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

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SUMMARY

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 $\approx$ 3X greater than autochthonous production. Conversely, in oligo/mesotrophic lakes algal production is typically $\approx$ 5X greater than the available flux of allochthonous basal resources.
3. Terrestrial particulate organic matter (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 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 likely to be 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 algal food resources.
5. Primary production to respiration ratios are not a meaningful index to assess consumer allochthony because respiration represents an oxidized carbon flux that cannot be utilized 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 favorable biochemical composition and greater availability, we conclude that microalgal production supports most animal production in freshwater ecosystems.

Introduction

Ecologists have long been fascinated by interfaces and the exchange of materials across aquatic-terrestrial boundaries (Summerhayes & Elton, 1923; Polis *et al.*, 1997). The stream ecology community has classically considered 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, heterotrophic rivers (Vannote *et al.*, 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 (Lewis *et al.*, 2001; Thorp & Delong, 2002; Bunn *et al.*, 2003; Brito *et al.*, 2006; Lau *et al.*, 2009a,b; Jardine *et al.*, 2015; Hayden *et al.*, 2016; Neres-Lima *et al.*, 2016, Thorp & Bowes, 2017). Conversely, lakes have classically been thought to be driven by autochthonous production (Carpenter *et al.*, 1985), but recent studies have suggested terrestrial carbon inputs support $\approx$ 30-70% of zooplankton as well as zoobenthos and fish production (Grey *et al.*, 2001; Karlsson *et al.*, 2003; Pace *et al.*, 2004; Carpenter *et al.*, 2005; Cole *et al.*, 2006; Jansson *et al.*, 2007; Pace *et al.*, 2007; Berggren *et al.*, 2010; Cole *et al.*, 2011; Berggren *et al.*, 2014; 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 characterized by high terrestrial carbon inputs are conducive to high rates of invertebrate and fish production.

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 subsidized 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; Hopkinson & Vallino, 1995; Gergel *et al.*, 1999). For example, France *et al.* (1996) calculated t-DOC export to the nearshore of oligotrophic forest lakes was reduced by a factor of 40 following riparian deforestation. Conversely, Webster *et al.* (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 (Skyllberg *et al.*, 2009) and lakes (Garcia & Carignan, 1999). Monteith *et al.* (2007) concluded recent increases in surface water DOC concentrations in glaciated regions of North America and Europe are a soil-mediated response to reduced atmospheric sulfate loading and recovery from acidification. Conversely, Schindler *et al.* (1997) showed a combination of forest fires, experimental acidification and especially drought reduced watershed t-DOC export to Canadian boreal lakes. Lepistö *et al.* (2014) stated 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 due to climate change in montane regions may be releasing stored t-DOC to aquatic ecosystems (Hood et al. 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 due to land-use and climate change, and this remains an important area for subsequent research.

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 to 10,000 years ago, Engstrom *et al.* (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 *et al.*, 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, as well as which photosynthetically active radiation (PAR) wavelengths are available at 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; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009) 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 (Schindler *et al.*, 1997; Prairie, 2008; 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; Steinberg *et al.*, 2006; Li & Brett, 2013), and it is common for much of the P within humic waters to be bound within only marginally bioavailable humic-iron complexes (Jones *et al.*, 1993). Due to 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; Wehr *et al.*, 1998; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009; Thrane *et al.*, 2014).

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 in regards to both direct nutrient and energy uptake (Tranvik *et al.*, 1989; Rothhaupt, 1996). The flagellated raphidophyte phytoplankter *Gonyostomum semen* is also characteristic of high DOC lakes, especially in Scandinavia where in some lakes it comprises $\approx$ 95% of total phytoplankton biomass (Johansson *et al.*, 2013a). It has been hypothesized that *Gonyostomum* is favored in humic lakes because it is particularly tolerant of low pH and weak light (Rengefors *et al.*, 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, due to its large size and defense system against grazing (e.g., expulsion of mucilaginous trichocysts), *Gonyostomum* is also not commonly consumed by metazoan zooplankton (Lebret *et al.*, 2012; but see Johansson *et al.*, 2013b).

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

(France *et al.*, 1996; Wetzel, 2001; Cole *et al.*, 2002; Jansson *et al.*, 2007; Prairie, 2008; Cole *et al.*, 2011). Despite the centrality of this assumption, it is not borne out by mass flux data for lakes. Brett *et al.* (2012) carried out a meta-analysis of studies that reported terrestrial carbon mass influx and algal primary production data for lakes with total phosphorus $\leqslant$ 20 µg L^{-1} (Fig. 1). This analysis showed 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) mg carbon m^{-2} d^{-1}, respectively (Fig. 1). These results indicate autochthonous production is 4 to 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 mg C m^{-2} d^{-1}), $\geqslant$ 98% of the t-DOC flux is advected because t-DOC is processed at only $\approx$ 0.1% d^{-1} (Hanson *et al.*, 2011; Brett *et al.*, 2012). Because of this very low degradation rate constant, advection is the main fate of t-DOC in lakes with water retention times less than 3 years (Hanson *et al.*, 2011; Brett *et al.*, 2012). Advected allochthonous organic matter cannot be used to support in-lake consumer production due to mass balance constraints.

Terrestrial organic matter loading to streams

The special volume edited by Webster & Meyer (1997) reported 28 cases where leaf litter inputs and benthic primary production were simultaneously determined for different streams. These data indicated the median leaf litter inputs and benthic algal production values were 454 (218-615) and 134 (63-514) mg carbon m^{-2} d^{-1}, respectively. When compared within systems, the median ratio of leaf litter inputs to algal production was 2.8 (0.6-7.8). Webster & Meyer (1997) also reported 13 cases where t-DOC loading to streams was quantified; these data had a median of 134 (94-634) mg carbon m^{-2} d^{-1}. Because t-DOC is metabolized 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.

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 analyzing gut contents and feeding behavior, 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 *et al.*, 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 observations of a substantial influx of leaf litter, reduced PAR for photosynthesis due to 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 & Likens (1987) determined that algae represented more than half the food consumed by the caddisfly *Neophylax aniqua* and was responsible for 75% of its energy needs, even though algal production was < 2% of total energy inputs. More recently, a survey of 70 streams and rivers, most forested, where isotopes had been measured in food webs found ^{13}C values indicating algal diets in scraping grazers from very small shaded headwater streams (draining 0.2 km^2) down through middle-sized rivers (drainage areas of 4000 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 *et al.*, 2008; Lau *et al.*, 2009a,b; Dudgeon *et al.*, 2010), but even in more temperate systems (e.g., Finlay, 2001; McNeeley *et al.*, 2007; Carroll *et al.*, 2016; Hayden *et al.*, 2016; Jonsson & Stenroth, 2016). 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 *et al.*, 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 emphasizing the supposed importance of net heterotrophy for upper trophic levels (Grey *et al.*, 2001; Jansson *et al.*, 2007; Karlsson, 2007; Berggren *et al.*, 2010). What the "net heterotrophy" literature actually shows is that allochthonous carbon inputs play an important role in the influx and efflux of CO_2 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 (Rosenfeld & Mackay, 1987; Thorp & Delong, 2002; Marcarelli *et al.*, 2011). 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_2 most likely via photochemical or bacterial degradation (Amon & Benner, 1996b; Cory *et al.*, 2014). Since animals use reduced carbon this also represents an oxidized 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 (Rosenfeld & Mackay, 1987; Brett *et al.*, 2012). There are also potentially important methodological issues in the net heterotrophy literature (see Carignan *et al.*, 2000; Abril *et al.*, 2015) 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 *et al.*, 1989; and revision of the RCC by Sedell *et al.*, 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 *et al.*, 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., Thorp *et al.*, 2006, 2008; Jardine *et al.*, 2012). Even in highly turbid lowland rivers, much of the consumer biomass, especially in higher trophic levels, is derived from algal sources (Power, 2001; Bunn *et al.*, 2003; Jardine *et al.*, 2013).

Tools to resolve this debate

Resolution of this nearly four-decade debate is hampered by a lack of detailed chemical analysis of carbon digestibility and by shortcomings in analytical techniques for tracking carbon sources, determining food chain length, and analyzing community relationships (e.g., Layman *et al.*, 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 *et al.*, 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 δ^{13}C autotrophic values of both terrestrial plants and algae. The values of both resources can vary substantially in time and space, especially for algae (Cloern *et al.*, 2002; Hadwen *et al.*, 2010; Bowes & Thorp, 2015). In an attempt to alleviate this problem, aquatic ecologists have often used isotopic values of herbivores, such as benthic bivalve molluscs or grazer macroinvertebrates (Vander Zanden & Rasmussen, 1999; Finlay, 2001). This is also problematic, however, because one needs to know: (a) 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); (b) from where within the river the food was primarily obtained (affecting the exact δ^{13}C value); and (c) 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^2 benthic algae had depleted ^{13}C values relative to terrestrial vegetation by 3 to 9‰, but for watershed surface areas ranging from 10 to 1,000 km^2 algal carbon isotope values varied widely and extensively overlapped with those for terrestrial C3 plants (Finlay *et al.*, 1999; Finlay, 2001). In relatively productive, unshaded, larger streams and rivers, the algae tend to incorporate dissolved atmospheric CO_2, which has a $\delta^{13}C$ value of about -8‰. Because of the relatively high demand for CO_2 in productive waters, algae discriminate relatively little towards the lighter isotope and thus incorporate a ^{13}C value which is enriched by about -15 to -23‰ relative to terrestrial C3 plants (which have nearly constant $\delta^{13}C$ values of $\approx$ -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 the less-productive shaded stream algae may have an abundance of CO_2 and thus fractionate more towards the lighter isotope, and become less enriched than the $\delta^{13}C$ 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 $\delta^{13}C$ values of periphyton, Finlay (2001) and Ishikawa *et al.* (2012) found a trend towards lighter values at a catchment size of approximately 0.2-10 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 $\delta^{13}C$ than the terrestrial material and hence provide the required discrimination between sources (e.g., Rounick *et al.*, 1982; Finlay, 2001).

Another approach for overcoming the source discrimination problem is to sample over large spatial scales and correlate the $\delta^{13}C$ (or $\delta^{15}N$) of consumers with the source of interest (e.g., benthic algae; see Rasmussen *et al.*, 2009; Rasmussen, 2010; Jardine *et al.*, 2012). 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 *et al.* (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 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., Li & Dudgeon, 2008; Lau *et al.*, 2009a,b; Hayden *et al.*, 2016), thus faunal representatives of terrestrial signature are expected to be more scarce in wider river channels where light availability and primary production are greater.

Another 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., McClelland & Montoya, 2002; Popp *et al.*, 2007; Chikaraishi *et al.*, 2009, 2014; Nielsen *et al.*, 2015; McMahon *et al.*, 2016), 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 *et al.*, in press). This technique links essential amino acids in the tissue of consumers with their ultimate autotrophic source because the consumers cannot synthesize essential amino acids. For example, the results of Thorp & 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 is clear evidence that algae are the main carbon source for herbivorous invertebrates (Mayer & Likens, 1987; Finlay, 2001; 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.

Enzymatic and biochemical constraints on the utilization 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 is due to kinetic, not energetic content limitations. For example, a variety of terrestrial plants have average energy contents of 19 ± 1 MJ kg^{-1} (± 1 SD) (Friedl *et al.*, 2005), which is slightly higher than for proteins and carbohydrates (i.e., 17 MJ kg^{-1}), but considerably less than the average energy content of fats (38 MJ kg^{-1}) and alcohols (29 MJ kg^{-1}) (Blaxter, 1989). It is obvious that many synthetic organic compounds such as plastics have a high-energy content (20-46 MJ kg^{-1}) while also being almost entirely resistant to attack by biological enzymes. Similarly, cellulose has extremely low bioavailability to the large majority of insects (Martin *et al.*, 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 hypothesize that aquatic animal consumers will grow best when utilizing diets that most closely match their own biochemical composition, or complement their endogenous capacity to modify and synthesize 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 comprised in large part of 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 *et al.*, 1988; Lynd *et al.*, 2002; Martinez *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 (Martinez *et al.*, 2005). The lignocellulosic component of the plant undergoes self-assembly at the site of biosynthesis and is composed of randomly polymerized 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 hypothesized to be an evolutionarily adaptive strategy to avoid attack by bacteria, fungi and herbivorous animals (Coley *et al.*, 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 metabolize 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 *et al.*, 2008).

White rot fungi are the best-known living organisms that specialize on using higher plant lignocellulose as their main substrate. They accomplish this feat by means of nonspecific extracellular oxidative enzymes (oxidoreductases) such as lignin and manganese peroxidases (Tuomela *et al.*, 2000). The forms of terrestrial carbon that are not metabolized 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 (Rasmussen *et al.*, 1989; Dillon & Molot, 1997; Canham *et al.*, 2004) 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 channeled towards methanogenesis (Schink, 1997), the degradation of organic matter in saturated anoxic conditions is slow and often incomplete for less energetically favorable 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 specialized 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 generalized attacks by reactive oxygen species such as H_2O_2 and ultraviolet radiation (UVR) in natural systems (Amon & Benner, 1996b), and chlorine, ozone, and UVR in engineered systems (Matilainen & Sillanpää, 2010). For example, it is widely recognized 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 metabolized by bacteria (Lindell *et al.*, 1995; Vähätalo *et al.*, 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 (Tulonen *et al.*, 1992; Amon & Benner, 1996a).

The colonization 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 colonization of decaying leaves does not lead to greater nutritional quality of leaf litter (due to 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*), but also increased the incorporation of low quality leaf litter into stream food webs (Guo *et al.*, 2016a). Although the shredders obtained most of their carbon by leaf consumption, they acquired and selectively retained their physiologically important fatty acids (ω3 PUFA) from high quality algae. Likewise, results from manipulative feeding experiments in Lau *et al.* (2013) showed pre-conditioned leaf litter alone could not sustain the somatic growth of the isopod *Asellus aquaticus*, which is a common benthic generalist in boreal freshwaters. 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* optimized 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.

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 unfertilized lakes (Cole *et al.*, 2006). However, as noted by Brett *et al.* (2009, 2012), t-POC inputs to these lakes are < 5% of algal primary production and because t-POC is a very low quality resource compared to 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 hypothesized 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 *et al.* (2015) found higher somatic growth, but no viable egg reproduction in *Daphnia magna* exposed to high t-DOC and attributed this growth response to the provision of bacteria rather than direct t-DOC utilization. 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 & Mostajir (2010) (i.e., $r^2 = 0.83$) and others (Bird & Kalff, 1984; $r^2 = 0.88$) suggests otherwise. Because DOC releases from algal production average about 20-30% of gross primary production (Cole *et al.*, 1982; Cole *et al.*, 2000), the flux of algal derived DOC will on average be similar (29-137 mg C m^{-2} d^{-1}) to the flux of t-DOC that is removed in oligo/mesotrophic lakes (37-165 mg C m^{-2} d^{-1}) (Brett *et al.*, 2012). Furthermore, Kritzberg *et al.* (2004, 2005) concluded heterotrophic bacteria preferentially utilize phytoplankton-derived DOC compared to 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; Karlsson, 2007; Farjalla *et al.*, 2009; Gudasz *et al.*, 2012; Kankaala *et al.*, 2013). The potential importance of a t-DOC to bacteria to zooplankton pathway is also contravened by bacterial production only averaging $\approx$ 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 comprised of bacteria; and when zooplankton consume mixed bacteria and phytoplankton diets, they very preferentially utilize the algal fraction of their diets (Martin-Creuzburg *et al.*, 2011; Taipale *et al.*, 2012; Wenzel *et al.*, 2012b; Taipale *et al.*, 2014).

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 oxidizing bacteria, can be used to definitively establish methane contributions to consumer production (Kankaala *et al.,* 2006b;

Deines *et al.*, 2007; Taipale *et al.*, 2008; 2012; Jones & Grey, 2011). 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 nutrient rich and humic 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 *et al.* (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 *et al.* (2012) showed that additions of algae (i.e., *Scenedesmus*) promoted substantially higher rates of CH_4 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 (Rudd & Hamilton, 1978; Molongoski & Klug, 1980). 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 (Rudd & Hamilton, 1978; Kankaala *et al.,* 2006a; Bastviken *et al.,* 2008; Schubert *et al.,* 2010). Thus, CH_4 contributions have been shown to be significant especially for chironomids in the profundal zone of some eutrophic lakes (Deines *et al.*, 2007; Ravinet *et al.,* 2010; Jones & Grey, 2011) and for pelagic cladocerans in seasonally stratified humic lakes (Taipale *et al.,* 2008; Kankaala *et al.*, 2013). Because methanogenesis is a less energetically favorable reaction in regards to Gibbs free energy, we hypothesize that the most easily metabolized 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. Hydrogenothrophic methanogens can utilize 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_2 does not contain usable energy. In nutrient poor environments the hydrogenothrophic pathway seems to be more important than acetoclastic methanogenesis (Casper, 1996; Galand *et al.*, 2010). At present the magnitude of methanogenic pathway from allochthonous organic and/or inorganic carbon to freshwater food webs is unknown.

You are what you eat, and you eat what you are

We hypothesize 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 synthesize structural molecules from dietary precursors. Considerable research also shows the lipid composition of herbivorous zooplankton is strongly influenced by their diets (Brett *et al.*, 2006; Ravet *et al.*, 2010; Burns *et al.*, 2011; Taipale *et al.*, 2011; Galloway *et al.*, 2015; Taipale *et al.*, 2015) (Fig. 2). In streams and larger rivers, caddis and mayfly larvae, amphipods, and snails similarly strongly reflect the fatty acid composition of their food (Steinman *et al.*, 1987; Torres-Ruiz *et al.*, 2007, 2010; Lau *et al.*, 2009a; Gladyshev *et al.*, 2012; Larson *et al.*, 2013; Guo *et al.*, 2016b). 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., $\approx$ 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 *et al.*, 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; 20:5ω3), docosahexaenoic acid (DHA; 22:6ω3), and arachidonic acid (ARA, 20:4ω6) (Mayer & Likens, 1987; Brett & Müller-Navarra, 1997; Sargent *et al.*, 1999; Brett *et al.*, 2009; Lau *et al.*, 2009a, 2012; Guo *et al.*, 2016c). 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 *et al.*, 2015; Hixson *et al.*, 2015). The short-chain ω-3 α-linolenic acid (α-LA; 18:3ω3) is commonly synthesized by distinct phytoplankton and benthic algal species including green algae and some cyanobacteria (Gugger *et al.*, 2002; Taipale *et al.*, 2016), but the long-chain ω-3 PUFA, including EPA and DHA are only synthesized by certain algal taxa (e.g., cryptophytes, diatoms, dinoflagellates, golden algae and raphidophytes; Ahlgren *et al.*, 1992; Taipale *et al.*, 2013, 2016), as well as some stream-dwelling moss species (Kalacheva *et al.*, 2009). Very few freshwater heterotrophic bacteria can synthesize ω-3 PUFA in significant amounts, although interestingly a small number of marine bacteria species do synthesize these molecules (Russell & Nichols, 1999). Higher plants can synthesize α-LA, but lack the enzymes necessary to elongate and desaturate this molecule to EPA and DHA (Guschina & Harwood, 2006), the physiologically active ω-3 molecules in animals. Some animals can elongate and desaturate α-LA to EPA and DHA, however, the conversion rate is low in many aquatic consumers (Koussoroplis *et al.*, 2014; Murray *et al*., 2014). For example, conversion is below 0.5% in herbivorous *Daphnia* (von Elert, 2002; Taipale *et al.*, 2011), 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 somatic growth and reproduction for which t-POC is also a poor source.

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 (especially salmonids and centracids) in small streams and the littoral regions of some lakes (Elliot, 1970; Wipfli, 1997; Nakano & Murakami, 2001; Francis & Schindler, 2009). 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 grow during years when rodent populations periodically erupt (Wyatt, 2013; Lisi *et al.*, 2014) (Fig. 3). Many tropical fish consume the fruits of terrestrial vegetation and thereby play an important role in seed dispersal (Boujard *et al.*, 1990; Correa *et al.*, 2007). In all of these cases, fish 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; Stenroth *et al.*, 2015; Recalde *et al.*, 2016). Bastow *et al.* (2002) even showed that supposedly “terrestrial” invertebrates obtained $\approx$ 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.

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* or *Spartina* spp. 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_{20} or C_{22} PUFA (Brett *et al.*, 2009). Submerged vascular plants tend to have lower C:N:P ratios than emergent vascular plants (Demars & Edwards, 2007), probably due to a lesser need for structural lignocellulose, and are therefore probably somewhat more palatable (e.g., Jacobsen & Sand-Jensen, 1994; Elger & Willby, 2003). Conversely, all algae whether phytoplankton or periphyton have little structural carbon, and oftentimes 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 (Jassby & Cloern, 2000; de Moura *et al.*, 2016), whereas the autochthonous production by *Phragmites* or *Spartina* would be expected to be very low 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 more important than whether this production is allochthonous or autochthonous.

To emphasize 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 *et al.*, 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 *et al.*, 2003), resident and juvenile anadromous salmoninds are also directly supported by very high food quality salmon eggs and flesh (Fig. 4). In this case, the marine derived carbon is clearly allochthonous to the salmon nursery streams, but outstanding fish growth rates are obtained (Denton *et al.*, 2009) due to the very high lipid and essential fatty acid content of this organic matter (Sargent *et al.*, 1999; Ravet *et al.*, 2010; 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.

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 utilizing 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 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 comprised 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 $\approx$ 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 $\approx$ 30%, which indicates the partial growth efficiency for the t-POC fraction of the diet was $\approx$ 20%. This clearly suggests that when offered a mixed diet, the *Daphnia* did realize a benefit from the terrestrial carbon available to them. It also suggests that utilization 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) hypothesized 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.* (2016) recently revealed that *Daphnia* utilize carbohydrates (glucose) from t-POC for energy and save essential fatty acids and amino acids for somatic growth and reproduction, thus using a “sparing strategy” to maximize their somatic growth and reproduction under nutritional stress.

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 Fig. 1). Brett *et al.* (2009), Wenzel *et al.* (2012a) and Taipale *et al.* (2014) also showed 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 to 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 (Fig. 5). When fed finely ground fresh red alder (*Alnus rubra*) leaves for 22 days, *Daphnia* had > 90% survival and produced an average of 3.1 ± 2.7 (± SD) neonates each. These individuals also grew to an average dry weight of 0.22 ± 0.05 mg individual^{-1} (Fig. 5). In contrast, *Daphnia* from the same maternal cohort fed the alga *Cryptomonas ozolinii* had 100% survival, produced an average of 69.5 ± 23.2 neonates ind.$^{-1}$, and had an average DW of 1.06 ± 0.16 mg ind.$^{-1}$ by the same age (Fig. 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 fed 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 ± 0.001 d^{-1}) similar to experimentally starved individuals (growth = -0.018 ± 0.002 d^{-1}) (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 ± 0.005 d^{-1}).

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 utilized 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 Fig. 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 Fig. 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.

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; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009), thereby increasing the relative availability of allochthonous energy sources. In oligotrophic clearwater lakes (DOC < 5 mg C L^{-1}), nutrients (nitrogen and phosphorus) associated with a moderate increase in t-DOC concentration may slightly stimulate primary production and/or brown-colored DOC may play a protective role in UV screening (Finstad *et al.*, 2014; Seekell *et al.*, 2015). However, due to PAR attenuation and phosphorus 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 similar phosphorus concentrations (Jones, 1992; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009; Thrane *et al.*, 2014). For example, del Giorgio & Peters (1994) reported strongly inhibitory effects of DOC on phytoplankton photosynthesis and showed that excess carbon (DOC) was respired as CO_2 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 *et al.*, 2003; Räsänen *et al.*, 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 *et al.*, 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 *et al.* (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^{-1}. Similarly, Karlsson *et al.* (2015) found a negative correlation between DOC concentration (7-22 mg C L^{-1}) 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 *et al.* (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 likely that algal primary production will be the most important resource supporting upper trophic levels in most oligotrophic lakes.

Benthic algal production is strongly related to mean lake depth and water-clarity which can be greatly inhibited by high algal biomass due to 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 *et al.* (2016) observed that in a small lake with very high t-DOC (ca. 30 mg C L^{-1}), and therefore a shallow euphotic zone (< 1m) with very low pelagic primary production, littoral algal primary production was relatively high and contributed to > 90% to the overall summertime primary production.

Interpreting stable isotope mixing models - 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 stable isotope mixing models (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 (Fry, 2013a,b; Brett, 2014b). 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 (Fry, 2013a; Brett, 2014b). Furthermore, fractionation-corrected consumers often fall well outside of the hypothesized resource polygons in this field literature (e.g., Cole *et al.*, 2011; Solomon *et al.*, 2011; Berggren *et al.*, 2014; 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 recognize obvious signs of a misspecified 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 estimates for the stable isotope values of the phytoplankton component of zooplankton diets (Brett, 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 *et al.*, 2006). A variety of methods have been employed to resolve this problem. For example, some authors estimate the δ^{13}C value of the phytoplankton by assuming a "photosynthetic fractionation factor" (ε_p) to predict the δ^{13}C value of the phytoplankton from directly determined δ^{13}C values for the CO_2 in the water (Brett, 2014a). Other studies have directly measured the δ^{13}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 (Pace *et al.*, 2007; Kankaala *et al.*, 2010; Berggren *et al.*, 2014; Taipale *et al.*, 2016) have estimated the δ^{13}C value using algal specific lipid biomarkers, especially PUFA. Other authors have simply assumed fixed δ^{13}C values for the phytoplankton within the seston (Karlsson *et al.*, 2012). Direct measurements δ^{13}C values of phytoplankton (Zohary *et al.*, 1994; Grey *et al.*, 2000; Vuorio *et al.*, 2006; Taipale *et al.*, 2016) have shown considerable variability (± 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.* (2016) recently found the δ^{13}C values of the dominant phytoplankton taxa could explain most of the variation in the δ^{13}C values of the zooplankton in humic lakes.

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 be due to 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; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009). 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 due to microbial respiration of terrestrial carbon and still have fish production strongly supported by an algae-invertebrate pathway (Thorp & Delong, 2002; Lau *et al.*, 2014). Support of upper trophic level production by terrestrial carbon inputs may depend on the simultaneous availability of essential biomolecules synthesized by algae. Stream studies suggest that even when allochthonous inputs greatly dominate, invertebrate and fish production is very preferentially supported by algal basal resources (Mayer & Likens, 1987; Bunn *et al.*, 2003; Brito *et al.*, 2006; Lau *et al.*, 2009a). 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 utilized a factor 5-10 less efficiently than algal basal resources. Not all carbon-based molecules are equally bioavailable, and specific biochemicals synthesized 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 synthesize 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 populations will respond to environmental changes that influence the fluxes, quality, and composition of their terrestrial and aquatic food sources.

Future perspectives

Both the lake and stream literature on reduced carbon influxes is characterized by small data sets. 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 stable isotope mixing models 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 hypothesized 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 utilize much lower quality terrestrial resources. These are particularly interesting lines of inquiry for future research.

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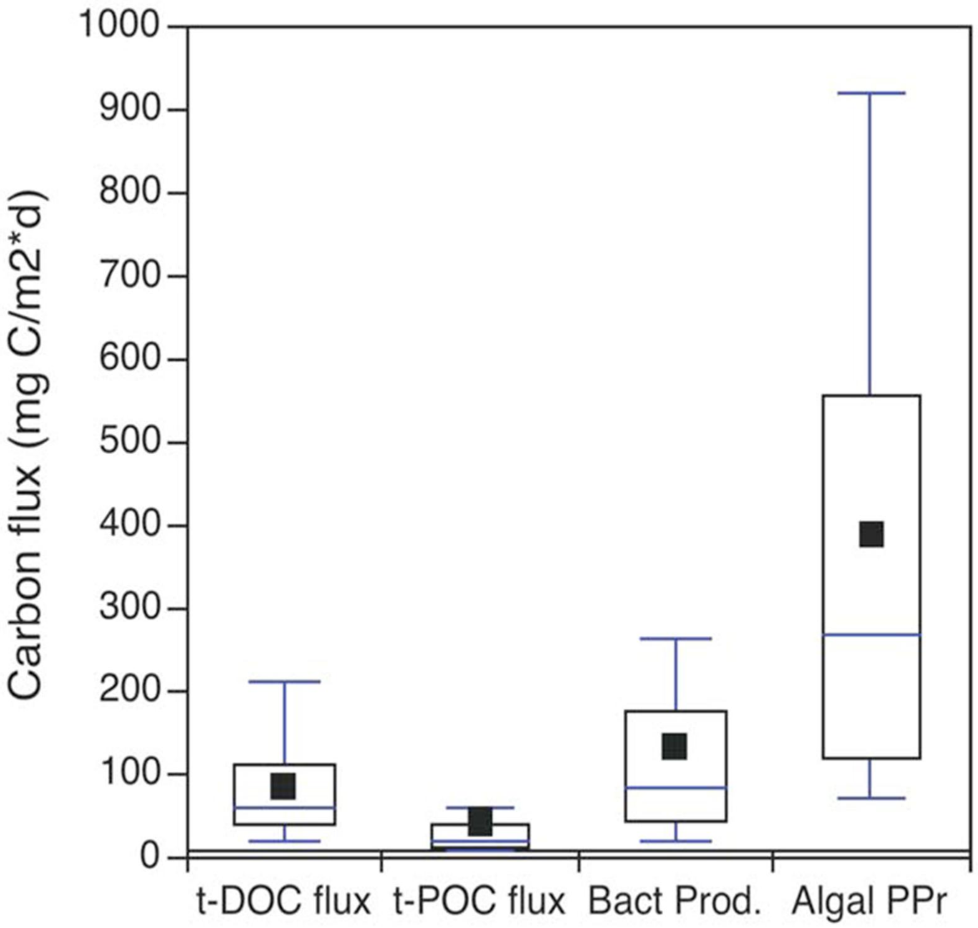

Fig. 1. The mass influx of dissolved and particulate carbon from terrestrial sources and the in-lake production of bacteria and benthic/pelagic algae based on individual lake observations (Brett *et al.*, 2012). Only algal production data from lakes with total phosphorus $\leqslant$ 20 µg L^{-1} were used. Terrestrial particulate loading was calculated based on direct the aeolian transport data from Preston *et al.* (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 data provided by Fouilland & 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.

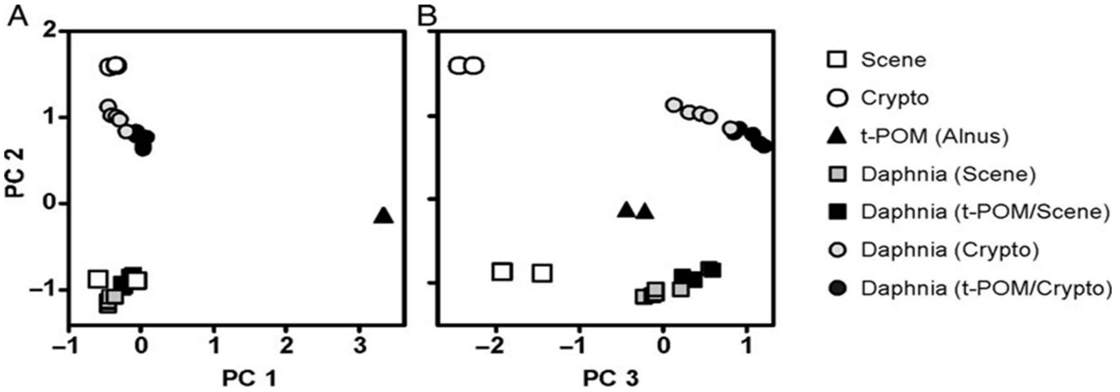

Fig. 2. A principal components analysis of the fatty acid composition of terrestrial detritus (i.e., finely-ground *Alnus rubra*; t-POM), phytoplankton (i.e., *Scenedesmus acutus* and *Cryptomonas ozolinii*), and *Daphnia* fed either pure or mixed diets of phytoplankton and t-POM (Taipale *et al.*, 2015). Diet samples are the fatty acid profiles of *Alnus* (t-POM; black triangle), *Scenedesmus* (Scene; open square), or *Cryptomonas* (Crypto; open circle). Samples labeled "Daphnia" represent *Daphnia* fatty acid profiles after consuming *Scenedesmus* (gray square), *Cryptomonas* (gray 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, 18:1ω9, and ALA, and negatively with SDA, EPA and DHA. The third PC explained 12.0% of the variability and separated *Daphnia* from their diets. This PC was positively correlated with ARA.

Fig. 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.

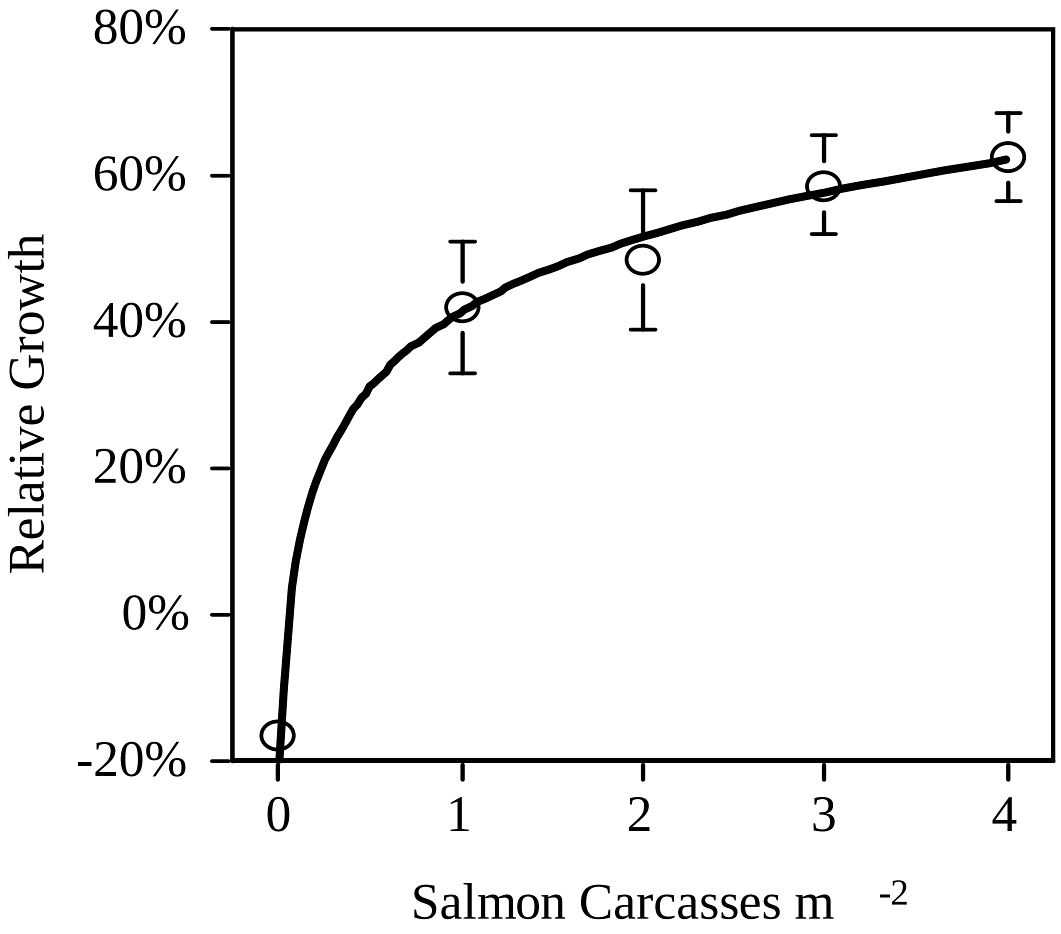

Fig. 4. Mean growth of juvenile Coho salmon (± SE) over 66 days when exposed to a gradient of salmon carcass additions. Adapted from Wipfli *et al.* (2003).

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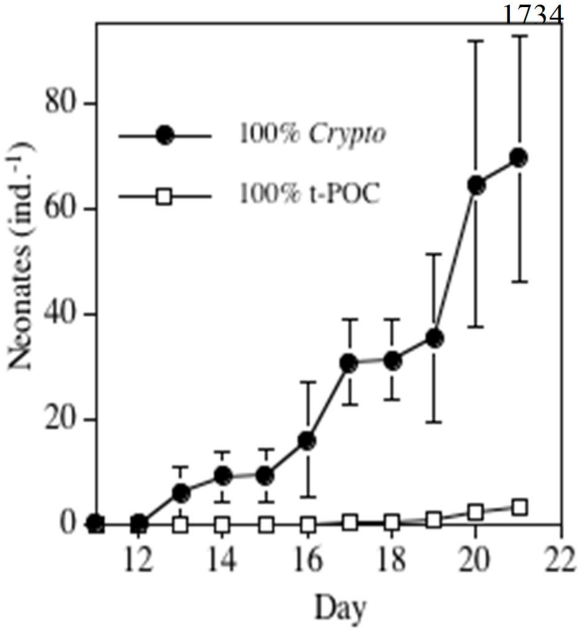
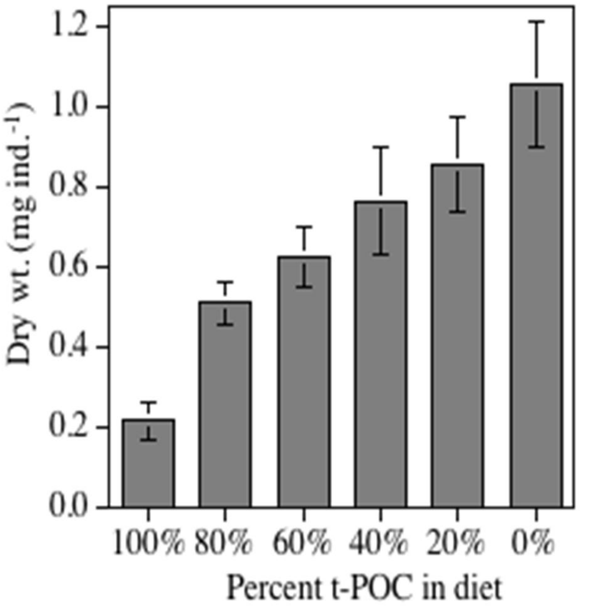

Neonates (ind.$^{-1}$)
0
20
40
60
80
12
14
16
18
20
22
Day
100% *Crypto*
100% t-POC


Dry wt. (mg ind.$^{-1}$)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
100%
80%
60%
40%
20%
0%
Percent t-POC in diet

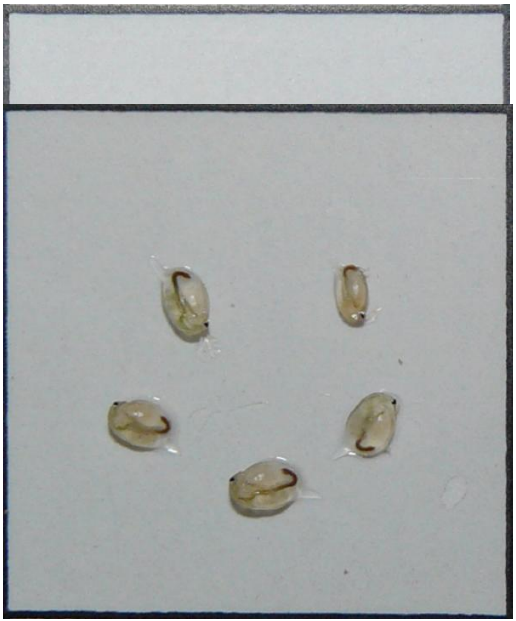


Fig. 5. The growth and reproduction responses of *Daphnia magna* fed phytoplankton or finely ground terrestrial detritus (Brett *et al.*, 2009). The upper left panel shows cumulative *Daphnia* neonate production when fed the phytoplankter *Cryptomonas ozolinii* or leaves of the riparian tree *Alnus rubra*. 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 day old *Daphnia* that have exclusively consumed *Rhodomonas lacustris*. The lower right panel shows 18 day 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 ± 1 SD.