaii (**Larned 2000**, Larned et al. 2001, 2003), Puerto Rico (Padget 1976, Crowl et al. 2001, Wright and Covich 2005), Central America (Stout 1980, Irons et al. 1994, Benstead 1996, Ardon et al. 2006, Ardon and Pringle 2008), South America (Dezzeo et al. 1998, **Mathuriau and Chauvet 2002**, Abhelo et al. 2005, Gonçalves et al. 2006a, **b**, 2007, **Rueda-Delgado et al. 2006**, **Wantzen and Wagner 2006**), the South Pacific Islands (Williams 2002), Africa (Mathooko et al. 2000a, b, Dobson et al. 2004), Hong Kong (Au et al. 1992, Dudgeon and Wu 1999, **Li and Dudgeon 2009**), and Australia (Pearson and Tobin 1989, Pearson and Connolly 2000, Boyero et al. 2006). Studies of organic matter decomposition also are becoming more common in open-canopy streams, such as those flowing through the grasslands of the central US (Tate and Gurtz 1986, Hooker and Marzolf 1987, McArthur and Marzolf 1987, Gurtz and Tate 1988, Hill et al. 1992) and New Zealand (Young et al. 1994, Niyogi et al. 2003), and through arid regions of the central and southwestern US (Mackay et al. 1992, Schade and Fisher 1997, Pomeroy et al. 2000, Kennedy and Hobbie 2004, Andersen and Nelson 2006, Nelson and Andersen 2007). Other systems that have gained attention in recent years include streams at high latitudes, such as those in the tundra of Alaska

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(Peterson et al. 1993, Benstead et al. 2005) and streams at high altitudes, such as those in Switzerland (Fabre and Chauvet 1998, **Gessner et al. 1998**, **Robinson et al. 2000**, Fleituch 2001, **Robinson and Jolidon 2005**).

Numerous studies of decomposition dynamics have been done in streams other than those flowing through temperate forested environments, but the perception remains that invertebrates play a large role in organic matter processing. However, in comparison to temperate forested streams, invertebrates are generally less important litter processors in tropical streams (**Gonçalves et al. 2006b**), in systems that lack seasonally timed leaf organic matter inputs (**Wantzen and Wagner 2006**), and in naturally disturbed systems, such as glacier-fed streams (**Robinson and Jolidon 2005**). Microorganisms play a larger role in decomposition in lotic systems that are unable to support an extensive community of shredding invertebrates. For example, organic matter processing in tropical streams occurs at a rapid rate because increased stream water temperatures increase microbial activity (**Mathuriau and Chauvet 2002**, Dobson et al. 2002, **Gonçalves et al. 2006b**). However, when present, large detritivores (e.g., shrimps, crabs) can play a significant role in organic matter decomposition (**Crowl et al. 2006**). Prairie streams that lack significant allochthonous inputs tend to support low densities of shredders, and leaf litter breakdown in these streams also is driven by microbial processing (**Hill et al. 1992**). The relative importance of invertebrates and microbes in organic matter decomposition might depend on the location and condition of the stream. However, the relative importance of microbial vs macroinvertebrate decomposition is still not well understood, and novel ways to address this question in a wider variety of lotic systems would be fruitful.

Recent papers in *J-NABS* have examined the effects of human land use on organic matter decomposition (several of these studies are reviewed in *Intrinsic and extrinsic factors affecting decomposition* above). Generally, decomposition of organic matter is more influenced by microorganisms or physical breakdown than by macroinvertebrates in streams where riparian zones have been removed and land use is dominated by row-crop agriculture, urban development, or timber harvest (**Sponseller and Benfield 2001**, **Meyer et al. 2005**, Chadwick et al. 2006, **Hagen et al. 2006**, Paul et al. 2006, Griffiths et al. 2009). In addition, contamination from mining operations reduces the importance of shredder activity to organic matter breakdown through decreases in pH (**Mulholland et al. 1987**, **Chaffin et al. 2005**, **Pascoal et al. 2005**). Sponseller and Benfield (**2001**) found slower decomposition rates in streams receiving high sediment loads from urbanization and agriculture. Similarly, Hagen et al. (**2006**) showed a positive relationship between shredder density and decomposition rates in agricultural streams. However, decomposition rates did not change predictably with changes in land use, probably because of stimulation of microbial activity from elevated inorganic nutrient concentrations. Changes in macroinvertebrate densities or biomass are often temporally variable and do not always change predictably along landuse gradients (**Hagen et al. 2006**) or following restorations that increase organic matter retention (Lepori et al. 2005, Entrekin et al. 2008). Examining the relative influence of fungi, bacteria, macroinvertebrates, and physical fragmentation on organic matter decomposition rates will be necessary to provide useful decomposition metrics for biological assessment. Stream ecologists have only begun to examine the effects of human land uses (e.g., urbanization and agriculture) on decomposition, especially compared to the wealth of studies conducted in intact systems. However, existing data should provide a foundation for developing appropriate metrics to be used for assessments.

*The importance of different forms of organic matter in decomposition dynamics.*—Most decomposition studies have focused on the breakdown of leaf litter within stream channels, probably because many decomposition studies were done in forested headwater streams and the litterbag method used to measure leaf litter decomposition is relatively straightforward. Several studies have been published on decomposition of other forms of organic matter, including detrital fruit (Larned et al. 2001), salmon carcasses (Minshall et al. 1991, Chaloner et al. 2002), and periodical cicadas (Menninger et al. 2008, **Pray et al. 2009**). Here we focus on wood and FPOM because *J-NABS* publications have contributed significantly in these areas.

Wood is integral to stream ecosystems because it retains organic matter, stabilizes banks, and provides refuge for stream-dwelling organisms. Wood decomposition has not been studied in detail, primarily because of methodological challenges associated with its lengthy decomposition time (>>1 y). Nevertheless, wood is an important substrate for biofilm development (Aumen et al. 1983, Sinsabaugh et al. 1991, **Tank et al. 1993**, Tank and Winterbourn 1995, 1996). Its decomposition is driven primarily by microbial activity because only a select few invertebrates are able to consume wood directly. Golladay and Sinsabaugh (1991) found that wood supported higher biofilm biomass per unit surface area than did leaves, perhaps because of the greater physical stability of wood. Thus, wood could provide a longer-term C supply compared to leaves. Further-

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more, fungal biomass, sporulation rate, microbial respiration, and wood breakdown rates increase with nutrient addition (Stelzer et al. 2003, Gulis et al. 2004, Ferreira et al. 2006b), and wood and leaf biofilms compete for limiting stream water nutrients (**Tank et al. 1998**). However, despite the importance of microbes to wood decomposition, breakdown of wood is a very slow process. Small sticks of wood (Webster et al. 1999) or wood surrogates, such as wood veneers, often are used in studies of wood decomposition, but use of these substrates can lead to overestimates of wood decomposition rates because such substrates have high surface area to volume ratios (**Spanhoff and Meyer 2004**).

FPOM is an important organic matter resource for microorganisms and invertebrates. However, our understanding of the decomposition dynamics of FPOM also is constrained by methodological limitations. Use of litterbag techniques to measure FPOM breakdown requires very fine-mesh (<52 μm) to enclose FPOM. However, fine mesh restricts exchange between the bag and the surrounding environment, so FPOM decomposition rates generally have been underestimated (**Sinsabaugh et al. 1994**). Furthermore, FPOM breakdown is difficult to predict because of heterogeneity of source material and, thus, quality of FPOM. Breakdown of leaf litter is a major source of FPOM in forested streams (**Ward 1986**), and investigators have assumed that the proportion of refractory material (e.g., lignin and cellulose) increases as FPOM sizes decrease (**Peters et al. 1989**). In an elegant study, Yoshimura et al. (**2008**) measured lignin, C:N, microbial respiration, and decomposition of FPOM produced by shredding amphipods fed 1 of 5 types of CPOM—wood, filamentous green algae, and conditioned leaves of ash, alder, and oak. They found that conversion of CPOM to FPOM reduced C quality (higher lignin content) and led to reduced microbial activity and slower decomposition rates of FPOM than of CPOM. In contrast, Sinsabaugh et al. (**1994**) and Jackson and Vallaire (**2007**) found that very-fine particulate organic matter (V-FPOM; 0.063–0.25 mm) decomposed more rapidly than FPOM (0.25–1 mm), and studies presented in Webster et al. (1999) showed that FPOM generally decomposes at a much faster rate than does CPOM. Ward (**1986**) found that smaller size classes of FPOM contained less lignin than did larger classes, a result suggesting that the processing patterns for benthic FPOM might be obscured by the coexistence of particles in a variety of decomposition states and from diverse origins, including CPOM decomposition, entrainment and flocculation of DOM from the riparian zone/soils, and fecal pellets from invertebrate feeding (**Joyce and Wotton 2008**). Bonin et al. (**2000**) explored the link between FPOM origin and FPOM quality by examining how quality varies seasonally in streams draining 3 successional age classes of forests (old growth to regenerating stands). They concluded that most FPOM in these Oregon streams was recalcitrant and from poor-quality sources (e.g., wood), and that the pool was supplemented seasonally by pulses of readily degradable FPOM from autochthonous and allochthonous (e.g., leaf litter) sources. Furthermore, streams draining regenerating stands generally had higher-quality FPOM and faster decomposition rates than did streams draining old growth stands. Overall, these studies demonstrate that assuming a single source (e.g., CPOM decomposition) and uniform quality of FPOM in streams is too simplistic.

*The influence of macroinvertebrates on decomposition rates.*—Macroinvertebrates play an important role in the decomposition of organic matter in streams, as demonstrated by numerous experiments that isolated the effect of macroinvertebrates on decomposition with coupled fine- and coarse-mesh litter bags (**Graça et al. 2001**, Langhans and Tockner 2006), electrical exclusion hoops (Pringle and Blake 1994, Pringle and Hamazaki 1997, Schofield et al. 2001), insecticide application (**Wallace et al. 1986**, Cuffney et al. 1990), and experimental CPOM exclusion (Eggert and Wallace 2003) and retention (**Tiegs et al. 2008**). For example, a unique approach was application of insecticide to small forested headwater streams (**Wallace et al. 1986**, Cuffney et al. 1990) with the result that leaf litter decomposition rates declined as invertebrate biomass and production declined.

The relationships between taxonomic composition and biomass of macroinvertebrates in leaf packs and variability in leaf processing rates also have been used to examine the importance of macroinvertebrates in organic matter decomposition. Of the 20 field studies published in *J-NABS* in which the relationship between invertebrates and organic matter processing rates was examined specifically, 70% reported shredder abundance, 30% reported both shredder abundance and biomass, and 20% reported taxon abundance and some measure of taxon richness as key variables controlling decomposition rates. Generally, increases in abundance, biomass, or richness corresponded to increases in decomposition rates. However, the diversity of metrics used in these studies make comparisons among studies challenging and emphasizes the need for standardized methods.

Biodiversity of detritivores and decomposition rates are linked. Community diversity, abundance, and dominance of certain taxa can all influence the processing rates of organic matter (Covich et al.

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2004, Dangles and Malmqvist 2004, Cardinale et al. 2006). Dangles and Malmqvist (2004) concluded that dominance by macroinvertebrates and crustaceans had a greater effect on decomposition rates than did species richness alone. Schofield et al. (2001) found that crayfish could process 33 to 50% of rhododendron leaves, a result indicating the potential importance of dominant macroconsumers to organic matter processing. Creed and Reed (**2004**) also concluded that leaf decomposition was faster when crayfish were present. However, these studies were unable to resolve the relative importance of shredder biomass vs taxonomic identity. Moreover, how nonshredding taxa affect processing rates remains unclear, although some evidence indicates that scrapers and gatherers facilitate the breakdown of organic matter when they are abundant. Orthocladiinae midges (Chironomidae) often are the first invertebrate colonists on experimental leaf bags and reach densities far in excess of other taxa (SAE, personal observation). Generalist feeders, such as gatherers and scrapers, might indirectly facilitate the breakdown of organic matter by browsing on organic matter biofilms, which in turn, remineralizes nutrients and stimulates the microbial community at the microscopic scale.

*Stream order influences the relative role of macroinvertebrates in organic matter processing.*—The relative importance of macroinvertebrates to decomposition dynamics can vary with stream order. For example, Graça et al. (**2001**) demonstrated that the role of shredders decreased as streams increased in size because of a decrease in shredder biomass with increasing stream size. In contrast, in a study of the role of macroinvertebrates in leaf decomposition in urban and agricultural watersheds, decomposition rates did not vary with stream size because shredders were scarce in these altered systems (**Pascoal et al. 2005**). Thus, stream order might determine the importance of shredders in relatively undeveloped forested watersheds, but other factors related to human land use probably will dictate shredder community structure and importance to decomposition.

*Organic matter quality influences the rate of processing by macroinvertebrates.*—Many *J-NABS* papers have addressed the importance of organic matter quality to invertebrate feeding preference and how assimilation of refractory material and various components of microbial biofilms influence processing rates. In general, lignified leaves are processed by invertebrates more slowly than are softer leaves (reviewed Webster and Benfield 1986), and water-column nutrient concentrations often mediate microbial production (Gulis et al. 2006). More feeding experiments addressing this topic have been published in *J-NABS* than in other aquatic journals, and these studies have demonstrated that leaf chemistry, stoichiometry, and enzyme activity in invertebrate guts are all important components of feeding preference. Caddisfly feeding preference and higher rates of processing were associated with high nutrient (N and phosphorus) and low lignin and polyphenol concentrations in leaves in a tropical stream (**Rincón and Martínez 2006**). Adams et al. (**2003**, **2005**), and Kominoski et al. (**2007a**) showed that elevated atmospheric $CO_2$ concentrations reduced the quality of leaf organic matter and its preference by crayfish. Organic matter processing also is influenced by stoichiometric relationships between invertebrates and organic matter. Stonefly shredders altered C:N of leaf organic matter via mineralization that was regulated by stoichiometry (**Balseiro and Albarino 2006**). Bärlocher and Porter (**1986**) concluded that the mechanism used by invertebrates to digest organic matter might be taxon specific. For example, *Tipula* can hydrolyze proteins of unconditioned maple leaves, whereas *Gammarus* does not produce cellulase, but instead produces endoglucanases and β-glucosidase to break down organic matter (**Bärlocher and Porter 1986**). Therefore, species-specific physiology influences organic matter processing rates.

Since Cummins (1974) likened biofilms to peanut butter on crackers, a wealth of studies (largely published in *J-NABS*) have examined the influence of microbial conditioning on invertebrate processing of organic matter (see **Findlay 2010**). Findlay et al. (**1986**; Fig. 1) were the first to measure the rate of bacterial and fungal assimilation by *Peltoperla* and *Tipula*, and they found that only 1% of the bacteria and 25% of the fungi were assimilated. Others have shown that different fungal mycelia are preferred by invertebrates, and fungal identity might affect assimilation by invertebrates (**Arsuffi and Suberkropp 1986, 1988** [Fig. 1]). Extracellular polysaccharides from bacteria are important sources of nutrition for blackflies, and this result could extend to other detritivores (**Couch et al. 1996**). Future studies should consider the relative importance of fungi, bacteria, and microbial community structure on invertebrate processing of organic matter.

Invertebrates also might influence wood processing rates in aquatic ecosystems. Decaying wood and wood biofilms (epixylon) are important sources of nutrition for aquatic invertebrates and microorganisms, but their importance varies with decay state, tree species, and relative amount of available leaf litter (Tank and Webster 1998, **Collier and Halliday 2000**, **Simon and Benfield 2001**, **Spanhoff et al. 2001**). Wood is a food source for xylophagous invertebrates

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(Anderson 1989, **Collier and Halliday 2000**), and epixylon can be assimilated more efficiently, in some cases, than leaf biofilms by shredding invertebrates, such as stoneflies and *Tipula* sp. craneflies (Golladay and Sinsabaugh 1991, Eggert and Wallace 2007). Given that wood and associated microbes can be an important food resource, macroinvertebrates might accelerate wood decomposition rates when leaf litter is rare, and thus, dead wood might be more important to the aquatic food web than its chemical quality (e.g., C:N ratio or lignin content) suggests. The importance of invertebrates to rates of wood decomposition in freshwater ecosystems is an area in need of additional research.

## Future Directions and Applications

*Global climate change.*—The study of the effects of global climate change on organic matter dynamics, including organic matter budgets, decomposition, and metabolism, presents a novel research opportunity. Numerous drivers, such as increased $CO_2$, are influencing the type and quality of organic matter entering aquatic ecosystems (**Rier et al. 2002**, 2005, **Adams et al. 2003**, **2005**, Tuchman et al. 2003, **Kominoski et al. 2007a**). For example, Rier et al. (2005) demonstrated that elevated atmospheric $CO_2$ concentrations can change leaf chemistry and can have implications for its processing in streams. Other widespread anthropogenic changes, such as N deposition, terrestrial herbivore outbreaks, and changes in precipitation patterns associated with climate change, could influence the quality of the allochthonous litter entering aquatic ecosystems (Hall et al. 2005, Henry et al. 2005, Frost and Hunter 2008). Widespread changes in climate might influence the timing of leaf fall, and at present, the overall expected effect of increased global temperature is a delay in leaffall (Menzel et al. 2006). Delayed leaffall and shifts in riparian forest composition might have consequences for organic matter processing and aquatic ecosystem function, but more research in this area is needed.

Changes in climate are predicted to result in concomitant changes in water temperature and hydrology, both of which are strong drivers of biological activity and organic matter processing. Increased water temperature in streams has been predicted to increase bacterial respiration from 26 to 63% (Sand-Jensen et al. 2007). Studies linking global climate change, aquatic assemblages, and organic matter dynamics are not common. However, a wealth of data (much of it published in *J-NABS*) demonstrates the links between bacteria, fungi, and macroinvertebrates, organic matter dynamics, and water temperature. A fruitful line of research will be to link these processes and scale them up to understand how regional climate changes influence instream organic matter dynamics.

*Landuse change.*—Global land use is changing at a staggering pace and probably will continue to change long into the future (Ellis and Ramankutty 2007). Changes to stream ecosystems associated with human land use, including changes in hydrology and suspended sediments, riparian vegetation composition, macroinvertebrate assemblages, and nutrient concentrations, affect organic matter dynamics (**Sponseller and Benfield 2001**, Schofield et al. 2004, Paul et al. 2006, **McTammany et al. 2007**, Griffiths et al. 2009). Moreover, specific landuse changes, such as conversion of forest land to agricultural uses or conversion of agricultural land to suburban uses, can have multiple effects on instream organic matter dynamics, with potentially cascading effects on the aquatic food web. For example, compositional changes in riparian species associated with landuse change can alter litter composition, and in turn, influence the processing rates of organic matter in aquatic ecosystems (**McArthur et al. 1994**, **Swan and Palmer 2004**, LeRoy and Marks 2006, Kominoski et al. 2007b, Lecerf et al. 2007a). Understanding organic matter dynamics in a changing landscape will continue to pose a challenge to benthologists.

*Biomonitoring applications.*—Interest in using organic matter decomposition (Gessner and Chauvet 2002, **Young et al. 2008**) and whole-stream metabolism as metrics of ecosystem integrity (Fellows et al. 2006, **Young et al. 2008**) is increasing because of the wealth of information on the importance of organic matter processing in stream ecosystems (much of these data were published in *J-NABS*; see also **Dolédec and Statzner 2010**). Decomposition is a sensitive indicator of stream integrity (Pascoal et al. 2003, Gulis et al. 2006, Lecerf et al. 2006, Mesquita et al. 2007, Castela et al. 2008, Lecerf and Chauvet 2008a), but some papers question the utility of this approach (**Hagen et al. 2006**, Bergfur 2007, Bergfur et al. 2007). Recent papers suggest that combining decomposition rates with structural metrics (e.g., invertebrate composition, aquatic hyphomycetes composition, and spore production) might provide some of the most effective indicators of stream integrity (Lecerf et al. 2006, Castela et al. 2008, Lecerf and Chauvet 2008a). A comprehensive review of decomposition and metabolism as indicators of stream health was published in *J-NABS* (**Young et al. 2008**). In particular, Young et al. (**2008**) provided 2 recommendations for ways to use to these strategies effectively for biomonitoring: 1) decomposition rates at test sites should be compared

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to those at reference sites and 2) metabolism measurements can be compared as long as the rates that represent reference conditions include measurements made at sites similar to the test sites (see **Hawkins et al. 2010** for a discussion of benchmarks). Inclusion of decomposition and metabolism in assessing stream integrity moves biomonitoring beyond traditional static metrics to include functional metrics with an emphasis on organic matter dynamics. The European Union has supported research on use of litterbag techniques to develop a continent-wide functional assessment of streams (RIVFunction project; http://www.ecolab.ups-tlse.fr/rivfunction/), and a program in southeast Queensland, Australia, includes ecosystem metabolism as an integrated measure of ecosystem health (Ecosystem Health Monitoring Program; http://www.ehmp.org/). The utility of organic matter metrics for biomonitoring has great potential, and learning from these new programs that incorporate functional metrics will be a novel way to incorporate organic matter dynamics into conservation.

## Synthesis and Summary

Stream ecologists have synthesized our understanding of organic matter dynamics in streams into several conceptual models that have fueled much research. For example, the River Continuum Concept (Vannote et al. 1980) and the Serial Discontinuity Concept (Ward and Stanford 1983) emphasized longitudinal linkages among stream reaches. Downstream reaches depend on energy subsidies from inefficient organic matter processing in upstream reaches. These models were developed with a focus on forested watersheds, and as such, generally fit observed patterns in those landscapes. The Flood Pulse Concept (Junk et al. 1989) emphasized lateral linkages whereby stream reaches depend on periodic energy subsides from adjacent floodplains. This model best describes moderately sized rivers that are well connected to their floodplains. The Riverine Productivity Model (Thorp and Delong 1994) proposed that upstream sources of organic matter are recalcitrant, and therefore, are less important energy sources than the comparatively labile material from instream primary production and locally generated allochthonous inputs. This model tends to fit large rivers that are constricted, highly branched, or otherwise isolated from floodplains or upstream inputs (Bunn et al. 2003). No single conceptual framework is universally applicable to all lotic systems. However, the process of evaluating these models for different systems has led to a more nuanced understanding of functional differences among different types of stream networks (Gawne et al. 2007).

The 158 publications on organic matter dynamics in *J-NABS* is similar to the body of work contributed by Freshwater Biology (~152) over the period since 1986. Papers in *J-NABS* have added substantially to 3 areas: 45% of papers within the broad category of organic matter dynamics focused on decomposition (evenly split between microbial and macroinvertebrate contributions), 44% focused on organic matter budgets, and 11% examined metabolism (Fig. 3). The 1997 special issue on organic matter budgets included 16 organic matter budget papers and 8 synthesis papers that have been well cited and have contributed greatly to the body of literature on organic matter budgets (Fig. 4). In general, organic matter budget papers published in *J-NABS* had higher numbers of citations per paper (mean = 22) than did decomposition (mean = 14) and metabolism papers (mean = 12). These citation patterns demonstrate that authors of *J-NABS* publications have helped refine current conceptual models and our overall understanding of organic matter dynamics in lotic ecosystems.

Based on our review, we repeat the urging of Cummins et al. (1983) for continued synthesis of data into comprehensive organic matter budgets. The influential set of papers published in the *J-NABS* special issue in 1997 provided the foundation for further fruitful research on organic matter inputs, decomposition, and ecosystem metabolism across biomes. In addition, understanding organic matter dynamics in the face of changing climate and land use will be an important future challenge. Comparative studies can elucidate important drivers of organic matter dynamics and can assist us as we try to understand large continental/global changes that are occurring. Our research on organic matter dynamics certainly is not complete. Continued emphasis on synthesizing information into a larger framework for rivers will improve our overall understanding of the importance of organic matter in lotic ecosystems (sensu **Webster 2007**).

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