

**REVIEW**

# How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems?

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**Abstract**

1. Many freshwater systems receive substantial inputs of terrestrial organic matter. Terrestrially derived dissolved organic carbon (t-DOC) inputs can modify light availability, the spatial distribution of primary production, heat, and oxygen in aquatic systems, as well as inorganic nutrient bioavailability. It is also well-established that some terrestrial inputs (such as invertebrates and fruits) provide high-quality food resources for consumers in some systems.
2. In small to moderate-sized streams, leaf litter inputs average approximately three times greater than the autochthonous production. Conversely, in oligo/mesotrophic lakes algal production is typically five times greater than the available flux of allochthonous basal resources.
3. Terrestrial particulate organic carbon (t-POC) inputs to lakes and rivers are comprised of 80%–90% biochemically recalcitrant lignocellulose, which is highly resistant to enzymatic breakdown by animal consumers. Further, t-POC and heterotrophic bacteria lack essential biochemical compounds that are critical for rapid growth and reproduction in aquatic invertebrates and fishes. Several studies have directly shown that these resources have very low food quality for herbivorous zooplankton and benthic invertebrates.
4. Much of the nitrogen assimilated by stream consumers is probably of algal origin, even in systems where there appears to be a significant terrestrial carbon contribution. Amino acid stable isotope analyses for large river food webs indicate that most upper trophic level essential amino acids are derived from algae. Similarly,

profiles of essential fatty acids in consumers show a strong dependence on the algal food resources.

5. Primary production to respiration ratios are not a meaningful index to assess consumer allochthony because respiration represents an oxidised carbon flux that cannot be utilised by animal consumers. Rather, the relative importance of allochthonous subsidies for upper trophic level production should be addressed by considering the rates at which terrestrial and autochthonous resources are consumed and the growth efficiency supported by this food.
6. Ultimately, the biochemical composition of a particular basal resource, and not just its quantity or origin, determines how readily this material is incorporated into upper trophic level consumers. Because of its highly favourable biochemical composition and greater availability, we conclude that microalgal production supports most animal production in freshwater ecosystems.

#### KEYWORDS

allochthonous, autochthonous, biochemical composition, freshwater, resource utilisation

## 1 | INTRODUCTION

Ecologists have long been fascinated by interfaces and the exchange of materials across aquatic-terrestrial boundaries (Polis, Anderson & Holt, 1997; Summerhayes & Elton, 1923). The stream ecology community has classically considered the allochthonous inputs to be the key basal resource because of their quantitative dominance over in-stream primary production in low-order systems and larger, turbid, and heterotrophic rivers (Vannote, Minshall, Cummins, Sedell & Cushing, 1980). However, more recently there has been a shift in emphasis to the disproportionate importance of autotrophic producers to animal consumer production in streams and larger rivers (Brito, Moulton, De Souza & Bunn, 2006; Bunn, Davies & Winning, 2003; Hayden, McWilliam-Hughes & Cunjak, 2016; Jardine et al., 2015; Lau, Leung & Dudgeon, 2009a,b; Lewis, Hamilton, Rodríguez, Saunders & Lasi, 2001; Neres-Lima et al., 2016; Thorp & Bowes, 2017; Thorp & Delong, 2002). Conversely, lakes have classically been thought to be driven by autochthonous production (Carpenter, Kitchell & Hodgson, 1985), but recent studies have suggested that terrestrial carbon inputs support approximately 30%–70% of the zooplankton as well as zoobenthos and fish production (Berggren, Ziegler, St-Gelais, Beisner & del Giorgio, 2014; Berggren et al., 2010; Carpenter et al., 2005; Cole et al., 2006, 2011; Grey, Jones & Sleep, 2001; Jansson, Persson, De Roos, Jones & Tranvik, 2007; Karlsson, Jonsson, Meili & Jansson, 2003; Pace et al., 2004, 2007; Tanentzap et al., 2014). The following analysis explores these paradoxical viewpoints in the literature from the perspective of the mass fluxes of allochthonous and autochthonous carbon to and within aquatic systems, resource energetics and enzyme kinetics, and nutritional constraints on animal consumer growth and reproduction by examining the empirical evidence of allochthonous and autochthonous subsidies to animal consumers in lakes and rivers. This analysis will also address whether systems characterised by high terrestrial carbon

inputs are conducive to high rates of invertebrate and fish production.

## 2 | WHY DOES ALLOCHTHONY MATTER?

A better understanding of where and how allochthony modifies aquatic food web processes will improve our ability to predict how land-use and climate change affect organic carbon export from watersheds to lakes and rivers and how this matter influences upper trophic level production in aquatic systems. If invertebrate and fish consumers in rivers and lakes are strongly subsidised by allochthonous carbon inputs, then watersheds and especially riparian zone management will potentially have as much influence on lake and river food webs as nutrient inputs or within system processes.

Anthropogenic activities greatly modify watershed characteristics, which can affect the fluxes of nutrients and organic carbon to rivers and lakes (Dillon & Kirchner, 1975; Gergel, Turner & Kratz, 1999; Hopkinson & Vallino, 1995). For example, France, Culbert & Peters (1996) calculated t-DOC export to the nearshore of oligotrophic forest lakes was reduced by a factor of 40 following riparian deforestation. Conversely, Webster, Golladay, Benfield, D'Angelo & Peters (1990) reported that the loading of particulate organic matter to small streams increased somewhat, and the transport of this matter within streams increased greatly after logging. Watershed disturbance, such as forest fires and logging, can result in considerable additions of carbon and nutrients to streams (Skjyllberg, Westin, Meili & Björn, 2009) and lakes (Garcia & Carignan, 1999). Monteith et al. (2007) concluded that recent increases in surface water DOC concentrations in glaciated regions of North America and Europe are a soil-mediated response to reduced atmospheric sulphate loading and recovery from acidification. Conversely, Schindler et al. (1997) showed a combination of forest fires, experimental acidification and

especially drought had reduced watershed t-DOC export to Canadian boreal lakes. Lepistö, Futter, and Kortelainen (2014) stated that watershed DOC export was most closely related to seasonal and inter-annual variation in soil frost cycles, precipitation, runoff, and drought. It has also been shown that glacial melt because of the climate change in montane regions may be releasing stored t-DOC to aquatic ecosystems (Hood, Battin, Fellman, O'Neel & Spencer, 2015). Recent evidence from subalpine lakes of northern California suggests that elevation and resulting vegetation dominance may play an important role in governing the inputs of t-DOC into aquatic ecosystems (Piovia-Scott et al., 2016). These at times contradictory studies indicate it is unclear whether the export of terrestrial organic matter to aquatic ecosystems will increase or decrease in the future because of land-use and climate change, and this remains an important area for subsequent research.

### 3 | TERRESTRIAL CARBON INFLUENCES ON LAKE PROCESSES

It is well-established that the chemical properties and production in lakes are directly tied to terrestrial inputs. In fact, with the exception some aeolian inputs, virtually all inorganic constituents in lakes originate from watershed export. In a chronosequence of lakes formed by glacial retreat 10–10,000 years ago, Engstrom, Fritz, Almendinger, and Juggins (2000) found dramatic changes in lake water chemistry in response to natural soil weathering and successional changes in watershed vegetation. Watershed vegetation has also been shown to affect the balance between macro- and micro-nutrient limitation of phytoplankton (Goldman, 1960) and bacterial (Wehr, Petersen & Findlay, 1999) production in lakes.

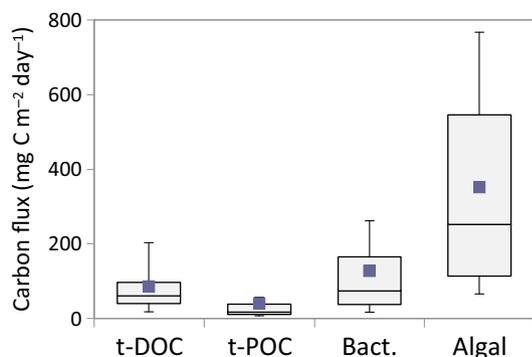
Terrestrial carbon inputs, and especially t-DOC, can influence the chemical and physical properties of lakes and rivers in a myriad of ways. For example, DOC dramatically affects the attenuation of visible and ultraviolet radiation (UVR) in surface waters, and also which photosynthetically active radiation (PAR) wavelengths are available at lake depth (Jones, 1992; Morris et al., 1995; Schindler et al., 1997; Von Einem & Granéli, 2010). As such, t-DOC affects where and how much primary production occurs (Jones, 1992; Karlsson, Byström, Ask, Persson & Jansson, 2009; Vadeboncoeur, Peterson, Vander Zanden & Kalff, 2008) and whether UVR will damage flora and fauna (Williamson & Rose, 2010). Similarly, t-DOC modifies heat retention, thermal stratification regimes, and oxygen availability within stratified water columns (Prairie, 2008; Schindler et al., 1997; Von Einem & Granéli, 2010). t-DOC also exerts strong control over the speciation and bioavailability of nutrients, in particular phosphorus (P) and to a lesser extent ammonium (Jones, 1992; Li & Brett, 2013; Steinberg et al., 2006), and it is common for much of the P within humic waters to be bound within only marginally bioavailable humic-iron complexes (Jones, Shaw & De Haan, 1993). Because of PAR attenuation and P sequestration, it is typical for high t-DOC lakes to have much less phytoplankton and benthic algal biomass and production than would be expected in clearwater lakes with

corresponding P concentrations (Jones, 1992; Karlsson et al., 2009; Thrane, Hessen & Andersen, 2014; Vadeboncoeur et al., 2008; Wehr, Holen, MacDonald & Lonergan, 1998).

For reasons that are not entirely clear, humic substances seem to inhibit the growth of some cyanobacteria (Steinberg et al., 2006) and certain chrysophyte species (Wehr et al., 1998), perhaps, because the humic matter sequesters iron. Conversely, cryptomonads are characteristically abundant in humic lakes (Klaveness, 1988), and it has been speculated that their ability to consume bacteria confers an advantage concerning both direct nutrient and energy uptake (Rothhaupt, 1996; Tranvik, Porter & Sieburth, 1989). The flagellated raphidophyte phytoplankton *Gonyostomum semen* (Vacuolariaceae) is also characteristic of high DOC lakes, especially in Scandinavia where in some lakes it comprises  $\approx 95\%$  of the total phytoplankton biomass (Johansson, Trigo, Vrede & Johnson, 2013). It has been hypothesised that *Gonyostomum* is favoured in humic lakes because it is particularly tolerant of low pH and weak light (Rengefors, Pålsson, Hansson & Heiberg, 2008). Having a mixotrophic feeding mode might also confer an advantage for *Gonyostomum* in light-limited systems relative to purely autotrophic algae (Berggren et al., 2010). However, because of its large size and defense system against grazing (e.g., expulsion of mucilaginous trichocysts), *Gonyostomum* is also not commonly consumed by metazoan zooplankton (Lebret, Fernandez, Hagman, Rengefors & Hansson, 2012; but see Johansson, Vrede, Lebret & Johnson, 2013).

### 4 | TERRESTRIAL ORGANIC MATTER LOADING TO LAKES

Much of the research suggesting allochthony as an important subsidy for animal consumers in lakes is based on the premise that terrestrial carbon inputs are often much larger than primary production in oligo/mesotrophic systems (Cole, Carpenter, Kitchell & Pace, 2002; Cole et al., 2011; France et al., 1996; Jansson et al., 2007; Prairie, 2008; Wetzel, 2001). Despite the centrality of this assumption, it is not borne out by mass flux data for lakes. Brett, Arhonditis, Chandra, and Kainz (2012) carried out a meta-analysis of studies that reported terrestrial carbon mass influx and algal primary production data for lakes with total phosphorus  $\leq 20 \mu\text{g/L}$  (Figure 1). This analysis showed that the median (interquartile range) terrestrial particulate organic carbon (t-POC), available dissolved organic carbon (t-DOC) inputs, and in-lake bacterial and algal production were 11 (8–17), 34 (11–78), 74 (37–165), and 253 (115–546)  $\text{mg carbon m}^{-2} \text{d}^{-1}$  respectively (Figure 1). These results indicate that autochthonous production is 4–7 times greater than the flux of terrestrial basal resources that is available to consumers in oligo/mesotrophic lakes (Brett et al., 2012). Lakes with high hydraulic flushing rates can also have very high loading of t-DOC. However, in lakes with the highest t-DOC inputs (i.e.,  $1000 \text{ mg C m}^{-2} \text{d}^{-1}$ ),  $\geq 98\%$  of the t-DOC flux is advected because t-DOC is processed at only approximately 0.1% per day (Brett et al., 2012; Hanson et al., 2011). Because of this very low-degradation rate constant, advection is the main fate of t-DOC in lakes with water retention times less than



**FIGURE 1** The mass influx of dissolved and particulate carbon from terrestrial sources and the in-lake production of bacteria and benthic/pelagic algae based on individual lake observations (Brett et al., 2012). Only algal production data from lakes with total phosphorus  $\leq 20$   $\mu\text{g/L}$  were used. Terrestrial particulate loading was calculated based on direct the aeolian transport data from Preston, Carpenter, Cole, and Pace (2008) while also assuming fluvial t-POC inputs are equal to 10% of t-DOC loading (Wetzel, 2001). Bacteria production was estimated from algal production based on a model derived from the data provided by Fouilland and Mostajir (2010). The mid-line in the box and whisker plots represents the sample median, the filled box represents mean, the outer margins represent the 25th and 75th percentiles and the whiskers represent the 10th and 90th percentiles. The sample sizes were  $n = 20, 8$  and  $58$ , respectively, for t-DOC, t-POC, and algal production mass fluxes [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

3 years (Brett et al., 2012; Hanson et al., 2011). Advected allochthonous organic matter cannot be used to support in-lake consumer production because of mass-balance constraints.

## 5 | TERRESTRIAL ORGANIC MATTER LOADING TO STREAMS

The special volume edited by Webster and Meyer (1997) reported 28 cases where leaf litter inputs and benthic primary production were simultaneously determined for different streams. These data indicated that the median leaf litter inputs and benthic algal production values were 454 (218–615) and 134 (63–514)  $\text{mg carbon m}^{-2} \text{d}^{-1}$ , respectively. Comparing within the systems, the median ratio of leaf litter inputs to algal production was 2.8 (0.6–7.8). Webster and Meyer (1997) also reported 13 cases where t-DOC loading to streams was quantified; these data had a median of 134 (94–634)  $\text{mg carbon m}^{-2} \text{d}^{-1}$ . Because t-DOC is metabolised very slowly and this fraction is advected in streams, these data suggest that particulate inputs will dominate the active terrestrial organic matter processing in streams.

## 6 | AUTOCHTHONY OR ALLOCHTHONY IN LOTIC ECOSYSTEMS

Conceptual theories on the relative importance of autochthonous and allochthonous carbon for animal production in lotic ecosystems are founded primarily on techniques for analysing gut contents and

feeding behaviour, and more recently, tracer techniques that track the incorporation of resources into tissue (e.g., bulk tissue, stable isotopes, and fatty acids). The dominant importance of algae in supporting animal production in areas where PAR reaches the stream bottom is almost universally acknowledged (e.g., arid zone streams – Minshall, 1978; Bunn, Balcombe, Davies, Fellows & McKenzie-Smith, 2006), but controversy continues over the primary carbon sources in forested headwaters and large turbid rivers. Terrestrial carbon from leaf litter has been thought to be the main carbon source in forested headwaters since at least publication of *The Stream And Its Valley* (Hynes, 1975) and development of the River Continuum Concept (or RCC: Vannote et al., 1980). This was primarily based on the observations of a substantial influx of leaf litter, reduced PAR for photosynthesis because of extensive riparia, a dearth of visible benthic algae, stream respiration much higher than production, and the dominance of shredding invertebrates and other detritivores. However, in one shaded headwater stream Mayer and Likens (1987) determined that algae represented more than half the food consumed by the caddisfly *Neophylax aniqua* (Trichoptera) and was responsible for 75% of its energy needs, even though the algal production was less than 2% of the total energy inputs. More recently, a survey of 70 streams and rivers, most forested, where isotopes had been measured in food webs found  $^{13}\text{C}$  values indicating algal diets in scraping grazers from very small shaded headwater streams (draining 0.2  $\text{km}^2$ ) down through middle-sized rivers (drainage areas of 4000  $\text{km}^2$ ) (Finlay, 2001). Other recent research has also challenged the RCC not only in low-latitude forest systems where sufficient PAR can stimulate benthic algal production (Brito et al., 2006; Davies, Bunn & Hamilton, 2008; Dudgeon, Cheung & Mantel, 2010; Lau et al., 2009a,b), but even in more temperate systems (e.g., Carroll, Thorp & Roach, 2016; Finlay, 2001; Hayden et al., 2016; Jonsson & Stenroth, 2016; McNeeley, Finlay & Power, 2007). Within the RCC model was the explicit assumption that at low-light levels, consumers would be limited by low algal production, and therefore, turn towards the lower quality but plentiful terrestrially derived resources. On the other hand, the flux of primary consumer production to predators and omnivores can be relatively high and imply top-down control of primary consumer populations (Hall, Likens & Malcom, 2001).

Wetzel (1995, 2001) suggested the metabolism of terrestrial origin particulate and especially dissolved organic matter by aquatic bacteria dominates both the material and energy fluxes of most aquatic ecosystems, especially small oligotrophic lakes and headwater streams. Many studies have also noted it is common for north temperature and boreal lakes to be net heterotrophic or have primary production to respiration (P/R) ratios  $<1$ , with the implication being this provides insights into whether the aquatic system being studied is on balance mainly supported by allochthony or autochthony (Odum, 1956; Vannote et al., 1980). Although the significance of low P/R ratios and/or net heterotrophy for upper trophic levels has been disputed (Rosenfeld & Mackay, 1987; Thorp & Delong, 2002), many of the papers in the zooplankton allochthony literature begin by emphasising the supposed importance of net heterotrophy for upper trophic levels (Berggren

et al., 2010; Grey et al., 2001; Jansson et al., 2007; Karlsson, 2007). What the "net heterotrophy" literature actually shows is that allochthonous carbon inputs play an important role in the influx and efflux of CO<sub>2</sub> in many lakes and streams (Duarte & Prairie, 2005). Understanding the role lakes play in the global carbon cycle is very important, but this research does not indicate the relative importance of allochthonous and autochthonous carbon subsidies for upper trophic levels. This latter question is addressed by considering the rates at which food of autochthonous and direct (t-POC inputs) or indirect (bacterial production supported by t-DOC) terrestrial origin are consumed and the growth efficiency with which this matter is used (Marcarelli, Baxter, Mineau & Hall, 2011; Rosenfeld & Mackay, 1987; Thorp & Delong, 2002). Furthermore, low P/R ratios are most commonly observed when apparent respiration is high, and high respiration indicates a high flux of organic matter being converted to CO<sub>2</sub> most probably via photochemical or bacterial degradation (Amon & Benner, 1996b; Cory, Ward, Crump & Kling, 2014). Since animals use reduced carbon this also represents an oxidised carbon flux that is not available to support upper trophic level production. The ratio of the bioavailable terrestrial and aquatic particulate organic matter fluxes is a more useful index of potential allochthonous subsidies to consumer production (Brett et al., 2012; Rosenfeld & Mackay, 1987). There are also potentially important methodological issues in the net heterotrophy literature (see Abril et al., 2015; Carignan, Planas & Vis, 2000) which need to be resolved before we have a clear understanding for the prevalence of this phenomenon in oligotrophic lakes and headwater streams.

Models of carbon sources for large rivers have focused either on the main channel (original RCC model), floodplains (Flood Pulse Concept, or FPC: Junk, Bayley & Sparks, 1989; and revision of the RCC by Sedell, Richey & Swanson, 1989), or the entire riverine landscape, especially the main and side channels of the riverscape (Riverine Productivity Model, or RPM: Thorp & Delong, 1994, 2002; and the Riverine Ecosystem Synthesis, or RES: Thorp, Thoms & Delong, 2006, 2008). Scientists supporting predictions of the RCC and FPC for large rivers could point to rates of downstream transport (rapid removal of algae from the system), the river's helical flow (continually taking phytoplankton into and out of the photic zone), the absence of PAR on the bottom across most of the river's width, and the high turbidities of many rivers. Consequently, Sedell et al. (1989) inferred that secondary production and system metabolism was principally supported by terrestrial carbon derived from upstream leakage of refractory carbon or lateral inputs from overland flow during flood and non-flood periods. Supporters of the RPM and RES argue instead that algal production in the main channel (e.g., Delong & Thorp, 2006), nearshore environments, and lateral slackwaters of the main and side channels provide sufficient labile carbon to support metazoan production during periods of maximum secondary production (e.g., Jardine et al., 2012a, 2012b; Thorp et al., 2006, 2008). Even in highly turbid lowland rivers, much of the consumer biomass, especially in higher trophic levels, is derived from algal sources (Bunn et al., 2003; Jardine et al., 2013; Power, 2001).

## 7 | TOOLS TO RESOLVE THIS DEBATE

Resolution of this nearly four-decade debate is hampered by a lack of detailed chemical analyses of carbon digestibility and by shortcomings in analytical techniques for tracking carbon sources, determining food chain length, and analysing community relationships (e.g., Layman, Arrington, Montaña & Post, 2007). From the biochemical perspective, however, our earlier conclusions for allochthonous carbon flowing into lakes should be directly applicable to allochthonous inputs to a river from headwaters to its terminus. From a sampling/analytical perspective, problems arise in determining source signatures, turnover rates and metabolic transformations within the consumer (e.g., effects of starvation: Bowes, Lafferty & Thorp, 2014) and among trophic levels (e.g., Bowes & Thorp, 2015) using standard techniques (see Jardine et al., 2014). Of these problems, determining source signatures is the most problematic, in part because scientists have until recently been limited to bulk tissue stable isotope techniques (the easiest, cheapest, and most widespread method) and fatty acid methods (good for specific source identification, but inappropriate for determining food chain length and other community metrics). The primary analytical problem in identifying primary food sources with bulk tissue techniques is reliably determining the  $\delta^{13}\text{C}$  autotrophic values of both terrestrial plants and algae. The values of both resources can vary substantially in time and space, especially for algae (Bowes & Thorp, 2015; Cloern, Canuel & Harris, 2002; Hadwen, Spears & Kennard, 2010). In an attempt to alleviate this problem, aquatic ecologists have often used isotopic values of herbivores, such as benthic bivalve molluscs or grazer macroinvertebrates (Finlay, 2001; Vander Zanden & Rasmussen, 1999). This is also problematic, however, because one needs to know: (1) what the mussel or other herbivore has been consuming and in what proportion (e.g., benthic or suspended algae and/or particulate organic matter of autochthonous or allochthonous origin); (2) from where within the river the food was primarily obtained (affecting the exact  $\delta^{13}\text{C}$  value); and (3) how the value changes as resources are conveyed through the food web under different physiological and environmental conditions.

Finlay and colleagues found that in streams with catchment areas <10 km<sup>2</sup> benthic algae had depleted <sup>13</sup>C values relative to terrestrial vegetation by 3‰–9‰, but for watershed surface areas ranging from 10 to 1,000 km<sup>2</sup> algal carbon isotope values varied widely and extensively overlapped with those for terrestrial C<sub>3</sub> plants (Finlay, 2001; Finlay, Power & Cabana, 1999). In relatively productive, unshaded, larger streams and rivers, the algae tend to incorporate dissolved atmospheric CO<sub>2</sub>, which has a  $\delta^{13}\text{C}$  value of about –8‰. Because of the relatively high demand for CO<sub>2</sub> in productive waters, algae discriminate relatively little towards the lighter isotope and thus incorporate a <sup>13</sup>C value which is enriched by about –15‰ to –23‰ relative to terrestrial C<sub>3</sub> plants (which have nearly constant  $\delta^{13}\text{C}$  values of approximately –28‰ from headwaters to downstream reaches of rivers, as expected given their well-mixed atmospheric source). Three factors conspire to reduce stable-isotope differences in small, shady, streams: (1) in less-productive shaded

streams algae may have an abundance of  $\text{CO}_2$  and thus fractionate more towards the lighter isotope, and become less enriched than the  $\delta^{13}\text{C}$  of terrestrial C3 plants; (2) the dissolved inorganic carbon in small shaded streams may derive in part from respired terrestrial organic matter and thus transfer this lighter isotopic value to the algae; (3) the epilithon may contain organic carbon derived from dissolved and fine particulate organic matter of terrestrial origin embedded within the matrix. Thus, studies of small streams may find that the values of periphyton and terrestrial material are not sufficiently different to be able to separate sources, whereupon they may abandon this approach (see Hall et al., 2001) or may simply not publish. Lack of publication of these findings creates a bias in the literature towards the cases in which stable isotopes provide a clear solution to the analysis of food sources. As previously noted, in meta-analyses of studies reporting the  $\delta^{13}\text{C}$  values of periphyton, Finlay (2001) and Ishikawa, Doi, and Finlay (2012) found a trend towards lighter values at a catchment size of approximately 0.2–10  $\text{km}^2$  and 75% canopy cover. This generally implies difficulty in discriminating algal and terrestrial resources in small, shaded streams, although in some studies, the algae can have a distinctly more depleted  $\delta^{13}\text{C}$  than the terrestrial material and hence provide the required discrimination between sources (e.g., Finlay, 2001; Rounick, Winterbourn & Lyon, 1982).

Another approach for overcoming the source discrimination problem is to sample over large spatial scales and correlate the  $\delta^{13}\text{C}$  (or  $\delta^{15}\text{N}$ ) of consumers with the source of interest (e.g., benthic algae; see Rasmussen, Trudeau & Morinville, 2009; Rasmussen, 2010; Jardine et al., 2012a, 2012b). In a meta-analysis of carbon and nitrogen isotope data from 92 sites across Australia and New Guinea, ranging from temperate forest streams to large arid zone rivers, Bunn, Leigh, and Jardine (2013) showed that 78% of the observed variation in consumer nitrogen isotopes was explained by variation in algal nitrogen isotopes and, importantly, the slope of this relationship was not different from 1. The close tracking of consumer and algal isotope values implies that most of the consumer nitrogen in these systems was derived from algae, and a similar relationship was found in data from 23 studies from North and South America, New Zealand, and Asia. The relationship for carbon isotopes was significant, but weaker (i.e., 48% of variability explained) and with a slope that was significantly less than 1, implying that other resources were also important (Bunn et al., 2013).

Even after one obtains a satisfactory signature from the aquatic herbivore, one would not have a reliable terrestrial signature for comparison because, first, the bulk tissue values of terrestrial plants also vary in space and time and the investigator would have to assume an equal mixture of organic carbon from various plant species and upstream locations; second, there are only a few, if any, aquatic primary consumers that assimilate only terrestrial resources and can truly represent a terrestrial end member. Empirical studies have shown that even obligate and facultative shredders (classified based on functional feeding) assimilate autochthonous algae in shaded streams (e.g., Hayden et al., 2016; Lau et al., 2009a,b; Li & Dudgeon, 2008), thus faunal representatives of terrestrial signature

are expected to be more scarce in wider river channels where light availability and primary production are greater.

A potential solution to this dilemma is through the use of a relatively new analytical technique: amino acid stable isotope analyses. This method has been employed in marine food web studies (e.g., Chikaraishi et al., 2009, 2014; McClelland & Montoya, 2002; McMahon, Thorrold, Houghton & Berumen, 2016; Nielsen, Popp & Winder, 2015; Popp et al., 2007), a stream field study (Ishikawa et al., 2014), a laboratory freshwater food web experiment (Bowes & Thorp, 2015), and several museum studies of freshwater piscivorous and invertivorous fishes collected from the Upper Mississippi and lower Ohio Rivers (Thorp & Bowes, 2017; Bowes, Thorp & Reuman, 2017). This technique links essential amino acids in the tissue of consumers with their ultimate autotrophic source because the consumers cannot synthesise essential amino acids. For example, the results of Thorp and Bowes (2017) demonstrated that on average, 60%–75% of the consumer amino acids were derived from algae in the rivers they studied.

Based on the biochemical analysis of terrestrial carbon in many studies and general conclusions from stable-isotope and fatty acid studies of mid-sized and large rivers, we contend that algae represent the primary carbon source supporting metazoan production during periods of somatic growth. The ultimate contributions of river algae during other seasons when animal growth is static or negative still needs to be resolved as does the contribution of algae to animal production in forested headwaters. However, even in these systems there exists clear evidence that algae are the main carbon source for herbivorous invertebrates (Finlay, 2001; Mayer & Likens, 1987; McNeeley et al., 2007). We also contend that algae represent the primary nitrogen source supporting metazoan production across a wide range of lotic and lentic systems.

## 8 | ENZYMATIC AND BIOCHEMICAL CONSTRAINTS ON THE UTILISATION OF TERRESTRIALLY DERIVED CARBON

The problem with using terrestrial derived carbon is not its energy content *per se*, but rather the accessibility of the energy contained within this material and the suitability of the biochemical composition of the resource for synthesis of new biomass in animals. Biological recalcitrance occurs because of the kinetic, not energetic content limitations. For example, a variety of terrestrial plants have average energy contents of  $19 \pm 1$  MJ/kg ( $\pm 1$  SD) (Friedl, Padouvas, Rotter & Varmuza, 2005), which is slightly higher than for proteins and carbohydrates (i.e., 17 MJ/kg), but considerably less than the average energy content of fats (38 MJ/kg) and alcohols (29 MJ/kg) (Blaxter, 1989). It is obvious that many synthetic organic compounds such as plastics have a high-energy content (20–46 MJ/kg) while also being almost entirely resistant to attack by biological enzymes. Similarly, cellulose has extremely low bioavailability to the large majority of insects (Martin, Jones & Bernays, 1991). True lignin digestion is thought to be restricted to a very small fraction of insects (Breznak

& Brune, 1994; Geib et al., 2008). This is important because we hypothesise that aquatic animal consumers will grow best when utilising diets that most closely match their own biochemical composition, or complement their endogenous capacity to modify and synthesise biochemicals.

Many bacteria are biochemical specialists and are equipped with specific enzymes that target particular molecular bonds. The structural carbon that dominates the tissues of many higher plants is present in large part as lignins and cellulose (Meyers & Ishiwatari, 1993). Lignocellulose degradation in terrestrial soil systems plays a central role in the global carbon budget, but currently the fundamental understanding of the degradation of these compounds is only rudimentary (Benner, Lay, K'nees & Hodson, 1988; Lynd, Weimer, van Zyl & Pretorius, 2002; Martínez et al., 2005). Cellulose is the most prevalent component of plant tissue comprising 35%–50% of dry weight, and is generally embedded in a biopolymer structural matrix including hemicelluloses (20%–35% of dry wt) and lignin (5%–30% of dry wt) (Lynd et al., 2002), with other biochemicals such as carbohydrates, lipids and proteins comprising a much smaller portion of plant tissues (Martínez et al., 2005). The lignocellulosic component of the plant undergoes self-assembly at the site of biosynthesis and is composed of randomly polymerised polyphenolics intertwined with hemicellulose, resulting in a hydrophobic crystalline or complex amorphous structure, which protects against biodegradation. Collectively, these physical properties of lignocellulose do not present well-defined enzymatic targets, making it difficult for enzymes to bind to susceptible sites and thereby conferring considerable resistance to microbial degradation (e.g., Moran & Hodson, 1989). These characteristics of higher plant structural material have been hypothesised to be an evolutionarily adaptive strategy to avoid attack by bacteria, fungi, and herbivorous animals (Coley, Bryant & Chapin, 1985; Rosenthal & Kotanen, 1994). By presenting a physical or enzymatic target with a random or tightly packed structure, the organism can prevent its consumers from refining an effective attack strategy. With the exception of termites (Ohkuma, 2003), very few animals are known to possess the requisite enzymes to metabolise the lignocellulosic biomass of terrestrial plants, and most of the degradation of lignocellulose in soils and aquatic systems is carried out by ascomycete fungi and various bacteria (Lynd et al., 2002; Simonis, Raja & Shearer, 2008).

White rot fungi are the best-known living organisms that specialise on using higher plant lignocellulose as their main substrate. They accomplish this feat by means of non-specific extracellular oxidative enzymes (oxidoreductases) such as lignin and manganese peroxidases (Tuomela, Vikman, Hatakka & Itävaara, 2000). The forms of terrestrial carbon that are not metabolised by bacteria and fungi within terrestrial soil systems are subsequently exported to streams and lakes. The aquatic realm is the recipient of the metabolic “leftovers” from the partial degradation of lignocellulose in the terrestrial system (Sutton & Sposito, 2005). High watershed t-DOC export is particularly associated with catchments with large wetland or saturated areas (Canham et al., 2004; Dillon & Molot, 1997; Rasmussen, Godbout & Schallenberg, 1989) and streams draining catchments with

well-drained soils typically have low t-DOC concentrations (Gergel et al., 1999). Because anoxic degradation (especially in lakes and wetlands) yields very little energy to microbes, with most energy channelled towards methanogenesis (Schink, 1997), the degradation of organic matter in saturated anoxic conditions is slow and often incomplete for less energetically favourable forms of terrestrial carbon.

Increased oxygen availability accelerates rates of lignin degradation by hydrogen peroxide, which is in turn derived from the metabolism of cellulose and hemicellulose in aerobic conditions (Sanchez, 2009). In the absence of oxygen, lignocellulose degradation to humic substances is much slower and less complete (Tuomela et al., 2000). In anoxic systems where methanogenesis prevails, optimal substrate metabolism generally requires syntrophic cooperation between two or more highly specialised bacteria species wherein the product of one species' metabolism is the resource for the other species (Schink, 1997). Optimal metabolic transfers between syntrophic bacteria occur when the cooperating species are in very close physical proximity, often as aggregates or flocs. However, this type of metabolic cooperation between bacteria species seems to be much less common in oxic environments (Schink, 1997).

Because of their complex and amorphous structure, humic and fulvic acids are, like their precursors, quite resistant to enzymatic hydrolysis. Therefore, they are most susceptible to generalised attacks by reactive oxygen species such as  $H_2O_2$  and UVR in natural systems (Amon & Benner, 1996b), and chlorine, ozone, and UVR in engineered systems (Matilainen & Sillanpää, 2010). For example, it is widely recognised that much of the degradation of complex t-DOC molecules in aquatic systems is a consequence of UVR-driven photooxidation (Cory et al., 2014), which in turn produces simpler molecules (e.g., formaldehyde, acetaldehyde, glyoxylate, and pyruvate) via cleavage of macromolecules into lower molecular weight compounds that can be more easily metabolised by bacteria (Lindell, Granéli & Tranvik, 1995; Vähätalo, Aarnos, Hoikkala & Lignell, 2011). Some research, however, suggests low molecular weight t-DOC is actually less bioavailable to microbial degradation because it is more diagenetically altered than most high molecular weight organic matter (Amon & Benner, 1996a; Tulonen, Salonen & Arvola, 1992).

The colonisation of decaying leaf litter by bacteria and fungi in smaller streams has been likened to peanut butter on crackers (e.g., Cummins, 1974), with the microbial biofilm converting detrital material into more labile and higher quality food sources for benthic invertebrates (Findlay, 2010). However, experimental studies suggest that microbial colonisation of decaying leaves does not lead to greater nutritional quality of leaf litter (because of very low quantities of  $\omega 3$  fatty acids), despite increases in bacterial and fungal fatty acids over time (Torres-Ruiz & Wehr, 2010). A recent feeding experiment showed that the presence of high-quality algae attached to leaf litter not only boosted the somatic growth of larvae of the shredding caddis (*Anisocentropus bicoloratus*; Trichoptera), but also increased the incorporation of low-quality leaf litter into stream food webs (Guo, Kainz, Valdez, Sheldon & Bunn, 2016a).

Although the shredders obtained most of their carbon by leaf consumption, they acquired and selectively retained their physiologically important fatty acids ( $\omega$ 3 PUFA) from high-quality algae. Likewise, results from manipulative feeding experiments in Lau, Goedkoop, and Vrede (2013) showed pre-conditioned leaf litter alone could not sustain the somatic growth of the isopod *Asellus aquaticus* (Isopoda), which is a common benthic generalist in boreal fresh waters. Supplying leaf litter and algae together, however, substantially enhanced somatic growth. This growth facilitation and the PUFA accumulation in *Asellus* were mediated by its seasonal physiological variation – *Asellus* optimised PUFA retention during the spring (i.e., the reproductive season) and somatic growth in the fall – yet in both seasons an algal diet was needed to satisfy its physiological requirements.

## 9 | TERRESTRIAL AND AUTOCHTHONOUS CARBON FLUXES TO AND WITHIN AQUATIC ECOSYSTEMS: OLIGO/MESOTROPHIC LAKES

Initially, it was concluded that the flux of terrestrial carbon to zooplankton via a t-DOC to bacteria pathway was very minor and only accounted for 1%–2% of zooplankton carbon (Cole et al., 2006). These authors concluded direct t-POC consumption was the main pathway by which terrestrial organic matter was routed to zooplankton with this pathway accounting for  $\approx$ 50% zooplankton carbon in unfertilised lakes (Cole et al., 2006). However, as noted by Brett, Kainz, Taipale, and Seshan (2009); and Brett et al. (2012), t-POC inputs to these lakes are <5% of algal primary production and because t-POC is a very low-quality resource compared with phytoplankton, it is unlikely that a small flux of low-quality resource could support  $\approx$ 50% of zooplankton production.

Cole et al. (2011) acknowledged that t-POC influxes were too low to support a large fraction of zooplankton production in their lakes. Instead these authors hypothesised that a microbially mediated t-DOC to bacteria pathway was the primary route by which zooplankton obtained terrestrial C (Cole et al., 2011). In a feeding experiment using t-DOC with algae, McMeans, Koussoroplis, Arts, and Kainz (2015) found higher somatic growth, but no viable egg reproduction in *Daphnia magna* exposed to high t-DOC concentration and attributed this growth response to the provision of bacteria rather than direct t-DOC utilisation. However, this pathway is contingent on t-DOC being the main resource for planktonic bacteria. The strong relationship between phytoplankton and bacteria production reported by Fouilland and Mostajir (2010) (i.e.,  $r^2 = .83$ ) and others (Bird & Kalff, 1984;  $r^2 = .88$ ) suggests otherwise. Because DOC releases from algal production average about 20%–30% of gross primary production (Cole, Likens & Strayer, 1982; Cole, Pace, Carpenter & Kitchell, 2000), the flux of algal-derived DOC will on average be similar (29–137 mg C m<sup>-2</sup> d<sup>-1</sup>) to the flux of t-DOC that is removed in oligo/mesotrophic lakes (37–165 mg C m<sup>-2</sup> d<sup>-1</sup>) (Brett et al., 2012). Furthermore, Kritzberg, Cole, Pace, Granéli, and Bade (2004); and Kritzberg, Cole, Pace, and Granéli

(2005) concluded heterotrophic bacteria preferentially utilise phytoplankton-derived DOC compared with t-DOC, and algal DOC resulted in higher bacterial growth efficiency. Several studies have also reported that bacteria production is not correlated with the standing pool of t-DOC in aquatic systems (Amon & Benner, 1996b; Carignan et al., 2000; Farjalla, Amado, Suhett & Meirelles-Pereira, 2009; Gudas, Bastviken, Premke, Steger & Tranvik, 2012; Kankaala, Bellido, Ojala, Tulonen & Jones, 2013; Karlsson, 2007). The potential importance of a t-DOC to bacteria to zooplankton pathway is also contravened by bacterial production only averaging approximately 30% of algal primary production in oligo/mesotrophic lakes (Fouilland & Mostajir, 2010). Finally, several authors have directly tested the food quality of heterotrophic bacteria for freshwater zooplankton. So far, all these studies have shown freshwater zooplankton cannot survive on diets solely comprise bacteria; and when zooplankton consume mixed bacteria and phytoplankton diets, they very preferentially utilise the algal fraction of their diets (Martin-Creuzburg, Beck & Freese, 2011; Taipale, Brett, Pulkkinen & Kainz, 2012; Taipale et al., 2014; Wenzel, Bergström, Jansson & Vrede, 2012b).

Methanogenesis and methanotrophy is another pathway by which terrestrial inputs might contribute to consumer production in aquatic food webs. Increasingly sophisticated stable isotope, and especially fatty acid biomarkers that are diagnostic for methane-oxidising bacteria, can be used to definitively establish methane contributions to consumer production (Deines, Bodelier & Eller, 2007; Jones & Grey, 2011; Kankaala et al., 2006; Taipale, Kankaala, Tirola & Jones, 2008; Taipale et al., 2012). However, these approaches do not establish the origin of the reduced carbon that originally supported methanogenesis. In a study of 207 Finnish boreal lakes, Juutinen et al. (2009) observed the greatest methane effluxes from shallow humic and nutrient-rich lakes. Deemer et al. (2016) recently showed water column chlorophyll *a* concentrations were the best predictor of methane effluxes from reservoirs. They also concluded that eutrophic reservoirs emitted an order of magnitude more methane than did oligotrophic reservoirs. Among 224 lakes from Quebec (Canada), Rasilo, Prairie, and del Giorgio (2015) found that methane effluxes were positively correlated with temperature and lake nutrient status, and negatively correlated with lake area and dissolved humic matter concentrations. West, Coloso, and Jones (2012) showed that additions of algae (i.e., *Scenedesmus*) (Scenedesmaceae) promoted substantially higher rates of CH<sub>4</sub> production than did equivalent additions of terrestrially derived organic matter (i.e., maple leaves) in laboratory experiments. Anoxia and high organic matter content promotes methanogenesis especially in the sediments of eutrophic lakes and reservoirs (Molongoski & Klug, 1980; Rudd & Hamilton, 1978). Hypolimnia with low oxygen or anoxia are also commonly encountered in small temperate and boreal humic lakes (Juutinen et al., 2009; Rinta et al., 2015). Methanotrophy predominately takes place at the interface zone between oxic and anoxic layers at the sediment surface or in the water column (Bastviken, Cole, Pace & Van de Bogert, 2008; Kankaala, Huotari, Peltonmaa, Saloranta & Ojala, 2006; Rudd & Hamilton, 1978; Schubert et al., 2010). Thus, CH<sub>4</sub> contributions have been shown to be significant especially for chironomids in the profundal zone of some

eutrophic lakes (Deines et al., 2007; Jones & Grey, 2011; Ravinet, Syväranta, Jones & Grey, 2010) and for pelagic cladocerans in seasonally stratified humic lakes (Kankaala et al., 2013; Taipale et al., 2008). Because methanogenesis is a less energetically favourable reaction concerning Gibbs free energy, we hypothesise that the most easily metabolised organic matter (e.g., algal and non-lignified littoral detritus) will preferentially support acetoclastic methane production, and thus methane-based food webs in freshwater ecosystems. Hydrogenotrophic methanogens can utilise carbon dioxide and hydrogen, both produced by fermenting and syntrophic bacteria during earlier steps of anaerobic organic matter decomposition (Conrad, 1999, 2005). In this pathway, the energy comes from the hydrogen because CO<sub>2</sub> does not contain usable energy. In nutrient-poor environments, the hydrogenotrophic pathway seems to be more important than acetoclastic methanogenesis (Casper, 1996; Galand, Yrjölä & Conrad, 2010). At present, the magnitude of methanogenic pathway from allochthonous organic and/or inorganic carbon to freshwater food webs is unknown.

## 10 | YOU ARE WHAT YOU EAT, AND YOU EAT WHAT YOU ARE

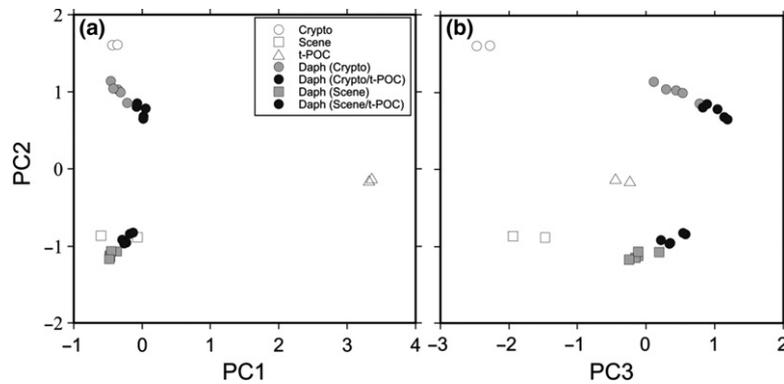
We hypothesise that organisms at the plant-animal interface preferentially consume and assimilate basal resources that best match their own biochemical composition, as well as their innate ability to synthesise structural molecules from dietary precursors. Considerable research also shows the lipid composition of herbivorous zooplankton is strongly influenced by their diets (Brett, Müller-Navarra, Ballantyne, Ravet & Goldman, 2006; Burns, Brett & Schallenberg, 2011; Galloway et al., 2015; Ravet, Brett & Arhonditsis, 2010; Taipale, Kainz & Brett, 2011, 2015) (Figure 2). In streams and larger rivers, caddis and mayfly larvae, amphipods, and snails similarly strongly reflect the fatty acid composition of their food (Gladyshev, Sushchik, Kalachova & Makhutova, 2012; Guo, Kainz, Sheldon & Bunn, 2016b; Larson et al., 2013; Lau et al., 2009a; Steinman, McIntire & Lowry, 1987; Torres-Ruiz, Wehr & Perrone, 2007, 2010). This link between the biochemical composition of the food and that of consumers is critical because terrestrially derived carbon has a profoundly different elemental and biochemical composition than does algae. Because of its very high proportion of lignocellulose, on a per carbon basis, the terrestrial carbon of higher plant origin is a poor carbon source for animal production. At the crudest stoichiometric level, terrestrial plant material is also nutritionally much more imbalanced than freshwater autotrophic matter relative to herbivorous invertebrate demands, with carbon to phosphorus and carbon to nitrogen ratios on average three times greater in terrestrial plants than aquatic autotrophs (Elser et al., 2000). This difference is a consequence of the previously mentioned prominence of carbon intensive structural molecules (i.e., approximately 90% cellulose, hemicelluloses, and lignin) in terrestrial plant tissues (Lynd et al., 2002). Variations in the nutrient stoichiometry and elemental imbalances of basal food sources also profoundly affect the excretion rates (and hence production efficiency) of certain

macroinvertebrates in streams, with greater retention of limiting nutrients (e.g., P) than would be predicted by a stoichiometric mass-balance model (Rothlisberger, Baker & Frost, 2008).

At a more detailed scale of biochemical resolution, terrestrial plants are devoid of the essential fatty acids upon which the nutritional physiology of zooplankton, benthic invertebrates, and especially fish production depends, such as eicosapentaenoic acid (EPA; 20:5 $\omega$ 3), docosahexaenoic acid (DHA; 22:6 $\omega$ 3), and arachidonic acid (ARA; 20:4 $\omega$ 6) (Brett & Müller-Navarra, 1997; Brett et al., 2009; Guo et al., 2016; Lau, Vrede, Pickova & Goedkoop, 2012; Lau et al., 2009a; Mayer & Likens, 1987; Sargent et al., 1999). The fatty acid composition of primary producers varies tremendously between terrestrial and aquatic basal resources and even within algal groups (Guschina & Harwood, 2006; Torres-Ruiz et al., 2007; Brett et al., 2009; Galloway & Winder, 2015; Guo, Kainz, Sheldon & Bunn, 2015; Hixson, Sharma, Kainz, Wacker & Arts, 2015). The short-chain  $\omega$ -3  $\alpha$ -linolenic acid ( $\alpha$ -LA; 18:3 $\omega$ 3) is commonly synthesised by distinct phytoplankton and benthic algal species including green algae and some cyanobacteria (Gugger et al., 2002; Taipale et al., 2013), but the long-chain  $\omega$ -3 PUFA, including EPA and DHA are only synthesised by certain algal taxa (e.g., cryptophytes, diatoms, dinoflagellates, golden algae, and raphidophytes; Ahlgren, Gustafsson & Boberg, 1992; Taipale et al., 2013), as well as some stream-dwelling moss species (Kalacheva, Sushchik, Gladyshev & Makhutova, 2009). Very few freshwater heterotrophic bacteria can synthesise  $\omega$ -3 PUFA in significant amounts, although interestingly a small number of marine bacteria species do synthesise these molecules (Russell & Nichols, 1999). Higher plants can synthesise  $\alpha$ -LA, but lack the enzymes necessary to elongate and desaturate this molecule to EPA and DHA (Guschina & Harwood, 2006), the physiologically active  $\omega$ -3 molecules in animals. Some animals can elongate and desaturate  $\alpha$ -LA to EPA and DHA, however, the conversion rate is low in many aquatic consumers (Koussoroplis, Nussbaumer, Arts, Guschina & Kainz, 2014; Murray, Hager, Tocher & Kainz, 2014). For example, this conversion is below 0.5% in herbivorous *Daphnia* (Taipale et al., 2011; Von Elert, 2002), and thus *Daphnia* require EPA directly from their diets. In addition to EPA and DHA, metazoan zooplankton require dietary sterols for optimal somatic growth and reproduction (Martin-Creuzburg & von Elert, 2009). The terrestrial organic carbon available to support aquatic production is almost entirely devoid of essential fatty acids and sterols (Brett et al., 2009; Taipale et al., 2014), regardless if this carbon is incorporated directly as t-POC or indirectly as t-DOC via a bacterial pathway. As terrestrial plant matter is processed by soil microbes, these elemental and biochemical imbalances are exacerbated. Furthermore, metazoans also require amino acids, vitamins, and other biomolecules for their somatic growth and reproduction for which t-POC is also a poor source.

## 11 | TERRESTRIAL RESOURCES CAN BE IMPORTANT PREY FOR FISH

It is well-established that terrestrial invertebrates (e.g., grasshoppers, ants, beetles and cicadas) are important prey for some fish species



**FIGURE 2** A principal components analysis of the fatty acid composition of terrestrial detritus (i.e., finely ground *Alnus rubra*; t-POC), phytoplankton (i.e., *Scenedesmus acutus* and *Cryptomonas ozolinii*), and *Daphnia* fed either pure or mixed diets of phytoplankton and t-POC (Taipale et al., 2015). Diet samples are the fatty acid profiles of *Alnus* (t-POC; black triangle), *Scenedesmus* (Scene; open square), or *Cryptomonas* (Crypto; open circle). Samples labeled “Daphnia” represent *Daphnia* fatty acid profiles after consuming *Scenedesmus* (grey square), *Cryptomonas* (grey circles), or mixed diets of *Alnus-Scenedesmus* (black squares) and *Alnus-Cryptomonas* (black/white circles). The first PC explained 21.7% of the variability and separated the *Alnus* from the phytoplankton diets and all *Daphnia*. This PC was strongly positively correlated with the SAFAs 14:0, 16:0, 20:0, 22:0 and 24:0. The second PC explained 53.8% of the variability and separated the two phytoplankton diets as well as *Daphnia* consuming these diets, and was positively correlated with LIN, 18:1 $\omega$ 9, and ALA, and negatively with SDA, eicosapentaenoic acid and docosahexaenoic acid. The third PC explained 12.0% of the variability and separated *Daphnia* from their diets. This PC was positively correlated with arachidonic acid

(especially salmonids and centrarcids) in small streams and the littoral regions of some lakes (Elliott, 1970; Francis & Schindler, 2009; Nakano & Murakami, 2001; Wipfli, 1997). This natural history knowledge has been familiar to most anglers for several centuries (Walton, 1653). It is also well-known that in New Zealand, Mongolia, and Alaska small rodents can be important prey for larger trout that facilitate rapid growth during years when rodent populations periodically erupt (Lisi, Bentley, Armstrong & Schindler, 2014; Wyatt, 2013) (Figure 3). Many tropical fishes consume the fruits of terrestrial vegetation and thereby play an important role in seed dispersal (Boujard, Sabatier, Rojasbeltran, Prevost & Renno, 1990; Correa, Winemiller, López-Fernández & Galetti, 2007). In all of these cases, fishes are consuming terrestrial resources with very low or no lignocellulose content and low C:N ratios. However, where riparian invertebrates are important for fish diets, it is also notable that it has been shown in some cases that the production of riparian invertebrates is strongly dependent on aquatic prey such as emergent insects (Power et al., 2004; Recalde, Postali & Romero, 2016; Stenroth, Polvi, Fältström & Jonsson, 2015). Bastow, Sabo, Finlay, and Power (2002) even showed that supposedly “terrestrial” invertebrates obtained approximately 90% of their carbon as well as most of their water from algal mats that were stranded along the river margin during the summer drought period.

## 12 | MARINE ALLOCHTHONY: THE EXCEPTION THAT PROVES THE RULE!

Because allochthonous means something transported from elsewhere into a particular system, technically riverine phytoplankton inputs to an estuary would be allochthonous, whereas primary production within the estuary by *Phragmites australis* (Poaceae) or *Spartina* spp. (Poaceae) would be autochthonous. However, from a

biochemical and nutritional perspective nearly all the important distinctions between allochthonous and autochthonous carbon subsidies relate to the differences between higher vascular plants and algae. Heterotrophic bacteria and cyanobacteria have other characteristics (such as a dearth of sterols and essential fatty acids) that place them into a third biochemical and low food quality category. As previously noted, terrestrial vascular plants have a high proportion of structural lignocellulose, high relative saturated fatty acid content, and no highly unsaturated C<sub>20</sub> or C<sub>22</sub> PUFA (Brett et al., 2009). Submerged vascular plants tend to have lower C:N:P ratios than emergent vascular plants (Demars & Edwards, 2007), probably because of a lesser need for structural lignocellulose, and are therefore probably somewhat more palatable (e.g., Elger & Willby, 2003; Jacobsen & Sand-Jensen, 1995). Conversely, all algae whether phytoplankton or periphyton have little structural carbon, and often-times high-essential fatty acid content (Brett & Müller-Navarra, 1997; Brett et al., 2009). It is probably biochemically irrelevant whether algal production in lakes is pelagic or benthic because, for example, benthic and pelagic diatoms are closely related and have similar nutritional value. From this biochemical perspective, riverine planktonic diatoms advected into an estuary would be expected to be high food quality for herbivorous invertebrates (De Moura, de Lucena Barbosa, Patrício, Nery & Gonçalves, 2016; Jassby & Cloern, 2000), whereas the autochthonous production by *Phragmites* or *Spartina* would be expected to be of very low in quality. A similar phenomenon has been observed in the Upper Mississippi, where consumers (bluegill sunfish, zebra mussels, pocketbook mussels) from the main channel (where diatoms predominated) had significantly higher long-chain PUFA content than the same species occupying backwater habitats, where detrital inputs and cyanobacteria were more prevalent (Larson et al., 2015). Therefore, the type of primary production (i.e., vascular plants or algae) is actually much



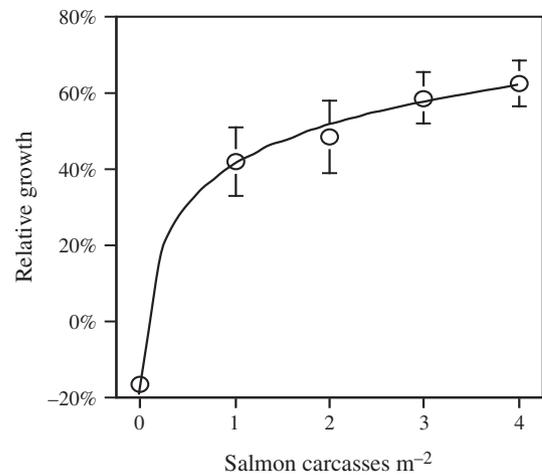
**FIGURE 3** An aquatic consumer (*Salmo trutta*) which has consumed a large mass of terrestrial resources (the house mouse *Mus musculus*). In New Zealand, mice populations often erupt when various trees (especially beech, *Nothofagus* spp.) have prolific seedfalls (Choquenot & Ruscoe, 2000). When these masting events occur, mice can become important prey for salmonid fish such as *S. trutta* and *Oncorhynchus mykiss*. Image taken by Steve Fox and used with permission

more important than whether this production is allochthonous or autochthonous.

To emphasise the point that the most salient difference between allochthonous and autochthonous subsidies to aquatic invertebrates is the biochemical composition of this material, consider the case of marine subsidies to salmonids in river systems in the north Pacific. The classic paradigm in these systems was that spawning Pacific salmon (*Oncorhynchus* spp.) support production within streams via an inorganic marine-derived nutrient pathway (Naiman, Bilby, Schindler & Helfield, 2002). However, as has long been known by anglers (Route, 1991) and recent research has shown (Naiman et al., 2002; Schindler et al., 2003; Wipfli, Hudson, Caouette & Chaloner, 2003), resident and juvenile anadromous salmonids are also directly supported by salmon eggs and flesh that have very high food quality. (Figure 4). In this case, the marine-derived carbon is clearly allochthonous to the salmon nursery streams, but outstanding fish growth rates are obtained (Denton, Rich & Quinn, 2009) because of the very high lipid and essential fatty acid content of this organic matter (Ravet et al., 2010; Sargent et al., 1999; Wipfli & Baxter, 2010). Ultimately, the growth of aquatic invertebrates and fish is predicated on the biochemical composition and nutritional value of their diets, and not the spatial origin of this matter.

### 13 | CATABOLIC AND ANABOLIC PARTITIONING OF BASAL RESOURCES

Karlsson (2007) presented the intriguing hypothesis that terrestrial carbon sources might be predominantly used to support catabolic metabolism, whereas algal-derived carbon is the primary support for anabolic production. According to this hypothesis, organisms utilising terrestrial carbon would obtain an energetic benefit from this resource, but this might leave almost no trace in their somatic lipid composition or stable-isotope ratios. This possibility presents



**FIGURE 4** The mean growth ( $\pm$ SE) of juvenile Coho salmon (*Oncorhynchus kisutch*) over 66 days when exposed to a gradient of salmon carcass additions. Adapted from Wipfli et al. (2003)

interesting challenges for field projects attempting to quantify terrestrial carbon subsidies to upper trophic levels. Brett et al. (2009) showed that when *Daphnia* were given diets composed of 50% high-quality phytoplankton and 50% low-quality t-POC, they obtained higher production rates than would have been expected had they only consumed half as much phytoplankton as used in the 100% phytoplankton treatment. When offered alone, this experiment showed t-POC resulted in a *Daphnia* growth efficiency of 5%, whereas pure phytoplankton diets resulted in growth efficiencies of approximately 40% (Brett et al., 2009). When offered a 50:50 t-POC and phytoplankton diet mixture the overall growth efficiency for the mixed diet was approximately 30%, which indicates the partial growth efficiency for the t-POC fraction of the diet was approximately 20%. This clearly suggests that when offered a mixed diet, the *Daphnia* did realise a benefit from the terrestrial carbon available to them. It also suggests that utilisation of low-quality terrestrial basal resources may be greatly enhanced by the simultaneous consumption of high food quality algae (Taipale et al., 2014). Wetzel (1995) hypothesised that allochthonous resources may function as a metabolic “lifeboat” by providing low-quality resources that allow consumers to survive during periods when more nutritious autochthonous resources are not available. Taipale et al. (2016a, 2016b) recently revealed that *Daphnia* utilise carbohydrates (glucose) from t-POC for energy and save essential fatty acids and amino acids for their somatic growth and reproduction, thus using a “sparing strategy” to maximise their somatic growth and reproduction under nutritional stress.

### 14 | ALLOCHTHONOUS INPUTS: SMALL FLUX AND LOW QUALITY

As previously noted, our analysis showed inputs of particulate terrestrial carbon and bacterial production are usually much smaller than the combined benthic and pelagic primary production in lakes (see Figure 1). Brett et al. (2009); Wenzel, Bergström, Jansson, and Vrede

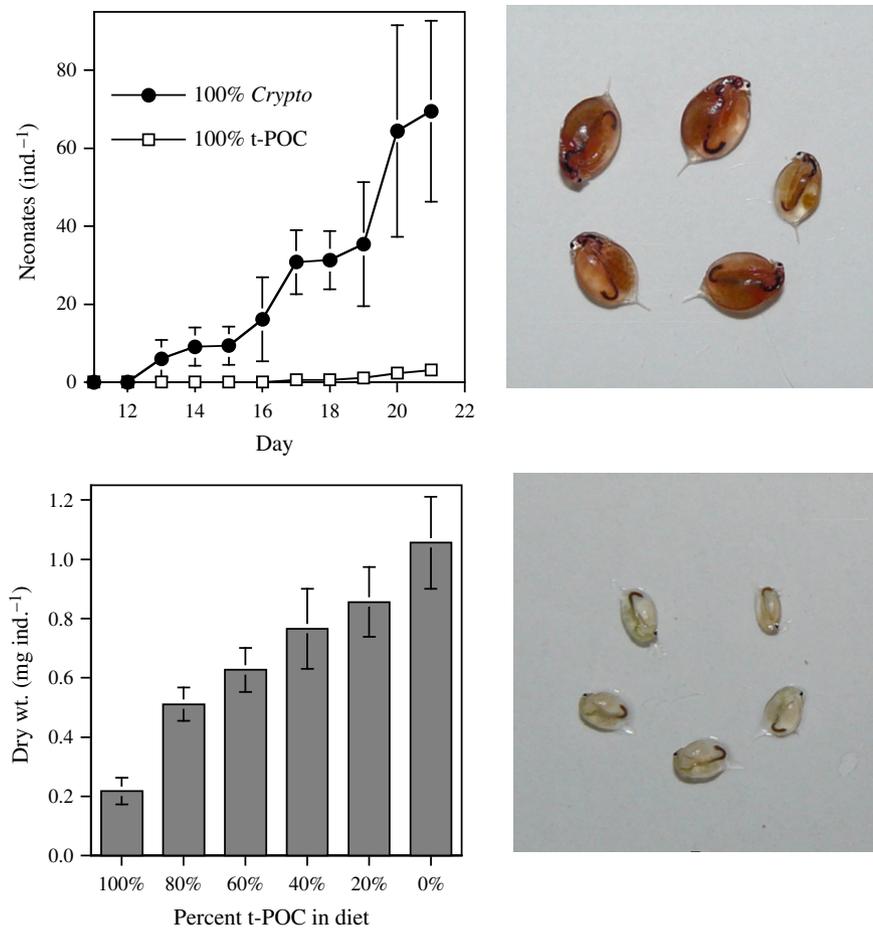
(2012a); and Taipale et al. (2014) also showed that t-POC is a much lower quality food resource for zooplankton growth and reproduction than many phytoplankton (although the food quality of cyanobacteria was similarly poor compared with the t-POC). So far, Brett et al. (2009) are the only authors to have successfully reared zooplankton through to reproduction on an exclusive diet of t-POC (Figure 5). When *Daphnia* were fed with finely ground fresh red alder (*Alnus rubra*) (Betulaceae) leaves for 22 days, they had >90% survival and produced an average of  $3.1 \pm 2.7$  ( $\pm$ SD) neonates each. These individuals also grew to an average dry weight of  $0.22 \pm 0.05$  mg/individual (Figure 5). In contrast, *Daphnia* from the same maternal cohort fed the alga *Cryptomonas ozolinii* (Cryptomonadaceae) had 100% survival, produced an average of  $69.5 \pm 23.2$  neonates/ind., and had an average DW of  $1.06 \pm 0.16$  mg/ind. by the same age (Figure 5). These results show fresh t-POC is a viable resource for aquatic herbivores, albeit a much lower quality one than nutrient-rich algae such as cryptophytes or diatoms. Similar results were observed with stream-dwelling benthic invertebrates, in which hydropsychid caddisfly larvae were fed with algae or autumn-shed leaves lost weight when switching from algal- to detritus-based diets (Torres-Ruiz et al., 2010). Similarly, shredder caddis larvae reached a smaller body size when fed on low-quality terrestrial leaf litter and their growth was substantially boosted as the availability of high-quality algae attached to leaf surfaces increased (Guo et al., 2016a). The benthic generalist isopod *Asellus aquaticus* also lost weight when solely fed leaf litter (growth =  $-0.017 \pm 0.001$  per day) similar to experimentally starved individuals (growth =  $-0.018 \pm 0.002$  per day) (Lau et al., 2013). Conversely, when *Asellus* was provided a mixed diet of algae and leaf litter its growth rate was greatly enhanced (growth =  $0.022 \pm 0.005$  per day).

The bacterial pathway to upper trophic level consumers entails two potentially large energetic penalties, i.e., low growth efficiency relative to algae if directly consumed by herbivores or additional trophic steps if utilised by protozoa prior to being consumed by zooplankton (Stockner & Porter, 1988). For example, Taipale et al. (2012) showed experimentally that all *Daphnia* fed only bacteria died before reproducing. However, Taipale et al. (2012) also showed *Daphnia* could tolerate bacteria-dominated diets, especially if mixed with very nutritious cryptophytes. These results suggest that bacteria are similarly poor nutritional quality as t-POC for herbivorous metazoan. For example, the fatty acid profiles of *Daphnia* experimentally fed t-POC derived from terrestrial leaves did not differ from animals that were experimentally starved (Galloway et al., 2014; Taipale et al., 2015). Similarly, when *Daphnia* were fed a 95% Actinobacteria and 5% cryptophyte dietary mixture, they had FA profiles that were much more similar to cryptophytes than Actinobacteria (Galloway et al., 2014). The median flux estimates from Figure 1 suggest t-POC, bacteria and algal carbon fluxes contribute  $\approx$ 5%,  $\approx$ 25% and  $\approx$ 70% of the particulate matter available for consumption by herbivorous zooplankton in lakes. If these flux estimates are corrected for the large differences in food quality (i.e., phytoplankton are a factor  $\approx$ 10 higher food quality than either t-POC or bacteria), then the median values presented in Figure 1 equate to t-POC plus processed t-DOC, bacteria and algae on

average supporting 1.7% (0.6%–4.9%), 2.9% (1.3%–5.6%), and 93.7% (87.7%–96.6%) of consumer production respectively.

## 15 | T-DOC SUPPRESSION OF UPPER TROPHIC LEVEL PRODUCTION

As has been previously noted, high-t-DOC concentrations in lakes may strongly suppress pelagic and benthic primary production (Jones, 1992; Karlsson et al., 2009; Vadeboncoeur et al., 2008), thereby increasing the relative availability of allochthonous energy sources. In oligotrophic clearwater lakes (DOC < 5 mg C L<sup>-1</sup>), nutrients (nitrogen and phosphorus) associated with a moderate increase in t-DOC concentration may slightly stimulate primary production and/or brown-coloured DOC may play a protective role in UV screening (Finstad, Helland, Ugedal, Hesthagen & Hessen, 2014; Seckell et al., 2015). However, because of PAR attenuation and phosphorus sequestration, it is typical for lakes with high t-DOC to have much less phytoplankton and benthic algal biomass and production than would be expected in clearwater lakes with similar phosphorus concentrations (Jones, 1992; Karlsson et al., 2009; Thrane et al., 2014; Vadeboncoeur et al., 2008). For example, del Giorgio and Peters (1994) reported strong inhibitory effects of DOC on phytoplankton photosynthesis and showed that excess carbon (DOC) was respired as CO<sub>2</sub> and therefore not available as reduced carbon for biomass production in higher trophic level consumers. Bacteria using t-DOC as their carbon source have generally poor growth efficiency (<10%) (e.g., del Giorgio & Cole, 1998; Eiler, Langenheder, Bertilsson & Tranvik, 2003; Räsänen, Kankaala, Akkanen, Tahvanainen & Saarnio, 2016) and additional steps within the microbial food web (heterotrophic nanoflagellates, ciliates) further increase respiratory losses. It was similarly demonstrated that primary production decreased with increasing DOC in oligotrophic lakes (Carpenter, Cole, Kitchell & Pace, 1998), suggesting that increasing DOC in aquatic ecosystems reduced light availability for primary production and consequently dietary energy for consumer production. This was supported by the results of Kelly, Solomon, Weidel, and Jones (2014) who found a negative relationship between t-DOC concentration and zooplankton biomass in ten temperate lakes within a DOC gradient of 5–25 mg C L<sup>-1</sup>. Similarly, Karlsson et al. (2015) found a negative correlation between DOC concentration (7–22 mg C L<sup>-1</sup>) and fish productivity in small boreal lakes, even though stable isotopes indicated t-DOC contributed to fish production. Rask et al. (2014) also reported that fish growth declined as lake t-DOC concentrations increased. Similar to this finding, Lau, Sundh, Vrede, Pickova, and Goedkoop (2014) also showed that consumer production and quality, measured as tissue PUFA concentrations, depended on the degree of autochthony in food chains of humic and oligotrophic lakes. Based on the very low food quality of t-POC and the low food quality and/or longer pathway for bacterial incorporation into upper trophic levels, it is probable that algal primary production will be the most important resource supporting upper trophic levels in most oligotrophic lakes.



**FIGURE 5** The growth and reproduction responses of *Daphnia magna* fed phytoplankton or finely ground terrestrial detritus (Brett et al., 2009). The upper left panel shows cumulative *Daphnia* neonate production when fed the phytoplankton *Cryptomonas ozolinii* or leaves of the riparian tree *Alnus rubra*. The lower left panel shows the size outcomes for *Daphnia* fed a gradient of *Alnus* and *Cryptomonas* for 14 days. The upper right panel shows 18 days old *Daphnia* that have exclusively consumed *Rhodomonas lacustris* (Cryptomonadaceae). The lower right panel shows 18 days old *Daphnia* that exclusively consumed a mixture of finely ground leaves from various riparian plants. The *Daphnia* in these panels were matched up from parallel maternal broods. The error bars in these plots represent  $\pm 1$  SD

Benthic algal production is strongly related to mean lake depth and water-clarity which can be greatly inhibited by high phytoplankton biomass because of eutrophication or as previously mentioned high t-DOC concentrations (Vadeboncoeur & Lodge, 2000; Vadeboncoeur et al., 2003). However, the role of t-DOC in suppressing total primary productivity may be complex. For example, Vesterinen, Devlin, Syväranta, and Jones (2016) observed that in a small lake with very high t-DOC (ca.  $30 \text{ mg C L}^{-1}$ ), and therefore, a shallow euphotic zone (<1 m) with very low-pelagic primary production, littoral algal primary production was relatively high and contributed to >90% to the overall summertime primary production.

## 16 | INTERPRETING STABLE ISOTOPE MIXING MODELS (SIMMS) – ASSUMPTIONS CAN BE VERY INFLUENTIAL

The most consistent evidence presented to suggest that terrestrial subsidies to aquatic consumers are strong, comes from the recent

outputs of Bayesian SIMMs. However, Bayesian SIMMs have several quirks that are currently poorly understood. For example, when the resource datasets considered in Bayesian SIMMs are highly variable or the models are mathematically under-determined, these analyses tend to produce outcomes that are strongly influenced by the prior generalist assumption (Brett, 2014b; Fry, 2013a,b). If a resource is included in a Bayesian SIMM, it will almost always be included in the solution at substantial levels even if it is of no real importance (Brett, 2014b; Fry, 2013a). Furthermore, fractionation-corrected consumers often fall well outside of the hypothesised resource polygons in this field literature (e.g., Berggren et al., 2014; Cole et al., 2011; Solomon et al., 2011; Tanentzap et al., 2014). These cases indicate there is a fundamental flaw in the dataset; for example, either an important food resource was left out of the analysis, or the wrong trophic enrichment factors were used for the consumer (see Bunn et al., 2013), or the correct foods with the wrong stable-isotope values were used in the analysis. Unfortunately, unlike conventional mass-balance analyses, current Bayesian SIMMs do not recognise obvious signs of a mis-specified model in their numerical outputs and these algorithms output a

result no matter how mismatched the underlying data are. To avoid these problems, scientists are encouraged to plot their data and make sure samples fall within the mixing polygons (Phillips et al., 2014), in addition to solely considering the numerical outputs from SIMMs.

One of the biggest challenges for these types of analyses is obtaining the estimates for the stable-isotope values of the phytoplankton component of zooplankton diets (Brett et al., 2014a). Because the phytoplankton are mixed with the detrital, bacterial, and protozoan components of the seston, it is rarely possible to obtain a direct estimate of phytoplankton stable-isotope values (but see Vuorio, Meili & Sarvala, 2006). A variety of methods have been employed to resolve this problem. For example, some authors estimate the  $\delta^{13}\text{C}$  value of the phytoplankton by assuming a “photosynthetic fractionation factor” ( $\epsilon_p$ ) to predict the  $\delta^{13}\text{C}$  value of the phytoplankton from directly determined  $\delta^{13}\text{C}$  values for the  $\text{CO}_2$  in the water (Brett et al., 2014a). Other studies have directly measured the  $\delta^{13}\text{C}$  values of large-sized phytoplankton, which can be separated from the seston using a variety of methods (Vuorio et al., 2006). A few studies (Berggren et al., 2014; Kankaala, Taipale, Li & Jones, 2010; Pace et al., 2007; Taipale et al., 2016a, 2016b) have estimated the  $\delta^{13}\text{C}$  value using algal-specific lipid biomarkers, especially PUFA. Other authors have simply assumed fixed  $\delta^{13}\text{C}$  values for the phytoplankton within the seston (Karlsson et al., 2012). Direct measurements  $\delta^{13}\text{C}$  values of phytoplankton (Grey, Jones & Sleep, 2000; Taipale et al., 2016a, 2016b; Vuorio et al., 2006; Zohary, Erez, Gophen, Berman-Frank & Stiller, 1994) have shown considerable variability ( $\pm 7\%$ ) in isotopic values between phytoplankton taxa, as well as within taxa between seasons and lakes. Using the stable isotope values of fatty acids that are characteristic for phytoplankton, Taipale et al. (2016a, 2016b) recently found the  $\delta^{13}\text{C}$  values of the dominant phytoplankton taxa could explain most of the variation in the  $\delta^{13}\text{C}$  values of the zooplankton in humic lakes.

## 17 | CONCLUSIONS

In a period of unprecedented global change from climate change, land-use alterations, and species invasions we should be asking, “Which basal resources are the most important to sustain the growth and reproduction of aquatic invertebrates and fish in aquatic ecosystems,” and “how might anthropogenic changes to temperature, nutrients, and light regimes change the supply of high-quality resources?” It is clear from the literature that aquatic systems that have the largest terrestrial inputs may also be the systems with the lowest rates of secondary production relative to basal carbon fluxes (Karlsson et al., 2015). This could occur because of the very low food quality of terrestrial carbon sources (Brett et al., 2009; Lau et al., 2013), as well as the fact that in some systems, large inputs of t-DOC actually inhibit pelagic and especially benthic algal production (Jones, 1992; Karlsson et al., 2009; Vadeboncoeur et al., 2008). The presence of a resource does not prove its importance. In fact, from a mass balance and kinetics perspective, a high standing stocking of a constituent (e.g., t-DOC) actually indicates that this constituent has low reactivity

and thus is unlikely to be an important resource for consumers (Brett et al., 2012). It is also entirely possible for the system to be net heterotrophic because of microbial respiration of terrestrial carbon and still have fish production strongly supported by an algae-invertebrate pathway (Lau et al., 2014; Thorp & Delong, 2002). Support of upper trophic level production by terrestrial carbon inputs may depend on the simultaneous availability of essential biomolecules synthesised by algae. Stream studies suggest that even when allochthonous inputs greatly dominate invertebrate and fish production is very preferentially supported by algal basal resources (Brito et al., 2006; Bunn et al., 2003; Lau et al., 2009a; Mayer & Likens, 1987). Lake studies suggest terrestrial carbon inputs generally have much lower mass fluxes and very low food quality, so the large majority of lake food webs are primarily supported by algal production. There is no doubt that in some systems, considerable amounts of terrestrially derived carbon are ingested and assimilated by herbivorous organisms; but because of the recalcitrant biochemical composition of this material, it is utilised a factor 5–10 less efficiently than algal basal resources. Not all carbon-based molecules are equally bioavailable, and specific biochemicals synthesised by particular primary producers may have an inordinate influence on the productivity of upper trophic levels. Fish production in particular may be highly dependent on specific basal producers that synthesise biochemically high-quality organic matter including large amounts of essential long carbon chain polyunsaturated fatty acids (Sargent et al., 1999). As we learn more about the nutritional underpinnings of consumer production in aquatic habitats, we can better predict how their communities will respond to environmental changes that influence the fluxes, quality, and composition of their terrestrial and aquatic food resources.

## 18 | FUTURE PERSPECTIVES

Both the lake and stream literature on reduced carbon influxes is characterised by small datasets. More field data for a much wide range of aquatic ecosystems will improve our understanding of when and where substantial terrestrial support of consumer production is plausible. Similarly, our current understanding of how land-use and climate change might affect the influx of terrestrial resources to aquatic systems and autochthonous production within these systems is only rudimentary. Much of what has been published on this topic is based on SIMMs that can be highly dependent on poorly constrained assumptions (e.g., the stable isotope values of phytoplankton, environmental water contributions to consumers, isotopic fractionation in consumers, missing isotopic data for protozoa, etc.). These types of analyses should be validated with direct evidence that the hypothesised scenarios are plausible from a nutritional perspective. Only a few studies have directly compared consumer growth and reproduction for algal, bacterial, and terrestrial organic matter dominated diets, and future studies could expand our understanding of what resources can actually support consumer production. Several studies have suggested that terrestrial and aquatic resources may support different aspects of consumer production

(i.e., catabolism and anabolism), and terrestrial resources might allow some consumers to survive periods when more nutritious resources are seasonally limited (i.e., the Wetzel lifeboat hypothesis). High-quality aquatic resources may also greatly enhance the ability of consumers to utilise much lower quality terrestrial resources. These are particularly interesting lines of inquiry for future research.

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