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1  
2 How important are terrestrial organic carbon inputs for secondary  
3 production in freshwater ecosystems?  
4

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29

30 **SUMMARY**

- 31 1. Many freshwater systems receive substantial inputs of terrestrial organic  
32 matter. Terrestrially derived dissolved organic carbon (t-DOC) inputs can  
33 modify light availability, the spatial distribution of primary production, heat  
34 and oxygen in aquatic systems, as well as inorganic nutrient  
35 bioavailability. It is also well established that some terrestrial inputs (such  
36 as invertebrates and fruits) provide high quality food resources for  
37 consumers in some systems.
- 38 2. In small to moderate-sized streams, leaf litter inputs average  $\approx 3X$  greater  
39 than autochthonous production. Conversely, in oligo/mesotrophic lakes  
40 algal production is typically  $\approx 5X$  greater than the available flux of  
41 allochthonous basal resources.
- 42 3. Terrestrial particulate organic matter (t-POC) inputs to lakes and rivers are  
43 comprised of 80-90% biochemically recalcitrant lignocellulose, which is  
44 highly resistant to enzymatic breakdown by animal consumers. Further, t-  
45 POC and heterotrophic bacteria lack essential biochemical compounds  
46 that are critical for rapid growth and reproduction in aquatic invertebrates  
47 and fishes. Several studies have shown that these resources have very  
48 low food quality for herbivorous zooplankton and benthic invertebrates.
- 49 4. Much of the nitrogen assimilated by stream consumers is likely to be of  
50 algal origin, even in systems where there appears to be a significant  
51 terrestrial carbon contribution. Amino acid stable isotope analyses for  
52 large river food webs indicate that most upper trophic level essential  
53 amino acids are derived from algae. Similarly, profiles of essential fatty  
54 acids in consumers show a strong dependence on algal food resources.
- 55 5. Primary production to respiration ratios are not a meaningful index to  
56 assess consumer allochthony because respiration represents an oxidized  
57 carbon flux that cannot be utilized by animal consumers. Rather, the  
58 relative importance of allochthonous subsidies for upper trophic level  
59 production should be addressed by considering the rates at which

60 terrestrial and autochthonous resources are consumed and the growth  
61 efficiency supported by this food.

62 6. Ultimately, the biochemical composition of a particular basal resource, and  
63 not just its quantity or origin, determines how readily this material is  
64 incorporated into upper trophic level consumers. Because of its highly  
65 favorable biochemical composition and greater availability, we conclude  
66 that microalgal production supports most animal production in freshwater  
67 ecosystems.

68

## 69 **Introduction**

70 Ecologists have long been fascinated by interfaces and the exchange of  
71 materials across aquatic-terrestrial boundaries (Summerhayes & Elton, 1923;  
72 Polis *et al.*, 1997). The stream ecology community has classically considered  
73 allochthonous inputs to be the key basal resource because of their quantitative  
74 dominance over in-stream primary production in low-order systems and larger,  
75 turbid, heterotrophic rivers (Vannote *et al.*, 1980). However, more recently there  
76 has been a shift in emphasis to the disproportionate importance of autotrophic  
77 producers to animal consumer production in streams and larger rivers (Lewis *et al.*,  
78 2001; Thorp & Delong, 2002; Bunn *et al.*, 2003; Brito *et al.*, 2006; Lau *et al.*,  
79 2009a,b; Jardine *et al.*, 2015; Hayden *et al.*, 2016; Neres-Lima *et al.*, 2016,  
80 Thorp & Bowes, 2017). Conversely, lakes have classically been thought to be  
81 driven by autochthonous production (Carpenter *et al.*, 1985), but recent studies  
82 have suggested terrestrial carbon inputs support  $\approx$  30-70% of zooplankton as  
83 well as zoobenthos and fish production (Grey *et al.*, 2001; Karlsson *et al.*, 2003;  
84 Pace *et al.*, 2004; Carpenter *et al.*, 2005; Cole *et al.*, 2006; Jansson *et al.*, 2007;  
85 Pace *et al.*, 2007; Berggren *et al.*, 2010; Cole *et al.*, 2011; Berggren *et al.*, 2014;  
86 Tanentzap *et al.*, 2014). The following analysis explores these paradoxical  
87 viewpoints in the literature from the perspective of the mass fluxes of  
88 allochthonous and autochthonous carbon to and within aquatic systems,  
89 resource energetics and enzyme kinetics, and nutritional constraints on animal  
90 consumer growth and reproduction by examining the empirical evidence of

91 allochthonous and autochthonous subsidies to animal consumers in lakes and  
92 rivers. This analysis will also address whether systems characterized by high  
93 terrestrial carbon inputs are conducive to high rates of invertebrate and fish  
94 production.

95

96 *Why does allochthony matter?*

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

105 Anthropogenic activities greatly modify watershed characteristics, which can  
106 affect the fluxes of nutrients and organic carbon to rivers and lakes (Dillon &  
107 Kirchner, 1975; Hopkinson & Vallino, 1995; Gergel *et al.*, 1999). For example,  
108 France *et al.* (1996) calculated t-DOC export to the nearshore of oligotrophic  
109 forest lakes was reduced by a factor of 40 following riparian deforestation.  
110 Conversely, Webster *et al.* (1990) reported that the loading of particulate organic  
111 matter to small streams increased somewhat, and the transport of this matter  
112 within streams increased greatly, after logging. Watershed disturbance, such as  
113 forest fires and logging, can result in considerable additions of carbon and  
114 nutrients to streams (Skylberg *et al.*, 2009) and lakes (Garcia & Carignan, 1999).  
115 Monteith *et al.* (2007) concluded recent increases in surface water DOC  
116 concentrations in glaciated regions of North America and Europe are a soil-  
117 mediated response to reduced atmospheric sulfate loading and recovery from  
118 acidification. Conversely, Schindler *et al.* (1997) showed a combination of forest  
119 fires, experimental acidification and especially drought reduced watershed t-DOC  
120 export to Canadian boreal lakes. Lepistö *et al.* (2014) stated watershed DOC  
121 export was most closely related to seasonal and inter-annual variation in soil frost

122 cycles, precipitation, runoff and drought. It has also been shown that glacial melt  
123 due to climate change in montane regions may be releasing stored t-DOC to  
124 aquatic ecosystems (Hood et al. 2015). Recent evidence from subalpine lakes of  
125 northern California suggests that elevation and resulting vegetation dominance  
126 may play an important role in governing the inputs of t-DOC into aquatic  
127 ecosystems (Piovia-Scott *et al.*, 2016). These at times contradictory studies  
128 indicate it is unclear whether the export of terrestrial organic matter to aquatic  
129 ecosystems will increase or decrease in the future due to land-use and climate  
130 change, and this remains an important area for subsequent research.

131

#### 132 *Terrestrial carbon influences on lake processes*

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

142 Terrestrial carbon inputs, and especially t-DOC, can influence the chemical  
143 and physical properties of lakes and rivers in a myriad of ways. For example,  
144 DOC dramatically affects the attenuation of visible and ultraviolet radiation (UVR)  
145 in surface waters, as well as which photosynthetically active radiation (PAR)  
146 wavelengths are available at depth (Jones, 1992; Morris *et al.*, 1995; Schindler *et al.*,  
147 1997; von Einem & Granéli, 2010). As such, t-DOC affects where and how  
148 much primary production occurs (Jones, 1992; Vadeboncoeur *et al.*, 2008;  
149 Karlsson *et al.*, 2009) and whether UVR will damage flora and fauna (Williamson  
150 & Rose, 2010). Similarly, t-DOC modifies heat retention, thermal stratification  
151 regimes and oxygen availability within stratified water columns (Schindler *et al.*,  
152 1997; Prairie, 2008; von Einem & Granéli, 2010). t-DOC also exerts strong

153 control over the speciation and bioavailability of nutrients, in particular  
154 phosphorus (P) and to a lesser extent ammonium (Jones, 1992; Steinberg *et al.*,  
155 2006; Li & Brett, 2013), and it is common for much of the P within humic waters  
156 to be bound within only marginally bioavailable humic-iron complexes (Jones *et*  
157 *al.*, 1993). Due to PAR attenuation and P sequestration, it is typical for high t-  
158 DOC lakes to have much less phytoplankton and benthic algal biomass and  
159 production than would be expected in clearwater lakes with corresponding P  
160 concentrations (Jones, 1992; Wehr *et al.*, 1998; Vadeboncoeur *et al.*, 2008;  
161 Karlsson *et al.*, 2009; Thrane *et al.*, 2014).

162 For reasons that are not entirely clear, humic substances seem to inhibit the  
163 growth of some cyanobacteria (Steinberg *et al.*, 2006) and certain chrysophyte  
164 species (Wehr *et al.*, 1998) perhaps because the humic matter sequesters iron.  
165 Conversely, cryptomonads are characteristically abundant in humic lakes  
166 (Klaveness, 1988), and it has been speculated that their ability to consume  
167 bacteria confers an advantage in regards to both direct nutrient and energy  
168 uptake (Tranvik *et al.*, 1989; Rothhaupt, 1996). The flagellated raphidophyte  
169 phytoplankter *Gonyostomum semen* is also characteristic of high DOC lakes,  
170 especially in Scandinavia where in some lakes it comprises  $\approx 95\%$  of total  
171 phytoplankton biomass (Johansson *et al.*, 2013a). It has been hypothesized that  
172 *Gonyostomum* is favored in humic lakes because it is particularly tolerant of low  
173 pH and weak light (Rengefors *et al.*, 2008). Having a mixotrophic feeding mode  
174 might also confer an advantage for *Gonyostomum* in light limited systems relative  
175 to purely autotrophic algae (Berggren *et al.*, 2010). However, due to its large size  
176 and defense system against grazing (e.g., expulsion of mucilaginous trichocysts),  
177 *Gonyostomum* is also not commonly consumed by metazoan zooplankton  
178 (Lebret *et al.*, 2012; but see Johansson *et al.*, 2013b).

179

#### 180 *Terrestrial organic matter loading to lakes*

181 Much of the research suggesting allochthony as an important subsidy for  
182 animal consumers in lakes is based on the premise that terrestrial carbon inputs  
183 are often much larger than primary production in oligo/mesotrophic systems

184 (France *et al.*, 1996; Wetzel, 2001; Cole *et al.*, 2002; Jansson *et al.*, 2007;  
185 Prairie, 2008; Cole *et al.*, 2011). Despite the centrality of this assumption, it is not  
186 borne out by mass flux data for lakes. Brett *et al.* (2012) carried out a meta-  
187 analysis of studies that reported terrestrial carbon mass influx and algal primary  
188 production data for lakes with total phosphorus  $\leq 20 \mu\text{g L}^{-1}$  (Fig. 1). This analysis  
189 showed the median (interquartile range) terrestrial particulate organic carbon (t-  
190 POC), available dissolved organic carbon (t-DOC) inputs, and in-lake bacterial  
191 and algal production were 11 (8-17), 34 (11-78), 74 (37-165), and 253 (115-546)  
192  $\text{mg carbon m}^{-2} \text{d}^{-1}$ , respectively (Fig. 1). These results indicate autochthonous  
193 production is 4 to 7 times greater than the flux of terrestrial basal resources that  
194 is available to consumers in oligo/mesotrophic lakes (Brett *et al.*, 2012). Lakes  
195 with high hydraulic flushing rates can also have very high loading of t-DOC.  
196 However, in lakes with the highest t-DOC inputs (i.e.,  $1000 \text{ mg C m}^{-2} \text{d}^{-1}$ ),  $\geq 98\%$   
197 of the t-DOC flux is advected because t-DOC is processed at only  $\approx 0.1\% \text{d}^{-1}$   
198 (Hanson *et al.*, 2011; Brett *et al.*, 2012). Because of this very low degradation  
199 rate constant, advection is the main fate of t-DOC in lakes with water retention  
200 times less than 3 years (Hanson *et al.*, 2011; Brett *et al.*, 2012). Advected  
201 allochthonous organic matter cannot be used to support in-lake consumer  
202 production due to mass balance constraints.

203

#### 204 *Terrestrial organic matter loading to streams*

205 The special volume edited by Webster & Meyer (1997) reported 28 cases  
206 where leaf litter inputs and benthic primary production were simultaneously  
207 determined for different streams. These data indicated the median leaf litter  
208 inputs and benthic algal production values were 454 (218-615) and 134 (63-514)  
209  $\text{mg carbon m}^{-2} \text{d}^{-1}$ , respectively. When compared within systems, the median  
210 ratio of leaf litter inputs to algal production was 2.8 (0.6-7.8). Webster & Meyer  
211 (1997) also reported 13 cases where t-DOC loading to streams was quantified;  
212 these data had a median of 134 (94-634)  $\text{mg carbon m}^{-2} \text{d}^{-1}$ . Because t-DOC is  
213 metabolized very slowly and this fraction is advected in streams, these data

214 suggest that particulate inputs will dominate the active terrestrial organic matter  
215 processing in streams.

216

### 217 *Autochthony or Allochthony in Lotic Ecosystems*

218 Conceptual theories on the relative importance of autochthonous and  
219 allochthonous carbon for animal production in lotic ecosystems are founded  
220 primarily on techniques for analyzing gut contents and feeding behavior, and  
221 more recently, tracer techniques that track the incorporation of resources into  
222 tissue (e.g., bulk tissue stable isotopes and fatty acids). The dominant  
223 importance of algae in supporting animal production in areas where PAR reaches  
224 the stream bottom is almost universally acknowledged (e.g., arid zone streams –  
225 Minshall, 1978; Bunn *et al.*, 2006), but controversy continues over the primary  
226 carbon sources in forested headwaters and large turbid rivers. Terrestrial carbon  
227 from leaf litter has been thought to be the main carbon source in forested  
228 headwaters since at least publication of *The Stream And Its Valley* (Hynes, 1975)  
229 and development of the River Continuum Concept (or RCC: Vannote *et al.*,  
230 1980). This was primarily based on observations of a substantial influx of leaf  
231 litter, reduced PAR for photosynthesis due to extensive riparia, a dearth of visible  
232 benthic algae, stream respiration much higher than production, and the  
233 dominance of shredding invertebrates and other detritivores. However, in one  
234 shaded headwater stream Mayer & Likens (1987) determined that algae  
235 represented more than half the food consumed by the caddisfly *Neophylax*  
236 *aniqua* and was responsible for 75% of its energy needs, even though algal  
237 production was < 2% of total energy inputs. More recently, a survey of 70  
238 streams and rivers, most forested, where isotopes had been measured in food  
239 webs found  $^{13}\text{C}$  values indicating algal diets in scraping grazers from very small  
240 shaded headwater streams (draining 0.2 km<sup>2</sup>) down through middle-sized rivers  
241 (drainage areas of 4000 km<sup>2</sup> (Finlay, 2001). Other recent research has also  
242 challenged the RCC not only in low-latitude forest systems where sufficient PAR  
243 can stimulate benthic algal production (Brito *et al.*, 2006; Davies *et al.*, 2008; Lau  
244 *et al.*, 2009a,b; Dudgeon *et al.*, 2010), but even in more temperate systems (e.g.,

245 Finlay, 2001; McNeeley *et al.*, 2007; Carroll *et al.*, 2016; Hayden *et al.*, 2016;  
246 Jonsson & Stenroth, 2016). Within the RCC model was the explicit assumption  
247 that at low light levels, consumers would be limited by low algal production and  
248 therefore turn towards the lower-quality but plentiful terrestrially-derived  
249 resources. On the other hand, the flux of primary consumer production to  
250 predators and omnivores can be relatively high and imply top-down control of  
251 primary consumer populations (Hall *et al.*, 2001).

252 Wetzel (1995, 2001) suggested the metabolism of terrestrial origin particulate  
253 and especially dissolved organic matter by aquatic bacteria dominates both the  
254 material and energy fluxes of most aquatic ecosystems, especially small  
255 oligotrophic lakes and headwater streams. Many studies have also noted it is  
256 common for north temperate and boreal lakes to be net heterotrophic or have  
257 primary production to respiration (P/R) ratios < 1, with the implication being this  
258 provides insights into whether the aquatic system being studied is on balance  
259 mainly supported by allochthony or autochthony (Odum, 1956; Vannote *et al.*,  
260 1980). Although the significance of low P/R ratios and/or net heterotrophy for  
261 upper trophic levels has been disputed (Rosenfeld & Mackay, 1987; Thorp &  
262 Delong, 2002), many of the papers in the zooplankton allochthony literature  
263 begin by emphasizing the supposed importance of net heterotrophy for upper  
264 trophic levels (Grey *et al.*, 2001; Jansson *et al.*, 2007; Karlsson, 2007; Berggren  
265 *et al.*, 2010). What the "net heterotrophy" literature actually shows is that  
266 allochthonous carbon inputs play an important role in the influx and efflux of CO<sub>2</sub>  
267 in many lakes and streams (Duarte & Prairie, 2005). Understanding the role  
268 lakes play in the global carbon cycle is very important, but this research does not  
269 indicate the relative importance of allochthonous and autochthonous carbon  
270 subsidies for upper trophic levels. This latter question is addressed by  
271 considering the rates at which food of autochthonous and direct (t-POC inputs) or  
272 indirect (bacterial production supported by t-DOC) terrestrial origin are consumed  
273 and the growth efficiency with which this matter is used (Rosenfeld & Mackay,  
274 1987; Thorp & Delong, 2002; Marcarelli *et al.*, 2011). Furthermore, low P/R ratios  
275 are most commonly observed when apparent respiration is high, and high

276 respiration indicates a high flux of organic matter being converted to CO<sub>2</sub> most  
277 likely via photochemical or bacterial degradation (Amon & Benner, 1996b; Cory  
278 *et al.*, 2014). Since animals use reduced carbon this also represents an oxidized  
279 carbon flux that is not available to support upper trophic level production. The  
280 ratio of the bioavailable terrestrial and aquatic particulate organic matter fluxes is  
281 a more useful index of potential allochthonous subsidies to consumer production  
282 (Rosenfeld & Mackay, 1987; Brett *et al.*, 2012). There are also potentially  
283 important methodological issues in the net heterotrophy literature (see Carignan  
284 *et al.*, 2000; Abril *et al.*, 2015) which need to be resolved before we have a clear  
285 understanding for the prevalence of this phenomenon in oligotrophic lakes and  
286 headwater streams.

287 Models of carbon sources for large rivers have focused either on the main  
288 channel (original RCC model), floodplains (Flood Pulse Concept, or FPC: Junk *et al.*  
289 *et al.*, 1989; and revision of the RCC by Sedell *et al.*, 1989), or the entire riverine  
290 landscape, especially the main and side channels of the riverscape (Riverine  
291 Productivity Model, or RPM: Thorp & DeLong, 1994, 2002; and the Riverine  
292 Ecosystem Synthesis, or RES: Thorp *et al.*, 2006, 2008). Scientists supporting  
293 predictions of the RCC and FPC for large rivers could point to rates of  
294 downstream transport (rapid removal of algae from the system), the river's helical  
295 flow (continually taking phytoplankton into and out of the photic zone), the  
296 absence of PAR on the bottom across most of the river's width, and the high  
297 turbidities of many rivers. Consequently, Sedell *et al.*, (1989) inferred that  
298 secondary production and system metabolism was principally supported by  
299 terrestrial carbon derived from upstream leakage of refractory carbon or lateral  
300 inputs from overland flow during flood and non-flood periods. Supporters of the  
301 RPM and RES argue instead that algal production in the main channel (e.g.,  
302 DeLong & Thorp, 2006), nearshore environments, and lateral slackwaters of the  
303 main and side channels provide sufficient labile carbon to support metazoan  
304 production during periods of maximum secondary production (e.g., Thorp *et al.*,  
305 2006, 2008; Jardine *et al.*, 2012). Even in highly turbid lowland rivers, much of

306 the consumer biomass, especially in higher trophic levels, is derived from algal  
307 sources (Power, 2001; Bunn *et al.*, 2003; Jardine *et al.*, 2013).

308

309 *Tools to resolve this debate*

310 Resolution of this nearly four-decade debate is hampered by a lack of  
311 detailed chemical analysis of carbon digestibility and by shortcomings in  
312 analytical techniques for tracking carbon sources, determining food chain length,  
313 and analyzing community relationships (e.g., Layman *et al.*, 2007). From the  
314 biochemical perspective, however, our earlier conclusions for allochthonous  
315 carbon flowing into lakes should be directly applicable to allochthonous inputs to  
316 a river from headwaters to its terminus. From a sampling/analytical perspective,  
317 problems arise in determining source signatures, turnover rates and metabolic  
318 transformations within the consumer (e.g., effects of starvation: Bowes *et al.*,  
319 2014) and among trophic levels (e.g., Bowes & Thorp, 2015) using standard  
320 techniques (see Jardine *et al.*, 2014). Of these problems, determining source  
321 signatures is the most problematic, in part because scientists have until recently  
322 been limited to bulk tissue stable isotope techniques (the easiest, cheapest, and  
323 most widespread method) and fatty acid methods (good for specific source  
324 identification, but inappropriate for determining food chain length and other  
325 community metrics). The primary analytical problem in identifying primary food  
326 sources with bulk tissue techniques is reliably determining the  $\delta^{13}\text{C}$  autotrophic  
327 values of both terrestrial plants and algae. The values of both resources can vary  
328 substantially in time and space, especially for algae (Cloern *et al.*, 2002; Hadwen  
329 *et al.*, 2010; Bowes & Thorp, 2015). In an attempt to alleviate this problem,  
330 aquatic ecologists have often used isotopic values of herbivores, such as benthic  
331 bivalve molluscs or grazer macroinvertebrates (Vander Zanden & Rasmussen,  
332 1999; Finlay, 2001). This is also problematic, however, because one needs to  
333 know: (a) what the mussel or other herbivore has been consuming and in what  
334 proportion (e.g., benthic or suspended algae and/or particulate organic matter of  
335 autochthonous or allochthonous origin); (b) from where within the river the food  
336 was primarily obtained (affecting the exact  $\delta^{13}\text{C}$  value); and (c) how the value

337 changes as resources are conveyed through the food web under different  
338 physiological and environmental conditions.

339 Finlay and colleagues found that in streams with catchment areas  $< 10 \text{ km}^2$   
340 benthic algae had depleted  $^{13}\text{C}$  values relative to terrestrial vegetation by 3 to  
341 9‰, but for watershed surface areas ranging from 10 to 1,000  $\text{km}^2$  algal carbon  
342 isotope values varied widely and extensively overlapped with those for terrestrial  
343 C3 plants (Finlay *et al.*, 1999; Finlay, 2001). In relatively productive, unshaded,  
344 larger streams and rivers, the algae tend to incorporate dissolved atmospheric  
345  $\text{CO}_2$ , which has a  $\delta^{13}\text{C}$  value of about -8‰. Because of the relatively high  
346 demand for  $\text{CO}_2$  in productive waters, algae discriminate relatively little towards  
347 the lighter isotope and thus incorporate a  $^{13}\text{C}$  value which is enriched by about -  
348 15 to -23‰ relative to terrestrial C3 plants (which have nearly constant  $\delta^{13}\text{C}$   
349 values of  $\approx -28$ ‰ from headwaters to downstream reaches of rivers, as  
350 expected given their well-mixed atmospheric source). Three factors conspire to  
351 reduce stable isotope differences in small, shady, streams: 1) in the less-  
352 productive shaded stream algae may have an abundance of  $\text{CO}_2$  and thus  
353 fractionate more towards the lighter isotope, and become less enriched than the  
354  $\delta^{13}\text{C}$  of terrestrial C3 plants; 2) the dissolved inorganic carbon in small shaded  
355 streams may derive in part from respired terrestrial organic matter and thus  
356 transfer this lighter isotopic value to the algae; 3) the epilithon may contain  
357 organic carbon derived from dissolved and fine particulate organic matter of  
358 terrestrial origin embedded within the matrix. Thus studies of small streams may  
359 find that the values of periphyton and terrestrial material are not sufficiently  
360 different to be able to separate sources, whereupon they may abandon this  
361 approach (see Hall *et al.*, 2001) or may simply not publish. Lack of publication of  
362 these findings creates a bias in the literature towards the cases in which stable  
363 isotopes provide a clear solution to the analysis of food sources. As previously  
364 noted, in meta-analyses of studies reporting the  $\delta^{13}\text{C}$  values of periphyton, Finlay  
365 (2001) and Ishikawa *et al.* (2012) found a trend towards lighter values at a  
366 catchment size of approximately 0.2-10  $\text{km}^2$  and 75% canopy cover. This  
367 generally implies difficulty in discriminating algal and terrestrial resources in

368 small, shaded streams, although in some studies the algae can have a distinctly  
369 more depleted  $\delta^{13}\text{C}$  than the terrestrial material and hence provide the required  
370 discrimination between sources (e.g., Rounick *et al.*, 1982; Finlay, 2001).

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

386 Even after one obtains a satisfactory signature from the aquatic herbivore,  
387 one would not have a reliable terrestrial signature for comparison because, first,  
388 the bulk tissue values of terrestrial plants also vary in space and time and the  
389 investigator would have to assume an equal mixture of organic carbon from  
390 various plant species and upstream locations; second, there are only few, if any,  
391 aquatic primary consumers that assimilate only terrestrial resources and can truly  
392 represent a terrestrial end member. Empirical studies have shown that even  
393 obligate and facultative shredders (classified based on functional feeding)  
394 assimilate autochthonous algae in shaded streams (e.g., Li & Dudgeon, 2008;  
395 Lau *et al.*, 2009a,b; Hayden *et al.*, 2016), thus faunal representatives of terrestrial  
396 signature are expected to be more scarce in wider river channels where light  
397 availability and primary production are greater.

398 Another solution to this dilemma is through the use of a relatively new  
399 analytical technique: amino acid stable isotope analyses. This method has been  
400 employed in marine food web studies (e.g., McClelland & Montoya, 2002; Popp  
401 *et al.*, 2007; Chikaraishi *et al.*, 2009, 2014; Nielsen *et al.*, 2015; McMahon *et al.*,  
402 2016), a stream field study (Ishikawa *et al.*, 2014), a laboratory freshwater food  
403 web experiment (Bowes & Thorp, 2015), and several museum studies of  
404 freshwater piscivorous and invertivorous fishes collected from the Upper  
405 Mississippi and lower Ohio Rivers (Thorp & Bowes, 2017; Bowes *et al.*, in press).  
406 This technique links essential amino acids in the tissue of consumers with their  
407 ultimate autotrophic source because the consumers cannot synthesize essential  
408 amino acids. For example, the results of Thorp & Bowes (2017) demonstrated  
409 that on average 60-75% of the consumer amino acids were derived from algae in  
410 the rivers they studied.

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

422

423 *Enzymatic and biochemical constraints on the utilization of terrestrially derived*  
424 *carbon*

425 The problem with using terrestrial derived carbon is not its energy content *per*  
426 *se*, but rather the accessibility of the energy contained within this material and  
427 the suitability of the biochemical composition of the resource for synthesis of new  
428 biomass in animals. Biological recalcitrance is due to kinetic, not energetic

429 content limitations. For example, a variety of terrestrial plants have average  
430 energy contents of  $19 \pm 1 \text{ MJ kg}^{-1}$  ( $\pm 1 \text{ SD}$ ) (Friedl *et al.*, 2005), which is slightly  
431 higher than for proteins and carbohydrates (i.e.,  $17 \text{ MJ kg}^{-1}$ ), but considerably  
432 less than the average energy content of fats ( $38 \text{ MJ kg}^{-1}$ ) and alcohols ( $29 \text{ MJ kg}^{-1}$ )  
433 (Blaxter, 1989). It is obvious that many synthetic organic compounds such as  
434 plastics have a high-energy content ( $20\text{-}46 \text{ MJ kg}^{-1}$ ) while also being almost  
435 entirely resistant to attack by biological enzymes. Similarly, cellulose has  
436 extremely low bioavailability to the large majority of insects (Martin *et al.*, 1991).  
437 True lignin digestion is thought to be restricted to a very small fraction of insects  
438 (Breznak & Brune, 1994; Geib *et al.*, 2008). This is important because we  
439 hypothesize that aquatic animal consumers will grow best when utilizing diets  
440 that most closely match their own biochemical composition, or complement their  
441 endogenous capacity to modify and synthesize biochemicals.

442 Many bacteria are biochemical specialists and are equipped with specific  
443 enzymes that target particular molecular bonds. The structural carbon that  
444 dominates the tissues of many higher plants is comprised in large part of lignins  
445 and cellulose (Meyers & Ishiwatari, 1993). Lignocellulose degradation in  
446 terrestrial soil systems plays a central role in the global carbon budget, but  
447 currently the fundamental understanding of the degradation of these compounds  
448 is only rudimentary (Benner *et al.*, 1988; Lynd *et al.*, 2002; Martinez *et al.*, 2005).  
449 Cellulose is the most prevalent component of plant tissue comprising 35-50% of  
450 dry weight, and is generally embedded in a biopolymer structural matrix including  
451 hemicelluloses (20-35% of dry wt.) and lignin (5-30% of dry wt.) (Lynd *et al.*,  
452 2002), with other biochemicals such as carbohydrates, lipids and proteins  
453 comprising a much smaller portion of plant tissues (Martinez *et al.*, 2005). The  
454 lignocellulosic component of the plant undergoes self-assembly at the site of  
455 biosynthesis and is composed of randomly polymerized polyphenolics intertwined  
456 with hemicellulose, resulting in a hydrophobic crystalline or complex amorphous  
457 structure, which protects against biodegradation. Collectively these physical  
458 properties of lignocellulose do not present well-defined enzymatic targets,  
459 making it difficult for enzymes to bind to susceptible sites and thereby conferring

460 considerable resistance to microbial degradation (e.g., Moran & Hodson, 1989).  
461 These characteristics of higher plant structural material have been hypothesized  
462 to be an evolutionarily adaptive strategy to avoid attack by bacteria, fungi and  
463 herbivorous animals (Coley *et al.*, 1985; Rosenthal & Kotanen, 1994). By  
464 presenting a physical or enzymatic target with a random or tightly packed  
465 structure, the organism can prevent its consumers from refining an effective  
466 attack strategy. With the exception of termites (Ohkuma, 2003), very few animals  
467 are known to possess the requisite enzymes to metabolize the lignocellulosic  
468 biomass of terrestrial plants, and most of the degradation of lignocellulose in soils  
469 and aquatic systems is carried out by ascomycete fungi and various bacteria  
470 (Lynd *et al.*, 2002; Simonis *et al.*, 2008).

471 White rot fungi are the best-known living organisms that specialize on using  
472 higher plant lignocellulose as their main substrate. They accomplish this feat by  
473 means of nonspecific extracellular oxidative enzymes (oxidoreductases) such as  
474 lignin and manganese peroxidases (Tuomela *et al.*, 2000). The forms of  
475 terrestrial carbon that are not metabolized by bacteria and fungi within terrestrial  
476 soil systems are subsequently exported to streams and lakes. The aquatic realm  
477 is the recipient of the metabolic "leftovers" from the partial degradation of  
478 lignocellulose in the terrestrial system (Sutton & Sposito, 2005). High watershed  
479 t-DOC export is particularly associated with catchments with large wetland or  
480 saturated areas (Rasmussen *et al.*, 1989; Dillon & Molot, 1997; Canham *et al.*,  
481 2004) and streams draining catchments with well-drained soils typically have low  
482 t-DOC concentrations (Gergel *et al.*, 1999). Because anoxic degradation  
483 (especially in lakes and wetlands) yields very little energy to microbes, with most  
484 energy channeled towards methanogenesis (Schink, 1997), the degradation of  
485 organic matter in saturated anoxic conditions is slow and often incomplete for  
486 less energetically favorable forms of terrestrial carbon.

487 Increased oxygen availability accelerates rates of lignin degradation by  
488 hydrogen peroxide, which is in turn derived from the metabolism of cellulose and  
489 hemicellulose in aerobic conditions (Sanchez, 2009). In the absence of oxygen,  
490 lignocellulose degradation to humic substances is much slower and less

491 complete (Tuomela *et al.*, 2000). In anoxic systems where methanogenesis  
492 prevails, optimal substrate metabolism generally requires syntrophic cooperation  
493 between two or more highly specialized bacteria species wherein the product of  
494 one species' metabolism is the resource for the other species (Schink, 1997).  
495 Optimal metabolic transfers between syntrophic bacteria occur when the  
496 cooperating species are in very close physical proximity, often as aggregates or  
497 flocs. However, this type of metabolic cooperation between bacteria species  
498 seems to be much less common in oxic environments (Schink, 1997).

499 Because of their complex and amorphous structure, humic and fulvic acids  
500 are, like their precursors, quite resistant to enzymatic hydrolysis. Therefore, they  
501 are most susceptible to generalized attacks by reactive oxygen species such as  
502 H<sub>2</sub>O<sub>2</sub> and ultraviolet radiation (UVR) in natural systems (Amon & Benner, 1996b),  
503 and chlorine, ozone, and UVR in engineered systems (Matilainen & Sillanpää,  
504 2010). For example, it is widely recognized that much of the degradation of  
505 complex t-DOC molecules in aquatic systems is a consequence of UVR driven  
506 photooxidation (Cory *et al.*, 2014), which in turn produces simpler molecules  
507 (e.g., formaldehyde, acetaldehyde, glyoxylate, and pyruvate) via cleavage of  
508 macromolecules into lower molecular weight compounds that can be more easily  
509 metabolized by bacteria (Lindell *et al.*, 1995; Vähätalo *et al.*, 2011). Some  
510 research, however, suggests low molecular weight t-DOC is actually less  
511 bioavailable to microbial degradation because it is more diagenetically altered  
512 than most high molecular weight organic matter (Tulonen *et al.*, 1992; Amon &  
513 Benner, 1996a).

514 The colonization of decaying leaf litter by bacteria and fungi in smaller  
515 streams has been likened to peanut butter on crackers (e.g., Cummins, 1974),  
516 with the microbial biofilm converting detrital material into more labile and higher  
517 quality food sources for benthic invertebrates (Findlay, 2010). However,  
518 experimental studies suggest that microbial colonization of decaying leaves does  
519 not lead to greater nutritional quality of leaf litter (due to very low quantities of  $\omega$ 3  
520 fatty acids), despite increases in bacterial and fungal fatty acids over time  
521 (Torres-Ruiz & Wehr, 2010). A recent feeding experiment showed that the

522 presence of high quality algae attached to leaf litter not only boosted the somatic  
523 growth of larvae of the shredding caddis (*Anisocentropus bicoloratus*), but also  
524 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  
525 consumption, they acquired and selectively retained their physiologically  
526 important fatty acids ( $\omega$ 3 PUFA) from high quality algae. Likewise, results from  
527 manipulative feeding experiments in Lau *et al.* (2013) showed pre-conditioned  
528 leaf litter alone could not sustain the somatic growth of the isopod *Asellus*  
529 *aquaticus*, which is a common benthic generalist in boreal freshwaters. Supplying  
530 leaf litter and algae together, however, substantially enhanced somatic growth.  
531 This growth facilitation and the PUFA accumulation in *Asellus* were mediated by  
532 its seasonal physiological variation – *Asellus* optimized PUFA retention during  
533 the spring (i.e., the reproductive season) and somatic growth in the fall – yet in  
534 both seasons an algal diet was needed to satisfy its physiological requirements.  
535

536

537 *Terrestrial and autochthonous carbon fluxes to and within aquatic ecosystems:*  
538 *oligo/mesotrophic lakes*

539 Initially, it was concluded that the flux of terrestrial carbon to zooplankton via  
540 a t-DOC to bacteria pathway was very minor and only accounted for 1-2% of  
541 zooplankton carbon (Cole *et al.*, 2006). These authors concluded direct t-POC  
542 consumption was the main pathway by which terrestrial organic matter was  
543 routed to zooplankton with this pathway accounting for  $\approx$  50% zooplankton  
544 carbon in unfertilized lakes (Cole *et al.*, 2006). However, as noted by Brett *et al.*  
545 (2009, 2012), t-POC inputs to these lakes are < 5% of algal primary production  
546 and because t-POC is a very low quality resource compared to phytoplankton, it  
547 is unlikely that a small flux of low quality resource could support  $\approx$  50% of  
548 zooplankton production.

549 Cole *et al.* (2011) acknowledged that t-POC influxes were too low to support a  
550 large fraction of zooplankton production in their lakes. Instead these authors  
551 hypothesized that a microbially-mediated t-DOC to bacteria pathway was the  
552 primary route by which zooplankton obtained terrestrial C (Cole *et al.*, 2011). In a

553 feeding experiment using t-DOC with algae, McMeans *et al.* (2015) found higher  
554 somatic growth, but no viable egg reproduction in *Daphnia magna* exposed to  
555 high t-DOC and attributed this growth response to the provision of bacteria rather  
556 than direct t-DOC utilization. However, this pathway is contingent on t-DOC being  
557 the main resource for planktonic bacteria. The strong relationship between  
558 phytoplankton and bacteria production reported by Fouilland & Mostajir (2010)  
559 (i.e.,  $r^2 = 0.83$ ) and others (Bird & Kalff, 1984;  $r^2 = 0.88$ ) suggests otherwise.  
560 Because DOC releases from algal production average about 20-30% of gross  
561 primary production (Cole *et al.*, 1982; Cole *et al.*, 2000), the flux of algal derived  
562 DOC will on average be similar ( $29\text{-}137 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) to the flux of t-DOC that is  
563 removed in oligo/mesotrophic lakes ( $37\text{-}165 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) (Brett *et al.*, 2012).  
564 Furthermore, Kritzberg *et al.* (2004, 2005) concluded heterotrophic bacteria  
565 preferentially utilize phytoplankton-derived DOC compared to t-DOC, and algal  
566 DOC resulted in higher bacterial growth efficiency. Several studies have also  
567 reported that bacteria production is not correlated with the standing pool of t-  
568 DOC in aquatic systems (Amon & Benner, 1996b; Carignan *et al.*, 2000;  
569 Karlsson, 2007; Farjalla *et al.*, 2009; Gudasz *et al.*, 2012; Kankaala *et al.*, 2013).  
570 The potential importance of a t-DOC to bacteria to zooplankton pathway is also  
571 contravened by bacterial production only averaging  $\approx 30\%$  of algal primary  
572 production in oligo/mesotrophic lakes (Fouilland & Mostajir, 2010). Finally,  
573 several authors have directly tested the food quality of heterotrophic bacteria for  
574 freshwater zooplankton. So far, all these studies have shown freshwater  
575 zooplankton cannot survive on diets solely comprised of bacteria; and when  
576 zooplankton consume mixed bacteria and phytoplankton diets, they very  
577 preferentially utilize the algal fraction of their diets (Martin-Creuzburg *et al.*, 2011;  
578 Taipale *et al.*, 2012; Wenzel *et al.*, 2012b; Taipale *et al.*, 2014).

579 Methanogenesis and methanotrophy is another pathway by which terrestrial  
580 inputs might contribute to consumer production in aquatic food webs.  
581 Increasingly sophisticated stable isotope, and especially fatty acid biomarkers  
582 that are diagnostic for methane oxidizing bacteria, can be used to definitively  
583 establish methane contributions to consumer production (Kankaala *et al.*, 2006b;

584 Deines *et al.*, 2007; Taipale *et al.*, 2008; 2012; Jones & Grey, 2011). However,  
585 these approaches do not establish the origin of the reduced carbon that originally  
586 supported methanogenesis. In a study of 207 Finnish boreal lakes, Juutinen *et al.*  
587 (2009) observed the greatest methane effluxes from shallow nutrient rich and  
588 humic lakes. Deemer *et al.* (2016) recently showed water column chlorophyll *a*  
589 concentrations were the best predictor of methane effluxes from reservoirs. They  
590 also concluded that eutrophic reservoirs emitted an order of magnitude more  
591 methane than did oligotrophic reservoirs. Among 224 lakes from Quebec  
592 (Canada), Rasilo *et al.* (2015) found that methane effluxes were positively  
593 correlated with temperature and lake nutrient status, and negatively correlated  
594 with lake area and dissolved humic matter concentrations. West *et al.* (2012)  
595 showed that additions of algae (i.e., *Scenedesmus*) promoted substantially  
596 higher rates of CH<sub>4</sub> production than did equivalent additions of terrestrially  
597 derived organic matter (i.e., maple leaves) in laboratory experiments. Anoxia and  
598 high organic matter content promotes methanogenesis especially in the  
599 sediments of eutrophic lakes and reservoirs (Rudd & Hamilton, 1978; Molongoski  
600 & Klug, 1980). Hypolimnia with low oxygen or anoxia are also commonly  
601 encountered in small temperate and boreal humic lakes (Juutinen *et al.*, 2009;  
602 Rinta *et al.*, 2015). Methanotrophy predominately takes place at the interface  
603 zone between oxic and anoxic layers at the sediment surface or in the water  
604 column (Rudd & Hamilton, 1978; Kankaala *et al.*, 2006a; Bastviken *et al.*, 2008;  
605 Schubert *et al.*, 2010). Thus, CH<sub>4</sub> contributions have been shown to be significant  
606 especially for chironomids in the profundal zone of some eutrophic lakes (Deines  
607 *et al.*, 2007; Ravinet *et al.*, 2010; Jones & Grey, 2011) and for pelagic  
608 cladocerans in seasonally stratified humic lakes (Taipale *et al.*, 2008; Kankaala  
609 *et al.*, 2013). Because methanogenesis is a less energetically favorable reaction  
610 in regards to Gibbs free energy, we hypothesize that the most easily metabolized  
611 organic matter (e.g., algal and non-lignified littoral detritus) will preferentially  
612 support acetoclastic methane production, and thus methane-based food webs in  
613 freshwater ecosystems. Hydrogenotrophic methanogens can utilize carbon  
614 dioxide and hydrogen, both produced by fermenting and syntrophic bacteria

615 during earlier steps of anaerobic organic matter decomposition (Conrad, 1999;  
616 2005). In this pathway the energy comes from the hydrogen because CO<sub>2</sub> does  
617 not contain usable energy. In nutrient poor environments the hydrogenotrophic  
618 pathway seems to be more important than acetoclastic methanogenesis (Casper,  
619 1996; Galand *et al.*, 2010). At present the magnitude of methanogenic pathway  
620 from allochthonous organic and/or inorganic carbon to freshwater food webs is  
621 unknown.

622

623 *You are what you eat, and you eat what you are*

624 We hypothesize that organisms at the plant-animal interface preferentially  
625 consume and assimilate basal resources that best match their own biochemical  
626 composition, as well as their innate ability to synthesize structural molecules from  
627 dietary precursors. Considerable research also shows the lipid composition of  
628 herbivorous zooplankton is strongly influenced by their diets (Brett *et al.*, 2006;  
629 Ravet *et al.*, 2010; Burns *et al.*, 2011; Taipale *et al.*, 2011; Galloway *et al.*, 2015;  
630 Taipale *et al.*, 2015) (Fig. 2). In streams and larger rivers, caddis and mayfly  
631 larvae, amphipods, and snails similarly strongly reflect the fatty acid composition  
632 of their food (Steinman *et al.*, 1987; Torres-Ruiz *et al.*, 2007, 2010; Lau *et al.*,  
633 2009a; Gladyshev *et al.*, 2012; Larson *et al.*, 2013; Guo *et al.*, 2016b). This link  
634 between the biochemical composition of the food and that of consumers is critical  
635 because terrestrially derived carbon has a profoundly different elemental and  
636 biochemical composition than does algae. Because of its very high proportion of  
637 lignocellulose, on a per carbon basis, the terrestrial carbon of higher plant origin  
638 is a poor carbon source for animal production. At the crudest stoichiometric level,  
639 terrestrial plant material is also nutritionally much more imbalanced than  
640 freshwater autotrophic matter relative to herbivorous invertebrate demands, with  
641 carbon to phosphorus and carbon to nitrogen ratios on average three times  
642 greater in terrestrial plants than aquatic autotrophs (Elser *et al.*, 2000). This  
643 difference is a consequence of the previously mentioned prominence of carbon  
644 intensive structural molecules (i.e.,  $\approx$  90% cellulose, hemicelluloses and lignin)  
645 in terrestrial plant tissues (Lynd *et al.*, 2002). Variations in the nutrient

646 stoichiometry and elemental imbalances of basal food sources also profoundly  
647 affect the excretion rates (and hence production efficiency) of certain  
648 macroinvertebrates in streams, with greater retention of limiting nutrients (e.g., P)  
649 than would be predicted by a stoichiometric mass-balance model (Rothlisberger  
650 *et al.*, 2008).

651 At a more detailed scale of biochemical resolution, terrestrial plants are  
652 devoid of the essential fatty acids upon which the nutritional physiology of  
653 zooplankton, benthic invertebrates, and especially fish production depends, such  
654 as eicosapentaenoic acid (EPA; 20:5 $\omega$ 3), docosahexaenoic acid (DHA; 22:6 $\omega$ 3),  
655 and arachidonic acid (ARA, 20:4 $\omega$ 6) (Mayer & Likens, 1987; Brett & Müller-  
656 Navarra, 1997; Sargent *et al.*, 1999; Brett *et al.*, 2009; Lau *et al.*, 2009a, 2012;  
657 Guo *et al.*, 2016c). The fatty acid composition of primary producers varies  
658 tremendously between terrestrial and aquatic basal resources and even within  
659 algal groups (Guschina & Harwood, 2006; Torres-Ruiz *et al.*, 2007; Brett *et al.*,  
660 2009; Galloway & Winder, 2015; Guo *et al.*, 2015; Hixson *et al.*, 2015). The  
661 short-chain  $\omega$ -3  $\alpha$ -linolenic acid ( $\alpha$ -LA; 18:3 $\omega$ 3) is commonly synthesized by  
662 distinct phytoplankton and benthic algal species including green algae and some  
663 cyanobacteria (Gugger *et al.*, 2002; Taipale *et al.*, 2016), but the long-chain  $\omega$ -3  
664 PUFA, including EPA and DHA are only synthesized by certain algal taxa (e.g.,  
665 cryptophytes, diatoms, dinoflagellates, golden algae and raphidophytes; Ahlgren  
666 *et al.*, 1992; Taipale *et al.*, 2013, 2016), as well as some stream-dwelling moss  
667 species (Kalacheva *et al.*, 2009). Very few freshwater heterotrophic bacteria can  
668 synthesize  $\omega$ -3 PUFA in significant amounts, although interestingly a small  
669 number of marine bacteria species do synthesize these molecules (Russell &  
670 Nichols, 1999). Higher plants can synthesize  $\alpha$ -LA, but lack the enzymes  
671 necessary to elongate and desaturate this molecule to EPA and DHA (Guschina  
672 & Harwood, 2006), the physiologically active  $\omega$ -3 molecules in animals. Some  
673 animals can elongate and desaturate  $\alpha$ -LA to EPA and DHA, however, the  
674 conversion rate is low in many aquatic consumers (Koussoroplis *et al.*, 2014;  
675 Murray *et al.*, 2014). For example, conversion is below 0.5% in herbivorous  
676 *Daphnia* (von Elert, 2002; Taipale *et al.*, 2011), and thus *Daphnia* require EPA

677 directly from their diets. In addition to EPA and DHA, metazoan zooplankton  
678 require dietary sterols for optimal somatic growth and reproduction (Martin-  
679 Creuzburg & von Elert, 2009). The terrestrial organic carbon available to support  
680 aquatic production is almost entirely devoid of essential fatty acids and sterols  
681 (Brett *et al.*, 2009; Taipale *et al.*, 2014), regardless if this carbon is incorporated  
682 directly as t-POC or indirectly as t-DOC via a bacterial pathway. As terrestrial  
683 plant matter is processed by soil microbes, these elemental and biochemical  
684 imbalances are exacerbated. Furthermore, metazoans also require amino acids,  
685 vitamins and other biomolecules for somatic growth and reproduction for which t-  
686 POC is also a poor source.

687

688 *Terrestrial resources can be important prey for fish*

689 It is well established that terrestrial invertebrates (e.g., grasshoppers, ants,  
690 beetles and cicadas) are important prey for some fish species (especially  
691 salmonids and centracids) in small streams and the littoral regions of some lakes  
692 (Elliot, 1970; Wipfli, 1997; Nakano & Murakami, 2001; Francis & Schindler,  
693 2009). This natural history knowledge has been familiar to most anglers for  
694 several centuries (Walton, 1653). It is also well known that in New Zealand,  
695 Mongolia, and Alaska small rodents can be important prey for larger trout that  
696 facilitate rapid growth during years when rodent populations periodically erupt  
697 (Wyatt, 2013; Lisi *et al.*, 2014) (Fig. 3). Many tropical fish consume the fruits of  
698 terrestrial vegetation and thereby play an important role in seed dispersal  
699 (Boujard *et al.*, 1990; Correa *et al.*, 2007). In all of these cases, fish are  
700 consuming terrestrial resources with very low or no lignocellulose content and  
701 low C:N ratios. However, where riparian invertebrates are important for fish diets,  
702 it is also notable that it has been shown in some cases that the production of  
703 riparian invertebrates is strongly dependent on aquatic prey such as emergent  
704 insects (Power *et al.*, 2004; Stenroth *et al.*, 2015; Recalde *et al.*, 2016). Bastow  
705 *et al.* (2002) even showed that supposedly “terrestrial” invertebrates obtained  $\approx$   
706 90% of their carbon as well as most of their water from algal mats that were  
707 stranded along the river margin during the summer drought period.

708

709 *Marine allochthony: the exception that proves the rule!*

710 Because allochthonous means something transported from elsewhere into a  
711 particular system, technically riverine phytoplankton inputs to an estuary would  
712 be allochthonous, whereas primary production within the estuary by *Phragmites*  
713 *australis* or *Spartina* spp. would be autochthonous. However, from a biochemical  
714 and nutritional perspective nearly all the important distinctions between  
715 allochthonous and autochthonous carbon subsidies relate to the differences  
716 between higher vascular plants and algae. Heterotrophic bacteria and  
717 cyanobacteria have other characteristics (such as a dearth of sterols and  
718 essential fatty acids) that place them into a third biochemical and low food quality  
719 category. As previously noted, terrestrial vascular plants have a high proportion  
720 of structural lignocellulose, high relative saturated fatty acid content, and no  
721 highly unsaturated C<sub>20</sub> or C<sub>22</sub> PUFA (Brett *et al.*, 2009). Submerged vascular  
722 plants tend to have lower C:N:P ratios than emergent vascular plants (Demars &  
723 Edwards, 2007), probably due to a lesser need for structural lignocellulose, and  
724 are therefore probably somewhat more palatable (e.g., Jacobsen & Sand-  
725 Jensen, 1994; Elger & Willby, 2003). Conversely, all algae whether  
726 phytoplankton or periphyton have little structural carbon, and oftentimes high  
727 essential fatty acid content (Brett & Müller-Navarra, 1997; Brett *et al.*, 2009). It is  
728 probably biochemically irrelevant whether algal production in lakes is pelagic or  
729 benthic because, for example, benthic and pelagic diatoms are closely related  
730 and have similar nutritional value. From this biochemical perspective, riverine  
731 planktonic diatoms advected into an estuary would be expected to be high food  
732 quality for herbivorous invertebrates (Jassby & Cloern, 2000; de Moura *et al.*,  
733 2016), whereas the autochthonous production by *Phragmites* or *Spartina* would  
734 be expected to be very low quality. A similar phenomenon has been observed in  
735 the Upper Mississippi, where consumers (bluegill sunfish, zebra mussels,  
736 pocketbook mussels) from the main channel (where diatoms predominated) had  
737 significantly higher long-chain PUFA content than the same species occupying  
738 backwater habitats, where detrital inputs and cyanobacteria were more prevalent

739 (Larson *et al.*, 2015). Therefore, the type of primary production (i.e., vascular  
740 plants or algae) is actually much more important than whether this production is  
741 allochthonous or autochthonous.

742 To emphasize the point that the most salient difference between  
743 allochthonous and autochthonous subsidies to aquatic invertebrates is the  
744 biochemical composition of this material, consider the case of marine subsidies  
745 to salmonids in river systems in the north Pacific. The classic paradigm in these  
746 systems was that spawning Pacific salmon (*Oncorhynchus* spp.) support  
747 production within streams via an inorganic marine derived nutrient pathway  
748 (Naiman *et al.*, 2002). However, as has long been known by anglers (Route,  
749 1991) and recent research has shown (Naiman *et al.*, 2002; Schindler *et al.*,  
750 2003; Wipfli *et al.*, 2003), resident and juvenile anadromous salmonids are also  
751 directly supported by very high food quality salmon eggs and flesh (Fig. 4). In this  
752 case, the marine derived carbon is clearly allochthonous to the salmon nursery  
753 streams, but outstanding fish growth rates are obtained (Denton *et al.*, 2009) due  
754 to the very high lipid and essential fatty acid content of this organic matter  
755 (Sargent *et al.*, 1999; Ravet *et al.*, 2010; Wipfli & Baxter, 2010). Ultimately, the  
756 growth of aquatic invertebrates and fish is predicated on the biochemical  
757 composition and nutritional value of their diets, and not the spatial origin of this  
758 matter.

759

#### 760 *Catabolic and anabolic partitioning of basal resources*

761 Karlsson (2007) presented the intriguing hypothesis that terrestrial carbon  
762 sources might be predominantly used to support catabolic metabolism, whereas  
763 algal derived carbon is the primary support for anabolic production. According to  
764 this hypothesis, organisms utilizing terrestrial carbon would obtain an energetic  
765 benefit from this resource, but this might leave almost no trace in their somatic  
766 lipid composition or stable isotope ratios. This possibility presents interesting  
767 challenges for field projects attempting to quantify terrestrial carbon subsidies to  
768 upper trophic levels. Brett *et al.* (2009) showed that when *Daphnia* were given  
769 diets comprised of 50% high quality phytoplankton and 50% low quality t-POC,

770 they obtained higher production rates than would have been expected had they  
771 only consumed half as much phytoplankton as used in the 100% phytoplankton  
772 treatment. When offered alone, this experiment showed t-POC resulted in a  
773 *Daphnia* growth efficiency of 5%, whereas pure phytoplankton diets resulted in  
774 growth efficiencies of  $\approx 40\%$  (Brett *et al.*, 2009). When offered a 50:50 t-POC  
775 and phytoplankton diet mixture the overall growth efficiency for the mixed diet  
776 was  $\approx 30\%$ , which indicates the partial growth efficiency for the t-POC fraction of  
777 the diet was  $\approx 20\%$ . This clearly suggests that when offered a mixed diet, the  
778 *Daphnia* did realize a benefit from the terrestrial carbon available to them. It also  
779 suggests that utilization of low quality terrestrial basal resources may be greatly  
780 enhanced by the simultaneous consumption of high food quality algae (Taipale *et al.*  
781 *et al.*, 2014). Wetzel (1995) hypothesized that allochthonous resources may  
782 function as a metabolic "lifeboat" by providing low quality resources that allow  
783 consumers to survive during periods when more nutritious autochthonous  
784 resources are not available. Taipale *et al.* (2016) recently revealed that *Daphnia*  
785 utilize carbohydrates (glucose) from t-POC for energy and save essential fatty  
786 acids and amino acids for somatic growth and reproduction, thus using a "sparing  
787 strategy" to maximize their somatic growth and reproduction under nutritional  
788 stress.

789

#### 790 *Allochthonous inputs: small flux and low quality*

791 As previously noted, our analysis showed inputs of particulate terrestrial  
792 carbon and bacterial production are usually much smaller than the combined  
793 benthic and pelagic primary production in lakes (see Fig. 1). Brett *et al.* (2009),  
794 Wenzel *et al.* (2012a) and Taipale *et al.* (2014) also showed t-POC is a much  
795 lower quality food resource for zooplankton growth and reproduction than many  
796 phytoplankton (although the food quality of cyanobacteria was similarly poor  
797 compared to t-POC). So far, Brett *et al.* (2009) are the only authors to have  
798 successfully reared zooplankton through to reproduction on an exclusive diet of t-  
799 POC (Fig. 5). When fed finely ground fresh red alder (*Alnus rubra*) leaves for 22  
800 days, *Daphnia* had > 90% survival and produced an average of  $3.1 \pm 2.7$  ( $\pm$  SD)

801 neonates each. These individuals also grew to an average dry weight of  $0.22 \pm$   
802  $0.05$  mg individual<sup>-1</sup> (Fig. 5). In contrast, *Daphnia* from the same maternal cohort  
803 fed the alga *Cryptomonas ozolinii* had 100% survival, produced an average of  
804  $69.5 \pm 23.2$  neonates ind.<sup>-1</sup>, and had an average DW of  $1.06 \pm 0.16$  mg ind.<sup>-1</sup> by  
805 the same age (Fig. 5). These results show fresh t-POC is a viable resource for  
806 aquatic herbivores, albeit a much lower quality one than nutrient rich algae such  
807 as cryptophytes or diatoms. Similar results were observed with stream-dwelling  
808 benthic invertebrates, in which hydropsychid caddisfly larvae fed algae or  
809 autumn-shed leaves lost weight when switching from algal- to detritus-based  
810 diets (Torres-Ruiz *et al.*, 2010). Similarly, shredder caddis larvae reached a  
811 smaller body size when fed on low quality terrestrial leaf litter and their growth  
812 was substantially boosted as the availability of high quality algae attached to leaf  
813 surfaces increased (Guo *et al.*, 2016a). The benthic generalist isopod *Asellus*  
814 *aquaticus* also lost weight when solely fed leaf litter (growth =  $-0.017 \pm 0.001$  d<sup>-1</sup>)  
815 similar to experimentally starved individuals (growth =  $-0.018 \pm 0.002$  d<sup>-1</sup>) (Lau *et al.*,  
816 2013). Conversely, when *Asellus* was provided a mixed diet of algae and leaf  
817 litter its growth rate was greatly enhanced (growth =  $0.022 \pm 0.005$  d<sup>-1</sup>).

818 The bacterial pathway to upper trophic level consumers entails two potentially  
819 large energetic penalties, i.e., low growth efficiency relative to algae if directly  
820 consumed by herbivores or additional trophic steps if utilized by protozoa prior to  
821 being consumed by zooplankton (Stockner & Porter, 1988). For example, Taipale  
822 *et al.* (2012) showed experimentally that all *Daphnia* fed only bacteria died before  
823 reproducing. However, Taipale *et al.* (2012) also showed *Daphnia* could tolerate  
824 bacteria dominated diets, especially if mixed with very nutritious cryptophytes.  
825 These results suggest that bacteria are similarly poor nutritional quality as t-POC  
826 for herbivorous metazoan. For example, the fatty acid profiles of *Daphnia*  
827 experimentally fed t-POC derived from terrestrial leaves did not differ from  
828 animals that were experimentally starved (Galloway *et al.*, 2014; Taipale *et al.*,  
829 2015). Similarly, when *Daphnia* were fed a 95% Actinobacteria and 5%  
830 cryptophyte dietary mixture, they had FA profiles that were much more similar to  
831 cryptophytes than Actinobacteria (Galloway *et al.*, 2014). The median flux

832 estimates from Fig. 1 suggest t-POC, bacteria and algal carbon fluxes contribute  
833  $\approx 5\%$ ,  $\approx 25\%$  and  $\approx 70\%$  of the particulate matter available for consumption by  
834 herbivorous zooplankton in lakes. If these flux estimates are corrected for the  
835 large differences in food quality (i.e., phytoplankton are a factor  $\approx 10$  higher food  
836 quality than either t-POC or bacteria), then the median values presented in Fig. 1  
837 equate to t-POC plus processed t-DOC, bacteria and algae on average  
838 supporting 1.7% (0.6-4.9%), 2.9% (1.3-5.6%), and 93.7% (87.7-96.6%) of  
839 consumer production, respectively.

840

#### 841 *t-DOC suppression of upper trophic level production*

842 As has been previously noted, high t-DOC concentrations in lakes may  
843 strongly suppress pelagic and benthic primary production (Jones, 1992;  
844 Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009), thereby increasing the relative  
845 availability of allochthonous energy sources. In oligotrophic clearwater lakes  
846 ( $\text{DOC} < 5 \text{ mg C L}^{-1}$ ), nutrients (nitrogen and phosphorus) associated with a  
847 moderate increase in t-DOC concentration may slightly stimulate primary  
848 production and/or brown-colored DOC may play a protective role in UV screening  
849 (Finstad *et al.*, 2014; Seekell *et al.*, 2015). However, due to PAR attenuation and  
850 phosphorus sequestration, it is typical for high t-DOC lakes to have much less  
851 phytoplankton and benthic algal biomass and production than would be expected  
852 in clearwater lakes with similar phosphorus concentrations (Jones, 1992;  
853 Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009; Thrane *et al.*, 2014). For  
854 example, del Giorgio & Peters (1994) reported strongly inhibitory effects of DOC  
855 on phytoplankton photosynthesis and showed that excess carbon (DOC) was  
856 respired as  $\text{CO}_2$  and therefore not available as reduced carbon for biomass  
857 production in higher trophic level consumers. Bacteria using t-DOC as their  
858 carbon source have generally poor growth efficiency ( $<10\%$ ) (e.g., del Giorgio &  
859 Cole, 1998; Eiler *et al.*, 2003; Räsänen *et al.*, 2016) and additional steps within  
860 the microbial food web (heterotrophic nanoflagellates, ciliates) further increase  
861 respiratory losses. It was similarly demonstrated that primary production  
862 decreased with increasing DOC in oligotrophic lakes (Carpenter *et al.*, 1998),

863 suggesting that increasing DOC in aquatic ecosystems reduced light availability  
864 for primary production and consequently dietary energy for consumer production.  
865 This was supported by the results of Kelly *et al.* (2014) who found a negative  
866 relationship between t-DOC concentration and zooplankton biomass in ten  
867 temperate lakes within a DOC gradient of 5-25 mg C L<sup>-1</sup>. Similarly, Karlsson *et al.*  
868 (2015) found a negative correlation between DOC concentration (7-22 mg C L<sup>-1</sup>)  
869 and fish productivity in small boreal lakes, even though stable isotopes indicated  
870 t-DOC contributed to fish production. Rask *et al.* (2014) also reported that fish  
871 growth declined as lake t-DOC concentrations increased. Similar to this finding,  
872 Lau *et al.* (2014) also showed that consumer production and quality, measured  
873 as tissue PUFA concentrations, depended on the degree of autochthony in food  
874 chains of humic and oligotrophic lakes. Based on the very low food quality of t-  
875 POC and the low food quality and/or longer pathway for bacterial incorporation  
876 into upper trophic levels, it is likely that algal primary production will be the most  
877 important resource supporting upper trophic levels in most oligotrophic lakes.

878 Benthic algal production is strongly related to mean lake depth and water-  
879 clarity which can be greatly inhibited by high algal biomass due to eutrophication  
880 or as previously mentioned high t-DOC concentrations (Vadeboncoeur & Lodge,  
881 2000; Vadeboncoeur *et al.*, 2003). However, the role of t-DOC in suppressing  
882 total primary productivity may be complex. For example, Vesterinen *et al.* (2016)  
883 observed that in a small lake with very high t-DOC (ca. 30 mg C L<sup>-1</sup>), and  
884 therefore a shallow euphotic zone (< 1m) with very low pelagic primary  
885 production, littoral algal primary production was relatively high and contributed to  
886 > 90% to the overall summertime primary production.

887

888 *Interpreting stable isotope mixing models - assumptions can be very influential*

889 The most consistent evidence presented to suggest that terrestrial subsidies  
890 to aquatic consumers are strong comes from the recent outputs of Bayesian  
891 stable isotope mixing models (SIMMs). However, Bayesian SIMMs have several  
892 quirks that are currently poorly understood. For example, when the resource  
893 datasets considered in Bayesian SIMMs are highly variable or the models are

894 mathematically under-determined, these analyses tend to produce outcomes that  
895 are strongly influenced by the prior generalist assumption (Fry, 2013a,b; Brett,  
896 2014b). If a resource is included in a Bayesian SIMM, it will almost always be  
897 included in the solution at substantial levels even if it is of no real importance  
898 (Fry, 2013a; Brett, 2014b). Furthermore, fractionation-corrected consumers often  
899 fall well outside of the hypothesized resource polygons in this field literature (e.g.,  
900 Cole *et al.*, 2011; Solomon *et al.*, 2011; Berggren *et al.*, 2014; Tanentzap *et al.*,  
901 2014). These cases indicate there is a fundamental flaw in the dataset; for  
902 example, either an important food resource was left out of the analysis, or the  
903 wrong trophic enrichment factors were used for the consumer (see Bunn *et al.*,  
904 2013), or the correct foods with the wrong stable isotope values were used in the  
905 analysis. Unfortunately, unlike conventional mass balance analyses, current  
906 Bayesian SIMMs do not recognize obvious signs of a misspecified model in their  
907 numerical outputs and these algorithms output a result no matter how  
908 mismatched the underlying data are. To avoid these problems, scientists are  
909 encouraged to plot their data and make sure samples fall within the mixing  
910 polygons (Phillips *et al.*, 2014), in addition to solely considering the numerical  
911 outputs from SIMMs.

912 One of the biggest challenges for these types of analyses is obtaining  
913 estimates for the stable isotope values of the phytoplankton component of  
914 zooplankton diets (Brett, 2014a). Because the phytoplankton are mixed with the  
915 detrital, bacterial and protozoan components of the seston, it is rarely possible to  
916 obtain a direct estimate of phytoplankton stable isotope values (but see Vuorio *et al.*,  
917 2006). A variety of methods have been employed to resolve this problem. For  
918 example, some authors estimate the  $\delta^{13}\text{C}$  value of the phytoplankton by  
919 assuming a "photosynthetic fractionation factor" ( $\epsilon_p$ ) to predict the  $\delta^{13}\text{C}$  value of  
920 the phytoplankton from directly determined  $\delta^{13}\text{C}$  values for the  $\text{CO}_2$  in the water  
921 (Brett, 2014a). Other studies have directly measured the  $\delta^{13}\text{C}$  values of large  
922 sized phytoplankton, which can be separated from the seston using a variety of  
923 methods (Vuorio *et al.*, 2006). A few studies (Pace *et al.*, 2007; Kankaala *et al.*,  
924 2010; Berggren *et al.*, 2014; Taipale *et al.*, 2016) have estimated the  $\delta^{13}\text{C}$  value

925 using algal specific lipid biomarkers, especially PUFA. Other authors have simply  
926 assumed fixed  $\delta^{13}\text{C}$  values for the phytoplankton within the seston (Karlsson *et*  
927 *al.*, 2012). Direct measurements  $\delta^{13}\text{C}$  values of phytoplankton (Zohary *et al.*,  
928 1994; Grey *et al.*, 2000; Vuorio *et al.*, 2006; Taipale *et al.*, 2016) have shown  
929 considerable variability ( $\pm 7\text{‰}$ ) in isotopic values between phytoplankton taxa, as  
930 well as within taxa between seasons and lakes. Using the stable isotope values  
931 of fatty acids that are characteristic for phytoplankton, Taipale *et al.* (2016)  
932 recently found the  $\delta^{13}\text{C}$  values of the dominant phytoplankton taxa could explain  
933 most of the variation in the  $\delta^{13}\text{C}$  values of the zooplankton in humic lakes.  
934

### 935 *Conclusions*

936 In a period of unprecedented global change from climate change, land use  
937 alterations, and species invasions we should be asking, “Which basal resources  
938 are the most important to sustain the growth and reproduction of aquatic  
939 invertebrates and fish in aquatic ecosystems”, and “how might anthropogenic  
940 changes to temperature, nutrients, and light regimes change the supply of high  
941 quality resources?” It is clear from the literature that aquatic systems that have  
942 the largest terrestrial inputs may also be the systems with the lowest rates of  
943 secondary production relative to basal carbon fluxes (Karlsson *et al.*, 2015). This  
944 could be due to the very low food quality of terrestrial carbon sources (Brett *et al.*,  
945 2009; Lau *et al.*, 2013), as well as the fact that in some systems large inputs of t-  
946 DOC actually inhibit pelagic and especially benthic algal production (Jones,  
947 1992; Vadeboncoeur *et al.*, 2008; Karlsson *et al.*, 2009). The presence of a  
948 resource does not prove its importance. In fact, from a mass balance and kinetics  
949 perspective, a high standing stocking of a constituent (e.g., t-DOC) actually  
950 indicates that this constituent has low reactivity and thus is unlikely to be an  
951 important resource for consumers (Brett *et al.*, 2012). It is also entirely possible  
952 for the system to be net heterotrophic due to microbial respiration of terrestrial  
953 carbon and still have fish production strongly supported by an algae-invertebrate  
954 pathway (Thorp & Delong, 2002; Lau *et al.*, 2014). Support of upper trophic level  
955 production by terrestrial carbon inputs may depend on the simultaneous

956 availability of essential biomolecules synthesized by algae. Stream studies  
957 suggest that even when allochthonous inputs greatly dominate, invertebrate and  
958 fish production is very preferentially supported by algal basal resources (Mayer &  
959 Likens, 1987; Bunn *et al.*, 2003; Brito *et al.*, 2006; Lau *et al.*, 2009a). Lake  
960 studies suggest terrestrial carbon inputs generally have much lower mass fluxes  
961 and very low food quality, so the large majority of lake food webs are primarily  
962 supported by algal production. There is no doubt that in some systems  
963 considerable amounts of terrestrially derived carbon are ingested and assimilated  
964 by herbivorous organisms; but because of the recalcitrant biochemical  
965 composition of this material, it is utilized a factor 5-10 less efficiently than algal  
966 basal resources. Not all carbon-based molecules are equally bioavailable, and  
967 specific biochemicals synthesized by particular primary producers may have an  
968 inordinate influence on the productivity of upper trophic levels. Fish production in  
969 particular may be highly dependent on specific basal producers that synthesize  
970 biochemically high quality organic matter including large amounts of essential  
971 long carbon chain polyunsaturated fatty acids (Sargent *et al.*, 1999). As we learn  
972 more about the nutritional underpinnings of consumer production in aquatic  
973 habitats, we can better predict how their populations will respond to  
974 environmental changes that influence the fluxes, quality, and composition of their  
975 terrestrial and aquatic food sources.

976

#### 977 *Future perspectives*

978 Both the lake and stream literature on reduced carbon influxes is  
979 characterized by small data sets. More field data for a much wide range of  
980 aquatic ecosystems will improve our understanding of when and where  
981 substantial terrestrial support of consumer production is plausible. Similarly, our  
982 current understanding of how land-use and climate change might affect the influx  
983 of terrestrial resources to aquatic systems and autochthonous production within  
984 these systems is only rudimentary. Much of what has been published on this  
985 topic is based on stable isotope mixing models that can be highly dependent on  
986 poorly constrained assumptions (e.g., the stable isotope values of phytoplankton,

987 environmental water contributions to consumers, isotopic fractionation in  
988 consumers, missing isotopic data for protozoa, etc.). These types of analyses  
989 should be validated with direct evidence that the hypothesized scenarios are  
990 plausible from a nutritional perspective. Only a few studies have directly  
991 compared consumer growth and reproduction for algal, bacterial and terrestrial  
992 organic matter dominated diets, and future studies could expand our  
993 understanding of what resources can actually support consumer production.  
994 Several studies have suggested that terrestrial and aquatic resources may  
995 support different aspects of consumer production (i.e., catabolism and  
996 anabolism), and terrestrial resources might allow some consumers to survive  
997 periods when more nutritious resources are seasonally limited (i.e., the Wetzel  
998 lifeboat hypothesis). High quality aquatic resources may also greatly enhance the  
999 ability of consumers to utilize much lower quality terrestrial resources. These are  
1000 particularly interesting lines of inquiry for future research.  
1001

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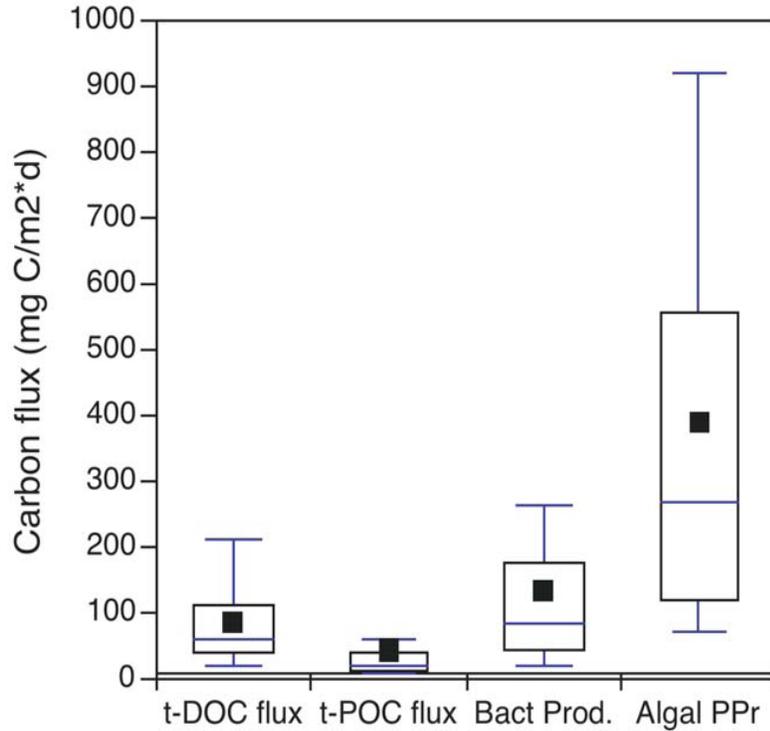
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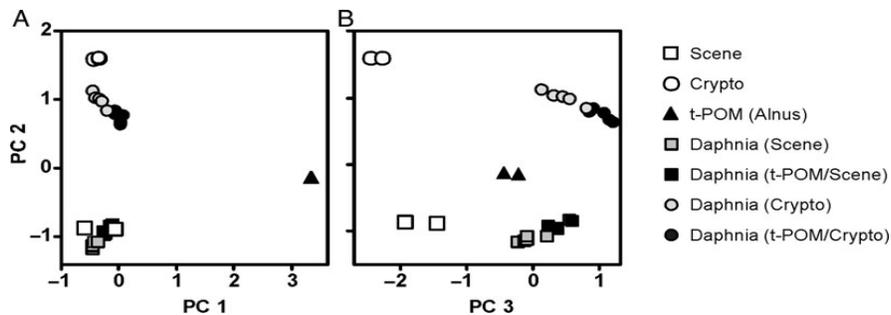
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1690  
 1691 Fig. 1. The mass influx of dissolved and particulate carbon from terrestrial  
 1692 sources and the in-lake production of bacteria and benthic/pelagic algae based  
 1693 on individual lake observations (Brett *et al.*, 2012). Only algal production data  
 1694 from lakes with total phosphorus  $\leq 20 \mu\text{g L}^{-1}$  were used. Terrestrial particulate  
 1695 loading was calculated based on direct the aeolian transport data from Preston *et al.*  
 1696 (2008) while also assuming fluvial t-POC inputs are equal to 10% of t-DOC  
 1697 loading (Wetzel, 2001). Bacteria production was estimated from algal production  
 1698 based on a model derived from data provided by Fouilland & Mostajir (2010). The  
 1699 mid-line in the box and whisker plots represents the sample median, the filled  
 1700 box represents mean, the outer margins represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles  
 1701 and the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentiles. The sample sizes were  
 1702  $n = 20, 8$  and  $58$ , respectively, for t-DOC, t-POC, and algal production mass  
 1703 fluxes.  
 1704



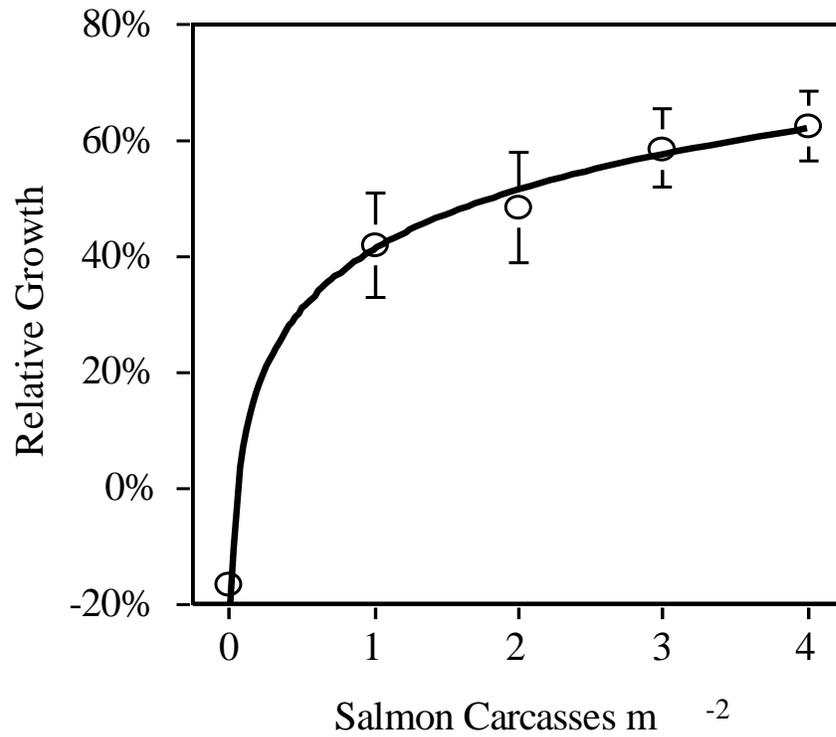
1705  
 1706 Fig. 2. A principal components analysis of the fatty acid composition of terrestrial  
 1707 detritus (i.e., finely-ground *Alnus rubra*; t-POM), phytoplankton (i.e.,  
 1708 *Scenedesmus acutus* and *Cryptomonas ozolinii*), and *Daphnia* fed either pure or  
 1709 mixed diets of phytoplankton and t-POM (Taipale *et al.*, 2015). Diet samples are  
 1710 the fatty acid profiles of *Alnus* (t-POM; black triangle), *Scenedesmus* (Scene;  
 1711 open square), or *Cryptomonas* (Crypto; open circle). Samples labeled “Daphnia”  
 1712 represent *Daphnia* fatty acid profiles after consuming *Scenedesmus* (gray  
 1713 square), *Cryptomonas* (gray circles), or mixed diets of *Alnus-Scenedesmus*  
 1714 (black squares) and *Alnus-Cryptomonas* (black/white circles). The first PC  
 1715 explained 21.7% of the variability and separated the *Alnus* from the  
 1716 phytoplankton diets and all *Daphnia*. This PC was strongly positively correlated  
 1717 with the SAFAs 14:0, 16:0, 20:0, 22:0 and 24:0. The second PC explained 53.8%  
 1718 of the variability and separated the two phytoplankton diets as well as *Daphnia*  
 1719 consuming these diets, and was positively correlated with LIN, 18:1 $\omega$ 9, and ALA,  
 1720 and negatively with SDA, EPA and DHA. The third PC explained 12.0% of the  
 1721 variability and separated *Daphnia* from their diets. This PC was positively  
 1722 correlated with ARA.  
 1723



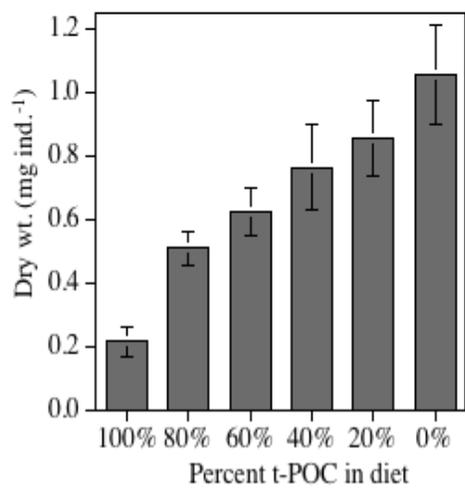
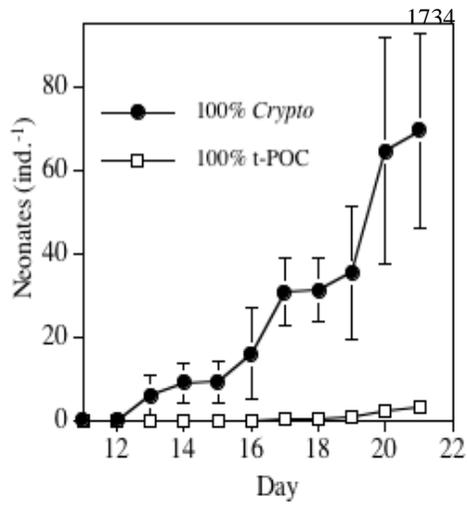
1724

1725 Fig. 3. An aquatic consumer (*Salmo trutta*) which has consumed a large mass of  
1726 terrestrial resources (the house mouse *Mus musculus*). In New Zealand mice  
1727 populations often erupt when various trees (especially beech, *Nothofagus* spp.)  
1728 have prolific seedfalls (Choquenot & Ruscoe, 2000). When these masting events  
1729 occur, mice can become important prey for salmonid fish such as *S. trutta* and  
1730 *Oncorhynchus mykiss*. Image taken by Steve Fox and used with permission.

1731



1732 Fig. 4. Mean growth of juvenile Coho salmon ( $\pm$  SE) over 66 days when exposed  
1733 to a gradient of salmon carcass additions. Adapted from Wipfli *et al.* (2003).





1752

1753 leaves from various riparian plants. The *Daphnia* in these panels were matched up from  
 1754 parallel maternal broods. The error bars in these plots represent  $\pm 1$  SD.

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