

The role of mobile consumers in lake nutrient cycles: a brief review

Simon D. Stewart  · David P. Hamilton · W. Troy Baisden · Piet Verburg · Ian C. Duggan

Received: 9 November 2017 / Revised: 9 March 2018 / Accepted: 27 March 2018 / Published online: 4 April 2018
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Abstract We summarise current understanding of consumer recycling in lake nutrient cycles and expand on it by integrating emerging knowledge from food web ecology. The role of consumer nutrient recycling (CNR) is initially framed in the wider context of lake nutrient cycling, which includes hydrodynamic and biogeochemical processes, and their responses to global environmental change. Case studies are used to demonstrate that effects of CNR on lake ecosystems range widely, from reduced nutrient cycling rates to exacerbation of eutrophication. CNR depends on consumer biomass, body size and diet, remaining relatively consistent through the year and becoming important as other fluxes seasonally ebb. Universal patterns in food web structure, for example,

consumer–resource biomass ratios, body size scaling and relationships between trophic level and diet breadth, are used to demonstrate the predictability of CNR effects. Larger, mobile, top predators excrete nutrients at a lower rate but over a wider range, linking nutrient cycles across habitats. Smaller-bodied, lower trophic level consumers have strong localised nutrient cycling effects associated with their limited mobility. Global environmental-change drivers that alter food web structure are likely to have the greatest impact on CNR rates and should direct future studies.

Keywords Food web · Recycling · Excretion · Body size · Biomass · Littoral pelagic coupling

Handling editor: Karl E. Havens

S. D. Stewart (✉) · D. P. Hamilton · I. C. Duggan
School of Science, University of Waikato, Hamilton 3225,
New Zealand
e-mail: simondstewart@hotmail.com

D. P. Hamilton
Rivers Institute, Griffith University, Queensland,
Australia

W. T. Baisden
National Isotope Centre, GNS Science, Lower Hutt 5010,
New Zealand

P. Verburg
NIWA Ltd, Gate 9 Silverdale Rd, Hamilton 3225, New
Zealand

Introduction

Nutrient cycling is a critical processes governing ecosystem function in lakes (Vitousek et al., 1997; Carpenter et al., 2011). It mediates the eutrophication from catchment nutrient inputs and determines the extent of productivity available to higher trophic levels (Smith & Schindler, 2009; Moss, 2012). Arguably eutrophication represents the most pressing challenge to the stability of lake ecosystems (Carpenter et al., 2011; Steffen et al. 2015) and, accordingly, nutrient cycling has received substantial research attention in limnology for over 60 years. This has resulted in catchment (Hamilton et al., 2016), physical

hydrodynamic (Boehrer & Schultze, 2008), and microbial biogeochemical processes (White et al., 1991; Cotner & Biddanda, 2002; Fenchel, 2008) being integrated into nutrient cycling models. This integration has substantially improved the understanding of nutrient cycling in lakes, particularly through demonstrating interactive effects between processes (Lewis, 2010; Moss, 2012). Interactive effects have demonstrated that rapid threshold changes in nutrient supply can occur with small environmental changes which affect multiple processes (Scheffer & Carpenter 2003; Rockström et al. 2009). For example, in deep lakes, climatic and catchment drivers can interact with hydrodynamic and biogeochemical processes resulting in hypolimnetic anoxia and strongly elevated sediment nutrient releases (Lehmann et al., 2015; Jenny et al., 2015). However, the drivers of change in nutrient cycling rates, particularly for oligotrophic lakes, remain uncertain (Lewis, 2010; Moss, 2012). There are still critical processes which enhance understanding of drivers of temporal and spatial variation in nutrient cycling rates that have not yet been integrated into lake nutrient cycling models.

Consumer nutrient cycling (CNR), the role of large mobile consumers on nutrient cycles, is one such area that is yet to be integrated into lake nutrient models. Microbial biogeochemical cycling is the dominant mechanism for regenerating bioavailable nutrients (White et al., 1991; Cotner & Biddanda, 2002; Fenchel, 2008), however, a growing number of case studies have demonstrated that mobile consumer recycling can also have a significant effect on nutrient cycles (He et al., 1993; Schindler et al., 1993; Vanni & Layne, 1997; Attayde & Hansson, 2001; Vanni et al., 2006). Specifically, the ability of many larger consumers to move between habitats (Vanni et al., 2006; Baustian et al., 2014) paired with long (generally > 1 year) consumer life cycles (Shostell & Bukaveckas, 2004), impacts nutrient cycling through displacement of nutrients in time and space. Despite the substantial impact of consumer nutrient recycling (CNR) on nutrient cycles at a lake ecosystem scale (Carpenter et al., 1987, 1992; Allgeier et al., 2017), there is no general conceptual framework for understanding the role of CNR. Food web theory has been used to understand the dynamics of consumer communities with particular reference to factors controlling biomass fluctuations (Thompson et al., 2012; Barraquand et al., 2017). Applying food web theory to

understanding CNR may provide clarity on the contribution of this process to lake nutrient cycles.

Recent developments in food web ecology show general, scalable patterns of food web structure which have the potential to elucidate the role of CNR. Food web research as a whole has focused heavily on the role of complexity in providing resilience to external stressors and how internal feedbacks can drive fluctuations (Layman et al., 2015; Barraquand et al., 2017). Attempts to describe complexity have identified common patterns across a diverse range of food web structures. For example, the number and strength of consumer–resource trophic links have been associated with important food web attributes such as productivity (Neutel et al., 2007), stability (McCann et al., 1998) and top-predator abundance (Estes et al., 2011). This approach has led to ‘rules of thumb’ for scaling across biomes, which enables ecosystem function to be predicted from observations of food web architecture (Thompson et al., 2012). These scaling rules can be extended to better understand how food web structure impacts nutrient cycles via CNR (Thompson et al., 2012; Layman et al., 2015).

Food web structure can affect the magnitude of CNR fluxes and the availability of nutrients for primary producers (Carpenter et al., 1992; He et al. 1993; Vanni et al., 2013; Higgins et al., 2014). Integrating current food web knowledge with CNR-mediated processes may provide a mechanism for identifying and mitigating nonlinear threshold responses. Most of the focus of critical threshold responses to date has been on nonlinear primary productivity responses, establishing the concepts of alternate states or regime shifts of the dominant primary producers (Carpenter, 2003; Scheffer et al. 2001; Angeler & Allen, 2016) and the resultant changes in phytoplankton biomass (Carpenter, 2003). The effect on, and responses of, mobile CNR have received substantially less attention (Carpenter et al., 1992; Sterner, 2008).

An approach of drawing on food web science could promote ecosystem-based lake and fisheries management to complement the current nutrient management paradigm. The aim of this review is therefore to synthesise emerging concepts from food web ecology in order to promote integration of CNR into assessments of nutrient cycling at whole-lake scale. The review covers:

- (1) a brief examination of contemporary understanding of the roles of hydrodynamic and microbial biogeochemical processes in lake nutrient cycles;
- (2) a review of current literature on mobile CNR;
- (3) a summary of emergent macro-scale patterns in lake food web ecology;
- (4) application of common patterns in food web ecology that inform CNR; and
- (5) discussion and comparison of the factors driving critical nutrient responses to hydrodynamic, biogeochemical and CNR processes.

Current concepts of lake nutrient cycling

Historically, progress in understanding primary productivity responses to nutrients in lakes can be viewed as “demystifying the black box” (Fig. 1). At an elementary level, the earliest workers regarded lakes as largely closed systems independent of their terrestrial environment (Forbes, 1887). The advent of cultural eutrophication (Valentine, 1974) provided an underlying impetus to connect lake responses to changes in catchment nutrient loads. This environmental phenomenon was fundamental to the development of catchment nutrient load models (e.g. OECD, 1982). Interest in the time-varying responses of lakes, particularly connected to seasonal mixing-stratification cycles (Imberger & Patterson, 1990), led to focus on how nutrients are transported within lakes (Bohrer & Schultze, 2008). Food web responses add a further

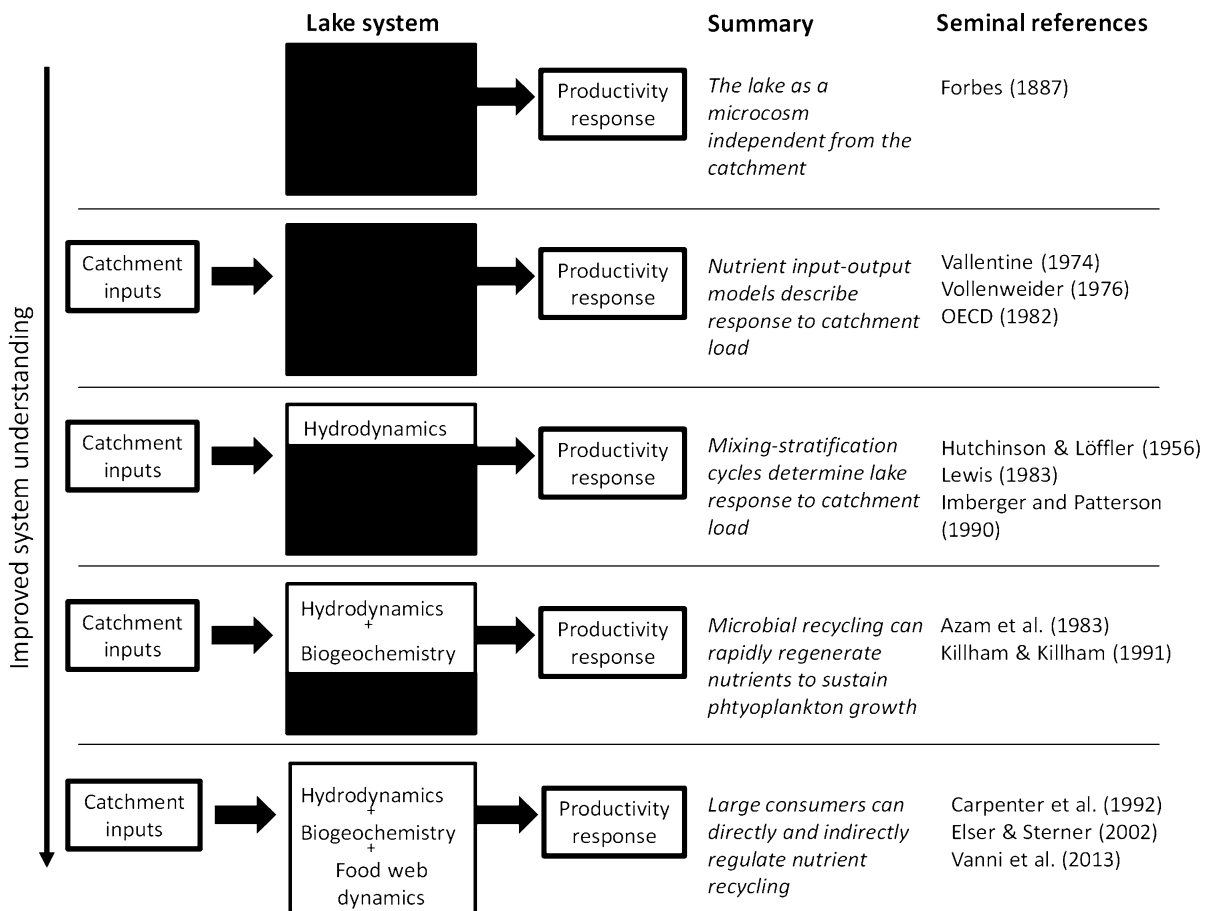


Fig. 1 “Demystifying the black box” of lake responses to nutrient inputs based on progression in the understanding of the controls on lake nutrient cycling. Seminal papers are listed against major advances

layer of complexity, but are necessary to understand ecological responses to changing catchment nutrient loads (Sommer et al., 2012; Allgeier et al., 2017). Such responses are yet to be integrated into dynamic lake system models to the resolution that has been achieved for hydrodynamic or biogeochemical processes (Fussmann, 2008; Hellweger, 2017).

Controls on nutrient cycling have traditionally been viewed as hierarchical, predominantly from catchment loads down to in-lake hydrodynamic processes (Valentine, 1974; Boehrer & Schultze, 2008), but there has been increasing recognition of the role of recycling, which cuts across this hierarchy at multiple levels, from microbial transformations through to higher levels in the food web. In this context, broad generalisations of the relative importance of the different controls are less easily generalised due to geographical, morphological and ecological variations amongst lakes. For example, physical mixing has a greater role in nutrient supply for lakes closer to the poles, whilst biogeochemical cycling is relatively more important in equatorial lakes (Kilham & Kilham, 1990; Lewis, 2010). Figure 1 shows the trajectory that studies into lake hydrodynamics and biogeochemistry have taken; there is a vast amount of accumulated knowledge and current research on these topics. We provide brief contemporary summaries on these two topics to lay a foundation for a review of CNR in lakes and to prepare for changes expected under global environmental change.

Hydrodynamic-mediated nutrient cycling

Turbulent mixing processes operate over a wide range of scales, from entire lakes (e.g. basin-scale seiching; Antenucci & Imberger, 2001) to millimetres (e.g. Kolmogorov scale; Wüest & Lorke, 2003). Here we focus on thermal stratification and other large-scale processes. The periodicity of complete water column mixing (i.e. frequency of mixis), as well as trophic state, are the most common ways in which lakes are characterised. Water column mixing allows oxygen-rich surface water to be transported to profundal habitats and reintroduces nutrients which have accumulated in the hypolimnion into surface waters. Thermal stratification hinders mixing between surface and bottom waters. Particulate material that is denser than water sinks rapidly under the prevailing density gradient and nutrients recycled from this material

accumulate in bottom waters. The mixing of bottom waters and surface waters in stratified lakes can be a significant nutrient input into the surface trophogenic zone, and stimulates production (O'Reilly et al., 2003; Verburg et al., 2003; Boehrer & Schultze, 2008). Complete water column mixing (i.e. redistribution of nutrients through the lake volume) may alleviate phytoplankton nutrient limitation and can be associated with an annual peak of phytoplankton production in some temperate (Vincent, 1983) and many tropical lakes (Lewis, 1996, 2010), whilst in other lakes it may be associated with the annual minimum of production (Boehrer & Schultze, 2008; Sommer et al., 2012). Winter mixing regulates primary production by reducing nutrient limitation through redistribution of nutrients accumulated in bottom waters and altering light limitation by changing the ratio of euphotic depth to mixed depth (Vincent, 1983). Localised introductions from the hypolimnion into trophogenic waters, in the absence of complete mixing, can alleviate nutrient limitation, albeit temporarily, even in the presence of strong stratification. Upwelling events that introduce hypolimnetic water into near-shore littoral zones may be associated with wind-derived currents (Bocaniov et al., 2014) or more generally with large-scale and small-scale turbulence (Boehrer & Schultze, 2008; MacIntyre et al., 2009) driving substantially elevated littoral production (Corman et al., 2010). Similarly, shallow littoral areas may show strong diurnal gradients in temperature which can drive vertical exchange with metalimnetic waters or horizontal exchange with offshore pelagic waters (Monismith et al., 1990; Boehrer & Schultze, 2008).

Hydrodynamic responses to global environmental-change drivers

Most physical transport mechanisms are extremely sensitive to climate warming (Boehrer & Schultze, 2008; Adrian et al., 2010; Kraemer et al., 2015). Warmer air temperatures increase the energy accumulated in the surface waters of lakes and result in prolonged and stronger thermal stratification. This may ultimately lead to incomplete mixing of monomictic or dimictic lakes that currently mix fully on annual cycles (Adrian et al., 2010; Sahoo et al., 2016) and lead to some polymictic lakes becoming persistently stratified on seasonal time scales (Kraemer et al., 2015). Prolonged climate-induced

stratification has been linked to changes in the timing of autumn blooms in Lake Washington (Winder & Schindler, 2004) and reduced pelagic productivity in Lake Tanganyika (O'Reilly et al., 2003; Verburg et al., 2003). A predicted stronger thermocline in Lake Tanganyika, due to climate warming, is expected to also reduce the magnitude of upwelling into the littoral zone and reduce the observed remarkably high rates of littoral production (Corman et al., 2010). In temperate and arctic lakes, a reduction in periods of weak stratification has been linked to reductions in the frequency of pelagic upwelling events (Bocaniov et al., 2014; Pöschke et al., 2015; Troitskaya et al., 2015). Whether climate warming ultimately increases or decreases productivity may be highly lake specific and could also have strong seasonality (O'Reilly et al., 2015). For example, prolonged stratification could potentially eliminate seasonal overturn events in some large lakes whilst reducing upwelling events in most lakes. Reduced upwelling would be expected to reduce productivity, but could also fuel increased productivity at overturn in association with prolonged build-up of nutrients in the hypolimnion, especially if upwelling brought about extended periods of anoxia and large sediment nutrient releases (Sahoo et al., 2016).

Biogeochemical nutrient cycling mediated by the microbial loop

Microbial recycling is the primary mechanism for regenerating nutrients from organic matter (Paerl & Pinckney, 1996; Cotner & Biddanda, 2002). Bacteria and protozoa adhere to and metabolise detrital particles, releasing dissolved nutrients for uptake by primary producers (Paerl & Pinckney, 1996; Biddanda et al., 2001; Fenchel, 2008). Free-living microbes also metabolise dissolved organic nutrients which would otherwise be unavailable to primary producers. In lakes, most microbial nutrient recycling occurs in the benthos where organic matter accumulates (Moss, 2012; Jenny et al., 2016). During periods of stratification this typically results in recycled nutrients accumulating below the thermocline (O'Reilly et al., 2003; Verburg et al., 2003; Lehmann et al., 2015). By contrast, where microbial metabolism of organic particles or dissolved organic matter occurs above the thermocline, nutrients are likely to be retained within the trophogenic zone, leading to tight coupling of productivity to microbial mineralisation (Kilham &

Kilham, 1990). The importance of microbial cycling to productivity varies substantially amongst lakes and is partly associated with the balance of bottom-up and top-down regulation of productivity (Ptacnik et al., 2010).

While top-down control of productivity by heterotrophic microbial communities has traditionally been considered a minor structuring effect, there is growing recognition of strong interactions amongst microbial communities (Beisner, 2001; Ptacnik et al., 2010). Environmental filtering (bottom-up control of community composition) is a dominant structuring mechanism (Beisner et al., 2006), but other mechanisms typical of macrofaunal communities, such as predator–prey interactions and competition (Ptacnik et al., 2014), are also present in microbial communities. These interactions can directly impact rates of nutrient cycling. For example, nitrification may be regulated by microbial predation (Lavrentyev et al., 1997). Top-down control of heterotrophic bacteria by predatory protozoa has also been shown to inhibit phytoplankton growth due to reduced nutrient availability (Steiner et al., 2005; Li & Stevens, 2010; Ptacnik et al., 2010). The composition of microbial communities in lakes therefore affects rates of nutrient recycling and primary production.

Bottom-up control of microbial processes is primarily due to temperature and nutrient availability (Cotner & Biddanda, 2002). Microbial metabolism increases with temperature, and nutrient recycling rates are correspondingly higher towards the equator (Lewis, 2010). Microbial growth rates also increase with nutrient availability, whilst maintenance costs, which increase with mismatch between food resource quality and nutritional requirements, decrease (White et al., 1991). Microbial communities in nutrient-rich lakes, especially those in lakes of warmer regions, are therefore able to convert a greater proportion of their nutrient intake into biomass than those in nutrient-depauperate lakes.

Biogeochemical responses to global environmental-change drivers

Strong temperature control on microbial metabolism suggests that microbial communities will be sensitive to climate warming (Paerl & Pinckney, 1996; Carey et al., 2012; Amado et al., 2013). Observed latitudinal patterns in microbial metabolism and phytoplankton

community composition have been the primary basis for projected biogeochemical responses to warming. Higher microbial recycling rates are observed in lower latitude—warmer lakes (Kilham & Kilham, 1990; Lewis, 2010; Amado et al., 2013). Within phytoplankton communities, heat-tolerant cyanobacteria are present in higher proportions than eukaryotic phytoplankton in tropical lakes compared with temperate lakes (Kilham & Kilham, 1990; Lewis, 2010). Abundance of cyanobacteria is expected to increase in lakes globally as a result of climate warming, particularly in temperate lakes (Carey et al., 2012; O’Neil et al., 2012; Paerl & Huisman 2008). Changes in phytoplankton communities and higher overall growth rates of phytoplankton are expected to increase the strength of nutrient cycling interactions between microbial heterotrophs and phytoplankton under climate warming (Lewis, 2010). Recent laboratory experiments demonstrate that phytoplankton N demands increase with temperature faster than P demands (Thrane et al., 2017), suggesting that microbial-phytoplankton N cycling interactions will be more sensitive to warming than for P cycling.

The impact of climate warming on top-down controls on microbial nutrient recycling has received relatively little attention. Top-down effects on microbial nutrient recycling would be expected to change in a nonlinear way if distinct heterotrophic microbial functional groups had different responses to warming (Sentis et al., 2017). There is, however, little empirical evidence that supports this hypothesis. Microbial top-down effects, and responses to environmental variation, are likely to mimic macrofauna responses (i.e. predator–prey dynamics) (Ptacnik et al., 2010). Hence, an improved understanding of macrofaunal CNR may also inform microbial processes.

Mobile consumer nutrient recycling

Based on two ecological principles, mobile consumers are often considered to have insignificant effects on nutrient recycling compared with microbial consumers. The first principle is that biomass of consumer species in an ecosystem is invariably negatively related to average species’ body size (Cohen et al., 2003) and therefore microbial consumers will dominate biomass within lakes (Cotner & Biddanda, 2002). The second is that metabolic rate scales negatively

with body size (Brown et al., 2004; Hall et al., 2007; McIntyre et al., 2008). Per unit biomass, therefore, small-bodied consumers will excrete more than large-bodied consumers (Hall et al., 2007). However, large mobile consumers have several traits that can have considerable effects on lake nutrient cycles. These traits include: the ability to move rapidly between spatially distinct habitats; lifespans of greater duration than seasonal fluctuations in nutrient supply; and the potential to control the distribution and biomass of lower trophic levels. Large reductions in ecosystem productivity due to loss of spawning salmonid-derived nutrients observed in many boreal freshwater ecosystems (Wipfli et al., 2007) highlight the importance of considering large mobile consumers, and their traits, for understanding nutrient cycles.

Translocation of nutrients through CNR

The role of animal excretion in transporting nutrients between spatially separate ecosystem habitats is well documented empirically (Vanni & McIntyre, 2016). Here we describe several examples involving lakes spanning a range of trophic states (oligotrophic to hypertrophic), where fish couple benthic and pelagic nutrient cycles. Benthivorous fish excretion can supply nutrients for primary producers in the pelagic zone (Vadeboncoeur et al., 2002; Vanni et al., 2005; Sereda et al., 2008). Excretion by the benthic-feeding gizzard shad [*Dorosoma cepedianum* (Lesueur, 1818)] can more than meet the pelagic phytoplankton P demand, exacerbating eutrophication driven by catchment nutrient loads (Vanni et al., 2006). Fish, by transporting nutrient into areas, have been shown to have higher rates of primary production than areas without fish (McIntyre et al., 2008). The lack of mobility, on the other hand, of sessile freshwater mussels (Spooner et al., 2013) and gardening caddis flies (larvae that actively maintain and defend a territory of benthic substrate; Ings et al., 2017) has been shown to increase recycling; subsequently increasing the biomass and diversity of benthic algae.

The enhancement of primary production accounted for by CNR depends on the biomass, feeding strategy (e.g. filter or benthic feeders) and diet composition of mobile consumers, as well as the nutrient demand of the primary producers. A larger standing stock of fish will naturally mobilise more nutrients (Schindler et al., 1993), benthivorous-feeding fish are typically a larger

net source of nutrients for pelagic primary producers than pelagic feeding fish (Vanni et al., 2013), and impacts on primary producers of consumer recycling will be greatest in low-nutrient systems (Carpenter et al., 1992). It follows that CNR has been implicated as one of the mechanisms by which bottom-feeding benthivorous fish act as a catalyst for tipping lakes from clear, macrophyte dominated states to turbid, phytoplankton dominated states (Søndergaard et al. 2007, 2017).

Temporal variations of CNR

Temporal variability of nutrient supply can determine primary producer community composition (Lagus et al., 2007; Oliver et al., 2012). Through mediating periodicity of nutrient pulses, CNR also has significant impacts on community composition (Weber & Brown, 2013). Biomass, distribution and persistence of microbial and micro-invertebrate consumers in lakes typically vary substantially over an annual cycle due to changes in resource supply (Sommer et al., 2012). Large-bodied consumers, however, can persist over multiple seasons despite such resource variations (McMeans et al., 2015). Excretion by larger consumers can therefore be a significant source of nutrients during low-nutrient periods. Shostell & Bukaveckas (2004) demonstrated that, in a eutrophic reservoir, consumer recycling became the primary source of pelagic nutrients during periods when catchment nutrient loads were reduced. Demand for consumer derived nutrients by pelagic primary producers is greatest when nutrients are most scarce, such as during late summer in deep lakes after prolonged stratification (Carpenter et al., 1987; Carpenter et al., 1992). Similarly, vertical migration of zooplankton, and their excretion in the surface layer at night, may have the greatest impact on pelagic primary productivity not necessarily when zooplankton biomass is greatest but when pelagic nutrient availability is very low (Baustian et al., 2014). Over long (e.g. annual) time scales, recycling by macrofaunal consumers can exceed that by microbial consumers (Attayde & Hansson, 2001) because the biomasses of smaller-bodied, lower trophic level organisms reduce at a much faster rate than that of larger-bodied higher trophic level organisms in response to resource depletion. The consumer traits most influential on recycling, wide foraging range and long lifespans, are inherently

related to consumer body size (McCann et al., 2005; McMeans et al., 2015).

Top-down effects on nutrient recycling

Consumers are able to alter nutrient recycling indirectly through two mechanisms; firstly, through in the relation between body size and metabolism, and secondly, through consumer–resource N:P stoichiometric mismatches. Replacing smaller-bodied consumers by large consumers will reduce community-level metabolic rates and nutrient recycling rates (Hall et al., 2007). In lakes, as for many other aquatic ecosystems, body size strongly correlates with trophic position (i.e. size structured food web) (McCann et al., 2005; Blanchard et al., 2010; DeLong et al., 2015). Top predators tend to be large bodied, whilst primary consumers are small bodied. Hence, the introduction of a top predator could be expected to reduce the biomass of small-bodied consumers. An increase in mean consumer body size would decrease ecosystem metabolism and nutrient excretion. The effect on nutrient cycling of changes in mean consumer body size has been documented in case studies of introduction or removal of species and the subsequent ecosystem response. Schindler et al. (1993) demonstrated that introduction of an invertebrate planktivore (*Chaoborus* sp.) into a lake food web where larger-bodied fish were previously the dominant planktivore, increased the rate of phosphorus recycling. Similarly, proliferation of invasive filter feeding dreissenid mussels [*Dreissena polymorpha* (Pallas, 1771) and *D. bugensis* Andrusov, 1897] in the Great Lakes has drastically increased the mean body size of the filter feeding primary consumer biomass, which was previously dominated by smaller bodied crustaceans (Higgins et al., 2014). The resultant reduction in nutrient recycling rates, as well as low predation rates on the mussels, has reduced the phosphorus availability to phytoplankton and decreased productivity at the lake ecosystem scale (Conroy et al., 2005).

Stoichiometric effects

Variations in the relative excretion rates of N and P by consumers can influence phytoplankton growth responses depending on stoichiometry of the phytoplankton demand (Elser et al., 2000). Stoichiometry of consumer excretion is the result of the N:P ratios in

consumer diet, as well as specific turnover rates of N and P. Inter-specific differences in N and P requirements arise because various tissue types have distinct N and P compositions. Protein, the largest N pool in organisms, largely controls N excretion rates (Hall et al., 2007; Vanni et al., 2013) along with body size (i.e. a metabolic control) (Houlihan, 1991; Hall et al., 2007). Structural and armouring tissue (i.e. bone and scales) is P-rich, and can be a strong predictor of P requirements of an organism, whilst ATP and RNA are the largest labile P pools in consumers (Vanni et al., 2013). Requirements for P increase during periods of rapid growth because tissue growth requires increased RNA production (Elser et al., 2003). A mismatch in N:P composition between the consumer diet and body tissue will enhance the excretion of the nutrient in excess and reduce the excretion of the under-supplied nutrient. Cladoceran zooplankton generally have lower N:P ratios and greater P demand than copepods, resulting in an increase in water column N:P when cladocerans dominate (McCarthy and Irvine, 2010; Sterner & Elser, 2002). Fish predation of cladocerans can, in turn, increase phytoplankton production in P-limited systems by promoting higher P recycling rates (Sterner & Elser, 2002).

The examples presented above demonstrate mechanisms by which the size of mobile consumers can have a substantial influence on lake nutrient cycles. However, few quantitative estimates of CNR are available to validate these mechanisms. Nonetheless, these independent lines of research show that variation in CNR is regulated by the interactions between the consumers in the lake. Understanding trophic interactions (i.e. food web dynamics) within a food web may improve the integration of CNR into lake nutrient dynamics.

Synthesising macro-scale patterns in lake food web ecology

Food web research is a diverse field but two areas emerge where there has been rapid development. These are, firstly, general scaling relationships for biomass, body size and metabolism, and second, patterns in the structure of trophic interactions. Concepts adapted from these two research themes have been important in developing an understanding

of food web structural and functional traits (Layman et al., 2015).

Trophic level, biomass and body size scaling relationships

Developing general scaling relationships in food web ecology has been assisted by access to multiple food web datasets from around the world (Cohen et al., 2003; Cebrian, 2015; Hatton et al., 2015). The resulting relationships have reinforced Kleiber's law that metabolism scales to the $-3/4$ power of body size (Brown et al., 2004). Given that excretion rates, in particular those of nitrogen (Houlihan, 1991), are primarily driven by metabolism, these relationships can be used to infer nutrient excretion rates from body size. As such, Hall et al. (2007) demonstrated that N excretion rates approximated a $-3/4$ power relationship with body size based on a diverse range of freshwater taxa. Given that higher trophic level consumers are typically larger bodied, metabolism would logically decrease with trophic level.

Biomass of predators and their prey typically scale in a universal manner (McCann et al., 2005). This was recently formalised by showing that predator biomass scales to a $-3/4$ power of prey biomass across a diverse range of ecosystems (Hatton et al., 2015). The value of the exponent (K), however, varies amongst major ecosystem types. When expressed in log–log terms, the ratio of predator to prey biomass for lake food webs was on average 0.68 (Hatton et al., 2015). A large biomass of predators relative to prey is indicative of strong top-down control within a food web (Vadeboncoeur et al., 2005; Casini et al., 2009; DeLong et al., 2015). Through time, K can vary as a response to cycles in predator–prey dynamics and associated biomass oscillations (Barraquand et al., 2017). Food webs that tend to demonstrate higher average K values (e.g. for pelagic planktivores) are assumed to have high productivity, despite relatively low producer biomass, and are often vulnerable to perturbations (Vadeboncoeur et al., 2005; Casini et al., 2009).

Body size also scales predictably between predators and prey (McCann et al., 2005; Brose et al., 2006). Averaged across a range of ecosystems, the exponent (M) for this relationship is 1.16 and not significantly different between major ecosystems (i.e. freshwater marine and terrestrial). The exponent varies between

invertebrates and vertebrate ectotherms (fish) predators, however, with average values of 4.15 and 0.96 for fish and invertebrates, respectively; this predator-type effect varies between aquatic and terrestrial ecosystems (Brose et al., 2006). Predator–prey body–size ratios have an important role in structuring food webs, and ratios have consistently increased over the last 500×10^6 years (Klompaker et al., 2017). Greater predator–prey body–size ratios are associated with a greater number of prey species in a predator’s diet (Petchey et al., 2008). This results in lower trophic efficiency and greater potential for top-down control in food webs (Barnes et al., 2010).

Universal patterns of trophic structure

The structure of trophic interactions, or food web architecture, has been studied mostly in the context of understanding mechanisms that promote stability of ecological communities. Understanding of these mechanisms has been supported by numerical modelling (McCann et al., 1998; Post et al., 2000), experimental studies (Steiner et al., 2006; Li & Stevens, 2010) and empirical observations (Rooney et al., 2006; McMeans et al., 2016; Stewart et al., 2017) of lake food webs. The traditional view of pelagic and littoral food webs as being largely independent, with energy being transferred within each food chain but with little interaction between the two, has now been superseded by recognition that lake consumers (particularly those from higher trophic levels) feed on both pelagic and littoral resources (Polis et al., 1997; Schindler & Scheuerell, 2002; Vadeboncoeur et al., 2002; Rooney & McCann, 2012; McMeans et al., 2015). The basis for this change is embedded in observations that many food webs have weak trophic interactions, with strong trophic interactions rarely observed (McCann et al., 1998). Weak trophic interactions act to stabilise food webs because a consumer that feeds on multiple resources is less exposed to fluctuations in one of their food resources than a consumer reliant on fewer resources (McCann et al., 1998). Large fluctuations in primary producer biomass are therefore dampened when a top predator consumes organisms from multiple trophic channels (Post et al., 2000; Vadeboncoeur et al., 2005; Blanchard et al., 2010; Ward et al., 2015). Recently, theory from network science has been integrated into food web ecology (Proulx et al., 2005; Stouffer &

Bascompte, 2011). Two general patterns of food web structure that have arisen from network science integration are asymmetric nested (i.e. ‘A-frame’ shaped distribution of interaction) food webs and compartmentalisation within food webs.

Asymmetric or nested food web structure occurs when higher trophic level consumers have multiple weak trophic interactions with prey resources, whilst lower trophic level consumers have strong trophic interactions but fewer food resources (Rooney et al., 2006). Nested structures are the result of several organismal functional traits related to the trophic level. Species and functional diversity correlate negatively with trophic level (Cohen et al., 2003), and organisms from lower trophic levels are commonly small and fast growing (Cohen et al., 2003; Beisner et al., 2006). These attributes of lower trophic levels favour trophic specialisation on basal resources which commonly have patchy distributions in space and time (Rooney et al., 2006; Neutel et al., 2007). Conversely, top predators are typically slow growing and long lived (McCann et al., 2005), requiring a more diverse diet to insure them against fluctuations in prey abundance (McMeans et al., 2016; Stewart et al., 2017). The large number of prey species of top predators explains why they can have disproportionately strong effects on food web dynamics despite low biomass (Estes et al., 2011).

A food web compartment is defined as a subset of species that can be identified as having stronger trophic interactions amongst one another than other constituents of the food web. Multiple food web compartments will typically be connected through a few weak interactions (Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011). It is argued that compartmentalisation promotes food web stability, because perturbations are more likely to be contained within an individual compartment, rather than being propagated throughout the entire food web (Krause et al., 2003; Stouffer & Bascompte, 2010; Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011). The relative importance of compartmentalisation increases with the number of species in a food web (Stouffer & Bascompte, 2011).

The food web patterns discussed here, biomass and body size food web scaling relationships, as well as nested structure and compartmentalisation within food webs, are well documented in lake food webs. Biomass relationships amongst trophic levels have

been widely studied (Carpenter, 2003; Cohen et al., 2003) and lake food webs are known to be highly size structured (McCann et al., 2005; Romanuk et al., 2011; McMeans et al., 2016). Lower trophic levels of lake food webs are commonly compartmentalised into littoral and pelagic consumer groups (Rooney et al., 2006; Thébault & Fontaine, 2010; Stouffer & Bascompte, 2011; McMeans et al., 2016). The degree to which consumers link littoral and pelagic compartments (i.e. the evenness of their littoral–pelagic diet contributions) is positively related to trophic level (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002; Vadeboncoeur et al., 2011; Rooney et al., 2006). Taken together, these food web patterns regulate patterns of consumer biomass within lakes in space and time. They dictate the degree to which consumers will link pelagic and littoral nutrient cycles as well as temporal patterns of biomass between trophic levels. Lake food webs, particularly pelagic food webs, are typically characterised by relatively large and abundant top predators (high *M* and *K*, respectively). This lends pelagic food webs to exhibiting oscillations in consumer biomass across trophic levels (Barraquand et al., 2017), a phenomena that is regulated by the extent of littoral habitat coupling. Given that consumer biomass is a significant factor determining CNR rates, this suggests that food web dynamics, and changes therein, will have the greatest effect on controlling CNR rates.

Applying food web theory to understand consumer nutrient recycling

Biomass and body size food web scaling relationships demonstrate how biomass becomes progressively smaller with the increasing trophic level, whilst body size becomes larger (Fig. 2). The distributions of biomass and body size predicted from these scaling relationships can inform patterns of CNR (Wang & Brose, 2017). Using the example of nitrogen cycling, where all nitrogen pools are expressed as a percentage of primary producer biomass-N, annual CNR rates should vary between $> 100\%$ for first trophic level herbivores to $< 0.001\%$ for tertiary level top-predators (Fig. 2). Food web structural patterns predict that higher trophic level consumers will have a greater diet breadth, foraging over a wider spatial area; a mechanism that will link habitats within an ecosystem

(Fig. 2). Thus, CNR from higher trophic level consumers is expected to disperse nutrients over a greater area, transporting them between littoral and pelagic areas and invoking more source–sink dynamics (Fig. 2). Conversely, lower trophic level consumers will primarily recycle nutrients in situ reflecting their spatially restricted diet and more localised distributions (McCann et al., 2005; Beisner et al., 2006; McMeans et al., 2015; Stewart et al., 2017). Food web knowledge also suggests that CNR will demonstrate unique spatial and temporal patterns as well as a higher prevalence of feedback effects when compared with hydrodynamic and biogeochemical processes.

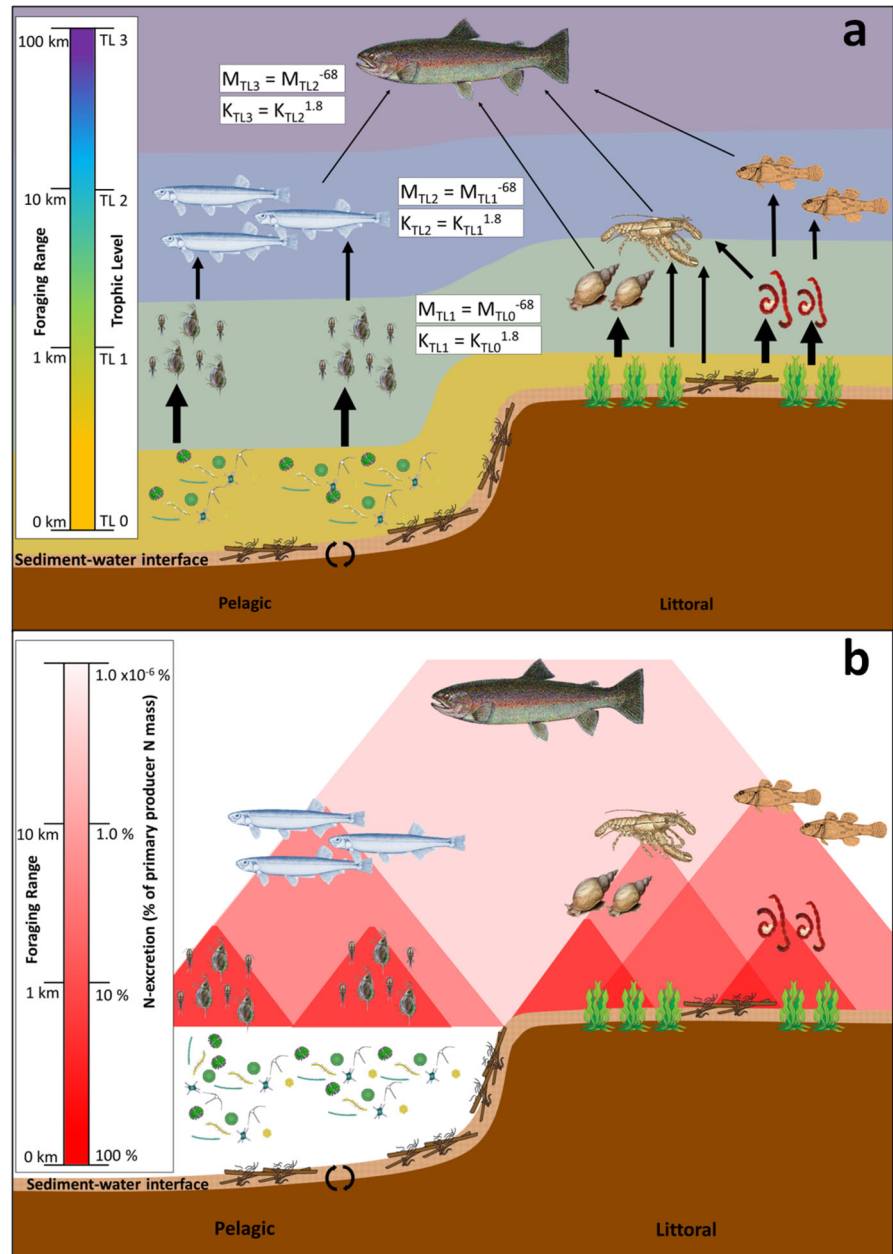
Spatial patterns

The spatial pattern of CNR fluxes differs from nutrient fluxes related to hydrodynamics and microbial biogeochemistry. The distribution of CNR within a lake follows observed nested food web structure (Fig. 2). A nested distribution of CNR rates in space enables self-organisation of lake biogeochemical cycles, where local processes cause emergent macro-scale patterns (Levin, 1999; Dong et al., 2017; Farnsworth et al., 2017). Self-organisation of nutrient cycles had the second-largest effect in determining spatial patterns, after catchment geomorphology in a perennial desert stream (Dong et al., 2017). Self-organisation processes have strong feedback loops and, by virtue of these, offer a degree of resilience to perturbation (Levin, 1999; Scheffer & Carpenter, 2003; Farnsworth et al., 2017).

Temporal patterns

The temporal patterns of CNR fluxes are also expected to differ from those driven by hydrodynamic and microbial biogeochemical processes. CNR dampens temporal variability of nutrient cycling rates in lakes (Vanni et al., 2013). Expected temporal patterns of the three processes are compared over the seasonal cycle of a monomitic lake (Fig. 3). Physical mixing delivers nutrients in abrupt pulses which are then retained within the system through microbial recycling (Lewis, 2010). Larger organisms respond less rapidly to pulses than microbes, and retain a smaller fraction of the initial pulse, but persist for longer after an initial pulse (Cohen et al., 2003). Hence, periods when CNR contributions to plant-available nutrient pools are

Fig. 2 Conceptualised structure of (a) the food web and (b) consumer nutrient recycling (CNR) in a lake ecosystem with pelagic and littoral habitats and three trophic levels (TL1–TL3). Arrow width in (a) represents proportional mass flux from resource to consumer group; covarying trophic level and foraging range are represented by colour bands. Food web structure is adapted from McMeans et al. (2016). Consumer–resource body size (Brose et al., 2006) and biomass (Hatton et al., 2015) ratios (K and M , respectively) are mean values for freshwater systems (in boxes). Body size was referenced against the average size of common freshwater TL3 fishes, salmoniform (Romanuk et al., 2011). The given body size and biomass ratios were used to calculate CNR rates for each trophic level. CNR rates are expressed as a percentage of mean annual phytoplankton biomass-N and are depicted using the red intensity scale. Spatial extent of CNR for each consumer group reflects covarying trophic level and foraging range



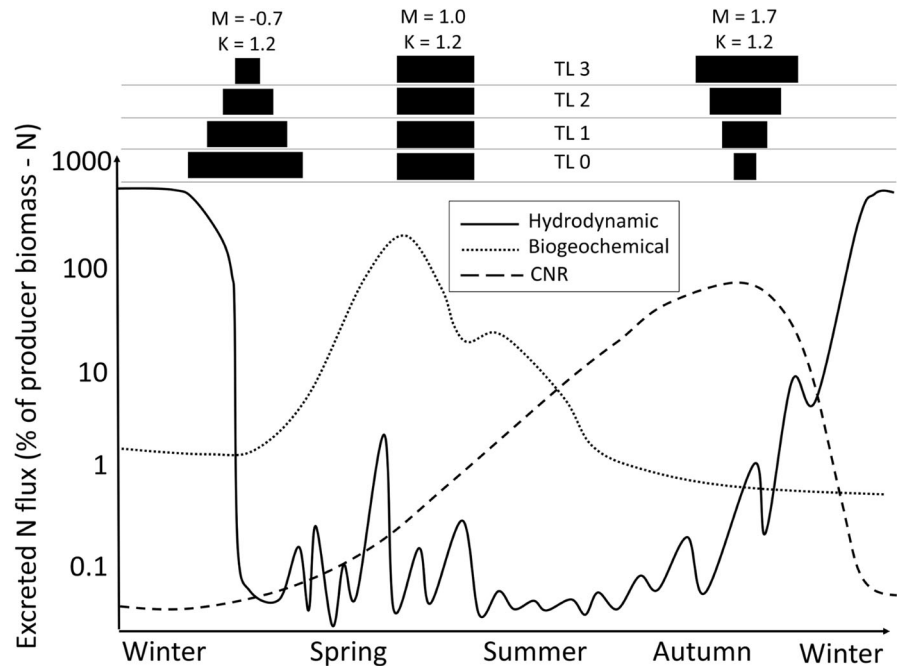
greatest likely coincide with greater biomass of higher trophic level rather than lower trophic level organisms (i.e. $M < 1$) (Fig. 3). Such periods likely occur seasonally within many lakes (McMeans et al., 2015). When primary producer biomass is relatively low, CNR inputs should be relatively high (Fig. 3). Furthermore, CNR is more likely to act as a nutrient source to low primary producer areas within the lake

as higher trophic level consumers have a greater diet breadth.

Feedback effects

CNR processes are likely to be susceptible to longer-term feedback effects corresponding to inter-annual population cycles of higher trophic level consumers. This trait distinguishes CNR from physical

Fig. 3 Conceptualised seasonal patterns in nutrient fluxes produced from hydrodynamic, biogeochemical and consumer nutrient recycling (CNR) processes for a hypothetical temperate monomictic lake. Seasonal patterns for hydrodynamic and biogeochemical processes were adapted from Lewis, 2010 and are indicative only. M (trophic-level biomass scaling ration) was varied seasonally to simulate slower responses of higher trophic levels to reductions in resource than lower trophic levels. Nutrient fluxes are expressed as a percentage of mean annual phytoplankton biomass N



hydrodynamic and microbial biogeochemical processes. Consumer population cycles are prone to intrinsic (e.g. predator–prey interactions) and external (e.g. environmental periodicity) drivers (Barraquand et al., 2017) over multi-year time scales. These fluctuations could introduce substantial variation in CNR rates that is out of phase with physical hydrodynamics and microbial biogeochemical processes which are far more responsive to intra-annual variance (Lewis, 2010; Sommer et al., 2012). These ‘out of phase’ responses suggests that variation in CNR induced by population cycles will likely dampen rather than accentuate anomalous annual patterns in physical hydrodynamics and microbial biogeochemical processes. The converse of this ‘out of phase’ response is that CNR may make lakes resilient to restoration actions such as oligotrophication (Søndergaard et al., 2007).

Responses of consumer nutrient recycling to global environmental change

CNR processes are expected to be more sensitive to indirect drivers of climate change in contrast to the strong direct effects observed for physical hydrodynamic and microbial biogeochemical processes. The most significant impacts on CNR rates are from

stressors which alter structural characteristics of aquatic food webs such as body size–biomass distribution and trophic interactions (Carpenter et al., 1992). Although direct (i.e. metabolic) effects of climate warming on food web structure are likely to be of less consequence for CNR than species invasions and extinctions, many studies have described the effects of warming. The effects of warming on food web structure have received substantial research attention and inform inferences on CNR responses. Habitat warming increases consumer metabolic rates which can lead to reduced consumer body size (Horne et al., 2015; Sentis et al., 2017) and changes in biomass between trophic levels (Lang et al., 2017). Lower trophic level, smaller bodied consumers show greater body size reductions with increased temperature than higher trophic levels (Garzke et al., 2015); hence, warmer temperatures are expected reduce carnivore biomass but increase herbivore biomass (Lang et al., 2017). This suggests that, with warming, CNR contributions from lower trophic levels will increase and higher trophic level contributions will decrease potentially resulting in stronger localised CNR effects and less spatial coupling.

Global environmental change drivers other than climate warming have stronger impacts on food web structure and should be the basis of targeted

management. Species invasions and extinctions directly alter food web structure. Species invasion case studies have invariably demonstrated the strongest effects on ecosystem nutrient cycling (Schindler et al., 1993; Walsh et al., 2016). Warmer temperatures are expected to increase the geographical ranges of many species leading to expected higher rates of species invasion and extinctions (Rolls et al., 2017). Eutrophication also has the ability to indirectly impact CNR by creating physical conditions more conducive to novel species and changes in lake communities (Ludsin et al., 2001). Over-fishing of top predators truncates food web biomass distribution (i.e. lower trophic transfer efficiency) and reduced consumer mean body size (due to fewer large predators) (Jennings & Blanchard, 2004) and in itself can have significant impacts on CNR. Impacts from species invasions and over-fishing represent the best avenues for management aiming to conserve CNR processes in the face of global environmental change.

Strong climate-induced changes on hydrodynamic and biogeochemical processes may affect the relative role of CNR. With warmer waters, the significance of CNR is expected to increase relative to hydrodynamic processes (Lewis, 2010), but to a lesser extent than microbial biogeochemical processes (Moss, 2012; Garzke et al., 2015). During periods when nutrient fluxes from hydrodynamic and microbial biogeochemical processes are both reduced (e.g. prolonged stratification; O'Reilly et al., 2003; Verburg et al., 2003; Moss, 2012), CNR fluxes will become increasingly important for sustaining pelagic productivity. By virtue of facilitating food web structures that promote resilience to perturbations, CNR is expected to display a degree of resilience to global environmental change stressors (Levin, 2005; Dong et al., 2017). However, recent research indicates that CNR responses may vary in the face of multiple stressors; impacts from warming should be greater when nutrient concentrations are lowest (Sentis et al., 2017). Such conditions are also when ecosystem effects of CNR are also greatest (Carpenter et al., 1992; Moss, 2012). With predicted increases in stratification duration under climate warming projections (Adrian et al., 2010; Kraemer et al., 2015), active management of CNR will become increasingly important. Effective management of CNR is compatible with most contemporary lake management frameworks (e.g. limiting catchment nutrient loads, sustaining fisheries and

preventing species invasions). Explicitly accounting for CNR has the potential to improve lake management in the face of larger scale global change effects.

Future research directions

The scarcity of data quantifying responses of CNR to a range of stressors represents a substantial research gap. Field studies, experimental work and modelling need to be fully integrated and their interdependencies acknowledged (Fussmann, 2008; Sommer et al., 2012). Arguably, field studies will provide the ultimate validation for CNR processes but also are the most challenging data of these approaches. CNR field studies have so far been limited due to the scale of the work required (see: Schindler et al., 1993; Attayde & Hansson, 2001; Vanni et al., 2006; Sereda et al., 2008). Stable isotope studies hold promise as a field-based approach for understanding consumer nitrogen cycling processes in particular. Stable isotopes are widely used for quantifying fluxes of nitrogen between compartments and processes in ecosystem studies (Robinson, 2001; Middelburg 2014). Nitrogen and carbon stable isotopes are well established in food web ecology for quantifying food web structure and biomass fluxes (Middelburg 2014). Lake food web studies commonly use stable isotope analyses to quantify littoral and pelagic diet contributions (Vander Zanden & Vadeboncoeur, 2002; McMeans et al., 2016). Consumer $\delta^{15}\text{N}$ values indicate trophic level as $\delta^{15}\text{N}$ values are consistently enriched $\sim 3\text{‰}$ relative to their diet (Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001). The converse of nitrogen trophic enrichment is that consumer excretion $\delta^{15}\text{N}$ is concomitantly $\sim 3\text{‰}$ depleted relative to their diet (Minagawa & Wada, 1984; Somes et al., 2010). Hence, ^{15}N depletion of DIN pools could be used as a measure of the contribution of CNR.

Analytical techniques provide $\delta^{15}\text{N}$ values of specific DIN compounds, nitrate, nitrite and ammonium, to be differentiated, enabling high resolution of N cycling dynamics (Bartrons et al., 2010). $\delta^{15}\text{N}$ – NH_4^+ values are of particular interest as it is the primary N excretory product of aquatic consumers (Vanni et al., 2013). Such measurements can now be obtained from oligotrophic lakes, where CNR effects are expected to be greatest, as technical advancements enable $\delta^{15}\text{N}$ values of nitrate and particularly ammonium at low concentrations (e.g. $< 2 \text{ mg m}^{-3}$) to be

determined (Xue et al., 2009; Bartrons et al., 2010). Ammonium in oligotrophic lakes is typically at low concentrations and readily removed by phytoplankton or nitrification (Kumar et al., 2008). Hence, it is expected that $\delta^{15}\text{N-NH}_4^+$ values primarily reflect localised sources (e.g. excretion). Expected $\delta^{15}\text{N}$ values of CNR can be demonstrated through applying the same framework as above for exploring CNR effects across trophic levels (Figs. 2, 3). Assuming that DIN inputs for the lake are 1‰ and there is a 3‰ trophic fractionation effect per trophic level within a closed system, net CNR is expected to result in excreted ammonium ranging $-1-0\%$. The more negative $\delta^{15}\text{N}$ values are associated with relatively greater biomass at lower trophic levels (i.e. lower trophic level biomass scaling factor–K) and the more positive ones with relatively greater biomass of higher trophic levels (higher K). In this example, the closed system assumption tightly constrains the effect of CNR on $\delta^{15}\text{N-NH}_4^+$ values. Fractionation effects are open-system dynamics control mass transfers (Middleburg 2014). When CNR is the primary factor controlling source–sink dynamics between habitats within a lake (an open system), with all metabolic and trophic structure assumptions kept constant, $\delta^{15}\text{N-NH}_4^+$ values can vary substantially ($> 40\%$) over the scale of days. This is because predation, as an N vector, is preferentially removing organic material with high $\delta^{15}\text{N}$ values, resulting in localised $\delta^{15}\text{NH}_4^+$ depletion. Viewed at the ecosystem level, CNR resulting from such source–sink dynamics would be expected to result in high spatial and temporal variability in $\delta^{15}\text{NH}_4^+$ values. In contrast, $\delta^{15}\text{NH}_4^+$ values resulting from biogeochemical and hydrodynamic processes should be relatively consistent (Somes et al., 2010). Compound-specific amino-acid $\delta^{15}\text{N}$ analyses are an emerging technique that enables isotopic effect within consumers associated with baseline variation to be separated from trophic fractionation effects (Chikaraishi et al., 2009; Steffan et al., 2013). Such analyses, when integrated into field studies, will enable isotopic evidence of nutrient cycling processes to be integrated with food web dynamics. Through stable isotope field studies, relationships between food web structure and CNR could be compared amongst lakes over gradients such as length of stratified season, nutrient enrichment, predator–prey biomass ratios, and degree of pelagic–littoral coupling. The quantitative patterns of biomass, body–

size, metabolic rate and trophic interactions, which all scale with trophic level, provide a framework for developing estimates of CNR and how it affects food web structure. Ultimately, these approaches may identify critical areas or processes in space and time for targeted management of CNR.

Conclusions

CNR is an important process within lake nutrient cycles. It is distinct from hydrodynamic and microbial biogeochemical nutrient cycling processes, both in terms of spatial and temporal distributions, and it may offer some resilience to global environmental change. While hydrodynamic and microbial biogeochemical nutrient cycling processes have rightfully received significant research attention, understanding how lakes might respond to global environmental change will require a greater focus on mobile CNR processes. An improved mechanistic understanding is possible by integrating food web theory and will provide greater context to the current case studies such as those discussed here. Specifically, we suggest that stable isotope-based field studies provide a promising research avenue moving forward. As demonstrated here, even broad insights from food web research can substantially inform understanding of CNR processes and demonstrate their sensitivity to food web alteration. The research synthesised in this review should provide impetus and direction for integrating food web ecology into lake nutrient cycling research, ultimately benefiting lake management.

Acknowledgements Mark McCarthy and two anonymous reviewers provided helpful comments that improved on an earlier draft of this manuscript. SS was funded by a Ph.D. scholarship from the Advocates for the Tongariro River. SDS, DPH, PV and ICD were assisted by funding from the Ministry of Business, Innovation and Employment for Enhancing the Health and Resilience of New Zealand Lakes (UOWX1503). WTB was supported by NZ funding to GNS Science (GCT84 and GWR43).

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