Freshwater Biology

Freshwater Biology (2015) **60,** 439–442 doi:10.1111/fwb.12517

Consumer-driven nutrient dynamics in freshwater ecosystems: an introduction

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SUMMARY

1. Over the past decade, studies of the effects of consumer-driven nutrient dynamics have become more common. This work has demonstrated that animals can function as sources and sinks of elements, but few studies have broadly compared these processes among organisms and across ecosystems.

2. Collectively, the articles in this special issue elucidate the important roles that organisms can play in nutrient dynamics in lotic, lentic and wetland ecosystems. These papers show how species-specific traits, such as body stoichiometry and trophic ecology, and abiotic variables, including ambient water chemistry, govern the net impacts of consumer-driven nutrient dynamics in freshwater ecosystems.

3. Globally, the introduction of non-native species and the loss of native biodiversity compromise the functional integrity of freshwater ecosystems. The work featured in this issue will help ecologists and conservation biologists integrate species-specific traits with ecosystem-specific conditions to understand the potential effects of changing biodiversity on ecosystem function in fresh waters.

Keywords: biogeochemistry, conservation, consumers, ecological stoichiometry, fresh water

Introduction

Research in both terrestrial and aquatic ecosystems has demonstrated that animals can play integral roles in the storage and remineralisation of elements (Augustine & Mcnaughton, 2006; Vanni *et al.*, 2006; Vaughn, 2010; Coetsee, Stock & Craine, 2011). Such studies have shown the role of organisms is often species-specific and is influenced by biotic and abiotic environmental conditions (Mcintyre *et al.*, 2007; Benstead *et al.*, 2010). Throughout the globe, freshwater ecosystems are threatened by habitat modifications, non-native species invasions and the loss of native species (Dudgeon, 2010; Strayer & Dudgeon, 2010). To conserve the integrity of fresh waters and protect ecosystem function in systems threatened by species invasion and/or species extinction, it is imperative to understand the functional roles aquatic organisms play in ecosystem processes, such as nutrient dynamics.

Over the past decade, investigations documenting the functional role of consumers in biogeochemical processes have become more common. For example, many studies have considered the contribution of migrations of anadromous fish to nutrient dynamics in stream ecosystems (e.g., Walters, Barnes & Post, 2009; Holtgrieve & Schindler, 2011; Tiegs *et al.*, 2011). However, there are still fundamental questions about consumer-driven nutrient dynamics (CND) that need to be addressed. For instance, the potential ecosystem-level effects of nutrient remineralisation, transport and storage by small or elusive animals such as tadpoles or macroinvertebrates, or exceptionally large aquatic or semi-aquatic organisms, such as hippopotami are largely unknown. Similarly, few studies have quantitatively compared the relative importance of the various mechanisms by which animals affect nutrient cycling. For example, many studies on CND have focused on animals as sources of nutrients through excretion and nutrient sinks through growth; yet, few have considered how the immigration and emigration of consumers from fresh waters influences nutrient dynamics.

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Recent work has attempted to address the context dependence of species effects on biogeochemical cycling. For instance, work on Trinidadian guppies has shown that local environmental conditions can influence organismal stoichiometry, subsequently influencing the role of guppies on nutrient dynamics (El-Sabaawi *et al*., 2012a,b; Marshall *et al*., 2012). In addition, Benstead *et al.* (2010) documented the importance of both water flow and organismal biomass in influencing the contribution of freshwater shrimp to ambient nutrient concentrations in tropical streams. As a whole, this research demonstrates the ecosystem-level impact of consumer-driven nutrient dynamics is taxon specific and strongly influenced by environmental variables. However, the number of studies quantifying the ecosystem-level impacts of CND in fresh waters is limited.

Scientists and natural resource managers are challenged to find commonalities in CND across taxa and ecosystems in diverse geographical areas. The collection of studies included in this special issue arose from special sessions organised at the 2012 and 2013 meetings of the Society for Freshwater Science and the 2012 meeting of the Ecological Society of America (Capps *et al*., 2012). These sessions had three purposes. First, we wanted to highlight the influence of a wide variety of taxa from geographically diverse areas on biogeochemical cycles in a range of aquatic habitats. Second, we asked authors to directly link CND with changes in community structure and ecosystem function. Third, we challenged participants to examine their work through a comparative lens in an attempt to synthesise patterns in CND across organisms and systems.

Themes in this special issue

In this special issue, we have included research that addresses the biotic and abiotic factors that influence CND and the ecosystem characteristics that determine whether CND is important at larger spatial scales in freshwater ecosystems. Together, the articles here emphasise the important role aquatic organisms can play in nutrient dynamics in lotic, lentic and wetland ecosystems. They elucidate the effect of organism-specific traits, such as body stoichiometry and trophic ecology, on the net impacts of CND in fresh waters. The papers also emphasise the influence of abiotic factors, such as ambient nutrient concentrations and stream discharge, on the net effects of consumers on biogeochemical cycles.

A suite of the manuscripts included in the special issue emphasises, from both ecological and evolutionary perspectives, the influence of species-specific traits on the role organisms play in nutrient dynamics. For example, a few of the papers address stoichiometric flexibility in consumers and how this influences diet choice and remineralisation stoichiometry (e.g., Halvorson *et al*., 2015; Moody *et al*., 2015; Snyder, Small & Pringle, 2015). Additionally, work featured in this issue reports how species traits and trophic ecology influence the role aquatic organisms play nutrient cycling (e.g., El-Sabaawi *et al*., 2015; Sterrett & Maerz, 2015). Finally, papers here highlight the influence of consumer ontogeny on the net flux of elements (e.g., Capps, Berven & Tiegs, 2015; Snyder *et al*., 2015).

Another common theme is the ability of freshwater consumers to transport large quantities of materials across ecosystem boundaries. For instance, Childress & Mcintyre (2015) measured the transport of elements from a lake into a tributary by excretion and egg deposition by a freshwater fish. Similarly, Subalusky *et al.* (2015) documented the important role hippopotami play in transporting nutrients from the savannah to rivers in the Serengeti.

Work in this issue highlights the importance of spatial and temporal scaling of remineralisation and storage stoichiometry in CND. Many of the study sites experienced pronounced wet and dry seasons, and the authors discussed the impact of this seasonality on the functional role of aquatic organisms in nutrient dynamics (e.g., Atkinson & Vaughn, 2015; Rantala *et al*., 2015). Additionally, this special issue emphasises the importance of using long-term data sets to document interannual variability in the flux of elements and the ecosystem response to CND in fresh waters (Capps *et al*., 2015; Rantala *et al*., 2015; Subalusky *et al*., 2015).

Many of the papers in this issue integrate the role of consumers in ecosystem processes with abiotic environmental conditions. For example, Wheeler, Miller & Crowl (2015) and Atkinson & Vaughn (2015) directly addressed the effects of stream discharge on the roles of fish and mussel excretion on ecosystem processes in streams. Ambient nutrient concentrations may also influence the role organisms play in ecosystem processes (Wilson & Xenopoulos, 2011; Spooner *et al*., 2013). In this issue, Datri *et al.* (2015) and Snyder *et al.* (2015) presented work addressing the synergistic effects of aquatic consumers and ambient nutrient concentrations on biogeochemical cycling. Additionally, Boros, Talacs & Vanni (2015) examined the abiotic conditions under which consumers function as sources or sinks of elements in fresh waters.

Potential impact of this special issue

One of the great challenges in ecology and conservation biology is the preservation of ecosystem function in the wake of habitat loss and changes in biodiversity. In ecosystems subject to rapid anthropogenic change, including many fresh waters, it is difficult to employ theory to predict how ecosystem processes will be affected (Woodward, 2009). Freshwater animals directly affect biogeochemical processes by remineralising nutrients through waste production and by sequestering nutrients in body tissues (Vanni, Boros & Mcintyre, 2013); therefore, changes in native species abundance and biodiversity could strongly influence nutrient dynamics (Strayer, 2014). Declines in native freshwater biodiversity far exceed those in most terrestrial ecosystems due to a combination of interacting factors including excess nutrients and sediments, flow alterations and climate change. Moreover, predictions suggest the rate of species decline will increase through time (Strayer & Dudgeon, 2010; Vaughn, 2010). Freshwater biodiversity and ecosystem function are also are threatened by the growing number of non-native species introductions (Strayer, 2010). Many CND studies have documented the important role a single species can play in biogeochemical dynamics in fresh waters (e.g., Flecker, 1996) and more recent work (e.g., Whiles *et al.*, 2013), including some of the work in this special issue (e.g., Rantala *et al.*, 2015) demonstrates how changes in the abundance and diversity of consumers can alter nutrient dynamics. The introduction or extirpation of suites of organisms to or from an ecosystem has the potential to alter CND even more than changes resulting from the loss or addition of a single species (Capps, Atkinson & Rugenski, 2015).

Scientists are challenged to quantify how environmental change may affect CND in fresh waters to predict changes in ecosystem function in response to altered species abundance and diversity. Work in this special issue discusses the potential effects of water withdrawals (Atkinson & Vaughn, 2015), dam construction (Childress & Mcintyre, 2015), non-native species invasion (Datri *et al.*, 2015) and land use change (Capps, Berven & Tiegs 2015), on CND in a variety of freshwater ecosystems. Additionally, Rantala *et al.* (2015) explicitly addressed changes in ecosystem function after amphibian declines due to the introduction of chytrid fungus, a global conservation challenge. The large body of CND research suggests that environmental change can alter the functional role of individual species and entire communities of organisms in ecosystem-level nutrient dynamics. Thus, being able to realistically scale up from individual CND to ecosystem processes is critical to preserving the functional integrity of fresh waters.

Acknowledgments

We thank Mike Vanni, Alex Flecker, Caryn Vaughn and Matt Whiles for their advice and support developing ideas that supported our graduate research, our initial collaboration in research on consumer-driven nutrient dynamics and the development of the special sessions that led to this special issue; they are all wonderful mentors. We thank all of the authors who contributed to the special sessions at the Ecological Society of America and the Society for Freshwater Science and those who contributed to this special issue. We appreciate the rapid response time and wonderful support of Penny Wallis in coordinating this special issue. Finally, we thank Dave Strayer for his insightful comments, for his seemingly endless patience and for giving us this wonderful opportunity.

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(Manuscript accepted 3 November 2014)