2-1-2021

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CURRENT EVIDENCE

Thinking like a consumer: Linking aquatic basal metabolism and consumer dynamics

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Scientific Significance Statement

High-frequency metabolic data are increasingly available for aquatic systems and provide the opportunity to measure energy provision at the short time scales relevant to the demands of consumers. However, scientists currently lack a conceptual framework for this new research frontier where metabolic regimes are viewed as an emergent property of food webs. We aim to advance the integration of disparate fields of research to produce a more holistic understanding of riverine productivity.

Abstract

The increasing availability of high-frequency freshwater ecosystem metabolism data provides an opportunity to identify links between metabolic regimes, as gross primary production and ecosystem respiration patterns, and consumer energetics with the potential to improve our current understanding of consumer dynamics (e.g., population dynamics, community structure, trophic interactions). We describe a conceptual framework linking metabolic regimes of flowing waters with consumer community dynamics. We use this framework to identify three emerging research needs: (1) quantifying the linkage of metabolism and consumer production data via food web theory and carbon use efficiencies, (2) evaluating the roles of metabolic dynamics and other

environmental regimes (e.g., hydrology, light) in consumer dynamics, and (3) determining the degree to which metabolic regimes influence the evolution of consumer traits and phenology. Addressing these needs will improve the understanding of consumer biomass and production patterns as metabolic regimes can be viewed as an emergent property of food webs.

Animals eat to satisfy their energetic demands. Most of our inferences about the energy available to animals have been based on the biomass or standing stock of their food resources, which research has often shown to be a poor proxy for energy availability to consumers (Lindeman 1942). Hairston et al. (1960) recognized this problem many decades ago for terrestrial ecosystems, where much of the "green" biomass is structurally or chemically defended against herbivores. In most aquatic ecosystems, however, the problem is inverted. Single-celled algae with short lifespans dominate ecosystem productivity, and typically only small standing stocks of autotrophs support a much larger biomass of herbivores or secondary consumers. Such "inverted biomass pyramids" (sensu Elton 2001) in freshwaters are most likely to be explained by high rates of energetic flux through algal communities (Odum and Barrett 1971; Wang et al. 2009). Additionally, many consumers within aquatic ecosystems are supported by detritus and associated detritivores (Hall and Meyer 1998; Marks 2019; Robbins et al. 2020). Similar to the "green food webs," in so called "brown food webs", standing stocks of detritus are a poor proxy for the amount of energy available from organic matter to higher trophic levels (Srivastava et al. 2009). Indeed, the organic matter that tends to accumulate in ecosystems is not palatable to most consumers (Freeman et al. 2001; Allison 2006; Schmidt et al. 2011; Marks 2019). In both aquatic and terrestrial ecosystems, the biomass of consumers is better explained by the energy transferred between trophic levels than by the overall standing stocks of resources in green or brown food webs.

Consumer energetics include the conversion of their food into biomass, known as secondary production. Historically, the energy transferred from basal resources to consumers has been measured in labor intensive collections of biomass of primary producers, allochthonous organic matter, and consumer standing stocks (Tank et al. 2010). As it is difficult to collect and separate the biomass of different resource pools, estimates made using these labor-intensive methods may not be sufficiently accurate to document the changes to overall standing stocks and processes occurring over short time spans that correspond to rapid energy transfer. Thus, we historically have had limited ability to measure energy transfer at the short time scales relevant to the energy demands of consumers. The advent of high-resolution ecosystem metabolism time series, due to technological advances in oxygen sensors and the development of statistical and modeling methods, now allows us to capture energy fluxes through the ecosystem at fine temporal resolution (Roberts et al. 2007; Appling et al. 2018; Bernhardt et al. 2018). Specifically, we can estimate organic carbon (C) fixation into biomass (measured as gross primary production [GPP]) and inorganic C release from organic matter and by primary producers (measured as ecosystem respiration [ER]) at daily time steps in any stream instrumented with the necessary sensors. These advances provide an opportunity to bridge infrequent measurements of biomass with *in situ* high-resolution estimates of production and consumption of organic C. The availability of ecosystem metabolism data creates opportunities to understand how the bioenergetics of individual organisms are linked to the energetics of entire ecosystems as proposed by Brown's metabolic theory of ecology (Brown et al. 2004) (Fig. 1; Box 1) and estimated for oceans (López-Urrutia et al. 2006). A major challenge now becomes actually connecting ecosystem metabolism and secondary production in streams.

Environmental regimes drive both ecosystem metabolism and consumers in aquatic systems. We have long known that light and thermal regimes (Olden and Naiman 2010; Hill et al. 2012), hydrologic regimes (Lytle and Poff 2004; Sabo et al. 2010), and resource supply regimes (Elser et al. 2000; Rosemond et al. 2001) together shape the structure of lotic food webs by altering consumer abundance, biomass, functional diversity, and trophic relationships. These physical and chemical regimes also constrain stream ecosystem metabolism. Light and nutrient supply determine the potential for C fixation (Roberts et al. 2007), hydrologic events can reduce or subsidize algal and organic matter standing stocks (Uehlinger et al. 2003), and temperature and nutrient supply each alter the degradation of organic matter (Woodward et al. 2012; Rosemond et al. 2015; Follstad Shah et al. 2017). Through their influence on metabolic regimes, the effects of environmental conditions could then be propagated indirectly to consumers by impacts on the magnitude, timing, and form of energy supply. At times, such indirect effects on energy supply may amplify, counterbalance, or mitigate the direct effects of physical and chemical controls on aquatic organisms and their interactions. Using continuous measures of environmental conditions such as flow and integrating those measures with high-resolution time series of ecosystem metabolism, we have the opportunity to determine when and where the impacts of physical constraints and disturbance on energy resources may constrain community membership or reduce the total consumer production and biomass. For example, studies using high-frequency measurements of ecosystem metabolism and GPP have already revealed that in many systems low flows coincide with periods of high light availability (Hensley et al. 2019; Hosen et al. 2019) resulting in higher rates of photosynthetic autochthonous production (Hall et al. 2015; Hosen et al. 2020). These integrated studies suggest that autochthonous production may counterbalance
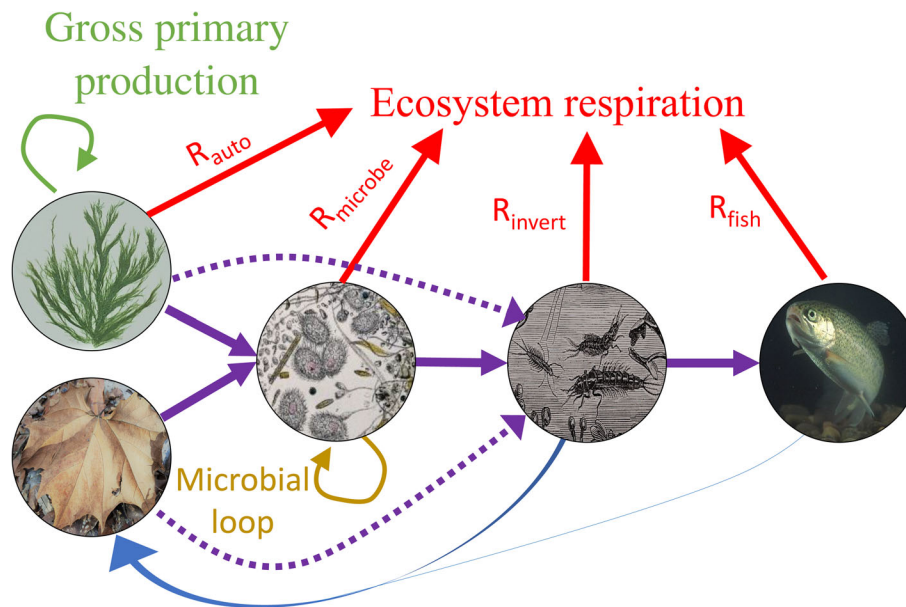
Fig. 1. Conceptual framework of food web dynamics and how they relate to ecosystem metabolism metrics. In this simplified food web, red arrows illustrate contributions to respiration, purple arrows indicate the energy uptake pathways, blue arrows address contributions from higher trophic levels to detritus (including potential nutrient subsidies), and the brown arrow represents the microbial loop. Generally, we would expect the magnitude of the fluxes from a trophic level through energy uptake to higher trophic levels (purple arrow) to be smaller than the magnitude of the corresponding flux through respiration (red arrow).

allochthonous production in temperate stream networks with potential implications for consumer production and biomass.

In order to mechanistically link patterns in ecosystem metabolism with secondary production, a framework connecting consumer- and ecosystem-level energetics that accounts for variable environmental conditions across spatial and temporal scales is needed. The conceptual framework we propose here is based on the interactions of environmental conditions and metabolism (Bernhardt et al. 2018) and considerations of consumer energetic constraints in the form of physical conditions, such as temperature, and necessary food resources. Our framework considers metabolism to be an emergent property of food webs (Figs. 1, 2). How this new property links to the traditional, mostly organismal based, food web ecology is an exciting new area of research (Fig. 2) (*see* also Benke 2018). We focus on a bottom-up view of food webs, tracing how resources drive consumer production, to illustrate how high-frequency GPP and ER data can be linked to consumer production via the conservation of energy as carbon is transferred through food webs. We hypothesize that distinguishing direct impacts of the environment on consumers through their physiological effects ("longer" mono-colored arrows), from indirect impacts through their resources in the form of GPP ("shorter" mono-colored arrows) will lead to new insights into food webs and ecosystem energetics. How these interactions affect the use of basal resources, as described by GPP, the amount of ER that is attributable to

macroscopic consumers, and the balance between consumer respiration and production are areas of needed research (multi-colored arrows). When these complex interactions play out over long time scales, we believe them to influence consumer phenology (time axis). Our conceptual framework leverages not only conservation of mass and energy, but also the growing availability of high-frequency data. These high-frequency data are particularly useful for linking phenology to basal resources, including autochthonous production via GPP (Hayden et al. 2016; Thorp and Bowes 2017) and allochthonous inputs from dissolved organic matter (Wagner et al. 2019).

The interactions among environment, metabolism and consumers (i.e., "arrows" in the framework) are expanded upon in the next three sections. The first focuses on the understanding of how energy is transferred to consumers, and on when ER might serve as a proxy for consumer production. The second section addresses when and where energy supply limits consumer abundance and biomass, especially in relation to the environment. In this section, we acknowledge that consumer respiration is a part of ER and discuss how this can result in feedbacks where consumers have top-down impacts on metabolic regimes. The third section explores how variation in the form, timing, and magnitude of energy supply affects the traits of aquatic consumers. Each section serves to outline the corresponding parts of the framework more clearly. Our framework offers new opportunities to

BOX A primer on metabolism (or the many meanings of metabolism).

The concept of metabolism unifies a large suite of disciplines in ecology (Brown et al. 2004; Sibly et al. 2012) and has been used to predict impacts of global change on food webs and ecosystem fluxes at the scale of biomes (e.g., oceans, López-Urrutia et al. 2006). Synthesizing across these disciplines requires an understanding of the different conceptual frameworks, and different units of measurement, commonly used in these disciplines.

Stream ecologists are increasingly estimating aerobic metabolism (in units of oxygen, g O_2 m^{-2} d^{-1}) at the scale of stream reaches from high-frequency measurements of oxygen using the simple model:

$$d\text{DO}/dt = \text{GPP} + \text{ER} + K\,(\text{DO}_{\text{sat}} - \text{DO})$$

where $d\text{DO}/dt$ is the change in dissolved oxygen concentration through time, GPP is the rate of photosynthetic O_2 production, ER is the rate of oxygen consumption through both autotrophic and heterotrophic respiration and $K\,(\text{DO}_{\text{sat}} - \text{DO})$ is the physical net exchange of oxygen between the water column and the overlying air governed by a per unit time gas exchange rate K.

The challenge is to integrate estimates of ecosystem GPP and ER with existing knowledge regarding respiration and production by various groups of autotrophs and heterotrophs. The link between these two types of measurements is clear if we examine the basic equation governing aerobic respiration:

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + \text{energy}$$

Oxygen production and consumption by aerobic metabolism indicates production and consumption of organic matter by organisms. While population or community studies may focus on aspects of production of biomass at higher levels (i.e., "energy" measured either in units of mass or energy) or the efficiency of energetic transfer between trophic levels (i.e., the conversion of glucose to energy in percent), respiration (consumption of oxygen) is a related quantity.

To facilitate integration, it is also important to understand how studies in different disciplines conceptualize and estimate metabolism and respiration. For example, laboratory-based studies of fish bioenergetics frequently measure metabolism of individual fish based on the oxygen they consume (i.e., fish respiration) and convert these measurements to units of energy or tissue mass and combine them with estimates of excretion, *Continued*

BOX 1. A primer on metabolism (or the many meanings of metabolism).—cont'd

egestion, and consumption to predict fish growth under varying conditions. Field-based studies of fish bioenergetics often take a simpler tact, lumping various processes into assimilation efficiency estimates to convert biomass intake into energetic intake, which is then combined with metabolic costs to predict consumer energy budgets, growth, or overall production of a stock. Field studies of food webs often take an even simpler approach combining estimates of assimilation efficiency and net production efficiency, the latter of which accounts for metabolic losses (i.e., respiration). Thus, while production is often the object of inference, respiration is frequently estimable from studies done in various disciplines.

understand and predict the impacts of global change on stream ecosystem processes and community ecology.

Consumer dynamics as part of ecosystem metabolism

To link aquatic metabolism to aquatic communities, we must estimate the degree to which ER can predict production across higher trophic levels. Trophic position and trophic transfer efficiencies are critical pieces of information needed to complete this task (Pauly and Christensen 1995; Cremona et al. 2014). Ecosystem models that estimate transfer of basal resources to higher trophic levels have been successfully developed for marine and lentic (i.e., standing water) freshwater systems, but are less common for streams (Pauly and Christensen 1995; Cremona et al. 2014; Hayden et al. 2016; Thorp and Bowes 2017). Studies that measure secondary production in conjunction with ecosystem metabolism in streams are rare and limited in scope (cf. Marcarelli et al. 2011, but *see* Huryn and Benstead 2019). In stream ecosystems, both allochthonous (Tank et al. 2010) and autochthonous (Larned 2010) food resources, which support secondary production, are variable over time and space. Yet, there are many knowledge gaps preventing researchers from linking ecosystem metabolism to consumer food webs. Only production of autochthonous resources via GPP is readily estimated with high-frequency data. Further, the proportion of GPP that is available to heterotrophic consumers is limited by the fraction of GPP that is consumed by autotrophic respiration (Hall and Beaulieu 2013). Allochthonous resources that enter stream food webs are by definition produced outside the ecosystem (Thurman 2012) and must therefore be inferred indirectly through estimates of aerobic ER (Marcarelli et al. 2011). Thus, direct studies of metabolic regimes that include both GPP and

ER and estimates of biomass inputs are needed to account for use of resources by consumers. Such estimates require extensive sampling and are rarely undertaken at the ecosystem scale (Cole et al. 1984; McDowell and Likens 1988).

Such unique challenges have likely contributed to the lack of studies linking ecosystem metabolism to secondary production in streams. Because invertebrate and fish secondary production studies are prohibitively time-intensive, the consumer data needed to populate models are rare (Cross et al. 2013). Therefore, methods applying high resolution ER measurements to approximate consumer production may permit estimates of higher resolution of consumer production at shorter time scales.

Estimates of ER are a summation of the respiration of autotrophs, microbes, and other consumers:

$$ER = R_{autotroph} + R_{heterotrophs-microbial} + R_{heterotrophs-consumers}$$

where $R_{autotroph}$ is autotrophic respiration as autotrophs convert part of their primary production directly into reduced compounds; $R_{heterotrophs-microbial}$ is microbial respiration, representing all the micro-organisms contributing to respiration, including fungi, bacteria, and archaea; and $R_{heterotrophs-consumers}$ is respiration of all multicellular organisms such as macroinvertebrates or fish (Fig. 1). Recognizing the fundamental differences between these two heterotrophic groups, we have elected to separate respiration by micro- and macroconsumers. This recognizes that there is a microbial food web that may feed production to invertebrates and fish or dissipate energy endogenously (Meyer 1994). While transfer of microbial secondary production to higher trophic levels is generally low in marine ecosystems (Azam et al. 1983), stream microbial communities and autochthonous production are frequently important food resources for invertebrates and fish (Meyer 1994; Hall and Meyer 1998; Bernhardt et al. 2002; Hayden et al. 2016; Thorp and Bowes 2017) and are thus accounted for in our conceptual approach.

To link *in situ* metabolism measurements to infrequent biomass estimates, we propose a conceptual approach based on trophic transfer efficiencies along the food chain. Transfer efficiencies can be used to provide predictions on how much production can occur at higher trophic levels for a given amount of ecosystem production and respiration. Carbon use efficiencies describe the amount of carbon incorporated into an organism's biomass compared to the amount ingested. Carbon fixed by autochthonous primary producers is a basal energy source in freshwaters, but a substantial proportion of photosynthetic production is respired by autotrophs before it is ever released to the environment (Hall and Beaulieu 2013). Depending on temperature, light, and nutrient availability, respiration by autotrophs can range from 20% to over 40% of primary production (Graham et al. 1985; Duarte and Cebrián 1996; McIntire et al. 1996). For heterotrophic organisms, carbon use efficiencies can range from 1% to 50% for

bacteria (del Giorgio and Cole 1998; Berggren et al. 2010; Amado et al. 2013), 5% to 40% for zooplankton (*Daphina*, Brett et al. 2017), 4% to 82% for macroinvertebrate species (Heal and MacLean 1975; McCullough et al. 1979; Sweeney and Vannote 1981; Webster 1983; Friberg and Jacobsen 1999), and from negligible to 40% for fish (e.g., alewife, Stewart et al. 2010), trout (Meyer and Poepperl 2004), salmon (Madenjian et al. 2004)). Additionally, food chain lengths can differ among aquatic ecosystems (e.g., 2.5–4.5 streams and 3.0–5.5 for lakes; Vander Zanden and Fetzer 2007). However, with a theoretical, simplified food chain, we can assign the basal resources used (autochthony vs. allochthony), assume the proportion of microbial biomass that is transferred to higher trophic levels of the consumer food web, and set the food chain length (Fig. 1). With a further assumption of the degree of carbon use efficiency at higher trophic levels, we can estimate how much consumed biomass is "lost" toward respiration or egestion rather than going toward production. With this combined information we can estimate biomass production via ER (Fig. 3, lines; Cole et al. 1989; Marcarelli et al. 2011; Demars et al. 2020). We are then able to estimate the expected biomass production of consumers such as fish, based on available allochthonous resources or autochthonous GPP.

In freshwater ecosystems, basal food resources, meaning allochthonous detritus and products of autochthonous primary production, are transferred to multicellular consumers (e.g., macroinvertebrates, fish) through both direct and indirect pathways. Many multicellular freshwater organisms consume basal detrital resources and primary producers such as phytoplankton, diatoms, and macrophytes. In other cases, these basal organic matter resources are first consumed by microbial communities that are subsequently consumed by multicellular consumers. Somewhat counterintuitively, both pathways will result in similar overall efficiency of 10% from basal resource to primary non-microbial consumer. Trophic efficiencies are higher for microorganisms (~ 30%; Cole et al. 1988) vs. metazoans (i.e., multicellular consumers) (~ 10%; Perry et al. 1987; Eggert and Wallace 2007) when basal resources are consumed. Further, carbon use efficiencies are typically higher (Anderson and Sedell 1979; Neres-Lima et al. 2017) when invertebrates feed on heterotrophic microbes (~ 30%; Benke and Wallace 1980; Eggert and Wallace 2007) than when allochthonous basal resources are consumed (~ 10% as above). If basal resources are first consumed by bacteria (trophic efficiency = 30%) and then consumed by a metazoan (trophic efficiency = 30%), the total trophic transfer efficiency of 9% ($0.30 \times 0.30 = 0.09$) is very similar to the trophic transfer efficiency of 10% that is expected if metazoans feed directly on basal organic matter resources. Thus, the inclusion or exclusion of microbial communities has a limited effect on the overall efficiency of ~ 10% from basal resource to the primary non-microbial consumer (assuming one microbial trophic level between resource and consumer).
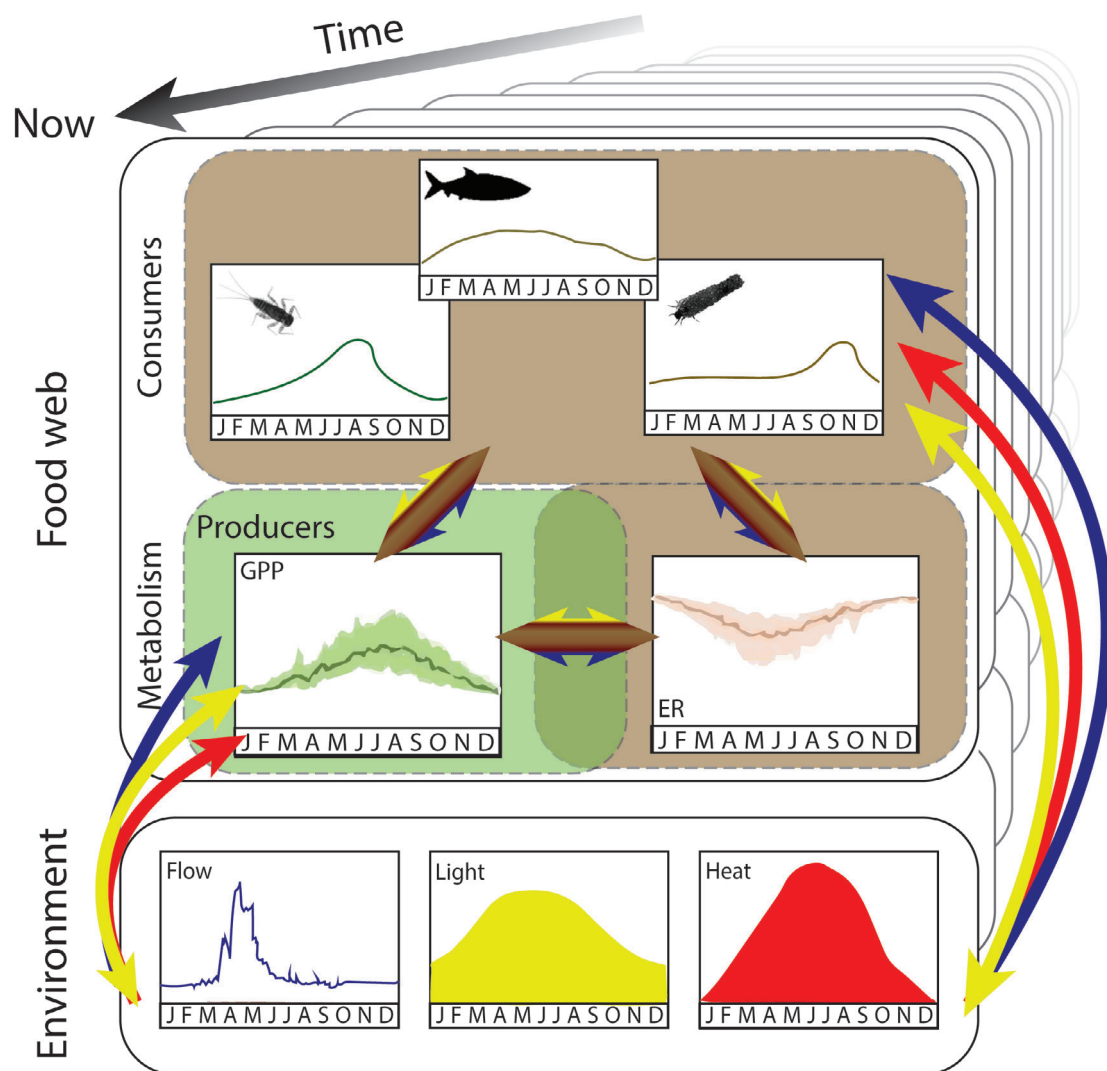
Fig. 2. Our conceptual framework considers metabolism as an emergent property of aquatic food webs. Here, we propose that the links between this emergent property and traditional, organismal-based food web ecology are modulated by the environment. The environment, here depicted as the physical stream environment including flow, light and temperature regimes, affects both the metabolic regimes via influences on GPP (indicated by the shorter blue, yellow and red arrows) and the provision of allochthonous resources, as well as the consumers directly through physiological effects (indicated through the longer blue, yellow and red arrows). Research needs to determine to what degree ER represents macroscopic consumer respiration as opposed to autotrophic or microbial respiration, and whether those ratios are altered by environmental influences (width of arrow between GPP and ER depends on the environment), and if primary production conversion to consumer production and biomass is modulated by the environment (with of arrow between ER/GPP and consumers). Consumer patterns presented here are hypothetical at the moment. The research into current patterns, here expressed on an annual basis, we believe to have developed over time to arrive at the current state of consumer traits and phenology.

Thus, we do not include the microbial level separately and assume a 10% efficiency per trophic level as a conservative estimate based on the carbon use efficiencies summarized above.

Applying the theoretical food chains detailed above, we can make predictions of consumer production based on GPP and ER data. Following this approach, we generated expected levels of secondary production assuming different mean food chain lengths (2.0, 2.5, 3.0) using both GPP (Fig. 3A) and ER (Fig. 3B) based on different levels of GPP. Using three studies

that provide information on fish production, trophic level, and ecosystem metabolism, we can see that fish production can be higher, similar, or lower than predicted from GPP or ER (Colorado, USA: Cross et al. 2013; Hall et al. 2015; Tonle Sap, Cambodia: Holtgrieve et al. 2013; globally: Pauly and Christensen 1995). For example, in the Tonle Sap, GPP underpredicts the amount of fish production observed, probably because of the important contribution of allochthony (Holtgrieve et al. 2013), so utilizing ER provided more reasonable predictions (Fig. 3B). This approach can be used to
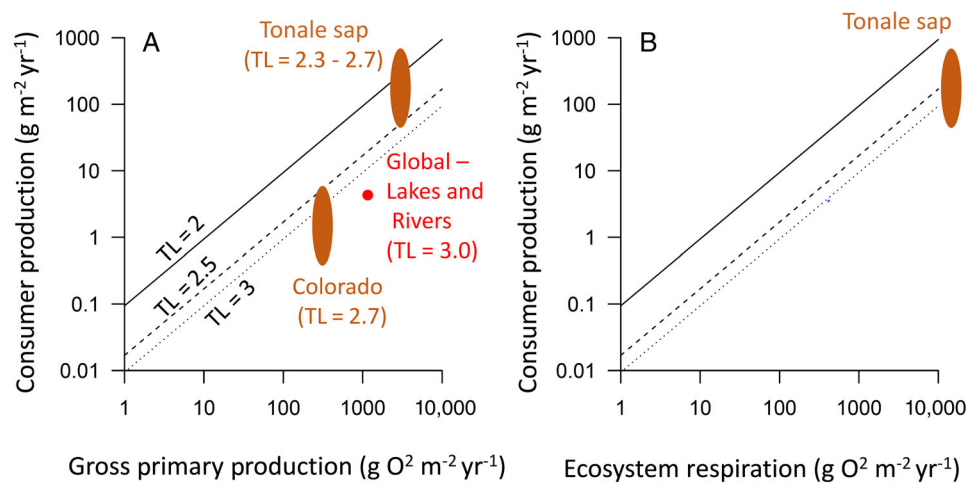
Fig. 3. Comparison of primary production and consumer production within an ecosystem can provide insights into the basis of fish production and the efficiency of the food web. Figures assume trophic transfer efficiencies of 10% to convert GPP (**A**) or ER (**B**) (measured in terms of oxygen) to fish production (measured in terms of tissue biomass), and allows us to estimate how much of GPP and ER should flow into fish production (see text for more detail on the model/calculations). "TL" indicates the trophic level at which production is being calculated. Specifically, Colorado estimates are based on a study area near the confluence of Diamond Creek and the Colorado River and previously reported in Hall et al. (2015) and Cross et al. (2013) (GPP = 290 g O_2 m^{-2} yr^{-1}, Consumer production = 0.5 – 3.5 g m^{-2} yr^{-1}). Tonle Sap estimates were reported in Holtgrieve et al. (2013) (GPP = 3900 g O_2 m^{-2} yr^{-1}, ER = 19'000 g O_2 m^{-2} yr^{-1}, Consumer production = 50 - 500 g m^{-2} yr^{-1}). Global lake and streams estimates are from Pauly and Christensen (1995) (GPP = 1500 g O_2 m^{-2} yr^{-1}, Consumer production = 4.3 g m^{-2} yr^{-1}). Note that data were converted to units of g O_2 m^{-2} yr^{-1} for GPP and ER rates and g m^{-2} yr^{-1} of catch for consumer production, where necessary to allow for comparison across studies.

evaluate other aspects of trophic energetics and carbon cycling. If the microbial loop is responsible for dissipating substantial amounts of energy, as has been seen in some freshwater studies (Amado et al. 2013), actual rates of secondary production will fall well short of those predicted using our conceptual approach. Thus, information on mismatches between theoretical predictions and actual measurements can point to knowledge gaps in a specific system and our understanding of ecosystems.

Predicted consumer production may be over- or underestimated based on the metabolism metrics for several reasons. In general, we expect aerobic measurements of GPP and ER to underpredict production when other, non-aerobic, metabolic processes contribute a significant percentage of overall production in a system. On the production side, chemoautotrophic processes are very difficult to measure in streams and based on the limited evidence available are generally assumed to form a small fraction of overall production (Jones et al. 1994). Heterotrophic processes can be substantial, but are also highly variable. Anaerobic respiration (e.g., denitrification, methanogenesis) is a heterotrophic process with alternate terminal electron receptors not captured by our aerobic metabolism estimates (Richey et al. 1988; Schlesinger and Bernhardt 2013). On the other hand, GPP and ER will overpredict consumer production when there are inefficiencies in the food web (from the perspective of higher trophic levels). This occurs when 1st-order consumers are resistant to higher consumers (McNeely et al. 2007). For example, heterotrophic resources may not be transferred to higher trophic levels if

interactions between microbes result in energy dissipation entirely through consumption and respiration within microbial communities via the aforementioned microbial loop (Azam et al. 1983; Meyer 1994). Or, macrobiota with defenses or high mobility may be able to avoid predation (Vermeij and Covich 1978), hindering heterotrophic energy transfers to higher trophic levels. The presence of inefficiencies may also be linked to ecosystem characteristics including hydrological or thermal regimes and ultimately to anthropogenic influences (Power et al. 2015). Finally, as streams are open systems, carbon can be brought in from upstream (e.g., drift) or for the terrestrial (e.g., leaf fall) or can leave the system via downstream export or burial. These sources and sinks may not be captured by estimates of GPP and ER but could be important for consumer production and efficiencies.

Our proposed framework could be used to determine food web production based on either GPP, ER, or a combination of both, if deviations from the theoretical model can be explained using future studies. Temperature has emerged as a useful tool to understand how the environment controls energy and thus can be used to understand and infer processes. In an effort to make measurements at an ecosystem level comparable to cellular measurements, researchers calculate apparent activation energies of riverine processes such as GPP and ER. On a biochemical level, temperature dependence, and therefore apparent activation energies, are expected to be greater for respiration than for primary production (Allen et al. 2005). In some cases, apparent activation energies at the ecosystem level conform to these expectations

(Perkins et al. 2012; Huryn et al. 2014), such as when labile organic matter resources are consistently available (Jane and Rose 2018). In other cases, temperature dependence of GPP and ER deviate from theoretical expectations (Demars et al. 2016; Song et al. 2018; Hosen et al. 2019). In these cases, researchers have pointed to causes of mean system temperature (Song et al. 2018), N_2 fixation (Welter et al. 2015), and dynamic light availability (Hosen et al. 2019). We propose that such information about temperature-dependence of ecosystem processes can be used to infer how efficiently energy is transferred between trophic levels. For example, if apparent activation of ER greatly exceeds theoretical expectations, this could be an indication of high rates of respiration and low production efficiencies of heterotrophic organisms as organic matter is disproportionately directed to mineralization. The role of environmental conditions in the interaction of metabolism and consumers is explored in more details in the next section.

There are already opportunities to test these (summarized in Table 1, food webs) and other hypotheses related to the combined study of ecosystem metabolism and consumers. For example, in the U.S., StreamPulse (http://www.streampulse.org) and the USGS Powell Center provide metabolism data on many U.S. streams (Appling et al. 2018), and a number of state and federal agencies sample fish; however, estimates of fish production in freshwater systems are less common. Similarly, macroinvertebrate surveys are conducted in many streams as part of stream health monitoring, though production estimates are more difficult. Exploring the relationship between these limited fish or macroinvertebrate production and GPP and ER may nonetheless provide valuable first insights into the inner workings of stream food webs, as well as identify factors that may decrease fish or macroinvertebrate production from its potential based on either GPP or ER.

Intra-annual linkages among the environment, metabolism, and consumers

The biomass and production of stream consumers are jointly constrained by the stream climate, comprising the physical conditions (i.e., thermal, light, and hydrologic regimes), chemistry (i.e., nutrients, contaminants), and basal resources. The physical drivers influence consumers through both direct and indirect pathways. For example, a flood can directly affect consumers through physical displacement of individuals or indirectly through removal of basal resources. Changing light conditions can both signal changes in consumer activity (e.g., circadian rhythm) and affect primary production (Hensley et al. 2019; Hosen et al. 2019; Huryn and Benstead 2019). Similarly, increasing temperature can directly stimulate microbial growth during warmer months or indirectly shift consumer food resources from green to brown pathways. The direct effects of the thermal, light, and

Table 1. Proposed hypotheses based on our framework.

Food webs

- In food webs receiving substantial energy from allochthony, secondary production will be greater than predicted from gross primary productivity by a theoretical food web and closer to predictions derived from ecosystem respiration.
- In food webs receiving substantial energy from non-aerobic sources, secondary production will be greater than predicted from ecosystem respiration.
- In food webs where microbial loops dissipate substantial energy, secondary production will be less than predicted from gross primary productivity or ecosystem respiration by a theoretical food web.
- The storage of substantial biomass in intermediate trophic levels will lead to an overprediction of secondary production from gross primary productivity by a theoretical food web, especially in systems lacking regular disturbances.

Environmental linkages

- The greatest impacts of environmental control on higher trophic levels will be through indirect pathways related to their regulation of food resources.
- Knowledge of the mechanisms by which environmental influence on food resources is linked to consumers will provide new insights into the role of environmental drivers and better information on stream environmental management of consumers.
- In systems where gross primary productivity or allochthonous inputs are more predictable in time, consumers synchronize their life history to coincide with peaks in basal metabolism.
- Consumer production dynamics will not respond to short-term changes in primary productivity if environmental conditions (e.g., temperature), a phenological mismatch, or a specialist diet are directly limiting a consumer.

Communities

- The role of environmental conditions in structuring aquatic consumer communities is mediated through metabolic pathways.
- Temporal variation in grazer and scraper production and abundance evolved to track predictable seasonal variation in primary productivity.
- Temporal variation in shredder production and abundance evolved to track predictable seasonal variation in the availability of allochthonous inputs.
- Highly mobile consumers evolved to track peaks in resources throughout a watershed leading to an apparent disconnect between consumer and gross primary production at local scales.

hydrologic regimes on consumers are well described in the literature (Hill et al. 2001; Ruhi et al. 2015; Smith et al. 2017). However, in some circumstances, the indirect pathway of environmental control via food resources may be a larger and
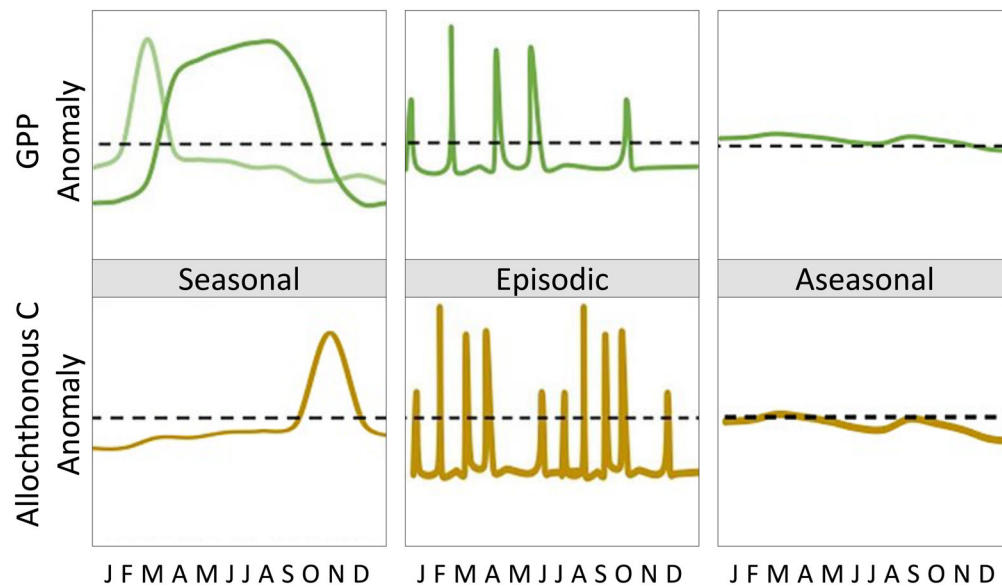
Fig. 4. Potential seasonal energetic regimes at the base of "green" and "brown" food webs within streams. In seasonal systems, terrestrial vegetation controls GPP via light availability and the timing and magnitude of allochthonous carbon subsidies. In episodic systems, flood scour and desiccation during droughts can constrain productivity, while storm pulses of organic matter and nutrients can subsidize both the green and brown food webs. In aseasonal systems, productivity and heterotrophy remain relatively constant year-round due to consistent supply of light or allochthonous carbon subsidies. Note that all regimes are graphed as anomalies from the mean to emphasize the timing of low and high energy supply rather than the magnitude of that energy flux.

more fundamental constraint, as the availability of autochthonous and allochthonous materials ultimately limits consumer biomass and productivity (Power 1992; Farrell et al. 2018). Thus, to understand consumer dynamics, we need to not only focus on the direct environmental (e.g., physical) effects, but determine when and where consumers are energy-limited as a result of constraints on primary productivity, the provisioning of organic matter, and/or inefficiencies in trophic transfers (e.g., microbial loop).

The variability of the environment (e.g., stable, predictably oscillating vs. stochastic, Fig. 4) likely defines whether systems are habitat- or energy-limited as it controls whether direct or indirect pathways, respectively, dominate. When the timing and magnitude of GPP is predictable, we expect the consumer to synchronize their growth and reproduction to coincide with the peaks in basal metabolism to become competitively dominant. In such cases, consumer production should track metabolic patterns as consumers optimize available energy from food resources (Huryn and Benstead 2019). Theoretically, in a predictable "green" ecosystem (i.e., autochthonous-dominant system), the magnitude of GPP approximates the upper limit of how much energy can be transferred to higher trophic levels (see previous section). Grazer or herbivore production will follow the patterns of GPP, which is constrained by the stream climate (i.e., indirect environmental control on consumers), representing bottom-up regulation of the system. GPP will increase with increasing light and temperature until grazing rates reduce standing algal biomass to a point when

grazers are energy-limited, thus shifting to a regulated system. The eventual decrease in consumers due to energy-limitation will lift top-down control on the resource, and GPP will again increase, and thus creating lagged oscillations in the phenology of grazer biomass and GPP (Carpenter 1989). Alternatively, in a "brown" ecosystem (i.e., allochthonous-dominant system) where the magnitude and timing of organic matter inputs are predictable, GPP is low and shows little temporal variation because autochthonous resources provide little to no energy for consumers. However, we can examine the ER time series along with stream climate data to infer consumer resource use. For example, in response to predictable inputs of leaf litter in the fall in temperate headwater streams, consumer productivity may increase, stimulating increases in ER (as $R_{heterotrophs-consumer}$). Predictable inputs of organic matter to streams often coincide with changes in light and temperature, affecting metabolic activity in the stream (Savoy et al. 2019). ER may respond by first increasing through microbial conditioning of organic matter ($R_{heterotophic-microbial}$) which will then be sustained by macroinvertebrates shredding, collecting, and gathering of the conditioned material.

Stream climate data allow for the interpretation of direct effects on the metabolic regime and consumers as well as energy-mediated indirect effects on consumers. With data on the environmental and metabolic (e.g., GPP or ER) regimes combined with traditional measurements of consumer biomass, turnover rate or productivity, we can test predictions about the consumers best adapted to take advantage of the

resources and how these advantages propagate through the food web at short, intra-annual time steps. For instance, with daily metabolic measurements (g O_2 m^{-2} d^{-1}) and weekly or monthly consumer biomass (g AFDM m^{-2}), we can consider whether the available energy is being utilized by the consumer community by converting metabolism estimates to carbon equivalents and applying carbon use efficiencies. An increase in daily GPP without a lagged increase in consumer biomass could indicate (1) a mismatch between consumers and the trophic base of production (e.g., unpalatable form of organic matter) or (2) a direct limitation on the consumer community by the stream climate (e.g., cold temperatures). Considering consumer biomass, daily GPP, and a metric of stream climate, such as hydrologic variability, would allow us to differentiate between direct and indirect effects. If GPP is correlated to hydrologic variability, but consumer biomass is unrelated to GPP, this could be evidence for a direct effect of hydrology on consumers (e.g., disturbance). A correlation between daily GPP and consumer biomass could indicate an indirect, energy-mediated effect of the stream climate. Any such insights will provide further information to understand why GPP and ER may or may not serve as predictors of consumer biomass and production.

Our testable, yet undeniably simplistic, theoretical examples of "green" and "brown" ecosystems provide starting points for how metabolism estimates can be used to explain and predict consumer dynamics at short time scales. However, we must consider how consumers in real systems, meaning systems that experience stochastic events (Rodriguez-Iturbe et al. 1987), interact with basal resources and the environment. Using flow variability as an example, stochastic floods can directly displace consumers and will decrease GPP, not only by scouring, but from increased light attenuation in the water column by particulate matter, representing an indirect constraint on energy flow to consumers (Grimm and Fisher 1989). In the "brown" model system, we could predict scouring and removal of organic matter during floods in the affected area, which represents an indirect constraint on energy availability to consumers in that reach. However, displacement of both autochthonous and allochthonous resources by flow makes that energy available to consumers downstream emphasizing the importance of not only temporal but also spatial scale.

For temporal aspects, we must consider that the timing, magnitude, and duration of predictable climate events as well as stochastic disturbance events will determine how phenologies of consumer production track with ecosystem metabolism. We must also consider whether direct, habitat-mediated or indirect, energy-mediated effects of environmental drivers are more important for determining consumer biomass and community membership and what combination thereof provides the most predictable variables. Even for systems with annual pulses of primary production, it may take time for consumers to take advantage of the new resources available based on how the timing of the resource aligns with the life

cycles and feeding strategies of the consumers. For instance, the ability of macroinvertebrates to use particular resources may vary by both feeding group and the nutritional content of the resource (Compson et al. 2018). Even if a predictable pulse of leaf litter occurs, if it is not their preference, there may be a sizable lag in consumption until the preferred resource is depleted. Thus, the time frame in which we consider consumer relationships to available energy will depend on the consumer community, especially their plasticity to respond to changing resources availability and to survive different disturbance events.

A fundamental entanglement exists between the environmental drivers, metabolic rate estimates, and the effects on consumers. Disentangling, or at least estimating, interactions between these factors may allow us to better predict consumer responses to anthropogenic change. For example, consider a forested headwater stream whose metabolic regime is dominated by predictable leaf litter inputs in the fall. As the consumers in this stream optimize their production based on this input of energy, we expect predictable resource and consumer synchronization based on this highly consistent annual event. However, in a changing climate (higher temperatures, more stochastic hydrologic events) with land cover conversion from forest to cropland, energy flow to consumers could be affected via direct and indirect pathways. As trees are removed, light availability increases and temperatures warm, stimulating primary production and fundamentally altering the base of the stream's energetics. Light thus indirectly affects consumers by altering the abundance and timing of food resources (see following section). More light may also warm the stream, modulating the metabolism of individual consumers (cf. Brown et al. 2004). More variable hydrology, as a result of vegetation removal, may increase scouring and downstream transfer of energy resources used by consumers while also directly displacing some consumers. The direct and indirect environmental effects together with changes in resource tracking ability by consumers can only be understood if the underlying mechanisms can be described, which are certain to be context-dependent and more complex than the above example.

Spatial scale is a large part of that context and important to consider because the scale at which we generally measure the stream climate, metabolic regime, and consumer effects, namely at the stream reach, is not necessarily the scale where we need information, such as the catchment scale (Finlay et al. 2002). Any extrapolation will require understanding how the mechanisms by which environmental effects, both indirect and direct, constraining consumers play out across spatial and temporal scales. The physical and chemical data necessary to do this have been available in a relatively continuous form for some time from stream gauges, satellites, and models. In contrast, only discrete standing stock measurements of basal resources were available, until recent advances provided fine scale metabolism data. The addition of high-frequency metabolism data to existing data on the stream climate and consumers provides us with

tools for disentangling direct and indirect pathways and thus defining the appropriate mechanisms. We propose a few hypotheses of interactions that could be tested in Table 1 (environmental linkages). The goal is for continued research to help disentangle the direct from indirect effects and to define what metrics of metabolism explain different elements of consumer biomass, production, or life histories. These metrics will build the base of the framework on current consumer dynamics and how dynamics may shift with anthropogenic influences (i.e., changes to the direct and indirect environmental control), such as climate change.

Synchrony between metabolic regimes and consumer ecology

The supply of energy and food is important for all organisms, and the timing of maximum and minimum resource availability act as potential agents of selection when looking at long temporal scales. Metabolic regimes could thus be important for current consumer dynamics and projected changes in the future, and can also be used to infer past conditions from current consumer life history traits.

Streams harbor a diversity of consumers that can be grouped by their feeding strategies (Cummins 1973). The concept of functional feeding groups, often applied to macroinvertebrate assemblages, uses behavioral mechanisms of food acquisition (e.g., way of feeding) and morphological characteristics (e.g., mouth parts) to distinguish consumers as shredders, collectors, grazers, predators, or scrapers (Cummins 1973). Another way consumers are often classified is more related to trophic levels and based on their food preference as either herbivorous, carnivorous, detritivorous, or omnivorous; these classifications are thus based on dietary preference for plants, animals, detritus, or any/all of those, respectively. Given these classifications, we propose that different consumers could experience stream metabolic regimes in different ways (Fig. 4), especially considering the "brown" and "green" stream food webs.

The temporal patterns of metabolic regimes in streams could explain consumer diversity and biomass, as different resources become available at different times and resource importance varies for each consumer type. For example, herbivores such as grazers or scrapers may have evolved life history traits that closely follow the variation and temporal patterns of instream primary production, while detritivores such as shredders evolved life history patterns that track the availability of allochthonous organic matter. If we imagine an example of a "brown" food web, such as a stream flowing through a deciduous temperate forest, light intensity and organic matter inputs peak at different times of the year (e.g., Walter Branch, Roberts et al. 2007). Here, GPP peaked in spring and early summer (May–June) and herbivores appeared to take advantage of this window of opportunity, leading to increases in their production and biomass. On the other hand, availability of allochthonous organic matter peaks in mid to late autumn and detritivores increased in biomass (Hall et al. 2000), suggesting higher consumer production during that time. A highly mobile consumer that can follow the resource or an omnivorous consumer could make use of whatever resource is currently peaking. These consumers may respond to both the "green" and "brown" food webs, or appear to be independent of the metabolic regime. Other consumers undergo ontogenetic shifts, where different life stages rely on different food resources and certain stages may track one food web type or the other. Evolutionary adaptation, in the form of consumer traits, can thus lead to both coupling and decoupling of metabolic regimes and consumer dynamics based on feeding strategy, life history stages, and mobility.

The selective force of metabolic regimes likely depends on both the regime itself and on the consumer, resulting in different evolutionary strategies to make use of energetic windows of opportunity and thus optimize the use of available resources. Metabolic regimes with short, predictable peaks in resources (Fig. 4, seasonal), such as primary production in spring before leaf-out or leaf litter fall in autumn, are likely to result in stronger selection than stochastic metabolic regimes, such as one might find in prairie streams. In such prairie streams, infrequent precipitation events scour algae but also entrain terrestrial organic matter during high flow, while the draw down that follows allows for high algal production (Dodds et al. 2014; Hall et al. 2015; Hosen et al. 2020). Thus, both the peaks of primary production and allochthonous organic matter provisions are tied to the unpredictable precipitation events (Fig. 4, episodic). A third metabolic regime can be described using spring streams, where environmental regimes are stable, with low intra-annual variation in flow and temperature, but resources are also few (Fig. 4, aseasonal). Thus, metabolic regimes are unlikely to lead to a strong selection of traits. We would expect that consumers evolved differently in response to the different metabolic regimes.

Regardless of the metabolic regime in question, consumer mobility will also play an important role. For example, in streams with predictable patterns, we would expect consumers with no or low mobility to be adapted to the metabolic regime of their native stream reach. On the other hand, a highly mobile or a migratory consumer can take advantage of the variation in metabolic regimes among reaches of the stream network, and the traits of the consumer may appear independent of the metabolic regimes of the stream reach currently occupied. Potamodromous fishes migrate hundreds of kilometers during their lifetimes, suggesting that their traits evolved to invest in movement and be independent of unpredictable metabolic regimes of a single stream reach (Barthem et al. 2017). Migratory consumers can serve as resources subsidies or ecosystem engineers, meaning they alter the stream environment through their presence as has been well documented for Pacific salmon (Holtgrieve and Schindler 2011; Rüegg et al. 2020). Thus, reciprocal interactions can evolve between consumers and metabolic regimes.

Metabolic regimes are not the only evolutionary force acting upon consumers. Environmental conditions such as physical regimes can enhance or counteract the influence of metabolic regimes. In fact, timing peak resource abundance in the form of GPP or allochthonous organic carbon may not always match with physiological optima, such as temperature, of consumers. Production rates of both consumers (Ratkowsky et al. 1982; White et al. 1991) and producers (Demars et al. 2016) in streams are correlated with temperature, likely due to temperature dependence of cellular processes such as respiration (Gillooly et al. 2002). For example, allochthonous resources often enter the stream due to a change in environmental conditions, such as the change in air temperature from summer to winter for deciduous leaf fall, which may also create a lag between the availability of the resource and the temperature needed for a detritivore to capitalize on said resource. As a result, a consumer's apparent adaptation to environmental conditions may have been mediated and driven by the metabolic regime. For the "green" food webs, that might mean that primary and secondary production evolved under similar environmental conditions, suggesting a tight evolutionary link among the stream environmental regimes, metabolic regimes, and consumer ecology.

The influence of environmental regimes on aquatic biota has been much studied, especially those of the hydrological and thermal regimes. To give just a few examples, hydrological regimes can structure aquatic communities (Poff and Allan 1995; Poff and Zimmerman 2010) and/or cue migrations (Cañas and Pine 2011), while thermal regimes can influence egg and juvenile development as well as insect emergence (Olden and Naiman 2010). However, as detailed information on metabolic regimes was missing until recently, its importance on freshwater consumers may have been underestimated. In fact, metabolic regimes may mediate the influence of hydrological and thermal regimes on aquatic food webs and, as a result, play an important role in structuring aquatic consumer communities, determining consumer production and biomass, and regulating consumer mobility traits. We thus make the case that studies on evolutionary adaptations of aquatic consumers should consider not only the direct effects of environmental regimes on consumers, but also effects of metabolic regimes and any indirect environmental effect mediated through the metabolic regimes (Fig. 2). Specifically, we propose to start with the hypotheses based on the ideas presented in this section (Table 1, communities). Incorporating energetic considerations into future studies will enhance our understanding of consumer life histories.

Applications

The multi-faceted framework proposed here, combining the increasing coverage of fine-temporal scale metabolic regimes with consumer data to better understand what controls consumer dynamics, could help inform responses to the management and conservation challenges facing streams of the Anthropocene. Freshwater ecosystems experience changes through increased flow regulation, eutrophication, and rising temperatures that can alter the timing, magnitude, and fate of stream metabolites (Arroita et al. 2018). Simultaneously, changes due to fisheries harvest, invasive species, or local species extinctions can cause shifts in the identity, abundance, and activity of consumers (Baxter et al. 2007). However, changes to the stream environment and changes to the consumers likely combine to affect the dynamics between metabolic regimes and consumer ecology, either independently, synergistically, or antagonistically.

The framework we have proposed applies to this very interface between ecosystem energetics and consumer ecology. For example, a system experiencing regulated flow may also allow for species to invade a novel "window of opportunity" and cause shifts in native consumer populations. To restore such a highly impacted system, one could apply the understanding of when and where energy supply limits consumer abundance and biomass to identify the most efficient plan of action; whether the system exhibits (de)coupling of metabolic regimes and consumer dynamics could inform priority given to interventions that affect direct or indirect pathways of environmental influences on consumers. Additionally, consumer traits such as feeding strategy or mobility may provide critical information on the environmental and metabolic regimes that should serve as references. We believe that management and restoration of stream ecosystems could benefit from closer attention to energetic regimes in addition to the thermal and hydrological regimes currently considered (e.g., environmental flows and dam mitigation, Olden and Naiman 2010).

Future directions

There is currently little information linking metabolic regimes to food webs. We argue that this lack of data has limited understanding of both biogeochemical fluxes and trophic interactions in fluvial networks. Metabolic regimes are an emergent property of food webs, but how GPP and ER are actually linked to more traditional food web ecology is unclear (but see Benke 2018). To determine the interplay between environment, metabolism and consumers, and how that interplay evolved, studies that explicitly jointly examine metabolic regimes and consumer production are essential. Some initial research questions are presented in the three sections above, such as whether GPP and ER can be used to predict consumer production at short times scales. A critical area of consideration is the question of metrics: what metabolic and consumer metrics can we use to explore the relationship between metabolism and consumer dynamics? And how do we compare consumer metrics such as repeated richness and abundance measures, measures of standing stocks, allometric equations of consumer biomass, isotopic tracing of energy

flow, or food webs viewed through time to metabolism estimates? Resolving the challenge of an integrative view of metabolic regimes and consumers will provide fundamental insights and new predictive models. Quantifying how and when fundamental food resources are transferred to higher trophic levels, by answering research questions related to the spatial and temporal scale, the underlying mechanisms, the plasticity of metabolic and consumer responses and feedbacks, will lead to a better understanding of controls on ecosystem energetics in streams. While there is still much work to be done, the union of consumer dynamics and ecosystem energetics opens up exciting opportunities for research with the potential to improve our ability to predict how food webs in streams will respond to various aspects of global change.

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