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1. Introduction

Lake ecosystems receive large quantities of dissolved and particulate materials from the surrounding landscape, blurring what would once have been considered clearly defined habitat boundaries. Among these materials, dissolved and particulate organic matter, derived from terrestrial primary production, have particularly profound influences on carbon and energy flow within lake ecosystems. Recognition of the importance of dissolved organic matter loading in particular has forced revision of our understanding of lake ecosystem functioning. Indeed, it has been suggested that water colour should, in addition to lake trophic status, be one of the main conceptual axes that we use to categorise lake ecosystems and understand both their functioning, and responses to external pressures (Jones 1992, Williamson et al. 1999, Jansson et al. 2007).

The total pool of organic matter present within each lake ecosystem is a mixture of this *allochthonous* terrestrial material and additional *autochthonous* material. The latter is typically derived from (photosynthetic) primary production by phytoplankton, macrophytes and epiphytes in lake littoral zones (Wetzel 1992), and (chemosynthetic) primary production by methanotrophs (Jones and Grey 2011). The temporal dynamics of organic matter delivery are likely to be very different when comparing allochthonous and autochthonous sources. Loading of terrestrial organic matter is likely to be strongly episodic and associated with rainfall events (Berggren et al. 2010, Jennings et al. 2012), while inputs from littoral zone areas are likely to be continuous due to the high connectivity between the littoral zone and the pelagic, and the steady turnover of vegetative tissues in the former habitat (Wetzel 1992).

Dissolved and particulate detrital organic matter (DOM and POM, respectively) are the largest allochthonous inputs, and potential subsidies to most communities and ecosystems (Polis et al. 1997). In order to assess the impacts of changes in organic matter (OM) loading over time, it is important to understand the processing and transformation of these materials within the lake environment. For example, higher dissolved organic carbon (DOC) concentrations can lead to increased sedimentation of biologically recalcitrant allochthonous matter; an important pathway in the carbon cycle (von Wachenfeldt and Tranvik 2008). Laboratory experimentation suggests that the formation of detrital particles results from bacterial activity (von Wachenfeldt et al. 2009). Further, results from a Swedish enclosure experiment suggest that this flocculation of allochthonous DOC might also be mediated by light (von Wachenfeldt et al. 2008).

The organic matter pool is pivotally important to lake ecosystem functioning, but in order to be able to assess the impacts of organic matter and nutrients on lake food webs, complexities in the inter-relatedness of trophic levels and food web compartments have to be acknowledged (Vadeboncoeur et al. 2002). Modelling studies suggest that the stability and resilience of lake food webs may be enhanced by the continual supply of organic matter, which would provide a constantly replenishing resource base for consumers in addition to that provided by local

primary production (Moore et al. 2004). The wider energetic stability of lake ecosystems is likely to be enhanced by the continual but relatively slow microbial decomposition of a largely recalcitrant pool of dissolved organic matter (Wetzel 1995), as well as by chemosynthetic production (Jones and Grey 2011).

The importance of the organic matter pool within lakes also transcends the boundaries of these ecosystems. Active processing of organic matter in the lake environment mediates fluxes of carbon to the oceans and atmosphere (as CO₂ and CH₄), and to lake sediments. As such, cycling of organic matter in freshwaters plays an important role in the global carbon cycle (Algesten et al. 2004, Cole et al. 2007, Battin et al. 2008, Bastviken et al. 2011).

Since lake ecosystems provide many important goods and services to society, there is a pressing need for mechanistic understanding of the effects of organic matter loading upon the functioning of these systems. This research need is made more urgent by observations that organic matter (specifically DOC) concentrations in European and North American lakes have been increasing in recent decades (Monteith et al. 2007). Regional-scale reductions in acid and sea salt deposition have likely driven much of the change in DOC concentrations over broad geographic scales (Monteith et al. 2007, Evans et al. 2012). However, locally-variable temporal trends in temperature, precipitation and drought frequency/intensity (Schindler et al. 1997, Freeman et al. 2001, Tranvik and Jansson 2002), atmospheric nitrogen deposition (Pregitzer et al. 2004) and site-specific changes in land management (Armstrong et al. 2010, Yallop et al. 2010) have also been implicated as potential drivers of changing DOC concentrations.

Scope of the review

The vast majority of the material that comprises the lake organic matter pool is in dissolved, rather than particulate, form (Birge and Juday 1934, Cole et al. 2007) and this dissolved pool is a complex mixture of humic and non-humic substances (Table 1). For the purposes of the present review, we will focus upon the effects of terrestrially-derived dissolved and particulate organic carbon (DOC and POC) upon lake ecosystems. While we recognise that organic matter also contains other ecologically important chemicals and nutrients, it is fluxes of terrestrial carbon to lake systems that have received much research attention. In the review, we provide an overview of current understanding of the effects of DOC and POC upon different elements of the lake food web, and ecosystem scale processes. We then consider the likely combined effects of increasing DOC loading, eutrophication and climate change upon lake ecosystems.

Table 1: *Broad classes of compounds present within the dissolved organic matter pool (Wetzel 1983).*

Non-humic substances	Humic substances
Carbohydrates	Humic acids
Proteins	Fulvic acids
Peptides	Humin
Amino acids	
Fats	
Waxes	
Resins	
Pigments	

2. Organic matter and the lake ecosystem

2.1 Effects of changes in organic matter on thermal structure

2.1.1 Background

Any dissolved organic matter (DOM) that is not transparent will affect the depth at which solar radiation is absorbed within a lake. In so doing DOM may have profound effects on the thermal structure of the water column. The effects of non-transparent material on solar radiation are usually parameterised by the light attenuation coefficient, K_d (m^{-1}), which describes the exponential decay of irradiance with depth as,

$$I_z = I_0 e^{(-K_d \cdot z)}, \quad (1)$$

where I_0 ($W m^{-2}$) is the solar radiation penetrating the surface of the water and I_z ($W m^{-2}$) is the solar radiation at a depth z in the water column (Kirk 1983). Large values of K_d are therefore associated with very coloured, particulate-rich or eutrophic systems where light is mainly absorbed near the surface of the water column, while small values of K_d typify very transparent lakes in which light penetrates deep into the water.

A wide range of approaches have been used to investigate the impacts of differing transparency on lakes, including statistical comparisons across a number of lakes (e.g. Kling 1988, Fee et al. 1996), longitudinal studies on a single lake (e.g. Yan 1983, Gaiser et al. 2009a, Gaiser et al. 2009b) and numerical modelling work (e.g. Hocking and Straškraba 1999, Persson and Jones 2008). Some studies have specifically investigated effects of light changes mediated by DOC, some the impact of changes mediated by phytoplankton biomass and size structure and others have used generic descriptors of transparency, such as Secchi depth or the attenuation coefficient, irrespective of the root cause of differing transparencies. Generally

studies have involved an overall measure of transparency rather than investigating the impacts of changing light quality, although calculations by Hocking & Straškraba (1999) suggested that the error associated with ignoring spectral attenuation could be as much as 20%.

Varying DOC concentrations might be expected to change attenuation and, as a result, lake thermal structure. Many of these potential effects can be anticipated by considering absorption curves calculated from Eqn (1), for different values of the attenuation coefficient. For mixed layers greater than 8 m deep increases in attenuation coefficients beyond about 0.6 m^{-1} make little difference (Fig. 1) as virtually all the solar radiation will be absorbed in the mixed layer anyway. Even when mixed depths are as shallow as 2–3 m increases in attenuation coefficients beyond 1 m^{-1} would have little impact on the thermal structure of the lake. As mixed depth is also a function of wind speed and therefore lake size (Patalas 1984, Gorham and Boyce 1989), smaller lakes should be more sensitive to changes in a greater range of attenuation coefficients than larger lakes. Owing to the exponential nature of the light penetration curve, changes to small values of K_d have a greater impact than changes to large values of K_d on the location of heat absorption. Thus, the thermal structure of clear lakes will be more impacted than coloured lakes by changes in transparency (Read and Rose 2013).

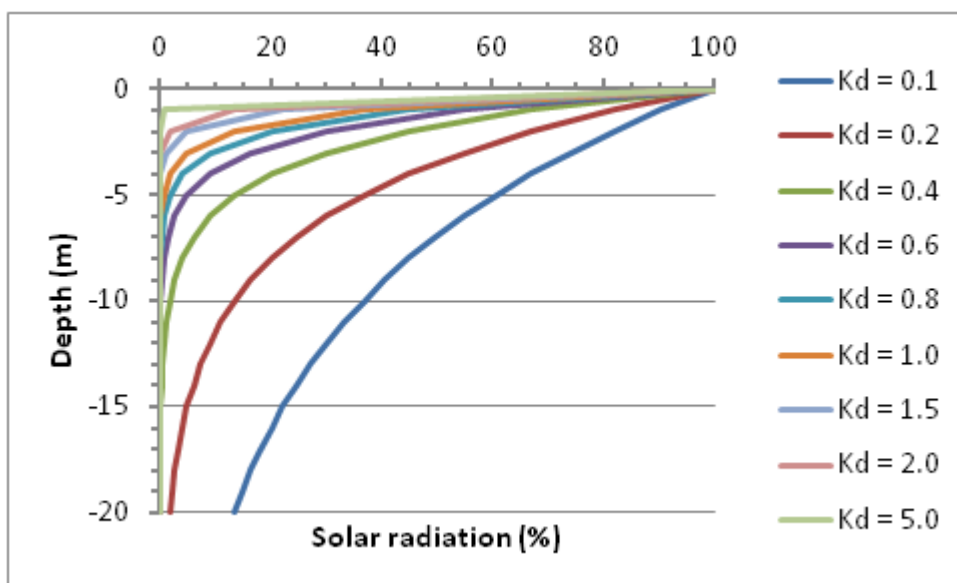


Figure 1 Change with depth of solar radiation for different attenuation coefficients, as a percentage of the solar radiation that penetrates the surface, calculated from Eqn 1.

2.1.2 Mixed depths

The most commonly studied effect of a varying K_d is the impact on thermal metrics such as epilimnetic and thermocline depths. Statistical comparisons across a relatively small number of lakes in Cameroon (Kling 1988), in Finland (Jones and

Arvola 1984) and in Canada (Fee et al. 1996, Pérez-Fuentetaja et al. 1999, Snucins and Gunn 2000, Keller et al. 2006) have all shown an increase in epilimnetic or thermocline depth accompanying an increase in transparency, whilst the same relationship has also been observed in Tasmanian lakes (Bowling 1990). Analysis of a larger dataset of North American lakes similarly suggested a statistical correspondence between greater transparency and greater epilimnetic depth (Mazumder and Taylor 1994). While Mazumder & Taylor (1994) expected the relationship between transparency and epilimnetic depth to continue across all lake sizes, Fee et al. (1996) suggested the influence of transparency would diminish for increasing surface areas and vanish for lakes sufficiently large that the mixed layer was deep enough to absorb all the solar radiation irrespective of transparency. They suggested a surface area of 5 km² to be an approximate threshold for the effect, but modelling work for the very large (500 km²) Lake Constance, Germany, focussing mainly on the effects of algae on attenuation, showed that changes in attenuation can affect very large lakes, if the attenuation coefficient becomes sufficiently small. In theory changes in attenuation can affect water even beyond 20 m deep (Fig. 1), but only for a very limited range of small attenuation coefficients, and thus is only likely to impact relatively few large lakes. Analysis of some small datasets have shown transparency can have an even greater influence on thermal metrics than lake size (Pérez-Fuentetaja et al. 1999, Keller et al. 2006), but this result will be dependent on the range of lake sizes and the range of K_d values studied.

Statistical comparisons across lakes allow the influence of variations in lake-size to be compared with the influence of variation in transparency, but cannot take into account the effect of all possible differences between individual lakes. Longitudinal studies on single lakes avoid this issue and also allow some quantification of the impact of changing attenuation, but can be restricted by the complicating effects of inter-annual variation in weather. Acidification of the 0.41 km² Lohi Lake (Ontario, Canada) resulted in a shift over 6 years in Secchi depth from 5.6 to 9.3 m and a change in mixed depth from 7.1 to 10.0 m, these changes having a significant correlation (Yan 1983). The change in DOC caused by re-acidification of the 0.77 km² Clearwater Lake (Ontario, Canada) caused an increase in K_d from 0.15 to 0.31 m⁻¹ in the 1990s and a related shallowing of the thermocline from 11 m to 7 m (Tanentzap et al. 2008). One-dimensional modelling of the lake ascribed both the increase in transparency and a concomitant reduction in wind speed, owing to deforestation, as being responsible for the alteration to mixed depth. In the 0.37 km² Lake Annie (Florida, USA) routine monitoring of environmental parameters since 1983 has shown a strong link between the Atlantic Multidecadal Oscillation (AMO) and the in-lake light attenuation (Gaiser et al. 2009b), which has varied between 0.3 and 1.9 m⁻¹, through the AMO's impact on precipitation and the corresponding DOC runoff into the lake. The observed changes in light attenuation were significantly correlated to the July thermocline depths varying between 4.6 and 12.7 m (Gaiser et al. 2009a).

Most of the observational studies hitherto carried out have relied on single, or infrequent, sets of measurements for assessing change. So far only modelling studies have provided high temporal resolution. A modelling study of the relatively large (24 km²) Lake Erken (Sweden) demonstrated a reduction in average thermocline depth over July and August from 11 m to 7 m accompanying attenuation coefficients rising from 0.2 to 1.0 m⁻¹, although no change in thermocline depth was shown for greater increases in attenuation (Persson and Jones 2008). Similarly, two comparison model runs of the similarly large (13.92 km²) Slapy Reservoir (Czech Republic) using attenuation coefficients of 0.2 and 2.0 m⁻¹ showed a reduction in mixed depth from 9.8 to 5.4 m (Hocking and Straškraba 1999). Thus, it has been well established, by several different methods, that alteration to light attenuation impacts epilimnetic and thermocline depths, can do so by several metres, if the light attenuation changes sufficiently, and that the impacts may be comparable to the effects of wind speed variations associated with differing fetch for relatively small lakes.

2.1.3 Temperatures

Although less frequently studied, decreases in light attenuation have also been shown to have a significant influence on metalimnion and hypolimnion temperatures, with decreases in transparency associated with cooler metalimnia and hypolimnia. Both metalimnia and hypolimnia may be expected to cool if there is a decrease in the depth to which solar radiation penetrates. In addition, water at a given depth may alter from being part of the (warmer) epilimnion to being part of the (cooler) metalimnion with a decrease in transparency, with consequent impact on its temperature. The extent of the cooling, particularly in the metalimnion, is striking. Studies of enclosures in which Secchi depth was substantially altered by changes in the phytoplankton community suggested that differing transparency could alter metalimnetic temperatures by anywhere between 3 and 8 °C, while in two lakes with contrasting Secchi depths the metalimnetic difference was up to 13 °C greater in the clearer lake (Mazumder et al. 1990). In Lake Annie the variation between extinction coefficient and July temperatures at 9 m (metalimnion) could be fitted to a simple log regression suggesting a change in temperature of about 10 °C accompanying attenuation coefficients varying between 0.3 and 1.4 m⁻¹ with the greatest changes happening at small attenuation coefficients. A similar log regression suggested about a 3 °C variation in temperatures at 19 m (hypolimnion), with all water below 5 m depth showing some significant reduction in temperature with increasing attenuation coefficients (Gaiser et al. 2009a). The modelling study in Lake Erken (Persson and Jones 2008) tested effects of changing attenuation coefficient on average July and August bottom water temperature and also showed a 3 °C reduction in bottom water temperature, as attenuation coefficients increasing from 0.2 to 1.0 m⁻¹, with little change exhibited for further increases in attenuation coefficient. Hocking & Straškraba (1999) compared model predictions of bottom water temperatures and metalimnetic temperatures in Slapy reservoir for attenuation coefficients between 0.2 and 1.0 m⁻¹ and found about a 4 °C change in the metalimnetic temperature, but

only about a 1 °C change in bottom water temperature. Meanwhile the longitudinal study in Clearwater Lake, where attenuation coefficients varied between 0.15 and 0.31 m⁻¹, showed bottom water temperatures varying by about 10 °C, although these were based on mid-summer profiles, not averaged data. Wind speed had changed systematically during the same period in this study, but model tests suggested it was not significantly responsible for alterations to the hypolimnetic temperature (Tanentzap et al. 2008). Another longitudinal study in Grane Langsø, Denmark (0.12 km²), showed a shift in attenuation coefficient from 0.24 m⁻¹ in 1960-61 to 0.44 m⁻¹ in 1994, mainly as a result of an increase in humic content, being accompanied by a 4 °C rise in hypolimnetic temperature (Riis and Sand-Jensen 1998). Stefan et al. (1996) used a computer model to systematically test the effects of both changing morphology and changing transparency on bottom temperatures, and found that, though bottom temperatures were a little higher in transparent lakes, the effect was dependent on the ratio of surface area to maximum depth.

While there is much evidence for a cooling impact on deep waters, there is much more uncertainty on the impact on epilimnetic temperatures of a decrease in transparency. Certainly the increase in absorption of solar radiation at the surface of the lake might be expected to increase the temperature there. Nevertheless, neither Gaiser et al. (2009a) nor Tanentzap et al. (2008) found a significant impact on surface water temperatures of changing transparency in Lake Annie and Lake Clearwater. In a comparison across six small Wisconsin lakes surface temperatures were shown to be even lower in the more coloured lakes than the clearer lakes (Houser 2006), while the enclosures studied by Mazumder et al. (1990) also showed a small decrease in surface temperature in those with shallower Secchi depths. In contrast, two very large enclosures, in a lake in northern England, housing very different phytoplankton concentrations exhibited a 0.5–1.0 °C rise in surface temperature in the less transparent enclosure (Jones et al. 2005). In modelling work on a small hypothetical lake in Wisconsin, USA (De Stasio et al. 1996), the impact of a shift in transparency from 0.1 to 1.2 m⁻¹ was a summer-averaged surface temperature increase of about a degree. Another modelling study on the very large (266 km²) Akkajaure reservoir in northern Sweden suggested an average surface temperature difference over the summer of between 0.1 and 0.3 °C driven by extinction coefficients varying from 0.2 to 1.0 m⁻¹ (Sahlberg 2003).

All these studies represent either summer averages, or a handful of single measurements. In contrast, several modelling studies (Hocking and Straškraba 1999, Persson and Jones 2008, Rinke et al. 2010) have produced daily values of surface water temperature. Each have indicated an increase in attenuation coefficient leads to an initially warmer lake surface at the start of the summer, but a reversal to a lower surface water temperature in the late summer, resulting from entrainment of the comparatively cooler metalimnion water that accompanies an increase in attenuation coefficient. There are several considerations that must be taken into account to explain all these results. The first is that surface temperatures

are highly related to air temperature (Kettle et al. 2004) and therefore individual measurements of surface temperature are unlikely to pick out the influence of a persistent characteristic such as attenuation coefficient. Similarly, any temporal averaging will diminish the strength of a signal, particularly if the sign of the signal varies over time. In addition, a rise in lake surface temperature is automatically accompanied by an increase in outward heat fluxes (Jones et al. 2005) acting to reduce the surface temperature, providing a negative feedback. The increase in cooling from below the epilimnion that accompanies a reduction in metalimnetic temperature induced by an increase in attenuation coefficient also acts as a negative feedback on the surface warming. Finally, as the summer extends, mixed layers tend to deepen, so the impact of additional surface warming is diluted (Persson and Jones 2008). In the absence of a series of high frequency measurements of the impacts of changes in DOC on thermal profiles, the consistency of the modelling studies probably provide the best overall picture of changes in surface temperature: in the early part of the summer surface temperatures are likely to be warmer with a decrease in transparency and become comparatively cooler towards the end of the summer, this pattern being highly variable, but over the whole summer the epilimnion is likely to be a few tenths of a degree warmer when transparency is lower.

Although the effects on surface temperatures are relatively uncertain, a number of studies have shown that a rise in attenuation coefficient effects a decrease in volume-averaged temperature. Two modelling studies (Persson and Jones 2008, Rinke et al. 2010), an enclosure experiment (Jones et al. 2005) and two longitudinal studies (Tanentzap et al. 2008, Gaiser et al. 2009a) have all shown a reduction in volume-averaged temperature for systems with higher attenuation coefficients compared with systems with lower attenuation coefficients, the effect being anything up to a monthly average of about 3 °C. Even those studies that have shown a correlation between lower transparency and a decrease in surface temperature (Mazumder et al. 1990, Houser 2006) have reported a reduction in heat content in the less transparent systems. These latter results are puzzling. If backscatter, and therefore net incoming solar radiation, is unaffected by changes in water clarity, then a reduction in heat content must be a result of an increase in outward heat flux. As the dominant outward heat fluxes are sensible and latent heat and outward long-wave radiation and each of these rise or fall with a rise or fall in surface temperature, then a reduction in lake heat content should be driven by an average fall in surface temperature over the summer, not a rise. This suggests either that changes in clarity can affect the total amount of solar radiation being absorbed in the lake, rather than just the location of absorption, or that those studies reporting a reduction in surface temperature with an increase in attenuation coefficient have been distorted by daily variability in weather conditions. Theoretical work on the effect of changes in surface temperature on the outgoing fluxes (Jones et al. 2005) has shown that a given change in surface temperature will cause a greater change in outward fluxes when wind speeds are high and in warmer climates, implying the effects of changing

attenuation coefficient on thermal structure will not be the same for different lakes or at different times.

2.1.4 Stratification

An increase in strength of stratification has also been shown to accompany a decrease in transparency, this being a natural consequence of deep water temperatures being cooled and surface temperatures warmed (Stefan et al. 1996, Persson and Jones 2008, Gaiser et al. 2009a, Gaiser et al. 2009b, Rinke et al. 2010). Of potentially greater consequence, though, is the impact on length of stratification. Gaiser et al. (2009) suggested that for Lake Annie a reduction in transparency may be responsible for a two and a half month elongation in stratification. A similar two and a half month transparency-induced elongation was suggested for stratification in Grane Langsø (Riis and Sand-Jensen 1998) while for Lake Erken, Persson & Jones (2008) calculated a possible increase of about two months in stratification with a reduction in transparency. Stefan et al. (1996) examined how stratification would change with decreasing Secchi depth for a wide range of lake morphologies and found that for large, shallow lakes the elongation could be as much as five months, potentially shifting polymictic lakes to become dimictic or monomictic, but for small deep lakes it may only alter stratification length by a few days.

2.1.5 Under-ice effects

Most work on the impact of transparency changes on thermal structure has taken place during the summer stratified season. In comparison there have been few studies on the effect of transparency when reverse stratification exists under ice in the winter, though they may be just as important for some lakes. In the winter season the heating of under-ice water is largely restricted to any penetration of solar radiation and a heat flux from the sediment. Towards the end of winter, as snow-cover melts, solar radiation becomes increasingly important, warming the upper part of the water column and causing convective mixing, as water is typically below 3.94 °C, the temperature of maximum density (Bertilsson et al. 2013). As wind mixing is effectively inhibited by the ice-cover the changes in transparency may be the most important impact on thermal structure at this time of year, for a wide range of lakes.

2.1.6 Summary

An increase in DOC is likely to: shallow the mixed depth and the thermocline, cool the hypolimnion, significantly cool the metalimnion, cause a net volume-averaged cooling and extend the stratified period. It will probably induce a warmer surface at the start of stratification with a cooler surface later on in the summer, but with an average warming effect on the epilimnion over the whole summer and much temporal variability. Effects will be dependent on lake morphology and are likely to be unimportant if attenuation coefficients are greater than 1 m^{-1} unless the lake is particularly small. In the winter it will cause the under-ice mixed layer to increase in size, through convective mixing of reverse stratification.

2.2 Organic matter and primary production

Many of the changes to the thermal structure of a lake associated with changes in transparency, and thus DOC (Section 2.1), are likely to impact primary production. In particular, epilimnetic depth, water temperature and length and strength of stratification are all important for phytoplankton growth, as is the direct change to light climate that takes place with changes in DOC. These physical effects will impact: sedimentation rates of algae, light availability, growth rates and internal nutrient supply.

As well as reducing the epilimnetic depth, an increase in DOC would also reduce the euphotic depth. Although some work has suggested that, for both some large (Jones 1992) and some small (Einem and Granéli 2010) lakes, the net result would be an overall worsening light climate for epilimnetic phytoplankton, this still remains unclear over a wide range of lake conditions. In addition, theoretical work and experiments in enclosures have shown that, while increasing light availability, a reduction in epilimnetic depth also increases the rate of sedimentation of phytoplankton from the mixed layer (Diehl 2002, Diehl et al. 2002), this sedimentation acting as a loss term for algal biomass. Modelling work on lakes in northern England has suggested that when changes in mixed depth, changes in photic zone and changes in sedimentation all take place, consequences are not straightforward and are likely to vary between lakes and at different times of year (Bernhardt et al. 2008). Thus, there is still uncertainty over the combined effects of a simultaneous shallowing of euphotic and epilimnetic depths, brought about by increasing DOC, on primary productivity, although there are suggestions that the most usual effect will be for a net reduction in algal biomass.

It also remains uncertain how the physical effects of DOC will affect phytoplankton community composition. Reduced mixed depths, for example, have been shown to favour cyanobacterial blooms (Jöhnk et al. 2008, Paerl and Huisman 2008), but this will not necessarily be true if the euphotic zone shrinks more than the epilimnion. Modelling work has also shown that a change in mixed layer depth can alter the effective retention time of a lake which has the potential to affect phytoplankton populations in those lakes with high flushing rates (Bernhardt et al. 2008, Jones et al. 2011), further complicating the likely impact of changes in DOC on epilimnetic phytoplankton.

Regardless of changes to epilimnetic depth, a DOC-driven reduction in transparency would lead to reduced availability of light for benthic algae. This is particularly important in the numerous small oligotrophic lakes of the world in which benthic algal production is a significant component of ecosystem energy fluxes, and where light limitation may be more important than nutrient limitation in controlling primary productivity (Karlsson et al. 2009). In addition, an increase in DOM would also

reduce the depth to which UV light penetrates which may have both beneficial and deleterious indirect effects on phytoplankton (Williamson and Rose 2010).

The summer-average increase in epilimnetic temperature expected from a DOC-driven decrease in transparency (see Section 2.1) would also favour phytoplankton growth and particularly cyanobacteria growth (Paerl and Huisman 2008), but as the change in temperature would be relatively small, the effect may not be of great magnitude, and possibly unimportant unless nutrient loading was high (Elliott et al. 2006, Brookes and Carey 2011). By promoting bacterial activity, deep water temperatures are thought to influence the extent of release of nutrients from the sediment and thereby impact internal loading (Boström et al. 1988, Pettersson 1998). The extensive cooling of metalimnia and hypolimnia that has been observed with a decrease in transparency suggests there could be a dramatic reduction in internal nutrient loading through this mechanism.

Changing DOC concentrations may also have important indirect effects upon primary producers, by influencing the length and strength of thermal stratification (Section 2.1). Stratification as weak as 0.5 °C over 13 m has been shown to promote hypolimnetic deoxygenation (Foley et al. 2012). The duration of stratification has a major influence on the amount of oxygen in the hypolimnion and the likelihood of anoxia (Lasenby 1975, Livingstone and Imboden 1996). Indeed, dramatic reductions in hypolimnetic oxygen following increases in the attenuation coefficient were seen in Grane Langsø (Riis and Sand-Jensen 1998) and predicted by a numerical model (Stefan et al. 1996). As anoxia promotes the release of phosphorus from lake sediment (Mortimer 1941) a lengthening of stratification is likely to increase the hypolimnetic phosphorus pool and therefore internal loading of phosphorus. While a lengthening of stratification may be expected to increase internal loading, the net effects of strengthening stratification are not clear. Stronger stratification is believed to decrease internal phosphorus loading from the hypolimnion by limiting vertical mixing (Soranno et al. 1997). Alternatively it has been argued that the bulk of internal phosphorus loading from the hypolimnion takes place in the late summer when the stratification is weak, and the hypolimnetic pool of soluble reactive phosphorus is at its largest. In this scenario stronger stratification further limits the supply of oxygen beneath the mixed layer, thereby raising the oxycline, increasing the extent of deep water anoxia and increasing the amount of soluble reactive phosphorus available for late summer release to the epilimnion (Mackay et al. 2014). Thus, the overall impact on internal loading and its consequent impact on primary productivity, of a strengthening and lengthening of stratification combined with a reduction in deep water temperatures remains far from certain.

Though DOM may have negative effects upon phytoplankton, by causing deterioration of the underwater light climate, increased organic matter concentrations may also stimulate total primary production or the growth of certain phytoplankton taxa (Blomqvist et al. 2001, Hessen et al. 2004, Kissman et al. 2013). This is likely because dissolved organic matter acts as a source of limiting nutrients, such as

nitrogen and phosphorus. These nutrients, initially incorporated in relatively recalcitrant organic molecules, can be transformed into more bioavailable inorganic forms by photochemical and bacterial mineralisation (Vahatalo et al. 2003). However, it has been suggested that this stimulating effect would likely only be important to primary producers in very oligotrophic systems and would otherwise be overridden by the negative effects of DOC-related shading and subsequent light limitation (Jones et al. 2012). Furthermore, many mixotrophic phytoplankton taxa are known to be capable of supplementing photosynthetic carbon fixation by using DOM directly, or by consuming bacteria that use this as a substrate (Saunders 1957, Graneli et al. 1999, Znachor and Nedoma 2010). Therefore, in addition to effects upon total phytoplankton biomass, individual taxa show variable responses to increasing concentrations of DOM (Blomqvist et al. 2001, Kissman et al. 2013). The result of this is that community composition may be dramatically altered by variations in organic matter loading.

Dissolved organic matter may also have more indirect effects upon primary producers. This was illustrated by Blomqvist *et al.* (2001): addition of DOM to oligotrophic Lake Siholma (Sweden) resulted in a decline in the abundance of large phytoplankton in favour of bacteria and mixotrophic flagellates. This suggested an increasing importance of bacterial production at the base of the food web under conditions of higher dissolved organic carbon availability (Jansson et al. 2000). As bacteria have higher nutrient uptake affinities under oligotrophic conditions, release from carbon limitation by increased DOC loading may increase the competitive advantage of bacteria over some phytoplankton for limiting nutrients, and bring about changes in phytoplankton biomass and community structure (Blomqvist et al. 2001). Increased DOM loading can also affect phytoplankton biomass and community composition via effects on zooplankton grazing. Stimulation of bacterial and phytoplankton production by elevated DOM concentrations may in turn increase zooplankton biomass (Kissman et al. 2013). Selective grazing by the zooplankton community would then feedback upon the phytoplankton community, potentially affecting biomass and composition.

2.3 Organic matter and the microbial loop

2.3.1 Overview

Bacteria have a central role in the decomposition of autochthonous and allochthonous organic matter in lakes. As a result, when organic matter enters a lake, it is microbial activity that makes the energy contained within this material available to the wider lake ecosystem. Microbial decomposition occurs both in the pelagic water column, and in lake sediments. The microbial loop facilitates the incorporation of organic matter (mostly as DOC) into lake food webs, allowing it to act as an alternative chemical energy source in addition to the energy transferred through the photosynthetically-based food web (Tranvik 1992). The concept of the

microbial loop originally assumed that the only organic matter source was the more labile autochthonous material, although a number of mechanisms have been proposed that would also allow more recalcitrant allochthonous material to be used simultaneously (Tranvik 1992). Once consumed by the bacteria, the mobilised energy passes through the food web via protozoa such as heterotrophic flagellates, and upwards to the macrozooplankton and fish (Hessen 1992, Jones et al. 1999, Jansson et al. 2000, Grey et al. 2001, Grey et al. 2004a, Ravinet et al. 2010, Jones and Grey 2011, see also Section 2.4). However, there is also evidence that the macrozooplankton can directly feed on bacteria (Vrede and Vrede 2005, Kankaala et al. 2006), shortening the energy pathway (Section 2.4). The following section considers a number of issues associated with the microbial loop in lakes, particularly the importance of bacterial production to lake food webs, the effects of quantity and quality of organic matter on bacteria and how changes in organic matter can effect bacterial community composition.

2.3.2 Bacterial contribution to lake food webs

Organic matter (specifically DOC) inputs to the lake environment stimulate bacterial production that represents a key component of ecosystem energy flux. This production is significantly positively related to phytoplankton production and thought to be twice as large as that of other secondary producers, such as zooplankton (Cole et al. 1988). Pelagic bacterial production is around 20% of primary production on a volumetric basis, and it has been suggested that around 60% of primary production is fluxed through bacteria (Cole et al. 1988). This metabolism of autochthonous and allochthonous organic carbon by bacteria may confer stability to lake food webs, (Wetzel 1983, 1995, Moore et al. 2004, see Section 1).

Despite the size and importance of bacterial production in lakes, very little DOC processed by bacteria is actually incorporated into its biomass or passed up the food web to higher trophic levels, since most is respired as CO₂ (Cole et al. 2002, Roehm et al. 2009). Energy transfer via the microbial pathway (from DOC) involves more steps than the transfer of photosynthetically-fixed carbon. This transfer is therefore considered less efficient, because relatively little DOC derived energy reaches macrozooplankton or fish (Jansson et al. 2000, Kalff 2002, but see Section 2.4.1). There is also some evidence to suggest that relatively little sediment DOC passes to benthic macroinvertebrates from bacteria, as grazing had little impact on the sediment bacterial community in a boreal lake study (Gudasz et al. 2012).

Although, in some lakes, little DOC may pass directly into lake food webs via bacterial pathways, much of the respired DOC forms the dissolved inorganic carbon (DIC) that is subsequently utilised by phytoplankton production (Cole et al. 2002). Thus, in addition to supplying limiting nutrients and resources for mixotrophic phytoplankton (see Section 2.2), bacterial processing of DOM may also provide a carbon subsidy to the photosynthetically-based food web. When not utilised by phytoplankton, CO₂ produced by bacterial mineralisation of allochthonous DOC may

be fluxed from the lake to the atmosphere (del Giorgio and Peters 1994, see also Section 2.7).

2.3.3 Quantity of organic matter

The amount of organic matter received by lakes has an important effect on the functioning of bacterial communities. Growth efficiency and growth rates of bacteria are both lower in oligotrophic environments and therefore less carbon passes to higher trophic levels in these lakes (Eiler et al. 2003). At higher DOC concentrations, growth efficiency and growth rate of bacteria are not constrained by the concentration of DOC in the water. The rate of pelagic bacterial DOC consumption, the total amount consumed and the size of the bacterial biomass are also strongly linked to initial DOC concentrations, where higher concentrations lead to more potential consumption and larger bacterial biomass (Tranvik 1988, Roehm et al. 2009). The amount of sediment bacterial production also appears to be positively related to the amount of organic matter present and the size of the sediment bacterial biomass (Cole et al. 1988).

2.3.4 Quality of organic matter

The ability and efficiency of bacteria to decompose organic matter depends on how labile or recalcitrant the source of organic matter is. Organic matter produced within the pelagic areas of the lake by plankton cells, and released as exudates, is assumed to be highly labile and readily consumed by bacteria (Wetzel 1983, Tranvik 1992). In contrast, littoral macrophyte or catchment sources are thought to be much more recalcitrant and decomposed only at slow rates (Tulonen et al. 1992, Wetzel 1995, Berggren et al. 2010). This simple divide between autochthonous and allochthonous sources in terms of their bioavailability is complicated by the occurrence of low and high molecular weight compounds within both of these source types. Low molecular weight autochthonous DOC has been found to be utilised more quickly and is therefore quantitatively more important for bacterial metabolism in pelagic bacteria than higher molecular weight compounds from the same source (Sundh 1992). Although high molecular weight compounds may have initially low utilisation by bacteria, the breakdown of these compounds into lower molecular weight compounds due to processes such as photochemical degradation can result in an increase in bacterial biomass (Lindell et al. 1995). Seasonality of autochthonous DOC sources also has an impact on the amount and quality of the substrate that is available to bacteria (Sundh 1992). Size distribution and composition of this DOC has been found to vary both between different lakes and over the growing season in lakes, which is likely to prompt a change in bacterial community succession or uptake kinetics of bacterial species.

Understanding the quality of allochthonous DOC as a bacterial substrate is important in the context of increased terrestrial DOC loading. Stoichiometric analysis of allochthonous DOC reveals that it often has a high C:P ratio, implying it is of a relatively poor quality (Hessen 1992). The higher the C:P ratio, the more DOC is respired by bacteria rather than being incorporated into biomass. High rates of

respiration also imply that bacteria are phosphorus limited and are therefore consumers of phosphorus bringing them into direct competition with phytoplankton for nutrients (Hessen 1992, Blomqvist et al. 2001). The presence of inorganic nutrients alongside more labile organic carbon also appears to be important from the perspective of bacterial production rates. In a study from an Arctic lake, the highest bacterial production rates were associated with the combination labile organic matter and other inorganic nutrients washed into the lake during spring (Crump et al. 2003). The quality of DOC from allochthonous sources for bacterial metabolism is also thought to vary between the sediments and water column. Allochthonous DOC is thought to be more available for bacterial production in the water column than the sediments as more labile compounds are utilised as it sinks, leaving mainly recalcitrant DOC reaching the sediment (Gudasz et al. 2012). An increase in terrestrial DOC loading is therefore likely to stimulate water column metabolism more than sediment metabolism.

2.3.5 Changes in bacterial communities in lakes

A change to organic matter loading may also affect the community composition of bacteria. It has already been implied by Sundh (1992) that species shifts are likely to occur seasonally due to the changing quality of autochthonous organic matter available to bacteria. Changes in bacterial community are also seen with changes in the trophic state of lakes, with α Proteobacteria only being present in oligotrophic lakes, while β Proteobacteria and Cytophaga-Flavobacteria occur along a trophic gradient and represent more cosmopolitan species (Eiler et al. 2003). The concept of cosmopolitan and transient bacterial species responding to specific organic matter fluxes has also been observed over a seasonal cycle in an Arctic lake. Cosmopolitan species were present all year but two groups of transient species were associated firstly, with a meltwater flux of organic matter in the spring, followed by their replacement by different populations associated with phytoplankton production in the summer (Crump et al. 2003). Similar variations in bacterial communities have been found in response to physical disturbances in lakes. Typhoon-induced mixing has been observed to “reset” bacterial communities in the epilimnion and hypolimnion of a subtropical lake, which subsequently diverged in their composition following these events, with some species showing persistence over time and others only present for a limited time during the re-establishment of stratification (Jones et al. 2008b). These dynamics of bacterial community composition in lakes are also likely to have effects on the structure and functioning of these communities. Changes to the source and bioavailability of DOM provided to bacteria have been found to alter community composition over relatively short timescales, with concomitant changes to production, metabolism and enzyme activity (Pinhassi et al. 1999, Findlay et al. 2003, Judd et al. 2008). Bacterial community composition is clearly linked to the supply of organic matter, both in terms of quantity and quality, which in turn affects the functioning of these communities and their role in processing carbon in lakes.

2.4 Organic matter and zooplankton communities

2.4.1 Effects on zooplankton nutrition

Much existing work on the effects of organic matter loading upon zooplankton communities has focussed upon the role of these materials as food resources. Studies based upon stable isotope techniques have shown that terrestrial carbon sources can provide an important subsidy to zooplankton production. Terrestrial organic matter is not only incorporated into crustacean zooplankton biomass, but may contribute a significant proportion of this biomass [e.g. ~50%, Jones et al. (1998); ~40% Grey et al. (2001) ; ~30-70% Cole et al. (2006); ~20-40% Cole et al. (2011)].

However, the relative contribution of terrestrial inputs of organic material to supporting zooplankton biomass production varies greatly among lakes. This contribution may be higher in humic lakes compared to clear water lakes (Jones 1992, Carpenter et al. 2005, Wilkinson et al. 2013), or in lakes where bacteria make a major contribution to the total pelagic production available to grazers (Karlsson et al. 2003). Also, there is potentially a greater dependence of zooplankton production on terrestrial organic matter in oligotrophic lakes than in eutrophic lakes (Jones 1992, Grey et al. 2000, Carpenter et al. 2005, Wilkinson et al. 2013). Among-lake comparisons of total planktonic production-respiration (P:R) ratios, and autotroph-heterotroph biomass ratios, are also consistent with the inference that the contribution of terrestrial carbon to pelagic production may vary with lake trophic state (del Giorgio and Peters 1994, del Giorgio and Gasol 1995).

Within lakes, the importance of terrestrial organic matter as a dietary source varies seasonally. Zooplankton grazers may “switch” between being heavily supported by terrestrial organic matter in the winter months, when there is little phytoplankton production, and by phytoplankton production in the summer months. For example, before the main phytoplankton growth period in Loch Ness, ~90% of zooplankton body carbon was of terrestrial origin compared to ~40% as an annual average (Grey et al. 2001). Also, in humic lakes, the contribution of terrestrial organic matter to zooplankton diets (accessed via ingestion of methanotrophic bacteria) may be higher during the autumnal mixing period than during the spring (Taipale et al. 2007, Kankaala et al. 2010b).

The direct (i.e. nutritional) effects of terrestrial organic matter will vary among zooplankton species. Taxa vary with respect to the extent to which they utilise terrestrial organic matter (Grey et al. 2001). Species abundant outside of the seasonal phytoplankton growth period would be more likely to be supported by terrestrial organic matter (Grey et al. 2001). Also, a number of studies have documented differences in allochthonous resource use between cladocera and calanoid copepods (Grey et al. 2000, Pulido-Villena et al. 2005, Faithfull et al. 2012, Karlsson et al. 2012, Berggren et al. 2014), perhaps due to differences in their feeding mechanisms. The more selective feeding mode of copepods may allow them

to actively select against direct ingestion of terrestrial detritus in favour of phytoplankton or micro-zooplankton that have themselves consumed terrestrially-supported bacterial populations (Section 2.3).

Once it has entered into the lake system, there exist a number of different pathways for the incorporation of terrestrial carbon into zooplankton biomass. These consumers may 1) ingest terrestrial particulate organic carbon (t-POC) (Hessen et al. 1990, Cole et al. 2006), 2) ingest heterotrophic bacteria and flagellates that have utilised terrestrial dissolved organic carbon (t-DOC) as a substrate (Jones 1992, Salonen et al. 1992b, Kankaala et al. 1996, Berggren et al. 2010), and 3) ingest inorganic particles to which t-DOC has adsorbed (Arruda et al. 1983). There is divergence among studies regarding the relative importance of these pathways. While some have shown that a greater proportion of the terrestrial carbon is accessed by zooplankton via the t-POC route (Hessen et al. 1990, Cole et al. 2006), others suggest that t-DOC processed by the microbial loop may be an important source of terrestrial carbon to zooplankton (Salonen and Hammar 1986, Grey et al. 2001), and that this transfer may be facilitated by UV-driven increases in the bioavailability of DOC (Cooke et al. 2006a). Stable isotope evidence from humic lakes also suggests a further pathway: zooplankton may access terrestrial carbon by consuming methanotrophic bacteria, which are in turn supported by methane generated by the decomposition of terrestrial carbon in deep anoxic waters (Jones et al. 1999, Bastviken et al. 2003, Santer et al. 2006, Taipale et al. 2007, Kankaala et al. 2010b). An additional complexity that hampers the generalisation of these findings is that zooplankton species likely differ with respect to the carbon pathways that they exploit (Hessen et al. 1990, Jansson et al. 2007, Berggren et al. 2014).

Despite the above evidence there is much debate over the likely importance of terrestrial organic matter to zooplankton nutrition, and regarding the extent to which zooplankton productivity actually benefits from the availability of this material. While inputs of terrestrial material are frequently viewed as subsidies to aquatic productivity (Cole et al. 2006, Cole et al. 2011, Jones et al. 2012), some have challenged the view that increased terrestrial organic carbon loading would actually stimulate the productivity of zooplankton populations. In some cases negative correlations between terrestrial organic carbon inputs and zooplankton production have been observed (Kelly et al. in press), in others only weak effects of terrestrial resource use upon zooplankton productivity have been found (Kankaala et al. 2010a, Faithfull et al. 2012). It has also been argued that, in short retention time lakes, DOC would likely be flushed from the system before significant trophic transfer could occur (Brett et al. 2012). Furthermore, recent evidence suggests that the contribution of terrestrial carbon to zooplankton biomass may be lower than would be expected based upon the relative availability of allochthonous and autochthonous resources (Marcarelli et al. 2011, Karlsson et al. 2012). This has been interpreted as “selection” against terrestrially-derived food resources though the mechanism is currently unclear, and such discrimination may occur during assimilation rather than ingestion. Such

observations are consistent with the fact that allochthonous organic matter is often nutritionally inferior to autochthonous material (Hessen et al. 1990, del Giorgio and Peters 1994, Elser et al. 2000), and that ingestion of DOC adsorbed to inorganic particles, may come at a cost of reduced consumption of higher-quality phytoplankton food resources (Arruda et al. 1983). Furthermore, use of terrestrial carbon sources by some zooplankton (particularly copepods) may be rather inefficient since these consumers access such sources through the microbial food chain, and much of the carbon is lost to respiration during trophic transfer (Kankaala et al. 1996, Kankaala et al. 2010a, see also Section 2.3). So, though terrestrial resources are clearly important to sustaining zooplankton populations, they may not dramatically stimulate zooplankton productivity directly and in-lake phytoplankton production may still have a disproportionate influence on the dynamics of these communities (del Giorgio and Peters 1994). However, it is possible that the productivity of zooplankton grazers may instead benefit from increased phytoplankton production in response to photochemical and microbial mineralisation of limiting nutrients from organic matter (Vahatalo et al. 2003, Hessen et al. 2004, Kissman et al. 2013, see also Section 2.2).

2.4.2 Non-nutritional effects upon zooplankton populations

In addition to affecting the quality and quantity of food resources available to zooplankton populations, terrestrial organic matter may influence these organisms more indirectly by affecting the underwater light climate. One aspect of this more indirect effect is that high concentrations of dissolved organic matter increase the vertical attenuation of ultra-violet radiation, thus protecting zooplankton from physiological damage (Williamson et al. 1996, Williamson et al. 1999, Rautio and Korhola 2002, Cooke et al. 2006b). As zooplankton species differ greatly in their physiological tolerance to ultra-violet radiation (Leech and Williamson 2000), the positive effect of increases in dissolved organic matter are likely to be highly species-specific and will be most beneficial to UV-sensitive taxa. In addition to physiological tolerance, zooplankton may migrate to greater depths as a means of avoiding ultra-violet radiation. The resulting depth-selection behaviour also varies greatly among species and is mediated by additional ecological factors, such as predation pressure at different depths in the water column (Boeing et al. 2004). As a result of these among-species differences in tolerances and responses to ultra-violet radiation, it is likely that increases in dissolved organic matter loading have the potential to affect zooplankton community structure and trophic relationships in complex ways.

In addition, organic matter also affects the vertical attenuation of visual-range solar radiation in the lake water column. As a result of this, high concentrations of dissolved organic carbon may reduce the effectiveness of visual predation by fish (see also Section 2.6), mediating this important determinant of zooplankton abundance and community structure. Under similar predation regimes, zooplankton abundance may be higher in the surface waters of coloured lakes than in clear lakes (Wissel et al. 2003). These observations are consistent with 1) a reduction in the

predation rate of visually-foraging planktivorous fish under conditions of reduced light intensity and 2) an extension of the low-light refuge available to zooplankton at high DOC concentrations.

Finally, the humic and fulvic acids contained in dissolved organic matter (Table 1) may influence zooplankton communities via effects on the pH of the lake environment. Species differ greatly with respect to their degree of acid sensitivity and so inputs of dissolved organic matter have the potential to profoundly affect community structure, by affecting the relative abundance of acid tolerant and acid sensitive species (Cooke et al. 2006a).

2.5 Organic matter and macro-invertebrate communities

2.5.1 Overview

The dynamics of most benthic invertebrate species are likely to be highly dependent upon allochthonous organic matter loading, since this material is an important source of energy for these consumers. Specifically, the quality and quantity of organic matter are important factors influencing community structure. Since complex interactions between benthic invertebrates and food webs can not only change species composition, but also lead to unexpected changes in freshwater ecosystems (Goedkoop and Johnson 1992, Covich et al. 1999, Vanni 2002), organic matter loading has the potential to affect numerous ecosystem processes via its effects upon macroinvertebrate communities. The effects of organic matter loading upon macroinvertebrate communities will be mediated by among-species differences in feeding modes, which determine what kind of organic matter they can ingest and assimilate.

When assessing the potential effects of organic matter on macroinvertebrate communities, it is important to consider the distribution of macroinvertebrate species within the lake ecosystem, because this will determine organic matter quality and availability. In order to discuss the effects that organic matter has on benthic macroinvertebrate communities, a rough division between littoral and profundal zones is made here. Lake macroinvertebrate communities typically differ between these zones, with two maxima of abundance and biomass that are usually found in littoral and profundal zones (Wetzel 2001, Jónasson 2004). However, interactions between organic matter and macroinvertebrates clearly demonstrate that these apparently different within-lake habitats are coupled with each other in multiple ways (Polis et al. 1997, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002).

2.5.2 Feeding habits and trophic relationships

Many benthic species are detritivorous and ingest substantial quantities of organic matter, including phytoplankton, submerged macrophytes, bacteria and other dead or living organic material (Jónasson 2004). Inputs of terrestrial POC (t-POC) into the pelagic environment can be a major source of nutrition for benthic invertebrates as

this material settles to the benthos, and may therefore fuel a large proportion of their production (e.g. ~60-85%, Cole et al. 2006). However, the relative contribution of this allochthonous material to macroinvertebrate nutrition may be rather lower (6% total energy use) when autochthonous (phytoplankton) production is stimulated (Cole et al. 2006). Under such conditions, dead phytoplankton may constitute a more important source of carbon to benthic invertebrates. In contrast however high concentrations of DOC may, through shading and subsequent light limitation of benthic algal food resources (see Section 2.2), alter the balance of autochthonous to allochthonous nutrition for benthic invertebrates (Solomon et al. 2011, Jones et al. 2012).

By consuming fine organic matter and storing this energy in their tissues, benthic invertebrates become themselves an important conduit for the transfer of this energy to higher trophic levels (Lindegaard 1994). For example, benthic macroinvertebrates comprise a dominant part of the diets of many fish species (e.g. Vander Zanden et al. 1997, Eloranta et al. 2010, Ravinet et al. 2010). Therefore, by limiting the production of benthic algal food resources (see Section 2.2), coloured terrestrial DOC may have important impacts upon both benthic macroinvertebrate production and, ultimately, fish biomass (Karlsson et al. 2009, Premke et al. 2010). This trophic transfer of energy derived from organic matter will be mediated by variations in feeding strategies during different stages of the macroinvertebrate life-cycle (Covich et al. 1999, Wetzel 2001, Jónasson 2004) thus making it challenging to assess the impacts of organic matter on benthic communities. Particular benthic macroinvertebrate groups have been proposed to have a special role in processing organic matter in freshwater ecosystems, by affecting its quality either directly or indirectly. For example, shredders that fragment organic matter without actually ingesting it, have been proposed as a vitally important group due to their relatively low species numbers and important role in organic matter processing (Palmer et al. 1997).

In summary, the trophic position and functional feeding groups of different species are pivotally important in understanding the effects of organic material on lake macroinvertebrate communities. However, studying the trophic position of aquatic consumers is challenging as it requires information on energy-flow and omnivory in complex lake food webs (see Polis and Strong 1996, Vander Zanden and Rasmussen 1999, Post 2002).

2.5.3 Littoral zone

The littoral zone has higher benthic species diversity than in the profundal zone (Wetzel 2001, Jónasson 2004), and littoral-benthic pathways have an important role in food web dynamics and lake production (Vadeboncoeur et al. 2002). Most of the world's lakes are small and have substantial littoral areas compared to their total lake area (Wetzel 1990). The depth of the euphotic zone determines how far this littoral zone extends and, at the same time, the maximum depth at which benthic primary production can occur (Jónasson 2004, see also Section 2.2). In clear-water and

shallow lakes, benthic algae can dominate primary production in the whole lake (Vadeboncoeur et al. 2003, Karlsson et al. 2009), thus making the benthic macroinvertebrates living there an important link between primary production and higher trophic levels.

In some lakes, a large share of the allochthonous organic matter in the littoral zone may originate from riparian vegetation (Schindler and Scheuerell 2002). In a study of eight Canadian Boreal Shield lakes, the results suggested a strong reliance of benthic primary consumers on leaf litter in seven of the lakes (Glaz et al. 2012). Another study revealed the importance of fine POM as a terrestrially derived subsidy for the recovery of littoral macroinvertebrate communities in industrially damaged lakes (Szkokan-Emilsson et al. 2011).

Most benthic macroinvertebrates in the littoral zone are herbivores or algivores consuming benthic periphyton, biofilms, associated bacteria and terrestrial carbon sources (Hecky and Hesslein 1995, Vadeboncoeur et al. 2003, Solomon et al. 2008, Solomon et al. 2011). For example, in a study of five north-temperate lakes in Wisconsin, U.S.A, consumer $\delta^{13}\text{C}$ values suggested specialization on benthic algae and also correlated with benthic primary production (Devlin et al. 2013). In the deeper sublittoral area, the share of phytoplankton and bacterial-coated detritus in the diets of benthic invertebrates increases, while the amount of benthic algae declines as the light starts to limit the productivity (Vadeboncoeur et al. 2003, Vadeboncoeur et al. 2008). Devlin et al. (2013) found that collector and predator $\delta^{13}\text{C}$ declined with depth and a strong correlation with the $\delta^{13}\text{C}$ of bulk periphyton.

2.5.4 Profundal zone

Most profundal species are detritivorous, feeding on phytoplankton and bacteria-coated detritus falling down from the upper water column (Jónasson 1972, Goedkoop and Johnson 1992, Gullberg et al. 1997, Jónasson 2004). Chironomid larvae often dominate macroinvertebrate communities in the profundal zone. The amount of sedimenting organic matter that is processed by benthic communities can be substantial, thus making them an important link in benthic-pelagic coupling (Jónasson 2004).

Due to the lack of light, the profundal zone is heterotrophic and dependent upon sedimenting organic matter which may be of terrestrial origin (Covich et al. 1999). Even though most of this material is of poor nutritional quality, some constituents of it may in fact represent high-quality resources. For example, many diatom species are rich in polyunsaturated fatty acids required by profundal macroinvertebrates (Johnson and Wiederholm 1992, Dunstan et al. 1993). It is perhaps for this reason that the profundal zone is able to support surprisingly high species diversity (Jónasson 1996).

Organic matter in anoxic sediments may form a substrate for methanogenic microbes and as methane diffuses upwards to more oxic layers, it may in turn become the energy source for methane-oxidising bacteria. Stable isotope studies

have been key in revealing how methane-derived carbon may contribute to benthic food webs, especially via tubicolous chironomid larvae (Grey et al. 2004b, Jones and Grey 2011). Indeed, from a study of 87 lakes across a wide latitudinal gradient, Jones et al. (2008a) concluded that 40% of those lakes contained chironomid larvae comprising a substantial proportion of methane-derived carbon. It was the stratifying lakes where this phenomenon was most pronounced and so, given the potential for increasing DOC to impact upon stratification duration and methane emissions (see Section 2.7), it will likely also affect methane cycling through food webs (Grey et al. 2004b, Jones and Grey 2011).

Environmental factors, such as hypolimnetic temperature, oxygen and availability of sedimenting organic matter (SOM), are all important in determining profundal macroinvertebrate community composition. The environmental factors are inter-related and they form a complex gradient, which has been studied e.g. in boreal (Jyväsjärvi et al. 2012) and arctic lakes (Brodersen and Anderson 2002). The profundal community composition correlated most strongly with $\delta^{13}\text{C}$ of sedimenting organic matter in a study of Finnish boreal lakes (Jyväsjärvi et al. 2012). The results of Jyväsjärvi et al. (2012) indicated the role of SOM in structuring the communities to be more important in oligotrophic sites. Correlation between carbon isotopic signature of marine POC and high-quality fatty acid abundance has indicated that $\delta^{13}\text{C}$ can possibly be used as a proxy of sedimenting organic matter quality (Veefkind 2003). It is, however, also important to recognize the indirect effects of increased DOC loading upon profundal macroinvertebrate communities. DOC impacts upon water temperature, by increasing surface heat absorption and potentially leading to a reduction in deep-water temperatures (see Section 2.1.3). This DOC-related reduction in deep water temperature is likely to be influential to benthic macroinvertebrate communities that are comprised entirely of ectothermic species.

2.6 Organic matter and fish communities

2.6.1 Effect on fish nutrition

Externally derived organic carbon may be channelled through planktonic and benthic food webs, and eventually become a valuable food resource for the fish (Jones et al. 1998, Carpenter et al. 2005, Cole et al. 2006, Premke et al. 2010, Solomon et al. 2011, Karlsson et al. 2012). Also, allochthonous matter contains potentially-limiting nutrients that may stimulate autochthonous production (see Section 2.2), and eventually fish production. However, if allochthonous organic matter colours lake water (brownification), the final outcome for fish production is less predictable as autochthonous production may decline substantially due to light limitation (Karlsson et al. 2009, see also Section 2.2). Furthermore, altered light, temperature and oxygen profiles with brownification further complicate predictions as they may alter

the foraging abilities of fish (Wissel et al. 2003, Ranåker et al. 2012), with possible consequences for zooplankton populations (Section 2.4).

In a study of a brownwater Swedish lake, with high input of humic water, Karlsson et al. (2012) found that allochthonous organic matter fuelled most (85%) of the total production at the base of the lake's food web (i.e., the sum of primary and bacterial production) and only contributed 42-65% to the biomass at primary consumer level (zooplankton and benthic invertebrates) and 57% of the biomass of fish. The disproportionately low reliance on allochthonous organic matter at higher trophic levels, compared with its high rates of input and high support of basic biomass production in the lake, suggests that autochthonous resources cannot be completely replaced by allochthonous resources and furthermore indicates an upper limit to terrestrial support of lake food webs (Karlsson et al. 2012). Concurrently Babler et al. (2011), in a study of 11 reservoirs with contrasting catchment areas, showed that the biomass of the predominant fish species (gizzard shad, *Dorosoma cepedianum*) was positively related to phytoplankton primary production but negatively to allochthony. This also suggests that phytodetritus is a higher quality resource than terrestrial detritus for organisms at higher trophic levels, and that highly coloured allochthonous input may reduce fish production if autochthonous production is reduced by enhanced light limitation. Babler et al. (2011) further found that allochthony was inversely related to total watershed area, as well as the absolute area of the watershed, but was independent of the proportion of agricultural land cover in the catchment. In a study of four nutrient-poor North American lakes, Solomon et al. (2011) also found that the contribution of allochthonous organic matter to fish biomass increased with increasing DOC, and subsequently reduced light conditions. However, while high input of coloured DOC may reduce light availability for primary producers and thus their role as basal resources for fish production, it also adds nutrients to the system, which to a various extent may compensate for the lower light, not least in nutrient-poor lakes. Hence, Leclerc et al. (2011) found a higher early growth of yellow perch (*Perca flavescens*) in lakes affected by forest harvesting than in control lakes (having less DOC) due to favourable feeding conditions after the perturbation. The perturbed lakes had higher algal biomass and *Daphnia* spp. abundance, and the authors hypothesised that the increase in *Daphnia* spp. abundance was due to higher productivity, as well as darkening of the water colour in perturbed lakes. These changes would reduce prey detection by predators, favour growth and then population recruitment. Using fish yield from standardised brown trout gill-net catches as a proxy, Finstad et al. (2014) showed a unimodal response of lake secondary productivity to DOC. They attributed this to a trade-off between positive and negative effects, where the initial increase may hinge upon several factors such as energy subsidising, screening of UV-radiation or enhanced P and N inputs associated with increased organic carbon loading. The subsequent decline in production with further increase in DOC was attributed to light limitation of primary production (see Section 2.2). They further showed that shallow lakes switch from positive to negative effects at higher carbon loads than deeper lakes.

2.6.2 Non-nutritional effects on fish populations

Water colour may also affect inter- and intra-specific interactions among fish species. Two key species, European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), in central European lakes (Bruce et al. 2013) differ in response to water colour, with perch being the inferior zooplankton predator competitor in coloured water (Estlander et al. 2010). Estlander et al. (2012) found that perch fed less in highly humic water than in clear water, and field data showed that water colour had a significant effect on the length at which perch shifted from feeding primarily on plankton to other food sources. High colour also limits the development of submerged macrophytes that are particularly suitable habitats for perch (Persson et al. 1991), making roach an even better competitor (Persson et al. 1991, Estlander et al. 2010). In this way, fewer perch may reach a size where they become partly piscivorous, which further makes roach a superior competitor in humic water. This has management implications. In Northern Europe selective removal of roach and bream has been used to restore degraded lakes after nutrient loading reduction, by promoting potentially piscivorous perch (Jeppesen et al. 2012). It is evident that the success of this method might be less pronounced in humic waters where roach is a stronger competitor than in similar clearwater lakes. This may perhaps explain why roach has returned quickly after biomanipulation in Finnish lakes (Olin et al. 2006).

As most fish are visual foragers, visual conditions in the water may alter the strength of predator regulation of prey fish. Jönsson et al. (2013) found that the encounter rate of Northern pike (*Esox lucius*) feeding on roach decreased in both turbid and humic water, which was not counteracted by increased searching activity. Capture success was non-linearly affected by humic water, being high in clear and highly humic waters but low in less humic water. In highly humic water, the visual range approached pike's strike distance and, together with its cryptic colours, pike may have initiated its attack before the prey detected it, limiting the possibility for prey evasive manoeuvres (Jönsson et al. 2013). Prey-size selectivity towards small prey in clear water was maintained in humic water. It was also evident from this study that, owing to its optical properties, turbidity degrades the quality of the visual information more through scattering than humic water does through absorption.

2.7 Fate of organic matter

Three dominant pathways determine the fate of organic matter in lakes. A fourth pathway, the transfer of energy from bacterial communities to higher trophic levels, has been considered extensively elsewhere in this review (Sections 2.3 and 2.4) and so is not covered in this section. Organic matter export, via lake outflows, forms part of the transfer of material from terrestrial to marine environments. Global estimates suggest that around 47% of carbon received by freshwaters is exported to the oceans (Cole et al. 2007). The importance of this route for individual lakes is likely to be dependent upon the lake retention time and discharge regime, as short retention times will increase the amount of organic matter flushed through the lake and reduce

time for sedimentation or microbial processing (Brett et al. 2012, Hanson et al. 2014). Where retention times are longer, more organic matter is likely to be lost to lake sediments or processed in the water column.

According to the estimates of Cole et al. (2007), the next largest pathway for carbon in freshwaters is the gaseous flux to the atmosphere of carbon dioxide (CO₂) and methane (CH₄). This is particularly the case for lakes, owing to their longer retention times than rivers. The relative importance of lakes as sites for the processing of DOC to DIC, as opposed to being the source of catchment produced DIC, appears to depend on the type of lake and catchment being considered (Jones et al. 2001, Duarte and Prairie 2005, Maberly et al. 2013). Variation in the fluxes of the two gases is also large and is related to a range of processes in the sediments and water column.

Large quantities of CO₂ are produced by the respiration of organic matter by bacterial communities, in both the water column and sediment (Wetzel 1983). Indeed, it has become evident that most lakes are net conduits of CO₂ to the atmosphere, and many studies have identified DOC as a key driver of partial pressure of CO₂ (pCO₂) (Cole et al. 1994, Sobek et al. 2005, Larsen et al. 2011). Bacterial respiration of terrestrial organic carbon in the epilimnion of eight lakes in southern Quebec (Canada) explained on average 60% of the estimated air-water CO₂ flux, suggesting it to be the major component of the flux (McCallister and del Giorgio 2008).

In addition, carbon in anoxic sediment can be transformed into CH₄. Wetzel (2001) suggests that between 20 – 59% of sediment sestonic carbon may be processed in this way. This CH₄ can be emitted from lakes either directly through the ebullition of gas bubbles, or by vertical transport through the water column as dissolved gas (Wetzel 1983). Within the water column, much of the CH₄ will be converted to CO₂ by methanotrophic bacteria, where the amount of CH₄ oxidised varies between 51 - 80% (Bastviken et al. 2008), but can be higher than 90% (Casper et al. 2000). A much higher proportion of CH₄ released from epilimnetic sediments is likely to reach the atmosphere, because the shallow water reduces the residence time of the gas to the lake surface (Bastviken et al. 2008). Reduction in the travel time of dissolved CH₄ is also seen during lake mixing and overturn, where much larger quantities of CH₄ reach the lake surface and are emitted (Rudd and Hamilton 1978). Recently, however, studies have shown that methanogenesis is also possible in oxic conditions (Grossart et al. 2011). The subsequent fate of CO₂ converted from CH₄ or other microbial respiration is either outgassing to the atmosphere or utilisation within the lake for other processes e.g. photosynthesis.

Sedimentation and burial of organic matter in lake sediments is the smallest of the three dominant carbon pathways, representing an accumulation of around 10% of terrestrial carbon received by freshwaters (Cole et al. 2007). However, carbon accumulation in sediments is very variable both within and between lakes types and

regions. High accumulation rates are found in small eutrophic lakes and artificial impoundments in agricultural landscapes ($150 - 17,000 \text{ g m}^{-2} \text{ yr}^{-1}$) (Downing et al. 2008), while accumulation rates are lower in more oligotrophic lakes and those in boreal landscapes ($3 - 128 \text{ g m}^{-2} \text{ yr}^{-1}$) (Mulholland and Elwood 1981, Ferland et al. 2012, Hanson et al. 2014). The microbial processing of organic matter to DIC results in less carbon accumulating in lake sediments (Wetzel 1983). The composition of organic matter determines how readily it can be decomposed, with the more labile forms and dissolved forms assimilated and mineralised more rapidly than humic or particulate materials (Wetzel 1983). The implication is that the organic carbon accumulating in lake sediments is largely the residue of the processes of decomposition and the rate of carbon accumulation will depend to some extent on both the amount of organic matter and the extent to which it can be decomposed.

2.8 Impacts upon ecosystem metabolism

Due to the large total pool of organic matter (OM) within lakes, loading of terrestrial DOC can significantly influence the energy pathways and metabolism of lake ecosystems (Salonen et al. 1992a, Tranvik 1992, Hessen 1998, Carpenter et al. 2005, Kankaala et al. 2006). The metabolic balance of lakes describes the relative magnitude of photosynthesis (gross primary production, GPP) in relation to ecosystem respiration (ER) (Hanson et al. 2003). If $GPP > R$, the metabolic balance is autotrophic, while $GPP < R$ implies heterotrophy where the respiratory breakdown of OM exceeds production of OM by photosynthesis. The role of allochthonous OM in lake metabolism has received much research attention in recent years due to improvements in estimating diel changes in dissolved oxygen (DO) using high-frequency measurements (Coloso et al. 2008, Van de Bogert and Staehr 2010), and also stable isotope techniques to analyze sources and origins of carbon in different food web components (e.g. Jones et al. 2008a). Recent studies have shown that POC, and in particular DOC, can significantly contribute to gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production ($NEP = GPP - ER$) in different lake habitats, i.e. the pelagial, littoral and benthic areas. However, it is important to realize that there are also other factors, e.g. physical, climate-related forces (wind and upwelling events), that influence pelagial metabolism in lakes (Bocaniov et al. 2013).

Despite variability among lakes with differing trophy and DOC content, several studies have shown a strong relation between community respiration and quantity and quality of DOC (Kritzberg et al. 2006, Sand-Jensen and Staehr 2009). Accordingly, the respiration of allochthonous organic carbon explains well the negative net ecosystem production in some lakes (Karlsson et al. 2007). It has been suggested that oligotrophic lakes are typically net heterotrophic and act as net sources of CO_2 while eutrophic lakes are generally net autotrophic and act as net CO_2 sinks (Cole et al. 1994, del Giorgio and Peters 1994). Hoellein et al. (2013) compared GPP and ER from diel oxygen curves measured in the open-water of 350

lakes, wetlands, estuaries, and streams. GPP and ER were strongly related in lakes and estuaries, but weakly related in streams and wetlands. Differences in the magnitude and variability of metabolism among ecosystems were attributable to landscape and water-column factors. In their study, watershed size and phosphorus (P) concentrations were positively related to GPP and ER across all ecosystems. Considered independently, lake and estuary GPP were driven by P concentrations.

Humic lakes rich in allochthonous DOC are thus typically considered net heterotrophic. Jansson et al. (2000) suggest that the threshold of DOC loading for a change between net autotrophy and net heterotrophy is ca. 5 mg/l DOC. Ask et al. (2012) studied 15 lakes with different concentrations of colored DOC of terrestrial origin in N-Sweden with respect to primary production and respiration in benthic and pelagic habitats. Primary production decreased and respiration increased on a whole-lake scale along the gradient of increasing DOC. Lakes became more net heterotrophic, i.e., had lower net ecosystem production, with increasing terrestrial DOC. They found that the single most important process for the increasing net heterotrophy along the DOC gradient was pelagic respiration of terrestrial organic carbon.

Staeher et al. (2012) studied the influence of lake morphometry, catchment conditions, light availability and nutrient input on lake metabolism in 25 lakes in Denmark. They found that GPP and community respiration (R) increased with algal biomass (chlorophyll concentration), DOC and TP. They concluded that, especially in small lakes with less incident light, and forest lakes with high DOC, net ecosystem production is negative ($NEP < 0$). Multiple regression models that combined water depth and chlorophyll concentration to predict GPP, and water depth and DOC to predict R, accounted for 57-63% of the variability of metabolism among the lakes. This highlights the importance of lake morphometry and catchment conditions when comparing metabolic responses of lakes to human impacts. The abnormally rainy summer of 2004 in Finland resulted in an upward shift in hydrology and an increase in DOC loading and consequently higher colour in many lakes (Jennings et al. 2012, Arvola et al. 2014). However, this did not clearly change R in all lakes (Arvola et al. 2014) which partly contradicts the findings that R and/or bacterial activity would respond to changes in allochthonous organic carbon load (Tranvik 1988, Kankaala et al. 1996).

Though the above literature suggests generalizations that can be made regarding environmental factors that influence lake ecosystem metabolism, there are considerable complexities associated with these patterns. For example, though high-DOC, oligotrophic lakes are often net heterotrophic, in some situations eutrophic lakes may also be net heterotrophic. This is due to their poor underwater light climate, e.g. as a result of suspended solids which limit phytoplankton photosynthesis (Staeher et al. 2010), analogous to increased light attenuation by coloured DOC compounds in humic lakes (see Section 2.2). Furthermore, the metabolic balance of a lake can also vary temporally and spatially (Sadro et al. 2011,

Arvola et al. 2014). For instance, in an oligotrophic high-altitude lake, except for a brief period of heterotrophy after snowmelt, littoral benthic metabolism was consistently net heterotrophic, despite the fact that the lake as a whole was autotrophic, due to higher pelagial production (Sadro et al. 2011). Working at a larger spatial scale, Solomon et al. (2013) analysed data from a global network of automated lake observatories. In their data, ER was tightly coupled to GPP at a daily scale in oligotrophic and dystrophic lakes and less strongly in meso- and eutrophic lakes. Mean annual GPP and ER ranged from 0.1 to 5.0 mg O₂/l/d and were positively related to TP, but not DOC.

3. Organic matter in a multiple stressors context

Changes in organic matter loading to lakes clearly have the potential to influence many inter-linked aspects of lake ecosystem structure and functioning. However, alterations in organic matter loading are but one of a wide array of different environmental stressors acting upon lake ecosystems. Given the need to sustainably manage lakes in an ever-changing world, it is essential to understand how changes to organic matter loading influence lake ecosystems when these occur in concert with other known stressors e.g. nutrient enrichment and climate change. However, a key concern is that the effects of increased organic matter loading in combination with other stressors, may be difficult to predict based upon existing knowledge of the effects of organic matter loading alone. The combined effects of multiple stressors may be non-additive (synergistic or antagonistic). For example, in alpine/montane lakes, increased DOC loading or warming alone may suppress phytoplankton production but, in combination, may actually enhance it (Weidman et al. 2014). Furthermore, dominance of potentially toxic cyanobacteria may increase dramatically in response to both warming and DOC loading, but not in response to either factor in isolation (Ekvall et al. 2013). These complexities in ecosystem responses underpin an urgent need to develop understanding of the effects of enhanced organic matter loading upon lake ecosystems, within a full multiple-stressors context. Herein we consider some possible effects of increased organic matter loading when in combination with eutrophication or climate change.

3.1 Interactions with climate change

The anticipated impacts of climate change on lakes appear to be related to increases in temperature, changes in stratification onset, strength and duration and changes to discharge regimes directly impacting retention times and indirectly affecting the flux of material from the catchment in response to altered rainfall patterns (De Stasio et al. 1996, Dillon and Molot 2005). This section considers how these factors are likely to interact with organic matter loading to lakes.

In addition to the direct effects on lakes, listed above, increases in air temperature associated with climate change are also likely to indirectly influence organic matter loading for some lakes as catchment soils warm, leading to melting of permafrost which could increase sources of labile DOC for lakes (Roehm et al. 2009). In

addition, increased variability in temperature could increase DOC export from soils where freeze-thaw cycles become more active, leading to more leaching from terrestrial organic matter (Hurst et al. 1985). However, the effect of warming on DOC loading is likely to be dependent on latitude, with more temperate lakes predicted to receive less DOC from catchments under climate change due to lower discharge (Fee et al. 1996).

Warmer water temperatures are associated with an increase in bacterial decomposition rates and bacterial biomass both in the water column and sediments (Cole et al. 1988, del Giorgio and Peters 1994). This suggests that bacterial activity may be enhanced because of warming but it is currently unclear the extent to which the whole of the water column and sediments may be expected to warm under climate change. Increases in surface temperatures are predicted but the earlier onset of stratification may lead to less change in hypolimnetic waters and the sediment (Livingstone 2003). Morphology is also likely to have an influence, with shallow lakes being anticipated to warm throughout the water column, in comparison to lakes which stratify and would be expected to warm more at the surface than at depth. The influence of temperature has a stronger effect on increasing bacterial decomposition rates than increasing rates of photosynthesis (del Giorgio and Peters 1994), which may result in some lakes becoming more heterotrophic.

The thermal structure changes expected due to an increase in the heat energy received by lakes as a result of climate change are very similar to those detailed in section 2.1 caused by increases in coloured organic matter loading. This is particularly true for the increases in early season surface temperature, the earlier onset of stratification (Hondzo and Stefan 1993, De Stasio et al. 1996), and greater lake stability. Indeed, the similarity of the effects combined with the observed increases in DOC loading implies the two drivers of change in lake thermal structure must be disentangled for long-term data records to be understood properly. Some likely effects of a warmer climate are less certain, and may be lake-dependent. There is currently insufficient evidence to say that mixed depths will always shallow with a warmer climate, or hypolimnetic temperatures will always increase (Fee et al. 1996, Livingstone 2003). In these cases it is particularly important to be aware of potential changes in light attenuation whilst investigating the likely impacts of a change in climate. For example, the potential late season cooling induced by a DOC-driven increase in the light attenuation coefficient K_d may even be antagonistic to the expected year round warming predicted under most future climate scenarios (Persson and Jones 2008). Similarly, the mean cooling attributed to an increase in coloured DOC concentration and subsequent increase in K_d could buffer temperature rises associated with climate change (Read and Rose 2013). As hypolimnetic temperatures are expected to experience a large cooling with an increase in DOC then it is likely this would override the small and uncertain warming hypolimnia would receive through an increase in atmospheric temperature. As epilimnetic temperatures are expected to be warmed by both climate change and an

increase in DOC, the coupled result would be even greater increases in temperature stratification than hitherto predicted.

Understanding the interaction of climate change and organic matter loading, associated with an increase in K_d , is likely to be difficult. While the general expectation is that climate change will lead to warming in lakes, changes in light attenuation are likely to be more variable, not only because of variations in DOC loading but also because a number of other factors can influence K_d , including changes in algal biomass, as discussed below.

Changes to precipitation and evapotranspiration as a result of climate change will lead to altered discharge regimes for inflowing streams and retention times for lakes. Predictions of how river discharge will change at a global level show enormous variation (Milly et al. 2005), depending on climatic region and individual catchment influences (Fowler and Kilsby 2007), as well as seasonal factors resulting in the prediction of large increases or decreases in flow (Nijssen et al. 2001). The uncertainty relating to discharge changes is also seen when considering the interaction with organic matter loading. Increased discharge due to storm events may increase allochthonous DOC loading, promoting heterotrophic energy mobilisation in some lakes (Jansson et al. 2000), while the reduction in retention time caused by higher discharge could simply increase DOC export through flushing (Brett et al. 2012). However, the catchment response and seasonality of discharge changes are also likely to be important when considering the impact of organic matter on the lake. Lateral flushing and water movements from littoral zones and wetlands surrounding lakes in response to summer rainfall events has been suggested as the source for increased concentrations of DOC and increased bacterial activity in pelagic waters in two boreal lakes (López Bellido et al. 2013). In contrast, lower flows are also thought to result in lower DOC input to lakes (Fee et al. 1996), relating the flow dependant nature of the source (Jones et al. 2011).

Altered loading of allochthonous OM under changing climate might markedly influence lake ecosystem metabolism (Bocaniov et al. 2013). Increased DOC is reported in surface waters in the northern hemisphere (Monteith et al. 2007). A shift in lake ecosystem metabolism towards heterotrophy is already supported by the impacts of increased DOC and POC loadings after extreme weather events (see Section 2.8), where the lakes have moved from net autotrophy to net heterotrophy (Tsai et al. 2011: a 28-852% increase in heterotrophy after typhoon in a subtropical lake in Taiwan, Jennings et al. 2012, Sadro and Melack 2012). However, it has been proposed that in boreal lakes increased loading of allochthonous DOC does not necessarily stimulate pelagial bacterial production and carbon transfer up the food web, because it strongly depends also on nutrient stoichiometry (C:N:P ratios) (Kankaala et al. 2010a).

3.2 Interactions with nutrient enrichment

Many lake ecosystems are likely to be impacted by changes in nutrient (especially phosphorus) delivery, at the same time as changes in DOC loading. The available literature suggests that simultaneous changes in these two pressures will act to influence the relative magnitude and importance of different trophic pathways within the lake ecosystem. Nutrient enrichment will most likely act to stimulate phytoplankton growth and therefore increase the contribution of phytoplankton primary production to the total resource base available to the food web (Jones 1992, Carpenter et al. 2005, Cole et al. 2006). On the other hand, increases in DOC loading will likely suppress in-lake primary production by shading phytoplankton and benthic algae (Carpenter et al. 1998, Karlsson et al. 2009, Jones et al. 2012, see Section 2.2) and will enhance bacterial production (Kankaala et al. 1996, Blomqvist et al. 2001, Karlsson et al. 2003, Kankaala et al. 2010a), thus increasing the contribution of external carbon sources to basal resource supply. In this way, relative changes in DOC and nutrient loading could alter the fundamental nature of the resource base available to consumers and shift the metabolic balance of lake systems between net autotrophy and heterotrophy (del Giorgio and Peters 1994, del Giorgio and Gasol 1995, Jansson et al. 2000, see Section 2.8).

The above literature would seem to suggest that nutrient enrichment would favour phytoplankton primary production over bacterial production, and that the reverse is true of elevated DOC loading. However, each of these stressors is capable of having opposing effects upon different lake ecosystems. For example, nutrient enrichment may also stimulate bacterial productivity, provided there is sufficient DOC to alleviate carbon limitation. Microbial decomposition of nutrient-poor DOC requires the presence of additional inorganic nutrients (Wetzel 1983). For example, in nitrogen limited boreal lakes, the addition of DOC will likely fail to dramatically enhance bacterial production unless there is a coincident increase in nitrogen availability (Kankaala et al. 2010a). Conversely increases in DOC concentrations may, in some circumstances, stimulate the production of some phytoplankton taxa (Saunders 1957, Graneli et al. 1999, Vahatalo et al. 2003, Znachor and Nedoma 2010). It is likely that the dominant effect of combined nutrient enrichment and DOC loading upon pelagic production will be highly system-specific. It is clear, then, that the ecological outcomes of simultaneous changes in nutrient and DOC concentrations will be highly context-specific.

The interactive effects of nutrient enrichment and DOC loading upon basal resource composition will change the relative contributions of different trophic pathways to the production of consumer organisms (Jansson et al. 2007), and thus propagate throughout the food web. For example, in lakes where DOC-based stimulation of bacterial production dominates over nutrient-driven stimulation of phytoplankton production, the enhanced bacterial production would not necessarily be available to zooplankton and fish populations because of high respiratory losses along the microbial food chain (Kankaala et al. 1996, Kankaala et al. 2010a, see Sections 2.3

and 2.4). However, if nutrient-driven stimulation of primary production was a more dominant influence than DOC-based stimulation of bacterial production, one might expect more efficient trophic transfer based upon a higher quality resource base (Jansson et al. 2007) and less dampened effects upon higher trophic levels.

As well as direct food web effects, combined changes in DOC and nutrient concentrations may also have more indirect effects upon lake ecosystems by influencing physical processes. Higher loading/in-lake concentrations of nutrients are associated with higher phytoplankton biomass (Dillon and Rigler 1974, Vollenweider and Kerekes 1980, Phillips et al. 2008). Crucially, a number of studies have shown light attenuation is influenced by changes in phytoplankton biomass and community composition as well as changes in DOC. Therefore, by stimulating phytoplankton growth, increases in nutrients could have a similar effect on thermal structure as increases in DOM (see Section 2.1). Experiments using nutrient (Jones et al. 2005) and planktivorous fish additions (Mazumder et al. 1990) have shown similar results induced by the change in light attenuation as studies carried out investigating effects of changes in colour. Similar results have also been shown by modelling studies that have deliberately targeted the effects of changes in phytoplankton on light attenuation (Rinke et al. 2010). Taken together these findings suggest that increases in DOM concentrations and in phytoplankton biomass, as a result of increases in nutrient concentrations, are likely to have additive effects on light attenuation and thus on the thermal structure of a lake. In addition, the influence of changes in algal biomass, is likely to interact with climate change as well as DOC loading. Reduced mixed depths and warmer surface temperatures are anticipated through both climate change and loss of transparency by increases in DOC or algal biomass. These synergistic consequences may then result in further changes to algal communities, favouring the growth of buoyant cyanobacterial species (Paerl and Huisman 2008, Posch et al. 2012), which may in turn further enhance light absorption near the surface.

3.3 Implications of interactive effects for management and restoration

Despite a growing body of literature on the effects of organic matter upon the structure and functioning of lake ecosystems, there is currently little understanding of the implications of organic matter loading for the way lakes are managed. However, the need for this knowledge is becoming increasingly urgent due to observed increases in organic matter, specifically DOC, concentrations in freshwaters throughout the Northern Hemisphere (Monteith et al. 2007).

In Europe, the Water Framework Directive (EC 2000) has been the major driver of lake management over the last ten years. Therein measures to reduce inputs of key limiting nutrients, specifically phosphorus, have been the focus of European lake management policy. The above literature suggests that measures to reduce phosphorus loading to lakes, in order to restore *good ecological status*, may also interact with changing organic matter loading in a way that affects the structure and functioning of lake ecosystems. Comparisons of lakes of differing productivity have

suggested that the structure and functioning of lake food webs, and ecosystem metabolism, may be dependent upon the relative availability of external carbon and in-lake primary production as basal resources (Jones 1992, del Giorgio and Peters 1994, del Giorgio and Gasol 1995, Carpenter et al. 2005, Wilkinson et al. 2013). Specifically, we may expect that measures to reduce phosphorus loading would reduce phytoplankton production in favour of bacterial production based upon external carbon sources (Jones 1992, Jansson et al. 2000, Karlsson et al. 2003, Jones et al. 2012). This change may be particularly pronounced for lakes experiencing elevated levels of DOC loading. Such a change would likely result in the re-structuring of phytoplankton communities (favouring mixotrophs) and would increase the relative importance of the microbial food chain as a conduit for energy flow to higher trophic levels. Ultimately, due to the energetic inefficiency of this pathway (Kankaala et al. 1996, Kankaala et al. 2010a), we may expect that the productivity of higher trophic levels (zooplankton, fish) could be affected as an unintended consequence of lake management. In addition, high levels of DOC loading are known to impose light-limitation upon phytoplankton and benthic algal communities (Jones et al. 2012). If, in humic systems, light is the primary limiting factor for phytoplankton growth then seeking to reduce primary producer biomass by cutting nutrient loads may not be as effective as anticipated.

In addition to the “traditional” focus on cutting external phosphorus loads to lakes of lower ecological status, measures to address internal phosphorus cycling are receiving increasing research attention (Spears et al. 2013). As yet, there is a need for a broad-scale assessment of the effectiveness and ecological implications of tackling internal phosphorus loading as a means of restoring lakes. However, it has been demonstrated that elevated concentrations of DOC may reduce the effectiveness of the phosphorus-binding chemicals that form the basis of these management techniques (Omoike and Vanloon 1999, Sonke and Salters 2006, Ross et al. 2008, Lüring and Faassen 2012).

Changes in lake DOC concentrations are also likely to have implications for more “top-down” management approaches i.e. biomanipulation via the trophic cascade (Carpenter and Kitchell 1993, Jeppesen et al. 2012). The effectiveness of this technique is contingent upon the intensity of planktivory, which impacts upon water quality/clarity by controlling the grazing pressure imposed by crustacean zooplankton. However, it has been suggested that the shading effects of elevated DOC concentrations may reduce the effectiveness of visual predation by fish and provide a more extensive dark predation-refuge for crustacean zooplankton (Wissel et al. 2003, see Section 2.4). In turn, this would suggest that high DOC concentrations could weaken top-down control on zooplankton grazers and thus may impact upon the strength of the trophic cascade, and the likelihood that manipulations to fish communities might be transmitted to phytoplankton and thus water clarity.

In addressing the implications of organic matter loading for lake restoration and management, there is a clear need to think beyond the physical boundaries of lake ecosystems and consider landscape scale processes, and the management decisions that impact upon them. Land use can have significant effects on the loading of organic matter to lakes. In order to understand these impacts it is therefore important to broaden the scope of scientific investigation to the catchment scale, including the stream network draining the catchment. Deforestation, agriculture and urbanization can alter the quantity and quality of organic matter inputs to running waters and receiving water bodies. For example, Kominoski and Rosemond (2012) suggest that organic matter resources should be taken into account during conservation and management planning for ecosystems along river networks, due to the recognised importance of organic matter for aquatic ecosystem structure and functioning.

4. Future directions

This review highlights the multi-faceted effects of organic matter loading upon complex lake ecosystems. Based upon the amassed literature, there are clear themes and issues that, currently, are not well understood and that should be considered as priorities for future research:

- *Evaluating the relative importance of organic matter quantity, quality and availability for recipient lake ecosystems.* Numerous studies have suggested the importance of allochthonous organic matter as source of energy to lake ecosystems. However consideration of organic matter retention within lakes, the nutritional quality of this material, and the inefficiency of relevant trophic pathways, have fuelled a debate over the extent to which this flux of material/energy represents a true ecosystem subsidy, and therefore increases ecosystem productivity. Future work is needed to resolve the quality and quantity aspects of organic matter loading, in order to develop a more generic understanding of the ecological contexts within which lake ecosystem productivity is, or is not, enhanced by inputs of allochthonous material. In the first instance, this could be addressed by developing a conceptual model of the role of organic matter subsidies along axes of lake size, clear water-humic water and dystrophy-eutrophy.
- *Understanding interactions between organic matter loading and other environmental pressures.* Organic matter clearly has many, diverse, effects on lake ecosystem structure and functioning. However, knowledge of these first-order effects may be insufficient to predict the future implications of altered organic matter loading, when this occurs at the same time as ongoing climate change and eutrophication. The potential for synergistic and antagonistic interactions between organic matter loading and other stressors, necessitates future experimental and modelling studies that will allow us to develop the mechanistic insight we need to project future ecological impacts.

- *Organic matter and lake restoration.* Currently, little is known of the likely implications of altered organic matter loading for the efficacy of lake restoration measures. There is an urgent need to investigate and test plausible restoration measures under different organic matter loading scenarios, as a means of providing this knowledge.
- *Organic matter and implications for lake management.* The issue of organic matter processing clearly demonstrates the presence of ecologically-important linkages between aquatic and terrestrial ecosystems. Furthermore, this review has shown that changes in the quantity and quality of this organic matter have numerous impacts upon lakes. Thus, land use induced changes in organic matter quality and quantity should be taken into account in decision-making processes concerning lakes and their catchments. Taking the fluxes of these organic matter resources into account is a prerequisite for successful lake management.
- *High resolution monitoring.* Process understanding will require data acquisition at the resolution of the relevant time-scales. Automatic monitoring stations on lakes are gaining popularity and provide data at sufficiently high resolution to improve understanding of the impact of changes in DOM. In particular, temperature profiles and sub-surface light measurements are relatively standard measured parameters on buoys and offer a treasure-trove of data at the correct resolution for resolving some of the outstanding issues involving in-water radiative effects on thermal structure, such as the extent and timing of changes in epilimnetic temperatures.
- *Comparing light-induced changes in euphotic and epilimnetic depths.* An increase in DOM is likely to shrink both the euphotic depth and the epilimnetic depth of a lake, but it is not clear how the ratio of the two will be affected. Determining under which environmental conditions the euphotic depth is impacted more than the epilimnetic depth will be crucial for unlocking the resultant impact on epilimnetic primary productivity.

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