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Food webs and biogeochemistry in freshwater systems

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Introduction

Early views of lakes as self-contained ecosystems have changed radically. Lakes (and rivers) are now viewed as integral components of a wider catchment-scale system. Delivery of nutrients, especially phosphorus (P), from catchments is well-established as a key process determining lake productivity and water quality. More recently, evidence has been accumulating that in more lakes than previously suspected productivity can be regulated by nitrogen (N) availability. However, it is important to recognise that the biogeochemical cycles of many of the key nutrients in lakes are closely coupled. For example, Finlay *et al*. (2013) showed how increased P inputs from human activities have stimulated N removal processes in many lakes. The corollary of this is that efforts to improve lake water quality by P removal will promote accumulation of N in the water column of lakes and its subsequent export. Hence alteration of one biogeochemical cycle can be expected to have ramifications in other, coupled cycles. Freshwaters are also now recognised to be strongly implicated in the global carbon (C) cycle, with one recent estimate of the global C emission from inland waters put at 2.1 $PgCyr^{-1}$, or greater than the transport of C from the continents to the oceans (Raymond *et al*. 2013). This emitted carbon derives both from degassing of CO_2 from supersaturated catchment drainage water entering lakes (e.g. Maberly *et al*. 2012) and from CO_2 produced by processing of organic carbon of terrestrial origin transported into lakes, but the balance between these mechanisms is still poorly understood. My focus here is on how loading of terrestrial organic matter to lakes can affect lake carbon fluxes through its impact on food webs, coupling terrestrial and aquatic carbon biogeochemical cycles.

A changing view of lake carbon fluxes

Accumulating evidence, especially from stable isotope studies, is showing how allochthonous (terrestrial) organic carbon can enter lake food webs, mainly via a microbial link between dissolved organic matter (DOM) and zooplankton (Fig. 1). Grey *et al*. (2001) used natural abundance stable, isotope analysis to show that around 40% of zooplankton carbon in Loch Ness could be traced to allochthonous carbon. To circumvent the frequent overlap of $\delta^{13}C$ signatures of autochthonous and allochthonous end members in lakes, some studies have used whole-lake tracer additions of ^{13}C-labelled bicarbonate to label the phytoplankton. Such studies have generally also shown an important contribution of allochthonous C to zooplankton consumers (e.g. Taipale *et al*. 2008), at least in moderately brownwater lakes. A whole-lake addition of cane sugar (from a C4 plant) to a small humic lake in southern Finland allowed the distinct $\delta^{13}C$ signature of the sugar-C to be traced into zooplankton and littoral zoobenthos, and

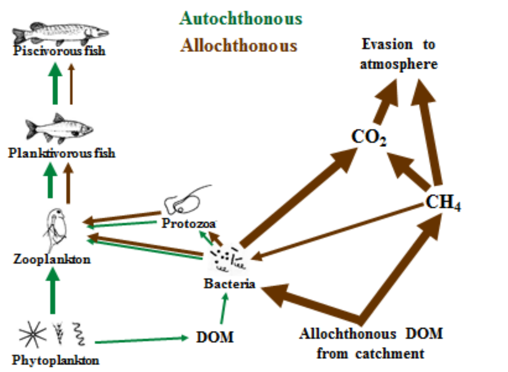

Fig.1. How allochthonous organic matter can contribute to lake food webs in parallel with autochthonous production. The magnitude of the contribution in different lake types is still contentious.

thence to fish, and suggested that around 20-30% of fish carbon in the lake could be derived from allochthonous C. However, the sugar addition produced a less than expected change in emissions of CO_2 from the lake (Peura *et al*. 2014), probably due to P and N availability constraining processing of DOM. This illustrates why efforts to understand likely impacts on lakes of increased transport of C from catchments as a predicted consequence of climate change will need to take into account the tight coupling between C, N and P cycles. Biogenic methane produced in the anaerobic sediments and hypolimnetic waters of lakes has also been identified as contributing widely to lake food webs (Jones & Grey 2011). Around 20% of ruffe carbon biomass in Lake Jyväsjärvi was traceable to biogenic methane (Ravinet *et al*. 2010). In some lakes, especially in the boreal zone, this biogenic methane may derive largely from allochthonous organic matter originating in the lake catchment.

Future studies

Ecological mechanisms can only properly be revealed and confirmed by experimentation. Ecological experiments have been conducted at various scales, offering a different balance between reliability and realism of the information produced (Fig. 2). Realistic and meaningful information regarding coupled biogeochemical cycles can probably only be obtained from experiments at the whole-ecosystem scale, but such experiments have been rare and the information obtained has generally been of low reliability, because of the very high costs of large-scale experiments and the difficulty of incorporating any true replication. Therefore researchers and funding agencies need to think big for the future. Well-designed whole-lake-catchment manipulation studies of coupled biogeochemical cycles that will yield reliable information are badly needed, but will require innovative approaches to funding if they are to receive the levels of resources necessary to underpin them properly.

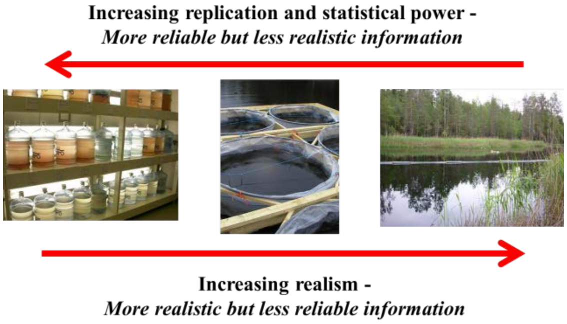

Fig.2. The balance between reliability and realism in experiments at different ecological scales..

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