REVIEW

The importance of high-quality algal food sources in stream food webs – current status and future perspectives

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SUMMARY

1. While many streams and rivers are dominated by terrestrial inputs of organic carbon, algae are an important trophic base for stream food webs. However, the nutritional importance of algae for stream invertebrates only recently has been highlighted. Algae are acknowledged as higher quality food than terrestrial organic matter for the growth and reproduction of invertebrates. In part, this is because of higher algal polyunsaturated fatty-acid (PUFA) content. Here, we review the important influence of algal food quality, as assessed by PUFA, in stream food webs.

2. Current field investigations have mainly focused on the fatty-acid dynamics of macroinvertebrates, and indicate that algal eicosapentaenoic acid (EPA), α-linolenic acid (ALA) and linoleic acids (LIN) are present in all macroinvertebrates. However, fungal and bacterial tracers have also been observed in a range of macroinvertebrates. The omega-3 (ω3)/omega-6 (ω6) ratio >1 in most macroinvertebrates strongly indicates that dietary energy of algae is highly retained in stream food webs. Interspecific differences in PUFA composition seem to be affected by dietary PUFA and consumer physiology.

3. Some studies have suggested that besides dietary EPA, the shorter chain C18 PUFA LIN and ALA also can improve growth and reproduction of stream invertebrate consumers. Some macroinvertebrates may preferentially retain or synthesise long-chain PUFA from C18 PUFA when experiencing low-quality food. However, this process is controversial since other species have shown very limited ability to synthesise long-chain PUFA.

4. Algal PUFA composition is strongly influenced by abiotic factors, particularly light, nutrients, and temperature. Human disturbance (i.e. riparian vegetation removal and nutrient inputs) on algal PUFA content and their consequent effects on macroinvertebrates and fish clearly warrant further scientific attention. Controlled feeding trials and manipulative studies are required to measure PUFA conversion capacities and reproductive investment of stream macroinvertebrates under different food quality conditions, which will provide insights into how freshwater species can cope with different nutritional food conditions due to human disturbance and climate change.

Keywords: aquatic invertebrates, human disturbance, polyunsaturated fatty acids, reproduction, somatic growth

Introduction

Food webs in streams and rivers are often complex, incorporating aspects of both terrestrial and aquatic systems. Stream food sources, such as terrestrial matter and algae, are strongly influenced by seasonal changes, flow conditions and anthropogenic activity (Dodds & Whiles, 2010), resulting in spatial and temporal variation in food availability and quality which consequently affects the growth and fitness of consumers (Torres-Ruiz, Wehr &
Perrone, 2007). Therefore, mixed feeding modes and a high degree of omnivory are increasingly reported for freshwater consumers, particularly for those in running waters (Woodward et al., 2005, 2010; Anderson & Cabana, 2007). This flexibility makes elucidating the exact consumer-resource relationships in streams complicated.

Polysaturated fatty acids (PUFA) are becoming an increasingly informative biochemical tracer for assessing consumer-resource relationships in aquatic food webs (Galloway et al., 2015). Animals are unable to synthesise certain PUFA de novo, such as eicosapentaenoic acid (EPA, 20:5ω-3) and docosahexanoic acid (DHA, 22:6ω-3), which can be abundant in algae, and therefore they must take up PUFA from their diets to meet physiological requirements (Brett & Müller-Navarra, 1997). Those PUFA could be transferred from food sources to consumers with no or minimal modification, and may represent long-term dietary information (Iversen, 2009). In stream ecosystems, PUFA have been used to detect the relative importance of food sources and elucidate trophic relationships (Torres-Ruiz et al., 2010). More- ever, dietary PUFA composition is also an indicator of nutritional quality, which is critical not only for invertebrate growth and reproduction, but also affects energy transfer efficiency (Müller-Navarra et al., 2000; Gladyshev et al., 2011). Diatoms with high concentrations of EPA and DHA are considered as high-quality food for invertebrates (Brett & Müller-Navarra, 1997), while cyanobacteria are usually low-quality food because they lack these specific PUFA as well as sterols (Martin-Creuzburg, Von Elert & Hoffmann, 2008). Higher algal food quality has been shown to support higher growth rates and reproduction of consumers (Müller-Navarra, 1995; Müller-Navarra et al., 2000), and stimulate energy transfer efficiency to upper trophic levels (Müller-Navarra et al., 2000; Kainz, Arts & Mazumder, 2004; Gladyshev et al., 2011). Basal consumers feeding on high-quality food will also be of high nutritional quality for secondary consumers, such as fish (Brett & Müller-Navarra, 1997). However, current studies on algal PUFA and their effect on invertebrates are mainly from lacustrine systems, and only a few studies have explicitly investigated algal PUFA in streams.

In stream food webs, basal food sources are known to differ markedly in their nutritional quality (Cross et al., 2003, 2005; Lau et al., 2009a). Compared with terrestrial organic matter, algae are considered as higher quality food for invertebrates because of higher PUFA content (Torres-Ruiz et al., 2007; Lau et al., 2009a). In streams and rivers, algal PUFA are mostly contained in the periphyton (Cashman, Wehr & Truhn, 2013; Guo et al., 2015) or biofilms (Ziegler & Lyon, 2010) that grow on stream substrates, and form basal dietary sources for consumers. Based on studies using a number of biochemical tracers, including stable isotopes, fatty acids and compound-specific stable isotopes, the algal component of the periphyton has been demonstrated as the major basal component of stream food webs (Bunn, Davies & Winning, 2003; Lau et al., 2009a; Descroix et al., 2010). Nonetheless, only recently has the importance of algal food quality, as distinct from just food quantity, been highlighted in stream food web studies. It is time to assess algal food quality and identify key factors that determine ‘quality’. This paper will examine the role of algal food quality, measured by PUFA composition, in stream food webs by summarising the nutritional quality of food sources, evaluating the role of algal food quality for the growth and reproduction in stream macroinvertebrates, discussing the influence of human disturbance on trophic energy flow across the plant–animal interface, and proposing future study directions. This review will bring together our understanding about nutritional quality, biochemistry and animal physiology to answer broad ecosystem questions, and may help us better understand how human disturbances (climate change, riparian clearing and nutrient enrichment) can influence fundamental ecosystem properties.

**PUFA terminology and physiological functions**

Fatty acids (FA) are usually divided into three major groups: saturated FA (SAFA), monounsaturated FA (MUFA) and PUFA, according to the degree of unsaturation and the length of carbon chain (Arts & Wainmann, 1999) (Table 1). Highly unsaturated FA (HUFA) are a subset of PUFA with 20 or more carbon atoms, mainly discriminating the long-chain PUFA, such as DHA, EPA and arachidonic acid (ARA, 20:4ω-6), from the shorter chain C18 PUFA, such as α-linolenic (ALA, 18:3ω-3) and linoleic (LIN, 18:2ω-6) (Bell & Tocher, 2009).

Fatty acids are the main components of neutral and polar lipids in all biota. SAFA are usually used for energy storage and are preferentially catabolised (Brett & Müller-Navarra, 1997). PUFA commonly regulate cell membrane fluidity and serve as precursors for animal hormones (Brett & Müller-Navarra, 1997). Among PUFA, LIN and ALA are structural starting molecules that can be converted to long-chain ω6 PUFA, including ARA, or long-chain ω3 PUFA, such as EPA and DHA. LIN and ALA are essential fatty acids for animals.
Table 1 Fatty-acid terminology.

<table>
<thead>
<tr>
<th>Abbreviations</th>
<th>Full name</th>
<th>Nomenclature</th>
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<tbody>
<tr>
<td>FA</td>
<td>Fatty Acid</td>
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<tr>
<td>SAFA</td>
<td>Saturated Fatty Acid</td>
<td>10:0, 11:0, 12:0, 13:0, 14:0, 15:0, 16:0, 17:0, 18:0, 20:0, 22:0, 23:0, 24:0</td>
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<tr>
<td>MUFA</td>
<td>Monounsaturated Fatty Acid</td>
<td>14:1, 15:1, 16:1, 17:1, 18:1ω9/ω7, 20:1, 22:1ω9/ω11, 24:1</td>
</tr>
<tr>
<td>PUFA</td>
<td>Polyunsaturated Fatty Acid</td>
<td>FA with 2 or more double bonds</td>
</tr>
<tr>
<td>HUFA</td>
<td>Highly Unsaturated Fatty Acid</td>
<td>PUFA with 20 or more carbon atoms</td>
</tr>
<tr>
<td>Cx</td>
<td>Refers to the number of carbons in fatty acids</td>
<td>e.g. C18=18 carbons</td>
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<tr>
<td>ω3: ω6</td>
<td>ω3: ω6 PUFA ratio</td>
<td></td>
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<tr>
<td>LIN</td>
<td>Linoleic acid</td>
<td>18:2ω-6</td>
</tr>
<tr>
<td>ALA</td>
<td>α-linolenic acid</td>
<td>18:3ω-3</td>
</tr>
<tr>
<td>ARA</td>
<td>Arachidonic acid</td>
<td>20:4ω-6</td>
</tr>
<tr>
<td>EPA</td>
<td>Eicosapentaenoic acid</td>
<td>20:5ω-3</td>
</tr>
<tr>
<td>DHA</td>
<td>Docosahexaenoic acid</td>
<td>22:6ω-3</td>
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because enzymes, which are usually found in algae and other plants (Kelly & Scheibling, 2012), are required to convert 18:1ω-9 to LIN (Δ12 desaturase) and further to ALA (Δ15 desaturase) (Cook & Mcmaster, 2002). Although it has been reported that many invertebrates and fish have the ability to convert dietary LIN and ALA to other PUFA (Jones, Kanazawa & Ono, 1979; Waldock & Holland, 1984; Goulden & Place, 1993; Sargent et al., 1999), this generally occurs at a level that is too limited and too low to support optimal growth (Brett & Müller-Navarra, 1997), but see Murray et al. (2014) for ALA conversion into DHA in the freshwater Alpine charr). Accordingly, it is necessary for freshwater animals to have access to adequate amounts of dietary PUFA, particularly in stream ecosystems, which are typically poor in dietary long-chain PUFA.

Eicosapentaenoic acid, ARA and DHA are the most physiologically important PUFA for invertebrates (Stanley-Samuelson, 1994a,b). EPA and ARA are precursors to eicosanoids, which are critical cellular signalling compounds required for development, reproduction and hormone regulation in many invertebrates (Stanley-Samuelson, 1994a; Gurr, Harwood & Frayn, 2002). EPA is required for insect emergence and reproduction (Stanley-Samuelson, 1994a), gastropod and mussel spawning (Morse et al., 1977), and hydra tissue regeneration (Stanley-Samuelson, 1994b).

Although the role of EPA in consumer physiology is well studied, the physiological function of ARA for invertebrates needs clarification. ARA has been shown to support somatic growth and reproduction of chironomids and ephemerids (Ahlgren, Vrede & Goedkoop, 2009). However, the patterns are not consistent; zooplankton did not improve their somatic growth or reproduction when small amounts of cyanobacteria containing 2.5% ARA were added to their diet (Ravet, Brett & Müller-Navarra, 2003).

Due to its high number of double bonds, DHA has a greater effect on membrane fluidity than the other long-chain PUFA (i.e. EPA and ARA) (Niebylski & Salem, 1994), even at low temperatures (Stillwell & Wassall, 2003). DHA is also associated with neural tissue, in particular the retina, playing an important role in neural development and vision functions (Sargent et al., 1993; Böh m et al., 2014).

Algal food quality in stream food webs

Terrestrial matter versus algae

A fundamental question regarding energy flow in streams is whether the basal component of the food web is predominantly driven by allochthonous or autochthonous sources. Earlier river conceptual models, the River Continuum Concept (RCC) (Vannote et al., 1980) and the Flood Pulse Concept (FPC) (Junk, Bayley & Sparks, 1989), had advocated that allochthonous carbon from either upstream (RCC) or lateral floodplains (FPC) fuelled stream food webs. Most of those studies supporting these models were based primarily on consumer ingestion, such as direct observations of gut content and feeding behaviour. However, in recent years, the widespread use of biochemical tracers, in particular stable isotopes and more recently FA, amino acids and isotopes of FA and amino acids, has challenged the view of dominant terrestrial sources, and highlighted the importance of algal food sources in stream food webs. Specific algal biochemical tracers have been found in animal tissues, even in streams whose conditions are not conducive for algal growth (Bunn et al., 2003; Lau et al., 2009a). Algae have been demonstrated as the trophic base of food webs and the main driver of consumer production in temperate rivers (Torres-Ruiz et al., 2007; Descroix et al., 2010), arid rivers (Bunn et al., 2003), tropical inland rivers (March & Pringle, 2003) and also tropical forest and headwater streams (Brito et al., 2006; Lau et al., 2009a). Despite these findings, several recent studies in lake food webs that drew on isotope data have again challenged this view (Cole et al., 2011; Zigah et al., 2012). Therefore, a better functional understanding of
the physiological mechanism behind the interaction between stream consumers and their food sources will help address this controversy.

**Algal food quality**

Why are stream food webs often dependent on inconspicuous algae? As the research emphasis has changed from consumer ingestion to assimilation, it has become increasingly clear that food quality, and not quantity, is the more important factor regulating the efficiency of energy flow through stream ecosystems (Torres-Ruiz et al., 2007; Lau, Leung & Dudgeon, 2008, 2009b; Lau et al., 2009a). The existing literature shows that allochthonous and autochthonous sources differ in their nutritional quality for invertebrates (Cross et al., 2005; Lau et al., 2009a).

Allochthonous food sources, such as leaf litter, and fungi and bacteria colonising leaves, are considered lower quality food for invertebrates compared with algae (Cross et al., 2005; Torres-Ruiz et al., 2007; Lau et al., 2009a). Live terrestrial leaf matter of vascular plants is typically characterised by high C : N and C : P ratios, relatively high levels of C18 PUFA (i.e. LIN and ALA), but non-detectable HUFA (Napolitano, 1999; Mills et al., 2001; Allan & Castillo, 2007). C18 PUFAs are usually lost when leaves are dead (Torres-Ruiz & Wehr, 2010). After leaves enter stream channels, fungi and bacteria colonising decomposing leaves can increase their nutritional quality in terms of decreased C : N ratios and increased protein content (Bärlocher & Kendrick, 1975; Cornut et al., 2015; Manning et al., 2015; Tant et al., 2015). Colonised or conditioned detritus is more rapidly consumed and assimilated by invertebrates and supports better growth than sterile detritus (Bärlocher & Kendrick, 1975; Allan & Castillo, 2007; Manning et al., 2015). Nevertheless, fungi and bacteria are still rather poor quality diets for invertebrates, because they generally lack HUFA, that is, EPA and DHA. Studies on terrestrial and marine fungi reported that 16:0, 18:0, 18:1ω9 and LIN are the most common FA in fungi (Cooney et al., 1993; Stahl & Klug, 1996). Bacteria are generally rich in 15:0, 17:0 and their branched derivatives, as well as vaccenic acid 18:1ω7 (Desvillettes et al., 1997; Kainz & Mazumder, 2005), and methanotrophs are unique in containing 16:1ω8 and 18:1ω8 (Sundh, Bastviken & Tranvik, 2005).

In contrast, algae have been recognised as higher quality food sources than terrestrial matter for the growth and reproduction of invertebrates because of their lower C : N and C : P ratios (Frost & Elser, 2002; Cross et al., 2005; Lau et al., 2009a) and higher PUFA content (Torres-Ruiz et al., 2007; Lau et al., 2009a). Most studies on the FA composition of stream periphyton are consistent with results from marine and lacustrine systems. Diatoms are best characterised by EPA, 16:1ω7 and C16 PUFA, while green algae are rich in LIN and ALA (Napolitano et al., 1994; Torres-Ruiz et al., 2007). Some cyanobacteria also contain LIN and ALA, but typically lack HUFA (Napolitano et al., 1994; Napolitano, 1999). The difference between marine and freshwater systems is that the DHA content of stream periphyton is very low, which may consequently influence the growth and reproduction of consumers.

**Environmental factors affecting algal food quality**

Most studies regarding the effect of environmental factors on algal PUFA have been conducted on single algal species under laboratory conditions, aiming to improve algal nutritional value (aquaculture), to increase PUFA production (the pharmaceutical industry), or to enhance lipid content (biodiesel production). Light intensity, nutrient availability, as well as temperature, have been shown to be the most important environmental factors affecting algal PUFA content (Guschina & Harwood, 2009) (Table 2). Algae adapt to low temperature by increasing the degree of unsaturation, leading to an increase in long-chain PUFA content (Morgan-Kiss et al., 2006; Piepho, Arts & Wacker, 2012). Algal PUFA biosynthesis is regulated by light levels (Wainman et al., 1999; Guschina & Harwood, 2006b), and strongly affected by nutrient regimes (Guschina & Harwood, 2009). In addition, elevated CO2 (Thompson, 1996; Muradyan et al., 2004), pH stress (Tatsuzawa et al., 1996; Guschina & Harwood, 2009) and environmental pollutants (Chia et al., 2012, 2013) also have impacts on algal PUFA (Table 2). However, few studies have considered the effect of environmental factors on algal PUFA content in stream food webs (Mcintire, Tinsley & Lowry, 1969; Steinman, McIntyre & Lowry, 1988; Hill, Rinchard & Czesny, 2011; Cashman et al., 2013; Guo et al., 2015), and the consequent effect on macroinvertebrates.

**The role of algal food quality for growth and reproduction in stream invertebrates**

Evidence of the influence of algal PUFA content on consumer growth and reproduction comes primarily from freshwater zooplankton (i.e. copepods and cladocera) (Harrison, 1990; Kleppel, Burkart & Houchin, 1998; Müller-Navarra et al., 2000; Brett et al., 2006) and...
To know how macroinvertebrates utilise algal PUFA, to achieve success in stream macroinvertebrates, it is essential to understand the importance of algal PUFA for somatic growth and reproduction (Goedkoop et al., 2004; Sinanoglou, Meimaroglou & Miniadis-Meimarakoglou, 2014). Thus, to better understand the nutritional importance of algal PUFA for somatic growth and reproductive success in stream macroinvertebrates, it is essential to know how macroinvertebrates utilise algal PUFA, to what extent macroinvertebrate FA composition is influenced by dietary PUFA, and if their capacity to synthesise HUFA from shorter homologues can meet physiological requirements during periods of active somatic growth and reproduction. This information is essential to estimate energy transfer efficiency in stream food webs.

Only a limited number of studies have referred to the importance of algal PUFA for stream macroinvertebrates. Current field investigations mainly focus on the FA dynamics of macroinvertebrates, such as temporal and spatial changes, and influencing factors (food sources and consumer physiology), emphasising the importance of algal HUFA with an eye towards their nutritional availability to fish. Existing laboratory feeding experiments primarily try to address the role of algal PUFA composition for the somatic growth and reproduction in macroinvertebrates and their PUFA metabolism.

**Fatty-acid composition of stream macroinvertebrates**

The present field data have been drawn mainly from studies in northern temperate rivers, such as the Yenisei River (Russia), River Allan (Scotland) and the Muscoot River (New York).
River, tributary systems of Lake Michigan and a range of natural running water habitats in the US (Table 3) (Hanson et al., 1985; Bell, Ghioni & Sargent, 1994; Ghioni, Bell & Sargent, 1996; Sushchik et al., 2003, 2006, 2007; Torres-Ruiz et al., 2007; Makhatova et al., 2011; Gladyshev et al., 2012; Volk & Kiffney, 2012; Larson et al., 2013; Lau, Goedkoop & Vrede, 2013; Smits, Schindler & Brett, 2015). Direct comparisons of the FA composition among different studies are difficult because of differences in sampling methods, measured FA (i.e. some measured MUFA as Cx: 1 without specifying the position of double bonds), and methods of expressing data (i.e. some authors use mg/g wet weight, and others report relative values as %). However, from across the data some general FA patterns of macroinvertebrates can be elucidated (Table 3). In general, 16:0 is the most dominant SAFA, followed by 18:0 and 14:0 (Table 3). 16:1ω7, 16:1ω9, 18:1ω7 and 18:1ω9 are the most abundant MUFA. Among PUFA, EPA is the most abundant ω3 PUFA in most macroinvertebrates, followed by ALA, and LIN is the most abundant ω6 PUFA, followed by ARA. DHA content is generally higher in Bivalvia, Crustacea, Oligochaeta and Turbellaria, but considerably less or completely lacking in Insecta.

It is worth noting that insect larvae with well-developed nervous systems and complex behaviour do not accumulate DHA. The lack of DHA may reflect a low activity conversion of precursor FA to DHA, low DHA retention requirements, and/or a limited dietary supply (Bell et al., 1994). DHA is usually present in cryptophytes and diatoms. Compared with the DHA content in marine cryptophytes (6.5 ± 2.2%) and diatoms (2.9 ± 1.7%), and freshwater cryptophytes (2.9 ± 1.8%) and diatoms (2.5 ± 3.0%) (Brett, Müller-Navarra & Persson, 2009b), stream periphyton as a whole has much lower DHA content, mostly <1% (Napolitano et al., 1994; Hill et al., 2011; Guo et al., 2015; Honeyfield & Maloney, 2015). DHA, as well as EPA and ARA are the most physiologically important HUFA for invertebrates (Stanley-Samuelson, 1994a). Insects may need more EPA and ARA for growth and reproduction than DHA (Ahlgren et al., 2009). Proper neural and retinal tissue development is probably fulfilled in insects by EPA, which may account for the high abundance of C20 PUFA in the retina of the butterfly (Ogg, Howard & Stanley-Samuelson, 1991). Nevertheless, insects are important food sources for freshwater fish, which retain high DHA contents. Fish may choose more nutritionally complete macroinvertebrates, such as Crustacea, or may obtain DHA from conversion of dietary EPA or ALA. The presence of biochemical conversion from dietary EPA to DHA in some freshwater fish, including rainbow trout and grayling, has been presented experimentally (Buzzi, Henderson & Sargent, 1997; Murray et al., 2014) and proposed based on field observations (Ahlgren, Carlstein & Gustafsson, 1999; Sushchik et al., 2006). Freshwater fish appear to have a greater capacity to elongate and desaturate C18 PUFA to DHA than marine fish (Sargent et al., 1993).

The FA composition of stream macroinvertebrates reflects the diversity of their food sources. Algal FA tracers for diatoms, green algae and cyanobacteria are present in all macroinvertebrates. Bacterial and fungal tracers also exist in higher levels in Ephemeroptera, Trichoptera, Chironomidae, Gammaridae and Oligochaeta in comparison with other recorded taxa. In streams, the ω3/ω6 ratio of invertebrates is of great importance since it has been used to identify food sources (terrestrial matter versus algae) (Pollero, Brenner & Gros, 1981; Desvillettes et al., 1994; Torres-Ruiz et al., 2007). Among all studied stream macroinvertebrates, the ω3/ω6 ratio >1 confirms that algae are the more important food sources fuelling stream food webs. Although macroinvertebrates use different feeding modes, feeding results may be similar in that they all require high-quality algae to improve their growth and survival. Algae may be scraped by grazers feeding on periphyton, collected by filter feeders in the water column, or gathered by collectors feeding in depositional areas. The dominance of EPA in most macroinvertebrates indicates the nutritional importance of diatoms as a trophic base for stream macroinvertebrates.

Highly unsaturated fatty-acid content, in particular EPA, ARA and DHA increases with stream trophic position, while SAFA, especially 16:0 decreases, which is consistent with findings from lacustrine systems (Persson & Vrede, 2006; Lau et al., 2012). The greater HUFA content in predators compared with non-predators is suggested to be chiefly dependent on food sources (Bell et al., 1994). Recent field studies found that algal resources are even more important for secondary than primary consumers in benthic habitats (Lau et al., 2014), and the basal resource support from biofilm is substantially higher for benthic predators than for primary consumers. This suggests that benthic predators can selectively choose invertebrates that are rich in HUFA or feed on diatoms. The accumulation of HUFA in subsequent trophic levels can enhance consumer growth and reproduction, and allow more efficient trophic transfer, while SAFA are preferentially catabolised decreasing their relative abundance (Brett et al., 2009a; Gladyshev et al., 2011; Lau et al., 2014).

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Table 3 Current field investigations on the fatty-acid composition of macroinvertebrates in streams. FA, fatty acid; PUFA, polyunsaturated fatty acids; DHA, docosahexaenoic acid (22:6\(\omega-3\)); EPA, eicosapentaenoic acid (20:5\(\omega-3\)); ARA, arachidonic acid (20:4\(\omega-6\)); ALA, \(\alpha\)-linolenic acid (18:3\(\omega-3\)); LIN, linoleic acid (18:2\(\omega-6\)).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Species</th>
<th>Abundant FA</th>
<th>(\alpha3/\omega6)</th>
<th>Study area</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ephemeroptera</td>
<td><em>Ephemerella setigera</em></td>
<td>EPA, ALA and LIN, 18:4(\omega-3) and C16 PUFA</td>
<td>4.9</td>
<td>The Yenisei River, Russia</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td></td>
<td><em>Ephemerella spp</em></td>
<td>(\alpha3) PUFA, EPA, ALA</td>
<td>5.5</td>
<td>The Muscoot River, south-eastern New York</td>
<td>Torres-Ruiz et al. (2007)</td>
</tr>
<tr>
<td></td>
<td><em>Ephemera lineata</em>, <em>Ephemera ignita</em>, <em>Pothamantis lutes</em></td>
<td>EPA, ARA, 16:1(\omega-9), 16:1(\omega-7) and 18:1(\omega-7)</td>
<td>2.8</td>
<td>The Yenisei River, Russia</td>
<td>Sushchik et al. (2003)</td>
</tr>
<tr>
<td></td>
<td><em>Ecdyonurus venosus</em>, <em>Caenis</em>, <em>Ephemerella</em></td>
<td>EPA, ALA, LIN, ARA</td>
<td>4.9-6.8</td>
<td>River Allan, Scotland</td>
<td>Ghioni et al. (1996)</td>
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<tr>
<td></td>
<td><em>Heptageniidae</em></td>
<td>EPA, ALA, 18:1(\omega-9) and 16:1</td>
<td>4.8</td>
<td>Streams, western Washington state</td>
<td>Volk &amp; Kiffney (2012)</td>
</tr>
<tr>
<td></td>
<td><em>Trichoptera</em></td>
<td>EPA, ALA, LIN, ARA</td>
<td>2.8-6.9</td>
<td>The Muscoot River, south-eastern New York</td>
<td>Torres-Ruiz et al. (2007)</td>
</tr>
<tr>
<td></td>
<td><em>Hydropsyche spp</em></td>
<td>(\alpha3) PUFA, EPA, ALA, 16:0(\omega-4)</td>
<td>2.8-6.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Apatania crymophila</em></td>
<td>EPA, (\alpha3), (\alpha6), C18 and C20 PUFA</td>
<td>5.5</td>
<td>The Yenisei River, Russia</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td></td>
<td><em>Apatania crymophila</em></td>
<td>EPA, ALA, LIN, 18:4(\omega-3), C16 PUFA, 16:4(\omega-3) and 16:3(\omega-3)</td>
<td>3.2-13.0</td>
<td>As above</td>
<td>Sushchik et al. (2006)</td>
</tr>
<tr>
<td></td>
<td><em>Apatania crymophila</em>, <em>Aethaloptera evanescens</em></td>
<td>18:1(\omega-9), EPA, ALA</td>
<td>3.8</td>
<td>As above</td>
<td>Sushchik et al. (2003)</td>
</tr>
<tr>
<td></td>
<td><em>Apatania crymophila</em></td>
<td>16:1(\omega-7), 18:1(\omega-9), EPA, ALA</td>
<td>6.6</td>
<td>As above</td>
<td>Gladyshev et al. (2012)</td>
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<td></td>
<td><em>Hydropsychidae</em></td>
<td>EPA, ALA, LIN, ARA</td>
<td>3.2</td>
<td>Tributary systems of Lake Michigan</td>
<td>Larson et al. (2013)</td>
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<td></td>
<td><em>Glossosomatidae</em></td>
<td>EPA, ALA and 18:1(\omega-9)</td>
<td>5.7</td>
<td>Streams, western Washington state</td>
<td>Volk &amp; Kiffney (2012)</td>
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<tr>
<td>Crustacea,</td>
<td><em>Eulimnogammarus viridis</em></td>
<td>EPA, DHA, ALA, LIN, ARA</td>
<td>6.2 ± 1.1</td>
<td>The Yenisei River, Russia</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td>Gammaridae</td>
<td><em>Eulimnogammarus viridis</em></td>
<td>EPA, DHA, ALA, LIN, ARA</td>
<td>As above</td>
<td></td>
<td>Sushchik et al. (2007)</td>
</tr>
<tr>
<td></td>
<td><em>Eulimnogammarus viridis</em></td>
<td>EPA, DHA, ALA, LIN, ARA</td>
<td>2.9-7.3</td>
<td>As above</td>
<td>Sushchik et al. (2006)</td>
</tr>
<tr>
<td></td>
<td><em>Eulimnogammarus viridis</em>, <em>Gmelinoides fasciatus</em></td>
<td>EPA, DHA, 22:5(\omega-3), 18:1(\omega-9)</td>
<td>3.8</td>
<td>As above</td>
<td>Sushchik et al. (2003)</td>
</tr>
<tr>
<td></td>
<td><em>Eulimnogammarus viridis</em></td>
<td>16:1(\omega-7), 18:1(\omega-9), EPA, ALA</td>
<td>5.7</td>
<td>As above</td>
<td>Gladyshev et al. (2012)</td>
</tr>
<tr>
<td>Turbellaria</td>
<td><em>Dendrocoelopsis sp</em></td>
<td>EPA, DHA 22:5(\omega-3), ALA, LIN</td>
<td>5.9 ± 0.4</td>
<td>As above</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td>Bivalvia</td>
<td><em>Dreissenia bugensis</em>, <em>Dreissenia polymorpha</em></td>
<td>DHA, EPA, 22:5(\omega-3), 22:5(\omega-6) and ARA</td>
<td>1.3-1.8</td>
<td>As above</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td></td>
<td><em>Dreissenia mussels</em> (presumably <em>Dreissenia polymorpha</em>)</td>
<td>EPA, DHA, ALA</td>
<td>2.1</td>
<td>Tributary systems of Lake Michigan</td>
<td>Larson et al. (2013)</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td><em>Lumbriculus variegatus</em>, <em>Tubifex tubifex</em></td>
<td>EPA, LIN, ALA, ARA and DHA</td>
<td>2.8-3.5</td>
<td>The Yenisei River, Russia</td>
<td>Makhututova et al. (2011)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>EPA, C16 PUFA</td>
<td>3.5</td>
<td>The Muscoot River, south-eastern New York</td>
<td>Torres-Ruiz et al. (2007)</td>
</tr>
<tr>
<td></td>
<td><em>Lumbriculus variegatus</em>, <em>Pristinella biloba</em>, <em>Stylaria lacustris</em></td>
<td>EPA, DHA ARA and iso- and anteiso-fatty acids</td>
<td>3.3 ± 0.4</td>
<td>The Yenisei River, Russia</td>
<td>Sushchik et al. (2007)</td>
</tr>
</tbody>
</table>

In addition to food sources, variations in FA composition of stream macroinvertebrates are also affected by sampling season and locations (Sushchik et al., 2006; Torres-Ruiz et al., 2007), and phylogenetic differences (Makhutova et al., 2011). The latter is considered to be more important (Makhutova et al., 2011). At the class level, the FA composition of Trichoptera and Ephemeroptera differed significantly (Smits et al., 2015). At lower taxonomic levels, despite having the same feeding strategies, separate populations of the same species showed distinct PUFA compositions (Makhutova et al., 2011), reflecting different FA metabolism abilities. Additionally, larvae in different developmental stages also have different dietary requirements or preferences for FA (Cargill et al., 1985a,b). Therefore, even if stream macroinvertebrates probably ingest similar food varieties and/or proportions, differences in FA assimilation can lead to different FA levels, suggesting that stream macroinvertebrates are not simple ‘collectors’, but rather ‘selective retainers’ of dietary FA.

Consumer reproduction requires large HUFA investment to eggs. Thus far, studies on the impact of algal PUFA on the reproduction of macroinvertebrates are limited to zebra mussels, *Dreissena polymorpha*. Algal PUFA content strongly affects their egg quantity and quality (Wacker & Von Elert, 2003, 2004). *D. polymorpha* fed diets rich in EPA and ARA invested 2X more EPA and ARA in eggs and released 3X more eggs than mussels fed PUFA-deficient food. Mussels were still able to allocate ARA and EPA to oocytes and spawn under PUFA-deficient food, which suggests the allocation of internal reserves to oocytes. More species need to be studied to improve our understanding of how stream macroinvertebrates invest their PUFA for reproduction under different quality foods.

The ability of stream macroinvertebrates to synthesise HUFA

Controlled feeding experiments provide a better understanding of the observed interspecific differences in fatty-acid composition in the field (Table 4). Zebra mussels, *D. polymorpha*, showed better survival and higher growth when fed diets rich in EPA and ARA compared to treatments with green algae and cyanobacteria (Wacker, Becher & Von Elert, 2002). Without dietary EPA and ARA only 50% of the larvae survived 2–3 weeks (Wacker & Von Elert, 2004), suggesting these larvae lacked the capacity to convert short-chain PUFA to HUFA. Similarly, the FA composition of net-spinning caddisfly larvae *Hydropsyche* sp. consistently matched those of the diets provided, and showed very limited ability to synthesise and elongate ARA and EPA even when supplied with their precursors LIN and ALA.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Species</th>
<th>Abundant FA</th>
<th>(\omega3/\omega6)</th>
<th>Study area</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lumbriculus variegatus, Pristinella bilobata, Stylaria lacustris</td>
<td>EPA, LIN, ALA, ARA and DHA</td>
<td></td>
<td></td>
<td>Sushchik et al. (2006)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chironomidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prodiamesa olivacea, Chironomus plumosus</td>
<td>EPA, LIN, ALA</td>
<td>1.1–3.6</td>
<td>The Yenisei River, Russia</td>
<td>Makhutova et al. (2011)</td>
</tr>
<tr>
<td></td>
<td>Prodiamesa olivacea, Pseudodiamesa branickii</td>
<td>(\omega3 C20, \omega6 C18, \omega3 C18, \omega4 + \omega7 C16)</td>
<td>As above</td>
<td>As above</td>
<td>Sushchik et al. (2007)</td>
</tr>
<tr>
<td></td>
<td>Prodiamesa olivacea, Pseudodiamesa branickii</td>
<td>EPA, LIN, ALA, ARA</td>
<td>2.3–5.3</td>
<td>As above</td>
<td>Sushchik et al. (2006)</td>
</tr>
<tr>
<td></td>
<td>Diamesa baikalensis, three other species</td>
<td>16:1(\omega9), 16:1(\omega7), 18:1(\omega7), EPA, ALA, LIN, ARA</td>
<td>2.7</td>
<td>As above</td>
<td>Sushchik et al. (2003)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>EPA, LIN, ARA</td>
<td>2.0</td>
<td>River Allan, Scotland</td>
<td>Ghioni et al. (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16:1(\omega9), 18:1(\omega7), 18:1(\omega9), 16:1(\omega7), EPA, ALA, LIN, ARA</td>
<td>2.2</td>
<td>As above</td>
<td>Bell et al. (1994)</td>
</tr>
<tr>
<td>Plecoptera</td>
<td></td>
<td>EPA, ALA, LIN, ARA</td>
<td>3.5–3.8</td>
<td>As above</td>
<td>Ghioni et al. (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>EPA, ALA, LIN, ARA</td>
<td>4.0</td>
<td>As above</td>
<td>Bell et al. (1994)</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>1.9–3.6</td>
<td>As above</td>
<td>Bell et al. (1994); Ghioni et al. (1996)</td>
</tr>
<tr>
<td>Corixidae</td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>2.6–3.9</td>
<td>As above</td>
<td>Ghioni et al. (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>3.2</td>
<td>As above</td>
<td>Bell et al. (1994)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>3.2–3.9</td>
<td>As above</td>
<td>Ghioni et al. (1996)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>3.7</td>
<td>As above</td>
<td>Bell et al. (1994)</td>
</tr>
<tr>
<td>Notonecta</td>
<td></td>
<td>ALA, EPA, LIN, ARA</td>
<td>3.0</td>
<td>As above</td>
<td>Ghioni et al. (1996)</td>
</tr>
</tbody>
</table>

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Clistoronia magnifica (Trichoptera) may also be able to synthesise HUFA from shorter homologues since they accumulated 20:4 and 20:5 when fed HUFA-free diets (Hanson et al., 1983). Furthermore, the freshwater benthic generalist Asellus aquaticus (Isopoda, Asellidae) are suggested to regulate their PUFA content according to season-specific physiological status and dietary quality (Lau et al., 2013).

**Future directions**

*The influence of human disturbance on the energy flow from algae to upper trophic levels*

Disturbances to streams include alterations to the light regime (i.e. riparian vegetation removal and turbidity), increased nutrient concentrations from point and non-point sources (i.e. agricultural and urban sewage), and environmental pollutant inputs (i.e. heavy metals or PCBs) (Bunn, Davies & Mosisch, 1999). Ecologists have long recognised that these human disturbances to streams can impact in-stream algal primary production and then secondary production (Bilby & Bisson, 1992; Bunn et al., 1999). Nevertheless, only recently the impact of human disturbance on algal food quality has been considered.

Riparian vegetation is effective in intercepting solar radiation, which determines the light intensity reaching the stream (Hill, Ryon & Schilling, 1995; Hill, Mulholland & Marzolf, 2001). Removal of riparian vegetation leads to an increase in light intensity, often causing a shift in the composition of primary producers from high-quality diatoms to low-quality filamentous green algae and ultimately macrophytes (Davies et al., 2008) and resulting in increases in the biomass and density of macroinvertebrate functional feeding groups except grazers (Moldenke & Ver Linden, 2007). Nonetheless, few studies have been concerned with the mechanisms behind these two processes. As well as riparian vegetation removal, aquatic ecosystems are under increasing threats from nutrient inputs associated with anthropogenic activity (Malmqvist & Rundle, 2002; Liess et al., 2012). In lacustrine ecosystems, lake trophic status significantly affects seston EPA and DHA composition (Müller-Navarra et al., 2004), and Daphnia growth rates are expected to be highest in lakes with intermediate trophic status (Persson et al., 2007). In lotic ecosystems, nutrient inputs are also strongly associated with the FA composition of basal food sources (Boéchat et al., 2011, 2014; Larson et al., 2013; Guo et al., 2015), but their consequent effects on macroinvertebrates need further exploration. Additionally, global warming may interact with human induced light and nutrients to influence the PUFA metabolism of algae and macroinvertebrates. Other factors, such as flow conditions (e.g. intermittent droughts or floods) and geomorphology (e.g. catchment slope and substratum size) could also act in concert, making the energy transfer more complicated.

To date, in stream ecosystems, few studies have been concerned with the influence of human disturbance on algal PUFA content and the consequent effects on macroinvertebrates and fish. As mentioned above, algal PUFA are sensitive, but not limited, to variations in light, nutrients and temperature (Table 2). In natural streams, algal PUFA are influenced simultaneously by gradients of environmental factors (Hill et al., 2011; Cashman et al., 2013; Guo et al., 2015). It should be a priority to identify the most important factors affecting
algal PUFA, and provide this advice to stream managers. Further field surveys and manipulative studies need to focus on how algal PUFA vary with gradients of environmental factors in streams, since algae are the primary sources of PUFA for invertebrates and fish.

Variations in algal PUFA content may potentially influence the growth and reproduction of primary consumers in lotic ecosystems. When exposed to high food quality conditions, consumers may grow faster and have higher reproductive rates, which in turn make them more resilient to over-exploitation by upper trophic levels (Persson et al., 2007). However, how do stream macroinvertebrates deal with low-quality food? If stream macroinvertebrates are limited in converting dietary PUFA, survival on low food quality would result in slow growth and development (Goedkoop et al., 2007), and may negatively affect the fitness of their offspring. In contrast, if stream macroinvertebrates are able to perform sufficient PUFA conversion into support their somatic growth and reproduction, they are then capable of upgrading low-quality food into high-quality for fish and may enhance the energy transfer efficiency of stream food webs. However, only several species have been considered to be able to synthesise PUFA or convert one PUFA molecule to another in stream food webs. More importantly, nutritional stress on the female influences larvae development (Bayne, 1976; Gabbott, 1976) as lipids and particularly HUFA are heavily invested in reproduction (Arts, 1999; Lee, Hagen & Kattner, 2006). D. polymorpha have been found to produce a smaller number but larger eggs when food quality was low (Wacker & Von Elert, 2003, 2004). Large eggs can improve the ability of neonates to withstand starvation (Tessier & Consolatti, 1989; Gliwicz & Guisande, 1992). However, our knowledge on the PUFA reproductive response of macroinvertebrates to different food quality conditions is thus far limited to zebra mussels.

Among all trophic levels, the plant-animal interaction is the most variable and least predictable link (Brett & Goldman, 1997; Müller-Navarra et al., 2000). Due to the variety of human disturbances, this link is more complex in stream food webs. Studies on the effects of human disturbances on the energy flow from algae to macroinvertebrates are just beginning and require further exploration. More controlled feeding trials and manipulative studies are needed to understand PUFA conversion capacities and reproductive investment of stream macroinvertebrates under different food quality conditions. This information will provide insights into how freshwater species cope with different nutritional food conditions from human disturbance such as riparian vegetation clearance and/or nutrient inputs, which should be integrated into the conservation and restoration of streams and riparian zones.

Interaction between algal food quality and invertebrate shredders

Although algal tracers EPA, ALA and LIN are abundant in most stream macroinvertebrates, tracers of allochthonous sources, fungi and bacteria, are also observed in a range of macroinvertebrates. Fungi and bacteria conditioning appears to be the major process determining the fate of terrestrial matters in lotic food webs. The potential interaction between allochthonous and autochthonous sources could arise from small amounts of labile carbon exudates released by algae, accelerating the decomposition of more recalcitrant organic matter (e.g. leaf litter) (Guenet et al., 2010). Algae have been observed to mediate the interactions between bacteria and fungi, and algal presence in combination with fungi increased leaf litter decomposition, and improved the nutritional quality of detritus (Danger et al., 2013).

In stream ecosystems, macroinvertebrates, mainly from the shredder functional feeding group, can be responsible for up to 70% of the leaf litter reduction (Cuffney, Wallace & Lugthart, 1990). By feeding on leaves, shredders also actively participate in leaf fragmentation and produce abundant faecal pellets (Allan & Castillo, 2007). Recent studies have established the links between invertebrate shredders, leaf litter decomposition, fungi, bacteria and environmental factors (i.e. light and nutrients), and proposed that algae can be an important component of the nutritional value of the leaf biofilm for invertebrate shredders (Franken et al., 2005; Albarino, Villanueva & Canhoto, 2008). However, the nutritional importance of algae for invertebrate shredders has yet to be reported. Shredders may have an impact on the interaction between the two types of food sources, and their feeding choices between algae, fungi and bacteria directly affect the transfer of allochthonous sources into stream food webs. Further studies are needed to explore how stream shredders acquire high-quality algae through feeding on leaf litter, and if they are performing an important ecological function in upgrading low-quality food to high-quality food.

Influence of algal food quality from individual invertebrates to ecosystem levels

The majority of the above studies has focussed on consumer-resource interactions at small scales, and/or
between individuals, whereas stream ecology has moved to a broader landscape perspective of aquatic ecosystems (Allan, 2004). The importance of cross-system movements of materials for local food-web structure has been well recognised (Polis, Anderson & Holt, 1997; Baxter, Fausch & Carl Saunders, 2005), and the transfer of algal PUFA along food chains and around food webs likely affect how different animal species thrive or survive (Lands, 2009). Food webs that lack algal PUFA may demonstrate trophic decoupling, leading to a significant increase in primary productivity with little corresponding increase in consumer biomass. Algal PUFA composition could be the possible link between species survival, community dynamics and ecosystem functions across ecosystems. We suggest that (i) Algal PUFA content could be developed as an efficient biomarker of human impacts on aquatic ecosystems, indicating ecosystem functions or health, since algal PUFA are more sensitive to environmental changes than algal community composition (Guo et al., 2015; Honeyfield & Maloney, 2015); (ii) consumer PUFA composition indicates the fitness of populations, with the potential to explain community dynamics (Smyntek et al., 2008); (iii) the PUFA dynamics in stream food webs could be a potential proxy of climate change because total lipid content of fish has been connected to climate-induced community changes (Litvow, 2006), and FA are promising compounds to reconstruct palaeo-environments (Ouyang, Guo & Bu, 2015). Progress along those lines will be enhanced by further creative thinking and cross-system interactions.

Conclusions

The study of algal food quality effects on energy transfer is helping to define a more holistic perspective of stream ecosystems, but also has the potential to shape new directions for ecology. There have been numerous studies of spatial and temporal patterns of macroinvertebrates and their food sources. However, conceptual models that could help explain the underlying mechanisms of such patterns and set the ground for future research lag behind. This review emphasises the importance of algal food quality, assessed by dietary PUFA, which influences the somatic growth and reproductive success of stream macroinvertebrates and ultimately the energy transfer to fish and humans. We propose that algal PUFA transfer in stream food webs provides a powerful approach to integrate our understanding of the complex relationships between different food sources and patterns of abundance and production of invertebrates and other higher order consumers. This integration will provide a profound understanding of how stream ecosystems respond to human disturbance and an important future focus for stream management.

Acknowledgments

The authors thank Dr Alan Steinman and two anonymous reviewers for their valuable comments on the manuscript. The research was supported by a PhD grant from Griffith University to F.G.

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(Manuscript accepted 21 February 2016)