Author(s): Brett, Michael T.; Bunn, Stuart E.; Chandra, Sudeep; Galloway, Aaron W. E.; Guo, Fen; Kainz, Martin J.; Kankaala, Paula; Lau, Danny C. P.; Moulton, Timothy P.; Power, Mary E.; Rasmussen, Joseph B.; Taipale, Sami; Thorp, James H.; Wehr, John D.

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

Year: 2017

Version:

Please cite the original version:

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

4

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29

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

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
78 al.*, 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 (Skyllberg *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*

147   *al.*, 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 $\leqslant$ 20 µg 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 mg carbon m^{-2} 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 mg C m^{-2} d^{-1}), $\geqslant$ 98%

197 of the t-DOC flux is advected because t-DOC is processed at only $\approx$ 0.1% 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 mg carbon m^{-2} 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) mg carbon m^{-2} 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}C values indicating algal diets in scraping grazers from very small
240 shaded headwater streams (draining 0.2 km^2) down through middle-sized rivers
241 (drainage areas of 4000 km^2 (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_2

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_2 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*
289 *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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 km^2

340 benthic algae had depleted ^{13}C values relative to terrestrial vegetation by 3 to

341 9‰, but for watershed surface areas ranging from 10 to 1,000 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 CO_2, which has a δ^{13}C value of about -8‰. Because of the relatively high

346 demand for CO_2 in productive waters, algae discriminate relatively little towards

347 the lighter isotope and thus incorporate a ^{13}C value which is enriched by about -

348 15 to -23‰ relative to terrestrial C3 plants (which have nearly constant δ^{13}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 CO_2 and thus

353 fractionate more towards the lighter isotope, and become less enriched than the

354 δ^{13}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 δ^{13}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 km² 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 $\delta^{13}C$ 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 $\delta^{13}C$ (or $\delta^{15}N$) 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 ± 1 MJ kg^{-1} (± 1 SD) (Friedl *et al.*, 2005), which is slightly

431 higher than for proteins and carbohydrates (i.e., 17 MJ kg^{-1}), but considerably

432 less than the average energy content of fats (38 MJ kg^{-1}) and alcohols (29 MJ kg^{-1})

433 ^{1}) (Blaxter, 1989). It is obvious that many synthetic organic compounds such as

434 plastics have a high-energy content (20-46 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_2O_2 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 ω3
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*

525 *al.*, 2016a). Although the shredders obtained most of their carbon by leaf

526 consumption, they acquired and selectively retained their physiologically

527 important fatty acids (ω3 PUFA) from high quality algae. Likewise, results from

528 manipulative feeding experiments in Lau *et al.* (2013) showed pre-conditioned

529 leaf litter alone could not sustain the somatic growth of the isopod *Asellus*

530 *aquaticus*, which is a common benthic generalist in boreal freshwaters. Supplying

531 leaf litter and algae together, however, substantially enhanced somatic growth.

532 This growth facilitation and the PUFA accumulation in *Asellus* were mediated by

533 its seasonal physiological variation – *Asellus* optimized PUFA retention during

534 the spring (i.e., the reproductive season) and somatic growth in the fall – yet in

535 both seasons an algal diet was needed to satisfy its physiological requirements.

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 (29-137 mg C m^{-2} d^{-1}) to the flux of t-DOC that is
563 removed in oligo/mesotrophic lakes (37-165 mg C m^{-2} 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_4 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_4 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. Hydrogenothrophic 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_2 does

617 not contain usable energy. In nutrient poor environments the hydrogenothrophic

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; 20:5ω3), docosahexaenoic acid (DHA; 22:6ω3),

655 and arachidonic acid (ARA, 20:4ω6) (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 ω-3 α-linolenic acid (α-LA; 18:3ω3) 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 ω-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 ω-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 α-LA, but lack the enzymes

671 necessary to elongate and desaturate this molecule to EPA and DHA (Guschina

672 & Harwood, 2006), the physiologically active ω-3 molecules in animals. Some

673 animals can elongate and desaturate α-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 grow 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

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

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 salmoninds 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*

781   *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 ± 2.7 (± SD)

801 neonates each. These individuals also grew to an average dry weight of 0.22 ±

802 0.05 mg individual^{-1} (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 ± 23.2 neonates ind.$^{-1}$, and had an average DW of 1.06 ± 0.16 mg ind.$^{-1}$ 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 ± 0.001 d^{-1})

815 similar to experimentally starved individuals (growth = -0.018 ± 0.002 d^{-1}) (Lau *et*

816 *al.*, 2013). Conversely, when *Asellus* was provided a mixed diet of algae and leaf

817 litter its growth rate was greatly enhanced (growth = 0.022 ± 0.005 d^{-1}).

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 (DOC < 5 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 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^{-1}. Similarly, Karlsson *et al.*

868 (2015) found a negative correlation between DOC concentration (7-22 mg C L^{-1})

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^{-1}), 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*

917   *al.*, 2006). A variety of methods have been employed to resolve this problem. For

918   example, some authors estimate the $\delta^{13}C$ value of the phytoplankton by

919   assuming a "photosynthetic fractionation factor" (ϵ_p) to predict the $\delta^{13}C$ value of

920   the phytoplankton from directly determined $\delta^{13}C$ values for the CO_2 in the water

921   (Brett, 2014a). Other studies have directly measured the $\delta^{13}C$ 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 $\delta^{13}C$ value

925 using algal specific lipid biomarkers, especially PUFA. Other authors have simply

926 assumed fixed $\delta^{13}C$ values for the phytoplankton within the seston (Karlsson *et*

927 *al.*, 2012). Direct measurements $\delta^{13}C$ 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 (± 7‰) 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 $\delta^{13}C$ values of the dominant phytoplankton taxa could explain

933 most of the variation in the $\delta^{13}C$ 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

References

Abril G., Bouillon S., Darchambeau F., Teodoru C.R., Marwick T.R., Tamooh F. *et al.* (2015) Technical Note: Large overestimation of pCO_2 calculated from pH and alkalinity in acidic, organic-rich freshwaters. *Biogeosciences,* **12,** 67-78.

Ahlgren G., Gustafsson I.B. & Boberg M. (1992) Fatty acid content and chemical composition of fresh-water microalgae. *Journal of Phycology, * **28,** , 37-50.

Amon R.M. & Benner R. (1996a) Bacterial utilization of different size classes of dissolved organic matter. *Limnology and Oceanography*, **41**, 41-51.

Amon R.M.W. & Benner R. (1996b) Photochemical and microbial consumption of dissolved organic carbon and dissolved oxygen in the Amazon River system. *Geochimica et Cosmochimica Acta,* **60**, 1783-1792.

Bastviken D., Cole J.J., Pace M.L. & Van de Bogert M.C. (2008) Fates of methane from different lake habitats: Connecting whole-lake budgets and CH_4 emissions. *Journal of Geophysical Research: Biogeosciences,* **113**, G02024, doi: 10.1029/2007JG000608.

Bastow J.L., Sabo J.L., Finlay J.C. & Power M.E. (2002) A basal aquatic-terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. *Oecologia*, **131**, 261-268.

Benner R., Lay L., K'nees E. & Hodson R.E. (1988) Carbon conversion efficiency for bacterial growth on lignocellulose: implications for detritus-based food webs. *Limnology and Oceanography*, **33**,1514-1526.

Berggren M., Strom L., Laudon H., Karlsson J., Jonsson A., Giesler R. *et al.* (2010) Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. *Ecology Letters*, **13**, 870-880.

Berggren M., Ziegler S.E., St-Gelais N.F., Beisner B.E., & del Giorgio P.A. (2014) Contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes. *Ecology*, **95**, 1947-1959.

Bird D.F. & Kalff J. (1984) Empirical relationships between bacterial abundance and chlorophyll concentration in fresh and marine waters. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1015-1023.

Blaxter K.L. (1989) Energy metabolism in animals and man. Cambridge University Press.

Boujard T., Sabatier C., Rojasbeltran R., Prevost M.F. & Renno J.F. (1990) The food-habits of 3 allochthonous feeding characoids in French Guiana. *Revue d'écologie - la Terre et la Vie,* **45**, 247-258.

Bowes R.E. & Thorp J.H. (2015) Consequences of employing amino acid vs. bulk-tissue, stable isotope analysis: a laboratory trophic position experiment. *Ecosphere* **6,** Article 14.

Bowes R.E., Lafferty M.H. & Thorp J.H. (2014) Less means more: nutrient stress leads to higher $\delta^{15}N$ ratios in fish. *Freshwater Biology*, **59**, 1926-1931.

Bowes R.E., Thorp J.H. & Reuman D.C. (2017) Multidimensional metrics of niche space for use with diverse analytical techniques. *Nature Scientific Reports*, (In Press)

Brett M.T. (2014a) Are phytoplankton in northern Swedish lakes extremely ^{13}C depleted? (comment to Karlsson et al. 2012). *Limnology and Oceanography*, **59**, 1795-1799.

Brett M.T. (2014b) Resource polygon geometry predicts Bayesian stable isotope mixing model bias. *Marine Ecology Progress Series,* **514**, 1-12.

Brett M.T. & Benjamin M.M. (2008) A reassessment of lake phosphorus retention and the nutrient loading concept in limnology. *Freshwater Biology,* **53**, 194-211.

Brett M.T. & Müller-Navarra D.C. (1997) The role of essential fatty acids in aquatic food web processes. *Freshwater Biology*, **38**, 483-499.

Brett M.T., Müller-Navarra D.C., Ballantyne A.P., Ravet J.L. & Goldman C.R. (2006) *Daphnia* fatty acid composition reflects that of their diet. *Limnology and Oceanography*, **51**, 2428-2437.

Brett M.T., Arhonditsis G.B., Chandra S. & Kainz M.J. (2012) Mass flux calculations show strong allochthonous support of freshwater zooplankton production is unlikely. *PLoS ONE,* **7**, e39508.

Brett M.T., Kainz M.J., Taipale S.J. & Seshan H. (2009) Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 21197-21201.

Breznak J.A. & Brune A. (1994) Role of microorganisms in the digestion of lignocellulose by termites. *Annual Review of Entomology*, **39**, 453-487.

35

Brito E.F., Moulton T.P., De Souza M.L. & Bunn S.E. (2006) Stable isotope analysis indicates microalgae as the predominant food source of fauna in a coastal forest stream, south-east Brazil. *Austral Ecology*, **31**, 623-633.

Bunn S.E., Balcombe S.R., Davies P.M., Fellows C.S. & McKenzie-Smith F.J. (2006) Aquatic productivity and food webs of desert river ecosystems. In: R.T. Kingsford (ed). *Ecology of Desert Rivers* pp 76-99. Cambridge Press.

Bunn S.E., Davies P.M. & Winning M. (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology*, **48**, 619-635.

Bunn S.E., Leigh C. & Jardine T.D. (2013) Diet-tissue fractionation of δ^{15}N by consumers from streams and rivers. *Limnology and Oceanography*, **58**, 765-773.

Burns C.W., Brett M.T. & Schallenberg M. (2011) A comparison of the trophic transfer of fatty acids in freshwater plankton by cladocerans and calanoid copepods. *Freshwater Biology*, **56**, 889-903.

Canham C.D., Pace M.L., Papaik M.J., Primack A.G.B., Roy K.M., Maranger R.J. *et al.* (2004) A spatially explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes. *Ecological Applications*, **14**, 839-854.

Carignan R., Planas D. & Vis C. (2000) Planktonic production and respiration in oligotrophic shield lakes. *Limnology and Oceanography*, **45**,189-199.

Carpenter S.R., Cole J.J., Pace M.L., Van de Bogert M., Bade D.L., Bastviken D. *et al.* (2005) Ecosystem subsidies: Terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology*, **86**, 2737-2750.

Carpenter S.R., Cole J.J., Kitchell J.F. & Pace M.L. (1998) Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography*, **43**, 73-80.

Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634-639.

Carroll T.M., Thorp J.H. & Roach K.A. (2016) Autochthony in karst spring food webs. *Hydrobiologia*, **776**, 173-191.

Casper P. (1996) Methane production in littoral and profundal sediments of an oligotrophic and a eutrophic lake. *Archiv für Hydrobiologie, Special Issues, Advances in Limnology* **48**, 253-259.

Chikaraishi Y., Ogawa N.O., Kashiyama Y., Takano Y., Suga H., Tomitani A. *et al.* (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography Methods,* **7**, 740-750.

Chikaraishi Y., Steffan S.A., Ogawa N.O., Ishikawa N.F., Sasaki Y., Tsuchiya M. *et al.* (2014) High-resolution food webs based on nitrogen isotopic composition of amino acids. *Ecology and Evolution*, **4**, 2423-2449.

Choquenot D. & Ruscoe W.A.(2000) Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology,* **69**, 1058-1070.

Cloern J.E., Canuel E.A., Harris D. (2002) Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography,* **47**, 713-729.

Cole JJ, Carpenter S.R., Kitchell J.L., Pace M.L., Solomon C.T. & Weidel B. (2011) Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1975-1980.

Cole J.J., Carpenter S.R., Pace M.L., Van de Bogert M.C., Kitchell J.L. & Hodgson J.R. (2006) Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters*, **9**, 558-568.

Cole J.J., Likens, G.E. & Strayer, D.L. (1982) Photosynthetically produced dissolved organic carbon: An important carbon source for planktonic bacteria. *Limnology and Oceanography,* **27**, 1080-1090.

Cole J.J., Pace M.L., Carpenter S.R. & Kitchell J.F. (2000) Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. *Limnology and Oceanography*, **5**, 1718-1730.

1112 Cole J.J., Carpenter S.R., Kitchell J.F. & Pace M.L. (2002) Pathways of organic carbon utilization
1113   in small lakes: results from a whole-lake ^{13}C addition and coupled model. *Limnology and*
1114   *Oceanography*, **47**, 1664-1675.
1115 Coley P.D., Bryant J.P. & Chapin F.S. (1985) Resource availability and plant antiherbivore
1116   defense. *Science*, **230**, 895-899.
1117 Conrad R. (1999) Contribution of hydrogen to methane production and control of hydrogen
1118   concentrations in methanogenic soils and sediments. *FEMS Microbiology Ecology* **28**, 193-
1119   202.
1120 Conrad R. (2005) Quantification of methanogenic pathways using stable carbon isotope
1121   signatures: a review and a proposal. *Organic Geochem*istry, **36**, 739-752.
1122 Correa S.B., Winemiller K.O., López-Fernández H. & Galetti M. (2007) Evolutionary perspectives
1123   on seed consumption and dispersal by fishes. *Bioscience*, **57**, 748-756.
1124 Cory R.M., Ward C.P., Crump B.C. & Kling G.W. (2014) Sunlight controls water column
1125   processing of carbon in arctic fresh waters. *Science*, **345**, 925-928.
1126 Cummins K. (1974) Structure and function of stream ecosystems. *BioScience*, **24**, 631-641.
1127 Davies P.M., Bunn S.E. & Hamilton S.K. (2008) Primary production in tropical rivers. In: D.
1128   Dudgeon (ed). pp 24-43. Tropical Stream Ecology. Academic Press.
1129 Deemer B.R., Harrison J.A., Li S., Beaulieu J.J., DelSontro T., Barros N., *et al.* (2016)
1130   Greenhouse gas emissions from reservoir water surfaces: A new global synthesis.
1131   *BioScience*, p.biw117.
1132 Deines P., Bodelier P.L. & Eller G. (2007) Methane‐derived carbon flows through methane‐
1133   oxidizing bacteria to higher trophic levels in aquatic systems. *Environmental Microbiology*, **9**,
1134   1126-1134.
1135 Demars B.O. & Edwards A.C. (2007) Tissue nutrient concentrations in freshwater aquatic
1136   macrophytes: high inter‐taxon differences and low phenotypic response to nutrient supply.
1137   *Freshwater Biology*, **52**, 2073-2086.
1138 de Moura G.C., de Lucena Barbosa J.E., Patrício J., Nery J.F. & Gonçalves A.M.M. (2016)
1139   Seasonal and spatial shifts in copepod diets within tropical estuaries measured by fatty acid
1140   profiles. *Ecological Indicators*, **69**, 284-294.
1141 del Giorgio P.A. & Cole J.J. (1998) Bacterial growth efficiency in natural aquatic systems. *Annual*
1142   *Review of Ecology and Systematics*, **29**, 503–541.
1143 del Giorgio P.A. & Peters R.H. (1994) Patterns in planktonic P:R ratios in lakes: Influence of lake
1144   trophy and dissolved organic carbon. *Limnology and Oceanography,* **39**, 772-787.
1145 Delong M.D. & Thorp J.H. (2006) Significance of instream autotrophs in trophic dynamics of the
1146   Upper Mississippi River. *Oecologia*, **147**, 76-85.
1147 Denton K.P., Rich Jr, H.B. & Quinn, T.P. (2009) Diet, movement, and growth of Dolly Varden in
1148   response to sockeye salmon subsidies. *Transactions of the American Fisheries Society,* **138**,
1149   1207-1219.
1150 Dillon P.J. & Kirchner W.B. (1975) The effects of geology and land use on the export of
1151   phosphorus from watersheds. *Water Research*, **9**, 135-148.
1152 Dillon P.J. & Molot L.A. (1997) Effect of landscape form on export of dissolved organic carbon,
1153   iron, and phosphorus from forested stream catchments. *Water Resources Research,* **33**,
1154   2591-2600.
1155 Duarte C.M. & Prairie Y.T. (2005) Prevalence of heterotrophy and atmospheric CO_2 emissions
1156   from aquatic ecosystems. *Ecosystems*, **8**, 862-870.
1157 Dudgeon D., Cheung F.K.W. & Mantel S.K. (2010) Foodweb structure in small streams: do we
1158   need different models for the tropics? *Journal of the North American Benthological Society,*
1159   **29**, 395-412.
1160 Eiler A., Langenheder S., Bertilsson S. & Tranvik L.J. (2003) Heterotrophic bacterial growth
1161   efficiency and community structure at different natural organic carbon concentrations. *Applied*
1162   *and Environmental Microbiology,* **69**, 3701-3709.
1163 Elger A. & Willby N.J. (2003) Leaf dry matter content as an integrative expression of plant
1164   palatability: the case of freshwater macrophytes. *Functional Ecology*, **17**, 58-65.
1165 Elliott J.M. 1970 Diel changes in invertebrate drift and the food of trout *Salmo trutta* L. *Journal of*
1166   *Fish Biology,* **2**, 161-165.

1167 Elser J.J., Fagan W.F., Denno R.F., Dobberfuhl D.R., Folarin A., Huberty A. *et al.* (2000)
1168   Nutritional constraints in terrestrial and freshwater food webs. *Natur*e, **408**, 578-580.
1169 Engstrom D.R., Fritz S.C., Almendinger J.E. & Juggins S. (2000) Chemical and biological trends
1170   during lake evolution in recently deglaciated terrain. *Nature*, **408**, 161-166.
1171 Farjalla V.F., Amado A.M., Suhett A.L. & Meirelles-Pereira F. (2009) DOC removal paradigms in
1172   highly humic aquatic ecosystems. *Environmental Science and Pollution Research*, **16**, 531-
1173   538.
1174 Findlay S. (2010) Stream microbial ecology. *Journal of the North American Benthological Society,*
1175   **29**, 170-181.
1176 Finlay J.C. (2001) Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic
1177   food webs. *Ecology,* **82**, 1052-1064.
1178 Finlay J.C., Power M.E., & Cabana G. (1999) Effects of water velocity on algal carbon isotope
1179   ratios: Implications for river food web studies. *Limnology and Oceanography,* **44**, 1198-1203.
1180 Finstad A.G., Helland I.P., Ugedal O., Hesthagen T. & Hessen D.O. (2014) Unimodal response of
1181   fish yield to dissolved organic carbon. *Ecology Letters*, **17**, 36-43.
1182 Fouilland E. & Mostajir B. (2010) Revisited phytoplanktonic carbon dependencyof heterotrophic
1183   bacteria in freshwaters, transitional, coastal and oceanic waters. *FEMS Microbiology*
1184   *Ecology,* **73**, 419-429.
1185 France R., Culbert H., & Peters R. (1996) Decreased carbon and nutrient input to boreal lakes
1186   from particulate organic matter following riparian clear-cutting. *Environmental Management*,
1187   **20**, 579-583.
1188 Francis T.B. & Schindler D.E. (2009) Shoreline urbanization reduces terrestrial insect subsidies to
1189   fishes in North American lakes. *Oikos*, **118**, 1872-1882.
1190 Friedl A., Padouvas E., Rotter H. & Varmuza K. (2005) Prediction of heating values of biomass
1191   fuel from elemental composition. *Analytica Chimica Acta*, **544**, 191-198.
1192 Fry B. (2013a) Review: Alternative approaches for solving underdetermined isotope mixing
1193   problems. *Marine Ecology Progress Series*, **472**, 1-13.
1194 Fry B. (2013b) Minmax solutions for underdetermined isotope mixing problems: Reply to
1195   Semmens et al. (2013). *Marine Ecology Progress Series*, **490**, 291-294.
1196 Galand P.E., Yrjälä K. & Conrad R. (2010) Stable isotope fractionation during methanogenesis in
1197   three boreal peatland ecosystems. *Biogeosciences* **7**, 3893-3900.
1198 Galloway A.W.E. & Winder M. (2015) Partitioning the relative importance of phylogeny and
1199   environmental conditions on phytoplankton fatty acids. *PLoS ONE,* **10**, e0130053.
1200 Galloway A.W.E., Britton-Simmons K.H., Duggins D.O., Gabrielson P.W. & Brett M.T. (2012)
1201   Fatty acid signatures differentiate marine macrophytes at ordinal and family ranks. *Journal of*
1202   *Phycology,* **48**, 956-965.
1203 Galloway A.W.E., Taipale S.J., Hiltunen M., Peltomaa E., Strandberg U., Brett M.T. *et al.* (2014)
1204   Diet specific biomarkers show that high quality phytoplankton fuels herbivorous zooplankton
1205   in large boreal lakes. *Freshwater Biology,* **59**, 1902-1915.
1206 Galloway A.W.E., Brett M.T., Holtgrieve G.W., Ward E.J., Ballantyne A.J., Burns C.W., *et al.*
1207   (2015) A fatty acid based Bayesian approach for inferring diet in aquatic consumers. *PLoS*
1208   *ONE*, **10**, e0129723.
1209 Garcia E. & Carignan R (1999) Impact of wildfire and clear-cutting in the boreal forest on methyl
1210   mercury in zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences,* **56**, 339-345.
1211 Geib S.M., Filley T.R., Hatcher P.G., Hoover K., Carlson J.E., del Mar Jimenez-Gasco M. *et al.*
1212   (2008) Lignin degradation in wood-feeding insects. *Proceedings of the National Academy of*
1213   *Sciences of the United States of America,* **105**, 12932-12937.
1214 Gergel S.E., Turner M.G. & Kratz T.K. (1999) Dissolved organic carbon as an indicator of the
1215   scale of watershed influence on lakes and rivers. *Ecological Applications*, **9**, 1377-1390.
1216 Gladyshev M.I., Sushchik N.N., Kalachova G.S. & Makhutova O.N. (2012) Stable isotope
1217   composition of fatty acids in organisms of different trophic levels in the Yenisei River. *PloS*
1218   *ONE,* **7,** e34059.
1219 Goldman C.R. (1960) Primary productivity and limiting factors in 3 lakes of the Alaska Peninsula.
1220   *Ecological Monographs,* **30**, 208-230.
1221 Grey J., Jones R.I. & Sleep D. (2000) Stable isotope analysis of the origins of zooplankton carbon
1222   in lakes of differing trophic state. *Oecologia,* **123**, 232-240.

1223 Grey J., Jones R.I. & Sleep D. (2001) Seasonal changes in the importance of the source of
1224   organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope
1225   analysis. *Limnology and Oceanography,* **46**, 505-513.
1226 Gudasz C., Bastviken D., Premke K., Steger K. & Tranvik L.J. (2012) Constrained microbial
1227   processing of allochthonous organic carbon in boreal lake sediments. *Limnology and*
1228   *Oceanography,* **57**, 163-175.
1229 Gugger M., Lyra C., Suominen I., Tsitko I., Humbert J.F., Salkinoja-Salonen M.S. *et al.* (2002)
1230   Cellular fatty acids as chemotaxonomic markers of the genera *Anabaena, Aphanizomenon,*
1231   *Microcystis, Nostoc* and *Planktothrix* (cyanobacteria). *International Journal of Systematic and*
1232   *Evolutionary Microbiology,* **52**, 1007-1015.
1233 Guo F., Kainz M.J., Sheldon F. & Bunn S.E. (2015) Spatial variation in periphyton fatty acid
1234   composition in subtropical streams. *Freshwater Biology*, **60**, 1411-1422.
1235 Guo F., Kainz M.J., Valdez D., Sheldon F. & Bunn S.E. (2016a) High-quality algae attached to
1236   leaf litter boost invertebrate shredder growth. *Freshwater Science*, **35**, 1213-1221.
1237 Guo F., Kainz M.J., Sheldon F. & Bunn S.E. (2016b) Effects of light and nutrients on periphyton
1238   and the fatty acid composition and somatic growth of invertebrate grazers in subtropical
1239   streams. *Oecologia,* **181**, 449-462.
1240 Guo F., Kainz M.J., Sheldon F. & Bunn S.E. (2016c) The importance of high-quality algal food
1241   sources in stream food webs–current status and future perspectives. *Freshwater Biology,* **61**,
1242   815-831.
1243 Guschina I.A. & Harwood J.L. (2006) Lipids and lipid metabolism in eukaryotic algae. *Progress in*
1244   *Lipid Research,* **45**, 160-186.
1245 Hadwen W.L., Spears M. & Kennard M.J. (2010) Temporal variability of benthic algal δ^{13}C
1246   signatures influences assessments of carbon flows in stream food webs. *Hydrobiologia,* **651**,
1247   239-251.
1248 Hall R.O., Likens G.E. & Malcom H.M. (2001) Trophic basis of invertebrate production in 2
1249   streams at the Hubbard Brook Experimental Forest. *Journal of the North American*
1250   *Benthological Society,* **20**, 432-447.
1251 Hanson P.C., Hamilton D.P., Stanley E.H., Preston N., Langman O.C. & Kara E.L. (2011) Fate of
1252   allochthonous dissolved organic carbon in lakes: a quantitative approach. *PLoS ONE*, **6,**
1253   e21884.
1254 Hayden B., McWilliam-Hughes S.M. & Cunjak R.A. (2016) Evidence for limited trophic transfer of
1255   allochthonous energy in temperate river food webs. *Freshwater Science,* **35**, 544-558.
1256 Hixson S.M., Sharma B., Kainz M.J., Wacker A. & Arts M.T. (2015) Production, distribution, and
1257   abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy
1258   between freshwater and terrestrial ecosystems. *Environmental Reviews,* **23**, 414-424.
1259 Hood E., Battin T.J., Fellman J., O'Neel S. & Spencer R.G. (2015) Storage and release of organic
1260   carbon from glaciers and ice sheets. *Nature Geoscience*, **8**, 91-96.
1261 Hopkinson C.S. & Vallino J.J. (1995) The relationships among man's activities in watersheds and
1262   estuaries: A model of runoff effects on patterns of estuarine community metabolism.
1263   *Estuaries,* **18**, 598-621.
1264 Hynes H.B.N. (1975) Edgardo Baldi memorial lecture. The stream and its valley. *Verhandlungen*
1265   *der Internationalen Vereinigung für theoretische und angewandte Limnologie,* **19**, 1-15.
1266 Ishikawa N.F., Kato Y. Togashi H. Yoshimura M. Yoshimizu C. Okuda N. & Tayasu. I. (2014)
1267   Stable nitrogen isotopic composition of amino acids reveals food web structure in stream
1268   ecosystems. *Oecologia*, **175**, 911-922.
1269 Ishikawa N., Doi H. & Finlay J. (2012) Global meta-analysis for controlling factors on carbon
1270   stable isotope ratios of lotic periphyton. *Oecologia*, **170**, 541-549.
1271 Jacobsen D. & Sand-Jensen K. (1995) Variability of invertebrate herbivory on the submerged
1272   macrophyte Potamogeton perfoliatus. *Freshwater Biology*, **34**, 357-365.
1273 Jansson M., Persson L., De Roos A.M., Jones R.I. & Tranvik L.J. (2007) Terrestrial carbon and
1274   intraspecific size-variation shape lake ecosystems. *Trends in Ecology & Evolution,* **22**, 316-
1275   322.
1276 Jardine T.D., Woods R., Marshall J., Fawcett J., Lobegeiger J., Valdez D. *et al.* (2015)
1277   Reconciling the role of organic matter pathways in aquatic food webs by measuring multiple
1278   tracers in individuals. *Ecology*, **96**, 3257-3269.

Jardine T.D., Hadwen W.L., Hamilton S.K., Hladyz S., Mitrovic S.M., Kidd K.A. *et al.* (2014) Understanding and overcoming baseline isotopic variability in running waters. *River Research and Applications*, **30**, 155-165.

Jardine T.D., Hunt R.J., Faggotter S.J., Valdez D., Burford M.A. & Bunn S.E. (2013) Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river. *River Research and Applications*, **29**, 560-573.

Jardine T.D., Pettit N.E., Warfe D.M., Pusey B.P., Ward D.P., Douglas M.M. *et al.* (2012) Consumer-resource coupling in wet-dry tropical rivers. *Journal of Animal Ecology,* **81**, 310-322.

Jardine T.D., Pusey B.P., Hamilton S.K., Pettit N.E., Davies P.M., Sinnamon V. *et al.* (2012). Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. *Oecologia*, **168**, 829-38.

Jassby A.D. & Cloern J.E. (2000) Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). *Aquatic Conservation-Marine and Freshwater Ecosystems,* **10**, 323-352.

Johansson K.S.L., Trigal C., Vrede T. & Johnson R.K. (2013a) Community structure in boreal lakes with recurring blooms of the nuisance flagellate *Gonyostomum semen. Aquatic Sciences*, **75**, 447-455.

Johansson K.S.L., Vrede T., Lebret K. & Johnson R.K. (2013b) Zooplankton feeding on the nuisance flagellate *Gonyostomum semen. PLoS ONE,* **8**, e62557.

Jones R.I. (1992) The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia,* **229**, 73-91.

Jones R.I. & Grey J. (2011) Biogenic methane in freshwater food webs. *Freshwater Biology*, **56**, 213-229.

Jones R.I., Shaw P.J. & De Haan H. (1993) Effects of dissolved humic substances on the speciation of iron and phosphate at different pH and ionic strength. *Environmental Science & Technology,* **27**, 1052-1059.

Jonsson M. & Stenroth K. (2016) True autochthony and allochthony in aquatic–terrestrial resource fluxes along a landuse gradient. *Freshwater Science,* **35**, doi:10.1086/68784

Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river–floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences Special Publication,* **106**, 110-127.

Juutinen S., Rantakari M., Kortelainen P., Huttunen J.T., Larmola T., Alm J. *et al.* (2009) Methane dynamics in different boreal lake types. *Biogeosciences*, **6**, 209-223.

Kalacheva G.S., Sushchik N.N., Gladyshev M.I. & Makhutova O.N. (2009) Seasonal dynamics of fatty acids in the lipids of water moss *Fontinalis antipyretica* from the Yenisei River. *Russian Journal of Plant Physiology,* **56**, 795-807.

Kankaala P., Bellido J.L., Ojala A., Tulonen T. & Jones R.I. (2013) Variable production by different pelagic energy mobilizers in boreal lakes. *Ecosystems*, **16**, 1152-1164.

Kankaala P., Huotari J., Peltomaa E., Saloranta T. & Ojala A. (2006a) Methanotrophic activity in relation to methane efflux and total heterotrophic bacterial production in a stratified, humic, boreal lake. *Limnology and Oceanography*, **51,** 1195-1204.

Kankaala P., Taipale S.J., Grey J., Sonninen E, Arvola L. & Jones R.I. (2006b) Experimental δ ^{13}C evidence for a contribution of methane to pelagic food webs in lakes. *Limnology and Oceanography*, **51**, 2821-2827.

Kankaala P., Taipale S.J., Li L. & Jones R.I., 2010. Diets of crustacean zooplankton, inferred from stable carbon and nitrogen isotope analyses, in lakes with varying allochthonous dissolved organic carbon content. *Aquatic Ecology*, **44**, 781-795.

Karlsson J., Berggren M., Ask J., Byström P., Jonsson A., Laudon H. *et al.* (2012) Terrestrial organic matter support of lake food webs: evidence from lake metabolism and stable hydrogen isotopes of consumers. *Limnology and Oceanography*, **57**, 1042-1048.

Karlsson J., Bergström A.-K., Byström P., Gudasz C., Rodríguez P. & Hein C. (2015) Terrestrial organic matter input suppresses biomass production in lake ecosystems. *Ecology,* **96**, 2870-2876.

Karlsson J., Jonsson A., Meili M. & Jansson M. (2003) Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. *Limnology and Oceanography*, **48**, 269-276.

1335 Karlsson J. (2007) Different carbon support for respiration and secondary production in
1336   unproductive lakes. *Oikos*, **116**, 1691-1696.
1337 Karlsson J., Byström P., Ask J., Persson L. & Jansson M. (2009) Light limitation of nutrient-poor
1338   lake ecosystems. *Nature*, **460**, 506-509.
1339 Kelly P.T., Solomon C.T., Weidel B.C. & Jones S.E. (2014) Terrestrial carbon is a resource, but
1340   not a subsidy, for lake zooplankton. *Ecology,* **95**, 1236-1242.
1341 Klaveness D. (1988) Ecology of the Cryptomonadida - a first review. In: Sandgren, C.D. (ed.):
1342   Growth and Reproductive Strategies of Freshwater Phytoplankton, 105-133. Cambridge
1343   University Press, New York. 442 pp.
1344 Koussoroplis A.M., Nussbaumer J., Arts M.T., Guschina I.A. & Kainz, M.J. (2014) Famine and
1345   feast in a common freshwater calanoid: Effects of diet and temperature on fatty acid
1346   dynamics of *Eudiaptomus gracilis*. *Limnology and Oceanography*, **59**, 947-958.
1347 Kritzberg E.S., Cole J.J., Pace M.L. & Graneli W. (2005) Does autochthonous primary production
1348   drive variability in bacterial metabolism and growth efficiency in lakes dominated by terrestrial
1349   C inputs? *Aquatic Microbial Ecology,* **38**, 103-111.
1350 Kritzberg E.S., Cole J.J., Pace M.L., Granéli W. & Bade D. (2004) Autochthonous versus
1351   allochthonous carbon sources to bacteria: Results from whole lake ^{13}C addition experiments.
1352   *Limnology and Oceanography*, **49**, 588-596.
1353 Larson J.H., Bartsch M.R., Gutreuter S., Knights B.C., Bartsch L.A., Richardson W.B. *et al.* 2015.
1354   Differences between main-channel and off-channel food webs in the upper Mississippi River
1355   revealed by fatty acid profiles of consumers. *Inland Waters*, **5**, 101-106.
1356 Larson J.H., Richardson W.B., Knights B.C., Bartsch L.A., Bartsch M.R., Nelson J.C. *et al.* (2013)
1357   Fatty acid composition at the base of aquatic food webs is influenced by habitat type and
1358   watershed land use. *PLoS ONE,* **8,** e70666.
1359 Lau D.C.P., Goedkoop W. & Vrede T. (2013) Cross-ecosystem differences in lipid composition
1360   and growth limitation of a benthic generalist consumer. *Limnology and Oceanography*, **58**,
1361   1149-1164.
1362 Lau D.C.P., Leung K.M.Y. & Dudgeon D. (2009a) Are autochthonous foods more important than
1363   allochthonous resources to benthic consumers in tropical headwater streams? *Journal of the*
1364   *North American Benthological Society,* **28**, 426-439.
1365 Lau D.C.P., Leung K.M.Y. & Dudgeon D. (2009b) What does stable isotope analysis reveal about
1366   trophic relationships and the relative importance of allochthonous and autochthonous
1367   resources in tropical streams? A synthetic study from Hong Kong. *Freshwater Biology*, **54**,
1368   127-141.
1369 Lau D.C.P., Sundh I., Vrede T., Pickova J., & Goedkoop W. (2014) Autochthonous resources are
1370   the main driver of consumer production in dystrophic boreal lakes. *Ecology*, **95**, 1506-1519.
1371 Lau D.C.P., Vrede T., Pickova J. & Goedkoop W. (2012) Fatty acid composition of consumers in
1372   boreal lakes – variation across species, space and time. *Freshwater Biology*, **57**, 24-38.
1373 Layman C.A., Arrington D.A., Montaña C.G. & Post D.M. (2007) Can stable isotope ratios provide
1374   for community-wide measures of trophic structure? *Ecology*, **88**, 42-48.
1375 Lebret L., Fernandez M.F., Hagman C.H.C., Rengefors K. & Hansson L.-A. (2012) Grazing
1376   resistance allows bloom formation and may explain invasion success of *Gonyostomum*
1377   *semen*. *Limnology and Oceanography*, **57**, 727–734.
1378 Lepistö A., Futter M.N. & Kortelainen P. (2014) Almost 50 years of monitoring shows that climate,
1379   not forestry, controls long‐term organic carbon fluxes in a large boreal watershed. *Global*
1380   *Change Biology*, **20**, pp.1225-1237.
1381 Lewis Jr., W.M., Hamilton S.K., Rodríguez M.A., Saunders III J.F. & Lasi M.A. (2001) Foodweb
1382   analysis of the Orinoco floodplain based on production estimates and stable isotope data.
1383   *Journal of the North American Benthological Society*, **20**, 241-254.
1384 Li A.O.Y. & Dudgeon D. (2008) Food resources of shredders and other benthic
1385   macroinvertebrates in relation to shading conditions in tropical Hong Kong streams.
1386   *Freshwater Biology*, **53**, 2011-2025.
1387 Li B. & Brett M.T. (2013) The influence of dissolved phosphorus molecular form on recalcitrance
1388   and bioavailability. *Environmental Pollution*, **182**, 37-44.

1389 Lindell M.J., Granéli W. & Tranvik L.J. (1995) Enhanced bacterial growth in response to
1390   photochemical transformation of dissolved organic matter. *Limnology and Oceanography*, **40**,
1391   195-199.
1392 Lisi P.J., Bentley K.T., Armstrong J.B. & Schindler D.E. (2014) Episodic predation of mammals by
1393   stream fishes in a boreal river basin. *Ecology of Freshwater Fish*, **23**, 622-630.
1394 Lynd L.R., Weimer P.J., van Zyl W.H. & Pretorius I.S. (2002) Microbial cellulose utilization:
1395   Fundamentals and biotechnology. *Microbiology and Molecular Biology Reviews*, **66**, 506-577.
1396 Marcarelli A.M., Baxter C.V., Mineau M.M. & Hall, R.O. (2011) Quantity and quality: unifying food
1397   web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*,
1398   **92**, 1215-1225.
1399 Martin M.M., Jones C.G. & Bernays E.A. (1991) The evolution of cellulose digestion in insects
1400   [and Discussion]. *Philosophical Transactions of the Royal Society of London B: Biological*
1401   *Sciences*, **333**, 281-288.
1402 Martin-Creuzburg D., Beck B. & Freese H.M. (2011) Food quality of heterotrophic bacteria for
1403   *Daphnia magna*: evidence for a limitation by sterols. *FEMS Microbiology Ecology*, **76**, 592-
1404   601.
1405 Martin-Creuzburg D. & von Elert E. (2009) Ecological significance of sterols in aquatic food webs.
1406   In Lipids in Aquatic Ecosystems (pp. 43-64). Springer New York.
1407 Martínez A.T., Speranza M., Ruiz-Dueñas F.J., Ferreira P., Camarero S., Guillén F. *et al.* (2005)
1408   Biodegradation of lignocellulosics: microbial, chemical, and enzymatic aspects of the fungal
1409   attack of lignin. *International Microbiology*, **8**, 195-204.
1410 Matilainen A. & Sillanpää M. (2010) Removal of natural organic matter from drinking water by
1411   advanced oxidation processes. *Chemosphere*, **80**, 351-365.
1412 Mayer M.S. & Likens G.E. (1987) The importance of algae in a shaded headwater stream as food
1413   for an abundant caddisfly (Trichoptera). *Journal of the North American Benthological Society*.
1414   **6**, 262-269.
1415 McClelland J.W. & Montoya J.P. (2002) Trophic relationships and the nitrogen isotopic
1416   composition of amino acids in plankton. *Ecology*, **83**, 2173-2180.
1417 McMahon K.W., Thorrold S.R., Houghton L.A. & Berumen M.L. (2016) Tracing carbon flow
1418   through coral reef food foods using a compound-specific stable isotope approach. *Oecologia*,
1419   **180**, 809-821.
1420 McMeans B.C., Koussoroplis A.-M., Arts, M.T. & Kainz M.J. (2015) Allochthonous dissolved
1421   organic matter pathways support somatic growth and reproduction of *Daphnia magna* when
1422   algae are limiting. *Journal Plankton Research*, **37**, 1201-1209.
1423 McNeeley C., Finlay J.C. & Power M.E. (2007) Grazer traits, competition, and carbon sources to
1424   a headwater-stream food web. *Ecology*, **88**, 391-401.
1425 Meyers P.A. & Ishiwatari R. (1993) Lacustrine organic geochemistry - an overview of indicators of
1426   organic matter sources and diagenesis in lake sediments. *Organic Geochemistry*, **20**, 867-
1427   900.
1428 Minshall G.W. (1978) Autotrophy in stream ecosystems. *BioScience*, **28**, 767-771.
1429 Molongoski J.J. & Klug M.J. (1980) Anaerobic metabolism of particulate organic matter in the
1430   sediments of a hypereutrophic lake. *Freshwater Biology,* **10**, 507-518.
1431 Monteith D.T., Stoddard J.L., Evans C.D., de Wit H.A., Forsius M., Høgåsen T. *et al. (*2007)
1432   Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry.
1433   *Nature*, **450**, 537-540.
1434 Moran M.A. & Hodson R.E. (1989) Formation and bacterial utilization of dissolved organic-carbon
1435   derived from detrital lignocellulose. *Limnology and Oceanography,* **34**, 1034-1047.
1436 Morris D.P., Zagarese H., Williamson C.E., Balseiro E.G., Hargreaves B.R., Modenutti B. *et al.*
1437   (1995) The attentuation of solar UV radiation in lakes and the role of dissolved organic
1438   carbon. *Limnology and Oceanography*, **40**, 1381-1391.
1439 Murray D.S., Hager H.H., Tocher D.R. & Kainz M.J. (2014) Effect of partial replacement of dietary
1440   fish meal and oil by pumpkin kernel cake and rapeseed oil on fatty acid composition and
1441   metabolism in Arctic charr (*Salvelinus alpinus). Aquaculture*, **431**, 85-91.
1442 Naiman R.J., Bilby R.E., Schindler D.E. & Helfield J.M. 2002. Pacific salmon, nutrients, and the
1443   dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399-417.

Nakano S. & Murakami M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 166-170.

Nielsen J.M., Popp B.N. & Winder M. (2015) Meta- analysis of amino acid stable nitrogen isotope ratios for estimating trophic position in marine organisms. *Oecologia*, **178**, 631-642.

Neres-Lima V., Brito E.F., Krsuloviḳ F.A.M., Detweiler A.M., Hershey A.E. & Moulton T.P. (2016) High importance of autochthonous basal food source for the food web of a Brazilian tropical stream regardless of shading. *International Review of Hydrobiology* (in press).

Odum H.T. (1956) Primary productivity in flowing waters. *Limnology and Oceanography,* **1,** 102-117.

Ohkuma M. (2003) Termite symbiotic systems: efficient bio-recycling of lignocellulose. *Applied Microbiology and Biotechnology*, **61**, 1-9.

Pace M.L., Cole J.J., Carpenter S.R., Kitchell J.F., Hodgson J.R., Van de Bogert M.C. *et al.* (2004) Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature*, **427**, 240-243.

Pace M.L., Carpenter S.R., Cole J.J., Coloso J.J., Kitchell J.F., Hodgson J.R. *et al.* (2007) Does terrestrial organic carbon subsidize the planktonic food web in a Clearwater lake? *Limnology and Oceanography*, **52**, 2177-2189.

Phillips D.L, Inger R., Bearhop S., Jackson A.L., Moore J.W., Parnell A.C. *et al.* (2014) Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, **92**, 823-835.

Piovia-Scott J., Sadro S., Knapp R.A., Sickman J., Pope K. & Chandra S. (2016) Variation in reciprocal subsidies between lakes and land: perspectives from the mountains of California. *Canadian Journal of Fisheries and Aquatic Sciences*, **73**, 1691-1701.

Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289-316.

Popp B.N, Graham B.S., Olson R.J., Hannides C., Lott M.J., López-Ibarra G.A. *et al.* (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. *Terrestrial Ecology*, **1**, 173-190.

Power M.E. (2001) Field biology, food web models, and management: Challenges of context and scale. *Oikos*, **94**, 118-129.

Power M.E., Rainey W.E., Parker M.S., Sabo J.L., Smyth A., Khandwala S., *et al.* (2004) River to watershed subsidies in an old-growth conifer forest. Pages 217-240 in G.A. Polis, M.E. Power, and G. Huxel, editors. Food webs and Landscapes. Univ. Chicago Press, Chicago.

Prairie Y.T. (2008) Carbocentric limnology: looking back, looking forward. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 543-548.

Preston N.D., Carpenter S.R., Cole J.J. & Pace M.L. (2008) Airborne carbon deposition on a remote forested lake. *Aquatic Sciences*, **70**, 213-224.

Räsänen N.H.J., Kankaala P., Akkanen J., Tahvanainen T. & Saarnio S. (2016) Effects of mire-originated dissolved organic carbon, nitrogen, and phosphorus on microbial activity in boreal headwaters. *Inland Waters*, **6**, 65-76.

Rasilo T., Prairie Y.T. & Del Giorgio P. (2015) Large-scale patterns in summer diffusive CH4 fluxes across boreal lakes, and contribution to diffusive C emissions. *Global Change Biology*, **21**, 1124–1139.

Rask M., Sairanen S., Vesala S., Arvola L., Estlander S. & Olin, M. (2014) Population dynamics and growth of perch in a small, humic lake over a 20-year period – importance of abiotic and biotic factors. *Boreal Environment Research*, **19**, 112-124.

Rasmussen J.B. (2010) Estimating terrestrial contribution to stream invertebrates and periphyton using a gradient-based mixing model for δ^{13}C. *Animal Ecology*, **78**, 674-685.

Rasmussen J.B., Godbout L. & Schallenberg M. (1989) The humic content of lake water and its relationship to watershed and lake morphometry. *Limnology and Oceanography*, **34**, 1336-1343.

Rasmussen J.B., Trudeau V. & Morinville G. (2009) Estimating the scale of fish feeding movements in rivers using δ^{13}C signature gradients. *Journal of Animal Ecology* **, 79**, 393-402.

1499 Ravet J.L., Brett M.T. & Arhonditsis G.B. (2010) The effects of seston lipids on zooplankton fatty
1500   acid composition in Lake Washington. *Ecology*, **91**, 180-190.
1501 Ravinet M., Syväranta J., Jones R.I. & Grey J. (2010) A trophic pathway from biogenic methane
1502   supports fish biomass in a temperate lake ecosystem. *Oikos*, **119**, 409-416.
1503 Recalde F.C., Postali T.C., & Romero G.Q. (2016) Unravelling the role of allochthonous aquatic
1504   resources to food web structure in a tropical riparian forest. *Journal of Animal Ecology*, **85**,
1505   525-536.
1506 Rengefors K., Pålsson C., Hansson L.A. & Heiberg L. (2008) Cell lysis of competitors and
1507   osmotrophy enhance growth of the bloom-forming alga *Gonyostomum semen*. *Aquatic*
1508   *Microbial Ecology*, **51**, 87-96.
1509 Rinta, P., Bastviken D., van Hardenbroek M., Kankaala P., Leuenberger M., Schilder J. *et al.*
1510   (2015) An inter-regional assessment of concentrations and $\delta^{13}C$ values of methane and
1511   dissolved inorganic carbon in small European lakes. *Aquatic Sciences*, **77**, 667-680.
1512 Rosenfeld J.S. & Mackay R.J. (1987) Assessing the food base of stream ecosystems:
1513   alternatives to the P/R ratio. *Oikos,* **50,** 141-147.
1514 Rosenthal J.P. & Kotanen P.M. (1994) Terrestrial plant tolerance to herbivory. *Trends in Ecology*
1515   *& Evolution*, **9**, 145-148.
1516 Rothhaupt K.O. (1996) Laboratory experiments with a mixotrophic chrysophyte and obligately
1517   phagotrophic and phototrophic competitors. *Ecology*, **77**, 716-724.
1518 Rothlisberger J.D., Baker M.A. & Frost P.C. (2008) Effects of periphyton stoichiometry on mayfly
1519   excretion rates and nutrient ratios. *Journal of the North American Benthological Society*, **27**,
1520   497-508.
1521 Rounick J.S., Winterbourn M.J. & Lyon G.L. (1982) Differential utilization of allochthonous and
1522   autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable
1523   carbon isotope study. *Oikos*, **39**, 191-198.
1524 Route A.J. (1991) Flies for Alaska. Spring Creek Press.
1525 Rudd J.W.M. & Hamilton R.D. (1978) Methane cycling in an eutrophic shield lake and its effects
1526   on whole lake metabolism. *Limnology and Oceanography*, **23**, 337-348.
1527 Russell N.J. & Nichols D.S. (1999) Polyunsaturated fatty acids in marine bacteria—a dogma
1528   rewritten. *Microbiology*, **145**, 767-779.
1529 Sanchez C. (2009) Lignocellulosic residues: Biodegradation and bioconversion by fungi.
1530   *Biotechnology Advances*, **27**, 185-194.
1531 Sargent J., McEvoy L., Estevez A., Bell G., Bell M., Henderson J. *et al.* (1999) Lipid nutrition of
1532   marine fish during early development: current status and future directions. *Aquaculture*, **179**,
1533   217-229.
1534 Schindler D.E., Scheuerell M.D., Moore J.W., Gende S.M., Francis T.B. & Palen W.J. (2003)
1535   Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the*
1536   *Environment*, **1**, 31-37.
1537 Schindler D.W., Curtis P.J., Bayley S.E., Parker B.R., Beaty K.G. & Stainton M.P. (1997) Climate-
1538   induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochemistry*,
1539   **36**, 9-28.
1540 Schink B. (1997) Energetics of syntrophic cooperation in methanogenic degradation. *Microbiology*
1541   *and Molecular Biology Reviews*, **61**, 262-280
1542 Schubert C.J., Lucas F.S., Durisch-Kaiser E., Stierli R., Diem T., Scheidegger O. *et al.* (2010)
1543   Oxidation and emission of methane in a monomictic lake (Rotsee, Switzerland). *Aquatic*
1544   *Sciences* **72,** 455-466.
1545 Sedell I.R., Richey J.E. & Swanson F.I. (1989) The river continuum concept: a basis for the
1546   expected behavior of very large rivers? Pages 49-55 in D.P. Dodge, editor. *Proceedings of*
1547   *the International Large River Symposium, Canadian Special Publications in Fisheries and*
1548   *Aquatic Sciences*, **106**, 49-55.
1549 Seekell D.A., Lapierre J.F., Ask J., Bergström A.K., Deininger A., Rodríguez P. *et al.* (2015) The
1550   influence of dissolved organic carbon on primary production in northern lakes. *Limnology and*
1551   *Oceanography*, **60**, 1276-1285.
1552 Simonis J.L., Raja H.A. & Shearer C.A. (2008). Extracellular enzymes and soft rot decay: Are
1553   ascomycetes important degraders in freshwater? *Fungal Diversity*, **31**, 135-146.

44

1554 Skyllberg U., Westin M.B., Meili M. & Björn E. (2009) Elevated concentrations of methyl mercury
1555   in streams after forest clear-cut: a consequence of mobilization from soil or new methylation?
1556   *Environmental Science & Technology*, **43**, 8535-8541.
1557 Solomon C.T., Carpenter S.R., Clayton M.K., Cole J.J., Coloso J.J., Pace M.L. *et al.* (2011).
1558   Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian
1559   mixing model. *Ecology*, **92**, 1115-1125.
1560 Steinberg C.E., Kamara S., Prokhotskaya V.Y., Manusadǯianas L., Karasyova T.A., Timofeyev,
1561   M.A. *et al.* (2006) Dissolved humic substances - ecological driving forces from the individual
1562   to the ecosystem level? *Freshwater Biology,* **51**, 1189-1210.
1563 Steinman A.D., McIntire C.D. & Lowry R.R. (1987) Effects of herbivore type and density on
1564   chemical composition of algal assemblages in laboratory streams. *Journal of the North*
1565   *American Benthological Society*, **6**, 189-197.
1566 Stenroth K., Polvi L.E., Fältström E. & Jonsson M. (2015) Land-use effects on terrestrial
1567   consumers through changed size structure of aquatic insects. *Freshwater Biology*, **60**, 136-
1568   149.
1569 Stockner J.G. & Porter K.G. (1988) Microbial food webs in freshwater planktonic ecosystems. In
1570   Complex interactions in lake communities (pp. 69-83). Springer New York.
1571 Summerhayes V.S. & Elton C.S. (1923) Bear Island. *Journal of Ecology*, **11**, pp.216-233.
1572 Sutton R. & Sposito G. (2005) Molecular structure in soil humic substances: the new view.
1573   *Environmental Science & Technology*, **39**, 9009-9015.
1574 Taipale S.J., Brett M.T., Hahn M.W., Martin-Creuzburg D., Yeung S., Hiltunen M. *et al.* (2014)
1575   Differing *Daphnia magna* assimilation efficiencies for terrestrial, bacterial and algal carbon
1576   and fatty acids. *Ecology*, **95**, 563-576.
1577 Taipale S.J., Brett M.T., Pulkkinen K., & Kainz M.J. (2012) The influence of bacteria-dominated
1578   diets on *Daphnia magna* somatic growth, reproduction, and lipid composition. *FEMS*
1579   *Microbiology Ecology*, **82**, 50-62.
1580 Taipale S.J., Galloway A.W.E, Aalto A.L., Kahilainen K.K., Strandberg U. & Kankaala P. (2016a)
1581   Terrestrial carbohydrates support freshwater zooplankton during phytoplankton deficiency.
1582   *Scientific Reports,* **6,** 30897 | DOI: 10.1038/srep30897
1583 Taipale S.J., Kainz M.J. & Brett M.T. (2011) Diet switching experiments show rapid accumulation
1584   and preferential retention of highly unsaturated fatty acids in *Daphnia*. *Oikos*, **120**, 1674-
1585   1682.
1586 Taipale S.J., Kainz M.J. & Brett M.T. (2015) A low ω-3:ω-6 ratio in *Daphnia* indicates terrestrial
1587   resource utilization and poor nutritional condition. *Journal of Plankton Research*, **37**, 596-610.
1588 Taipale S.J., Kankaala P., Tiirola M. & Jones R.I. (2008) Whole-lake dissolved inorganic 13C
1589   additions reveal seasonal shifts in zooplankton diet. *Ecology*, **89**, 463-474.
1590 Taipale S.J., Strandberg U., Peltomaa E., Galloway A.W., Ojala A. & Brett M.T. (2013) Fatty acid
1591   composition as biomarkers of freshwater microalgae: analysis of 37 strains of microalgae in
1592   22 genera and in seven classes. *Aquatic Microbial Ecology*, **71**, 165-178.
1593 Taipale S.J., Vuorio K., Brett M.T., Peltomaa E., Hiltunen M., & Kankaala P. (2016b) Lake
1594   zooplankton $\delta^{13}C$ values are strongly correlated with the $\delta^{13}C$ values of distinct phytoplankton
1595   taxa. *Ecosphere* (in press).
1596 Tanentzap A.J., Szkokan-Emilson E.J., Kielstra B.W., Arts M.T., Yan N.D. & Gunn J.M. (2014).
1597   Forests fuel fish growth in freshwater deltas. *Nature Communications*, **5**, 4077.
1598 Thorp J.H. & Bowes R.E. (2017) Carbon sources in riverine food webs: new evidence from amino
1599   acid isotopic techniques. Ecosystems (in press) DOI: 10.1007/s10021-016-0091-y.
1600 Thorp J.H. & Delong M.D. (1994) The riverine productivity model: an heuristic view of carbon
1601   sources and organic processing in large river ecosystems. *Oikos*, **70**, 305-308.
1602 Thorp J.H. & Delong M.D. (2002) Dominance of autochthonous autotrophic carbon in food webs
1603   of heterotrophic rivers. *Oikos*, **96**, 543-550.
1604 Thorp J.H., Thoms M.C. & Delong M.D. (2006) The riverine ecosystem synthesis: biocomplexity
1605   in river networks across space and time. *River Research and Applications*, **22**, 123-147.
1606 Thorp J.H., Thoms M.C. & Delong M.D. (2008) The riverine ecosystem synthesis. Academic
1607   Press, Boston, MA, USA. 208 p.
1608 Thrane J.E., Hessen D.O. & Andersen T. (2014) The absorption of light in lakes: negative impact
1609   of dissolved organic carbon on primary productivity. *Ecosystems*, **17**, 1040-1052.

1610 Torres-Ruiz M. & Wehr J.D. (2010) Changes in the nutritional quality of decaying leaf litter in a
1611   stream based on fatty acid content. *Hydrobiologia*, **651**, 265-278.
1612 Torres-Ruiz M., Wehr J.D. & Perrone A.A. (2007) Trophic relationships in a stream food web: the
1613   importance of fatty acids for macroinvertebrate consumers. *Journal of the North American*
1614   *Benthological Society*, **26**, 509-522.
1615 Torres-Ruiz M., Wehr J.D. & Perrone A.A. (2010) Are net-spinning caddisflies what they eat? An
1616   investigation using controlled diets and fatty acids. *Journal of the North American*
1617   *Benthological Society*, **29**, 803-813.
1618 Tranvik L.J., Porter K.G. & Sieburth J. McN. (1989) Occurrence of bacterivory in *Cryptomonas*, a
1619   common freshwater phytoplankter. *Oecologia*, **78**, 473-476.
1620 Tulonen T., Salonen K. & Arvola L. (1992) Effects of different molecular weight fractions of
1621   dissolved organic matter on the growth of bacteria, algae and protozoa from a highly humic
1622   lake. *Hydrobiologia*, **229**, 239-252.
1623 Tuomela M., Vikman M., Hatakka A. & Itävaara M. (2000) Biodegradation of lignin in a compost
1624   environment: a review. *Bioresource Technology*, **72,** 169-183.
1625 Vadeboncoeur Y. & Lodge D.M. (2000) Periphyton production on wood and sediment:
1626   substratum-specific response to laboratory and whole-lake nutrient manipulations. *Journal of*
1627   *the North American Benthological Society*, **19**, 68-81.
1628 Vadeboncoeur Y., Peterson,G., Vander Zanden M.J. & Kalff J. (2008) Benthic algal production
1629   across lake size gradients: interactions among morphometry, nutrients, and light. *Ecology*,
1630   **89**, 2542-2552.
1631 Vadeboncoeur, Y., Jeppesen E., Vander Zanden M.J., Schierup H.H., Christoffersen K. & Lodge
1632   D.M. (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic
1633   pathways in lakes. *Limnology and Oceanography*, **48**, 1408-1418.
1634 Vähätalo A.V., Aarnos H., Hoikkala L. & Lignell R. (2011) Photochemical transformation of
1635   terrestrial dissolved organic matter supports hetero-and autotrophic production in coastal
1636   waters. *Marine Ecology Progress Series*, **423**, 1-14.
1637 Vander Zanden M.J. & Rasmussen J.B. (1999) Primary consumer δ^{13}C and δ^{15}N and the trophic
1638   position of aquatic consumers. *Ecology*, **80**, 1395-1404.
1639 Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river
1640   continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137.
1641 Vesterinen J., Devlin S.P., Syväranta J. & Jones R.I. (2016) Accounting for littoral primary
1642   production by periphyton shifts a highly humic boreal lake towards net autotrophy.
1643   *Freshwater Biology*, **61**, 265-276.
1644 von Einem J. & Granéli W. (2010) Effects of fetch and dissolved organic carbon on epilimnion
1645   depth and light climate in small forest lakes in southern Sweden. *Limnology and*
1646   *Oceanography*, **55**, 920-930.
1647 von Elert E. (2002) Determination of limiting polyunsaturated fatty acids in *Daphnia galeata* using
1648   a new method to enrich food algae with single fatty acids. *Limnology and Oceanography*, **47**,
1649   1764-1773.
1650 Vuorio K., Meili M. & Sarvala J. (2006) Taxon-specific variation in the stable isotopic signatures
1651   (δ^{13}C and δ^{15}N) of lake phytoplankton. *Freshwater Biology*, **51**, 807-822.
1652 Walton I. (1653) The Compleat Angler. Charles Lamb Publisher.
1653 Webster J.R., Golladay S.W., Benfield E.F., D'Angelo D.J. & Peters G.T. (1990) Effects of forest
1654   disturbance on particulate organic matter budgets of small streams. *Journal of the North*
1655   *American Benthological Society*, **9**, 120-140.
1656 Webster J.R. & Meyer J.L. (1997) Organic matter budgets for streams: a synthesis. *Journal of the*
1657   *North American Benthological Society*, **16**, 141-161.
1658 Wehr J.D., Holen D.A., MacDonald M.M. & Lonergan S.P. (1998) Effects of different carbon
1659   sources on a freshwater plankton community. *Canadian Journal of Fisheries and Aquatic*
1660   *Sciences*, **55**, 2150-2160.
1661 Wehr J.D., Petersen J. & Findlay S. (1999) Influence of three contrasting detrital carbon sources
1662   on planktonic bacterial metabolism in a mesotrophic lake. *Microbial Ecology*, **37**, 23-35.
1663 Wenzel A., Bergström, A.K., Jansson, M. & Vrede, T. (2012a) Poor direct exploitation of terrestrial
1664   particulate organic material from peat layers by *Daphnia galeata*. *Canadian Journal of*
1665   *Fisheries and Aquatic Sciences*, **69**, 1870-1880.

1666 Wenzel A., Bergström A.-K., Jansson M. &Vrede T. (2012b) Survival, growth and reproduction of
1667   *Daphnia galeata* feeding on single and mixed *Pseudomonas* and *Rhodomonas* diets.
1668   *Freshwater Biology*, **57**, 835-846.
1669 West W.E., Coloso J.J. & Jones S.E. (2012) Effects of algal and terrestrial carbon on methane
1670   production rates and methanogen community structure in a temperate lake sediment:
1671   Methanogen response to trophic change. *Freshwater Biology*, **57,** 949-955.
1672 Wetzel R.G. (1995) Death, detritus and energy flow in aquatic ecosystems. *Freshwater Biology*,
1673   **35**, 83-89.
1674 Wetzel R.G. (2001) Chapter 23, Detritus: organic carbon cycling and ecosystem metabolism. *In*
1675   Limnology, Lake and River Ecosystems, 3rd edition. Academic Press.
1676 Williamson C.E. & Rose K.C. (2010) When UV meets fresh water. *Science,* **329**, 637-639.
1677 Wipfli M.S. & Baxter C.V. (2010) Linking ecosystems, food webs, and fish production: subsidies in
1678   salmonid watersheds. *Fisheries*, **35**, 373-387.
1679 Wipfli M.S., Hudson J.P., Caouette J.P. & Chaloner D.T. (2003) Marine subsidies in freshwater
1680   ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids.
1681   *Transactions of the American Fisheries Society*, **132**, 371-381.
1682 Wipfli M.S. (1997) Terrestrial invertebrates as salmonid prey and nitrogen sources in streams:
1683   contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA.
1684   *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1259-1269.
1685 Wyatt B. (2013) What trout want: the educated trout and other myths. Stackpole Books, 2013.
1686 Zohary T., Erez J., Gophen M., Berman-Frank I. & Stiller M. (1994) Seasonality of stable carbon
1687   isotopes within the pelagic food web of Lake Kinneret. *Limnology and Oceanography*, **39**,
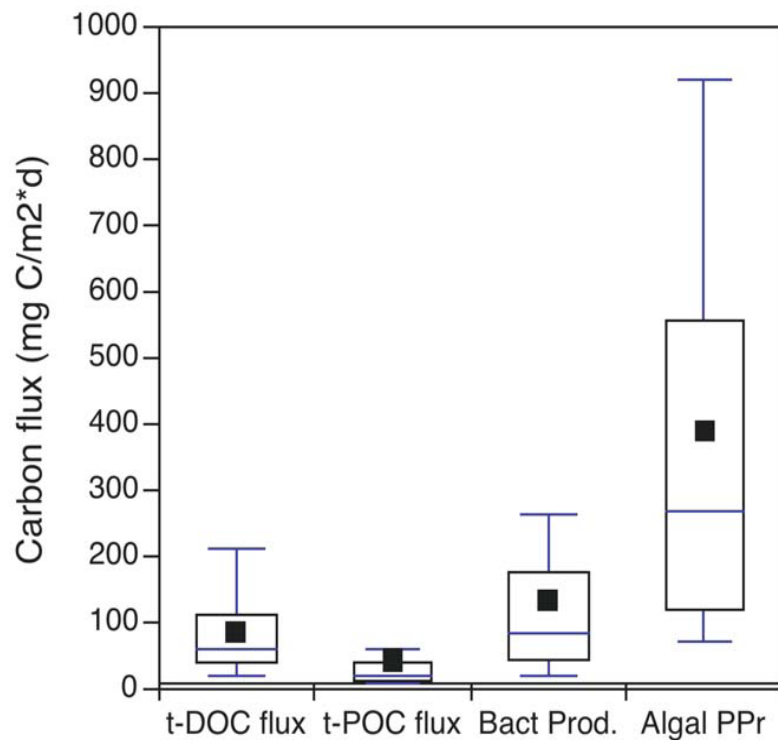1688   1030-1043.
1689

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.
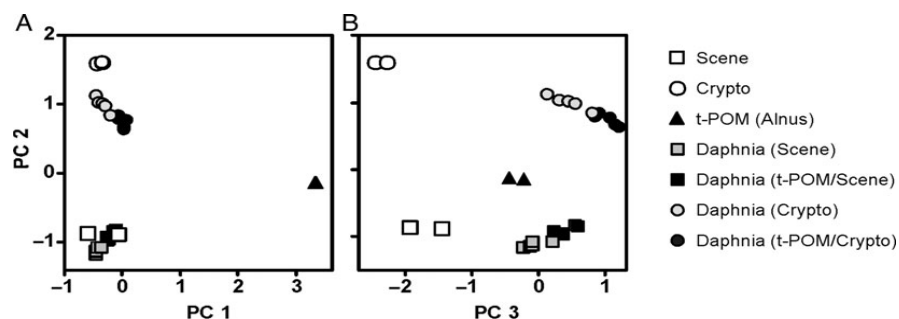
Fig. 2. A principal components analysis of the fatty acid composition of terrestrial detritus (i.e., finely-ground *Alnus rubra*; t-POM), phytoplankton (i.e., *Scenedesmus acutus* and *Cryptomonas ozolinii*), and *Daphnia* fed either pure or mixed diets of phytoplankton and t-POM (Taipale *et al.*, 2015). 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.

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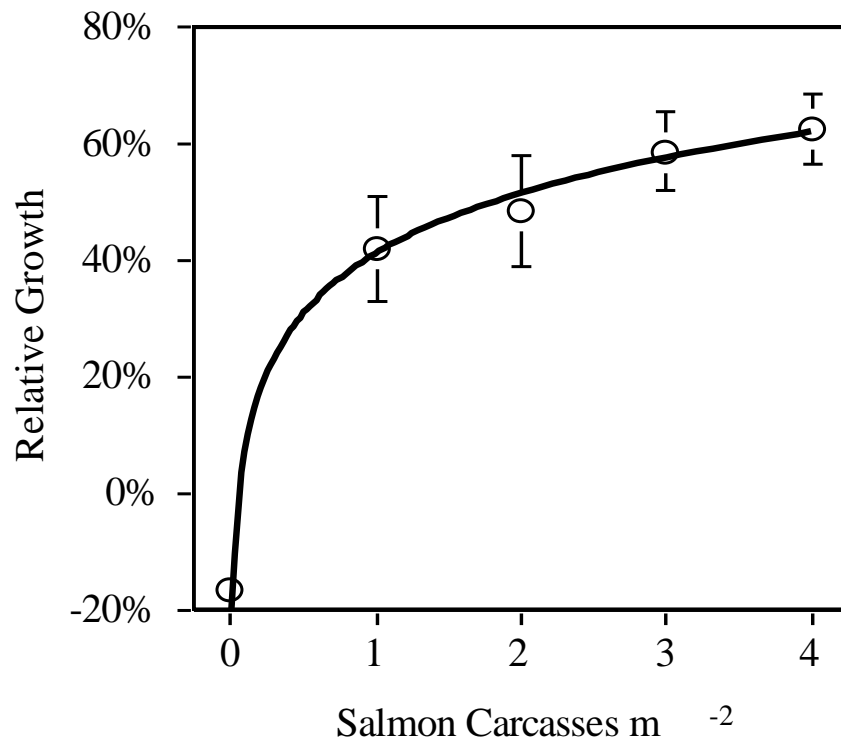
Fig. 4. Mean growth of juvenile Coho salmon (± SE) over 66 days when exposed
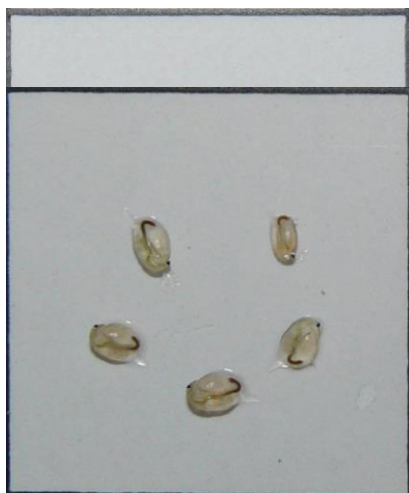to a gradient of salmon carcass additions. Adapted from Wipfli *et al.* (2003).

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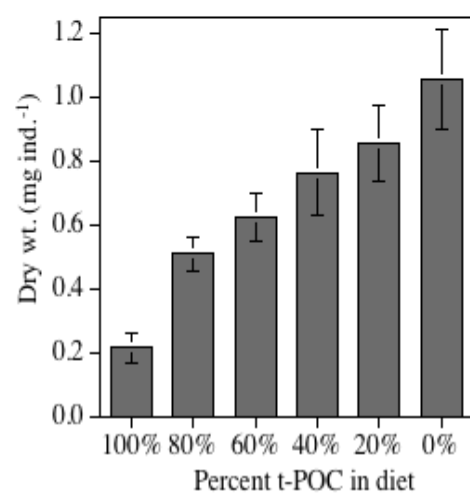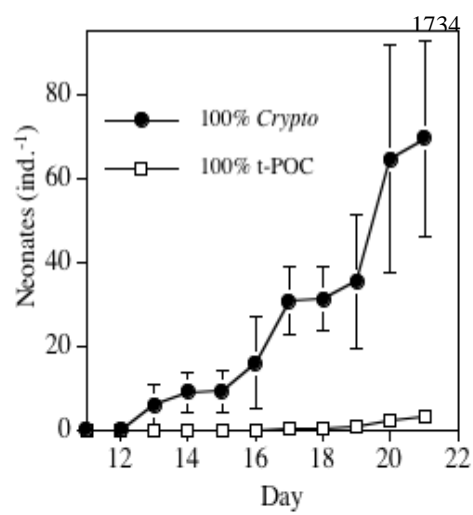
Fig. 5. The growth and reproduction responses of *Daphnia magna* fed phytoplankton or finely ground terrestrial detritus (Brett *et al.*, 2009). The upper left panel shows cumulative *Daphnia* neonate production when fed the phytoplankter *Cryptomonas ozolinii* or leaves of the riparian tree *Alnus rubra*. 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.