Seasonal and spatial patterns in nitrogen cycling and food web interactions in Lake Taupō New Zealand

A thesis

submitted in fulfilment

of the requirements for the degree

of

Doctor of Philosophy in Science

at

The University of Waikato

by

Simon Donald Stewart

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2018

Abstract

Lakes with high water quality and low productivity, commonly referred to as 'oligotrophic', are often viewed as relatively pristine and highly aesthetic ecosystems, but may still require management of nutrient inputs and fisheries. The ecosystem processes that determine functions in oligotrophic lakes are often distinct from those in eutrophic lakes, which are traditionally more actively managed. This is particularly true for nitrogen cycling which, in oligotrophic lakes, is closely coupled with food web dynamics. Strong nitrogen cycling-food web coupling in oligotrophic systems is partly related to greater significance of consumer nutrient recycling. Given that processes affecting nutrient cycles and food web dynamics can be actively managed (e.g., through catchment nutrient load regulation and fisheries management, respectively), understanding the interactions between these two processes is key to management of oligotrophic lakes globally. This thesis examines interactions between nitrogen cycling and food web dynamics in oligotrophic Lake Taupō.

Lake Taupō is a large (616 km^2 in area), deep (92 m mean depth), warm monomictic lake in the North Island of New Zealand. It shares many of the characteristics typical of large, deep oligotrophic lakes globally and can be viewed as a model system to examine nutrient cycling-food web interactions. Since 2008, nitrogen loads to the lake have been restricted by local government regulation with the objective to maintain high standards of water quality. Lake Taupō is the only example globally of exclusively N management for water quality purposes.

Abundance of rainbow trout (*Oncorhynchus mykiss*: Salmonidae), the top predator in the Taupō system, is managed through a regulated recreational fishery. Coincident with a period of declining water quality between 1995 and 2005, the trout in Lake Taupō underwent a drastic decline in abundance and individual size. However, connection between the changes in water quality and trout abundance has never been examined. Globally, there have been few empirical studies, and little research generally, to examine interactions of food web dynamics and nutrient availability, despite growing awareness of the impact of these interactions on primary production.

One component of this study synthesises literature and case studies of lakes to present a contemporary understanding of food web ecology and N-cycling

processes. The synthesis indicates that consumer nutrient recycling effects on lake productivity are likely to be seasonally specific and act to supplement demand by primary producers, especially during periods when other nutrient supply processes (e.g., hypolimnetic upwelling) are suppressed. Consumer nutrient recycling itself is regulated by food web structure, with smaller organisms contributing disproportionately to recycling locally and large mobile organisms acting as nutrient dispersal vectors across boundaries (e.g., the thermocline). Tightly coupled nutrient cycling-food web interactions have the potential to provide ecosystem resilience to global environmental change drivers such as climate change.

In this thesis I build on findings from the literature synthesis and use three methods to investigate nitrogen cycling food web interactions in Lake Taupō. First, $\delta^{15}N$ and $\delta^{13}C$ stable isotope analyses are used to quantify intra-annual patterns in, and drivers of, food web dynamics. The focus is on littoral-pelagic diet coupling by mobile consumers in response to variation in pelagic resource availability. Second, spatially resolved samples (littoral and pelagic surface waters, metalimnetic and hypolimnetic waters) taken at seasonal intervals over one year are used to contribute information towards consumer nutrient recycling. Stable isotope analyses of $\delta^{15}N$-POM (particulate organic matter), $\delta^{15}N$-NH_4^+, $\delta^{15}N$-NO_3^- and $\delta^{18}O$-NO_3^-; ^{15}N are used to indicate how consumer nutrient recycling contributes to nitrogen availability. Third, food web dynamics and consumer nutrient recycling are used as inputs to a nitrogen mass-balance model for pelagic surface waters. This model explicitly considers littoral-pelagic exchange using a coupled three-dimensional hydrodynamic model to resolve advection and mixing. Littoral-derived nitrogen fluxes to the pelagic surface waters and nitrogen fluxes from hypolimnetic to pelagic surface waters were estimated from the three-dimensional hydrodynamic model and nitrogen concentrations of the respective layers. Output from the hydrodynamic model was used in combination with other nitrogen influxes to the pelagic surface waters (e.g., hypolimnetic upwelling, littoral exchange, catchment loading, atmospheric deposition and N-fixation) in a mass balance model quantifying the role of recycling fluxes in sustaining phytoplankton nitrogen uptake.

Collectively, these research chapters demonstrated that there is close coupling of nitrogen cycling and the food web in Lake Taupō and that this coupling is strongly seasonally forced. Pelagic nutrient availability was strongly influenced by phytoplankton biomass. Highest nutrient availability was associated with winter

mixing and the period of highest phytoplankton biomass. These conditions resulted in an increased reliance on pelagic trophic resources across all trophic levels with little evidence from stable isotope analyses for substantial nutrient recycling during this period. During summer stratification, however, surface water nutrient concentrations and pelagic phytoplankton abundance reached an annual minimum. Correspondingly, zooplankton abundance decreased while trout and smelt consumed more littoral resources. Strong littoral-pelagic dietary coupling was demonstrated by smelt and trout. This finding is contrary to previous assumptions that the Lake Taupō food web is predominantly supported by pelagic production but aligns with current theories that postulate that food web interactions are dynamic and adaptive to environmental conditions.

Surface water POM, NH_4^+ and NO_3^- all became increasingly δ^{15}N-depleted over the period of summer stratification, indicated increased reliance on consumer nutrient recycling. Depleted $\delta^{15}N\text{-}NO_3^-$ was associated with enriched $\delta^{18}O\text{-}NO_3^-$, indicative of high heterotrophic biomass relative to primary producers. Strong correlations between $\delta^{15}N\text{-}NH_4^+$ excreted by zooplankton and $\delta^{15}N\text{-}NH_4^+$ in water taken from the deep chlorophyll maximum suggest particularly strong coupling of primary production and consumer nutrient recycling at this depth. Collectively, these findings demonstrate that seasonal alternation of bottom-up and top-down processes control nitrogen cycling and food web interactions in Lake Taupō.

The pelagic surface water nitrogen mass balance model, inclusive of physical transport using the three-dimensional hydrodynamic model, quantified the seasonal contributions of consumer nitrogen recycling to pelagic primary production. Nitrogen fluxes from littoral to pelagic waters originating from consumer transport were greater than those arising from physical transport during early and mid-summer stratified periods. Physical transport of littoral-derived-N into pelagic surface waters was greatest during autumn, prior to destratification and were minimum during mid-stratification. *In situ* recycling accounted for between 75 and 95% of phytoplankton nitrogen demand throughout the year. Nitrogen recycling rates were found to be greatest during winter mixing when phytoplankton biomass was highest. A positive linear relationship between surface water $\delta^{15}N\text{-}NO_3^-$ and modelled recycling rates suggests that phytoplankton nitrogen excretion, which is not ^{15}N-depleted, drives much of the seasonal variation in nitrogen recycling and that consumer nutrient recycling provides a relatively constant nitrogen supply

throughout the year. Given that nitrogen recycling rates were positively related to phytoplankton biomass, nitrogen recycling may act as a positive feedback, amplifying the growth response of phytoplankton to external nutrient supplies. The base level of consumer nutrient recycling, on the other hand, may provide resilience to strong seasonal fluctuations in nitrogen supply associated with other sources.

This study demonstrates strong bi-directional interactions between nitrogen cycling and food web dynamics in Lake Taupō. These findings can be used to understand the reciprocating effects of observed long-term changes in nutrient concentrations and trout abundance in Lake Taupō. The observed inter-decadal variations observed in top-predator abundance could have substantial impacts on nitrogen availability for phytoplankton in the pelagic zone through changes in food web structure and consumer nutrient recycling. In oligotrophic lakes such as Taupō, management should be adopted to consider the interactions between food web dynamics and nutrient cycling. One potential action includes adapting trout harvest based on winter pelagic primary productivity data as a measure of resource availability. A second potential action is adapting trout harvest to regulate smelt populations, thus altering the degree of littoral-derived nutrient translocation during the stratified period. This thesis supports the growing recognition that ecosystem-level management of lakes will increasingly be required to counter multiple interacting ecosystem stressors (e.g., climate change, invasive species, fishery exploitation and cultural eutrophication). Informed management using these approaches will be critical for maintaining resilient oligotrophic lakes.

Acknowledgements

Ngāti Tūwharetoa, holding manawhenua and kaitiakitanga over Lake Taupō, and as legal owners of the bed of Lake Taupō, provided access to the lake as well as feedback on initial study design.

I would like to thank my supervisory committee for working together so well to help create a piece of work that I am proud of. Chief supervisor David Hamilton provided patience, support, mentoring with writing and belief in the project. I am extremely grateful to have started my research career under David's mentorship. I thank Troy Baisden for given key insights at key times and always keeping the bigger picture/strategy in mind. Troy always kept my personal development as the primary goal. Ian Duggan, with his astute eye and willingness to look for detail was always approachable and supportive, taking this project on as chief supervisor at the 11th hour. Piet Verburg provided immense knowledge and held me to account on ideas, helping to tease them out into something defensible. Brendan Hicks was always willing to share ideas, information and data, much of which were discussed while out running.

Researchers outside of my committee also provided support. Michel Dedual was always willing to share his immense knowledge of fisheries and Lake Taupō. This project would not be half of what it is without him. Brittaney Graham mentored me on amino-acid compound-specific stable isotope applications, providing expertise that helped clarify and refine the food web paper. I was extremely lucky to have four international visiting professors, Helene Cyr, Jake Vander Zanden, Catherine O'Reilly and Bill Perry, within our lab group throughout this project. All of them provided enthusiastic discussion and great advice.

Heath Cairns and Johno Uniwai from the Taupō Harbour Master's Office, Nick Bradford, John Crawley, Chester Boyes, Anna Sintenie (and Freyja), Derek Roberts and Warrick Powrie all provided willing and able field assistance in a 'diverse range' of weather conditions. Dudley Bell in particular was instrumental in guiding me through the initial stages of fieldwork. Cam Branch is thanked for always providing a welcoming house for the troupe to stay throughout the year.

Andy Philips, Ashleigh Immers, Joanne Fitzgerald, and Karyne Rogers provided laboratory assistance at the National Isotope Centre in Lower Hutt. Anjana Rajendram and Jude Holt provided further assistance at the Waikato Stable Isotope

Unit. I would not have finished without their lab assistance. Ron Ram provided timely nutrient concentration analyses. Lance Buckthought, Rickoh and Liv Luoni, and Giselle Clarkson and James Pettengell provided accommodation in Wellington. Kohji Muraoka, Derek Roberts, Chris McBride, Matt Allen and Chris Dallimore all provided invaluable assistance on the set-up and troubleshooting of the hydrodynamic model.Other than those already mentioned, I was lucky to have a great group of colleagues in our research group who helped immensely along the way. In no particular order, I would like to thank Hannah Mueller, Ari Santoso, Tom Moore, Michelle Melchoir, Wang Me, Theo Kpodonu, Tina Ulrich, Donya Novin, Grant Tempero, Kevin Collier, Ian Kusabs, Joe Butterworth, Steph Monahan, Vera Rullens, Moritz Lehmann, Lena Schallenberg, Vanessa Cottrell, Vanessa Barabosa and Lee Laborie.

This project was primarily supported by a scholarship funded equally by Great Lake Taupō District Council, the Department of Conservation and the Pharazyn Trust. The scholarship was organised by the Advocates for the Tongariro who maintained support and enthusiasm throughout the project and were a pleasure to work with. Additional funding was provided by the MBIE-funded project "Enhancing the resilience of New Zealand's lakes", the Bruce Cronin Trust Scholarship and the Project Tongariro Natural History Scholarship. International travel to conferences and workshops throughout PhD candidature was supported by the SIL Trust travel award, the Rotorua Lakes Water Quality Society and a GLEON Student Travel Award fellowship.

Finally, I would like to thank my friends and family. Without their support and banter, I would be a shell of a man by now. The "Farmily" have made home in Raglan a special place for the last four years. Constant visits from Carl and Nina were always a welcome escape from the thesis. My father-in-law, Ad, my siblings Dane and Gina and their families, and Mum and Dad have been everything you could want from a family over the last four years.

Anna, thank you so much for discussing ecology, doing fieldwork, editing my drafts, keeping me going when I wasn't doing enough and distracting me when I was doing too much. I can't express how amazing you have been. Freyja and Athol, Papa has been 'doing his thesis' your entire lives. Despite being very proud of this work, it pales in comparison to how proud you two make me feel.

Table of contents

List of figures

List of tables

Chapter one

Introduction

1.1 Theoretical background

Lakes with high water quality and low productivity, commonly referred to as 'oligotrophic', provide significant benefits to society. They are valued for drinking water, fisheries, recreation, aesthetics and spiritual connections (Carpenter et al. 2011; Keeler et al. 2012). Understanding the ecosystem processes operating in these systems, specifically those that maintain an oligotrophic state, is critical for their management (Carpenter 2003; Folke et al. 2004). To date, much of our understanding of lake ecosystem processes has come from lakes that have already been severely impacted by anthropogenic nutrient enrichment, known as cultural eutrophication. Research investigating critical transitions and state-shifts of these systems in response to eutrophication demonstrates the importance of interactions of food webs and nutrient cycles (Scheffer et al. 2001; Folke et al. 2004; Seekell 2016). However, knowledge gained from investigating these systems is not necessarily transferable to oligotrophic systems that inherently function in a distinct ecosystem state (Scheffer et al. 2001; Scheffer & Carpenter 2003).

Oligotrophic lakes tend to be strongly governed by multiple interacting processes that connect various pools of nutrients, with strong feedback effects that maintain an oligotrophic state (Scheffer et al. 2001; Carpenter 2003). Cultural eutrophication amplifies a specific subset of these interactions within the nutrient cycle, resulting in the decoupling of feedbacks (Seekell 2016). Decoupled feedbacks result in a press effect (a unidirectional change in ecosystem condition), eventually driving the ecosystem past a critical threshold and into an alternate state (Folke et al. 2004; Seekell 2016). Understanding the feedbacks that maintain an oligotrophic state is critical for management and requires a systems-based approach that integrates aspects of lake ecology (e.g., catchment nutrient management and fisheries management) that are typically studied and managed independently (Carpenter et al. 2011).

Strong feedbacks can result from temporal and spatial gradients within ecosystems (Dong et al. 2017). In oligotrophic lakes these gradients have received substantial research attention. The strongest driver of temporal dynamics in lakes is mixing of

the water column associated with thermal changes (Lewis 1983; Boehrer and Schultze 2008). Water column mixing reintroduces nutrients into the euphotic waters. These nutrients have mostly accumulated in the hypolimnion during stratification (Boehrer and Schultze 2008; Sommer et al. 2010). Stratification results in a surface mixed layer that is often closely related in depth to the euphotic zone, resulting in high light availability for phytoplankton entrained in the surface mixed layer (Lewis 2010). Depending on water clarity and nutrient availability, periods of stratification can be associated with the timing of either maximum or minimum phytoplankton abundance, resulting in strong seasonal patterns in pelagic phytoplankton abundance (Vincent 1983; Sommers et al. 2010). Periods of stratification also determine the vertical distribution of phytoplankton in pelagic waters. A metalimnetic peak in phytoplankton abundance, a deep chlorophyll maximum (DCM), commonly occurs during stratification in oligotrophic lakes (Hamilton et al. 2010; Leach et al. 2017). In contrast to the strong seasonal variation in pelagic primary production, production in the littoral zone varies little seasonally (Hawes and Smith 1994; Vadeboncoeur et al. 2008). As a result, the relative contribution of littoral production to total lake production can vary substantially over an annual cycle (Hawes and Smith 1994). Physical exchange of water, and thus nutrients, between littoral and pelagic habitats can reduce the seasonal gradients of pelagic and littoral production (Boehrer and Schultze 2008; Corman et al. 2010), however, mobile consumers are able to adjust their diet to compensate for these gradients (Francis et al. 2011; Hayden et al. 2014; Eloranta et al. 2015).

A growing body of evidence demonstrates that consumers frequently adjust their spatial distribution and diet composition according to seasonally available resources (McMeans et al. 2015). Along gradients of environmental conditions, planktonic grazers vary the depth from which they primarily feed (Winder et al. 2004; Francis et al. 2012) and higher trophic level consumers display a wide variation in littoral-pelagic diet resource use (Vadeboncoeur et al. 2003; Hayden et al. 2014; Eloranta et al. 2015). Diet changes in oligotrophic lake food webs provide important feedback mechanisms that help maintain an ecosystem within a given state (Vadeboncoeur et al. 2005). Associated changes in distributions of mobile consumers additionally have the potential to change a habitat from a source to a sink of consumer excreted nutrients. In nutrient depauperate ecosystems, consumer nutrient recycling (CNR) can be a significant localised nutrient source (McIntyre et al. 2008; Spooner et al. 2013). The role of CNR in maintaining resilient ecosystem

function in oligotrophic lakes is rarely considered. More generally, most assessments of oligotrophic lakes do not consider food web dynamics, CNR, and seasonally varying physical conditions in an integrated manner. Understanding the interactions between these ecosystem processes is critical for oligotrophic lakes where feedbacks are particularly strong. Such integration requires consumer-scale through to lake-scale processes to be synthesised. Practically, such an integrated assessment requires novel methodologies and a more detailed and process-focused approach on ecosystem components.

1.2 Methodological approaches

Stable isotopes provide a method to quantify multiple ecosystem processes in an integrated way and to consider interactions between nitrogen cycling and food web dynamics (Robinson 2001; Middelburg 2014). Distinct isotopic fractionation effects on $\delta^{15}N$ values at each step of the nitrogen cycle enable tracing of the movement of nitrogen from catchment sources into a lake and through the food chain. An even greater degree of resolution is gained when $\delta^{15}N$ measurements are paired with those of $\delta^{13}C$ of organic components and $\delta^{18}O$ of dissolved nitrate (del Rio 2009; Xue et al. 2009). Stable isotope analyses have been used on fluxes of nitrogen associated with organic matter decomposition (Michelsen et al. 1996; Menge et al. 2011), nitrification (Finlay et al. 2007), denitrification (Johannsen et al. 2008; Wells et al. 2016), anaerobic ammonium oxidation (Buchwald et al. 2012; Gammons et al. 2010), ammonium volatilisation (Tozer et al. 2005; Fogel et al. 2008), atmospheric deposition (Anisfeld et al. 2007; Barnes et al. 2012), N-fixation (Kohzu et al. 2008; Ryabenko et al. 2012), autotrophic nitrogen uptake (Michelsen et al. 1996; Deutsch et al. 2009; Menge et al. 2011), animal and human septic waste inputs (McLarin et al. 1999; Anisfeld et al. 2007; Barr et al. 2013), dietary assimilation (Minagawa & Wada 1984; Peterson & Fry 1987) and cross-ecosystem subsidies (Helfield & Naiman 2001; Harding et al. 2006). Broadly, this body of literature can be categorised into two groups: work analysing trophic dynamics using organic $\delta^{15}N$ and $\delta^{13}C$ analyses and work analysing dissolved nitrogen cycling using ammonium $\delta^{15}N$ as well as nitrate $\delta^{15}N$ and $\delta^{18}O$. Rarely is research from these two fields integrated, although there are exceptions (e.g., Kristensen et al 2016 and Norman et al. 2017). Simultaneously combining nitrogen cycling and food web dynamic studies presents a powerful tool to understand the effects of CNR in oligotrophic lakes.

1.3 Study setting: Lake Taupō

In this thesis I use Lake Taupō as a case study ecosystem for investigating the interactions between nitrogen cycling and food web dynamics. Lake Taupō is a large (area 616 km^2), deep (max. depth 155 m), oligotrophic lake in New Zealand's central North Island. It is the second largest lake in Oceania, consisting of a single deep basin within a rhyolitic caldera formed (in its current state) around 1800 years before present (232 AD) during the Hatepe eruption (Hogg et al. 2012). The Hatepe eruption blew out with an easterly orientation, resulting in steep plunging cliffs along most of western and northern shorelines and more gradually inclined beaches along the southern and eastern shores (Hawes and Smith 1994). This morphology results in relatively limited area of littoral habitat; approximately 9% of the lake surface area. Lake Taupō has a relatively small catchment area (3,487 km^2) for its volume, resulting in a long residence time of 10.5 years. The Waikato River, which drains to the north, is the sole outlet.

Lake Taupō is monomictic, typically being stratified for 288 ± 21 days per year (Piet Verburg, NIWA, *unpublished data*). Exceptional years of incomplete mixing are associated with El Niño weather patterns (Hamilton et al. 2013). Pelagic primary production is maximal during winter and, as such, winter mixing duration and depth are important determinants of production in the lake (Vincent 1983). The typical annual pattern is due to a combination of mild winter conditions (the duration of winter day-light does not fall below 9.5 hours), nutrient depauperate waters and high water clarity. During this time, the phytoplankton community is dominated by diatom species (Vincent 1983). Summer pelagic primary production is characterised by a DCM comprising a similar diatom community to winter mixed conditions (Hamilton et al. 2010). Colony forming cyanobacteria (*Dolichospermum* sp.) and chlorophytes (*Botryococcus* sp.) can occur periodically in the surface water during calm periods of late summer stratification. The catchment has abundant highly soluble phosphorus-rich volcanic rock (e.g., pumice) which, in combination low catchment nitrogen inputs, results in low N:P in inflows (Vincent 1983). Pelagic primary production in Lake Taupō is therefore considered to be N-limited (White and Payne 1978; Vincent 1983; Vant 2013).

In its current oligotrophic state, Lake Taupō provides a range of ecosystem services. It is an iconic waterbody that has significant cultural, recreational and economic values for New Zealanders (Vant 2013). The shores of Lake Taupō are the ancestral

home of the iwi (tribe) Ngāti Tūwharetoa and the lake itself is considered a tupuna (ancestor) and resource for mahinga kai (food gathering; Tūwharetoa Māori Trust Board 2017). Lake Taupō is used as a reservoir for hydroelectric generation along the Waikato River, producing > 10% of national electricity needs (Mercury Ltd 2017). Lake Taupō, including its riverine inflows, is important for recreation. In addition, 28 $m^3 s^{-1}$ is diverted from adjacent catchments to the south-east of Lake Taupō into the lake via the Tongariro Power Scheme. This scheme was commissioned in 1976 and reduced the residence time from 13.5 to 10.5 years (Hamilton and Wilkins 2005). Lake Taupō supports an internationally renowned rainbow trout (*Oncorhynchus mykiss*: Salmonidae) sport fishery, which was established after releases in the late 19th century (Rowe 1993). A study based on 1998 data (McDermott Fairgray 2001) indicated that tourism was the largest contributor ($90 million) to the annual local gross domestic product ($177 million) and that trout fishing alone contributed $70 million annually.

1.4 Lake Taupō water quality management

In the late 1990s and early 2000s public concern began to grow over decreased water quality in Lake Taupō and, in particular, an atypically severe cyanobacterial bloom in the northern bays during the 2002/2003 summer (Hamilton and Wilkins 2005). Over this period a trend of increasing total nitrogen coincident with increasing chlorophyll-a (Chl-*a*) concentration was detected in Lake Taupō (Hamilton and Wilkins 2005; Vant 2013). Concern about declining water quality precipitated research to quantify the catchment nitrogen budget. The catchment nitrogen budget was divided into background natural sources beyond the scope of management intervention (non-manageable) and sources that were the result of anthropogenic modification to the catchment (manageable). Agricultural land-use was identified as the primary contributor to the manageable N-load (Table 1-1). Stakeholder consultation (iwi and the wider public) and freshwater scientists developed lake water quality targets for management. These qualitative targets were benchmarked against quantitative water quality monitoring values, and water quality parameters extant in 2001 were set as management targets (Table 1-2).

*Table 1-1: Contributions of primary sources of N to Lake Taupō, divided into manageable (grey shaded) and non-manageable sources (see text), used to inform catchment N management. Values were adapted from Waikato Regional Plan 3.10 (2011). *The Tongariro Power Scheme constitutes a source of diverted water from outside of the catchment.*

Source	**Load (t yr^{-1})**	**Percent**	**Effective yield (kg N ha^{-1} yr^{-1})**

Atmospheric deposition	272	20%	4.2
Undeveloped land	331	23%	4
Tongariro power scheme*	87	6%	
Pine on unimproved land	112	9%	2
Pine on unimproved pasture	12	1%	2.7
N-fixing scrub (gorse & broom)	7	<1%	12
Pine on improved pasture	3 – 8	<1%	4.2 – 6
Non-dairy pasture	442	33%	8.6
Dairy pasture	68	5%	29
Urban run-off	16	1%	8
Sewage	17	1%	
Total	**Approx. 1367 - 1372**		

A new legal framework was developed for managing Lake Taupō water quality. The 2001 water quality attributes were mandated as Objective 1 in the Waikato Regional Plan Variation Five (RPV 5 – operative, chapter 3.10 in the Waikato Regional Plan as of 2011). A lake water quality model (DYRESM-CAEDYM) was used to calculate required catchment N-load reductions for long-term restoration of lake water quality (Spigel 2001). In order to achieve Objective 1 (requiring targets to be reached by 2080), manageable catchment nitrogen emissions were capped (Policy 3) and a nitrogen reduction target of 20% of the 2001 load from land use activities was instated with provision for 10-year review of the target required to achieve Objective 1 (Policies 4 and 5) (Waikato Regional Plan 3.10 2011). This necessitated management of land-use activities to reduce nitrogen leaching, particularly from farming activities, to facilitate restoration to water quality levels of 2001, set out in Objective 2 (Waikato Regional Plan 3.10 2011).

Managing catchment N loads required modification of land property rights. The management of the nitrogen cap was enabled through setting N discharge rights for properties based on their average 2001 leaching rates from the rooting zone of plants. The required 20% reduction was applied across all properties, to be achieved incrementally over 15 years from 2005. Nitrogen allocation enabled discharges to be traded between rights owners within the catchment, creating a flexible management framework. An $81.5 million public fund, supported by central and local government, was initiated to then buy back cost-effective portions of the

targeted 20% of manageable catchment load from right holders. This was a mechanism to incentivise land-owners to convert their agricultural land to low-N-emission land-uses such as forestry. The cap-and-trade nutrient management system implemented for Lake Taupō was considered an innovative case-study internationally, and it is a world-first example of setting N limits for restoration of lake water quality (Abell et al. 2010; Duhon et al. 2011; Schindler et al. 2016).

Table 1-2: 2001 water quality attributes in Lake Taupō set as management targets to be maintained by 2080. Values adapted from Waikato Regional Plan 3.10 (2011).

Water quality attribute	**Mean**	**Standard dev.**	**Unit**
Total nitrogen (TN)	70.3	19.1	(mg m^{-3})
Total phosphorus (TP)	5.6	1.4	(mg m^{-3})
Chlorophyll *a* (Chl-*a*)	1.2	0.6	(mg m^{-3})
Secchi depth	14.6	2.7	(m)

1.5 Science gaps within the current management

The Lake Taupō Catchment Water Quality Management Plan focuses on protecting values which are held in high regard by the community. It includes opportunities for adaptive management that could include new science related to the most important values: clear water in the lake, water of high quality flowing into the lake and good trout fishing (Waikato Regional Plan 3.10 2011). Initially, no attributes of Lake Taupō food web constituents beyond pelagic primary production (Chl-*a*) were explicitly included in the plan. In 2006 the rainbow trout population began a rapid year-on-year decline which saw the weight, condition factor (weight/length) and catch rate (catch per unit effort; CPUE) of anglers' catches concomitantly decline. Trout size and abundance have since remained low for over a decade (Figure 1-1). Anecdotal evidence suggested that caught trout had noticeably fewer smelt (*Retropinna retropinna* – a pelagic zooplanktivore and predominant food source) in their stomachs, and therefore that the pelagic food chain may have undergone a drastic decline. The unexpected nature of the trout population decline highlighted the limited understanding of food web dynamics in Lake Taupō and particularly how these dynamics interact with pelagic primary production, and management thereof. This is an important consideration for the overall management of the lake given the importance of trout for the Lake Taupō fishery as well as indigenous species such as kākahi (freshwater mussel, *Echyridella menziesi*) and

kōura (freshwater crayfish, *Paranephrops planifrons*) which are taonga (treasured) species for Ngāti Tūwharetoa. Given the potential for food web dynamics to influence nutrient availability and Chl-*a* concentrations, it is also an important consideration for water quality management (i.e., Waikato Regional Plan 3.10 2011).

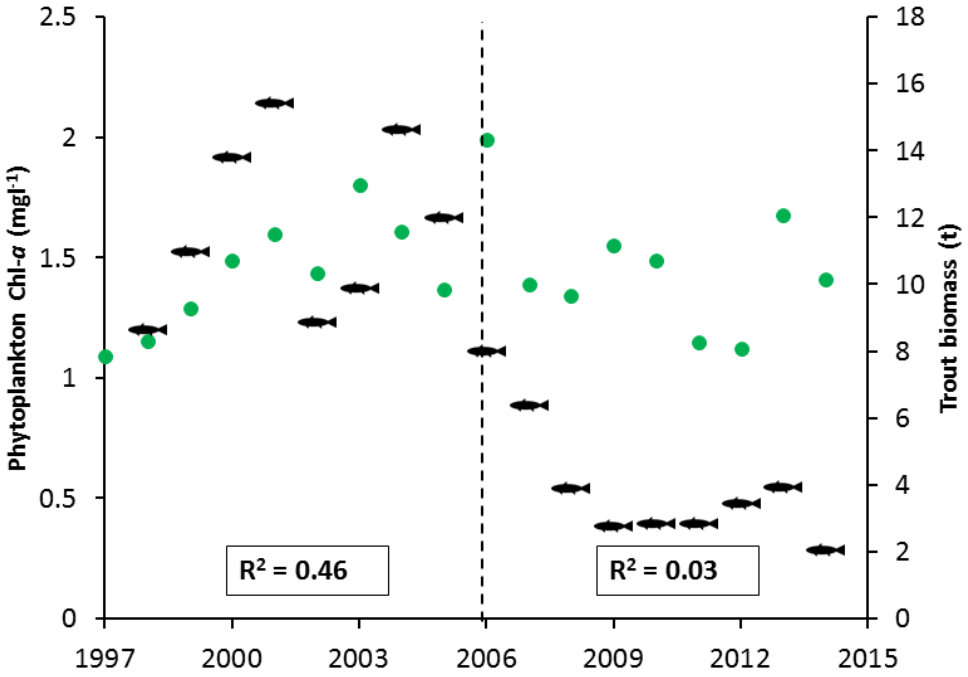


Figure 1-1: Records of annual trout biomass (fish symbols) recorded at the Waipa fish trap and mean winter (June – August) chlorophyll a concentration (green circles) between 1998 and 2015 in Lake Taupō.

Established food web theory can, to an extent, provide information on the interactions between pelagic production and food web dynamics. Pelagic food chains, such as in Lake Taupō, are characterised by strong trophic interactions between few consumers (i.e., predators' diet consists of few species) (Blanchard et al. 2010). Such food chains commonly undergo predator-prey stable limit cycles (Lotka-Volterra oscillations) due to the strong predator-prey interactions (Vadeboncoeur et al. 2005; Barraquand et al. 2017). This suggests that trout and smelt populations should naturally vary year-to-year. However, increased productivity typically accentuates these oscillations, resulting in food web destabilisation (Vadeboncoeur et al. 2005; Blanchard et al. 2010; Ward et al. 2015). Varying pelagic consumer abundances are expected to have flow-on effects for predation on littoral food chain consumers such as kākahi and kōura (Vadeboncoeur et al. 2005; Ward et al. 2015). Furthermore, given that consumer biomass

constitutes a high proportion of the N pool in oligotrophic lakes, relative to N-enriched systems, food web dynamics may also have a substantial impact on productivity through the contribution of consumer excretion to phytoplankton N demand (Dong et al. 2017). Understanding how these independent theories specifically apply to Lake Taupō requires a detailed ecosystem-level study. For example, given the dominant role of seasonal mixing-stratification cycles in structuring pelagic productivity (Vincent 1983), food web interactions and nutrient recycling feedbacks are expected to be highly seasonally sensitive. Limited understanding of how nutrient cycling and food web dynamics interact is also a feature of lakes globally (Vanni et al. 2013). Given the commonalities of Lake Taupō with other oligotrophic lakes globally, detailed findings from a system-specific study will enhance ecological understanding for oligotrophic lakes generally.

1.6 Thesis outline

The objective of this thesis is to improve understanding of how food web dynamics interact with nutrient cycling in large monomictic Lake Taupō. This information is fundamental to understanding ecosystem structure and functioning of large oligotrophic lakes globally, and for managing water quality and food web processes in Lake Taupō specifically. The thesis has four chapters and a concluding synthesis, which collectively test the overriding hypotheses that: i) *reciprocal interactions between nitrogen cycling and food web dynamics play a significant role in structuring the Lake Taupō ecosystem*; and ii) *these interactions are seasonally dependent*.

This thesis addresses the hypotheses using a literature review and three chapters examining data collected over an annual cycle (September 2014 – August 2015). Chapter 2 is a review of current literature on food web dynamics and nutrient cycling. It summarises commonly accepted primary components of lake nutrient cycles, hydrodynamic and biogeochemical processes, and synthesises this information to provide a current understanding of the role of CNR. Emerging concepts from food web literature are then synthesised and integrated with CNR concepts to provide novel insights into the role of CNR in lakes, particularly during stratification. General scaling patterns for food web structure are used to demonstrate how expected seasonal food web patterns in lakes can determine the contributions of CNR.

Chapter 3 uses $\delta^{15}N$ and $\delta^{13}C$ stable isotope analyses of the primary pelagic and littoral food web components collected over a complete annual cycle to examine food web responses to seasonal patterns in pelagic productivity. The results demonstrate that a combination of top-down and bottom-up interactions control phytoplankton-zooplankton interactions over the annual cycle. Higher trophic levels, meso- and top-predators respond to changes in lower trophic levels by switching their diet from pelagic to littoral prey as pelagic resources decline.

Chapter 4 involves utilisation of $\delta^{15}N\text{-}NH_4^+$, nitrate $\delta^{15}N$ and $\delta^{18}O$ and, POM- $\delta^{15}N$ isotopes to examine the contribution of CNR to nitrogen cycling in Lake Taupō over an annual cycle. Consumer nutrient excretion incubations were used to determine $\delta^{15}N\text{-}NH_4^+$ excretion values to validate that CNR results in ^{15}N-deplete DIN pools and to examine relationships between zooplankton excretion and ambient water $\delta^{15}NH_4^+$ values. Zooplankton contribute substantially to ammonium availability in the DCM layer. At the lake scale, CNR was found to be greatest during late summer stratification when the lake was net-heterotrophic.

Chapter 5 uses a 3D hydrodynamic model simulation with hypolimnetic and epilimnetic tracers, to quantify exchange of water between littoral, hypolimnetic, metalimnetic and epilimnetic habitats of Lake Taupō. These data were analysed with nutrient concentration and stable isotope data to examine the comparative and interactive effects between physical transport and recycling (inferred from stable isotope data) over an annual cycle. The results demonstrate complex interactions between nutrient recycling and hydrodynamics within the DCM and that these can be quite independent from surface waters. Seasonal estimates for physical transport of littoral dissolved inorganic nitrogen (DIN) to the epilimnion were then incorporated into a surface water DIN mass-balance model including hypolimnetic upwelling, N-fixation, atmospheric deposition, riverine N load, and excretion of littoral-derived N from mussels, smelt, bullies and trout which was balanced against phytoplankton uptake to solve for *in situ* recycling. Results suggest that smelt excretion transports more littoral N to the epilimnion during early stratification than physical water exchange and that *in situ* recycling accounts for > 75% of phytoplankton N-demand.

The four research chapters which comprise this thesis collectively demonstrate the importance of considering food web –nitrogen cycling interactions in Lake Taupō. When synthesised and integrated with the wider literature, the findings of this thesis

provide a novel understanding of the role of nutrient-food web interactions in oligotrophic lakes generally.

Each of the research chapters has been written in the first instance as a manuscript for submission to a peer-reviewed scientific journal. As such, formatting varies lightly between chapters so that each confirms to target journal requirements. Furthermore, to keep integrity with submitted and published work, collective pronouns (i.e., 'we' and 'our') are used rather than the personal pronouns ('I' and 'me') which are used in the thesis introduction and conclusion. Except when referenced, the material in this thesis was produced from my own ideas and research while working under the chief supervision of Prof. David Hamilton and Dr Ian Duggan, and the supervisory committee of Prof. Troy Baisden, Dr Piet Verburg and Prof. Brendan Hicks. Where specialist assistance was received for specific chapters, additional co-authors were included. Chapter 3 was published in *Freshwater Biology*, chapter 2 is accepted in *Hydrobiologia* and chapter 4 will imminently be submitted to *Limnology & Oceanography*. Chapter 5 has been prepared to be submitted at a later date.

1.7 References

Abell, J. M., D. Özkundakci, and D. P. Hamilton. 2010. Nitrogen and phosphorus limitation of phytoplankton growth in New Zealand lakes: implications for eutrophication control. Ecosystems **13**: 966–977.

Anisfeld, S. C., R. T. Barnes, M. A. Altabet, and T. X. Wu. 2007. Isotopic apportionment of atmospheric and sewage nitrogen sources in two Connecticut rivers. Environ. Sci. Technol. **41**: 6363–6369.

Barnes, R. T., and P. a Raymond. 2010. Land-use controls on sources and processing of nitrate in small watersheds: insights from dual isotopic analysis. Ecol. Appl. **20**: 1961–78.

Barr, N. G., B. D. Dudley, K. M. Rogers, and C. D. Cornelisen. 2013. Broad-scale patterns of tissue-δ^{15}N and tissue-N indices in frondose *Ulva* spp.; Developing a national baseline indicator of nitrogen-loading for coastal New Zealand. Mar. Pollut. Bull. **67**: 203–216.

Barraquand, F., S. Louca, K. C. Abbott, and others. 2017. Moving forward in circles : challenges and opportunities in modelling population cycles. Ecol. Lett. **20:** 1074-1092

Blanchard, J. L., R. Law, M. D. Castle, and S. Jennings. 2010. Coupled energy pathways and the resilience of size-structured food webs. Theor. Ecol. **4**: 289–300.

Boehrer, B., and M. Schultze. 2008. Stratification in lakes. Rev. Geophys. **46**: RG2005

Buchwald, C., A. E. Santoro, M. R. McIlvin, and K. L. Casciotti. 2012. Oxygen isotopic composition of nitrate and nitrite produced by nitrifying cocultures and natural marine assemblages. Limnol. Oceanogr. **57**: 1361–1375.

Carpenter, S. R. 2003. The need for fast and frugal models, *In* C.D. Canham, J.J. Cole, and W.K. Lauenroth [eds.], Models in Ecosystem Science. Princeton University Press.

Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annu. Rev. Environ. Resour. **36**: 75–99.

Corman, J. R., P. B. McIntyre, B. Kuboja, and others. 2010. Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa. Limnol. Oceanogr. **55**: 214–224.

Deutsch, B., M. Voss, and H. Fischer. 2009. Nitrogen transformation processes in the Elbe River: Distinguishing between assimilation and denitrification by means of stable isotope ratios in nitrate. Aquat. Sci. **71**: 228–237.

Dong, X., A. Ruhí, and N. B. Grimm. 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proc. Natl. Acad. Sci. **114**: E4744-E4752

Duhon, M., J. Young, and S. Kerr. 2011. Nitrogen Trading in Lake Taupo: An Analysis and Evaluation of an Innovative Water Management Strategy. *New Zealand Agricultural and Resource Economics Society Annual Conference*. Motu Economic and Public Policy Research. 1–30.

Eloranta, A. P., K. K. Kahilainen, P. A. Amundsen, R. Knudsen, C. Harrod, and R. I. Jones. 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecol. Evol. **5**: 1664–1675.

Finlay, J. C., R. W. Sterner, and S. Kumar. 2007. Isotopic evidence for in-lake production of accumulating nitrate in Lake Superior. Ecol. Appl. **17**: 2323–32.

Fogel, M. L., M. J. Wooller, J. Cheeseman, B. J. Smallwood, Q. Roberts, I. Romero, and M. J. Meyers. 2008. Unusually negative nitrogen isotopic compositions ($\delta^{15}N$) of mangroves and lichens in an oligotrophic , microbially-influenced ecosystem. Biogeosciences **5**: 1693–1704.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity. Ann. Rev. Ecol. Syst. **35**: 557-581

Francis, T. B., D. E. Schindler, G. W. Holtgrieve, E. R. Larson, M. D. Scheuerell, B. X. Semmens, and E. J. Ward. 2011. Habitat structure determines resource use by zooplankton in temperate lakes. Ecol. Lett. **4**: 364–372.

Gammons, C. H., J. N. Babcock, S. R. Parker, and S. R. Poulson. 2010. Diel cycling and stable isotopes of dissolved oxygen, dissolved inorganic carbon, and nitrogenous species in a stream receiving treated municipal sewage. Chem. Geol. **283**: 44–55.

Hamilton, D. P., C. G. McBride, D. Ozkundukci, M. Schallenberg, and P. Verburg. 2013. Climate warming in New Zealand Lakes, *In* C.R. Goldman, M. Kumagai, and R. Roberts [eds.], Climate change and global warming of inland waters. John Wiley & Sons, Ltd.

Hamilton, D. P., K. R. O'Brien, M. A. Burford, J. D. Brookes, and C. G. McBride. 2010. Vertical distributions of chlorophyll in deep, warm monomictic lakes. Aquat. Sci. **72**: 295–307.

Hamilton, D., and K. Wilkins. 2005. Review of science underpinning the 20% nitrogen reduction target for Lake Taupo. Report to the Ministry for the Environment. Centre for Biodiversity and Ecology Research, University of Waikato.

Harding, J. S., D. J. Hawke, R. N. Holdaway, and M. J. Winterbourn. 2004. Incorporation of marine-derived nutrients from petrel breeding colonies into stream food webs. Freshw. Biol. **49**: 576–586.

Hawes, I., and R. Smith. 1994. Seasonal dynamics of epilithic periphyton in oligotrophic Lake Taupo, New Zealand. New Zeal. J. Mar. Freshw. Res. **28**: 1–12.

Hayden, B., C. Harrod, and K. K. Kahilainen. 2014. Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. J. Anim. Ecol. **83**: 1501–1512.

Helfield, J. I., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology **82**: 2403–2409.

Hogg, A., D. J. Lowe, J. Palmer, G. Boswijk, and C. B. Ramsey. 2011. Revised calendar date for the Taupo eruption derived by ^{14}C wiggle-matching using a New Zealand kauri ^{14}C calibration data set. The Holocene **22**: 439–449.

Johannsen, A, K. Dahnke, and K. Emeis. 2008. Isotopic composition of nitrate in five German rivers discharging into the North Sea. Org. Geochem. **39**: 1678–1689.

Keeler, B. L., S. Polasky, K. A. Brauman, K. A. Johnson, J. C. Finlay, and A. O. Neill. 2012. Linking water quality and well-being for improved assessment and valuation of ecosystem services. Proc. Natl. Acad. Sci. **109**: 18619-18624

Kohzu, A., T. Miyajima, I. Tayasu, and others. 2008. Use of stable nitrogen isotope signatures of riparian macrophytes as an indicator of anthropogenic n inputs to river ecosystems. Environ. Sci. Technol. **42**: 7837–7841.

Kristensen, P. B., T. Riis, H. E. Dylmer, and others. 2016. Baseline identification in stable-isotope studies of temperate lotic systems and implications for calculated trophic positions. Freshw. Sci. **35**: 909–921.

Leach, T., B. Beisner, C. Carey, and others. 2017. Relative importance of light and thermal stratification in prediting the structure of deep chlorophyll maxima among lakes. Limnol. Oceanogr. **63**: 628-646

Lewis, W. M. J. 1983. Revised classification of lakes based on mixing. Can. J. Fish. Aquat. Sci. **40**: 1779–1787.

McDermott Fairgray. 2001. The impact of alternative land uses in Taupo catchment. Report prepared by Landcare Research for the Ministry for the Environment in association with Environment Waikato (document # 926638)

McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. M. Hood, B. W. Taylor, and S. A Thomas. 2008. Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? Ecology **89**: 2335–46.

McLarin, W., G. Bekesi, L. Brown, and M. Jack. 1999. Nitrate contamination of the unconfined aquifer, Manakau, Horowhenua, New Zealand. J. Hydrol. **38**: 211–235.

McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2015. Food web structure in temporally-forced ecosystems. Trends Ecol. Evol. **30**: 662–672.

Menge, D. N. L., W. T. Baisden, S. J. Richardson, D. A. Peltzer, and M. M. Barbour. 2011. Declining foliar and litter $\delta^{15}N$ diverge from soil , epiphyte and input $\delta^{15}N$ along a 120 000 yr temperate rainforest chronosequence. New Phytol. **190**: 941–952.

Mercury^{Ltd}. 2017. Summary of Waikato River hydroelectric power scheme: https://www.mercury.co.nz/About/Renewable-Energy/Hydro-Generation. Accessed 19/10/2017

Michelsen, A., I. K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia **105**: 53–63.

Middelburg, J. J. 2014. Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences **11**: 2357–2371.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of $\delta^{15}N$ along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta **48**: 1135–1140.

Norman, B. C., M. R. Whiles, S. M. Collins, and others. 2017. Drivers of nitrogen transfer in stream food webs across continents. Ecology. **98**: 3044-3055

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

del Rio, C. M., N. Wolf, S. a Carleton, and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. Camb. Philos. Soc. **84**: 91–111.

Robinson, D. 2001. ^{15}N as an integrator of the nitrogen cycle. Trends Ecol. Evol. **16**: 153–162.

Rowe, D. K. 1993. Disappearance of koaro, Galaxias brevipinnis, from Lake Rotopounamu, New Zealand, following the introduction of smelt, Retropinna retropinna. Environ. Biol. Fishes **36**: 329–336.

Ryabenko, E., A. Kock, H. W. Bange, M. A. Altabet, and D. W. R. Wallace. 2012. Contrasting biogeochemistry of nitrogen in the Atlantic and Pacific Oxygen Minimum Zones. Biogeosciences **9**: 203–215.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**: 591-596

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends Ecol. Evol. **18**: 648–656.

Schindler, D. W., S. R. Carpenter, S. C. Chapra, R. E. Hecky, and D. M. Orihel. 2016. Reducing phosphorus to curb lake eutrophication is a success. Environ. Sci. Technol. **50**: 8923–8929.

Seekell, D. 2016. Passing the point of no return. Science **354**: 1109–1109.

Sommer, U., R. Adrian, L. De Senerpont Domis, and others. 2012. Beyond the Plankton Ecology Group (PEG) Model: mechanisms driving plankton succession. Annu. Rev. Ecol. Evol. Syst. **43**: 429–448.

Spigel, R, (2001): A coupled hydrodynamic-ecosystem study of Lake Taupo – A preliminary model. NIWA Client Report CHC01/52. NIWA, Christchurch.

Spooner, D. E., P. C. Frost, H. Hillebrand, M. T. Arts, O. Puckrin, and M. a Xenopoulos. 2013. Nutrient loading associated with agriculture land use dampens the importance of consumer-mediated niche construction. Ecol. Lett. **16**: 1115–25.

Tozer, W. C., D. Hackell, D. B. Miers, and W. B. Silvester. 2005. Extreme isotopic depletion of nitrogen in New Zealand lithophytes and epiphytes ; the result of diffusive uptake of atmospheric ammonia? Oecologia **144**: 628–635.

Tūwharetoa Māori Trust Board. 2017. Summary of settlement deed: https://www.tuwharetoa.co.nz/declaratoryjudgment/http://www.tuwharetoa.iwi.nz/. Accessed 18/10/2017.

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. S. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48**: 1408–1418.

Vanni, M. J., G. Boros, and P. B. McIntyre. 2013. When and fish sources vs. sinks of nutrients in lake ecosystems? Ecology **94**: 2195–2206.

Vant, B. 2013. Recent changes in the water quality of Lake Taupo and its inflowing streams. New Zeal. J. For. **58**: 27–30.

Vincent, W. F. 1983. Phytoplankton production and winter mixing: contrasting effects in two oligotrophic lakes. J. Ecol. **71**: 1–20.

Ward, C. L., K. S. McCann, and N. Rooney. 2015. HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. Ecol. Lett. **18**: 1190-1197

Wells, N. S., W. T. Baisden, T. Horton, and T. J. Clough. 2016. Spatial and temporal variations in nitrogen export from a New Zealand pastoral catchment revealed by stream water nitrate isotopic composition. Water Resour. Res. **52**: 2840–2854.

Winder, M., P. Spaak, W. M. Mooij, S. Ecology, and N. Jul. 2004. Trade-offs in Daphnia habitat selection. Ecology **85**: 2027–2036.

White, E. & Payne, G. W. 1977. Chlorophyll production, in response to nutrient additions, by the algae in Lake Taupo water. NZ. J. Mar. Freshwater Res, **11**:

501-507.

Xue, D. M., J. Botte, B. De Baets, and others. 2009. Present limitations and future prospects of stable isotope methods for nitrate source identification in surface- and groundwater. Water Res. **43**: 1159–1170.

Chapter two

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

This chapter was published as: Stewart, S. D., Hamilton, D. P., Baisden W. T., Verburg, P., Duggan I. C. 2018. The role of mobile consumers in lake nutrient cycles: a brief review. *Hydrobiologia* DOI: 10.1007/s10750-018-3603-2

2.1 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 relationship 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 spatial 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.

Key words: food web, recycling, excretion, body size, biomass, littoral pelagic coupling

2.2 Introduction

Nutrient cycling is a critical process 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 and Schindler, 2009; Moss, 2012). Arguably, eutrophication represents the most pressing challenge to the stability of lake

ecosystems (Carpenter et al., 2011) 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 & Baddina, 2002; Finchel, 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. 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., 2016). However, the drivers of change in nutrient cycling rates, particularly for oligotrophic lakes, remain uncertain (Lewis, 2010; Moss, 2012). The development in understanding of lake nutrient cycling models is currently limited by knowledge of several critical processes driving temporal and spatial variation in nutrient cycling rates.

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 & Baddina, 2002; Finchel, 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., 1992; Schindler et al., 1993; Layne & Vanni, 1997; Attyade & Hansson, 2001; Vanni et al., 2006). Specifically, the ability of many larger consumers to move between habitats (Vanni et al., 2006; Baustain et al., 2014) paired with long (generally > 1 year) consumer life cycles (Schostell & Bukaveckas, 2004), control 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; Carpenter et al., 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 has 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., 2012). 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 affects 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., 1992; 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 non-linear threshold responses. Most of the focus of critical threshold responses to date has been on non-linear primary productivity responses, establishing the concepts of alternate states or regime shifts of the dominant primary producers (Carpenter et al., 2005; Scheffer et al., 2012; Angeler and 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. This 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;
(5) discussion and comparison of the factors driving critical nutrient responses to hydrodynamic, biogeochemical and CNR processes.

2.3 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" (Figure 2-1). 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 (Vallentyne 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 and Patterson 1990), led to focus on how nutrients are transported within lakes (Boehrer & Schultze 2008). Food web responses add a further 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 (Fussman et al. 2008; Hellweger 2017).

Controls on nutrient cycling have traditionally been viewed as hierarchical, predominantly from catchment loads down to in-lake hydrodynamic processes (Vollenweider 1974; Boehrer & Schultze 2008), but there is 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 made 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, while biogeochemical cycling is relatively more important in equatorial lakes (Kilham & Kilham 1990; Lewis 2010). Figure 2-1 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.

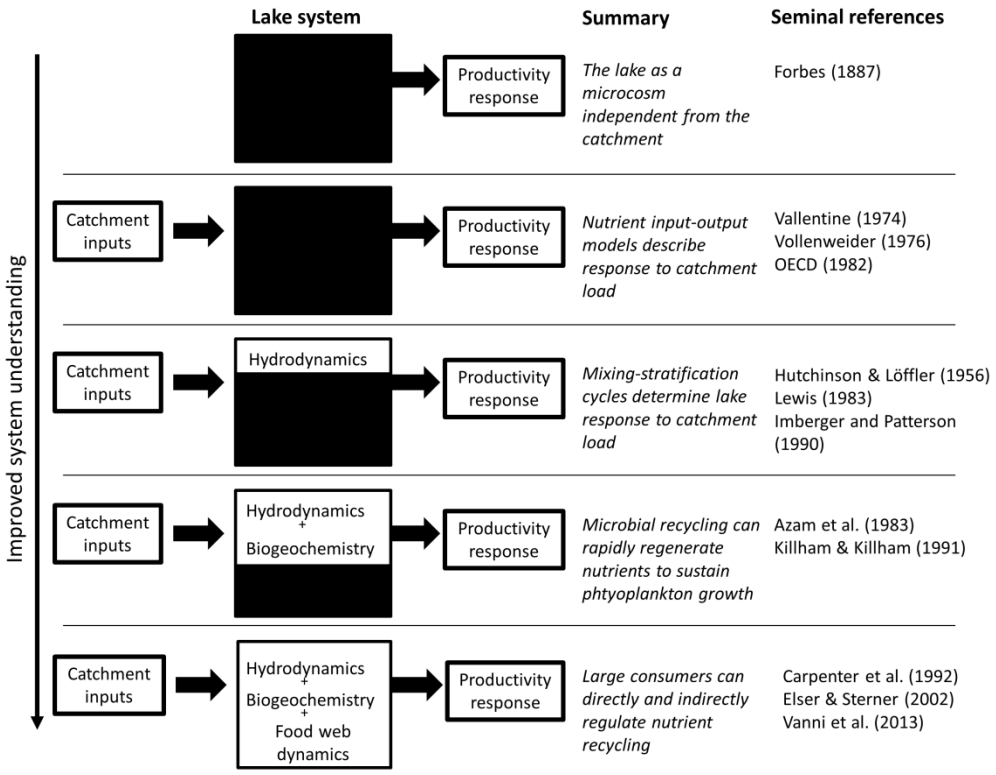


Figure 2-1: "Demystifying the black box" of lake responses to nutrient inputs based on progression in the understanding of the controls on lake nutrient cycling. Seminal papers are listed against major advances.

2.3.1 Hydrodynamic mediated nutrient cycling

Turbulent mixing processes operate over a wide range of scales, from entire lakes (e.g., basic-scale seiching; Antenucci and Imberger, 2001) to millimetres (e.g., Kolmogorov scale; Wüest and 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 and 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; Lewis 2013), while in other lakes it may be associated with the annual minimum of production (Boehrer and Schultze 2008; Sommer et al. 2012). The response of primary production to mixing is regulated by lake depth and water clarity, as well as the extent of alleviation of nutrient limitation (Vincent 1983). Localised nutrient 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 and 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 and Schultze 2008).

Hydrodynamic responses to global environmental change drivers – Most physical transport mechanisms are extremely sensitive to climate warming (Boehrer and Schultze 2008; Adrian et al. 2009; 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. 2009; Sahoo et al. 2015) 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 later timing of autumn blooms in Lake Washington (Winder and Schindler 2007) and reduced pelagic productivity in Lake Tanganyika (Verburg et al. 2003; O'Reilly 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 (Bokaniov et al. 2014; Poschke 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 could reduce productivity, but may 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. 2015).

2.3.2 Biogeochemical nutrient cycling mediated by the microbial loop

Microbial recycling is the primary mechanism for regenerating nutrients from organic matter (Paerl and Pinckney 1996; Cotner and Baddina 2002). Bacteria and protozoa adhere to and metabolise detrital particles, releasing dissolved nutrients for uptake by primary producers (Paerl and Pinckney 1996; Biddanda et al. 2001; Fenchel 2014). Free-living microbes also metabolise dissolved organic nutrients that 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). Higher relative benthic recycling rates typically results in nutrients accumulating below the thermocline during periods of stratification (Verburg et al. 2003; O'Reilly et al. 2003; Lehman 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 and 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 (Ptacknic 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 among microbial communities (Ptacknic 2010; Beisner 2001). Environmental filtering (bottom-up control of community composition) is a dominant structuring mechanism (Beisner et al. 2006), but others typical of macrofaunal communities, such as predator-prey interactions and competition (Ptacknik et al. 2014), are also present in microbial communities. These interactions can directly control 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 and Stevens 2010; Ptacknik 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 (Cottner and 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 decrease, resulting in increased growth efficiencies (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 controls on microbial metabolism suggest that microbial communities will be sensitive to climate warming (Paerl and Pinckney 1996; Carey et al. 2012; Amando 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, i.e., warmer lakes (Kilham and Kilham 1990; Lewis 2010; Amando 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 and 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). 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 non-linear 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. The best indication of potential responses may come from observations of the response of macrofauna (i.e. predator-prey dynamics) to changes in temperature (Ptacknic et al. 2010) and will benefit from an improved understanding of CNR.

2.4 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 body size (Cohen et al. 2003) and therefore microbial consumers will dominate biomass within lakes (Cotner and Baddina 2002). The second is that mass-specific metabolic rates scale negatively with body size (Brown et al. 2004; Hall et al. 2007; McIntyre et al. 2008). Therefore, small-bodied consumers will excrete more than large-bodied consumers per unit biomass (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.

2.4.1 Translocation of nutrients through CNR

The role of animal excretion in transporting nutrients between spatially separate ecosystem habitats is well documented empirically (Vanni and 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*) can more than meet the pelagic phytoplankton P demand, exacerbating eutrophication driven by catchment nutrient loads (Vanni et al. 2006). Areas with fish have been shown to have higher rates of primary production than areas without fish (McIntyre et al.

2008), while biomass of sessile freshwater mussels (Spooner et al. 2013) and gardening caddis flies larvae (which actively maintain and defend a territory of benthic substrate; Ings et al. 2017) has been positively correlated with biomass and diversity of benthic algae.

The enhancement of primary production 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 fish standing stock will naturally mobilise more nutrients (Schindler et al. 1993), benthivorous fish are typically a net source of nutrients for pelagic primary producers (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 the strongest impacts of CNR have been attributed to bottom feeding by benthivorous fish which has been implicated as a catalyst for tipping lakes from clear, macrophyte dominated states to turbid, phytoplankton dominated states (Søndergaard et al. 2008, 2017).

2.4.2 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 and 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 and 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 at 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 (Baustain et al. 2014). Over annual time scales, recycling by consumers can exceed that by microbial consumers

(Attayde and Hansson 2001) because the biomass of smaller bodied, lower trophic level organisms reduces at a must faster rate than larger bodied higher trophic level organisms in response to resource depletion. The consumer traits most influential on recycling, including wide foraging range and long lifespans, are inherently related to consumer body size (McCann et al. 2005; McMeans et al. 2015).

2.4.3 Top-down effects on nutrient recycling

Consumers are able to alter nutrient recycling indirectly through two mechanisms; firstly, through 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) (Blanchard et al. 2010; McCann et al. 2005; DeLong et al. 2015). Top predators tend to be large-bodied while 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 species introductions or removals 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* and *D. bugensis*) 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).

2.4.4 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 diet N:P ratios, as well as consumer species-specific N and P turnover rates. 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, while 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 and Elser 2002). Fish predation of cladocerans can, in turn, increase phytoplankton production in P-limited systems by promoting higher P recycling rates (Sterner and 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, little is known of quantitative estimates of CNR. Nonetheless, these independent lines of research show that variation in CNR is regulated by the interactions between 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.

2.5 Synthesising food web ecology macro-scale patterns in lakes

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

2.5.1 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; Hatton et al. 2015; Cebrian 2015). The resulting relationships have reinforced Kleiber's law that metabolism scales to the -3/4 power of body size (Brown 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, mass-specific 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 (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 x 106 years (Klompmaker 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).

2.5.2 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 and 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 transferred within each food chain but with little interaction between the two, has now been superseded by recognition that lake consumers feed on both pelagic and littoral resources (Polis et al. 1997; Vadeboncoeur et al. 2002; Schindler and Scheuerell 2002; Rooney and McCann 2012; McMeans et al. 2015). This basis for this change is embedded in observations that many food webs have weak trophic interactions, with strong trophic interactions rarely observed (McCann 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 2000). Intermediate levels of prey preference (i.e., neither completely random selection of prey nor exclusive reliance on a single resource) optimise food web stability (Post et al. 2000). 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 and 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, while 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; Beinser 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. 2008). 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 and Fontaine 2010; Stouffer and 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 and Bascompte 2010; Thébault and Fontaine 2010; Stouffer and Bascompte 2011). The relative importance of compartmentalisation increases with the number of species in a food web (Stouffer and 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 and Cohen 2003) and lake food webs are known to be highly size structured (McCann et al. 2005; Romanuk et al. 2011; McMeans et al. 2016). Lake food webs are commonly compartmentalised into littoral and pelagic consumer groups (Rooney et al. 2006; Thébault and Fontaine 2010; Stouffer and 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 and Scheuerell 2002; Vander Zanden and 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 phenomenon 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.

2.6 Applying food web theory to understand consumer nutrient recycling

Biomass and body size food web scaling relationships demonstrate how biomass becomes progressively smaller with increasing trophic level while body size becomes larger (Figure 2-2). The distributions of biomass and body size predicted from these scaling relationships can inform patterns of CNR (Wang and 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 (Figure 2-2). 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 (Figure 2-2). 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 (Figure 2-2). 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. 2014; 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.

2.6.1 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 nested food web structure (Figure 2-2). A nested distribution of CNR rates in space enables self-organisation (i.e., regulating feed-back loops) 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 and Carpenter 2003; Farnsworth et al. 2017).

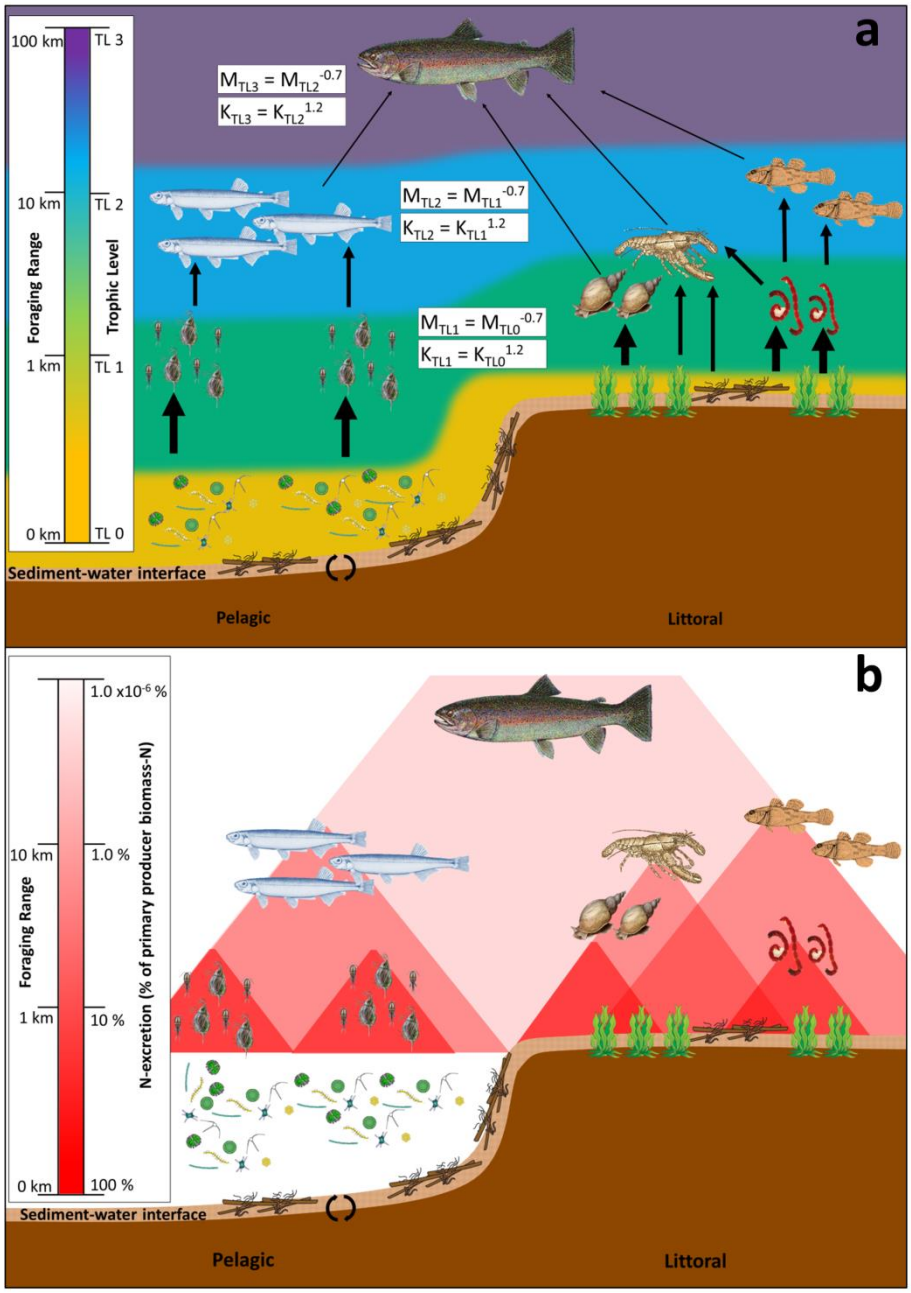


Figure 2-2: Conceptualised structure of (a) the food web and (b) consumer nutrient recycling (CNR) in a lake ecosystem with pelagic and littoral habitat and three trophic levels (TL1 to TL3). Arrow width in (a) represents proportional mass flux from resource to consumer group, co-varying trophic level and foraging range are represented by colour bands.

2.6.2 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 monomictic lake (Figure 2-3). 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 greatest likely coincide with greater biomass of higher trophic level than lower trophic level organisms (i.e., $M < 1$) (Figure 2-3). Such periods likely occur seasonally within many lakes (McMeans et al. 2015). When primary producer biomass is relatively low, CNR inputs should be high (Figure 2-3). 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.

2.6.3 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 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 are out of phase with physical hydrodynamics and microbial biogeochemical processes, and which are far more responsive to intra-annual variance (Lewis 2010; Sommer et al. 2012). These 'out of phase' responses suggest 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).

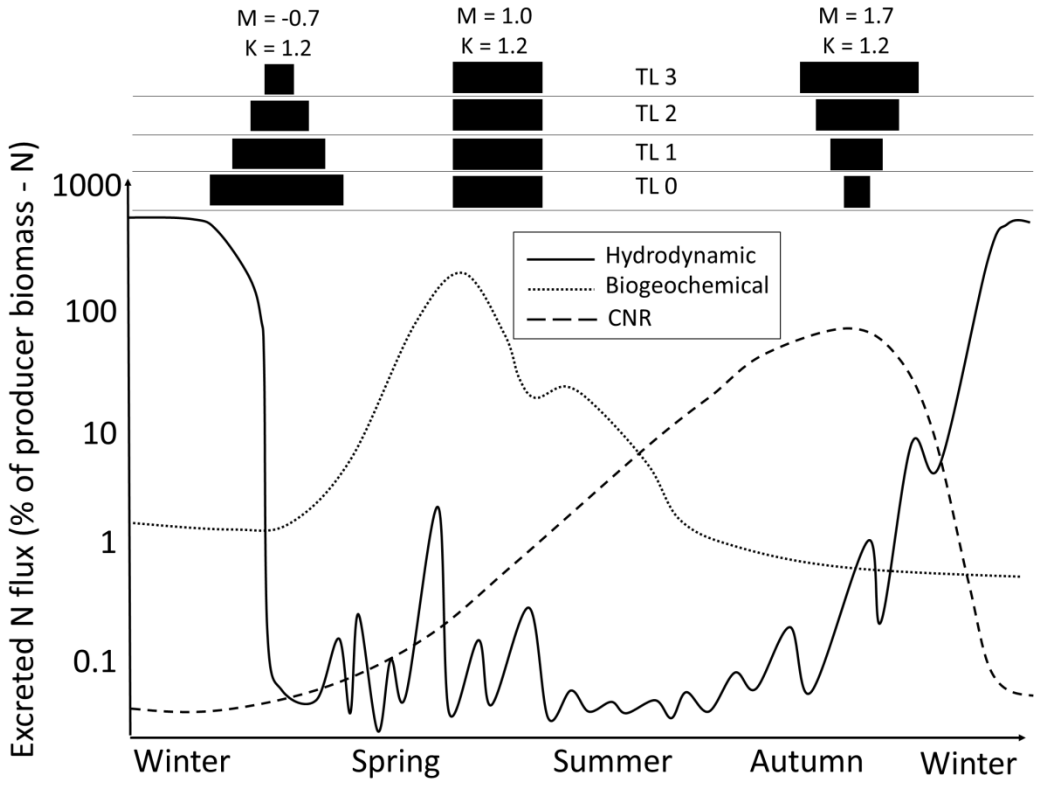


Figure 2-3: Conceptualised seasonal patterns in nutrient fluxes produced from hydrodynamic, biogeochemical and consumer nutrient recycling (CNR) processes for a hypothetical temperate monomictic lake.

2.6.4 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 that alter structural characteristics of aquatic food webs such as body size – biomass distribution and trophic interactions (Carpenter et al. 1992). Although direct effects of climate warming are likely less consequential for CNR, there are many studies describing effects of warming on food web structure. 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 that 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 to 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. This would be expected to result in stronger localised CNR effects and less spatial coupling.

Global environmental change drivers other than climate warming have stronger impacts of 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 stronger effects on ecosystem nutrient cycling than other drivers (Schindler et al. 1993; Walsh et al. 2016). Warmer temperatures will change the geographic 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 and 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. Warmer temperatures increase the significance of microbial biogeochemical processes (Moss et al. 2010; Garzke et al. 2015) and decrease the significance of physical hydrodynamic processes (Lewis et al. 2010) relative CNR nutrient fluxes. 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 2010), 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 et al. 2010). The duration of stratification for most lakes is predicted to increase under climate warming projections (Adrian et al. 2010; Kraemer et al. 2015). Hence 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.

2.6.5 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). Field and experimental studies will both inform modelling studies (e.g., providing parameterisation data) and in turn be informed by modelling (as a tool for rapid generation and exploration of hypotheses) (Fussmann 2008). The quantitative macro-scale patterns of food web structure demonstrated in this review provide a starting point for pursuing future modelling, experimental and field studies. 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; Attydae and Hansson 2001; Vanni et al. 2006; Sereda et al. 2008). Stable isotope studies hold particular promise as a field-based approach for understanding consumer nitrogen cycling processes. 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 and Vadeboncoeur 2002, McMeans et al. 2016). Consumer $\delta^{15}N$ values indicate trophic level as $\delta^{15}N$ values are consistently enriched ~3 ‰ relative to their diet (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). The converse of nitrogen trophic enrichment is that consumer excretion $\delta^{15}N$ is concomitantly ~3‰ deplete relative to their diet (Minagawa and 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 $\delta^{15}N$ values of specific DIN compounds, nitrate, nitrite and ammonium, to be differentiated, enabling high resolution of N cycling dynamics (Bartrons et al. 2010). $\delta^{15}N\text{-}NH_4^+$ values are of particular interest as

ammonium 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 advances enable $\delta^{15}N$ values of nitrate and particularly ammonium at low concentrations (e.g., < 2 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 $\delta^{15}N\text{-}NH_4^+$ values primarily reflect localised sources (e.g., excretion). Expected $\delta^{15}N$ values of CNR can be demonstrated through applying the same framework as above for exploring CNR effects across trophic levels (Figures 3-2 and 3-3). 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 from -1 to 0‰. The more negative $\delta^{15}N$ 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 $\delta^{15}N\text{-}NH_4^+$ 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, $\delta^{15}N\text{-}NH_4^+$ 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 $\delta^{15}N$ values, resulting in localised $\delta^{15}NH_4^+$ 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 $\delta^{15}NH_4^+$ values. In contrast, $\delta^{15}NH_4^+$ values resulting from biogeochemical and hydrodynamic processes should be relatively consistent (Sommes et al. 2010). Compound-specific amino-acid $\delta^{15}N$ 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.

2.7 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.

2.8 Acknowledgements

Mark McCarthy and two anonymous reviewers provided helpful comments 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).

2.9 References

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. B. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. van Donk, G. A. Weyhenmeyer,

& M. Winder, 2010. Lakes as sentinels of climate change. Limnology & Oceanography 54: 2283–2297.

Allgeier, J. E., D. E. Burkepile, & C. A. Layman, 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Global Change Biology: **23**: 2166-2178.

Amado, A. M., F. Meirelles-Pereira, L. O. Vidal, H. Sarmento, A. L. Suhett, V. F. Farjalla, J. B. Cotner, & F. Roland, 2013. Tropical freshwater ecosystems have lower bacterial growth efficiency than temperate ones. Frontiers in Microbiology 4: 167.

Angeler, D. G., & C. R. Allen, 2016. Quantifying resilience. Journal of Applied Ecology 53: 617–624.

Antenucci, J. P., & J. Imberger, 2001. Energetics of long internal gravity waves in large lakes. Limnology and Oceanography 46: 1760–1773.

Attayde, J. L., & L.-A. Hansson, 2001. Fish-mediated nutrient recycling and the trophic cascade in lakes. Canadian Journal of Fisheries and Aquatic Sciences 58: 1924–1931.

Barraquand, F., S. Louca, K. C. Abbott, C. A. Cobbold, D. L. DeAngelis, B. D. Elderd, J. W. Fox, P. Greenwood, F. Hilker, D. L. Murry, C. R. Stieha, R. A. Taylor, K. Vitense, G. S. K. Wolkiwicz, & R. C. Tyson, 2017. Moving forward in circles : challenges and opportunities in modelling population cycles. Ecology Letters: **20**: 1074-1092

Bartrons, M., L. Camarero, & J. Catalan, 2010. Isotopic composition of dissolved inorganic nitrogen in high mountain lakes : variation with altitude in the Pyrenees. Biogeosciences 7: 1469–1479.

Baustian, M. M., G. J. a. Hansen, A. de Kluijver, K. Robinson, E. N. Henry, L. B. Knoll, K. C. Rose, & C. C. Carey, 2014. Linking the bottom to the top in aquatic ecosystems: mechanisms and stressors of benthic-pelagic coupling. Eco-DAS X Symposium Proceedings 25–47.

Beisner, B. E., 2001. Plankton community structure in fluctuating environments and the role of productivity. Oikos 95: 496–510.

Beisner, B. E., P. R. Peres-Neto, E. S. Lindstrom, A. Barnett, & M. L. Longhi, 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87: 2985–2991.

Blanchard, J. L., R. Law, M. D. Castle, & S. Jennings, 2010. Coupled energy pathways and the resilience of size-structured food webs. Theoretical Ecology 4: 289–300.

Bocaniov, S. A., C. Ullmann, K. Rinke, K. G. Lamb, & B. Boehrer, 2014. Internal waves and mixing in a stratified reservoir: Insights from three-dimensional modeling. Limnologica 49: 52–67.

Boehrer, B., & M. Schultze, 2008. Stratification in lakes. Reviews of Geophysics 46: 1–27.

Brose, U., T. Jonsson, E. L. Berlow, P. H. Warren, C. Banasek-Richter, L.-F. Bersier, J. L. Blanchard, T. Brey, S. R. Carpenter, M.-F. Cattin Blandenier, L. Cushing, H. A. Dawah, A. I. Dell, F. Edwards, S. Harper-Smith, U. Jacob, M. E. Ledger, N. D. Martinez, J. Memmott, K. Mintenbeck, J. K. Pinnegar, B. C. Rall, T. S. Rayner, D. C. Reuman, L. Ruess, W. Ulrich, R. J. Williams, G. Woodward, & J. E. Cohen, 2006. Consumer-resource body-size relationships in natural food webs. Ecology 87: 2411–2417.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, & G. B. West, 2004. Toward a metabolic theory of ecology. Ecology 85: 1771–1789.

Carey, C. C., B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton, & J. D. Brookes, 2012. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. Water Research 46: 1394–1407.

Carpenter, S. R., 2003. Regime shifts in lake ecosystems: pattern and variation. Excellence in Ecology, Volume 15. Oldendorf/Luhe (Germany): International Ecology Institute. ISSN: 0932–2205. 2003

Carpenter, S. R., K. L. Cottingham, & D. E. Schindler, 1992. Biotic feedbacks in lake phosphorus cycles. Trends in Ecology & Evolution 7: 332–336.

Carpenter, S. R., J. R Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, and X. He. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876

Carpenter, S. R., E. H. Stanley, & M. J. Vander Zanden, 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annual Review of Environment and Resources 36: 75–99.

Casini, M., J. Hjelm, J.-C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, & G. Kornilovs, 2009. Trophic cascades promote threshold-like shifts. Proceedings of the National Acadamy of Science 106: 197–202.

Cebrian, J., 2015. Energy flows in ecosystems. Science 349: 1053–1054.

Chikaraishi, Y., N. O. Ogawa, Y. Kashiyama, Y. Takano, H. Suga, A. Tomitani, H. Miyashita, H. Kitazato, & N. Ohkouchi, 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnology and Oceanography: Methods 7: 740–750.

Cohen, J. E., T. Jonsson, & S. R. Carpenter, 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences 100: 1781–1786.

Conroy, J. D., W. J. Edwards, R. a. Pontius, D. D. Kane, H. Zhang, J. F. Shea, J. N. Richey, & D. A. Culver, 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshwater Biology 50: 1146–1162.

Corman, J. R., P. B. McIntyre, B. Kuboja, W. Mbemba, D. Fink, C. W. Wheeler, C. Gans, E. Michel, & A. S. Flecker, 2010. Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa. Limnology and Oceanography 55: 214–224.

Cotner, J. B., & B. A. Biddanda, 2002. Small players, large role: Microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems 5: 105–121.

DeLong, J. P., B. Gilbert, J. B. Shurin, V. M. Savage, B. T. Barton, C. F. Clements, A. I. Dell, H. S. Greig, C. D. G. Harley, P. Kratina, K. S. McCann, T. D. Tunney, D. A. Vasseur, & M. I. O'Connor, 2015. The body size dependence of trophic cascades. The American Naturalist 185: 354–366.

Dong, X., A. Ruhí, & N. B. Grimm, 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proceedings of the National Academy of Sciences: **114**: E4744-E4752.

Elser, J. J., K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan, J. Schade, J. Hood, & R. W. Sterner, 2003. Growth rate-stoichiometry couplings in diverse biota. Ecology Letters 6: 936–943.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, & R. W. Sterner, 2000. Nutritional constraints in terrestrial and freshwater food webs. Nature 408: 578–580.

Estes, J. a, J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. a Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, & D. A. Wardle, 2011. Trophic downgrading of planet Earth. Science 333: 301–306.

Farnsworth, K. D., L. Albantakis, & T. Caruso, 2017. Unifying concepts of biological function from molecules to ecosystems. Oikos, 126: 1367–1376.

Fenchel, T., 2008. The microbial loop – 25 years later. Journal of Experimental Marine Biology and Ecology 366: 99–103.

Finlay, J. C., G. E. Small, & R. W. Sterner, 2013. Human influences on nitrogen removal in lakes. Science 342: 247–250.

Fussmann, G. F., 2008. The lake as a system of differential equations - A paradigm for the aquatic ecologist of the 21st Century? International Review of Hydrobiology 93: 532–540.

Garzke, J., S. H. Ishmar, & U. Sommer, 2015. Climate change affects low trophic level marine consumers: warming decreases copepod size and abundance. Oikos 177: 849–860.

Hall, R. O., B. J. Koch, M. C. Marshall, B. W. Taylor, & L. M. Tronstad, 2007. How body size mediates the role of animals in nutrient clcying in aquatic ecosystems In Hildrew, A., D. Raffaelli, & R. Edmonds-Brown (eds), Body Size: The Structure and Function of Aquatic Ecosystems. Cambridge University Press, Cambridge: 286–305.

Hamilton, D.P., Salmaso, N. and Paerl, H.W. 2016. Mitigating harmful cyanobacterial blooms: strategies for control of nitrogen and phosphorus loads. Aquatic Ecology **50**: 351

Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, & M. Loreau, 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. Science 349: aac6284.

He, X., J. F. Kitchell, S. R. Carpenter, J. R. Hodgson, D. E. Schindler, & K. L. Cottingham, 1993. Food web structure and long-term phosphorus recycling: a simulation model evaluation. Transactions of the American Fisheries Society 122: 773–783.

Hellweger, F. L., 2017. 75 years since Monod: It is time to increase the complexity of our predictive ecosystem models. Ecological Modelling 346: 77–87.

Higgins, S. N., B. Althouse, S. P. Devlin, Y. Vadeboncoeur, & M. J. Vander Zanden, 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology 95: 2257–2267.

Horne, C. R., A. G. Hirst, & D. Atkinson, 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. Ecology Letters 18: 327–335.

Houlihan, D. F., 1991. Protein turnover in ectotherms and its relationships to energetics. In: Advances in Comparative and Environmental Physiology. Vol. 7. Springer Berlin, Heidelberg: 1–43.

Imberger, J., and J. C. Patterson. 1990. Physical limnology. Advances in Applied Mechanics, 27, 303–475.

Ings, N. L., J. Grey, L. King, S. McGowan, & A. G. Hildrew, 2017. Modification of littoral algal assemblages by gardening caddisfly larvae. Freshwater Biology 62: 507–518.

Jennings, S., & J. L. Blanchard, 2004. Fish abundance with no fishing: predictions based on macroecological theory. Journal of Animal Ecology 73: 632–642.

Jenny, J.-P., P. Francus, a. Normandeau, F. Lapointe, M.-E. Perga, a. E. K. Ojala, a. Schimmelmann, & B. Zolitschka, 2015. Global spread of hypoxia in freshwater

ecosystems during the last three centuries is caused by rising local human pressure. Global Change Biology 22: 1481–1489.

Jenny, J., A. Normandeau, P. Francus, Z. E. Taranu, I. Gregory-Eaves, F. Lapointe, J. Jautzy, A. E. K. Ojala, J.-M. Dorioz, A. Schimmelmann, & B. Zolitschka, 2016. Urban point sources of nutrients were the leading cause for the historical spread of hypoxia across European lakes. Proceedings of the National Academy of Sciences 113: 12655 – 12660.

Jeppesen, E., M. Søndergaard, J. P. Jensen, K. E. Havens, O. Anneville, L. Carvalho, M. F. Coveney, R. Deneke, M. T. Dokulil, B. Foy, D. Gerdeaux, S. E. Hampton, S. Hilt, K. Kangur, J. Köhler, E. H. H. R. Lammens, T. L. Lauridsen, M. Manca, M. R. Miracle, B. Moss, P. Nõges, G. Persson, G. Phillips, R. Portielje, S. Romo, C. L. Schelske, D. Straile, I. Tatrai, E. Willén, & M. Winder, 2005. Lake responses to reduced nutrient loading - An analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50: 1747–1771.

Kilham, P., & S. Kilham, 1990. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshwater Biology 23: 379–389.

Klompmaker, A., M. Kowalewski, J. W. Huntley, & S. Finnegan, 2017. Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems. Science 356: 1178–1180.

Krause, A. E., K. A. Frank, D. M. Mason, R. E. Ulanowicz, & W. W. Taylor, 2003. Compartments revealed in food-web structure. Nature 426: 282–286.

Kumar, S., R. W. Sterner, & J. C. Finlay, 2008. Nitrogen and carbon uptake dynamics in Lake Superior. Journal of Geophysical Research 113: 1–15.

Lagus, A, J. Suomela, H. Helminen, J. Lehtimäki, J. Sipura, K. Sivonen, & L. Suominen, 2007. Interaction effects of N:P ratios and frequency of nutrient supply on the plankton community in the northern Baltic Sea. Marine Ecology Progress Series 332: 77–92.

Lang, B., R. B. Ehnes, U. Brose, & B. C. Rall, 2017. Temperature and consumer type dependencies of energy flows in natural communities. Oikos. doi:10.1111/oik.04419.

Lavrentyev, P. J., W. S. Gardner, & J. R. Johnson, 1997. Cascading trophic effects on aquatic nitrification - Experimental-evidence and potential implications. Aquatic Microbial Ecology 13: 161–175.

Layman, C. A., S. T. Giery, S. Buhler, R. Rossi, T. Penland, M. N. Henson, A. K. Bogdanoff, M. V. Cove, A. D. Irizarry, C. M. Schalk, & S. K. Archer, 2015. A primer on the history of food web ecology: Fundamental contributions of fourteen researchers. Food Webs 4: 14–24.

Lehmann, M. F., M. Simona, S. Wyss, J. Blees, C. H. Frame, H. Niemann, M. Veronesi, & J. Zopfi, 2015. Powering up the "biogeochemical engine": the impact of exceptional ventilation of a deep meromictic lake on the lacustrine redox, nutrient, and methane balances. Frontiers in Earth Science 3: 1–13.

Levin, S. A., 1999. Fragile Dominion: Complexity and the Commons. Perseus Books, Reading, MA.

Lewis, W. J., 2010. Biogeochemistry of tropical lakes. Verh. Int. Verein. Limnol. 30: 1595–1603.

Lewis, W. M. J., 1996. Tropical lakes: how latitude makes a difference. In: Perspectives in Tropical Limnology. Schiemer F & Boland K (eds). SPB Academic Publishing, Amsterdam, Netherlands. 43-64.

Li, W., & M. H. H. Stevens, 2010. How enrichment, ecosystem size, and their effects on species richness co-determine the stability of microcosm communities. Oikos 119: 686–695.

Ludsin, S. A., M. W. Kershner, K. A. Blocksom, R. L. Knight, & R. A. Stein, 2001. Life after death in Lake Erie: Nutrient cotrols drive fish soecies richness, rehabilitation. Ecological Applications 11: 731–746.

Macintyre, S., J. F. Clark, R. Jellison, & J. P. Fram, 2009. Turbulent mixing induced by nonlinear internal waves in Mono Lake, California. Limnology and Oceanography 54: 2255–2272.

McCann, K. S., A. Hastings, & G. R. Huxel, 1998. Weak trophic interactions and the balance of nature. Nature 395: 794–798.

McCann, K. S., J. B. Rasmussen, & J. Umbanhowar, 2005. The dynamics of spatially coupled food webs. Ecology Letters 8: 513–523.

McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. M. Hood, B. W. Taylor, & S. A Thomas, 2008. Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? Ecology 89: 2335–2346.

McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, & A. T. Fisk, 2015. Food web structure in temporally-forced ecosystems. Trends in Ecology and Evolution 30: 662–672.

McMeans, B. C., K. S. McCann, T. D. Tunney, A. T. Fisk, A. M. Muir, N. P. Lester, B. J. Shuter, & N. Rooney, 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecological Monographs 86: 4–19.

Minagawa, M., & E. Wada, 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48: 1135–1140.

Monismith, S. G., J. Imberger, & M. L. Morison, 1990. Convective Motions in the Sidearm of a Small Reservoir. Source: Limnology and Oceanography 35: 1676–1702.

Moss, B., 2012. Cogs in the endless machine: lakes, climate change and nutrient cycles: a review. The Science of the Total Environment 434: 130–142.

Neutel, A. M., J. A. P. Heesterbeek, J. van de Koppel, G. Hoenderboom, A. Vos, C. Kaldeway, F. Berendse, & P. C. de Ruiter, 2007. Reconciling complexity with stability in naturally assembling food webs. Nature 449, 599–602.

OECD. 1982. Eutrophication of waters—monitoring, assessment and control. Paris: Organisation for Economic Co-operation and Development. 154 pp.

O'Neil, J. M., T. W. Davis, M. A. Burford, & C. J. Gobler, 2012. The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. Harmful Algae 14: 313–334.

O'Reilly, C. M., S. R. Alin, P.-D. D. Plisnier, A. S. Cohen, & B. a McKee, 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature 424: 766–768.

O'Reilly, C. M., R. J. Rowley, P. Schneider, J. D. Lenters, P. B. Mcintyre, & B. M. Kraemer et al., 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42: 10,773–10,781.

Oliver, R. L., D. P. Hamilton, J. D. Brookes, & G. G. Ganf, 2012. Ecology of Cyanobacteria II. In: Whitton, B. A. (ed), Springer Netherlands, Dordrecht: 155–189.

Paerl, H. W., & J. Huisman, 2008. Blooms like it hot. Science 320: 57–58.

Paerl, H. W., & J. L. Pinckney, 1996. A mini-review of microbial consortia: Their roles in aquatic production and biogeochemical cycling. Microbial Ecology 31: 225–247.

Petchey, O. L., A. P. Beckerman, J. O. Riede, & P. H. Warren, 2008. Size, foraging, and food web structure. Proceedings of the National Academy of Sciences 105: 4191–4196.

Polis, G. A., W. B. Anderson, & R. D. Holt, 1997. Toward an integration of landscape and food web ecology : the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289–316.

Pöschke, F., J. Lewandowski, C. Engelhardt, K. Preuß, M. Oczipka, T. Ruhtz, & G. Kirillin, 2015. Upwelling of deep water during thermal stratification onset - A major mechanism of vertical transport in small temperate lakes in spring? Water Resources Research 51: 9612–9627.

Post, D. M., M. E. Conners, & D. S. Goldberg, 2000. Prey preference by a top predator and the stability of linked food chains. Ecology 81: 8–14.

Proulx, S. R., D. E. L. Promislow, & P. C. Phillips, 2005. Network thinking in ecology and evolution. Trends in Ecology and Evolution 20: 345–353.

Ptacknik, R., A. Gomes, S. J. Royer, T. M. Tsagaraki, A. F. Sazhin, S. A. Berger, A. Calbet, J. C. Nejstgaard, S. Isari, S. D. Moorthi, R. Ptacnikova, M. Striebel, S. Zervoudaki, K. Altoja, P. Dimitriou, P. Laas, A. Gazihan-Akoglu, R. A. Martínez, S. Schabhuttl, I. Santi, D. Sousoni, J. M. Gasol, & P. Pitta, 2014. A light-induced shortcut in the planktonic microbial loop. Scientific Reports: 6:29286.

Ptacknik, R., S. D. Moorthi, & H. Hillebrand, 2010. Hutchinson reversed , or why there need to be so many species. In: Woodward, G. (ed), Advances in Ecological Research. Academic Press, Burlington: 1–43.

Robinson, D., 2001. ^{15}N as an integrator of the nitrogen cycle. Trends in Ecology & Evolution 16: 153–162.

Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. Chapin, E. Lambin, T. M. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. a. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, & J. Foley, 2009. Planetary boundaries: Exploring the safe operating space for humanity. Ecology and Society 14: 472–475.

Rolls, R. J., B. Hayden, & K. K. Kahilainen, 2017. Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. Ecology and Evolution 7:4109–4128.

Romanuk, T. N., A. Hayward, & J. A. Hutchings, 2011. Trophic level scales positively with body size in fishes. Global Ecology and Biogeography 20: 231–240.

Rooney, N., K. McCann, G. Gellner, & J. C. Moore, 2006. Structural asymmetry and the stability of diverse food webs. Nature 442: 265–269.

Rooney, N., & K. S. McCann, 2012. Integrating food web diversity, structure and stability. Trends in Ecology and Evolution 27: 40–46.

Sahoo, G. B., A. L. Forrest, S. G. Schladow, J. E. Reuter, R. Coats, & M. Dettinger, 2016. Climate change impacts on lake thermal dynamics and ecosystem vulnerabilities. Limnology and Oceanography 61: 496–507.

Scheffer, M., & S. R. Carpenter, 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends in Ecology and Evolution 18: 648–656.

Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, & K. L. Cottingham, 1993. Food web structure and phosphorus cycling in lakes. Transactions of the American Fisheries Society 122: 756–772.

Schindler, D. E., & M. D. Scheuerell, 2002. Habitat coupling in lake ecosystems. Oikos 98: 177–189.

Schindler, D. W., S. R. Carpenter, S. C. Chapra, R. E. Hecky, & D. M. Orihel, 2016. Reducing phosphorus to curb lake eutrophication is a success. Environmental Science and Technology 50: 8923–8929.

Sentis, A., A. Binzer, & D. S. Boukal, 2017. Temperature-size responses alter food chain persistence across environmental gradients. Ecology Letters 20: 852–862

Sereda, J. M., J. J. Hudson, W. D. Taylor, & E. Demers, 2008. Fish as sources and sinks of nutrients in lakes. Freshwater Biology 53: 278–289.

Shostell, J., & P. A. Bukaveckas, 2004. Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. Aquatic Ecology 38: 359–373.

Smith, V. H., & D. W. Schindler, 2009. Eutrophication science: where do we go from here? Trends in Ecology and Evolution 24: 201–207.

Somes, C. J., A. Schmittner, E. D. Galbraith, M. F. Lehmann, M. A. Altabet, J. P. Montoya, R. M. Letelier, A. C. Mix, A. Bourbonnais, & M. Eby, 2010. Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochemical Cycles 24: 1–16.

Sommer, U., R. Adrian, L. De Senerpont Domis, J. J. Elser, U. Gaedke, B. Ibelings, E. Jeppesen, M. Lürling, J. C. Molinero, W. M. Mooij, E. van Donk, & M. Winder, 2012. Beyond the Plankton Ecology Group (PEG) Model: mechanisms driving plankton succession. Annual Review of Ecology, Evolution, and Systematics 43: 429–448.

Søndergaard, M., E. Jeppesen, T. L. Lauridsen, C. Skov, E. H. Van Nes, R. Roijackers, E. Lammens, & R. Portielje, 2007. Lake restoration: Successes, failures and long-term effects. Journal of Applied Ecology 44: 1095–1105.

Søndergaard, M., T. L. Lauridsen, L. S. Johansson, & E. Jeppesen, 2017. Nitrogen or phosphorus limitation in lakes and its impact on phytoplankton biomass and submerged macrophyte cover. Hydrobiologia 795: 1–14.

Spooner, D. E., P. C. Frost, H. Hillebrand, M. T. Arts, O. Puckrin, & M. a Xenopoulos, 2013. Nutrient loading associated with agriculture land use dampens the importance of consumer-mediated niche construction. Ecology Letters 16: 1115–1125.

Steffan, S. A, Y. Chikaraishi, D. R. Horton, N. Ohkouchi, M. E. Singleton, E. Miliczky, D. B. Hogg, & V. P. Jones, 2013. Trophic hierarchies illuminated via amino acid isotopic analysis. PloS one 8: e76152.

Steffen, W., K. Richardson, J. Rockstrom, S. E. Cornell, I. Fetzer, E. M. Bennett, R. Biggs, S. R. Carpenter, W. de Vries, C. A. de Wit, C. Folke, D. Gerten, J. Heinke, G. M. Mace, L. M. Persson, V. Ramanathan, B. Reyers, & S. Sorlin, 2015. Planetary

boundaries: Guiding human development on a changing planet. Science 347: 1259855-10.

Steiner, C. F., Z. T. Long, J. a. Krumins, & P. J. Morin, 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. Ecology Letters 8: 819–828.

Steiner, C. F., Z. T. Long, J. A. Krumins, & P. J. Morin, 2006. Population and community resilience in multitrophic communities. Ecology 87: 996–1007.

Sterner, R. W., 2008. On the phosphorus limitation paradigm for lakes. International Review of Hydrobiology 93: 433–445.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA.

Stewart, S. D., Hamilton, D. P., Baisden, W. T., Dedual, M., Duggan, I. C., Hicks, B. J., Graham, B. S. 2017 Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. Freshwater Biology. 62: 2008–2025.

Stouffer, D. B., & J. Bascompte, 2010. Understanding food-web persistence from local to global scales. Ecology Letters 13: 154–161.

Stouffer, D. B., & J. Bascompte, 2011. Compartmentalization increases food-web persistence. Proceedings of the National Academy of Sciences of the United States of America 108: 3648–3652.

Thébault, E., & C. Fontaine, 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329: 853–856.

Thompson, R. M., U. Brose, J. a Dunne, R. O. Hall, S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer, & J. M. Tylianakis, 2012. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27: 689–697.

Thrane, J.E., D. O. Hessen, & T. Andersen, 2017. Plasticity in algal stoichiometry: experimental evidence of a temperature-induced shift in optimal supply N:P ratio. Limnology & Oceanography 62: 1346–1354.

Troitskaya, E., V. Blinov, V. Ivanov, A. Zhdanov, R. Gnatovsky, E. Sutyrina, & M. Shimaraev, 2014. Cyclonic circulation and upwelling in Lake Baikal. Aquatic Sciences 77: 171–182.

Vadeboncoeur, Y., K. S. McCann, M. J. Vander Zanden, & J. B. Rasmussen, 2005. Effects of multi-chain omnivory on the strength of trophic control in lakes. Ecosystems 8: 682–693.

Vadeboncoeur, Y., P. B. McIntyre, & M. J. Vander Zanden, 2011. Borders of biodiversity: life at the edge of the world's large lakes. BioScience 61: 526–537.

Vadeboncoeur, Y., M. J. Vander Zanden, & D. M. Lodge, 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. BioScience 52: 44–54.

Vallentyne, J. R. 1974. The algal bowl: lakes and man. Fisheries Research Board of Canada. Misc. Spec. Publ. 22: 186

Vander Zanden, M. J., & J. B. Rasmussen, 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography 46: 2061–2066.

Vander Zanden, M. J., & Y. Vadeboncoeur, 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83: 2152–2161.

Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. Gonzalez, W. H. Renwick, P. A. Soranno, & R. A. Stein, 2005. Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. Bioscience 55: 155–167.

Vanni, M. J., G. Boros, & P. B. McIntyre, 2013. When and fish sources vs. sinks of nutrients in lake ecosystems?. Ecology 94: 2195–2206.

Vanni, M. J., A. M. Bowling, E. M. Dickman, R. S. Hale, K. A. Higgins, M. J. Horgan, L. B. Knoll, W. H. Renwick, & R. A Stein, 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. Ecology 87: 1696–1709.

Vanni, M. J., & C. D. Layne, 1997. Nutrient recycling and herbivory as mechanisms in the " top-down " effect of fish on algae in lakes. Ecology 78: 21–40.

Vanni, M. J., & P. B. McIntyre, 2016. Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: A global synthesis. Ecology 97: 3460–3471.

Verburg, P., R. E. Hecky, & H. Kling, 2003. Ecological consequences of a century of warming in Lake Tanganyika. Science 301: 505–508.

Vincent, W. F., 1983. Phytoplankton production and winter mixing: contrasting effects in two oligotrophic lakes. Journal of Ecology 71: 1–20.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, & J. M. Melillo, 1997. Human domination of Earth's ecosystems. Science 277: 494–499.

Vollenweider, J. R. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Istituto italiano di idrobiologia dott 33:53–83

Walsh, J. R., S. E. Munoz, & M. J. Vander Zanden, 2016. Outbreak of an undetected invasive species triggered by a climate anomaly. Ecosphere 7: e01628.

Wang, S., & U. Brose, 2017. Biodiversity and ecosystem functioning in food webs : the vertical diversity hypothesis. Ecology Letters 21: 9-20.

Ward, C. L., K. S. McCann, & N. Rooney, 2015. HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. Ecology Letters18: 1190-1197

Weber, M. J., & M. L. Brown, 2013. Continuous , pulsed and disrupted nutrient subsidy effects on ecosystem productivity , stability , and energy flow. Ecosphere 4: 1–13.

White, P. A., J. Kalff, J. B. Rasmussen, & J. M. Gasol, 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbial Ecology 21: 99–118.

Winder, M., & D. E. Schindler, 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85: 2100–2106.

Wipfli, M. S., J. S. Richardson, & R. J. Naiman, 2007. Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates, and wood down headwater channels. Journal of the American Water Resources Association 43: 72–85.

Wüest, A., & A. Lorke, 2003. Small scale hydrodynamics in lakes. Annual Review of Fluid Mechanics 35: 373–412.

Xue, D. M., J. Botte, B. De Baets, F. Accoe, A. Nestler, P. Taylor, O. Van Cleemput, M. Berglund, & P. Boeckx, 2009. Present limitations and future prospects of stable isotope methods for nitrate source identification in surface- and groundwater. Water Research 43: 1159–1170.

Chapter three

Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production

This chapter is published as: Stewart S. D., Hamilton D. P., Baisden W. T., Dedual M., Verburg P., Duggan I. C., Hicks B. J., Graham B. S. 2017. Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. *Freshwater Biology* 62: 2008–2025 (DOI: 10.1111/fwb.13046).

3.1 Abstract

1. Lakes are among the most seasonally forced ecosystems on Earth. Seasonal variation in temperature and light produce cyclic patterns in water column mixing, nutrient supply and phytoplankton biomass. Diet responses of consumers to these patterns have rarely been quantified. Moreover, pelagic-littoral coupling of dietary resources by mobile consumers is commonly considered to be static over annual cycles.

2. This study quantifies littoral-pelagic diet responses of multiple consumers to a strong shift in pelagic phytoplankton abundance over an annual cycle (September 2014 – August 2015) in a large (area 616 km^2), oligotrophic, monomictic lake (Lake Taupō, New Zealand). Intra-annual patterns in pelagic phytoplankton (chlorophyll *a*) and zooplankton were determined over multiple years. Major resource and consumer $\delta^{13}C$ and $\delta^{15}N$ were then collected over an annual cycle. Temporal patterns in in food web structure were examined using convex-hulls as a proxy of community trophic niche size. Diet was quantified using mixing models for zooplankton, meso-predatory zooplanktivorous common smelt (*Retropinna retropinna*) and benthivorous common bullies (*Gobiomorphus cotidianus*), as well as the top-predator rainbow trout (*Oncorhynchus mykiss*). Trophic structure patterns for smelt, bullies and trout where then independently examined using compound specific amino-acid $\delta^{15}N$ analyses (CSIA-AA).

3. Lake Taupō demonstrated similar food web patterns to other lakes globally. Phytoplankton and zooplankton demonstrated strong seasonal oscillations of abundance driven by both bottom-up (nutrient supply) and top-down (stable limit

cycle) drivers. The food web demonstrated the typical nested structure. It responded to seasonally low and high pelagic resource availability periods by expansion and contraction, respectively, of trophic niche space. In response to lower pelagic phytoplankton abundance during summer stratification, and phytoplankton accumulation at a deep chlorophyll maximum (DCM), zooplankton abundance reduced and their diet became dominated by phytoplankton from below the thermocline (i.e., the hypolimnion and DCM). This change may have been prompted by the combined drivers of avoidance of predation and depauperate food supply in surface-waters.

4. The diet of smelt and bullies switched from predominantly zooplankton to benthic macroinvertebrates, synchronous with the decline in pelagic zooplankton. Trout diet, inferred from comparison of isotopic signatures of tissues with different turnover rates, also increased littoral resource reliance over the stratified period. Smelt, bully and trout CSIA-AA data confirmed estimates of trophic position and indicated a greater degree of trophic complexity in the littoral than the pelagic food chain.

5. Food webs in large, deep lakes such as Taupō are expected to be primarily pelagic. This study demonstrates the need to re-examine this expectation due to seasonal variations in productivity. The relatively small littoral areas in large lakes, combined with meso-predators' highly seasonally variable littoral resource use, may drive strong seasonal top-down effects on littoral macroinvertebrate prey. Our study supports the notion that food web interactions are highly dynamic and responsive to seasonal forcing. By linking food web dynamics to dynamic environmental conditions, this study provides a framework for future studies research on understanding lake food web responses to a range of annual/seasonal and global environmental change drivers.

3.2 Introduction

Lakes are characterised by strong seasonal gradients (Lewis, 1983; Adrian *et al.*, 2010). Physical forcing by seasonal changes in temperature and light determines water column mixing, nutrient cycling and ultimately primary production within pelagic waters (Kilham & Kilham, 1990; Moss, 2012). Seasonal variations are reinforced by high variability of pelagic primary producer biomass compared with that of littoral producers (Vadeboncoeur *et al.*, 2003; Kraemer *et al.*, 2015). Therefore, seasonal effects are greater in large lakes which typically have higher

ratios of pelagic: littoral surface area and primary production than small lakes. While the responses of lake physical processes and biogeochemical cycles to seasonal climatic forcing have been extensively studied (Sommer *et al.*, 2012), much less is known about the responses of food webs (McMeans *et al.*, 2015). The significance of this knowledge gap relates to the global importance of fisheries in large lakes. Consumers with lifespans greater than one year (i.e., large, higher trophic level predators) typically do not exhibit seasonal biomass changes concomitant with fluctuations in food resources, suggesting that diet-switching to alternative resources is important for maintaining this biomass (McMeans *et al.*, 2015). Integrating food web theory into lake seasonal dynamics presents a promising avenue to better understand the connection of food resources to consumer production.

Strong physical forcing means that lakes are particularly vulnerable to external drivers such as climate change and nutrient enrichment. Climate warming is expected to prolong thermal stratification in many lakes, impacting primary production (Adrian *et al.*, 2010; O'Reilly *et al.*, 2015). In clear, oligotrophic lakes, prolonged stratification is expected to reduce primary production as nutrients are retained below the trophogenic zone (O'Reilly *et al.*, 2003; Verburg *et al.*, 2003). Conversely, in eutrophic lakes with strong light limitation, increased stratification is expected to increase primary production (Paerl & Huisman, 2008).

A review by McMeans and others (2015) applied food web theory to explore impacts of seasonal gradients and resource availability on lake consumers. The authors argued that, in the same way in which large mobile predators stabilise food webs by linking spatially distinct food webs through consumption, large long-lived predators dampen pulses in prey resources. Mobile consumers play a critical role in linking distinct trophic pathways, and this functional trait promotes food web resilience (McCann *et al.*, 2005; McMeans *et al.*, 2016). Large-bodied, higher trophic level predators have a larger number of trophic linkages (Rooney & McCann, 2012) and show less dietary specialisation than lower trophic level consumers (Rooney *et al.*, 2006; McMeans *et al.*, 2016). This nested food web structure is particularly well documented in lakes where fish act to link littoral and pelagic food chains (Schindler & Scheuerell, 2002; Vadeboncoeur *et al.*, 2002; Vander Zanden & Vadeboncoeur, 2002).

An increasing number of studies in a diverse range of aquatic systems have demonstrated food web responses to seasonal changes in productivity (see: Hayden *et al.*, 2014; Dalu *et al.*, 2017; Muzumder *et al.*, 2017; Peralta-Maraver et al. 2017). In smaller lakes, dietary shifts of predators to littoral and terrestrial resources have been observed when pelagic productivity declines (Eloraanta *et al.*, 2015; Dalu *et al.*, 2017; Peralta-Maraver *et al.*, 2017). However, similar observations are lacking in large lakes which have a relatively high proportion of pelagic: littoral habitat with strong seasonal variations in primary production (Vadeboncoeur *et al.*, 2008), are lacking. Eutrophication (Carpenter *et al.*, 2011; Moss *et al.*, 2012) and prolonged stratification (Verburg *et al.*, 2003; Adrian *et al.*, 2010) as a result of global environmental change are expected to substantially impact pelagic productivity. Theoretical arguments suggest that small-bodied consumers with short generation times (i.e., zooplankton) will rapidly adjust their biomass to the availability of resources (i.e., primary producers) and may potentially undergo diapause during resource depletion (Sommer *et al.*, 2012). In contrast, large mobile top predators respond to seasonal variations in pelagic and littoral productivity by switching their diet to alternate (littoral) resources (Hecky & Hesslein, 1995; Vander Zanden & Vadeboncoeur, 2002; Hayden *et al.*, 2014). Investigations of littoral-pelagic coupling have been enhanced greatly through the use of stable isotopes (Middelburg 2014; McMeans et al. 2016).

Food web structure is commonly quantified using $\delta^{15}N$ and $\delta^{13}C$ stable isotopic signatures of known consumers and resources within the food web. Signatures of $\delta^{15}N$ provide a reference for the trophic level of an organism and $\delta^{13}C$ values are used to distinguish littoral and pelagic energy channels. Benthic littoral algae typically have $\delta^{13}C$ values 10 – 15 ‰ higher than pelagic phytoplankton (Hecky & Hesslein, 1995). When depicted in $\delta^{15}N$ and $\delta^{13}C$ isotopic bi-space, lake food webs with a nested structure show a characteristic "A-frame" shape; consumers at lower trophic levels (i.e., with lower $\delta^{15}N$ values) have $\delta^{13}C$ values indicative of strong reliance on a single (i.e., either littoral or pelagic) resource and top predators have $\delta^{13}C$ signatures intermediate between littoral and pelagic food chains (i.e., indicative of strong coupling of these food chains) (McMeans *et al.*, 2016). Repeated measures of consumers through time can then be used to demonstrate resource switching by consumers over annual cycles (O'Reilly *et al.*, 2002). For large, long-lived top-predators that are inherently less abundant, and potentially rare, temporal changes in diet can be assessed by comparing tissues which have different

turnover rates (Vander Zanden *et al.,* 2015; Bond *et al.,* 2016). Several analytical tools are now available for determining aspects of food web structure using stable isotopes. Bayesian mixing models quantify consumer diet composition (Moore & Semmens, 2008; Semmens *et al.,* 2009; Layman *et al.,* 2012) while the range in consumer stable isotope values is used to indicate trophic niche size (Jackson *et al.,* 2011; Layman *et al.*, 2012). Trophic niche estimations of whole communities (e.g., using convex hull area) provide relative comparisons of the range of range of resources supporting food webs (Layman *et al.,* 2012). When integrated, these analytical tools enable specific (diet composition) and general (niche space) determination of lake food web responses to seasonal cycles. Recent analytical advancements, such as compound-specific amino-acid $\delta^{15}N$ analyses (CSIA-AA) provide precise alternative techniques for assessing key attributes of trophic structure such as trophic position (Bowes & Thorpe, 2015) and trophic diversity (Steffan *et al.,* 2015). These techniques can provide independent validation to inferences derived from conventional 'bulk' $\delta^{15}N$ and $\delta^{13}C$ analyses and can reveal 'cryptic' trophic interactions otherwise not identified by bulk isotope analyses (Steffan *et al.,* 2015).

In this study we demonstrate changes in food web consumer dietary responses to a strong seasonal gradient in pelagic productivity in Lake Taupō, New Zealand. This lake exemplifies other large, deep, oligotrophic lakes across the globe which may be subject to greater duration of stratification with climate change, with potential major implications for pelagic vs. littoral food resources and higher trophic levels including lake fisheries (O'Reilly *et al.,* 2003; Adrian *et al.,* 2010). Lake Taupō is the largest permanent lake in Oceania and supports an important rainbow trout (*Oncorhynchus mykiss,* family Salmonidae) fishery. Temporal patterns in producer and consumer dynamics were determined by repeat sampling across spatially distinct littoral and pelagic sites over the course of an annual cycle. First, we used an inter-annual time series of monthly pelagic chlorophyll *a* and zooplankton to examine seasonal biomass patterns. Second, seasonal variations in pelagic-littoral coupling and food web size (i.e. trophic niche) were quantified using $\delta^{13}C$ and $\delta^{15}N$ analyses. Compound-specific amino acid $\delta^{15}N$ analyses provided validation of broad food web structure inferred from mixing model analyses. We hypothesised that the strong seasonal gradient in pelagic phytoplankton abundance: i) will reflect changes in the food web trophic niche size, and ii) a higher degree of littoral-pelagic diet switching to compensate for resource variability. Implications of these findings

are discussed in the context of contemporary food web theory and understanding of lake food web responses to global environmental change.

3.3 Methods

3.3.1 Study site

Lake Taupō is an oligotrophic, warm monomictic lake within a rhyolitic caldera which was last active around 232 AD (Hogg *et al.*, 2011). The lake is characterised by a single basin (mean depth = 90 m) and relatively narrow littoral habitat, particularly in the western area where plunging cliffs constitute much of the shoreline (Figure 3-1). The Waikato River drains to the north and is the sole surface discharge. The mean Secchi depth has been stable at around 15 m over the last decade and commonly exceeds 18 m during summer stratification (Verburg & Albert, 2016). As a result of a combination of mild winters, high water clarity and seasonally elevated surface-water nutrient concentrations, Lake Taupō has a winter phytoplankton productivity maximum that is dominated by diatoms (Vincent, 1983). The summer phytoplankton assemblage is characterised by a deep chlorophyll maximum (DCM) with a similar diatom community to that observed during winter (Hamilton *et al.*, 2010). Colony-forming cyanobacteria (*Dolichospermum* sp., family Nostocaceae) and chlorophytes (*Botryococcus* sp., family Botryococcaceae) occur frequently in the surface-waters during summer stratification. Littoral primary production is dominated by benthic diatomaceous mats to 40 m depth. Non-native macrophyte beds are present sporadically around 5-18 m depth (Howard-Williams & Davies, 1988; Hawes & Smith, 1994). Strong seasonal patterns in pelagic phytoplankton abundance and seasonally stable littoral producer abundance results in seasonal variability in the littoral-pelagic production ratio (Table 3-1).

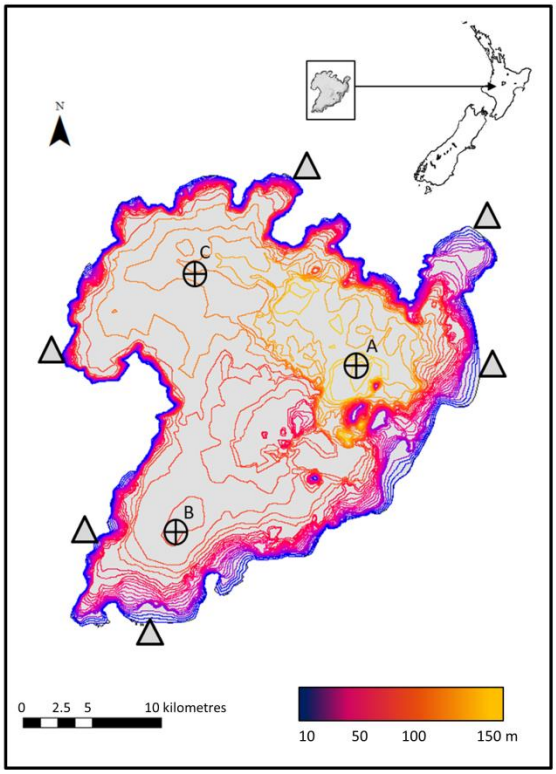


Figure 3-1 Bathymetric map of Lake Taupō showing the three pelagic sampling sites (crossed circles) and six littoral sampling sites (triangles) used in this study.

Native fauna recorded in Lake Taupō include benthivorous common bully (*Gobiomorphus cotidianus*, family Eleotridae), which occupy the littoral zone as adults, benthic invertebrates consisting of snails (*Potamopyrgus antipodarum*, family Tateidae), oligochaete worms and chironomids (e.g., *Chironomus zealandicus*, family Chironomidae), freshwater mussel/kākahi (*Echyridella menziesii*, family Unionidae) and freshwater crayfish/kōura (*Paranephrops planifrons*, family Parastacidae) (Forsyth & McCallum, 1981; Rowe *et al.*, 2002). The earliest zooplankton records indicate a community dominated by Crustacea, in particular the calanoid copepod *Boeckella propinqua* (family Centropagidae) and the cladocerans *Ceriodaphnia dubia* (family Daphniidae) and *Bosmina meridionalis* (family Bosminidae) (Jolly, 1965; Forsyth & McCallum, 1980). A land-locked population of the galaxiid kōaro (*Galaxias brevipinnis*, family Galaxiidae) existed historically within the lake in great abundance but is now largely limited to the tributaries isolated from predatory trout (Rowe, 1993). Eels (*Anguilla* spp., family Anguillidae) are historically absent due to natural and artificial migratory barriers. However, there have been either deliberate or

accidental releases of eels in recent years. These populations are not expected to be self-sustaining populations due to migratory barriers.

Table 3-1: Mean summer stratified and winter mixed Values of physical and chemical parameters (± standard deviation) for Lake Taupō, 2004-2014 (WRC 2015).

Parameter	Summer Stratification	Winter mixing
Mean stratification duration	288 ± 21 days	
Areal percent littoral habitat*	9.7 %	
Temperature	19.4 ± 1.0 °C	11.4 ± 1.2 °C
Secchi	17.6 ± 3.1 m	13.8 ± 2.1 m
TP	4.6 ± 1.8 mg m^{-3}	6.2 ± 2.0 mg m^{-3}
TN	84.5 ± 26.6 mg m^{-3}	81.3 ± 22.0 mg m^{-3}
Chlorophyll a	0.5 ± 0.2 mg m^{-3}	1.7 ± 0.5 mg m^{-3}
Littoral primary producer biomass as percent of lake gross**	16.2 ± 1.5%	1.8 ± 0.7%

A number of exotic fauna have been deliberately or unintentionally introduced. Brown trout (*Salmo trutta*, family Salmonidae) and rainbow trout (*Oncorhynchus mykiss*) were introduced in the late 19th century to establish a sport fishery. Planktivorous shoaling common smelt (*Retropinna retropinna*, family Retropinnidae) were introduced into Taupō from nearby Lake Tarawera in 1936, as a fodder fish for the trout (Ward *et al.*, 2005). Brown Bullhead catfish (*Ameiurus nebulosus*, family Ictaluridae) were either illegally or accidentally introduced to the lake in the early 1980s and the North American cladoceran *Daphnia galeata* (family Daphniidae) was identified in the lake in the early 2000s (Duggan *et al.*, 2006).

3.3.2 Sample collection

Seasonal pelagic primary production patterns – Seasonal patterns of variables in the pelagic zone of Lake Taupō were determined routine sampling at Site A (Figure 3-1). Chlorophyll *a* (Chl-*a*) and zooplankton abundance were assessed from samples collected at Site A by the regional environmental monitoring authority, Waikato Regional Council, from January 2000 to January 2009. Typically, 16 paired Chl-*a* and zooplankton samples were available annually. Chl-*a* samples were collected from the surface-water using a 2-m integrated tube and analysed by NIWA (Hamilton, New Zealand) using acetone pigment extraction and spectrofluorometric measurement (Verburg & Albert, 2016). Zooplankton samples were collected by hauling a net of 63 μm mesh and 100 mm diameter from 100 m depth to the surface. Samples were preserved in 4% formalin and stored until they were counted (3 subsamples) by an experienced technician using a compound

microscope (Verburg & Albert, 2016). A detailed account of sample collection is given in Verburg & Albert (2016). Vertical profiles of chlorophyll fluorescence and temperature were collected from Site A (Figure 3-1) between July 2014 and August 2015. Vertical profiles for temperature, dissolved oxygen and chlorophyll fluorescence were taken using a RBR XR620f Conductivity-Temperature-Depth profiling system fitted with a chlorophyll fluorometer (Seapoint Sensors Inc., New Hampshire, USA).

Food web sampling

Pelagic and littoral habitats were sampled bi-monthly six times between September 2014 and August 2015 to capture the annual mixing-stratification cycle. Six littoral sites and three deep-water pelagic sites were sampled (Figure 3-1). Littoral sites were chosen to be 200-600 m stretches of shoreline. The specific sampling site within this wider area was selected randomly by assigning the southern/western end of the shore a value of zero and the northern/eastern end a value of one, and then estimating the position along the shore that best aligned with a randomly generated decimal value between 0 and 1.

Pelagic sampling – The three pelagic sampling sites, A, B and C, were located at depths of 150, 100, and 110 m, respectively. A sample was taken at the epilimnion (near-surface), metalimnion (mid-water column/DCM) and hypolimnion (profundal bottom water) at each site with a 5 L Van Dorn water sampler. Profundal samples were collected 2 – 5 m above the lake bed. Mid-water column samples varied in depth as they targeted the metalimnetic DCM when it was present. This depth was determined through inspecting the vertical chlorophyll fluorescence profile taken immediately prior to sampling at each site. When no DCM was present (June and August sampling), mid-water-column samples were collected from 40 m depth. Water samples from each depth were filtered through pre-ashed and weighed 0.45 μm Whatman GF/C filters. Zooplankton samples were collected by hauling a 100 μm mesh net of 25 cm diameter through the length of the water column. A 100 μm mesh was used as the majority of zooplankton species in the lake (mostly crustaceans) are >100 μm (McCullum & Forsyth 1981), and the coarser mesh reduced contamination from phytoplankton.

Littoral sampling – Littoral sites were sampled at three depths; 1, 5 and 20 m. A 120 cm^2 Ponar sampler was used to collect three surface sediment samples for

benthic invertebrates as well as benthic particulate organic matter randomly within a 5 m radius of each sample location. Beach seine nets were used to catch smelt, bullies and juvenile trout (< 400 mm length). The seine net was 5 m long by 1.5 m high, and was dragged for 20 m along the shoreline in 0.4 – 1.5 m water depth. If < two smelt or bullies were caught at a site, the net was dragged a second time, for 50 m. Captured fish were immediately euthanized in a brine solution. Mussels were collected by snorkelling within a 15 m radius to 5 m depth. Attempts were made to collect crayfish in the same manner; however, these were successful only at one sampling site. In February SCUBA divers were used to collect mussels, crayfish and macrophytes from depths below 5 m. Divers descended to 15 m depth and progressively worked outwards in an increasing radius until 15 – 20 crayfish and 5 – 10 mussels had been obtained. Ten crayfish and five mussels were selected to represent the size spectrum of each species, with the remainder returned to the lake. The selected specimens were euthanized and stored in brine until returned to the laboratory.

Large trout sample collection – Samples of legal sized trout (>400 mm length) were collected from anglers' catches during an annual fishing competition in March 2015 and 2016. Fish were weighed and measured, and the tails (including white muscle) and livers were removed and stored on ice until return to the laboratory. These tissues were chosen as they are typically discarded by anglers and represent a gradient of tissue turnover rates (Heady & Moore, 2013). Collecting data from a fishing competition is typically biased towards larger fish (Hargrove *et al.*, 2015). However, this competition used a range of award categories that encouraged anglers to submit a spectrum of legal-sized fish. This range of sizes was considered to provide representative samples of adult trout (> 400 mm).

3.3.3 Sample preparation

In the field, sediment samples were stirred in a bucket with an equal volume of lake water. The sediment suspension was then passed through a pre-ashed and weighed 0.45 μm Whatman GF/C filter. The remaining water was drained from the sediment and the sediment was bagged and stored on ice until return to the laboratory. Surface-water was collected in a clean bucket at each site for analysis of particulate organic matter (POM). Up to three litres of sample water was passed through pre-ashed, pre-weighed 0.45 μm Whatman GF/C filters. All sample filters were oven dried at 48°C for >48 h upon return to the laboratory. Fish and invertebrate samples

stored in NaCl brine were washed in freshwater. Fish were weighed and fork-length measured. Mussels were measured along their longest shell axis and crayfish size was assessed using orbital carapace length. Tissue was removed for stable isotope analysis. For mussels and crayfish, samples were of the spatulate burrowing foot and tail muscle, respectively. Samples for smelt >15 mm, bullies >15 mm and trout <200 mm had their head and guts removed while smelt and bullies ≤15 mm were analysed in their entirety. For trout 200 – 400 mm, a segment of white muscle was removed for analysis. For trout > 400 mm, segments of liver, white muscle and fin were differentiated for sample analysis. Fin segment samples were taken down the length of the fin from base to tip, to provide a consistent ratio of soft and hard fin tissue, as isotopic variation occurs along the fin length (Hayden *et al.*, 2015). Zooplankton samples were examined under a dissection microscope (10X magnification) to remove non-zooplankton material. Samples were then centrifuged, decanted and diluted with reverse osmosis (RO) water five times, to remove salt. Benthic invertebrates were removed from sediment samples in the laboratory by sorting and identifying with the naked eye. Samples were sorted into coarse taxonomic/functional groups (i.e., Chironomidae, snails and oligochaete worms). All samples for stable isotope analysis were stored in 1.5 ml Eppendorf snap-lock tubes and were oven dried at 48°C for >48 h.

3.3.4 Organic sample $\delta^{15}N$ and $\delta^{13}C$ analysis

All samples except POM were analysed at the Waikato Stable Isotope Unit (University of Waikato) by combustion using a Dumas elemental analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20-20 Stable Isotope Analyser, Europa Scientific Ltd, Crewe, U.K.). POM samples were analysed at the GNS Science National Isotope Centre (Wellington) by the same procedure on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer (GV Instruments Ltd, Wythenshawe, U.k.). For both laboratories, results are reported with respect to VPDB and N-Air, normalized to an internal standard: leucine. The analytical precision is 0.3‰ and 0.5‰ for $\delta^{15}N$ and 0.2‰ and 0.3‰ for $\delta^{13}C$ for samples analysed in the GNS and University of Waikato laboratories, respectively.

Compound specific amino-acid $\delta^{15}N$ analysis of fish – Compound specific amino-acid (CSIA-AA) $\delta^{15}N$ analyses were performed on fish tissues to determine trophic position and corroborate bulk tissue $\delta^{15}N$ trophic position estimates. Consumer

trophic position can be estimated from amino-acid $\delta^{15}N$ values by calculating the difference between 'trophic' (amino acids that show strong trophic fractionation) and 'source' (show negligible trophic fractionation) amino-acids (Chikaraishi *et al.*, 2009). Three smelt, three trout and two bullies, all collected during February 2015, were selected for analysis representative of the size range for each species. CSIA-AA analyses were conducted at the NIWA stable isotope ecological laboratory (Wellington, New Zealand). The methodology used to determine amino-acid $\delta^{15}N$ values is described in detail in Chikaraishi *et al.* (2007). Briefly, fish tissues were hydrolysed in HCl followed by an n-hexane/dichloromethane wash to remove any hydrophobic constituents such as lipids then, finally, N-pivaloyl/isopropyl (Pv/iPr) derivatization. The $\delta^{15}N$ values of derivatised amino-acids were then determined using a Delta V Plus mass spectrometer interfaced with an Ultra Trace GC gas chromatograph through a GC IsoLink combustion furnace, and liquid nitrogen cold trap (Thermo Fisher Scientific, Darmstadt, Germany). Measured isotopic compositions were corrected relative to known $\delta^{15}N$ values for internal reference material (i.e., caffeine and leucine). All samples were analysed at least in triplicate. The average standard deviation of the multiple analyses per amino acid was 0.9‰, (range: 0.01 to 3.3‰).

Trophic position was subsequently estimated using three methods. The first method was through difference between glutamic acid (Glu) and phenylalanine (Phe) $\delta^{15}N$ values:

$$TP_{Glu-Phe} = [(\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4)/7.6] + 1$$

(Chikaraishi *et al.*, 2009). Second, trophic position was calculated through the difference between mean $\delta^{15}N$ of multiple 'trophic' and 'source' amino-acids:

$$TP_{Mean(troph-sou)} = [\bar{x}\,(\delta^{15}N_{Trophic}) - \bar{x}\,(\delta^{15}N_{Source} - 3.4)/7.6] + 1$$

where source amino acids were glycine and phenylalanine, and trophic amino acids were glutamic acid and alanine. Third, trophic position was estimated by difference between bulk tissue and an external baseline (Vander Zanden and Rasmussen 2001):

$$TP_{Bulk} = [\delta^{15}N_{Consumer} - \delta^{15}N_{Base}/3.4] + 1$$

where baselines were grazing snails and zooplankton for littoral and pelagic food chains, respectively. Trophic position estimates from littoral and pelagic food

chains were weighted for consumers based on estimated littoral-pelagic diet contribution.

3.3.5 Data analysis

Time series data analysis – All statistical relationships were performed in R (version 3.4.1; R core team 2017), using the base package linear model (lm) function. Type II sums of squares were used in all analyses due to the unbalanced study design and co-varying predictor variables (Crawley, 2007). Temporal patterns of Lake Taupō Chl-*a* concentration and zooplankton abundance between 2000 and 2008 were analysed to demonstrate the relationship between intra-annual patterns in pelagic primary and secondary producer biomass. Seasonal patterns in Chl-*a* and zooplankton as well as correlation between the two variables, were investigated by autocorrelation (ACF) and partial autocorrelation (partial ACF) models using the ">acf()" function within R (Crawley, 2007). Chl-*a* and zooplankton relationships were also graphically investigated by comparing mean monthly abundances. Graphical analysis of consumer vs. resource patterns, i.e. phase-plane analysis, is used to infer the nature of interactions. When consumer-resource abundances through time follow an orbital pattern, it indicates a stable limited cycle; the result of Lotka-Volterra predator-prey oscillations (Barraquand *et al.*, 2017). Vertical profiles of chlorophyll fluorescence and temperature from Site A between July 2014 and August 2015 were used to demonstrate pelagic seasonal dynamics for the study period. Thermocline depth was calculated for each month using the R package Lake Analyzer (Read *et al.*, 2011) and Chl-*a* vertical distribution patterns, as well as thermocline depth, were analysed from depth distribution graphs.

Bayesian isotope trophic niche analyses – Isotope based indices for trophic niche space were used to demonstrate food web level seasonal changes in diet diversity. The R package SIBER (Jackson *et al.*, 2011) was used to derive convex hulls for bi-annual food web niche space using a Bayesian inferenced model. Community level niche was estimated by pooling samples from September and December and comparing with samples from June and August. The September-December and June-August periods represented periods of high and low pelagic zooplankton abundance, respectively; hereafter referred to as zooplankton-abundant and -scarce periods. Consumer groups included in the community level niche analysis were limited to those collected within both periods; smelt, bullies, crayfish, mussels, zooplankton and benthic macroinvertebrates. Niche space estimates were derived

using default priors, as described in Jackson et al. (2011), and with > 10,000 Markov Chain Monte-Carlo run iterations.

Bayesian trophic mixing models – Stable isotope mixing-models using food web $\delta^{15}N$ and $\delta^{13}C$ data were employed to quantify consumer-resource interactions in Lake Taupō. First, overall annual food web interactions were quantified using MixSIAR (Stock & Semmens, 2016), a Bayesian mixing model used in R (version 3.3.2; R core team 2015). Consistent trophic discrimination factors of $\Delta^{15}N = 3.4‰$ and $\Delta^{13}C = 0.8‰$ were used across all consumer groups, similar to published values (Vander Zanden & Rasmussen, 2001; McCutchan *et al.*, 2003; Perkins *et al.*, 2013), and consumer $\delta^{13}C$ values were corrected for lipid content following published methods (Post *et al.*, 2007). All samples from the nine sampling sites and six months were combined and sorted by organism group. All mixing model runs were visually inspected to ensure that consumer $\delta^{15}N$ and $\delta^{13}C$ data were constrained within the resource $\delta^{15}N$ and $\delta^{13}C$ iso-space. Model runs were performed until all three Markov chains converged based on both Gelman and Geweke diagnostics (Stock & Semmens, 2016). Typical Markov chain length was between 100,000 and 1,000,000 iterations. All mixing models were performed using an uninformative prior.

Intra-annual dietary patterns for zooplankton, smelt and bullies – Diet composition for mobile consumers (smelt and bullies) was compared across the six sampling months using the six sampling sites as the true unit of replication. Seasonal dietary shifts of smelt and bullies were quantified in MixSiar using $\delta^{15}N$ and $\delta^{13}C$ data from zooplankton and benthic macro-invertebrates to represent two end-members (pelagic and littoral trophic resources, respectively). Sampling site was included as a random factor within the model and sampling month was nested as a factor within that to compare intra-annual dietary changes. Seasonal zooplankton diet composition was determined by partitioning pelagic POM samples by collection depth; surface, DCM and hypolimnion to produce a three end-member mixing mode. The three pelagic sites were the true unit of replication.

Intra-annual dietary patterns for trout – Trout > 400 mm were collected only during a single month so seasonal dietary patterns were not investigated. However, differences in stable isotopic turnover rates between liver (fast turnover), fin (intermediate turnover) and white muscle (slow turnover) (Heady & Moore, 2013) provide a practical method for qualitative assessment of diet changes within single

fish (Quevedo *et al.,* 2009; Bond *et al.,* 2016). Quantitative estimates of diet switching, on the other hand, are more difficult and require robust estimates of tissue-specific turnover rates (Bond *et al.,* 2016). Muscle turnover rates can be estimated for fish of a given body mass raised to the power of 0.13 whereas splanchnic tissue is determined by thermoregulation tactics (Thomas & Crowther, 2015). Heady & Moore (2013), who performed a controlled feeding experiment conducted on a population of rainbow trout, provide tissue turnover rates for muscle fin and liver. In brief, fish were conditioned on a $\delta^{13}C$ and $\delta^{15}N$ isotopically labelled diet for a period after which they were switched to a non-isotopically labelled diet. Individuals were sampled over the duration of the study, sacrificed and isotopic decay rates were quantified for various tissues (Heady & Moore, 2013). Estimated turnover rates for liver (range = 5 – 20, mean = 10 days) and fin (range = 10 – 35, mean = 15 days) were applied directly from Heady & Moore (2013). Muscle turnover rate was derived by applying a body mass correction (Thomas & Crowther, 2014) to the turnover rate (Heady and Moore, 2012) to account for the considerable body mass discrepancy between the experimental fish (mean = 150 g) and our study (mean = 2570 g). Based on these studies, we assumed the mean muscle turnover time for trout was 65 days with 55 – 150 days representing a credible range. Temporal patterns in diet of large trout were quantified from tissue $\delta^{13}C$ and $\delta^{15}N$ data using MixSIAR. Diet composition was estimated based on six potential prey groups (smelt, bullies and crayfish, catfish, benthic macroinvertebrates and snails) from trout liver, fin and muscle samples. Zooplankton were omitted as a diet end-member for two reasons. First, model runs were impractically slow and did not achieve suitable convergence with a seventh end-member of zooplankton included. Second, short runtime (50-iteration) models indicated that zooplankton were a negligible component of trout diet. $\delta^{15}N$ values were corrected for tissue-specific trophic discrimination factors ($\Delta^{15}N_{Liver}$ = 1.4‰, $\Delta^{15}N_{Fin}$ = 1.8‰, $\Delta^{15}N_{Muscle}$ = 3.4‰) and normalised to muscle values (Heady & Moore, 2013).

3.4 Results

3.4.1 Seasonal patterns in lake primary production

Long-term (Jan 2000 – Jan 2009) surface-water Chl-*a* at Site A showed a winter peak in phytoplankton biomass (July-August) and low surface-water concentrations during summer (December-January) (Figure 3-2). Zooplankton also demonstrated a single annual peak, albeit delayed; annual zooplankton maxima were typically in

November-December and minima in July-August. Annual minima for Chl-*a* and zooplankton were on average 22 ± 9% and 20 ± 15% of annual maxima, respectively. Zooplankton abundance (m^{-2}) and Chl-*a* between 2000 and 2009 each showed significant autocorrelation, with a 12 month lag (ACF = 0.3 and 0.7 respectively) indicating an annual cycle of abundance. Strong partial autocorrelation effects on zooplankton at 10 months (partial ACF = 0.3) and Chl-*a* at five months (partial ACF = -0.4) and 11 months (partial ACF = 0.4) provide statistical evidence of complex interdependencies of the two cycles (Figure 3-2). This statistical analysis supports the graphical interpretation (phase-plane) of the relationship between monthly mean Chl-*a* and zooplankton. Between October and March Chl-*a* and zooplankton showed a stable limit cycle. From April through September, however, zooplankton showed a negative linear relationship with Chl-*a* (Figure 3-2). Monthly chlorophyll fluorescence depth profiles from Site A between July 2014 and August 2015 show that biomass was greatest during winter mixing and that a DCM formed below the thermocline during summer (Figure 3-3).

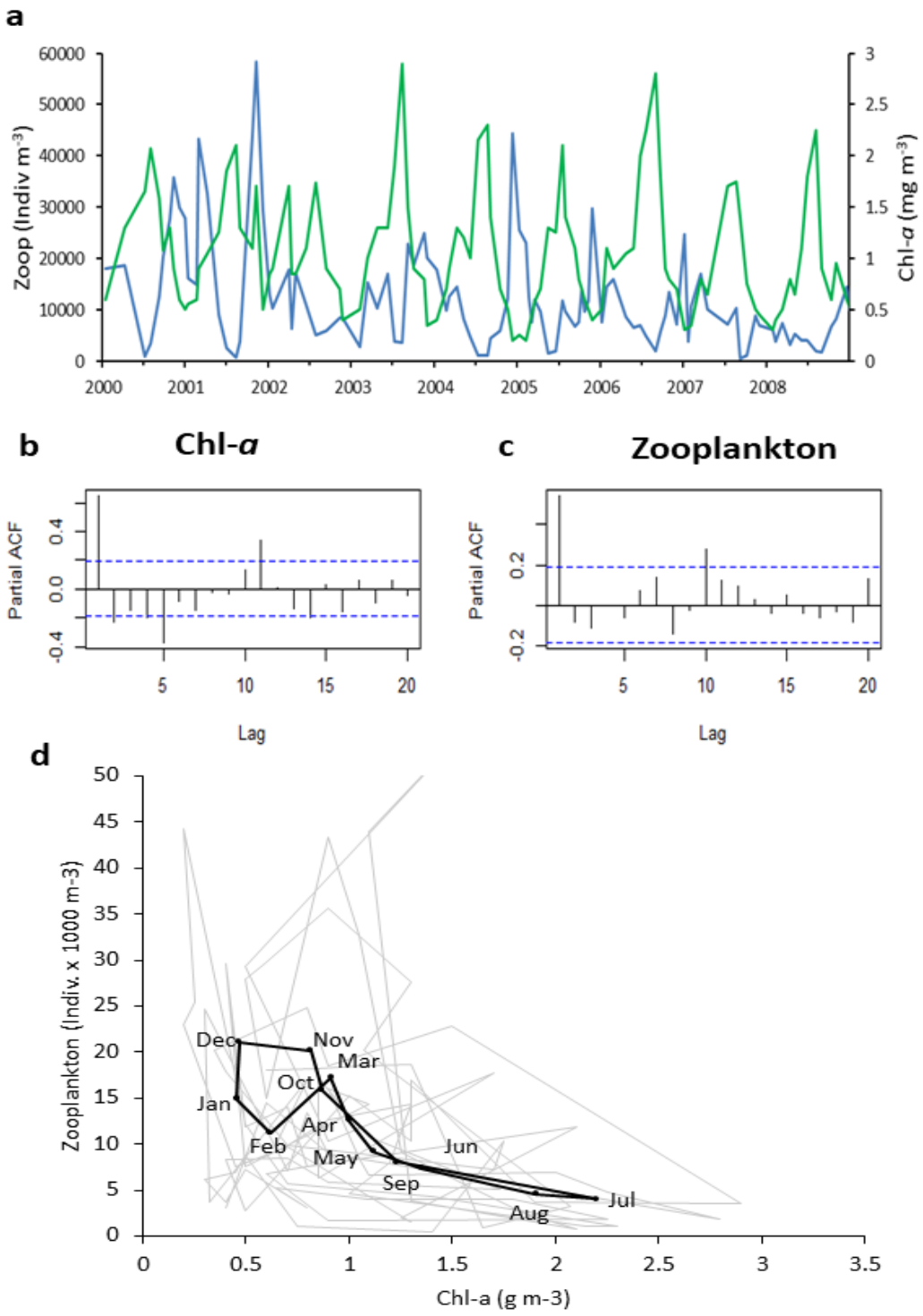


Figure 3-2: Relationships between Lake Taupō chlorophyll a concentration (green line) and zooplankton counts (blue line) both from Site A between January 2000 and January 2009.

3.4.2 Food web stable isotopes

The relative effects of time (i.e., sampling month) and habitat type on $\delta^{15}N$ and $\delta^{13}C$ of functional groups was substantially different between consumer groups. Generally, temporal effects increased and spatial effects decreased with increasing

trophic level (Appendix 3.1). Both $\delta^{15}N$ and $\delta^{13}C$ varied significantly with time (ANOVA: $P < 0.05$) in trout (using tissue turnover as a proxy for time effects), smelt and bullies. By contrast, zooplankton tissue varied with time only for $\delta^{13}C$ ($P < 0.05$), and there was no variation in $\delta^{15}N$ and $\delta^{13}C$ for pelagic POM, littoral POM, benthic POM, benthic macroinvertebrates and catfish. A summary of ANOVA analyses is provided in Appendix 3.2.

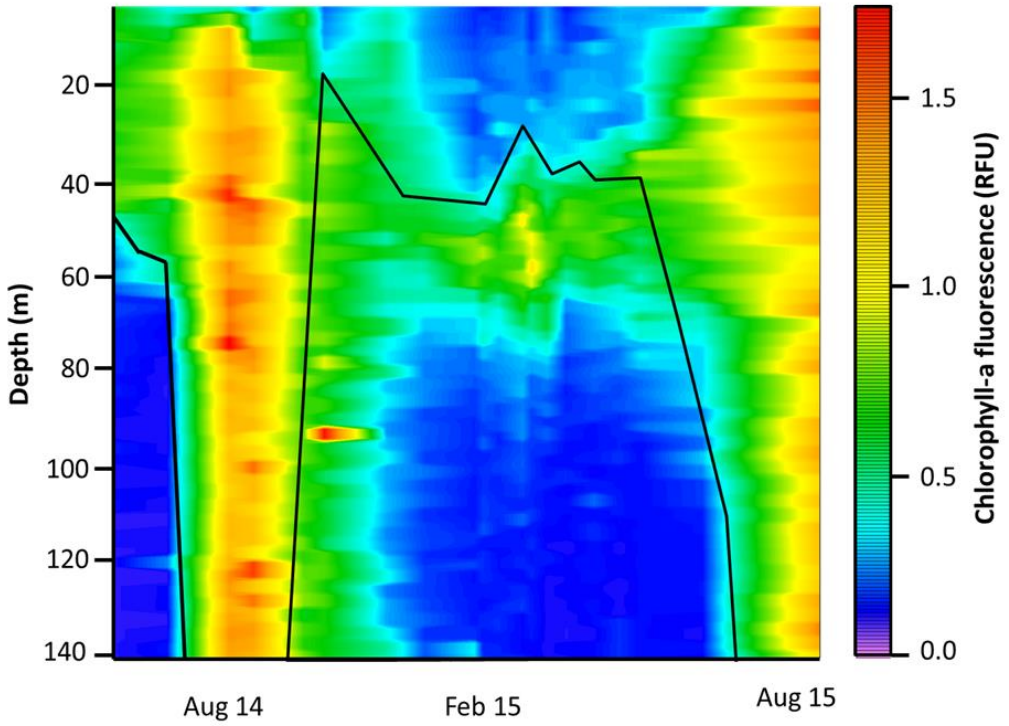


Figure 3-3: Contour plot showing vertical distribution of Chl-a in relative fluorescence units (RFU) from Lake Taupō at Site A between July 2014 and August 2015.

Food web structure – Annual averages of $\delta^{15}N$ and $\delta^{13}C$ for different trophic groups conformed to the "A-frame" shape of a nested food web in isotopic bi-plot space (Figure 3-4). Phytoplankton sampled across all three pelagic sites over the six months had a mean isotopic signature of $\delta^{15}N = -1.2 \pm 5.4$ (95% CI) ‰ and $\delta^{13}C = -24.9 \pm 3.3$‰, slightly lower than benthic microalgae ($\delta^{15}N = 1.9 \pm 1.5$‰ and $\delta^{13}C = -23.1 \pm 3.2$‰) but substantially different from littoral macrophytes/epiphytic algae ($\delta^{15}N = 1.8 \pm 2.2$‰ and $\delta^{13}C = -12.1 \pm 3.7$‰). The mixSIAR model indicated that trout > 400 mm received 69 ± 17% of their diet from pelagic resources. Large trout predominantly preyed upon smelt, with < 1 ± 3% cannibalistic predation on juvenile trout. The model indicated that bullies, catfish and crayfish comprised 14 ± 11, 7 ± 8, and 4 ± 6% respectively, of the diet of large trout. Juvenile trout and

smelt were predominantly zooplanktivorous, obtaining 96 ± 11% and 75 ± 17%, respectively, of their diet from zooplankton. The diet of bullies was predicted to be 73 ± 23% benthic macroinvertebrates. Crayfish and catfish were true omnivores. Crayfish diet was predicted to comprise 52 ± 13% and 47 ± 29% benthic macroinvertebrates and macrophytes, respectively, while catfish diet was 37 ± 22% macrophytes, 27 ± 9% koura, 26 ± 12% benthic macroinvertebrates and 12 ± 6% snails. Of the primary consumers, model output indicated zooplankton diet was > 99 % pelagic phytoplankton and benthic macroinvertebrate diet was 41 ± 15% macrophytes/epiphytic algae, 53 ± 29% benthic microalgae and 5 ± 14% phytoplankton. Freshwater mussel diet was 52 ± 17% phytoplankton and 46 ± 10% benthic microalgae.

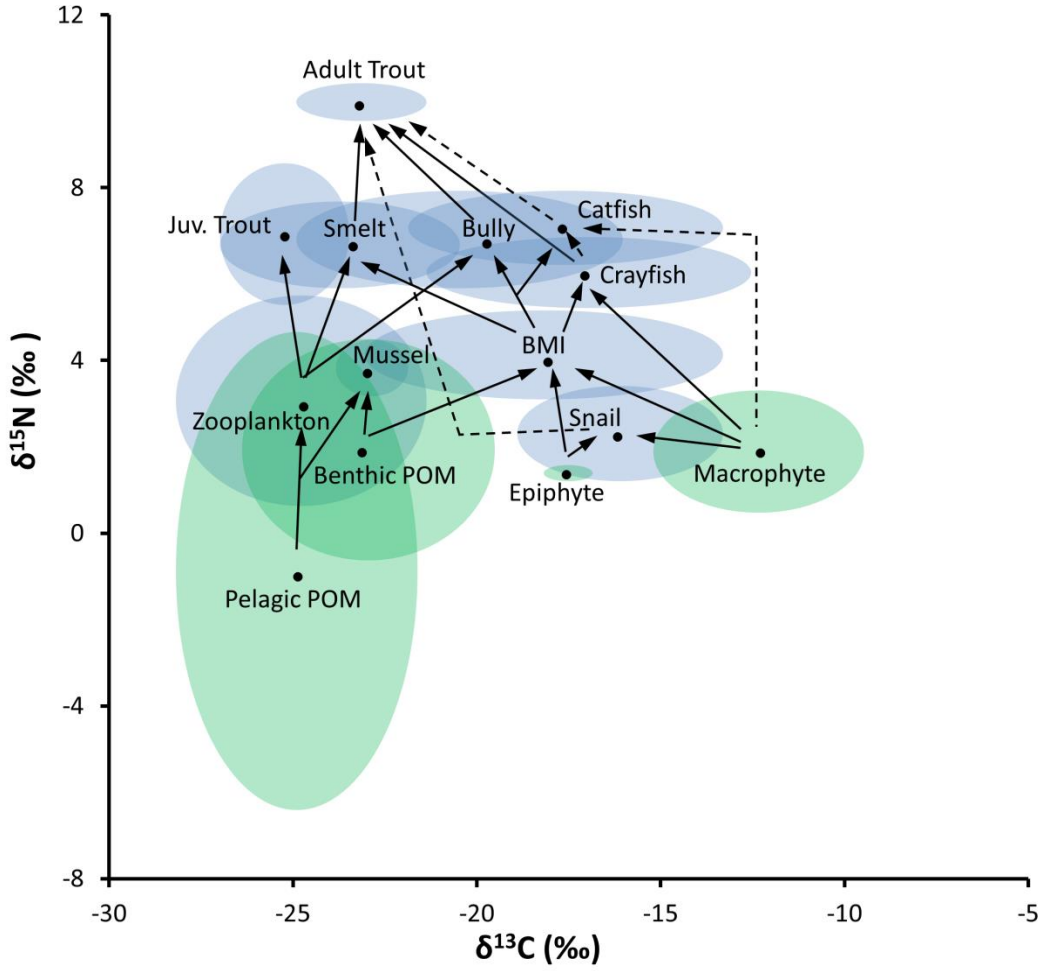


Figure 3-4: Values of $\delta^{15}N$ and $\delta^{13}C$ for food web constituents of Lake Taupō averaged across all nine sampling sites and six sampling events (2014-15). Black dots represent functional group mean values and ellipses represent one standard deviation.

Seasonal community niche space – The food web trophic niche space (convex hull area) was substantially greater during the period of scarce zooplankton abundance (21.5 ± 1.5‰^{2}) compared to during the period of high zooplankton abundance (16.3 ± 1.4‰^{2}) (Figure 3-5). The observed differences in niche space between the two periods was due to a larger range in $\delta^{15}N$ (2.1‰) and $\delta^{13}C$ (2.6‰) values during the scarce period than the abundant period. The overall community trophic position and littoral-pelagic ratio remained similar between the periods. The community centroid was similar between the two periods. During the scarce period the community centroid ($\delta^{15}N$ = 5.0‰, $\delta^{13}C$ = -20.8‰) was relatively lower in $\delta^{15}N$ space than during the abundant period ($\delta^{15}N$ = 5.1‰, $\delta^{13}C$ = -20.8‰), indicating that seasonal niche expansion was not biased towards a certain direction in iso-space (Figure 3-5).

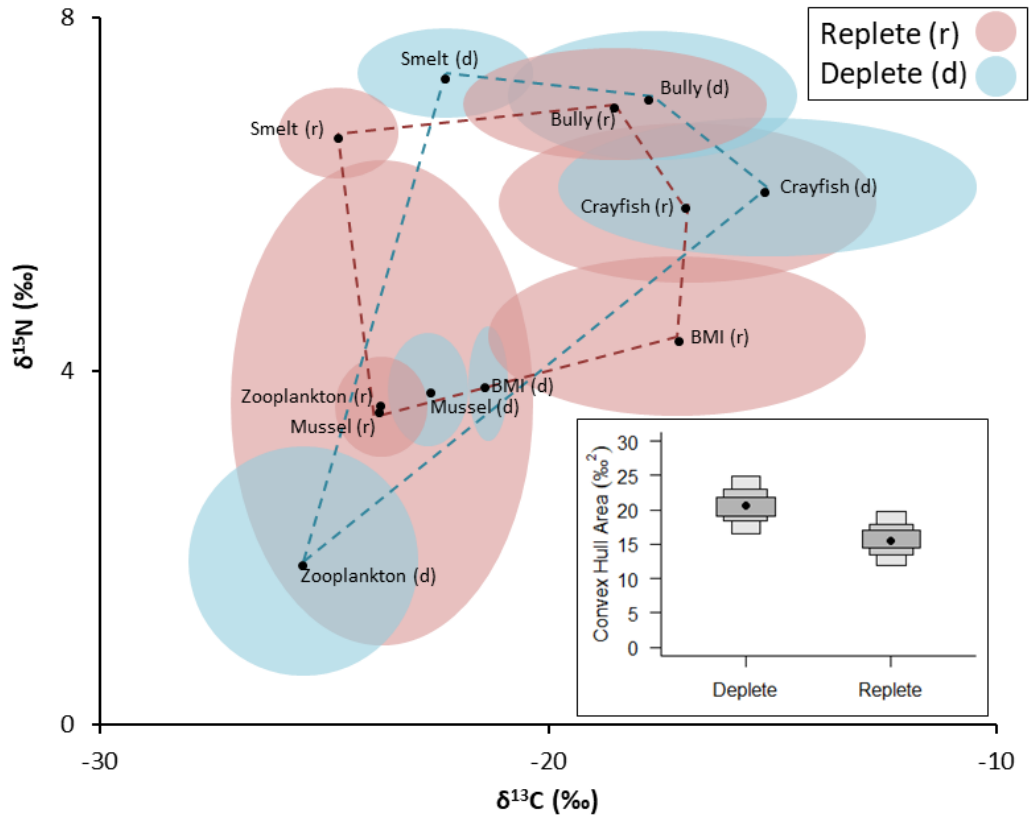


Figure 3-5: Community trophic niche space compared between replete (high pelagic resource availability) and deplete (low pelagic resource availability) periods for selected members of the Lake Taupō food web.

Temporal zooplankton mixing model – Mixing model results for estimating the contribution to zooplankton diet of phytoplankton from surface water, the DCM, and bottom water showed that zooplankton fed more in the bottom water during

stratification than in the mixing period (Figure 3-6). Phytoplankton from surface waters had the smallest contribution to zooplankton diet and bottom-water phytoplankton contributed most during December and April. The contribution of DCM phytoplankton to zooplankton diet was greatest during September and June, the beginning and end of stratification respectively (Figure 3-6).

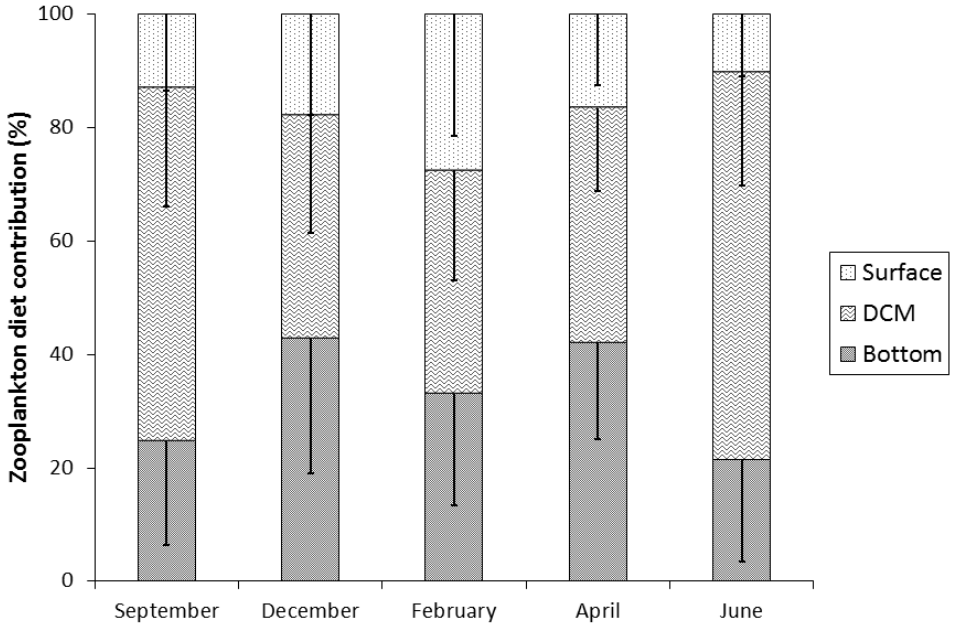


Figure 3-6: Zooplankton diet contribution from phytoplankton grouped by vertical habitat of surface water, deep chlorophyll maximum (DCM) and bottom water.

Temporal smelt and bully mixing model – Results from the mixing model for dietary contribution of zooplankton and benthic macroinvertebrates to smelt and bullies (i.e., mobile meso-predators) demonstrated that the dietary reliance on littoral resources varied substantially over the year for each species (Figure 3-7). Between September 2014 and August 2015 consumption of zooplankton fluctuated between 8 ± 8 and 52 ± 19% for bullies and 18 ± 22 and 84 ± 15% for smelt (Figure 3-7). This equated to an average increase in littoral diet contribution of 48% for smelt and 43% for bullies, which was greater than the difference (39%) of littoral-pelagic diet differentiation in smelt and bullies. Smelt and bully diets were strongly correlated ($R^2 = 0.96$) with the contribution of zooplankton greatest in September 2014 and declining to a minimum in August 2015. Variations in the contribution of

zooplankton to smelt and bully diet corresponded broadly with changes in zooplankton abundance.

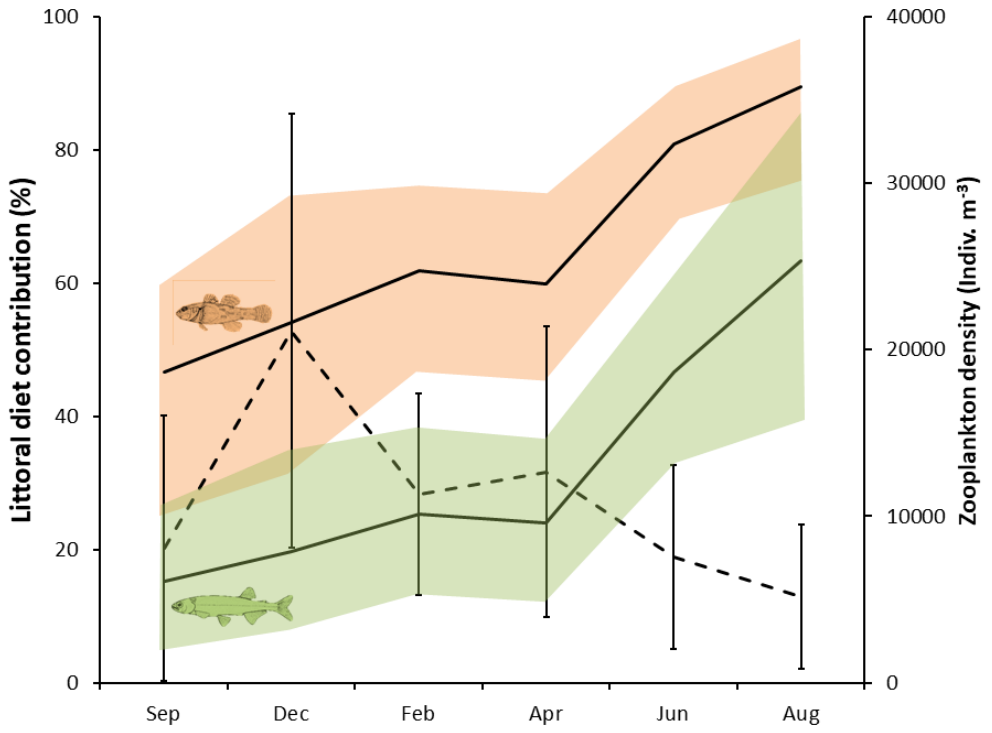


Figure 3-7: Patterns in littoral diet for smelt and bullies over an annual cycle, September 2014 – August 2015. Estimates of contribution of littoral resources to the diet of smelt and bullies are derived from the MixSIAR $\delta^{15}N$ and $\delta^{13}C$ mixing model.

Temporal trout mixing model – Results from mixing model analysis of stable isotope results from trout muscle (turnover 65 days), fin (15 days) and liver (10 days) tissue suggest that trout fed increasingly on littoral prey over a 65-day period (14 Jan to 14 Mar 2015). Based on muscle tissue, smelt comprised 69 ± 17% of trout diet, bullies 14 ± 5%, catfish 7 ± 6%, koura 4 ± 4%, snails 3 ± 2% and benthic macroinvertebrates 2 ± 1% (Figure 3-8). Based on liver samples, the contribution to trout diet from smelt, bully, catfish and crayfish diet was 61 ± 12, 8 ± 4, 8 ± 11 and 2 ± 2%, respectively, with much larger contributions from snails and benthic macroinvertebrates; 19 ± 17% and 7 ± 9%, respectively. Fin samples showed the lowest contribution of smelt to trout diet (52 ± 24%) of any of the tissues, while the contribution of all other prey increased (Figure 3-8). A comparison with previous trout and smelt diet records from Lake Taupō indicates that the littoral diet contribution and the degree of diet switching observed in trout and smelt was greater in our study than previously reported (Table 3-2). Mean littoral diet

contribution of trout and smelt changed from 80 ± 7% in 1989 to 70 ± 13% in this study and 94 ± 4% in 1983 to 82 ± 6% in this study respectively. These increases in littoral diet reliance were associated with changes in the intra-annual diet variation for trout (22% in 1989 and 35% in this study) and smelt (34% in 1989 and 72% in this study).

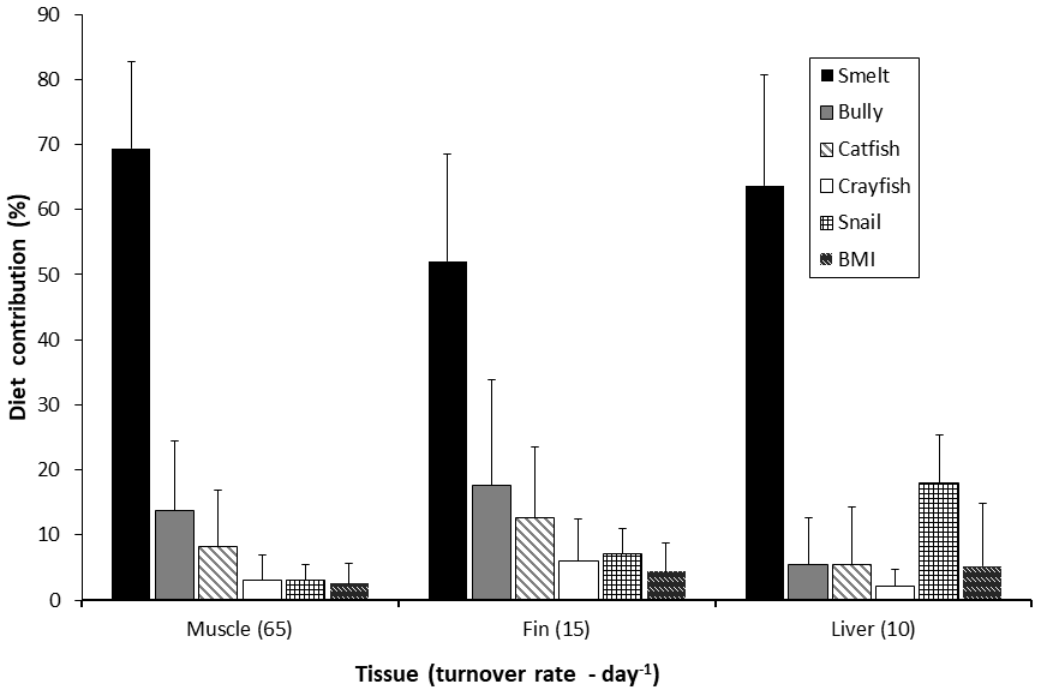


Figure 3-8: Diet composition of trout diet composition estimates derived from $\delta^{15}N$ and $\delta^{13}C$ values of muscle (60 – 150 days), fin (10 – 50 days) and liver (5 – 30 days) tissue (with different turnover rates).

Trophic position – Respective trophic position estimates for smelt, bullies and trout from the two CSIA-AA methods ('Glu-Phe' and 'averaged' trophic-source) produced similar values across fish species. Bulk isotope trophic position estimates were similar to the CSIA-AA methods for smelt and yielded slightly lower estimates for bullies and trout (Figure 3-9). The trophic position estimates for smelt were 2.6 ± 0.7, 2.4 ± 0.4 and 2.5 ± 0.0 (± 1 SD) based on the 'Glu-Phe', 'averaged' trophic-source and bulk isotope methods respectively. For bullies the trophic position estimates were 2.7 ± 0.2, 2.8 ± 0.1 and 2.1 ± 0.2 using the Glu-Phe, averaged and bulk methods. In the same order, trout trophic position estimates were 3.9 ± 0.1, 3.5 ± 0.1 and 3.1 ± 0.0. These results infer the same trophic structure as the mixing model analyses. A significant positive relationship was found between the littoral proportion of consumer's diet and the discrepancy between the CSIA-

AA and bulk isotope method ($P = 0.04$, $R^2 = 0.52$). Variance associated with smelt CSIA-AA values was substantially greater than for bullies and trout.

Table 3-2: Summary of trout and smelt diet obtained from pelagic resources from this study and previous studies. Data for trout are from Cryer (1991) and smelt from Stephens (1984).

	Year	Period	% Pelagic	± SD	Reference
Trout	2014-2015	Annual	70	13	This study
		January	87	15	
		March	52	17	
	1989	Annual	80	7	Cryer 1991
		December	95	2	
		April	73	16	
Smelt	2014-2015	Annual	82	6	This study
		September	98	2	
		August	26	13	
	1981	Annual	94	4	Stephens 1984
		January	99	1	
		August	65	28	

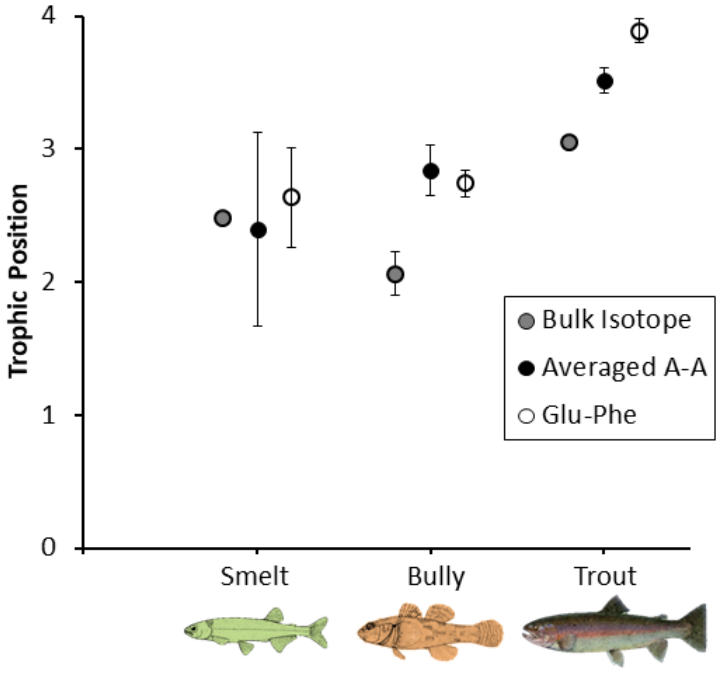


Figure 3-9: Trophic position estimates for common smelt, common bullies and rainbow trout compared between three methods; bulk isotope value, averaged essential and non-essential amino-acids and glutamine – phenylalanine.

3.5 Discussion

Phytoplankton and zooplankton seasonal abundance varied strongly in Lake Taupō and the food web shifted broadly between reliance on littoral and pelagic resources. Our hypotheses were therefore confirmed by findings that: i) seasonal peaks in pelagic resource abundance (zooplankton) corresponded to decreased food web trophic niche size; and ii), trout, smelt, bullies and zooplankton all showed diet changes in response to lower pelagic resource availability, with the magnitude of changes positively related to trophic level. The Lake Taupō food web resembles the generalised nested "A-frame" structure where higher trophic level consumers integrate pelagic and littoral food chains to a greater extent than lower trophic level consumers. This food web structure is seasonally dynamic. The findings of this study are addressed below by discussing: 1), seasonal dynamics of planktonic interactions; 2), seasonal patterns in food web structure; 3), diet patterns of consumer groups; and 4), food web dynamics in the context of GEC drivers.

3.5.1 Seasonal phytoplankton-zooplankton dynamics

Alternate periods of mixing and stratification led to strong temporal and spatial variations in the distribution of phytoplankton biomass and zooplankton abundance in Lake Taupō. During winter mixing, when phytoplankton biomass is evenly distributed throughout the water column, total volumetric pelagic Chl-*a* abundance is on average five times greater than during summer stratified periods (Vincent, 1983) when it is concentrated in the metalimnion (Hamilton *et al.,* 2010). Pelagic zooplankton abundance (individuals m^{-3}) also showed a concomitant seasonal cycle of similar magnitude to Chl-*a*. The significant partial-autocorrelation effects for zooplankton abundance and Chl-*a* concentration together with the phase-plane interpretation suggest highly variable interactions of phytoplankton and zooplankton over an annual cycle, with two distinct states; one from October through March when Chl-*a* and zooplankton display a stable limit cycle, indicative of Lotka-Volterra top-down grazing control (Barraquand *et al.,* 2017) and the second from April through September when nutrient availability determines bottom-up control of phytoplankton. These states reflect dominance by grazing interactions or seasonal mixing, respectively (Vasseur *et al.,* 2014). Conversely, as is typical for many other lakes (Vadeboncoeur *et al.,* 2008; Brothers, Vadeboncoeur & Sibley, 2016), littoral autotrophic biomass remains relatively constant throughout the year in Lake Taupō (Hawes & Smith, 1994). Benthic macroinvertebrate

abundance is correspondingly seasonally invariant in large lakes (Forsyth & McCullum, 1981; Vadeboncoeur *et al.,* 2003). Littoral production may be small relative to pelagic production, but can become a critical resource during periods of extended stratification.

3.5.2 Food web structure

The $\delta^{15}N$ and $\delta^{13}C$ values of the Lake Taupō food web resembled the previously observed nested 'A-frame' structure, adding to the growing recognition that mobile consumers play an important role in linking multiple food chains in aquatic systems (Vander Zanden & Vadeboncoeur, 2002; Sierszen *et al.,* 2014; McMeans *et al.,* 2016). Lower trophic levels showed strong association with either pelagic or littoral food chains while higher trophic levels increasingly integrated the two. The observed trophic structure was broadly confirmed by the CSIA-AA data. Bulk isotope and CSIA-AA-derived trophic position estimates were most similar in consumers that had greater pelagic diet contributions. Underestimating trophic chain length from bulk isotope methods is common (Steffan *et al.,* 2013; Bowes & Thorp, 2015) as CSIA-AA methods reveal 'cryptic' trophic diversity associated with microbial interactions such as detritivory (Steffan *et al.,* 2015). This 'cryptic' trophic diversity reflects the greater trophic complexity in littoral than pelagic food chains (Schindler & Scheuerell, 2002; Vadeboncoeur *et al.,* 2002; McMeans *et al.,* 2016). We expanded the nested 'A'-frame concept of trophic structure by demonstrating a dynamic response to seasonal environmental conditions. The food web contracted during the pelagic zooplankton-abundant period (the onset of a stable limit-cycle), and expanded during the zooplankton-scarce period. Consumers used a wider range of trophic-resources when zooplankton abundance was lowest. Given the dominant contribution of zooplankton to secondary production in Lake Taupō (James 1987), our study demonstrates that food web expansion compensates for resource scarcity. The extent food webs can expand and contract in response to perturbations determines stability (Tunney *et al.,* 2012). Considering seasonal dynamics of specific consumer groups will clarify the relationship between food web expansion and seasonally reduced resource availability.

3.5.3 Seasonal diet patterns of consumer

Coherent seasonal diet patterns were observed across trophic levels; zooplankton, meso- and top-predators. During summer stratification, when a substantial DCM

was present, zooplankton primarily fed on POM below the thermocline (i.e., in the DCM and hypolimnion). The high contribution of bottom-water POM to zooplankton diet at this time was unexpected given bottom-water POM was less abundant and had lower Chl-*a*/C ratios (Verburg & Albert, 2016) than POM from surface water and the DCM. Low Chl-*a*/C ratios indicate a low nutritional quality food resource (Francis *et al.*, 2011). Zooplankton migrate diurnally from dark bottom-waters where they avoid visual predation and ultraviolet radiation to feed within the trophogenic zone (Jolly, 1965; Rhode *et al.,* 2001; Winder *et al.,* 2004). As elevated hypolimnetic POM diet contributions coincide with annual recruitment of young-of-year planktivores (smelt) in Lake Taupō (Cryer, 1991), our data suggest predator avoidance drives zooplankton to increase time spent in bottom-waters and consume resources of low-quality during stratification.

Incidentally, the stratified period coincides with meso-predator (smelt and bully) diets becoming more littoral. Variations in pelagic primary production appear to determine switches in meso-predator diets. However, the highest pelagic zooplankton abundances (in December) were not coincident with the period of maximum zooplankton contribution to smelt diet (September); likely a reflection of zooplankton predator avoidance. Notably, littoral and pelagic resource use patterns by smelt and bullies were highly synchronous over the annual cycle. Synchronicity of seasonal abundance and/or resource use by species demonstrates predominance of bottom-up control as opposed to inter-specific competition (Vasseur *et al.*, 2014) and was surprising to observe in Lake Taupō given differential morphological adaptations and published diet records suggest smelt and bullies have strong niche differentiation (i.e., asynchronous dynamics) (Rowe *et al.*, 2001; Ward *et al.*, 2005). The seasonal pattern of pelagic resource availability (zooplankton abundance) was, however, the major influence on both species' diets. Smelt and bullies are functionally typical of meso-predatory zooplanktivores and benthivores, respectively (Rowe *et al.,* 2001; Ward *et al.,* 2005) and as such, demonstrated diet patterns likely representative of functional responses for lake food webs.

Rainbow trout showed the greatest littoral diet shift over the stratified period; 0.31% day^{-1} compared to 0.14 and 0.12% day^{-1} in smelt and bullies, respectively. Top predators typically have varied diets (McMeans *et al.*, 2016); a trait which provides stability to food webs (Rooney *et al.*, 2006; Wootton, 2017). Our study expands this understanding by demonstrating that top-predators adjust diet to resource

abundance more rapidly than lower trophic levels. Faster diet switching rates suggest top-predators may disproportionately regulate food web temporal dynamics (McMeans *et al.,* 2015). CSIA-AA data validated trout muscle tissue as an indicator of recent diet history (i.e., approx. 65 days prior to capture). Phenylalanine $\delta^{15}N$ (trophic source indicator) of trout tissue was enriched relative to smelt and bullies, indicating different trophic sources. The pelagic baseline (i.e., phytoplankton) $\delta^{15}N$ values in Lake Taupō varied seasonally, which is characteristic of lakes (Syväranta, Tiirola & Jones, 2008). The trophic baseline mismatch between trout and smaller bodied smelt and bullies reflects the longer turnover time of trout tissue (Thomas & Crowther, 2014).

3.5.4 Principles of seasonal lake food web dynamics

The Lake Taupō food web has been considered to be supported predominantly by pelagic production (Rowe & Schallenberg, 2004). Globally, food webs in large lakes are primarily pelagic-based due to lake morphology and productivity (Vadeboncoeur *et al.,* 2003; Eloranta *et al.,* 2015). Top-predator pelagic diet proportion decreases with relative littoral habitat area and reduced pelagic productivity (Vadeboncoeur *et al.,* 2003). Elevated pelagic productivity has the compounding effect of reducing littoral production through reduced water clarity (Vadeboncoeur *et al.,* 2008; Brothers, Vadeboncoeur & Sibley, 2016). Predictions of pelagic diet contribution to consumers commonly assume steady-state trophic interactions, as many systems are only sampled annually (Vadeboncoeur *et al.,* 2003; Janjua & Gerdeaux, 2011). Our study shows seasonal forcing is also a strong driver of littoral-pelagic coupling. Seasonal diet switching results from temporally differentiated resource pulses (Hayden *et al.,* 2014; Dalu *et al.,* 2017; Mazumder *et al.,* 2017; Peralta-Maraver *et al.,* 2017). These dynamics need to be considered for defining trophic structure. For example, during zooplankton-abundant periods zooplankton and mussels had indistinguishable $\delta^{15}N$ and $\delta^{13}C$ values, yet during scarce periods values were substantially different. Freshwater mussels are commonly used to represent $\delta^{15}N$ baselines of pelagic food chains (Vander Zanden & Rasmussen, 2001; Post, 2002) but our study suggests they would give erroneous pelagic $\delta^{15}N$ baseline estimates when pelagic productivity is low.

The temporal dynamics of food webs in lakes can be characterised by both pelagic-littoral coupling and resource variability. These two components represent research themes in food web theory. Pelagic-littoral coupling is addressed in research on

food chain linking, while the temporal variability in resource supply is considered in research on resource pulses. Principles from these research fields can be used to generalise our findings and inform seasonally explicit lake food web responses to altered environmental forcing conditions (e.g., due to GEC drivers). Consumption across food chains by consumers/predators is destabilising when the comparative productivity of the food chains is highly imbalanced (Holt, 1977; Ward, McCann & Rooney, 2015). In lakes, higher pelagic production and resulting increased biomass at higher trophic levels can increase top-down pressure on littoral food chains, making them more susceptible to collapse (Vadeboncoeur *et al.*, 2005; Ward, McCann & Rooney, 2015). Increasing the period between resource pulses in one food chain can increase the top-down pressure in a linked food chain (Holt, 2008; Nowlin, Vanni & Yang, 2008; Wollrab, Diehl & De Roos, 2012). Together, these food web responses suggest the resilience of large lake food webs will be compromised where there is an increase in either periods between pelagic production pulses or the ratio of pelagic to littoral production (i.e. increase pelagic or decrease littoral production).

3.5.5 A case study on seasonally explicit food web vulnerabilities

Our study provides a framework from which seasonally explicit effects of GEC drivers on lake food webs can be explored. Smelt and trout have historically (pre-1990) had a higher proportion of pelagic diet. The recent (post-2005) pelagic diet reduction coincides with a substantial decline in trout biomass (Dedual, *unpublished data*). The proportionately small littoral area in Lake Taupō results in a small benthic macroinvertebrate biomass (41 t dry wt) (Forsyth & McCallum, 1981) relative to zooplankton biomass (227 t) (James, 1987). Combined, these food sources support around 35 t of smelt (Cryer, 1991). During troughs in pelagic productivity, when > 75% of smelt diet can be comprised of benthic macroinvertebrates, smelt predation has the potential to strongly limit macroinvertebrate abundance (Vadeboncoeur *et al.*, 2005). This could be an important consideration for fisheries management. Environmental forcing, through the seasonal pelagic cycle, may alter food web dynamics and impact ecosystem resilience. Accounting for food web seasonal dynamics when considering lake food web responses to GEC effects (e.g., climate warming, eutrophication and increased DOC input) provides a novel perspective which identifies plausible food web responses and feasible management interventions warranting future investigation (Table 3-3). Conversely, the impacts of invasive species are species-specific and

less predictable. Invasive species, such as dreissenid mussels (Higgins *et al.*, 2014; Sterner *et al.*, 2017) and mysid shrimp (Ellis *et al*., 2011) can produce trophic bottlenecks. The recent invasion of *D. galeata* in Lake Taupō (Duggan *et al.* 2006), which has an affinity for low-light environments (Rhode *et al.*,2001; Winder *et al*., 2004), could limit pelagic resource availability for smelt and trout during the stratified period. These scenarios are broadly applicable to large oligotrophic lakes (Shimoda *et al.*, 2011; Sommer *et al.*, 2012; Sterner *et al.*, 2017).

3.5.6 Summary

Food webs are dynamic networks highly responsive to environmental conditions. Nevertheless, these interactions are often distilled into a static interpretation. We demonstrated food web responses to seasonal pelagic forcing patterns typical of deep, oligotrophic lakes. In doing so, we demonstrated the significance of environmental conditions (mixing processes and primary productivity) on food web dynamics. At lower (planktonic) trophic levels, environmental forcing results in abundance oscillations and switching between bottom-up and top-down control. At meso- and top-predator trophic levels, it results in seasonally dynamic littoral-pelagic food chain coupling. These responses manifest as expansion and contraction of the food web isotopic niche space to low and high pelagic resource availability. Considering the dynamic relationship between trophic interactions and environmental forcing, provides a framework from which food web responses to GEC scenarios can be considered and management responses evaluated. The findings observed here for Lake Taupō have broad implications for other large temperate lakes. Synthesising physical limnology, biogeochemistry and food web processes will help food web management of other large, deep and oligotrophic temperate lakes consider seasonal effects.

Table 3-3: Impacts of global environmental change (GEC) drivers of lake food webs when explicitly considering seasonal forcing patterns.

GEC driver	GEC response	Effect on seasonal pelagic resource fluctuation	Food web response	Example	Suggested food web management response
Climate warming	Prolonged stratification	Reduced frequency of pelagic pulse - extended period of low pelagic productivity	Littorification of lake food web	Lake Tanganyika (O'Reilly et al. 2003; Verburg et al. 2003)	Increased management focus on littoral chain
Increased surface run-off	Increased DOC input	Diminished fluctuation - elevated alternative energy source for zooplankton during periods of low phytoplankton production	Reduced coupling to littoral habitats by pelagic consumers	Scandinavian boreal lakes (Deininger et al. 2017)	Minimal intervention - positive food web effects
Eutrophication	Increased pelagic production	Increased seasonal fluctuation in phytoplankton production	Seasonally elevated top-down effects of littoral food chain	Food web models (Vadeboncoeur et al. 2005; Ward et al. 2015)	Catchment nutrient management
Lake-shore urbanisation	Littoral habitat degradation	Increased fluctuation - diminished littoral production	Reduced littoral secondary production to support higher trophic levels	North American temperate lakes (Francis and Schindler 2006; Sass et al. 2012)	Littoral habitat restoration, e.g. additions of woody debris

3.6 References

Adrian R., O'Reilly C.M., Zagarese H., Baines S.B., Hessen D.O., Keller W.B., *et al.* (2010) Lakes as sentinels of climate change. *Limnology & Oceanography* **54**, 2283–2297.

Barraquand F., Louca S., Abbott K.C., Cobbold C.A., DeAngelis D.L., Elderd B.D., *et al.* (2017) Moving forward in circles : challenges and opportunities in modelling population cycles. *Ecology Letters* **20:** 1074-1092.

Bond A.L., Jardine T.D. & Hobson K.A. (2016) Multi-tissue stable-isotope analyses can identify dietary specialization. *Methods in Ecology and Evolution* **7**: 1428–1437.

Bowes R.E. & Thorp J.H. (2015) Consequences of employing amino acid vs. bulk-tissue , stable isotope analysis: a laboratory trophic position experiment. *Ecosphere* **6:** 14 http://dx.doi.org/10.1890/ES14-00423.1.

Brothers S., Vadeboncoeur Y. & Sibley P. (2016) Benthic algae compensate for phytoplankton losses in large aquatic ecosystems. *Global Change Biology* **22**, 3865–3873.

Carpenter S.R., Stanley E.H. & Vander Zanden M.J. (2011) State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources* **36**, 75–99.

Chikaraishi Y., Kashiyama Y., Ogawa N.O., Kitazato H. & Ohkouchi N. (2007) Metabolic control of nitrogen isotope composition of amino acids in macroalgae and gastropods: Implications for aquatic food web studies. *Marine Ecology Progress Series* **342**, 85–90.

Chikaraishi Y., Ogawa N.O., Kashiyama Y., Takano Y., Suga H., Tomitani A., *et al.* (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography: Methods* **7**, 740–750.

Crawley M.J. (2007) *The R Book*, 1st edn. Wiley & Sons Ltd, Chichester.

Cryer M. (1991) *Lake Taupo trout production: a four year study of the rainbow trout fishery of Lake Taupo, New Zealand*. Wellington.

Dalu T., Wasserman R.J., Froneman P.W. & Weyl O.L.F. (2017) Trophic isotopic carbon variation increases with pond's hydroperiod: Evidence from an Austral ephemeral ecosystem. *Scientific Reports* **7**, 7572.

Duggan I.C., Green J.D. & Burger D.F. (2006) First New Zealand records of three non-indigenous zooplankton species: *Skistodiaptomus pallidus*, *Sinodiaptomus valkanovi*, and *Daphnia dentifera*. *New Zealand Journal of Marine and Freshwater Research* **40**, 561–569.

Ellis B.K., Stanford J. a, Goodman D., Stafford C.P., Gustafson D.L., Beauchamp D. a, *et al.* (2011) Long-term effects of a trophic cascade in a large lake ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 1070–1075.

Eloranta A.P., Kahilainen K.K., Amundsen P.A., Knudsen R., Harrod C. & Jones R.I. (2015) Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecology and Evolution* **5**, 1664–1675.

Forsyth D.J. & McCallum I.D. (1981) Benthic macroinvertebrates of Lake Taupo. *New Zealand Journal of Marine and Freshwater Research* **15**, 41–46.

Forsyth D.J. & McCallum I.D. (1980) Zooplankton of Lake Taupo. *New Zealand Journal of Marine and Freshwater Research* **14**, 65–69.

Francis T.B., Schindler D.E., Holtgrieve G.W., Larson E.R., Scheuerell M.D., Semmens B.X., *et al.* (2011) Habitat structure determines resource use by zooplankton in temperate lakes. *Ecology Letters* **4**, 364–372.

Hamilton D.P., O'Brien K.R., Burford M.A., Brookes J.D. & McBride C.G. (2010) Vertical distributions of chlorophyll in deep, warm monomictic lakes. *Aquatic Sciences* **72**, 295–307.

Hargrove J.S., Weyl O.L.F., Allen M.S. & Deacon N.R. (2015) Using tournament angler data to rapidly assess the invasion status of alien sport fishes (Micropterus spp.) in Southern Africa. *PLoS ONE* **10** (6): e0130056.

Hawes I. & Smith R. (1994) Seasonal dynamics of epilithic periphyton in oligotrophic Lake Taupo, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **28**, 1–12.

Hayden B., Harrod C. & Kahilainen K.K. (2014) Dual fuels: Intra-annual variation in the relative importance of benthic and pelagic resources to maintenance, growth and reproduction in a generalist salmonid fish. *Journal of Animal Ecology* **83**, 1501–1512.

Hayden B., Soto D.X., Jardine T.D., Graham B.S., Cunjak R.A., Romakkaniemi A., *et al.* (2015) Small tails tell tall tales - intra-individual variation in the stable isotope values of fish fin. *PLoS ONE* **10**: e0145154..

Heady W.N. & Moore J.W. (2013) Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia* **172**, 21–34.

Hecky R.E. & Hesslein R.H. (1995) Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *Journal of the North American Benthological Society* **14**, 631–653.

Higgins S.N., Althouse B., Devlin S.P., Vadeboncoeur Y. & Vander Zanden M.J. (2014) Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. *Ecology* **95**, 2257–2267.

Hogg A., Lowe D.J., Palmer J., Boswijk G. & Ramsey C.B. (2011) Revised calendar date for the Taupo eruption derived by ^{14}C wiggle-matching using a New Zealand kauri ^{14}C calibration data set. *The Holocene* **22**, 439–449.

Holt R.D. (1977) Predation, apparent competition, and structure of prey communities. *Theoretical Population Biology* **12**, 197–229.

Holt R.D. (2008) Theoretical perspectives on resource pulses. *Ecology* **89**, 671–681.

Howard-Williams C. & Davies J. (1988) The invasion of Lake Taupo by the

submerged water weed Lagarosiphon major and its impact on the native flora. *New Zealand Journal of Ecology* **11**, 13–19.

Jackson A.L., Inger R., Parnell A.C. & Bearhop S. (2011) Comparing isotopic niche widths among and within communities : SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**, 595–602.

James M.R. (1987) Seasonal changes in metabolic rates of zooplankton and their importance to phytoplankton production in two New Zealand lakes of contrasting trophic state. *New Zealand Journal of Marine and Freshwater Research* **21**, 573–583.

Janjua M.Y. & Gerdeaux D. (2011) Evaluation of food web and fish dietary niches in oligotrophic Lake Annecy by gut content and stable isotope analysis. *Lake and Reservoir Management* **27**, 115–127.

Jolly V.H. (1965) Diurnal surface concentrations of zooplankton in Lake Taupo, New Zealand. *Hydrobiologia* **25**, 466–472.

Kilham P. & Kilham S. (1990) Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. *Freshwater Biology* **23**, 379–389.

Kraemer B.M., Anneville O., Chandra S., Dix M., Kuusisto E., Livingstone D.M., *et al.* (2015) Morphometry and average temperature affect lake stratification responses to climate change. *Geophysical Research Letters* **10**, 4981–4988.

Layman C. A, Araujo M.S., Boucek R., Hammerschlag-Peyer C.M., Harrison E., Jud Z.R., *et al.* (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews of the Cambridge Philosophical Society* **87**, 545–62.

Lewis W.M.J. (1983) Revised classification of lakes based on mixing. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 1779–1787.

Mazumder D., Saintilan N., Wen L., Kobayashi T. & Rogers K. (2017) Productivity influences trophic structure in a temporally forced aquatic ecosystem. *Freshwater Biology* **62**, 1528–1538.

McCann K.S., Rasmussen J.B. & Umbanhowar J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters* **8**, 513–23.

McCutchan J.H.J., Lewis W.M.J., Kendall C. & Mcgrath C.C. (2003) Variation in trophic shift for stable isotope ratios of carbon , nitrogen , and sulfur. *Oikos* **102**, 378–390.

McMeans B.C., McCann K.S., Humphries M., Rooney N. & Fisk A.T. (2015) Food web structure in temporally-forced ecosystems. *Trends in Ecology and Evolution* **30**, 662–672.

McMeans B.C., McCann K.S., Tunney T.D., Fisk A.T., Muir A.M., Lester N.P., *et al.* (2016) The adaptive capacity of lake food webs: from individuals to ecosystems. *Ecological Monographs* **86**, 4–19.

Middelburg J.J. (2014) Stable isotopes dissect aquatic food webs from the top to the bottom. *Biogeosciences* **11**, 2357–2371.

Moore J.W. & Semmens B.X. (2008) Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters* **11**, 470–480.

Moss B. (2012) Cogs in the endless machine: lakes, climate change and nutrient cycles: a review. *The Science of the Total Environment* **434**, 130–42.

Nowlin W.H., Vanni M.J. & Yang L.H. (2008) Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* **89**, 647–659.

O'Reilly C.M., Alin S.R., Plisnier P.-D.D., Cohen A.S. & McKee B. A (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature* **424**, 766–768.

O'Reilly C.M., Hecky R.E., Cohen A.S. & Plisnier P.-D. (2002) Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. *Limnology and Oceanography* **47**, 306–309.

O'Reilly C.M., Rowley R.J., Schneider P., Lenters J.D., Mcintyre P.B., Kraemer B.M. et al. (2015) Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters* **42**, 10,773–10,781.

Paerl H.W. & Huisman J. (2008) Blooms like it hot. *Science* **320**, 57–58.

Peralta-Maraver I., Robertson A.L., Rezende E.L., Lemes da Silva A.L., Tonetta D., Lopes M., *et al.* (2017) Winter is coming: Food web structure and seasonality in a subtropical freshwater coastal lake. *Ecology and Evolution* **7**: 4534–4542.

Perkins M.J., McDonald R. A., van Veen F.J.F., Kelly S.D., Rees G. & Bearhop S. (2013) Important impacts of tissue selection and lipid extraction on ecological parameters derived from stable isotope ratios. *Methods in Ecology and Evolution* **4**, 944–953.

Post D.M. (2002) The long and short of food-chain length. *Trends in Ecology & Evolution* **17**, 269–277.

Post D.M., Layman C. a, Arrington D.A., Takimoto G., Quattrochi J. & Montaña C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–89.

Quevedo M., Svanbäck R. & Eklöv P. (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology* **90**, 2263–2274.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Read J.S., Hamilton D.P., Jones I.D., Muraoka K., Winslow L.A., Kroiss R., *et al.* (2011) Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling and Software* **26**, 1325–1336.

Rhode S.C., Pawlowski M. & Tollrian R. (2001) The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature* **412**, 69–72.

Rooney N., McCann K., Gellner G. & Moore J.C. (2006) Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–9.

Rooney N. & McCann K.S. (2012) Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution* **27**, 40–6.

Rowe D.K., Nichols S. & Kelly G.R. (2001) Depth distribution and abundance of the common bully, *Gobiomorphus cotidianus* (Eleotridae), in three oligotrophic New Zealand lakes, one of which is turbid. *Environmental Biology of Fishes* **61**, 407–418.

Rowe D.K., Shankar U. & James M. (2002) Use of GIS to predict effects of water level on the spawning area for smelt, *Retropinna retropinna*, in Lake Taupo, New Zealand. *Fisheries Management and Ecology* **9**, 205–216.

Schindler D.E. & Scheuerell M.D. (2002) Habitat coupling in lake ecosystems. *Oikos* **98**, 177–189.

Semmens B.X., Ward E.J., Moore J.W. & Darimont C.T. (2009) Quantifying inter- and intra-population niche variability using hierarchical bayesian stable isotope mixing models. *PLoS ONE* **4**, 1–9.

Shimoda Y., Azim M.E., Perhar G., Ramin M., Kenney M. A., Sadraddini S., *et al.* (2011) Our current understanding of lake ecosystem response to climate change: What have we really learned from the north temperate deep lakes? *Journal of Great Lakes Research* **37**, 173–193.

Sierszen M.E., Hrabik T.R., Stockwell J.D., Cotter A.M., Hoffman J.C. & Yule D.L. (2014) Depth gradients in food-web processes linking habitats in large lakes: Lake Superior as an exemplar ecosystem. *Freshwater Biology* **59**, 2122–2136.

Sommer U., Adrian R., De Senerpont Domis L., Elser J.J., Gaedke U., Ibelings B., *et al.* (2012) Beyond the Plankton Ecology Group (PEG) Model: mechanisms driving plankton succession. *Annual Review of Ecology, Evolution, and Systematics* **43**, 429–448.

Steffan S. A., Chikaraishi Y., Currie C.R., Horn H., Gaines-Day H.R., Pauli J.N., *et al.* (2015) Microbes are trophic analogs of animals. *Proceedings of the National Academy of Sciences* **112**, 201508782.

Steffan S. A, Chikaraishi Y., Horton D.R., Ohkouchi N., Singleton M.E., Miliczky E., *et al.* (2013) Trophic hierarchies illuminated via amino acid isotopic analysis. *PloS ONE* **8**, e76152.

Sterner R.W., Ostrom P., Ostrom N.E., Klump J.V., Steinman A.D., Dreelin E.A., *et al.* (2017) Grand challenges for research in the Laurentian Great Lakes. *Limnology and Oceanography* **62**, 2510–2523

Stock B.C. & Semmens B.X. (2016) Unifying error structures in commonly used biotracer mixing models. *Ecology* **97**, 2562–2569.

Syväranta J., Tiirola M. & Jones R.I. (2008) Seasonality in lake pelagic $\delta^{15}N$ values: patterns, possible explanations, and implications for food web baselines. *Fundamental and Applied Limnology / Archiv für Hydrobiologie* **172**, 255–262.

Thomas S.M. & Crowther T.W. (2015) Predicting rates of isotopic turnover across the animal kingdom: A synthesis of existing data. *Journal of Animal Ecology* **84**, 861–870.

Tunney T.D., McCann K.S., Lester N.P. & Shuter B.J. (2012) Food web expansion and contraction in response to changing environmental conditions. *Nature Communications* **3**, 1105.

Vadeboncoeur Y., Jeppesen E., Vander Zanden M.J., Schierup H.-H., Christoffersen K.S. & Lodge D.M. (2003) From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology and Oceanography* **48**, 1408–1418.

Vadeboncoeur Y., McCann K.S., Zanden M.J. Vander & Rasmussen J.B. (2005) Effects of multi-chain omnivory on the strength of trophic control in lakes. *Ecosystems* **8**, 682–693.

Vadeboncoeur Y., Peterson G., Vander Zanden M.J. & Kalff J. (2008) Benthic algal production across lake size gradients : interactions among morphometry , nutrients , and light. *Ecology* **89**, 2542–2552.

Vadeboncoeur Y., Vander Zanden M.J. & Lodge D.M. (2002) Putting the Lake Back Together: Reintegrating benthic pathways into lake food web models. *BioScience* **52**, 44–54.

Vasseur D.A., Fox J.W., Gonzalez A., Adrian R., Beisner B.E., Helmus M.R., *et al.* (2014) Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. *Proceedings of the Royal Society - Biological Sciences* **281**, 20140633.

Verburg P. & Albert A. (2016) *Lake Taupo Long-term Monitoring Programme, 2014 – 2015. Prepared for Waikato Regional Council*. NIWA Hamilton, Report: TR 2016/13.

Verburg P., Hecky R.E. & Kling H. (2003) Ecological consequences of a centuray of warming in Lake Tanganyika. *Science* **301**, 505–508.

Vincent W.F. (1983) phytoplankton production and winter mixing: contrasting effects in two oligotrophic lakes. *Journal of Ecology* **71**, 1–20.

Ward C.L., McCann K.S. & Rooney N. (2015) HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. *Ecology Letters*, **18**: 1190–1197.

Ward F.J., Northcote T.G. & Boubee J.A.T. (2005) The New Zealand common smelt: Biology and ecology. *Journal of Fish Biology* **66**, 1–32.

Winder M., Spaak P., Mooij W.M., Ecology S. & Jul N. (2004) Trade-offs in *Daphnia* habitat selection. *Ecology* **85**, 2027–2036.

Wollrab S., Diehl S. & De Roos A.M. (2012) Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. *Ecology letters* **15**, 935–46.

Wootton K.L. (2017) Omnivory and stability in freshwater habitats: does theory match reality? *Freshwater Biology* **62**, 821–832

Vander Zanden M.J., Clayton M.K., Moody E.K., Solomon C.T. & Weidel B.C. (2015) Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS ONE* **10** (1), e0116182.

Vander Zanden M.J. & Rasmussen J.B. (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography* **46**, 2061–2066.

Vander Zanden M.J. & Vadeboncoeur Y. (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology* **83**, 2152–2161.

3.7 Appendices

Appendix 3-4: Summary of Lake Taupō food web $\delta^{15}N$ and $\delta^{13}C$ values by functional group, month and habitat.

Functional group	N	Month	Habitat	$\delta^{13}C$	± 95% CI	$\delta^{15}N$	± 95% CI	Functional group	n	Month	Habitat	$\delta^{13}C$	± 95% CI	$\delta^{15}N$	± 95% CI
Benthic POM	1	September	Littoral - 1 m	-24.9		2.3		Macrophyte	2	Sept	Littoral - 5 m	-13.5	1.8	0.6	1.6
Benthic POM	6	February	Littoral - 1 m	-21.3	2.7	1.0	3.5	Macrophyte	1	Dec	Littoral - 5 m	-11.7		3.7	
Benthic POM	6	April	Littoral - 1 m	-21.2	2.5	0.7	1.9	Macrophyte	4	Feb	Littoral - 5 m	-13.0	2.7	2.7	0.5
Benthic POM	6	June	Littoral - 1 m	-23.8	3.0	2.3	1.2	Epiphyte	1	Sept	Littoral - 5 m	-18.0		1.5	
Benthic POM	6	August	Littoral - 1 m	-25.8	1.9	3.2	0.7	Epiphyte	2	Feb	Littoral - 5 m	-15.7	5.9	0.7	0.5
Benthic POM	3	September	Littoral - 5 m	-19.5	3.6	2.0	0.6	Benthic POM	2	February	Littoral - 20 m	-24.5	1.3	4.2	1.1
								Benthic POM	2	April	Littoral - 20 m	-24.3	0.3	2.9	1.5
Suspended POM	2	September	Pelagic - Bottom	-20.5	5.6	1.8	1.0	Suspended POM	3	September	Pelagic - DCM	-25.6	1.6	-4.8	12.4
Suspended POM	3	December	Pelagic - Bottom	-26.1	1.0	-0.4	4.5	Suspended POM	3	December	Pelagic - DCM	-25.0	0.9	-5.5	1.3
Suspended POM	3	February	Pelagic - Bottom	-23.3	0.7	2.3	1.2	Suspended POM	3	February	Pelagic - DCM	-26.7	4.8	-0.7	4.6
Suspended POM	3	April	Pelagic - Bottom	-20.4	3.3	3.4	1.4	Suspended POM	3	April	Pelagic - DCM	-24.9	1.7	-1.2	7.1
Suspended POM	2	June	Pelagic - Bottom	-26.7	1.5	0.0	0.0	Suspended POM	2	June	Pelagic - DCM	-23.4	2.4	0.0	0.0
Suspended POM	3	August	Pelagic - Bottom	-26.5	0.4	1.6	1.7	Suspended POM	3	August	Pelagic - DCM	-25.0	1.0	3.5	0.5
Suspended POM	5	September	Littoral	-24.0	2.7	-3.1	11.1	Suspended POM	3	September	Pelagic - Surface	-23.8	5.7	0.3	3.0
Suspended POM	5	December	Littoral	-25.1	0.9	-3.1	4.5	Suspended POM	3	December	Pelagic - Surface	-26.8	2.2	-2.1	8.2
Suspended POM	6	February	Littoral	-26.9	2.2	-9.6	4.8	Suspended POM	3	February	Pelagic - Surface	-23.2	2.7	-4.9	4.6
Suspended POM	6	April	Littoral	-22.8	1.2	-0.7	2.8	Suspended POM	3	April	Pelagic - Surface	-23.3	9.5	-1.1	6.2
Suspended POM	6	June	Littoral	-26.4	0.6	2.2	1.0	Suspended POM	2	June	Pelagic - Surface	-22.4	0.9	0.0	0.0
Suspended POM	6	August	Littoral	-27.9	0.6	1.2	2.7	Suspended POM	3	August	Pelagic - Surface	-23.3	2.3	3.8	0.3
Juv. Trout	1	September	Littoral	-24.8		9.7		Kakahi	36	February	Littoral	-22.6	0.3	3.7	0.2
Juv. Trout	12	December	Littoral	-24.8	0.7	6.4	0.6	Kakahi	16	September	Littoral	-23.7	0.5	3.6	0.3
Juv. Trout	1	February	Littoral	-29.8		5.5		Koura	19	February	Littoral	--15.2	2.1	6.0	0.4
Juv. Trout	1	August	Littoral	-25.6		10.6		Koura	13	June	Littoral	--16.9	2.3	5.8	0.5
BMI	1	September	Littoral - 1 m	-20.9		6.7		Zooplankton	8	Sept	Pelagic	-24.8	1.1	4.2	2.5
BMI	1	Dec	Littoral - 1 m	-23.6		4.3		Zooplankton	3	December	Pelagic	-21.6	2.6	2.0	1.1
BMI	1	June	Littoral - 1 m	-20.1		4.0		Zooplankton	5	February	Pelagic	-25.1	0.9	1.3	1.3
BMI	13	September	Littoral - 5 m	-14.8	0.8	3.5	0.2	Zooplankton	4	April	Pelagic	-18.7	1.8	3.6	1.1
BMI	1	April	Littoral - 5 m	-12.4		0.6		Zooplankton	6	June	Pelagic	-24.7	2.4	1.7	0.9
BMI	6	April	Littoral - 20 m	-21.4	0.3	3.8	0.5	Zooplankton	6	August	Pelagic	-26.3	1.6	1.9	1.3
Bully	24	September	Littoral	-22.0	1.7	6.0	0.3	Smelt	5	September	Littoral	-24.8	0.8	7.6	0.4
Bully	5	December	Littoral	-20.9	0.9	7.0	0.1	Smelt	12	December	Littoral	-24.8	0.9	5.8	0.8
Bully	19	February	Littoral	-19.8	1.4	6.7	0.5	Smelt	33	February	Littoral + pelagic	-24.5	0.8	6.1	0.1
Bully	15	April	Littoral	-20.9	1.1	6.9	0.3	Smelt	21	April	Littoral + pelagic	-22.3	1.1	6.5	0.2
Bully	21	June	Littoral	-18.0	1.5	7.0	0.3	Smelt	31	June	Littoral	-22.4	0.5	7.0	0.1
Bully	21	August	Littoral	-17.6	1.3	7.2	0.4	Smelt	23	August	Littoral	-22.2	1.0	6.4	0.4
Catfish	5	Muscle	Littoral	-17.7	3.8	7.0	0.8	Adult Trout	34	Muscle	Littoral + pelagic	-23.2	0.5	9.9	0.1
Catfish	5	Fin	Littoral	-15.9	3.0	6.5	0.9	Adult Trout	36	Fin	Littoral + pelagic	-21.7	0.5	9.1	0.1
Catfish	5	Liver	Littoral	-18.4	2.8	6.1	0.8	Adult Trout	36	Liver	Littoral + pelagic	-24.0	0.6	8.6	0.2

Appendix 3-5: Summary of linear model results for predictors of variation in tissue $\delta^{15}N$ and $\delta^{13}C$ values for Lake Taupō species groups.

			$\delta^{15}N$				$\delta^{13}C$			
	Response	**DF**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**
Trout	Tissue type	**2**	1.79	0.89	4.50	0.02	20.03	10.01	3.41	0.05
	Location caught	**5**	2.11	0.42	2.13	0.09	15.90	3.18	1.08	0.39
	Residuals	**28**	5.55	0.20			82.31	2.94		
Smelt	Site	**5**	7.97	1.59	6.13	< 0.01	156.61	31.32	14.62	< 0.01
	Month	**5**	28.25	5.65	21.73	< 0.01	132.56	26.51	12.38	< 0.01
	Month:Site	**13**	0.12	< 0.01	0.04		125.72	9.67	4.52	< 0.01
	Residuals	**95**	28.09	0.26			203.47	2.14		
Bully	Site	**5**	17.19	3.44	6.33	< 0.01	76.96	15.39	1.48	0.20
	Month	**5**	9.80	1.96	3.61	0.01	385.52	77.10	7.42	< 0.01
	Month:Site	**12**	4.03	0.34	0.62	0.82	96.07	8.01	0.77	0.68
	Residuals	**81**	44.02	0.54			851.90	10.39		
Zooplankton	Site	**2**	1.83	0.92	0.46	0.64	13.35	6.67	1.28	0.30
	Month	**4**	11.69	2.92	1.48	0.25	158.55	39.64	7.58	< 0.01
	Residuals	**17**	33.50	1.97			88.88	5.23		
BMI	Site	**3**	11.98	3.99	2.91	0.05	320.04	160.02	37.64	< 0.01
	Month	**3**	8.28	2.76	2.02	0.13	60.29	20.10	4.73	0.01
	Depth	**2**	9.39	4.70	3.43	0.04	24.16	8.06	1.89	0.15
	Species	**3**	7.15	2.38	1.74	0.18	20.58	6.86	1.61	0.20
	Residuals	**38**	52.04	1.37			161.56	4.25		
Pelagic POM	Location	**2**	36.87	18.43	1.03	0.36	7.40	3.70	0.36	0.70
	Month	**5**	159.90	31.98	1.79	0.14	49.88	9.98	0.98	0.44
	Depth	**2**	85.11	42.56	2.39	0.10	18.79	9.40	0.92	0.41
	Residuals	**41**	730.74	17.82			408.05	10.20		
Benthic POM	Location	**5**	31.74	6.35	0.88	0.52	52.99	10.60	1.07	0.42
	Month	**3**	24.36	8.12	1.13	0.37	90.28	30.09	3.04	0.06
	Residuals	**15**	108.26	7.22			148.58	9.91		

Chapter four

Seasonal and spatial variations in consumer nitrogen excretion in a large, oligotrophic lake: Evidence from stable isotope analyses

4.1 Abstract

Determining spatial and temporal patterns of contributions to nutrient cycling by consumer excretion, or consumer nutrient recycling (CNR), is an elusive goal. Stable isotope analysis of nitrogen has significant potential as it enables *in situ* contributions of CNR to nitrogen cycling to be examined. Trophic fractionation of nitrogen results in excretion of depleted $\delta^{15}N$ by consumers. Hence, substantially $\delta^{15}N$ depleted NH_4^+, NO_3^- and particulate organic matter (POM) is expected to indicate the contribution of CNR at any given point in space and time. This study applied stable isotope analyses to investigate the contribution of CNR in a large oligotropic lake, Lake Taupō, New Zealand, between habitats (epilimnion, metalimnetic deep chlorophyll maximum (DCM), hypolimnion and littoral zone) over an annual mixing cycle. Firstly, we compared consumer tissue and excretion $\delta^{15}N$ values to validate that consumer excretion produces a ^{15}N-depleted nutrient source; secondly, the spatial impact of zooplankton on pelagic nitrogen cycling was demonstrated through comparing their excretion $\delta^{15}NH_4^+$ to water $\delta^{15}NH_4^+$ at three depths (epilimnion, DCM and hypolimnion). Thirdly, $\delta^{15}NH_4^+$, POM $-\delta^{15}N$ and NO_3^- $-\delta^{15}N$ & $\delta^{18}O$ data over an annual mixing cycle demonstrated seasonal patterns in CNR contribution. Spatially, ^{15}N-depleted NH_4^+ values (commonly < -10.0 ‰) and strong correlation with zooplankton excretion ($R^2 = 0.91$) suggested substantial N supply from CNR at the DCM. Temporally, the CNR effect on $\delta^{15}NO_3^-$ was greatest during late stratification when the lake was net-heterotrophic. These results demonstrate that food web dynamics can regulate nitrogen cycling in a large oligotrophic lake.

4.2 Introduction

The role of consumer nutrient recycling (CNR) in nutrient cycles is receiving increasing attention (Vanni et al. 2013; Allgeier et al. 2017; Wing et al. 2017). CNR describes the dietary assimilation and excretion of organic nutrients by

heterotrophic consumers (herein referred to as consumers) and consists of *in situ* recycling (primarily by single celled and smaller bodied consumers) and nutrient translocation (primarily by large-bodied mobile consumers (Vanni et al. 2013; Allgeier et al. 2017). It can enhance primary productivity by translocating nutrients between habitats or by retaining nutrients within an otherwise open system. For example, benthivorous fish translocate nutrients from the bottom sediments to the water column (Vanni et al. 2006), while zooplankton metabolize organic matter that would otherwise sink out of the euphotic zone (Bruce et al. 2006; Higgins et al. 2014). CNR may enhance primary production in oligotrophic lakes to a greater extent than in eutrophic lakes, as oligotrophic lakes typically have higher ratios of biomass of consumers to primary producers (Carpenter et al. 1992; Cooke et al. 2016). Changes in food web structure can also affect rates of CNR and pelagic productivity (Schindler et al. 1993; Higgins et al. 2014). For example, high biomass of invasive dreissenid mussels can re-route pelagic nutrients into the benthos (Conroy et al. 2005; Higgins et al. 2014) and has been linked to fishery collapses (Johannsson et al. 2000; Kao et al. 2015).

The importance of CNR as a nutrient source in lakes will vary significantly spatially and temporally. Spatially, CNR may be relatively more important for phytoplankton in pelagic rather than littoral habitats (Carpenter et al. 1992; Vanni et al. 2013), due in part to enhanced nutrient supply in littoral habitats through interactions with highly microbially active bottom sediments (Figure 4-1). Temporally, the effects of CNR may be greatest in pelagic epilimnia of oligotrophic lakes during periods of stratification, when nutrient concentrations in euphotic surface waters are typically at an annual minimum (Figure 4-1). Climate warming is expected to prolong the duration and intensity of stratification in many lakes (Adrian et al. 2008; O'Reilly et al. 2015), potentially further magnifying the role of CNR during stratification periods (Kilham and Kilham 1992; Lewis 2010; Moss 2012).

Determining spatial and temporal variations in CNR has to date been constrained by methodological limitations. Some previous attempts to quantify the contribution of CNR to pelagic productivity have used consumer incubations to measure nutrient excretion rates (Schindler et al. 1992; Vanni et al. 2006; Sereda et al. 2008). This approach has three limitations: 1) a focus on selected species rather than the net effect of all food web interactions; 2) inability to account for spatio-temporal

mismatches between phytoplankton nutrient demand and consumer distributions (Vanni et al. 2013); and 3) lack of explicit consideration of food web structure in estimating nutrient translocations (Carpenter et al. 1992; Allgeier et al. 2017). Natural abundance $\delta^{15}N$ stable isotope analyses can be used to trace the flows of N through an ecosystem (Middelburg 2014) and hold promise for nitrogen cycling studies. In particular, ^{15}N depletion of dissolved inorganic (DIN) and primary producer N pools has been suggested as an indicator of significant N recycling (Robinson 2001; Somes et al. 2010). Two processes within the nitrogen cycle can lead to significant ^{15}N depletion; consumer N excretion and nitrification (Robinson 2001). The principles underpinning stable isotope analysis of consumer excretion are well established. When a consumer feeds on and metabolises dietary nutrients (for example, N), heavier isotopes (^{15}N) are preferentially assimilated into tissue, while lighter, more reactive isotopes (^{14}N) are preferentially metabolised and excreted back into the environment (Minagawa and Wada 1984) (Figure 4-1). Nitrification can result in an isotope effect of $\Delta^{15}N$ = -20‰, leading to enrichment and depletion of the source ammonium and product nitrate pools, respectively (Figure 4-1). However, isotopic fractionation is dependent on open system dynamics (i.e., chemical reactions not going to completion). Hence, the degree of fractionation during nitrification is negatively related to demand for ammonium and positively related to ammonium concentration (Liu et al. 2013; Denk et al. 2017). In N deficient systems, where nitrification approximates closed system cycling, N excretion from heterotrophic metabolism becomes the primary process of ^{15}N depletion. During periods of significant CNR, labile N pools with rapid turnover have more negative $\delta^{15}N$ values than slow-turnover pools (Minagawa and Wada 1984; Middelburg 2014). Isotopic effects of CNR may be most evident in oligotrophic systems (i.e., with low nitrogen availability) due to the increased importance of *in situ* recycling over external sources (Sigman et al. 2006; Xue et al. 2009). In the tropical Atlantic Ocean, ^{15}N-deplete nitrate has been used to indicate a significant contribution of zooplankton to CNR (Somes et al. 2010). In terrestrial ecosystems, ^{15}N deplete values in fast-turnover foliage compared with relatively ^{15}N enriched slow-turnover soil organic matter have been used to indicate high rates of nitrogen recycling in Arctic tundra (Michelsen et al. 1996) and temperate rain forest ecosystems (Menge et al. 2011). Analogously, isotopically deplete dissolved $\delta^{56}Fe$ values in the Southern Ocean have been attributed to high rates of recycling in these iron-limited waters (Wing et al. 2017).

The history of use of stable isotopes for N cycling in ecosystems originates from identifying sources of N (Anisfeld et al. 2007; Kendall et al. 2007; Bartrons et al. 2010) and assuming that these sources have unique processes determining their $\delta^{15}N$ values (Kendall et al. 2007; Sharp 2007). Ammonium and nitrate $\delta^{15}N$ have shown limited success in differentiating N sources. However, dual nitrate $\delta^{15}N$ and $\delta^{18}O$ determination has proved useful (Kendall et al. 2007). Nitrate $\delta^{18}O$ indicate $\delta^{18}O$ values of water and ambient oxygen characteristic to the environmental conditions during nitrate formation (Kendall et al. 2007; Xue et al. 2009). Often, however, source signatures are affected by N attenuation processes (Xue et al. 2009; Nestler et al. 2011). For example, denitrification and phytoplankton uptake preferentially remove nitrate with isotopically light N and O, which results in a positive linear relationship between nitrate $\delta^{15}N$ and $\delta^{18}O$ values (Sigman et al. 2005; Granger and Wankel 2016; Wells et al. 2016).

Increasingly, N isotopes are being used to study processes occurring in the N cycle (Finlay et al. 2007; Xue et al. 2009). This change has occurred in step with analytical method developments, which now enable robust analyses of $\delta^{15}N\text{-}NH_4^+$ values (Zhang et al. 2005) as well as dual nitrate $\delta^{15}N$ and $\delta^{18}O$ determination (Sigman et al. 2001; McIlvin and Altabet 2005) at concentrations as low as 2 mg N m^{-3}. This ability to accurately determine low concentration nitrate and ammonium $\delta^{15}N$ values enables differentiation of source effects (mixing) versus process effects (kinetic fractionation). Attenuation and mixing can be differentiated using the relationship between the isotope and the concentration of the atom according to the Keeling relationship (Keeling 1958; Sharp 2007; Bartrons et al. 2010). An linear inverse relationship between nitrate concentration and NO_3^-–$\delta^{15}N$ values (i.e., NO_3^-–$\delta^{15}N = f([NO_3^-]^{-1})$) indicates end-member mixing. Conversely, a natural log linear relationship (i.e., NO_3^-–$\delta^{15}N = f(\ln[NO_3^-])$) indicates kinetic fractionation (Sharp 2007). This is because fractionation effects are reduced at lower nitrate concentrations whereas effects of mixing are amplified. In the context of investigating CNR, the presence of an end-member mixing relationship could be used to quantify relative contributions of CNR-derived nitrate to other sources such as catchment inputs.

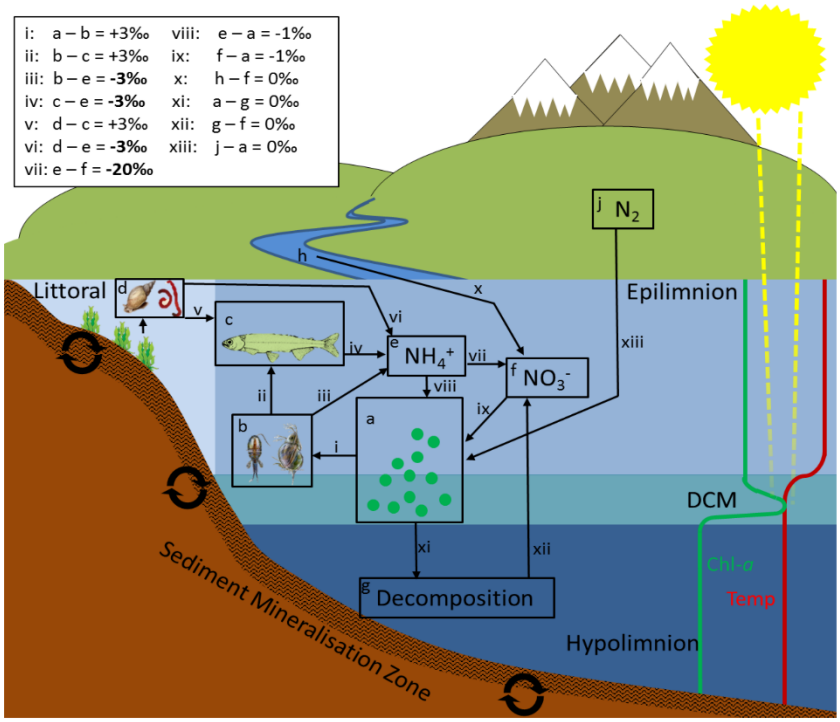


Figure 4-1: Conceptual model of Lake Taupō nitrogen cycle including consumer nutrient recycling, hydrodynamic, biogeochemical processes and catchment inputs. Arrows represent fluxes of nitrogen.

Based on previous studies, it can be suggest that nitrate $\delta^{18}O$ values track the ratio of productivity to respiration, providing a proxy for lake physiological status. In lakes, $\delta^{18}O$ of dissolved oxygen values has been used to estimate the ratio of production to respiration (P:R) (Kendall et al. 2007; Finlay et al. 2007; Wassenaar 2012). Dissolved oxygen $\delta^{18}O$ is transferred to nitrate $\delta^{18}O$ during nitrification (Xue et al. 2009; Finlay et al. 2007). Oxygen in nitrate is derived from dissolved oxygen (DO) and ambient water at a 1:2 ratio (Finlay et al. 2007; Xue et al. 2009). Where $\delta^{18}O$-H_2O values are relatively homogenous, variation in nitrate $\delta^{18}O$ reflects that of dissolved oxygen (Finlay et al. 2007). In the absence of biological activity, dissolved oxygen $\delta^{18}O$ is in equilibrium with the atmosphere ($\delta^{18}O$ = 23.5 ‰) (Wassenaar 2012). Relatively enriched ^{18}O indicates net ecosystem respiration and deplete ^{18}O indicates net ecosystem production (Wassenaar 2012). Photosynthesis results in ^{18}O depletion of DO as it generates oxygen derived from dissolved CO_2 which is in equilibrium with ambient water and has a much lower $\delta^{18}O$ value ($\delta^{18}O$ = -8 ± 7 ‰) than the atmosphere (Sharp 2007; Wassenaar 2012). Respiration results in ^{18}O enrichment of the DO pool as isotopically light oxygen is preferentially assimilated during respiration. The isotopic discrimination factor ($\Delta^{18}O$) for ecosystem respiration is close to 1 ‰ (Wassenaar 2012). Dual isotope NO_3^- ($\delta^{15}N$

and $\delta^{18}O$) analyses can provide important information on nitrogen cycling processes; $\delta^{15}N$ values indicate *loose* vs. *tight* cycling (i.e., the intensity of CNR) and $\delta^{18}O$ values indicate ecosystem metabolic state.

Our study uses advances in stable isotope analytical techniques to quantify the spatial and temporal significance of CNR as a component of the N cycle over an annual stratification cycle in a large (616 km^2) oligotrophic lake; Taupō, New Zealand. Analyses of $\delta^{15}N$ from consumer tissue and excretion as well as ammonium, POM and nitrate within the water are used to investigate CNR fluxes that operate at different rates. We first tested the assumption that consumer excretion by several consumers results in ^{15}N depletion of ammonium. Second, we used relationships between $\delta^{15}N$ values of zooplankton excretion and ambient water ammonium to determine the contribution of zooplankton excretion to CNR. Finally, we examined the effect of CNR on $\delta^{15}N$ values relative to transport and mixing processes in Lake Taupō. These three components enabled us to test the hypothesis that CNR is important to nitrogen cycling and highly spatially while being temporally variable in a large oligotrophic lake.

4.3 Methods

4.3.1 Study area

Lake Taupō, in the central North Island of New Zealand, is characteristic of other large lakes globally. It is oligotrophic, monomictic, and has a small ratio of littoral relative to pelagic habitat. Lake Taupō formed in a rhyolitic caldera that was last active around 232 AD (Hogg et al. 2012), with a single deep basin. The Waikato River drains to the north and is the sole surface discharge. The hypolimnion has a stable temperature of approximately 11.5 °C year-round, while the epilimnion fluctuates between ~11.5 °C during winter mixing and up to 20 – 25 °C during summer mixing (Vincent 1983). Primary production in Lake Taupō has been demonstrated to be predominantly N-limited (White and Payne 1977; Vincent 1983) and the lake is one of only a few globally where management is focused solely on catchment N controls (Schindler et al. 2016). Catchment surface water inflows contribute 82 % of the approximately 1200 t annual N budget (Vant 2013). Atmospheric wet deposition accounts for approximately 17 % of the N load while septic tanks and geothermal inputs account for the remainder (Hamilton and Wilkin 2005; Gibbs and Vant 2006). The annual mean Secchi depth has been relatively stable at around 15 m over the last decade and commonly exceeds 18 m during

summer stratification. As a result of a combination of mild winters, high water clarity and seasonally elevated surface-water nutrient concentrations, Lake Taupō has a winter phytoplankton productivity maximum which is dominated by diatoms (Vincent 1983). The summer phytoplankton assemblage is characterised by a deep chlorophyll maximum (DCM) at 40 – 60 m depth, which has a similar diatom community to that observed through the water column during winter (Hamilton et al. 2010). Cyanobacteria (e.g., *Dolichospermum* sp.) and chlorophytes (e.g., *Botryococcus* sp.) occur frequently in the surface waters during summer stratification. Littoral primary production is dominated by benthic diatomaceous mats to 40 m depth. Invasive macrophyte beds are present sporadically around 5-18 m depth (Howard-Williams and Davies 1988; Hawes and Smith 1994).

The fauna documented in Lake Taupō are typical of oligotrophic New Zealand lakes and are functionally typical of large oligotrophic lakes globally (Rowe and Schallenberg 2004). A detailed description of the food web is given in Stewart et al. (2017). Nutrient excretion incubations were performed on four consumer groups: common smelt, common bully, pelagic zooplankton grazers and freshwater mussels. These consumers represent primary and secondary consumers with comparable diets from both littoral and pelagic habitats (Stewart et al. 2017). Common smelt are a pelagic zooplanktivorous fish. Smelt grow to 70 mm (fork-length) in a year, after which the majority of the population die post-spawning (Ward et al. 2005). Common bullies are a littoral benthivorous fish preying on benthic macroinvertebrates (Stewart et al. 2017). Bullies grow up to 120 mm and are the most numerous littoral fish in most oligotrophic New Zealand lakes (Rowe 2003). The zooplankton community in Lake Taupō is dominated by Crustacea and consists of the calanoid copepod *Boeckella propinqua*, and the cladocerans *Ceriodaphnia dubia* and *Bosmina meridionalis* (Forsyth and McCallum 1980; James 1987) as well as the North American cladoceran *Daphnia galeata*, which was first identified in the lake in the early 2000s (Duggan et al. 2006). Zooplankton biomass typically peaks in late spring, a three to four month lag behind winter peak chlorophyll concentrations (Stewart et al. 2017). Freshwater mussels feed through a combination of filter feeding phytoplankton and foraging benthic organic particulates using their spatulate foot (Cyr et al. 2017). Freshwater mussels occupy littoral substrate between 2 m and 40 m depth in Lake Taupō (James 1985).

4.3.2 Sample collection

Sampling was carried out for four distinct lake zones, littoral, surface, metalimnetic/DCM and hypolimnetic water, (Figure 4-1) six times between September 2014 and August 2015. Three deep-water pelagic sites and six littoral sites were used as true replicates (Figure 4-2). Pelagic sites varied in depth from 100 to 150 m. Littoral sites included 200 to 600 m lengths of shoreline within which a specific sampling site was randomly selected by assigning the southern/western end of the shore a value of zero and the northern/eastern end a value of one, and then estimating the position along the shore that aligned with a randomly generated value between 0 and 1. Water samples were taken at each site bi-monthly between September 2014 and August 2015. Consumer $\delta^{15}N$ nutrient excretion incubations were done with zooplankton in February, June and August 2014, freshwater mussels in February 2014, and smelt and bully in February, April, June and August 2015.

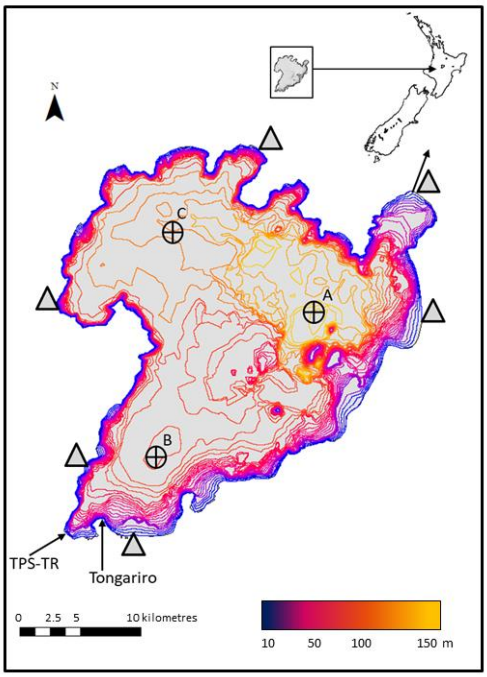


Figure 4-2: Bathymetric map of Lake Taupō showing the three pelagic sampling sites (crossed circles) and six littoral sampling sites (triangles) used in this study.

4.3.3 Excretion incubation experiments.

All excretion experiments were conducted in the field immediately following sample collection. Zooplankton samples were collected by hauling a 90 µm mesh net of 25 cm diameter through the length of the water column. This mesh was chosen because the majority of zooplankton species in the lake are crustaceans >100

μm in length (James 1987), and the coarse mesh reduced accidental collection of phytoplankton. Mussels were collected by snorkelling within a 15 m radius to 5 m depth. Up to 10 individuals were collected. Beach seine nets were used to catch smelt and bullies. The seine net was 5 m long by 1.5 m high, and was dragged for 20 m along the shoreline in 0.4 – 1.7 m water depth. If <2 smelt or bullies were caught at a site, the net was dragged a second time, for 50 m.

Consumers were kept in a bath of ambient lake water within an insulated, dark box until the start of the excretion experiment. The consumers were then placed in containers of reverse-osmosis (RO) filtered water. RO water was used in all cases rather than lake water in order to prevent bias when comparing $\delta^{15}N–NH_4^+$ values from the collected water sample to those excreted by consumers. For zooplankton samples, net contents were emptied into a 100 μm sieve to remove lake water, then rinsed in a jar containing 150 ml of RO filtered water. Three – ten mussels were lightly scrubbed with a cotton cloth and placed upright in 0.5 – 1.0 L of RO filtered water, depending on the number of individuals collected. Smelt and bullies were immediately identified from the seine net sample and three – fifteen individuals were rapidly transferred into 1 L of RO filtered water. Where <5 individuals were caught at a site, the incubation water was reduced to 500 ml to allow adequate sample concentration for subsequent analyses.

After 30 minutes of the consumer excretion incubations, a filtered water sample was taken. The water sample was split into two sub-samples; one to determine nutrient concentrations and the other for $\delta^{15}N–NH_4^+$ analysis. Samples for $\delta^{15}N$ analysis were preserved in the field by adding 1 % by volume of 10 mM HCl solution containing 25 μM of sulfanilic acid to reduce pH to < 4 and prevent microbial transformation while the sulfanilic acid removed nitrite from the sample. Nitrite has previously been demonstrated to interfere with $\delta^{15}N–NH_4^+$ and NO_3^-–$\delta^{15}N$ and $\delta^{18}O$ analyses (Granger and Sigman 2009).

Consumers used in the incubations were euthanized and stored in NaCl brine solution for subsequent tissue $\delta^{15}N$ analysis. Upon return to the laboratory, zooplankton samples were rinsed with RO-filtered water to remove NaCl by centrifuging and decanting five times. Zooplankton were examined under a dissection microscope (10X magnification) to remove non-zooplankton material. For mussels, samples were taken from the foot. Samples for smelt >15 mm and bullies >15 mm had their head and guts removed while smelt and bullies ≤15 mm

were analysed in their entirety. Samples were then rinsed to remove salt. Benthic invertebrates were removed from sediment samples in the laboratory and rinsed. All samples for stable isotope analysis were stored in 1.5 ml Eppendorf snap-lock tubes and were oven dried at 48 °C for >48 h. Samples were homogenised for stable isotope analysis.

4.3.4 Water chemistry sampling

Littoral water chemistry samples were collected from the 1-m depth contour at each site approximately 20 cm below the water surface. Pelagic water chemistry samples were collected from three depths; surface, DCM and hypolimnion, from each site. Pelagic sampling used a vertically positioned 5 L Van Dorn water sampler. Surface and hypolimnion samples were collected by lowering the Van Dorn sampler to 0.5 m below the surface and approximately 2 m above the bottom, respectively, at each site. The depth for DCM sampling was determined by first recording a vertical profile with an RBR XR620f Conductivity-Temperature-Depth profiling system fitted with a chlorophyll fluorometer (Seapoint Sensors Inc., New Hampshire). The vertical chlorophyll fluorescence profile was immediately inspected and the depth of maximum chlorophyll fluorescence was taken as the DCM sample collection depth. When no DCM was present (June and August sampling), mid-water column samples were collected from 40 m depth to standardise sampling.

Water chemistry samples were collected for determination of total nitrogen, total phosphorus (TN and TP respectively), nitrate, ammonium and phosphate concentrations as well as stable isotope values of NO_3^-–$\delta^{15}N$ and $\delta^{18}O$, $\delta^{15}N$–NH_4^+ and POM –$\delta^{15}N$. Sample containers were rinsed in triplicate with filtered sample water prior to filling. Water samples, excluding aliquots taken for TN and TP, were filtered through pre-ashed and weighed 0.45 μm Whatman GF/C filters. The filter papers were retained after sufficient sample water was passed through for determination of POM–$\delta^{15}N$. Upon return to the laboratory, POM filters were oven dried at 48 °C for >48 h, weighed, then stored for stable isotope determination. Nitrate–$\delta^{15}N$ and $\delta^{18}O$ and $\delta^{15}N$–NH_4^+ samples were preserved with HCl-sulfanilic acid solution to remove nitrite while all other samples were stored on ice in the dark until return to the laboratory.

4.3.5 Nutrient concentration determination

Dissolved nutrients (NH_4^+, NO_2^-, NO_3^- and PO_4^{3-}) were measured at the University of Waikato with an Aquakem 200 discrete analyser (Thermo Fisher, Scoresby,

Australia) using standard colorimetric methods (APHA, 1998). Limits of detection were 0.001 mg L^{-1} for NO_2^--N and NO_3^--N, 0.002 mg L^{-1} for NH_4^+-N and 0.001 mg L^{-1} for PO_4^{3-}-P. Total nitrogen (TN) and total phosphorus (TP) concentrations were determined through alkaline persulphate digestion (APHA, 1998) of an unfiltered sample and subsequent colorimetric analysis for NO_3^- and PO_4^{3-}, respectively, using a Lachat QuickChem flow injection analyser (Zellweger Analytics Inc.) Chlorophyll *a* concentrations were analysed at NIWA (Hamilton) using acetone pigment extraction and spectrofluorometric measurement as described by Verburg and Albert (2016).

4.3.6 Stable isotope analyses

Organic sample $\delta^{15}N$ analysis. Consumer tissue samples were analysed at the Waikato Stable Isotope Unit (University of Waikato) by combustion using a Dumas Elemental Analyser (Europa Scientific ANCA-SL) interfaced to an isotope mass spectrometer (Europa Scientific 20-20 Stable Isotope Analyser, Europa Scientific Ltd, Crewe, U.K.). POM samples were analysed at the GNS Science National Isotope Centre (Wellington) by the same procedure on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer (GV Instruments Ltd, UK). All results were normalized to an internal leucine standard (themselves calibrated to international standards USGS 25 and USGS26). The analytical precision for $\delta^{15}N$ is 0.3 ‰ and 0.5 ‰ for the GNS and University of Waikato laboratories, respectively.

$\delta^{15}N$–NH_4^+ analysis. Analyses were conducted at the GNS Science National Isotope Centre (Wellington) using the hypobromate oxidation-azide reduction method (Zhang et al 2007). Briefly, samples were initially injected with a hypobromate solution to quantitatively oxidise ammonium to nitrite. Arsenate was then added to remove residual hypobromate from the sample. A sodium azide – acetic acid buffer (2M) solution then quantitatively converted sample nitrite into nitrous oxide by injection into a septum-capped sample vial. This reaction was terminated after 30 minutes by injecting a 6M NaOH solution. The NaOH also scrubbed from the sample vial any ambient CO_2 which can interfere with N_2O stable isotopic determinations. Sample nitrous oxide was then removed from the sample vial using a purge and trap system (pre-concentrator, Isoprime) after which the sample was analysed by continuous flow mass spectrometry (GV Instruments Ltd, UK). All samples were measured with a comparable concentration range of standards and

blanks. Sample $\delta^{15}N$ values were corrected against four ammonium standards; IAEA-N1, IAEA-N2, USGS 25 and USGS 26.

NO_3^-–$\delta^{15}N$ & $\delta^{18}O$ analysis. All analyses were conducted at the GNS Science National Isotope Centre using the two-step cadmium and azide reduction method (McIlvin and Altabet 2005). In brief, samples were diluted where necessary, to achieve a concentration of 25 μM nitrate at pH 7. NaCl was added to obtain a 2 M concentration. pH was controlled by adding MgO to buffer the preservation acid. Acid-washed spongy cadmium was then added to each sample and placed on a shaker table overnight to allow complete conversion of nitrate to nitrite. The next day samples were further diluted, where necessary, to achieve a final concentration of 1 μM nitrite solution in a septum-capped vial. Sample $\delta^{15}N$ and $\delta^{18}O$ values analysed by continuous flow mass spectrometry were corrected using four nitrate standards; the international standards USGS 34, USGS 32 and IAEA-KNO_3 as well as an internal KNO_3 standard.

Correction of low-concentration samples. Samples with concentrations <1.4 mM m^{-3} NH_4^+-N or NO_3^--N had a correction applied. An inverse relationship between $\delta^{15}N$ values and these analyte concentrations indicated increasing interference by N_2O as the sample concentration decreased. Background N_2O (± SE) in deionised water blanks had stable concentrations (150 ± 0.1 μM N m^{-3}) and $\delta^{15}N$ values (-3.3 ± 0.09 ‰). The contributions of background N_2O to the sample $\delta^{15}N$ value was therefore able to be corrected using a two-point concentration dependent mixing model. The true sample $\delta^{15}N$ value was determined using the equation:

$$\delta^{15}N_{Observed} = \rho_B(\delta^{15}N_{Background}) + \rho_S(\delta^{15}N_{Sample})$$

where ρ_B and ρ_S are the proportionate contributions of background N_2O and true sample N_2O to the observed sample yield, respectively. The value of ρ_B was calculated using:

$$\rho_B = \frac{Peak\ height_{blank}}{Peak\ height_{observed\ sample}}$$

where peak height is the N_2O yield from a distilled water blank and from the sample, measured by mass spectrometry. ρ_S is determined as 1- ρ_B. For $\rho_B > 0.5$, sample values were discarded.

4.3.7 Data analysis

Statistical analyses were performed in R (version 3.3.2; R core team 2015), using the base package linear model (lm) function. Type II sums of squares were used in all analyses due to the unbalanced study design and co-varying predictor variables (Crawley 2007).

Excretion $\delta^{15}NH_4^+$ relationships – trophic discrimination factor between consumer tissue and excretion ($\Delta^{15}N_{TDF}$) was determined as:

$$\Delta^{15}N_{TDF} = \delta^{15}N_{Excretion} - \delta^{15}N_{Tissue}$$

for excretion values paired with mean consumer tissue values from each incubation. Factorial analysis was used to determine species and sampling month effects on tissue-excretion trophic discrimination. Regression analysis was used to examine relationships between zooplankton excretion $\delta^{15}NH_4^+$ and water $\delta^{15}NH_4^+$ values from surface water, DCM and hypolimnion samples at sampling sites. Models to determine the relationship between zooplankton excretion $\delta^{15}NH_4^+$ and water $\delta^{15}N$–NH_4^+ values were run for all three pelagic sites and with Site B samples excluded. The effect of Site B samples was examined because it is within 5 km of the two largest inflows, the Tongariro River, and the Tokaanu Power Scheme tailrace (Figure 4-2). Combined, these two inflows account for over 80 % of the total annual catchment input and approximately 38 % of the annual nitrogen load (Vant 2013). These inflows, at varying times of the year, can enter the lake as plunging discharges, surface plumes or mid-water column jets (Spigel et al. 2005).

NO_3^- isotopes – NO_3^-–$\delta^{18}O$ values were used as a proxy for *in situ* production: respiration (P:R) ratios. Lake Taupō water had a spatially and temporally consistent $\delta^{18}O$ value ($\delta^{18}O$–H_2O = -5.2 ± 0.1 ‰) throughout the study period (*Data appendix 1*). Given the intra-annual consistency of $\delta^{18}O$–H_2O values, variation in $\delta^{18}O$–NO_3^- reflects $\delta^{18}O$–DO values, hence P:R. Observed $\delta^{18}O$–NO_3^- data were compared against expected values using the isotopic nitrification equation:

$$NO_3^- - \delta^{18}O = \frac{2\,(\delta^{18}O_{Water})}{3} + \frac{\delta^{18}O_{Atmosphere}}{3} + \varepsilon_{diffusion}$$

where $\delta^{18}O_{Water}$ = -5.2 ‰, $\delta^{18}O_{Atmosphere}$ = 23.5 ‰ (Finlay et al. 2007) and $\varepsilon_{diffusion}$ is the fractionation effect on dissolved oxygen through diffusion into water (~1 ‰ – Wassenaar 2012). Using the data for Lake Taupō with the equation above, the expected $\delta^{18}O$–NO_3^- = 4.4 ‰. Observed nitrate with $\delta^{18}O$ values greater than and

less than this value were considered indicative of net heterotrophy and autotrophy, respectively.

Keeling relationships were used to examine the underlying mechanisms associated with linear relationships between NO_3^-–$\delta^{15}N$ and $\delta^{18}O$ values. Existence of a linear relationship between nitrate $\delta^{15}N$ and $([NO_3^-])^{-1}$ is used to infer end-member mixing, and a positive linear relationship between nitrate $\delta^{15}N$ and $\ln([NO_3^-])$ is used to infer kinetic fractionation processes.

4.4 Results

4.4.1 Validation of trophic fractionation from excretion

Mean consumer nutrient excretion $\delta^{15}N$–NH_4^+ values across all four sampling months (± 95 % CI) were 1.2 (4.4) ‰, -0.6 (4.1) ‰, -1.2 (0.9) ‰ and 1.0 (6.1) ‰ for smelt, bullies, mussels and zooplankton, respectively (Figure 4-3). The average $\Delta^{15}N_{TDF}$ for all consumer incubations over the study period was -5.6 ± 2.5 ‰. Significant differences between month were observed in $\Delta^{15}N_{TDF}$ values (Fig. 3), with stronger (i.e., more negative) $\Delta^{15}N_{TDF}$ in June than February and April ($P < 0.01$). No significant difference ($P = 0.12$) was observed between bullies (-7.5 ± 4.1 ‰), smelt (-5.7 ± 4.6 ‰), mussels (-4.8 ± 1.1 ‰), and zooplankton (-0.7 ± 5.7 ‰), respectively (Figure 4-3).

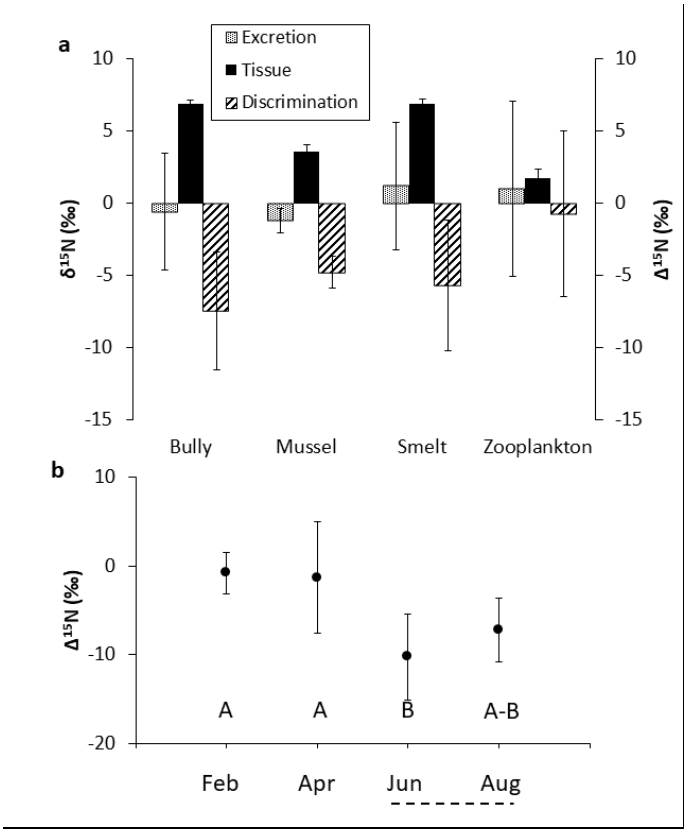


Figure 4-3: Consumer tissue-excretion trophic discrimination for four consumers. Error bars represent 95 % confidence interval. a) Mean $\delta^{15}N$ values for consumer excretion, tissue and the discrimination factor ($\Delta^{15}N$) between the two. b) Trophic discrimination factor $\Delta^{15}N$ as a mean for each of the four sample months.

Water-excretion $\delta^{15}NH_4^+$ relationships

Zooplankton excretion $\delta^{15}N–NH_4^+$ was significantly related to $\delta^{15}N–NH_4^+$ in the DCM samples:

$Water\ \delta^{15}N{-}NH_4^+ = 0.81 \times Zooplankton\ excretion\ \delta^{15}N - 6.1$ (R^2 = 0.58, P > 0.01) (Figure 4-4).

No significant relationships (P > 0.05) were observed between zooplankton excretion $\delta^{15}N–NH_4^+$ and surface or hypolimnion water values (Figure 4-4). DCM water $\delta^{15}N–NH_4^+$ values were slightly below the 1:1 line for the $\delta^{15}N–NH_4^+$water – excretion relationship, whereas surface and hypolimnion water $\delta^{15}N–NH_4^+$ values varied about the 1:1 line (Figure 4-4). The relationship improved with Site B samples excluded:

$Water\ \delta^{15}N - NH_4^+ = 0.91 \times Zooplankton\ excretion\ \delta^{15}N{-}NH_4^+ - 2.7$ (R^2 = 0.91, P = 0.015).

Excluding Site B data from the relationships between water and excretion $\delta^{15}N–NH_4^+$values for surface waters resulted in data points falling above the 1:1 line,

whereas exclusion of Site B had no discernible influence on the relationship for hypolimnetic water samples. Linear models indicated that the effect of sampling site (i.e. Site B) was greater within water $\delta^{15}N–NH_4^+$ values than within zooplankton excretion $\delta^{15}N–NH_4^+$. Variance in water $\delta^{15}N–NH_4^+$ values explained by sampling site was 23 %, 73 % and 41 % for DCM, surface and hypolimnion water respectively. Sampling site explained only 13 % of the total variance of zooplankton excretion $\delta^{15}N–NH_4^+$ values.

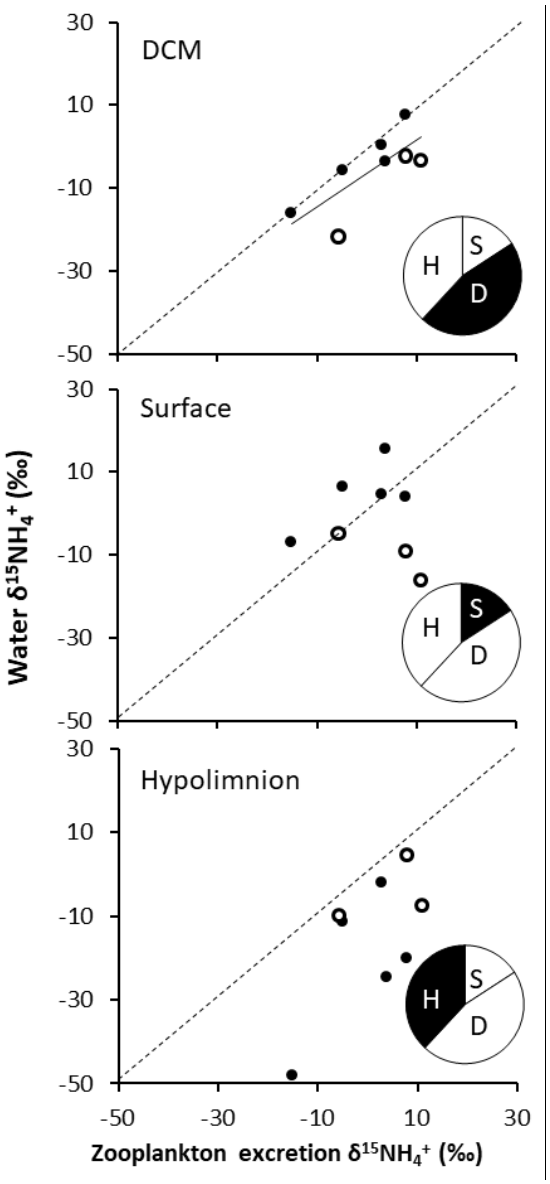


Figure 4-4: $\delta^{15}NH_4^+$ for zooplankton excretion and water samples from the a) surface water, b) DCM and c) hypolimnion. Dashed line represents the 1:1 line.

4.4.2 *Temporal patterns in Chl-a, POM –$\delta^{15}N$, $\delta^{15}N$–NH_4^+, and NO_3^-–$\delta^{15}N$ & $\delta^{18}O$ values across lake zones*

Surface water Chl-*a* concentrations were highest in September (2.4 mg m^{-3}) and lowest in December (0.4 mg m^{-3}). Chl-*a* was highest during winter mixing, when concentrations were largely homogeneous throughout the water column, and lowest during summer stratification when it was concentrated as a metalimnetic deep chlorophyll maximum (Figure 4-5).

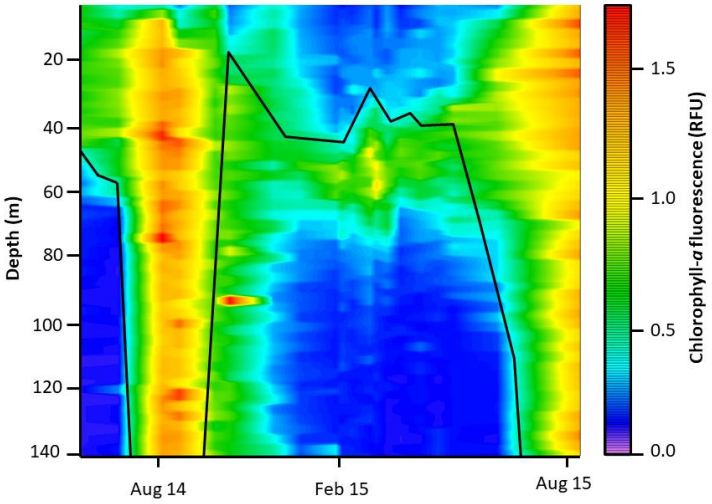


Figure 4-5: Depth distributions of chlorophyll a fluorescence (relative fluorescence units – RFU) from Lake Taupō at Site A between July 2014 and August 2015.

POM–$\delta^{15}N$ values from the four lake zones (surface, DCM, bottom and littoral water) were similar in the near-mixed/mixed periods of June and August (mean = 3.1 ± 0.7 ‰). From the onset of thermal stratification in September, POM–$\delta^{15}N$ values for surface, littoral and DCM waters became increasingly ^{15}N deplete with large 95 % confidence intervals (Figure 4-6). By February POM–$\delta^{15}N$ was strongly ^{15}N deplete for surface and littoral samples (-4.9 ± 4.0 ‰ and -9.6 ± 5.8 ‰), while bottom-water POM–$\delta^{15}N$ had become slightly more enriched (3.4 ± 1.2 ‰). POM–$\delta^{15}N$ values from each of the lake zones (surface, DCM, bottom and littoral) tended to converge again in June just prior to the onset of mixing. The C/N molar ratios in POM ranged from 6.1 to 35.0 over all lake zones. Ratios for the majority of these samples (61 %) were between 11.0 and 12.5, the reported range for freshwater phytoplankton. These samples also displayed a wide range of $\delta^{15}N$ values, -18.0 to +6 ‰) (Figure 4-7).

Across all N pools, $\delta^{15}N$ varied most widely for NH_4^+ (Figure 4-6). The range of $\delta^{15}N$ for NH_4^+ was 94.4 ‰ (-29.1 – 65.3 ‰) compared to 10.3 ‰ and 24 ‰ for

nitrate and POM, respectively. The variance in $\delta^{15}N–NH_4^+$ values was particularly high in the hypolimnion (44.3 ‰) in August. $\delta^{15}N–NH_4^+$ values were most negative for water samples from the surface (-9.4 ± 14.7 ‰) and hypolimnion (-12.9 ± 7.9 ‰) in February, for DCM samples (-7.0 ± 3.0 ‰) in August and September and for littoral samples in September (-10.4 ± 4.1 ‰) (Table 4-1). Values were highest for water samples from the surface (10.3 ± 8.2 ‰) in June, the DCM (5.7 ± 5.4 ‰) in December, the littoral (9.3 ± 9.3 ‰) in June and the hypolimnion (28.9 ± 19.4 ‰) in December. Temporal patterns within individual sites for $\delta^{15}N–NH_4^+$ and $\delta^{15}N–NO_3^-$ generally showed positive covariation (Supplementary Figure 4-10). The exceptions, periods when ammonium became ^{15}N enriched and nitrate ^{15}N deplete, were between February and April in littoral sites 'Kinloch' and 'Stump' and December to February in the surface water at pelagic Site C.

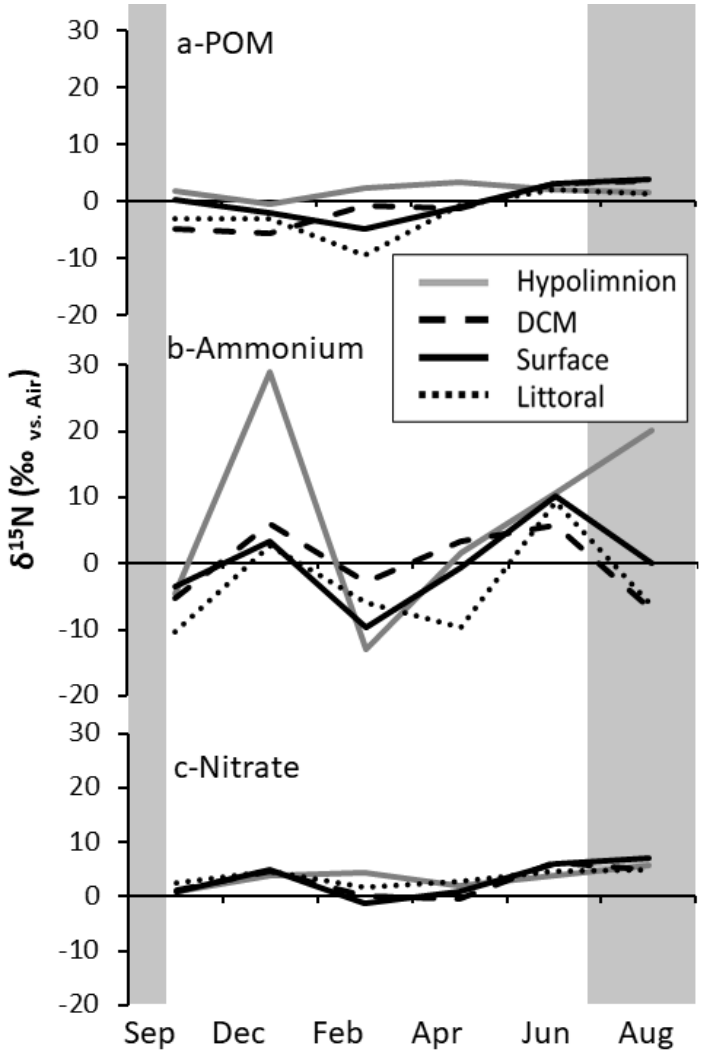


Figure 4-6: Mean $\delta^{15}N$ of water samples from the surface, DCM, littoral and hypolimnion for a) POM, b) ammonium and c) nitrate over the sampling months during 2014-2015.

$\delta^{15}N–NO_3^-$ values displayed a similar pattern to those of $\delta^{15}N$–POM with generally highest values during winter mixing and lowest around the end of summer. Samples had similar $\delta^{15}N–NO_3^-$ values across zones during winter mixing (Figure 4-6). Samples from the surface and DCM became ^{15}N deplete relative to the hypolimnion during summer stratification. The difference between surface and hypolimnion $NO_3^-–\delta^{15}N$ values was greatest during February stratification. $\delta^{15}N–NO_3^-$ varied less with season in the hypolimnion (from 1.0 ± 0.4 ‰ in September 2014 to 5.8 ± 1.0 ‰ in August 2015) compared with surface water (from -1.1 ± 1.0 ‰ in February 2014 to 7.0 ± 1.3 ‰ in August 2015) and DCM (from -1.1 ± 1.0 ‰ in April 2014 and 6.3 ± 2.2 ‰ in June 2015).

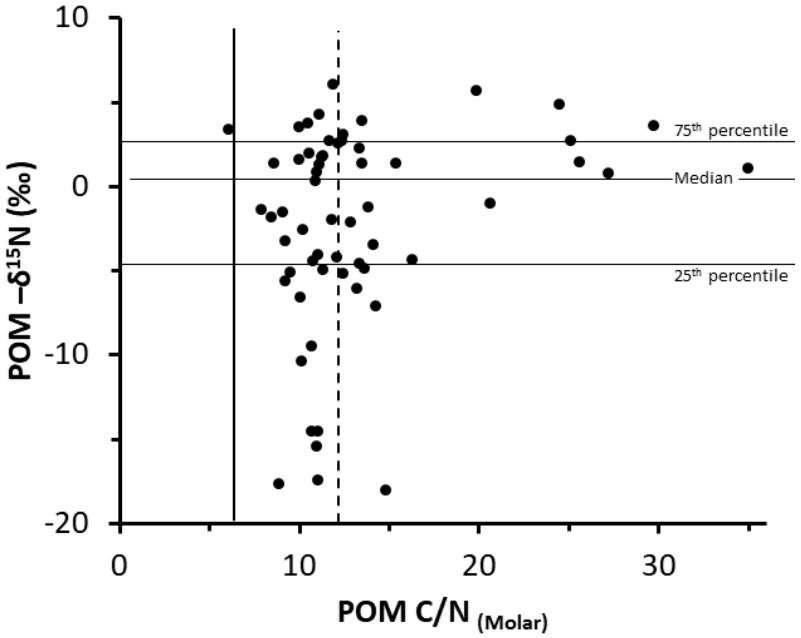


Figure 4-7: C/N molar ratio versus $\delta^{15}N$ of all POM samples (surface, DCM, hypolimnion and littoral water). Horizontal lines depict the 25th percentile, median and 75th percentile values for POM – $\delta^{15}N$.

$\delta^{18}O–NO_3^-$ from surface and DCM waters was enriched (i.e., heterotrophic) during summer stratification and depleted (autotrophic) during winter mixing (Figure 4-8). $\delta^{18}O–NO_3^-$ enrichment was greatest during February at the DCM (10.2 ± 4.0 ‰) and at the surface (8.4 ± 3.8 ‰) in April, and depletion was greatest during August for both DCM (-3.1 ± 0.6 ‰) and surface water (-4.1 ± 0.9 ‰). Surface water $\delta^{18}O–NO_3^-$ depletion (autotrophy) in August coincided with the highest Chl-*a* concentrations, and $\delta^{18}O–NO_3^-$ enrichment (heterotrophy) in summer coincided with low Chl-*a* concentrations (Figure 4-8). $\delta^{18}O–NO_3^-$ for samples from the littoral

zone varied between 3.0 ± 3.1 ‰ in April and 0.7 ± 0.7 ‰ in December. Littoral zone $\delta^{18}O–NO_3^-$ displayed a similar, albeit dampened, monthly pattern to that of surface and DCM samples. Littoral $\delta^{18}O–NO_3^-$ remained within the range of net autotrophy throughout the year.

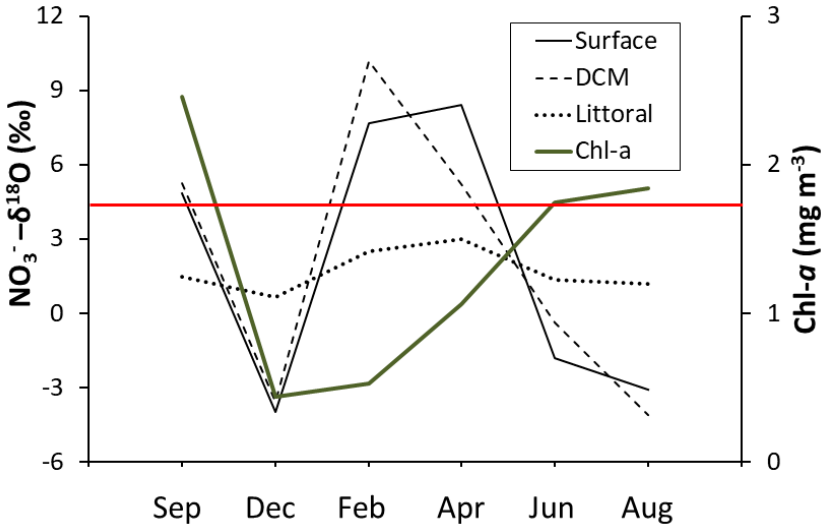


Figure 4-8: NO_3^-–$\delta^{18}O$ from surface, DCM and littoral samples. The red horizontal line indicates the NO_3^-–$\delta^{18}O$ value for a productivity:respiration ratio = 1 (see methods section for details).

When the $\delta^{18}O$ & $\delta^{15}N$ values in NO_3^- were compared against each other in isotopic bi-space, overall $\delta^{18}O$ was negatively related to $\delta^{15}N–NO_3^-$ ($R^2 = 0.52$, $P < 0.01$):

$NO_3^- - \delta^{18}O = -1.4 \times nitrate\ \delta^{15}N + 4.8$ (Figure 4-9).

Mean catchment surface water nitrate input ($\delta^{15}N = 4.2 \pm 0.5$ ‰ and $\delta^{18}O = 1.6 \pm 0.4$ ‰) fell on the mid-point of the lake NO_3^- $\delta^{18}O$ & $\delta^{15}N$ line (Figure 4-9). Two keeling relationship was observed for $\delta^{15}N–NO_3^-$ values. $\delta^{15}N–NO_3^-$ values showed a significant negative linear relationship with the inverse of nitrate concentration for samples collected during February and April:

$NO_3^- - \delta^{15}N = -0.17 \times \frac{1}{NO_3^- - N} + 7.96$ ($R^2 = 0.60$, $P < 0.01$)

where concentration is in mg l^{-1}. This suggests that the negative linear relationship between $\delta^{18}O$ & $\delta^{15}N$ values in NO_3^- was the result of two-point end-member mixing. The relationship for the remaining months was positive:

$NO_3^- - \delta^{15}N = 0.05 \times \frac{1}{NO_3^- - N} + 2.22$ ($R^2 = 0.53$, $P < 0.01$)

The ^{15}N-deplete nitrate end-member was associated with ^{18}O enriched values (i.e., heterotrophy) while the ^{15}N-enriched nitrate end-member was associated with ^{18}O deplete values (autotrophy) (Figure 4-9).

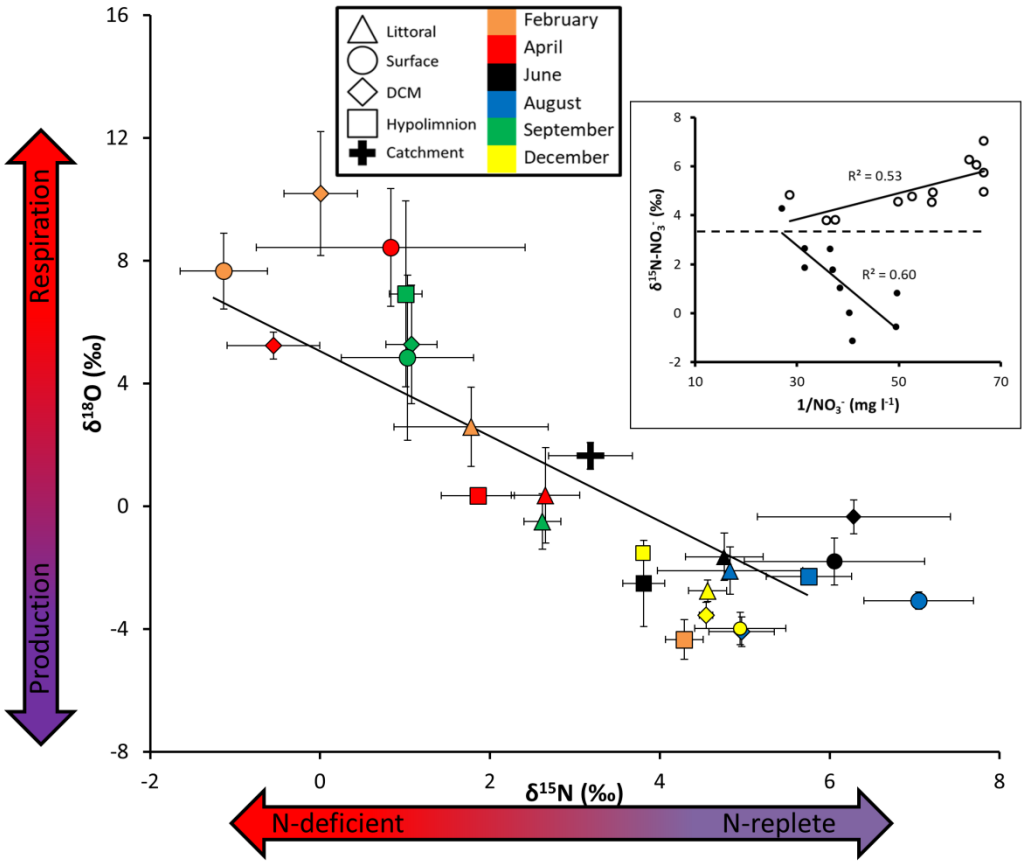


Figure 4-9: NO_3^-–$\delta^{15}N$ and $\delta^{18}O$ data, separated by sampling month (colours) and lake zones (symbols). All data points are described by the solid black line: $\delta^{18}O = -1.35 \times \delta^{15}N + 4.76$ ($R^2 = 0.52$, $p < 0.001$).

4.5 Discussion

4.5.1 Overview

The stable isotope data presented in this study of a large, oligotrophic lake, demonstrate that the importance of CNR to nutrient cycling is substantial but varies both spatially and temporally. On the balance of evidence, we argue that ^{15}N depletion of dissolved nitrogen pools observed during stratification is due to CNR. This effect was most evident in δ^{15}N values for nitrate, and to a lesser extent POM. The stratified period is characterised by low nitrogen availability and net heterotrophy. Spatially, CNR contributions are likely to be greatest at the DCM where zooplankton grazing is focussed, as there is a significant linear relationship between δ^{15}N-NH_4^+ values of zooplankton excretion and the ambient water in this

layer. Stable isotope analysis provides evidence for CNR at three levels: 1) negative isotopic trophic discrimination during excretion; 2) positive relationships between zooplankton $\delta^{15}N\text{-}NH_4^+$ of excretion and ambient water; and 3) seasonal changes in $\delta^{15}N$ values of N pools. Implications of variations in CNR in the context of global environmental change are further discussed below.

4.5.2 Patterns in trophic discrimination factors

Trophic discrimination factors for consumer $\delta^{15}N\text{-}NH_4^+$ excretion were negative over the four taxa studied in Lake Taupō (overall mean $\Delta^{15}N$ = -5.6 ‰). This is in line with other studies demonstrating that $\Delta^{15}N_{TDF}$ values are consistent across all ecosystem consumers and CNR will universally result in excretion that is ^{15}N depleted (Steffan et al. 2015). Importantly, consumer excretion is the only fractionation process that results in ^{15}N depletion of ammonium (Robinson 2001; Denk et al. 2017). The $\Delta^{15}N_{TDF}$ of excretion has not previously been measured, but rather inferred by mass balance from consumers' diet and tissue $\delta^{15}N$ under controlled feeding experiments (Minagawa and Wada 1984; Somes et al. 2010). These earlier calculations suggest less ^{15}N depletion of nitrogen excretion (-3.2 ‰) than observed in our study. The discrepancy observed between the two methods is likely due to our results reflecting the combined effects of diet switching and diet quality. Lower $\Delta^{15}N_{TDF}$ is associated with poorer diet quality (Olive et al. 2003; Chikaraishi et al. 2015) while rapid diet switching (i.e., faster than tissue turnover rates) can result in a mismatch between diet (hence excretion) and tissue $\delta^{15}N$ values (O'Reilly et al. 2002; Olive et al. 2003; Newsome et al. 2007; Mohan et al. 2016). In our study, $\Delta^{15}N_{TDF}$ values were significantly lower in June and August than in February and April and varied substantially within consumer groups. As is the case with oligotrophic lakes generally (McMeans et al. 2015), consumers in Lake Taupō rapidly switch their diet in response to seasonal changes in resource availability (Stewart et al.2017). A combination of diet switching and changes in diet quality may therefore be responsible for variation in $\Delta^{15}N_{TDF}$ values.

4.5.3 Patterns in $\delta^{15}N\text{-}NH_4^+$

Observed values of $\delta^{15}N\text{-}NH_4^+$ suggest strong coupling between zooplankton excretion and ammonium generated, particularly within DCM and surface waters. Site B, however, was an exception. For all depths, Site B was an outlier in the $\delta^{15}N\text{-}NH_4^+$ relationship between zooplankton excretion and water. Sampling site accounted for a substantially greater percentage of the total variance of $\delta^{15}N\text{-}NH_4^+$

values at all three depths than zooplankton excretion did. This indicates that the anomalies at Site B are driven by water column processes rather than zooplankton excretion. Samples from Site B in the southern basin of the lake are most likely to be influenced by intrusions of two major river inflows (Spigel et al. 2005). These depths where inflows enter the lake can vary from the hypolimnion to the surface (Spigel et al. 2005). Stronger site effects (i.e., associated variance) in surface and DCM water $\delta^{15}N\text{-}NH_4^+$ values than in the hypolimnion align with expected inflow intrusion being mostly into surface and metalimnetic waters.

The relationship of $\delta^{15}NH_4^+$ between zooplankton excretion and water was strongest for DCM samples from Sites A and C combined ($R^2 = 0.91$) and fell close to the 1:1 line. By comparison, ambient water $\delta^{15}N\text{-}NH_4^+$ for samples from surface and hypolimnion waters were higher and lower than zooplankton excretion $\delta^{15}N\text{-}NH_4^+$, respectively, indicating less of a role of zooplankton at these depths. Discrepancies in surface and hypolimnion waters may reflect either greater relative contributions of nitrogen excretion from higher (i.e., pelagic fish) or lower (i.e., microbial consumer) trophic levels to water $\delta^{15}N\text{-}NH_4^+$ (Shostell and Bukaveckas 2004) or nutrient source-sink dynamics within zooplankton excretion (Lampert 1989; Baustain et al. 2014). Zooplankton excretion has been implicated as an important source of nutrients for phytoplankton growth (Elser et al. 1996; Spillman et al. 2000; Bruce et al. 2006). Our results indicate that CNR effects are depth dependent. There is reciprocal coupling between zooplankton and phytoplankton at the DCM in Lake Taupō but less so in surface and hypolimnion waters. While zooplankton typically utilise the entire water column (Jolly 1965; Baustain et al. 2014), they tend to aggregate in the metalimnion of oligotrophic lakes due to higher food abundance (Winder et al. 2004). Our results highlight how biotic interactions spatially structure nutrient cycling processes in oligotrophic lakes.

The relationships between $\delta^{15}N\text{-}NH_4^+$ of zooplankton excretion and water from different zones did not translate to water $\delta^{15}N\text{-}NH_4^+$ values being a strong indicator of whole-lake patterns of CNR through time. Water $\delta^{15}N\text{-}NH_4^+$ values were highly variable between replicates from the same lake zone. Monthly mean water $\delta^{15}N\text{-}NH_4^+$ values showed a similar pattern to nitrate and POM $\delta^{15}N$ (i.e., summer stratification accompanied pelagic surface water ^{15}N depletion), but the high variance prevented conclusions being made about seasonal patterns in water $\delta^{15}N\text{-}NH_4^+$. Our results suggest that water $\delta^{15}N\text{-}NH_4^+$ values likely respond to a number

of localised nitrogen cycling processes which, collectively at the ecosystem level, produce high variability. Warmer water temperatures, higher incident light and lower nutrient concentrations during stratified periods result in faster nitrogen cycling rates (Goldman et al. 1996; Kumar et al. 2008; Bratič et al. 2012). During these periods, the rate of ammonium depletion (e.g., via photosynthetic uptake and nitrification) commonly balances generation (consumer excretion). As a result, the ammonium present in the water is transient (Goldman et al. 1996; Kumar et al. 2008). Under these conditions, nitrification and ammonium uptake, which remove ammonium, will display closed system dynamics (i.e., strongly supply-limited N transformation) and associated isotopic fractionation effects on $\delta^{15}N\text{-}NH_4^+$ values. (e.g., $^{15}N\text{-}NH_4^+$ enrichment) will be minimal (Bourbonnias et al. 2013; Liu et al. 2013; Denk et al. 2017). This suggests that processes generating ammonium (i.e., CNR) are driving the observed deplete $^{15}N\text{-}NH_4^+$ and $^{15}N\text{-}NO_3^-$ values during summer. Under oligotrophic conditions ammonium fluxes are highly isotopically heterogeneous, which likely reflects the spatial heterogeneity of recycling processes and potentially localised effects of fractionation during nitrification. Heterogeneous cycling processes are expected to confer resilience in nutrient cycles (Dong et al. 2017; Farnsworth et al. 2017). The substantial heterogeneity of $\delta^{15}N\text{-}NH_4^+$ documented in this study, if teased apart, could help identify critical rate-limiting processes and dynamics in N-cycling at a high resolution.

4.5.4 Patterns in nitrate $\delta^{15}N$ & $\delta^{18}O$

Nitrate $\delta^{15}N$ & $\delta^{18}O$ data indicated that Lake Taupō varied between two states over the year: heterotrophy with large contributions of CNR during stratification, and autotrophy during nitrogen replete mixing. Isotopically, the high-CNR, heterotrophic state was defined by high $\delta^{18}O\text{–}NO_3^-$ (10 ‰) and low $\delta^{15}N\text{–}NO_3^-$ (-1.5 ‰) while the autotrophic nutrient replete state was characterised by low $\delta^{18}O\text{–}NO_3^-$ (-4 ‰) and high $\delta^{15}N\text{–}NO_3^-$ (6 ‰). Enrichment and depletion of ^{18}O in nitrate indicates heterotrophy and autotrophy, respectively (Wassenaar 2012). CNR depletes $\delta^{15}N\text{–}NO_3^-$, while fractionation from phytoplankton uptake when nitrate is replete enriches ^{15}N in the nitrate pool (Kendall et al. 2007; Xue et al. 2009). These two states of the lake represented isotopic end-members; nitrate –$\delta^{15}N$ & $\delta^{18}O$ values were spread along a negative gradient between these two states. The two distinct linear (Keeling) relationships were due to mixing between the two end-member states. Catchment $\delta^{15}N\text{–}NO_3^-$ represented the common origin value for both of the seasonal keeling relationships. Similarly, nitrate–$\delta^{15}N$ & $\delta^{18}O$ values of

catchment inflows, the predominant external nitrate source, fell between the two end-member states along the mixing line. Isotopic fractionation associated with heterotrophic and autotrophic states drives these source nitrate–$\delta^{15}N$ & $\delta^{18}O$ values in different directions along the mixing line. Heterotrophy occurs during stratification as declining nutrient concentrations in the euphotic zone cause phytoplankton biomass to also decline, and ecosystem trophic level biomass pyramids tend to become inverted (Sommers et al. 2010; Stewart et al. 2017). The hypothesis that CNR contributions are greatest when consumer biomass is high and nutrient supply from other sources is low (Allgeier et al. 2017; Stewart et al. 2018), was supported by results from our study. Seasonal fluctuation in dissolved nutrient concentrations and phytoplankton biomass would be expected to be far greater in the absence of CNR (Lewis 2010). Greater temporal fluctuations in phytoplankton biomass have implications for food web stability (Li and Stevens 2017) and productivity (Yang et al. 2008), suggesting that CNR may provide an important feedback mechanism for maintaining resilience in aquatic food webs.

4.5.5 Patterns in POM–$\delta^{15}N$

POM–$\delta^{15}N$ data suggest that high rates of CNR were associated with phytoplankton as opposed to detrital POM. POM that was deplete in ^{15}N consistently had a C:N ratio ~11.5 which is a typical C:N ratio for freshwater phytoplankton (Hecky et al. 1993). Conversely, detrital POM had variable C:N frequently C:N > 13 and up to 35, with $\delta^{15}N$ consistently > zero. Detrital POM $\delta^{15}N$ values were similar to the annual mean for nitrate ($\delta^{15}N$ = 1.2 ± 1.3 ‰) suggesting a close association with decomposition (i.e., slow N turnover). The occurrence of isotopic values indicative of high rates of CNR (i.e., ^{15}N deplete) exclusively within phytoplankton-rich POM samples indicates that high rates of epilimnetic consumer nutrient recycling were disproportionately associated with phytoplankton uptake rather than detrital decomposition indicating tight nitrogen cycling. This concurs with current understanding that phytoplankton, or 'green', trophic channels are more responsive to changes in nutrient concentrations than detrital, or 'brown', trophic channels (Polis and Strong 1996; Blanchard et al. 2010; Zou et al. 2016).

CNR was most important for phytoplankton during stratification. Both littoral and pelagic surface water POM were most ^{15}N deplete during summer stratification (February-April) and coincided with the POM–$\delta^{15}N$ values being most similar to $\delta^{15}N$-NH_4^+ as opposed to $\delta^{15}N$–NO_3^-. Conversely, during winter mixing, values of

POM–$\delta^{15}N$ values were more similar to $\delta^{15}N$–NO_3^-. This seasonal pattern in POM-$\delta^{15}N$ indicates that phytoplankton is primarily sustained by: a) recycled ammonium during the strongly nutrient deficient summer stratified period, and b) during winter mixing by hypolimnetic nitrate, which accumulates over the stratified period and is entrained through the water column. Ammonium uptake is critical for sustaining phytoplankton growth during stratification in oligotrophic lakes with low availability of inorganic N (Suttle and Harrison 1988; Kumar et al. 2008) and tight coupling within the nitrogen cycle (Goldman et al. 1996; Ptacnik 2010). Comparing ammonium uptake by phytoplankton during stratification alongside the coupling between zooplankton excretion and water $\delta^{15}N$-NH_4^+ suggests that tight nitrogen recycling is influenced strongly by localised consumption and excretion by zooplankton in the metalimnion.

4.5.6 Consumer interactions provide new perspectives on lake nutrient cycling

CNR may have a positive feedback with phytoplankton abundance at the DCM during stratification. The depth of DCM in lakes is driven by interactions of physical conditions (light penetration, hypolimnetic nutrients, water density gradients; Hamilton et al. 2010; Leach et al. 2017) as well as zooplankton aggregation and excretion (Pannard et al. 2015). Zooplankton aggregate at the DCM due to relatively high food resource density (Winder et al. 2010), and their excretion becomes a localised nutrient source, producing a positive feedback on DCM phytoplankton growth. Evidence for such a positive feedback in Lake Taupō is provided firstly by the correlation between zooplankton excretion and water $\delta^{15}NH_4^+$ values at the DCM, and secondly by the high contribution of phytoplankton to zooplankton diet at the DCM (Stewart et al. 2017). Biotic interactions exhibit stronger positive and negative feedbacks on spatial and temporal patterns in nutrient cycles than purely abiotic drivers (Carpenter et al. 1992; Levin 1999; Herren et al. 2016; Dong et al. 2017). Such feedback mechanisms should be explicitly considered in lake nutrient management (Herren et al. 2016; Dong et al. 2017). Consumer interactions (i.e., food web dynamics) are not considered explicitly in lake nutrient management. On the basis of our results, however, food web dynamics should be taken into consideration in ecosystem management particularly in oligotrophic lakes.

4.5.7 Potential contributions from N-fixation

N-fixation is a potentially seasonally important additional N source that was not explicitly considered in this study. Heterocystous *Dolichospermum* sp. (cyanobacteria) colonies become most abundant during late stratification when and surface water N:P are typically lowest (Verburg and Albert 2016). N fixation produces $\delta^{15}N$ values of approximately 0 ‰ (Finlay et al. 2007; Somes et al. 2010). Surface-water POM–$\delta^{15}N$ values were closest to 0 ‰ during peak *Dolichospermum* sp. abundance. Zooplankton have been shown to avoid grazing cyanobacteria (Boon et al. 1994; Burns 1998). When N-fixing cyanobacteria biomass is not grazed by zooplankton, it has been shown to sink, then accumulate and decompose within the hypolimnion (Scott and McCarthy 2010). In the context of Lake Taupō, while we are unable to make definitive statements in the absence of measured N-fixation rates, cyanobacteria-fixed N likely becomes available for other non-N-fixing phytoplankton uptake during winter mixing after mineralisation in the hypolimnion.

4.5.8 Consumer nutrient recycling in the context of global environmental change

Variations in CNR have implications for the resilience of lakes to global environmental change. Given the similarities of food web structure (Stewart et al. 2017), nutrient concentrations, and mixing regime between Lake Taupō and other large oligotrophic lakes globally, we expect that our findings can be applied to spatio-temporal patterns in CNR across multiple systems. Increased duration of stratified period is predicted to occur in response to climate change (Adrian et al. 2008; Sahoo et al. 2016) and can result in reduced productivity (Verburg et al. 2003; O'Reilly et al. 2003; Verburg 2007). Previous research has alluded to CNR as a process which may partially offset this effect (Adrian et al. 2008; Lewis 2010). While CNR may dampen fluctuations in phytoplankton biomass between nutrient pulses (e.g., due to mixing events), our results suggest it does not affect production: respiration ratios. In other words, CNR cannot sustain primary production in the long-term but rather is a mechanism for alleviating periods of low nutrient supply. With increasing durations of stratification, CNR may partially offset declines in phytoplankton production for a period, after which the system approaches a threshold collapse (Farnsworth et al. 2017). The importance of CNR within lakes indicates that ecosystem processes typically considered outside of the scope of nutrient management should be explicitly considered for oligotrophic lakes.

4.5.9 Summary

Mechanisms controlling nutrient cycling in oligotrophic lakes are distinct from those in eutrophic lakes. This study demonstrates that stable isotope analysis of nitrogen pools within a lake can be applied to investigate the significance of CNR in lake nutrient cycling. CNR is an important factor in regulating and maintaining primary production in oligotrophic systems during periods of low nutrient availability. Catchment loads and mixing regime are the major determinants of productivity but CNR can have a critical role at specific periods of the year in large oligotrophic lakes. This may provide an important feedback between consumers and phytoplankton supporting consumers during ebbs between resource availability. The findings presented here support the growing call for integration of food web and nutrient management in large lakes.

4.6 Acknowledgments

Ngāti Tūwharetoa, holding manawhenua and kaitiakitanga over Lake Taupō, and as legal owners of the bed of Lake Taupō, provided access to the lake as well as feedback on initial study design. Dr Nick Bradford, Warrick Powrie and Dudley Bell are thanked for regular provision of field assistance. Andy Philips and Ashleigh Immers (GNS Science) assisted with stable isotope analyses. Catherine O'Reilly provided helpful comments on this manuscript. SDS was funded by a PhD scholarship from the Advocates for the Tongariro River. SDS, DPH, PV and ICD were supported by 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). All authors declare no conflicts of interest.

4.7 References

Adrian, R., C. M. O'Reilly, H. Zagarese, and others. 2010. Lakes as sentinels of climate change. Limnol. Oceanogr. **54**: 2283–2297.

Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Glob. Chang. Biol. **23**: 2166-2178

Anisfeld, S. C., R. T. Barnes, M. A. Altabet, and T. X. Wu. 2007. Isotopic apportionment of atmospheric and sewage nitrogen sources in two Connecticut rivers. Environ. Sci. Technol. **41**: 6363–6369.

Bartrons, M., L. Camarero, and J. Catalan. 2010. Isotopic composition of dissolved

inorganic nitrogen in high mountain lakes: variation with altitude in the Pyrenees. Biogeosciences **7**: 1469–1479.

Baustian, M. M., G. J. Hansen, A. de Kluijver, K. Robinson, E. N. Henry, L. B. Knoll, K. C. Rose, and C. C. Carey. 2014. Linking the bottom to the top in aquatic ecosystems: mechanisms and stressors of benthic-pelagic coupling. Eco-DAS X Symp. Proc. 25–47.

Blanchard, J. L., R. Law, M. D. Castle, and S. Jennings. 2010. Coupled energy pathways and the resilience of size-structured food webs. Theor. Ecol. **4**: 289–300.

Boon, P. I., S. E. Bunn, J. D. Green, and R. J. Shiel. 1994. Consumption of cyanobacteria by freshwater zooplankton: implications for the success of "top-down" control of cyanobacterial blooms in Australia. Mar. Freshw. Res. **45**: 875–887.

Bourbonnais, A., M. F. Lehmann, R. C. Hamme, C. C. Manning, and S. K. Juniper. 2013. Nitrate elimination and regeneration as evidenced by dissolved inorganic nitrogen isotopes in Saanich Inlet , a seasonally anoxic fjord. Mar. Chem. **157**: 194–207.

Bratič, A., M. Šturm, J. Faganeli, and N. Ogrinc. 2012. Semi-annual carbon and nitrogen isotope variations in the water column of Lake Bled, NW Slovenia. Biogeosciences **9**: 1–11.

Bruce, L. C., D. Hamilton, J. Imberger, G. Gal, M. Gophen, T. Zohary, and K. D. Hambright. 2006. A numerical simulation of the role of zooplankton in C, N and P cycling in Lake Kinneret, Israel. Ecol. Modell. **193**: 412–436.

Burns, C. W. 1998. Planktonic interactions with an austral bias: Implications for biomanipulation. Lakes Reserv. Res. Manag. **3**: 95–104.

Carpenter, S. R., K. L. Cottingham, and D. E. Schindler. 1992. Biotic feedbacks in lake phosphorus cycles. Trends Ecol. Evol. **7**: 332–336.

Chikaraishi, Y., S. A. Steffan, Y. Takano, and N. Ohkouchi. 2015. Diet quality influences isotopic discrimination among amino acids in an aquatic vertebrate. Ecol. Evol. **5**: 2048–2059.

Conroy, J. D., W. J. Edwards, R. a. Pontius, D. D. Kane, H. Zhang, J. F. Shea, J. N. Richey, and D. a. Culver. 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshw. Biol. **50**: 1146–1162.

Cooke, S. J., E. H. Allison, T. D. Beard, and others. 2016. On the sustainability of inland fisheries: Finding a future for the forgotten. Ambio **45**: 753–764.

Crawley, M. J. 2007. The R Book, 1st ed. Wiley & Sons Ltd.

Cyr, H., K. J. Collier, S. J. Clearwater, B. J. Hicks, and S. D. Stewart. 2016. Feeding and nutrient excretion of the New Zealand freshwater mussel *Echyridella menziesii* (Hyriidae, Unionida): implications for nearshore nutrient budgets in lakes and reservoirs. Aquat. Sci. **79**: DOI: 10.1007/s00027-016-0517-9.

Denk, T. R. A., J. Mohn, C. Decock, D. Lewicka-szczebak, E. Harris, K. Butterbach-bahl, R. Kiese, and B. Wolf. 2017. The nitrogen cycle : A review

of isotope effects and isotope modeling approaches. Soil Biol. Biochem. **105**: 121–137.

Dong, X., A. Ruhí, and N. B. Grimm. 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proc. Natl. Acad. Sci. **114**: E4744-E4752

Duggan, I. C., J. D. Green, and D. F. Burger. 2006. First New Zealand records of three non-indigenous zooplankton species: *Skistodiaptomus pallidus, Sinodiaptomus valkanovi,* and *Daphnia dentifera*. New Zeal. J. Mar. Freshw. Res. **40**: 561–569.

Elser, J. J., D. R. Dobberfuhl, N. Mackay, and J. H. Schampel. 1996. Size , and Life Stoichiomet Toward a unified view of cellular and ecosystem processes. Bioscience **46**: 674–684.

Farnsworth, K. D., L. Albantakis, and T. Caruso. 2017. Unifying concepts of biological function from molecules to ecosystems. Oikos **126:** 1367–1376.

Finlay, J. C., R. W. Sterner, and S. Kumar. 2007. Isotopic evidence for in-lake production of accumulating nitrate in Lake Superior. Ecol. Appl. **17**: 2323–32.

Forsyth, D. J., and I. D. McCallum. 1980. Zooplankton of Lake Taupo. New Zeal. J. Mar. Freshw. Res. **14**: 65–69.

Goldman, C. R., J. J. Elser, R. C. Richards, J. E. Reuters, J. C. Priscu, and A. L. Levin. 1996. Thermal stratification , nutrient dynamics , and phytoplankton productivity during the onset of spring phytoplankton growth in Lake Baikal, Russia. Hydrobiologia **331**: 9–24.

Granger, J., and D. M. Sigman. 2009. Removal of nitrite with sulfamic acid for nitrate N and O isotope analysis with the denitrifier method. Rapid Commun. Mass Spectrom. **23**: 3753–3762.

Granger J, Wankel S. D. 2016. Isotopic overprinting of nitrification on denitrification as a ubiquitous and unifying feature of environmental nitrogen cycling. Proc. Natl. Acad. Sci. **113**: E6391-E6400.

Hamilton, D. P., K. R. O'Brien, M. A. Burford, J. D. Brookes, and C. G. McBride. 2010. Vertical distributions of chlorophyll in deep, warm monomictic lakes. Aquat. Sci. **72**: 295–307.

Hamilton, D., and K. Wilkins. 2005. Review of science underpinning the 20% nitrogen reduction target for Lake Taupo. Report to the Ministry for the Environment. Centre for Biodiversity and Ecology Research, University of Waikato.

Hawes, I., and R. Smith. 1994. Seasonal dynamics of epilithic periphyton in oligotrophic Lake Taupo, New Zealand. New Zeal. J. Mar. Freshw. Res. **28**: 1–12.

Hecky, R. E., P. Campbell, and L. L. Hendzel. 1993. The stoichiometry of carbon , nitrogen , and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. **38**: 709–724.

Herren, C. M., K. C. Webert, M. D. Drake, M. J. Vander Zanden, Á. Einarsson, A. R. Ives, and C. Gratton. 2016. Positive feedback between chironomids and

algae creates net mutualism between benthic primary consumers and producers. Ecology **98**: 447–455.

Higgins, S. N., B. Althouse, S. P. Devlin, Y. Vadeboncoeur, and M. J. Vander Zanden. 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology **95**: 2257–2267.

Hogg, A., D. J. Lowe, J. Palmer, G. Boswijk, and C. B. Ramsey. 2011. Revised calendar date for the Taupo eruption derived by 14C wiggle-matching using a New Zealand kauri 14C calibration data set. The Holocene **22**: 439–449.

Howard-Williams, C., and J. Davies. 1988. The invasion of Lake Taupo by the submerged water weed Lagarosiphon major and its impact on the native flora. N. Z. J. Ecol. **11**: 13–19.

James, M. R. 1985. Distribution , biomass and production of the freshwater mussel , Hyridella menziesi (Gray), in Lake Taupo , New Zealand. Freshw. Biol. **15**: 307–314.

James, M. R. 1987. Seasonal changes in metabolic rates of zooplankton and their importance to phytoplankton production in two New Zealand lakes of contrasting trophic state. New Zeal. J. Mar. Freshw. Res. **21**: 573–583.

Johannsson, O. E., R. Dermott, D. M. Graham, J. a. Dahl, E. Scott Millard, D. D. Myles, and J. LeBlanc. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. J. Great Lakes Res. **26**: 31–54.

Jolly, V. H. 1965. Diurnal surface concentrations of zooplankton in Lake Taupo, New Zealand. Hydrobiologia **25**: 466–472.

Kao, Y. C., S. A. Adlerstein, and E. S. Rutherford. 2016. Assessment of top-down and bottom-up controls on the collapse of alewives (*Alosa pseudoharengus*) in Lake Huron. Ecosystems **19**: 803–831.

Keeling, C. D. 1958. The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas. Geochim. Cosmochim. Acta **13**: 322–34.

Kendall, C., E. M. Elliott, and S. D. Wankel. 2007. Tracing anthropogenic inputs of nitrogen to ecosystems, p. 375–449. *In* R. Michener and K. Lajtha [eds.], Stable isotopes in ecology and environmental science. Wiley Online Library.

Kilham, P., and S. Kilham. 1990. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshw. Biol. **23**: 379–389.

Kumar, S., R. W. Sterner, and J. C. Finlay. 2008. Nitrogen and carbon uptake dynamics in Lake Superior. J. Geophys. Res. **113**: 1–15.

Lampert, W. 2017. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. **3**: 21–27.

Leach, T., B. Beisner, C. Carey, Pernica, P. , Rose, K. C., Huot, Y. , Brentrup, J. A., Domaizon, I. , Grossart, H. , Ibelings, B. W., Jacquet, S. , Kelly, P. T., Rusak, J. A., Stockwell, J. D., Straile, D. and Verburg, P. 2017. Relative importance of light and thermal stratification in prediting the structure of deep chlorophyll maxima among lakes. Limnol. Oceanogr. **63**: 628-646

Levin, S. A. 1999. Fragile dominion: complexity and the commons. Perseus Books.

Lewis, W. J. 2010. Biogeochemistry of tropical lakes. Verh Int Verein Limnol **30**: 1595–1603.

Li, W., and M. H. H. Stevens. 2010. How enrichment, ecosystem size, and their effects on species richness co-determine the stability of microcosm communities. Oikos **119**: 686–695.

Liu, K., S. Kao, K. Chiang, G. Gong, and J. Chang. 2013. Concentration dependent nitrogen isotope fractionation during ammonium uptake by phytoplankton under an algal bloom condition in the Danshuei estuary , northern Taiwan. Mar. Chem. **157**: 242–252.

McIlvin, M. R., and M. a Altabet. 2005. Chemical conversion of nitrate and nitrite to nitrous oxide for nitrogen and oxygen isotopic analysis in freshwater and seawater. Anal. Chem. **77**: 5589–95.

McMeans, B. C., K. S. McCann, M. Humphries, N. Rooney, and A. T. Fisk. 2015. Food web structure in temporally-forced ecosystems. Trends Ecol. Evol. **30**: 662–672.

Menge, D. N. L., W. T. Baisden, S. J. Richardson, D. A. Peltzer, and M. M. Barbour. 2011. Declining foliar and litter $\delta^{15}N$ diverge from soil , epiphyte and input $\delta^{15}N$ along a 120 000 yr temperate rainforest chronosequence. New Phytol. **190**: 941–952.

Michelsen, A., I. K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia **105**: 53–63.

Middelburg, J. J. 2014. Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences **11**: 2357–2371.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta **48**: 1135–1140.

Mohan, J. A., S. D. Smith, T. L. Connelly, E. T. Attwood, J. W. Mcclelland, S. Z. Herzka, and B. D. Walther. 2016. Tissue-specific isotope turnover and discrimination factors are affected by diet quality and lipid content in an omnivorous consumer. J. Exp. Mar. Bio. Ecol. **479**: 35–45.

Moss, B. 2012. Cogs in the endless machine: lakes, climate change and nutrient cycles: a review. Sci. Total Environ. **434**: 130–42.

Nestler, A., M. Berglund, F. Accoe, S. Duta, D. M. Xue, P. Boeckx, and P. Taylor. 2011. Isotopes for improved management of nitrate pollution in aqueous resources: review of surface water field studies. Environ. Sci. Pollut. Res. **18**: 519–533.

Newsome, S. D., C. Martenez del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. Front. Ecol. Environ. **5**: 429–436.

O'Reilly, C. M., S. R. Alin, P.-D. D. Plisnier, A. S. Cohen, and B. A McKee. 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature **424**: 766–768.

O'Reilly, C. M., R. E. Hecky, A. S. Cohen, and P.-D. Plisnier. 2002. Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. Limnol. Oceanogr. **47**: 306–309.

O'Reilly, C. M., R. J. Rowley, P. Schneider, J. D. Lenters, P. B. Mcintyre, and B. M. Kraemer et al. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys. Res. Lett. **42**, 10,773–10,781.

Olive, P. J. W., J. K. Pinnegar, N. V. C. Polunin, G. Richards, and R. Welch. 2003. Isotopic trophic-step fractionation: a dynamic equilibrium model. J. Anim. Ecol. **72**: 608–617.

Pannard, A., D. Planas, and B. E. Beisner. 2015. Macrozooplankton and the persistence of the deep chlorophyll maximum in a stratified lake. Freshw. Biol. **60**: 1717–1733.

Polis, G. a., and D. R. Strong. 1996. Food Web Complexity and Community Dynamics. Am. Nat. **147**: 813.

Ptacnik, R., S. D. Moorthi, and H. Hillebrand. 2010. Hutchinson reversed , or why there need to be so many species, p. 1–43. *In* G. Woodward [ed.], Advances in Ecological Research. Academic Press.

Robinson, D. 2001. ^{15}N as an integrator of the nitrogen cycle. Trends Ecol. Evol. **16**: 153–162.

Rowe, D. K., S. Nichols, and G. R. Kelly. 2001. Depth distribution and abundance of the common bully, *Gobiomorphus cotidianus* (Eleotridae), in three oligotrophic New Zealand lakes, one of which is turbid. Environ. Biol. Fishes **61**: 407–418.

Rowe, D. K., and M. Schallenberg. 2004. Food webs in lakes, p. 23.1-23.14. *In* J.S. Harding, P. Mosley, C. Pearson, and B. Sorrell [eds.], Freshwaters of New Zealand. Caxton Press.

Sahoo, G. B., A. L. Forrest, S. G. Schladow, J. E. Reuter, R. Coats, and M. Dettinger. 2016. Climate change impacts on lake thermal dynamics and ecosystem vulnerabilities. Limnol. Oceanogr. **61**: 496–507.

Schindler, D. E., J. F. Kitchell, X. He, S. R. Carpenter, J. R. Hodgson, and K. L. Cottingham. 1993. Food web structure and phosphorus cycling in lakes. Trans. Am. Fish. Soc. **122**: 756–772.

Scott, J. T., and M. J. McCarthy. 2010. Nitrogen fixation may not balance the nitrogen pool in lakes over timescales relevant to eutrophication management. Limnol. Oceanogr. **55**: 1265–1270.

Sereda, J. M., J. J. Hudson, and P. D. Mcloughlin. 2008. General empirical models for predicting the release of nutrients by fish, with a comparison between detritivores and non-detritivores. Freshw. Biol. **53**: 2133–2144.

Sharp, Z. 2007. Principles of Stable Isotope Geochemistry, C. Rapp [ed.]. Pearson Prentice Hall.

Shostell, J., and P. A. Bukaveckas. 2004. Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. Aquat. Ecol. **38**: 359–373.

Sigman, D. M., K. L. Casciotti, M. Andreani, C. Barford, M. Galanter, and J. K.

Böhlke. 2001. A bacterial method for the nitrogen isotopic analysis of nitrate in seawater and freshwater. Anal. Chem. **73**: 4145–4153.

Sigman, D. M., J. Granger, P. J. DiFiore, M. M. Lehmann, R. Ho, G. Cane, and A. van Geen. 2005. Coupled nitrogen and oxygen isotope measurements of nitrate along the eastern North Pacific margin. Global Biogeochem. Cycles **19**: GB4022

Somes, C. J., A. Schmittner, E. D. Galbraith, and others. 2010. Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem. Cycles **24**: GB4019.

Spigel, R. H., C. Howard-Williams, M. Gibbs, S. Stephens, and B. Waugh. 2005. Field calibration of a formula for entrance mixing of river inflows to lakes: Lake Taupo, North Island, New Zealand. New Zeal. J. Mar. Freshw. Res. **39**: 785–802.

Spillman, C. M., J. Imberger, D. P. Hamilton, M. R. Hipsey, and J. R. Romero. 2007. Modelling the effects of Po River discharge , internal nutrient cycling and hydrodynamics on biogeochemistry of the Northern Adriatic Sea. J. Mar. Syst. **68**: 167–200.

Steffan, S. A., Y. Chikaraishi, C. R. Currie, H. Horn, H. R. Gaines-Day, J. N. Pauli, J. E. Zalapa, and N. Ohkouchi. 2015. Microbes are trophic analogs of animals. Proc. Natl. Acad. Sci. **112**: 15119-15124

Stewart S. D., Hamilton D. P., Baisden W. T., Dedual M., Verburg P., Duggan I. C., Hicks B. J., Graham B. S. 2017. Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. Freshwater Biology **62**: 2008–2025

Stewart, S. D., Hamilton, D. P., Baisden W. T., Verburg, P., Duggan I. C. 2018. The role of mobile consumers in lake nutrient cycles: a brief review. Hydrobiologia DOI: 10.1007/s10750-018-3603-2

Suttle, C. A., and P. J. Harrison. 1988. Rapid ammonium uptake by freshwater phytoplankton. J. Phycol. **24**: 13–16.

Vanni, M. J., G. Boros, and P. B. McIntyre. 2013. When and fish sources vs. sinks of nutrients in lake ecosystems? Ecology **94**: 2195–2206.

Vanni, M. J., A. M. Bowling, E. M. Dickman, and others. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. Ecology **87**: 1696–709.

Vant, B. 2013. Recent changes in the water quality of Lake Taupo and its inflowing streams. New Zeal. J. For. **58**: 27–30.

Vant, B., and M. Gibbs. 2006. Nitrogen and Phosphorus in Taupo Rainfall. Waikato Regional Council Technical Report: 2006/46, Hamilton.

Verburg, P. 2007. The need to correct for the Suess effect in the application of $\delta^{13}C$ in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. J. Paleolimnol. **37**: 591–602.

Verburg, P., and A. Albert. 2016. Lake Taupo Long-term Monitoring Programme, 2014 – 2015. Prepared for Waikato Regional Council, Report: TR 2016/13.

Verburg, P., R. E. Hecky, and H. Kling. 2003. Ecological consequences of a

centuray of warming in Lake Tanganyika. Science **301**: 505–508.

Vincent, W. F. 1983. Phytoplankton production and winter mixing: contrasting effects in two oligotrophic lakes. J. Ecol. **71**: 1–20.

Ward, F. J., T. G. Northcote, and J. A. T. Boubee. 2005. The New Zealand common smelt: Biology and ecology. J. Fish Biol. **66**: 1–32.

Wassenaar, L. I. 2012. Dissolved oxygen status of Lake Winnipeg: Spatio-temporal and isotopic ($\delta^{18}O$-O_2) patterns. J. Great Lakes Res. **38**: 123–134.

Wells, N. S., W. T. Baisden, T. Horton, and T. J. Clough. 2016. Spatial and temporal variations in nitrogen export from a New Zealand pastoral catchment revealed by stream water nitrate isotopic composition. Water Resour. Res. **52**: 2840–2854.

White, E. and Payne, G. W. 1977. Chlorophyll production, in response to nutrient additions, by the algae in Lake Taupo water. New Zealand Journal of Marine and Freshwater Research, 11, 501-507.

Winder, M., P. Spaak, W. M. Mooij, S. Ecology, and N. Jul. 2004. Trade-offs in Daphnia Habitat Selection. Ecology **85**: 2027–2036.

Wing, S. R., M. Gault-Ringold, C. H. Stirling, L. C. Wing, O. A. Shatova, and R. D. Frew. 2017. δ^{56} Fe in seabird guano reveals extensive recycling of iron in the Southern Ocean ecosystem. Limnol. Oceanogr. **62**: 1671-1681

Xue, D. M., J. Botte, B. De Baets, and others. 2009. Present limitations and future prospects of stable isotope methods for nitrate source identification in surface- and groundwater. Water Res. **43**: 1159–1170.

Yang, L. H., J. L. Bastow, K. O. Spence, A. N. Wright, S. Ecology, N. Mar, and N. Wright. 2008. What Can We Learn from Resource Pulses? Ecology **89**: 621–634.

Zhang, L., M. a Altabet, T. Wu, and O. Hadas. 2007. Sensitive measurement of NH_4^+ $^{15}N/^{14}N$ ($\delta^{15}NH_4^+$) at natural abundance levels in fresh and saltwaters. Anal. Chem. **79**: 5297–303.

Zou, K., E. Thabault, G. Lacroix, S. Barot, and S. Leroux. 2016. Interactions between the green and brown food web determine ecosystem functioning. Funct. Ecol. **30**: 1454–1465.

4.8 Supplementary information

Table 4-1: Standard deviations (‰) for $\delta^{15}N\text{-}NH_4^+$, $\delta^{15}N$-POM, $\delta^{15}N\text{-}NO_3^-$ and $\delta^{18}O\text{-}NO_3^-$ samples from all four lake habitats throughout all six sampling months. Colour scale reflects relative variance within the sample set with red reflecting the highest standard deviations.

Month	Habitat	n	$\delta^{15}N\text{-}NH_4^+$	$\delta^{15}N$-POM	$\delta^{15}N\text{-}NO_3^-$	$\delta^{18}O\text{-}NO_3^-$
September	Bottom	3	11.41	0.75	0.33	5.25
December	Bottom	3	17.13	4.01	0.24	0.86
February	Bottom	3	7.01	1.09	0.39	1.12
April	Bottom	3	1.45	1.22	0.74	0.14
June	Bottom	3	12.21	1.94	0.43	2.43
August	Bottom	3	39.12	1.51	0.87	0.33
September	DCM	3	9.21	11.00	0.52	3.34
December	DCM	3	0.45	1.18	0.14	0.74
February	DCM	3	7.19	4.09	0.75	3.49
April	DCM	3	4.75	6.29	0.95	0.76
June	DCM	3	4.80	1.51	1.97	0.96
August	DCM	3	2.68	0.45	0.66	0.83
September	Surface	3	13.50	2.61	1.35	4.66
December	Surface	3	2.92	7.25	0.93	0.91

February	Surface	3	15.62	4.06	0.89	2.14
April	Surface	3	3.13	5.48	2.74	3.32
June	Surface	3	7.25	0.28	1.84	1.33
August	Surface	3	7.47	0.28	1.12	0.49
September	Littoral	5	8.06	9.19	0.48	2.03
December	Littoral	6	5.49	7.95	0.55	0.86
February	Littoral	6	3.69	5.80	2.23	3.17
April	Littoral	6	18.14	3.28	0.99	3.81
June	Littoral	6	11.63	1.48	1.12	1.88
August	Littoral	6	6.54	2.36	1.71	1.53

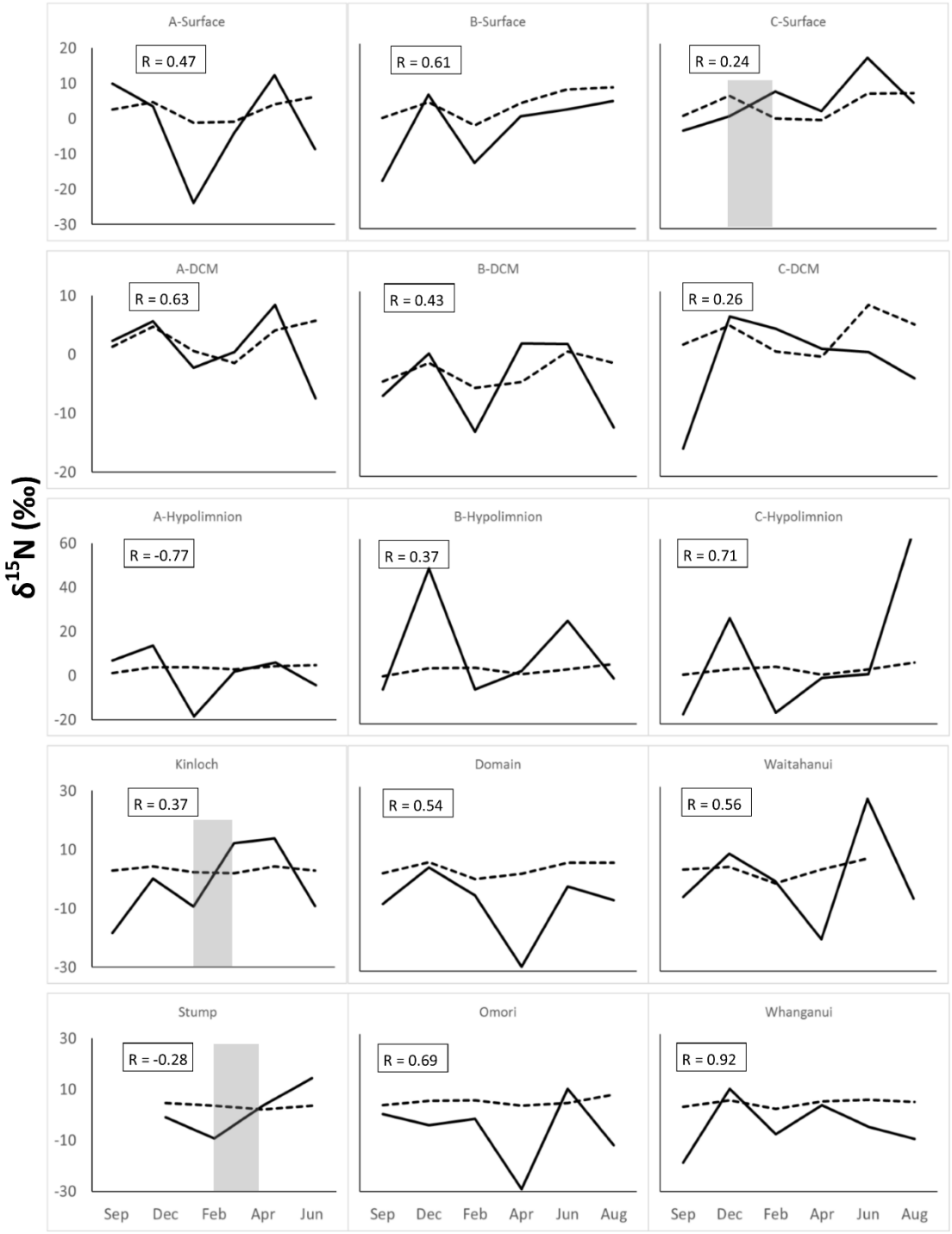


Figure 4-10 1: Time series of ammonium $\delta^{15}N$ (solid line) and nitrate $\delta^{15}N$ (dashed line) for individual sites across the six sampled months. Correlation coefficients (R) for temporal covariation between ammonium and nitrate $\delta^{15}N$ are displayed for each site. Periods of potential nitrification (i.e., coupled ^{15}N depletion of nitrate and enrichment of ammonium) are identified by grey blocks.

Chapter five

Biological nitrogen recycling and translocation exceed physical transport fluxes in a large oligotrophic lake: A coupled mass balance and hydrodynamic model evaluation

5.1 Abstract

Nitrogen (N) supply within lakes is the sum of 'new' influxes and recycling of 'old' fluxes. Understanding the relative contributions of these two processes is an important consideration for nutrient management in lakes. Physical influxes of littoral N into pelagic waters are known to be both substantial and variable, but are seldom considered in isolation. A three-dimensional hydrodynamic model was used in this study to quantify littoral-pelagic exchanges of water over an annual cycle in Lake Taupō; a large (59 km^3) warm monomictic, oligotrophic lake in North Island, New Zealand. Modelled littoral-pelagic exchanges and respective N concentrations, together with phytoplankton N uptake and other major N influxes were incorporated into the mass balance model. Calculated recycling rates were compared against nitrate, ammonium and POM $\delta^{15}N$ values to test if ^{15}N-depletion was related to high rates of consumer nutrient recycling. The model demonstrates that littoral-pelagic exchange acted as a net source of N to the pelagic surface waters throughout the year. However, during summer stratification (December and February), consumer excretion of littoral-derived N exceeded the physical transport influx. The mass balance model indicated that *in situ* recycling was the dominant flux (> 70%) throughout the year. Stable isotope data showed that much of the N recycling could be accounted for by phytoplankton excretion, related to the winter peak of biomass. By contrast, consumer recycling remained relatively consistent throughout the year. These results highlight the dominant role of biological interactions to recycle and transport nitrogen and drive phytoplankton production in lakes.

5.2 Introduction

Renewal of the dissolved inorganic nitrogen pool in lake ecosystems is due to two processes; influxes of allochthonous ('new') nitrogen and *in situ* recycling of organic ('old') nitrogen (Finlay et al., 2007; Allgeier et al., 2017). Understanding the relative contributions of these processes, and variations within each, is critical

for effective nutrient management (Carpenter et al., 2011; Schindler et al., 2016). Catchment land-management is most commonly used to attempt to achieve nitrogen concentration targets in lake pelagic waters (Hamilton et al., 2016) and the role of recycling in retaining N is rarely considered (Lewis and Wurtsbaugh, 2008). Recycling may be particularly important during periods of stratification when particulate nutrients settle out into the hypolimnion, leading to progressive nitrogen depletion (Kumar et al. 2008; Lewis, 2010). Nitrate, ammonium and POM $\delta^{15}N$ values in pelagic surface waters can be used to estimate the relative contribution of recycling to the dissolved inorganic nitrogen (DIN) pool from consumer (bacteria through to top-predator) excretion (see Chapter 4).

Influxes of new nitrogen can include: delivery of catchment N in riverine inflows (Abell and Hamilton, 2015), direct atmospheric deposition (Batrons et al., 2010), cyanobacteria N-fixation (Scott and McCarthy, 2010), translocation of nutrients in excretion by littoral feeding mobile consumers (Schostell and Bukavickas, 2004; Vanni et al., 2013); localised hypolimnetic upwelling events (Boehrer and Schultze, 2008; Bocaniov et al., 2010), and physical exchange of littoral and pelagic water (Monismith et al., 1990; Boehrer and Schultze, 2008). Littoral-pelagic exchange has received less attention than other physical transport processes such as hypolimnetic upwelling as a source of new nitrogen (see Boehrer and Schultze, 2008). However, littoral areas of lakes are typically highly productive environments which have higher DIN concentrations than pelagic waters (Hawes and Smith, 1994; Vadeboncoeur et al., 2003). Higher DIN concentrations in littoral waters are the result of multiple influxes of DIN, including *in situ* mineralisation (Brothers et al., 2016), mixing with riverine inputs (Spigel et al., 2005) and hypolimnetic upwelling (MacIntyre et al. 2009; Corman et al. 2010). Physical exchanges, along with movement of mobile consumers, can transport DIN from littoral to surface pelagic waters.

Littoral-pelagic exchange is controlled by water circulation patterns set up mostly by interactions of the prevailing wind field and the lake bed morphology (Rueda and MacIntyre, 2010), Coriolis effects (Csanady, 1977), riverine inflows (Spigel et al., 2005; Abell and Hamilton, 2015) and the internal wave field (Antenucci and Imberger, 2001). Quantifying littoral-pelagic exchanges of nitrogen will provide substantially improved understanding of how nitrogen enters and is cycled in the pelagic zone.

Three-dimensional (3-D) hydrodynamic models are a powerful tool to assist with understanding physical transport of water between areas of lake basins (Imberger et al., 2017). They can provide insights into littoral-pelagic water exchange, for example by labelling specific water volumes with inert tracers and quantifying the dilution of the tracers (Abell and Hamilton, 2015). When combined with DIN concentration data, 3-D models may allow littoral-pelagic exchange and hypolimnetic upwelling to be included in pelagic surface water nitrogen budgets. Combining this information with $\delta^{15}N$ data has the potential to quantify the relative importance of, and temporal variations in, physical transport and recycling of DIN (Figure 5-1).

This study applies a 3-D hydrodynamic model to Lake Taupō, a large (616 km^2), deep (mean depth = 90 m), oligotrophic lake in the North Island of New Zealand. Inert tracers are used in model simulations to quantify littoral-pelagic water exchange during six sampling periods over an annual cycle. Fluxes of water are combined with DIN concentration data as well as published and modelled calculations of all important DIN influxes in order to develop a N mass-balance budget for the pelagic surface waters. The pelagic surface water N budget is then used to: 1) compare supply of DIN from physical transport and consumer translocation from littoral to pelagic surface waters throughout the annual cycle; 2) calculate the role of *in situ* recycling; 3) test for relationships between nitrogen recycling rates and $\delta^{15}N$ of nitrate, ammonium and particulate organic matter (POM) $\delta^{15}N$ data. These analyses support testing the hypothesis that after the onset of summer stratification, *in situ* recycling becomes the primary source of DIN for pelagic surface waters and that $\delta^{15}N$-DIN values correspondingly become progressively negative.

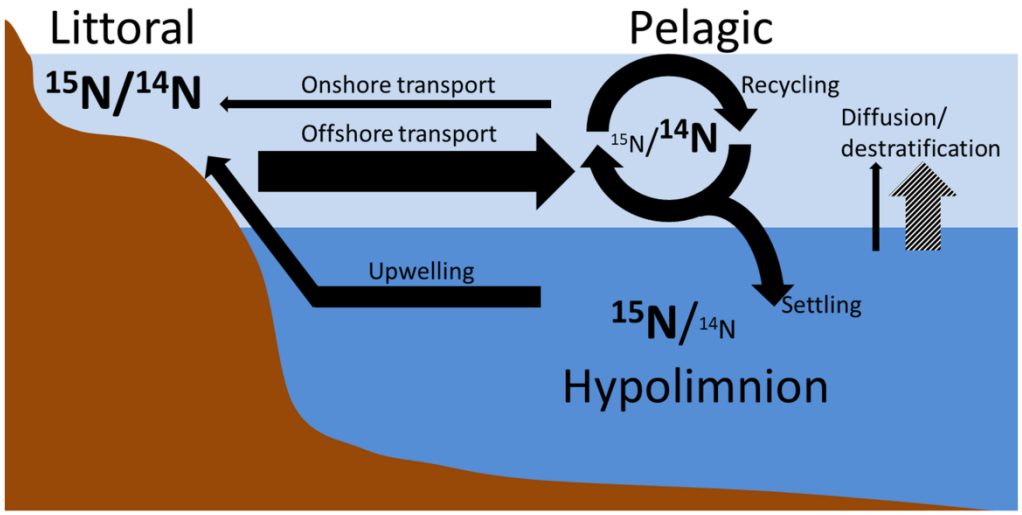


Figure 5-1: Conceptual representation of flows of N in a stratified lake and associated effects on $\delta^{15}N$ values. Font size of ^{14}N and ^{15}N demonstrates the relative isotope enrichment associated with the respective processes.

5.3 Methods

5.3.1 Study site

Lake Taupō is a large, deep (max. depth 160 m) caldera lake formed in 1257 CE (Hogg et al., 2011). The lake consists of a single basin and is characterised by a relatively small littoral area due to the steep shoreline (Figure 5-2). The mean shoreline gradient is 45° (Hawes and Smith, 1994). This steep gradient is partially due to the presence of vertically plunging cliffs along much of the western shoreline. The lake has a small natural catchment (3,487 km^2) relative to the lake volume (59 km^3), resulting in a lake water residence time of 13.5 years prior to the commissioning of the Tongariro power scheme between 1973 and 1983. This scheme diverts an additional 1.3 km^3 of water into the lake annually from neighbouring catchments and reduces the residence time to 10.5 years (Hamilton and Wilkins, 2005). Detailed descriptions of the ecology of Lake Taupō are provided in Stewart et al. (2017) and in Chapter 4. Briefly, Lake Taupō is a monomictic lake that, owing to high water clarity and temperate-subtropical location, has peak phytoplankton production during winter mixing when nutrient availability is greatest (Vincent 1983). During the remaining approximately ten months of stratification, when nutrient concentrations in the euphotic zone are progressively reduced, consumer excretion becomes a significant nutrient source (Chapter 4), at which time there is also a high degree of littoral-pelagic diet coupling (Stewart et al., 2017).

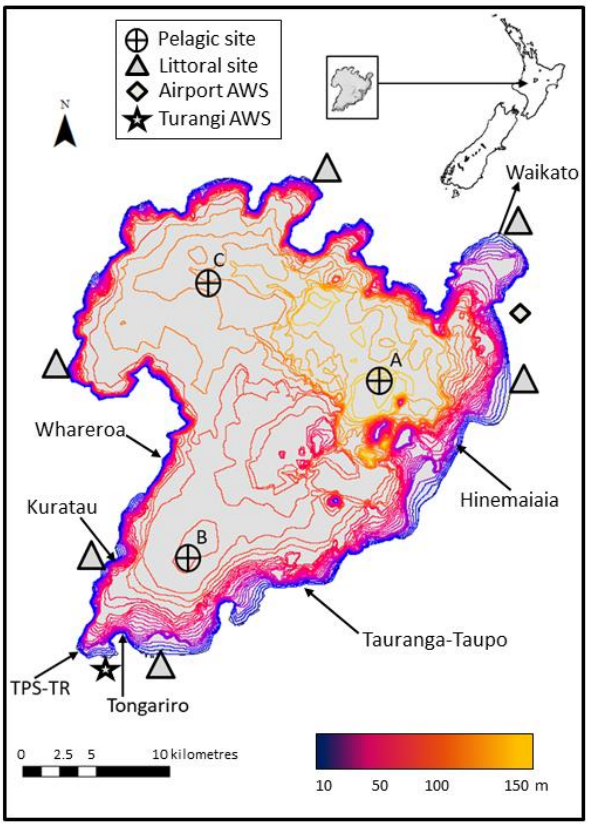


Figure 5-2: Bathymetric map of Lake Taupō showing the pelagic (circles) and littoral (triangles) sampling sites used in the study. Six inward-pointing arrows and one outward-pointing arrow show locations of the six gauged surface inflows and the surface outflow, respectively.

5.3.2 Model setup

The three-dimensional Aquatic Ecosystem Model (AEM3D – Hydronumerics, Victoria, Australia) was used to simulate hydrodynamics in Lake Taupō. The simulation period was 1 January 2014 to 18 October 2015. This period was chosen to coincide with a field sampling campaign between 10 September 2014 and 8 August 2015. AEM3D is a hydrostatic model based on the unsteady, viscous Navier-Stokes equations for incompressible flow (Hodges and Dallimore, 2015). A comprehensive overview of the model is provided in Imberger et al. (2017). Simulation modules include surface thermodynamics, inflows and outflows, water temperature and density, direct precipitation and Coriolis forcing. In short, the modelling process involved the following steps: 1) lake bathymetry was discretised into a 2-D configuration of bed elevation, 2) meteorological and catchment inflow forcing data were compiled and formatted for model input at an hourly time step, 3) model calibration and validation was performed, 4) a conservative tracer was employed within the pelagic zone to simulate littoral-pelagic exchange in cells corresponding to the sampling sites, 5) simulations of littoral-pelagic exchange

rates derived from the tracer were compared with concentrations of ammonium (NH_4^+-N), nitrate (NO_3^--N), total nitrogen (TN), as well as POM, nitrate and ammonium $\delta^{15}N$ data.

Bathymetry configuration – The lake surface area was converted into a grid of cells in ArcGIS Version 10.5.1 (ESRI Redlands, CA, USA). A 2 m (or higher) horizontal resolution bathymetry map from Land Information New Zealand (data.linz.govt.nz accessed: July 2012) was digitised to provide an average depth for each cell. Individual cells had dimensions of x = 500 m, y = 500 m and z (vertical) = 0.5 to 15 m. The vertical water column was divided into 35 layers of thickness 0.5 m at the surface, 3 m between 5 and 50 m depth, and then incrementally increasing up to 15 m at 120 m depth, below which the layer thickness was constant at 15 m. The variable thickness was chosen to enable higher resolution in the epilimnion and metalimnion layers.

5.3.3 Environmental forcing data

Meteorological information – Meteorological data were collected from two stations, both within 1 km of the lake shore, during the model period of September 2014 until August 2015 (Figure 5-2). Mean hourly atmospheric pressure, recorded at the Taupō Airport weather station on the north-eastern shore, was obtained from the New Zealand MetService. Hourly measurements of air temperature, wind speed and direction, solar radiation and rainfall were collected from National Institute of Water and Atmosphere (NIWA) at their Turangi weather station, at the southern end of the lake (Figure 5-2). Daily cloud cover was estimated from the ratio of observed solar radiation to potential radiation at midday for each day. Potential solar radiation was derived using the Bird Clear-sky model (Bird and Hulstrom, 1981). The installation of an autonomous monitoring buoy at Site A (Figure 5-2) in March 2015 provided *in situ* wind recordings for the centre of the lake from 13 March 2015 to 30 April 2015. Lake shore and mid-lake wind speed measurements provided an indication of wind speed variability within the lake wind-field (Antenucci and Imberger, 2003). AEM3D uses a constant wind-field over a lake, and commonly applies an average wind-speed over the lake (Hodges & Dallimore, 2015). Quartile regression between lake shore and mid-lake wind stations gave the following relationship of wind speed:

$$U_{Buoy} = 2.2\ x\ U_{Turangi}$$

where U is wind speed (m s^{-1}) and subscripts represent the two locations. Wind speed was adjusted to the 10 m elevation used as input to the model following equations described in Verburg and Antenucci, (2010). Scaling factors of 1 and 2.2 represented the minimum and maximum wind speeds within the Lake Taupō wind-field. The appropriate scaling factor for the mean wind speed was determined through an iterative process by matching modelled and observed water column profiles. This resulted in a scaling factor of 1.5 being applied to lake-shore meteorological station data, to represent mean wind speed for the Lake Taupō wind-field.

Inflows –Discharge (*Q*) and water temperature for all second-order and greater surface inflows to the lake (35 inflows in total) as well as the single surface outflow, the Waikato River, were included as boundary condition forcing data. A summary of forcing data and sources is provided in Table 1. Eight of the 35 natural inflows (Table 5-1), the Waikato River and water diverted into Lake Taupō from neighbouring catchments through the Tongariro Power Scheme (Genesis, 2017) had mean hourly *Q* values for the entire sampling period. Values of *Q* for the Tongariro Power Scheme were derived from records of hydro-electric power generation (MW) while all other measured values of *Q* were derived from calibrated flow gauging managed by various organisations (Table 5-1). For the remainder of inflows, the Catchment Land-Use model for Environmental Sustainability (CLUES: Elliot et al., 2011), was used to determine mean annual *Q* based on catchment area as well as topographic and land cover information. Within the gauged catchments, discharge varies substantially throughout the year. Hence prescribing a mean annual *Q* to the majority of inflows would produce substantial error in the lake water balance at more highly resolved time scales. Mean hourly *Q* used as model input was assigned for catchments with modelled mean annual *Q* data by matching discharge to the hydrograph of the nearest-neighbour gauged stream of similar catchment area (± 20%), corrected for the difference in mean annual *Q* between the two inflows.

Groundwater inputs – Groundwater inputs were assigned as the daily *Q* required to balance the water budget. Known terms within the water budget were the 35 surface inflows, the surface outflow, direct rainfall on the lake surface and evaporation from the lake surface. The residual of the water balance was calculated daily by fit of modelled and measured lake water level. The average of the previous seven days

was used for measured lake water level in order to dampen high-resolution surface oscillations and measurement error. The water balance residual yielded an annual mean *Q* of 13 ± 12.4 (SD) $m^3 s^{-1}$. This value represents the upper estimated ground water inputs of 5.36 to 13.8 $m^3 s^{-1}$ (Maxwell 2012). It should be noted that first order surface water inflows were not explicitly modelled as inputs and, hence, were also included in our groundwater inflow. Given that > 90% of ground water is estimated to enter the lake between depths of 1 and 15 m (Maxwell, 2012), combining first order surface inflows with groundwater was considered reasonable. A comparison was also made between assigning groundwater *Q* as a variable rate matched to the daily water balance residual and as a constant rate. The comparison allowed the modelled water balance to deviate from the measured one by approximately 0.2% of the total water mass, demonstrating that groundwater inputs had a negligible effect on modelled water transport within the lake. Correlations of pelagic surface water tracer dilutions between the two models gave $R^2 > 0.99$.

Surface inflow and ground water temperature – Daily stream inflow water temperature was required for forcing data input as temperature has a strong effect on how the inflow interacts with the receiving lake water (Spigel et al., 2005). Monthly spot water temperature measurements for 23 of the stream inflows (n = 24 – 28) were available from Waikato Regional Council (WRC) for the duration of the model simulation period. A non-linear regression model (Mohseni et al., 1998) provided mean daily inflow water temperatures using five-day average air temperatures and quadratic parameters accounting for minimum and maximum water temperature observed in the data series (January 2014 until December 2015) as well as hysteresis from warming and cooling seasons. The parameter values were determined by fitting the regression model to monthly observed temperatures. Twelve of the stream inflows did not have water temperature records, so modelled daily water temperature from the nearest neighbouring stream of similar catchment size (± 20%) was used as a surrogate. The Tokaanu Power Scheme discharge included mean hourly temperature for model input, as opposed to daily data, as this discharge is highly variable due to fluctuating water residence times within the power scheme network. The Tokaanu Power Scheme discharge represents approximately 27% of the annual water discharge to the lake. The depth at which this water enters the water column is related to its temperature relative to the lake water column temperature (Spigel et al., 2005). The mean annual air temperature (11.2 °C) was used for the groundwater temperature.

Table 5-1: Summary of model input data for the hydrodynamic model.

Model forcing variable	Data type	Frequency	Source	Location	Reference
Air temperature	Measured	Hourly	Cliflo*	Turangi	http://cliflo.niwa.co.nz/
Solar radiation	Measured	Hourly	Cliflo	Turangi	http://cliflo.niwa.co.nz/
Rainfall	Measured	Hourly	Cliflo	Turangi	http://cliflo.niwa.co.nz/
Wind speed/direction	Measured	Hourly	Cliflo	Turangi	http://cliflo.niwa.co.nz/
Atmospheric pressure	Measured	Hourly	MetService	Taupo Aero	AWS-93245
Lake level	Measured	Daily	Mighty River Power	Acacia Bay intake	
Outflow	Measured	Hourly	Mighty River Power	Waikato Control Gates	
Hinemaiaia River	Measured	Hourly	Waikato Regional Council (WRC)	Refer to Fig.5.2	
Tauranga-Taupo River	Measured	Hourly	WRC	Refer to Fig. 5.2	
Whareroa River	Measured	Hourly	WRC	Refer to Fig. 5.2	
Tongariro River	Measured	Hourly	NIWA	Refer to Fig. 5.2	
Kuratau River	Measured	Hourly	King Country Power	Refer to Fig. 5.2	
Tongariro Power Scheme	Measured	Hourly	Genesis Power	Refer to Fig. 5.2	
Ungauged surface inflows	Modelled	Hourly	Catchment area	Refer to Fig. 5.2	CLUES (Elliot et al 2011)
Groundwater	Modelled	Daily	Balance of lake water budget		Refer to text
Water temperature	Measured	Monthly	WRC	Site A	

Geothermal inputs – Lake Taupō sits within an active geothermal zone. The Tongariro volcanic centre terminates at the southern end of the lake and the Wairakei centre is situated near the northern shores. Active venting has been observed below 140 m depth in the lake, with water temperatures >180 °C (de Ronde et al., 2002). Measurements of these vents give localised heat leaving the sediment of 3.57 W m^{-2} (Whiteford, 1996). Average values across the geothermal field are estimated to be 0.39 W m^{-2} (Kissling and Weir, 2005). A conservative estimate of geothermal heat input was used in this study, 0.35 W m^{-2}. To implement this heat input, a geothermal water inflow of 5 m^3 s^{-1} at 95 °C from the benthic sediment, as per von Westernhagen (2010), was used in order to provide the minimum water volume while maintaining temperatures below boiling point. This input represented approximately 30% of the mean annual groundwater input and was distributed over a 16 km^2 area of the lake bed (80 – 145 m depth) in the area of documented geothermal activity (de Ronde et al., 2002).

5.3.4 Model parameter refinement

Light extinction coefficient (Kd) values for Lake Taupō were taken from the literature for input to the model. Leach et al. (2017) reported Kd = 0.086 m^{-1} in Lake Taupō during summer stratification, when water clarity is greatest. Davies-Colley (1983) reported Kd = 0.128 m^{-1} during winter mixing. A constant intermediate value of 0.10 m^{-1} was used as model input. Albedo was set to 0.08

corresponding to the mean annual value of ocean water at similar latitude to Lake Taupō (Payne, 1973).

5.3.5 Simulation tracer configuration

Conservative tracers were used in the model to simulate seasonal exchange of water between habitat areas. Tracers were initiated during September and December 2014 and February, April, June and August 2015, to coincide with field sampling campaigns in those months. In each instance tracers were released ten days prior to sampling of model output. Two tracers, hereafter referred to as the hypolimnetic and epilimnetic tracers, were assigned to pelagic cells for each initiation except August 2015 (Figure 5-3). In August, when the lake was fully mixed, a single tracer was used through the whole water column. Pelagic cells were defined as any non-boundary (perimeter) cell with depth >80 m (Figure 5-3). The hypolimnetic tracer was assigned to all pelagic cells between the thermocline and the lake bed. The thermocline depth was determined for each sampling period using temperature profile data (collected using a RBR XR620f Conductivity-Temperature-Depth profiling system: Seapoint Sensors Inc., New Hampshire, USA) from Site A during each field campaign. Lake Analyzer (Read et al., 2011) was used to calculate thermocline depth based on a 0.5 °C temperature difference threshold between vertically adjacent measurements in order to avoid detecting diurnal thermoclines during the mixed period. The epilimnetic tracer was assigned to all pelagic cells from the water surface to the thermocline. Tracer concentrations were set as 1 in relevant cells (i.e., 100% of tracer in the water within a given cell) and released for 12 h. Transport of water between littoral, epilimnetic, and hypolimnetic waters was then inferred by the daily rate of tracer accrual at specific sampling sites (i.e., cells). Tracer concentrations were directly proportionate to traced water; hence, water flux (m^3 d^{-1}) into a cell was calculated by multiplying tracer concentration by the cell volume. The mean flux was determined as the average daily change in concentration over a ten-day period directly preceding a sampling campaign. Tracer accrual was measured in nine surface water cells representing the six littoral sites and three pelagic sampling sites shown in Figure 5-2. Littoral water movement was inferred by calculating the enrichment/dilution of all tracer-free water (i.e., the sum of all water not from the pelagic epilimnion or hypolimnion regions). Littoral tracer concentration was defined using a mass balance assuming that the known concentrations of hypolimnetic and epilimnetic tracers, as well as unknown littoral tracer, within a given cell summed to 1. In practice, this included ‘new’ water

delivered to the lake from stream and groundwater inflows that became entrained with the littoral water and was transported to the pelagic surface water. This simplification of littoral water was used as it best aligned with the objective of the model simulation, to quantify fluxes of new water (and associated nutrients) into pelagic surface waters from physical transport processes.

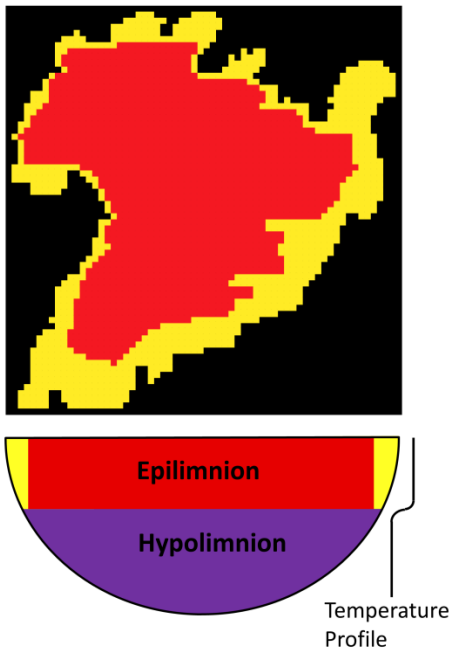


Figure 5-3: Schematic to demonstrate the horizontal (upper panel) and vertical (lower panel) distribution of tracer cells used in this study.

5.3.6 Pelagic surface water N budget

A budget for dissolved inorganic nitrogen (DIN) was developed for the pelagic surface waters for the six sampling periods between September 2014 and August 2015. As the model was focused on DIN, the fate of organic N after phytoplankton uptake was external to the model. Thus losses of organic N from the pelagic surface waters (e.g., phytoplankton settling) were considered implicitly; reduced phytoplankton biomass (i.e., PON) results in reduced phytoplankton DIN uptake. Here pelagic surface water was defined as the top 10 m of the open water (> 80 m depth) portion of the lake. This definition of pelagic surface water was applied as it corresponds to the scale of bi-weekly surface water monitoring as well as legislated water quality guidelines for Lake Taupō. Furthermore, analysis of the top 10 m, as opposed to the entire epilimnion, avoided variability associated with seasonal changes in the epilimnetic depth. The DIN budget included supply (inputs of new

N and recycling of old N), loss (phytoplankton uptake) and change in mass of the standing pool:

$$\Delta N = f + r - p$$

Where *ΔN*, *f*, *r* and *p* represent rates of daily change of the DIN pool; influxes of new DIN, regeneration rates of old DIN and phytoplankton uptake rates, respectively. All fluxes (rates) were expressed in t N day^{-1} relative to the total pelagic surface water (upper 10 m) N pool. The mass balance equation was rearranged to solve for recycling (*r*) using calculations of *ΔN*, *f* and *p*. Influxes of new DIN considered were; water exchange between littoral and hypolimnetic waters, riverine surface water inflows that entered the pelagic, atmospheric deposition, N-fixation, and consumer nutrient recycling. Groundwater N inputs were implicitly included in the littoral water exchange. In all instances DIN was calculated by summing the concentrations of NO_3^--N and NH_4^+-N.

Littoral and hypolimnion DIN exchange – Supply of littoral ($f_{Litt,}$) and hypolimnetic ($f_{Hyp,}$) DIN (t-N d^{-1}) to the surface water was determined as:

$$f_{litt} = w \times DIN_{litt}$$

where *w* and DIN_{litt} represent the monthly mean flux of littoral water into the pelagic surface water (m^3 d^{-1}) and the DIN concentration of source littoral water (g m^{-3}), respectively, and the subscripts denote the origin of the influx. To derive *w*, the mean daily rate of tracer water increase in the pelagic surface water (m^3 d^{-1}) was multiplied by the pelagic surface water volume (5.46 x 10^9 m^3) to derive a daily volume of water flux.

Riverine DIN input – DIN load from all surface water/riverine inflows (f_{Inflow}) was calculated following:

$$f_{Inflow} = \sum (Q_i \times DIN_i)$$

where Q_i and DIN_i are discharge (m^3 d^{-1}) and monthly mean DIN concentration (g m^{-3}) for a given inflow, respectively. Monthly DIN concentrations were provided by WRC. When DIN data were not available for an inflow, concentrations for the nearest neighbouring stream were used as a substitute. Due to the way littoral water was defined in the hydrodynamic model (including inputs of new water from inflows; see above), simulated littoral water exchange with surface pelagic waters

implicitly includes surface water inflows. Assuming that no catchment N inputs are attenuated within the littoral zone prior to moving off-shore to the pelagic zone, the model in its current set-up would otherwise include the catchment N load twice. However, N retention in the littoral zone can be substantial (Abell and Hamilton, 2015) and calculating the catchment N influxes independently of the littoral water transported to the pelagic zone is useful for understanding the extent to which receiving littoral areas attenuate DIN loads from inflows.

Atmospheric deposition – Rates of atmospheric deposition were taken from Vant and Gibbs (2006), who estimated 27 t yr^{-1} of total nitrogen deposition on the lake surface, of which DIN comprised on average of 38%. No seasonal variation in atmospheric deposition rates has been reported (Vant and Gibbs, 2006). As such, we used a constant atmospheric deposition rate to the lake of 0.03 t day^{-1} as DIN.

N-fixation – Nitrogen fixation by colony-forming cyanobacteria (*Dolichospermum* sp., family Nostocaceae) was estimated using the empirical model of Levine and Lewis (1987). In brief, fixation rates were based on their relationship between light availability and heterocyst daily N_2-fixation rate (N_2 $cell^{-1}$ d^{-1}). Total daily N influx from N-fixation to the Lake Taupō surface waters was then calculated by multiplying heterocyst N-fixation rates by the number of heterocyst cells present in the upper 10 m of the water column and applying units adjustments. Heterocyst numbers were derived from total cell counts for *Dolichospermum* sp. taken from phytoplankton samples collected annually from Site A during April and October by WRC between 2009 and 2014. Phytoplankton samples were collected using a 10 m integrated tube (Verburg and Albert, 2016). Cell counts (cells m^{-3}) were multiplied by the pelagic surface water volume (m^3). Independent samples collected using a 45 μm mesh net during September 2014 and April 2015, also from Site A, were used to derive the proportion of vegetative to heterocystous cells present in *Dolichospermum* sp. and using exponential linear interpolation between these two months to infer daily heterocystous cell abundances during the other modelled months. Heterocyst cell proportions and cell counts were used to calculate the total number of heterocysts in the upper 10 m, thereby informing modelled daily N-fixation rates.

Consumer nutrient recycling – Consumer nutrient recycling rates were estimated for smelt (*Retropinna retropinna*), mussels (*Echyridella menziesii*), bullies (*Gobiomorphus cotidianus*) and trout (*Oncorhynchus mykiss*). These species,

collectively, represent the majority of large-bodied (> 20 mg wet weight) biomass within the lake (James, 1985; Cryer, 1991; Stewart et al., 2017). Smelt, bully and trout excretion rates were estimated using length-specific N-excretion rate relationships for each species. Data used to derive these relationships were obtained for smelt and bullies (Hicks, *unpublished data*), and trout (Vanni et al. 2017). Smelt excretion rate, E_{smelt} (μg NH_4^+-N h^{-1} $Ind.^{-1}$) was determined as:

$$Ln(E_{Smelt}) = Ln(L) \times 0.78 + 3.0$$

where L is body length (mm) (Hicks, *unpublished data*). Seasonal patterns in mean body size and abundance of the Lake Taupō smelt population were taken from 1988-1989 survey data (Cryer, 1991). Bully excretion (E_{Bully}, μg NH_4^+-N h^{-1} $Ind.^{-1}$) was determined as:

$$Ln(E_{Bully}) = Ln(L) \times 0.63 + 2.8$$

where L is body length (mm) (Hicks, *unpublished data*). Mean size data for bullies were taken from Stewart et al. (2017) and annual mean abundance was matched to observed bully densities from similar oligotrophic lakes (Rowe et al., 2001). Seasonal variation in abundance of bullies was assumed to follow the same pattern as smelt. A comparison of mean annual abundances of smelt and bullies was used to obtain a density correction (0.12) to convert monthly smelt data to estimates of monthly bully biomass. Trout excretion (E_{Bully}, μg NH_4^+-N h^{-1} $Ind.^{-1}$) was determined as:

$$Ln(E_{Trout}) = Ln(W) \times 0.68 + 2.1$$

where W is dry weight (g) (Vanni et al., 2017). Seasonal patterns in mean body size and abundance were taken from 1988-1989 survey data of Lake Taupō trout populations (Cryer, 1991). A species-specific length-weight relationship (Jellyman et al., 2013) was used to convert length data into dry weight. The mean mussel DIN excretion rate (11 μg NH_4^+-N hr^{-1} $Ind.^{-1}$) was taken from observations in Lake Taupō (Cyr et al., 2017). This excretion rate was extrapolated to previously measured mussel densities in the Lake Taupō littoral area (James 1985). Consumer nutrient translocation was considered independently of physical nutrient exchange. While a degree of consumer excretion (e.g., excretion within the littoral zone by sessile mussels) will become available to pelagic phytoplankton through physical offshore transport, quantifying these fluxes independently enables a scrutiny of the relative contribution of physical transport and consumer translocation in pelagic

nutrient delivery. In order to maintain the independence of physical transport and consumer translocation, and to maintain parsimony, it was assumed that N excretion from all consumers was available for pelagic phytoplankton uptake. For smelt, pelagic smelt which supplement their diet with littoral resources during periods of pelagic resource scarcity and also represent the largest consumer biomass (Stewart et al., 2017), this was a valid assumption which aligns with previous studies (Vanni et al., 2013; Tunney et al., 2014). Given that mussels are sessile obligate littoral consumers, their entire N-excretion was considered as an influx of new DIN into the pelagic pool. Smelt, bullies and trout, being free swimming fish, spend a substantial amount of time in the pelagic water feeding *in situ*, where their excretion is considered to be recycling of old N rather than an influx of new N (Vanni et al., 2013). For this study, interest was in the potential for mobile consumers to transport N between littoral and pelagic waters (consumer nutrient translocation – CNT). To account for CNT explicitly, excretion fluxes were multiplied by the mean monthly littoral diet portion for each consumer. Monthly littoral-pelagic diet composition data were derived from stable isotope analysis (Stewart et al., 2017).

Phytoplankton DIN uptake – Uptake of DIN by phytoplankton was estimated form monthly measurements of carbon (C) uptake from the upper 10 m of Lake Taupō (Vincent, 1983) and a stoichiometric conversion. Areal C uptake rates (mg C m^{-2} h^{-1}), measured between 1979 and 1980, (Vincent 1983) were multiplied by the pelagic surface area of the lake. Carbon uptake was converted to N uptake using a constant $C:N_{molar}$ ratio of 11.6; the mean value for lentic phytoplankton globally and identical to the mean C:N for POM in Lake Taupō during the study period (see Chapter 4).

In situ N recycling processes – Calculated recycling rates were compared against estimates of two primary *in situ* N recycling processes, zooplankton excretion and phytoplankton N release, to test their validity. Zooplankton excretion was estimated by multiplying individual excretion rates, lake surface area and monthly areal zooplankton densities (Indiv. m^2). Mean monthly zooplankton densities were obtained from monthly monitoring data between 2000 and 2010 (see Stewart et al., 2017 for further details). A mixed species average excretion rate (0.003 µg N $Indiv.^{-1}$ h^{-1}) compiled from multiple published studies (Vanni et al., 2017) was used to represent zooplankton excretion. Zooplankton characteristically exhibit diel vertical migration (Jolly, 1965; Winder et al., 2004) meaning that, in the context of this study, zooplankton grazing-excretion may act as either a net source or sink of

N into the pelagic surface waters. Understanding zooplankton N source-sink dynamics requires vertical resolution of zooplankton diet and distribution; in the absence of these data, our zooplankton excretion estimate represents the maximum potential contribution. A substantial body of oceanography research can be used to infer phytoplankton N release rates where it is typically expressed as a percent of N uptake (Bronk et al., 1994; Lomas et al., 2000, Varela et al., 2003). We used a low and high estimate of phytoplankton N release (17.4 and 85.7% of daily uptake, respectively) for diatom dominated pelagic systems from the literature (Lomas et al., 2000).

5.3.7 Data analysis

Model calibration and validation – Calibration and validation of the model was performed for the lake water balance, water column temperature, thermocline depth and Schmidt stability. The water balance was assessed through comparing modelled and measured daily water level (Table 5-1). The model performance for the water column temperature was assessed using 30 CTD temperature profiles taken from Site A. Of these 30 profiles, six (i.e., 20%) were randomly selected to asses model performance, with the remainder used for calibration. The performance of the model was quantitatively assessed using root mean square error (RMSE) and Pearson's correlation coefficient values (Bennett et al., 2013) for water temperature. The depth and strength of stratification were quantified by calculating thermocline depth and Schmidt stability, respectively. Schmidt stability is a measure of mechanical mixing required to achieve uniform water column density (Read et al., 2011). Thermocline depth (as described above) and Schmidt stability were calculated using water temperature profiles and bathymetry data using Lake Analyzer (Read et al., 2011). These analyses were performed on both modelled and measured data and the results compared using RMSE and Pearson's correlation values.

Analyses of statistical relationships – All data were compiled and inspected using Microsoft Excel 2013 (Microsoft Corporation, Redmond WA USA). All reported statistical relationships were performed with R (version 3.4.1; R core team, 2017), using the base package linear model (lm) function and Type II sums of squares (Crawley, 2007). Physical transport rates into the pelagic surface water were compared against measurements of cumulative wind, total nitrogen (TN), ammonium-N (NH_4^+), nitrate-N (NO_3^-), ammonium-$\delta^{15}N$ ($\delta^{15}N$-NH_4^+), nitrate-

$\delta^{15}N$ ($\delta^{15}N$-NO_3^-) and POM-$\delta^{15}N$ ($\delta^{15}N$-POM) for each of the sampling locations. Cumulative wind was defined as the sum of hourly wind speeds (m s^{-1}) over the six 14-day tracer simulation periods. Total cumulative wind speed as well as cumulative south-westerly wind were both quantified. South-westerly wind (185° - 235°) was calculated separately as this represents the prevailing wind in the area. A detailed description of data collection and analysis is provided in Chapter 4 of this thesis. Mean monthly pelagic surface water ammonium-$\delta^{15}N$ and nitrate-$\delta^{15}N$ values were also compared against DIN recycling rates calculated from the pelagic surface water N mass balance model. For these relationships, DIN recycling rates for August were excluded because the water column mixing event, at the end of June, occurred prior to the tracer release period and was not represented. Annual overturn is the strongest determinant of pelagic primary production in Lake Taupō (Vincent, 1983; Stewart et al., 2017) and excluding this nutrient influx likely over-represented recycling rates during August. Moreover, the study was primarily focused on quantifying N fluxes during the stratified season.

5.4 Results

5.4.1 Model validation

The model produced a close fit to measured data for lake water level, thermocline depth, and Schmidt stability (Figure 5-4) as well as water column temperature (Figure 5-5). Quantitatively, the relationship between measured and observed water level, thermocline depth and stability gave Pearson's correlation coefficient values of 0.99, 0.99 and 0.99, and RMSE = 0.01 m, 5.19 m and 1040 kJ m^{-2} respectively. Divergence between modelled and measured water level and stability was greatest during summer stratification when modelled water level was underestimated (maximum difference = 0.02 m) and stability (maximum = 2100 kg m) and thermocline depth (maximum = 6 m) were overestimated (Figure 5-5).

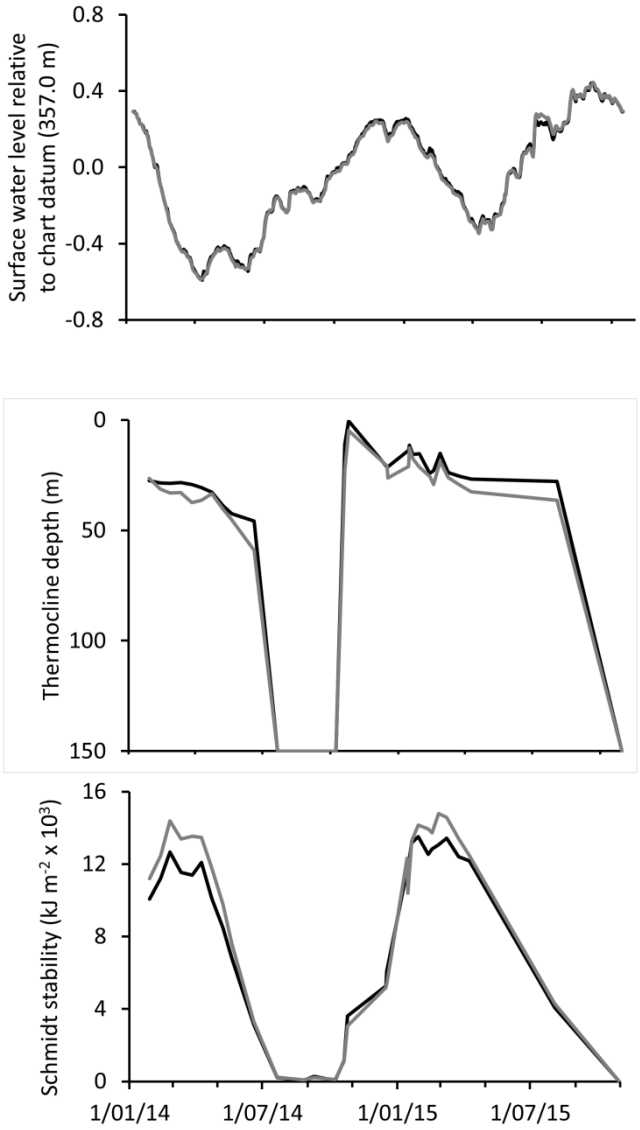


Figure 5-4: Comparison of observed (black) and modelled (grey) data for water level (Pearson's correlation = 0.99, RMSE = 0.01 m), thermocline depth (Pearson's correlation > 0.99, RMSE = 5.2 m) and Schmidt stability (Pearson's correlation = 0.99, RMSE = 1040 kJ m^{-2}).

Water column temperature was well represented by the model throughout the study period (Figure 5-6). Quantitatively, this was demonstrated by Pearson's correlation coefficient = 0.99 and RMSE = 0.45 ^{o}C. The model tended to slightly underpredict surface temperatures during winter mixing (maximum difference = 2.1 °C) and slightly over predict metalimnetic temperatures during stratification (maximum difference = 2.8 °C) (Figure 5-6).

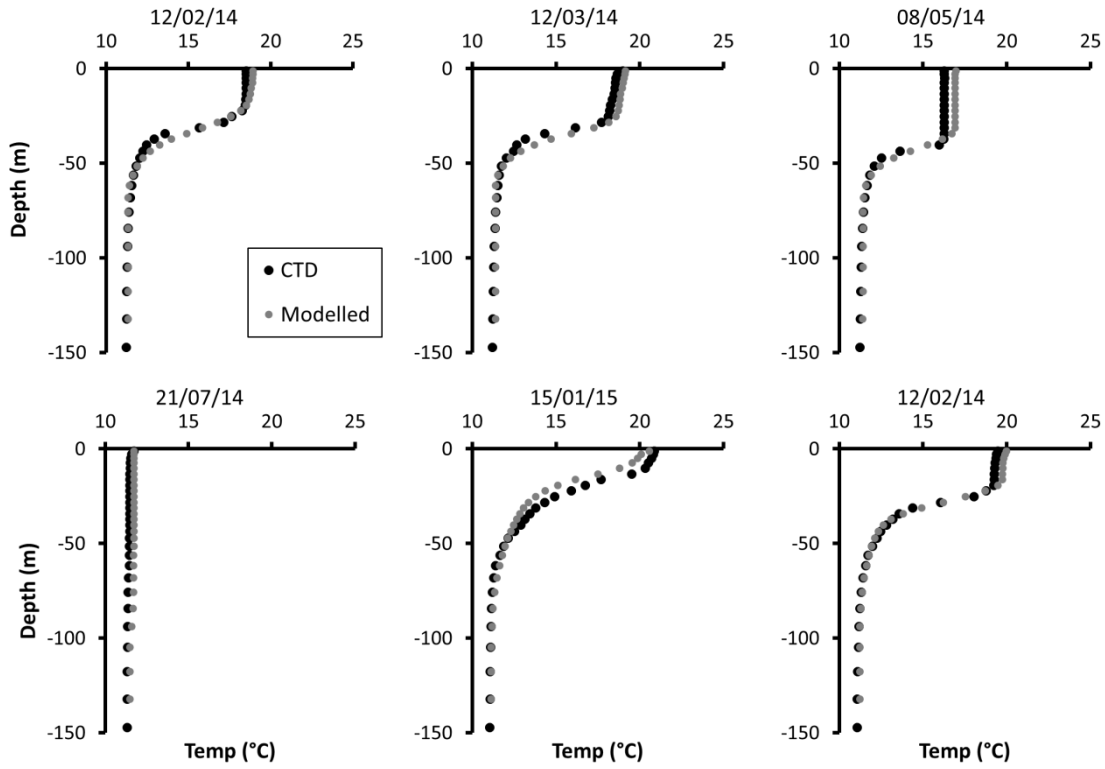


Figure 5-5: Comparison of observed (black) and modelled (grey) temperature profiles from Site A (see Fig. 1) for the six validation profiles.

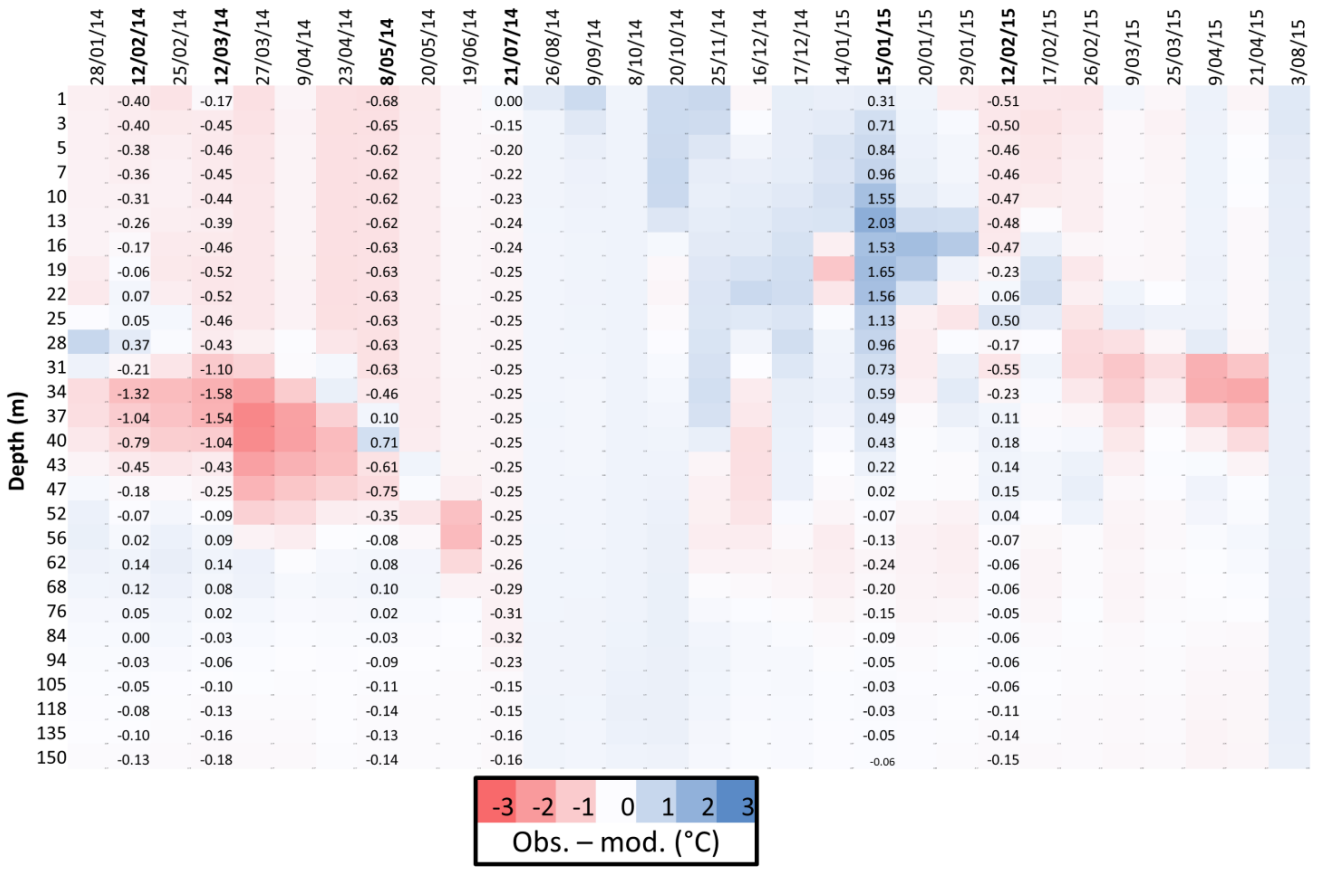


Figure 5-6: Model error for observed temperature – modelled temperature during all periods with corresponding model and measured profile data. Colour indicates relative over (red)/under (blue) prediction of water temperature by the model.

5.4.2 Littoral-pelagic exchange of water and nitrogen

Dispersal of the pelagic epilimnion tracer in the hydrodynamic model demonstrated the spatial and temporal patterns in littoral-pelagic water exchange across the lake. The water circulation, which determined littoral-pelagic water exchange, was driven by wind, bathymetry and the major riverine inflows at the southern end of the lake (Appendix 5–l). Water tended to be transported northward along the eastern shoreline. Accumulation of epilimnetic tracer water at littoral measuring sites was greatest when on-shore winds were strongest (Appendix 5-1). Transport of littoral water into the pelagic surface water varied between 0.3 ± 0.02% (SD) and 3.6 ± 1.1% of the pelagic surface water volume per day in December and April, respectively (Figure 5-7). During calm periods, when wind was minimal, tracer water movement highlighted three geostrophic gyres within Lake Taupō (Appendix 1). Influxes of littoral water to the pelagic surface water were greater than those of hypolimnion water in all months except December and June (Figure 5-7). Mean concentrations of DIN and TN were higher in the littoral water than pelagic surface water across all months (Figure 5-7). The littoral-pelagic difference in concentrations of DIN and TN was greatest in September (0.02 g m^{-3}) and April (0.21 g m^{-3}) respectively. Combined, these water transport rates and DIN concentrations resulted in a calculated influx of DIN from the littoral to pelagic surface waters of between 0.31 and 13.58 t N day^{-1} in December and April respectively (Figure 5-7).

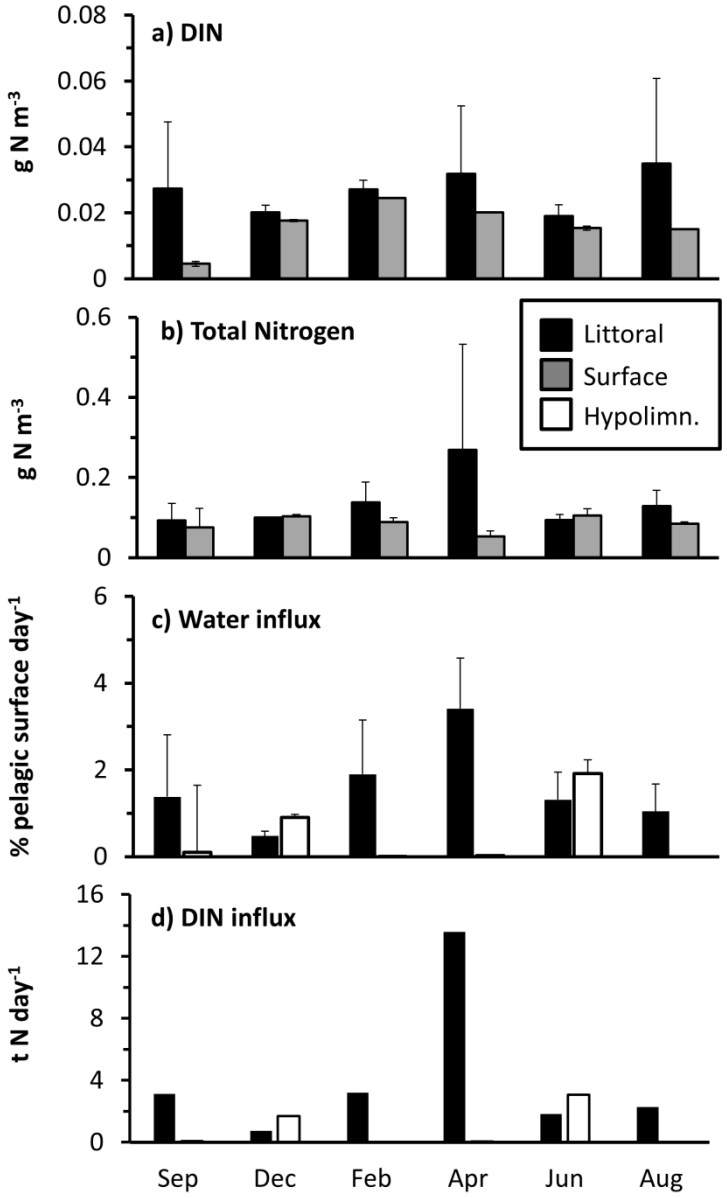


Figure 5-7: Comparisons of concentrations for DIN (a) and TN (b) between surface and littoral water as well as fluxes of water (c) and DIN (d) into the pelagic surface water from littoral and hypolimnion areas over the six sampled/modelled months.

Littoral-epilimnetic water exchange was positively related ($R^2 = 0.88$, $P = 0.02$) to the cumulative magnitude of south-westerly wind during the 14-day tracer simulation period (Figure 5-8). Conversely, the total cumulative wind magnitude showed no significant relationship ($R^2 = 0.10$, $P > 0.05$). Littoral water influx to pelagic surface water affected DIN present in the pelagic surface water (Figure 5-9) and was positively related to the percentage of DIN in TN ($R^2 = 0.64$, $P < 0.01$). No relationship was observed between littoral influx and either nitrate-$\delta^{15}N$ ($R^2 = 0.18$, $P = 0.66$) or ammonium-$\delta^{15}N$ ($R^2 = 0.07$, $P = 0.71$) values measured in the pelagic surface waters.

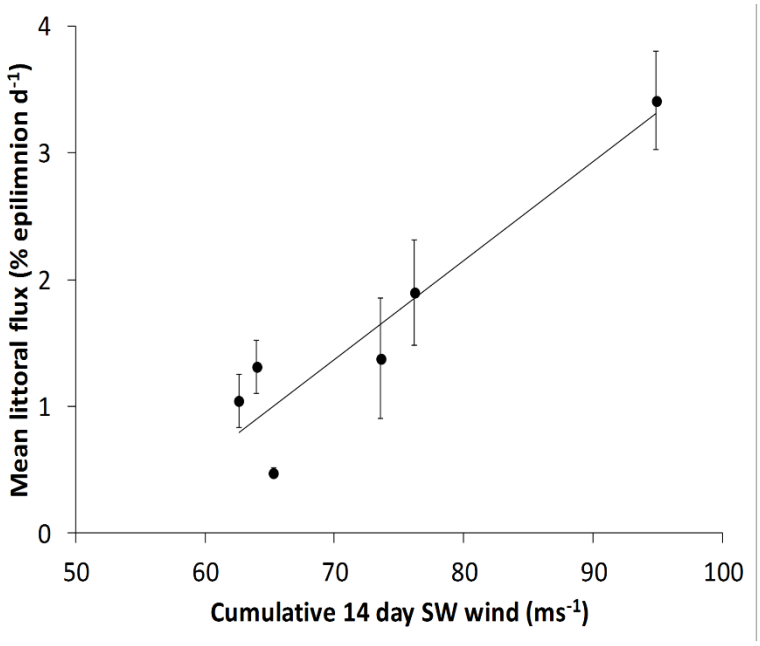


Figure 5-8: Relationship between littoral-epilimnetic water exchange and 14-day cumulative south-westerly wind (R^2 = 0.88, P = 0.02). South-westerly wind was defined as mean hourly wind periods between 185° – 235°. The 14 day cumulative period represented the periods of tracer release simulation.

Intra-annual patterns of DIN influxes to the pelagic surface water – The primary fluxes of DIN into the pelagic surface waters were estimated for the six sampling periods during the annual cycle (Figure 5-10). These included physical transport fluxes from littoral and hypolimnion water, DIN load delivered from surface/riverine inflows, atmospheric deposition, cyanobacterial N-fixation and consumer nutrient excretion. The calculated physical DIN transport flux from the littoral areas of the lake into the pelagic surface water was greater than the load delivered by riverine inflows entering the lake in all months except June and August, indicating that the littoral zone of Lake Taupō is generally ineffective as a nitrogen sink. The DIN transport flux from the littoral to the pelagic varied substantially over the year, between 1.0 t N day^{-1} in December and 14.2 t N day^{-1} in April (Figure 5-10). April was also the period of greatest total DIN flux into the pelagic surface waters and littoral flux was the primary source during this period. This period also had the highest calculated N-fixation rates (4.8 t N day^{-1}) (Figure 5-10).

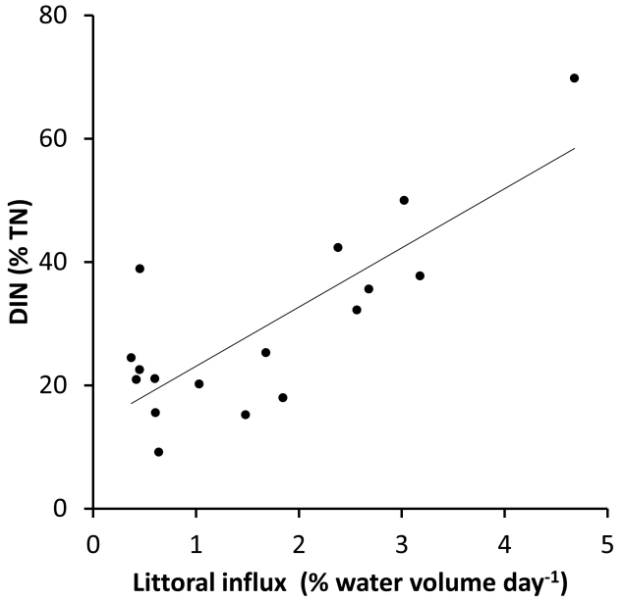


Figure 5-9: Relationship between littoral influx to pelagic surface water (upper 10 m) and dissolved inorganic nitrogen (DIN) as a percentage of the total nitrogen from the three pelagic sampling sites over the six sampled months: %DIN = 9.61 x Littoral influx + 13.51; R^2 = 0.64, P < 0.01.

CNT was a larger than physical transport of littoral DIN in all months except September and April, indicating that CNT exceeded physical transport in most months. The DIN flux from CNT was the largest influx to the pelagic surface water in December and February (9.2 and 9.7 t N day^{-1}, respectively). The large CNT-derived DIN influx during December and February coincided with the period when smelt biomass was greatest. Smelt excretion increased from 0.08 to 1.7 t N day^{-1} between September and December. The DIN flux delivered from the littoral to the pelagic surface water by CNT was greater than that from physical transport in December, February and June. Atmospheric deposition remained a relatively minor contribution throughout the year.

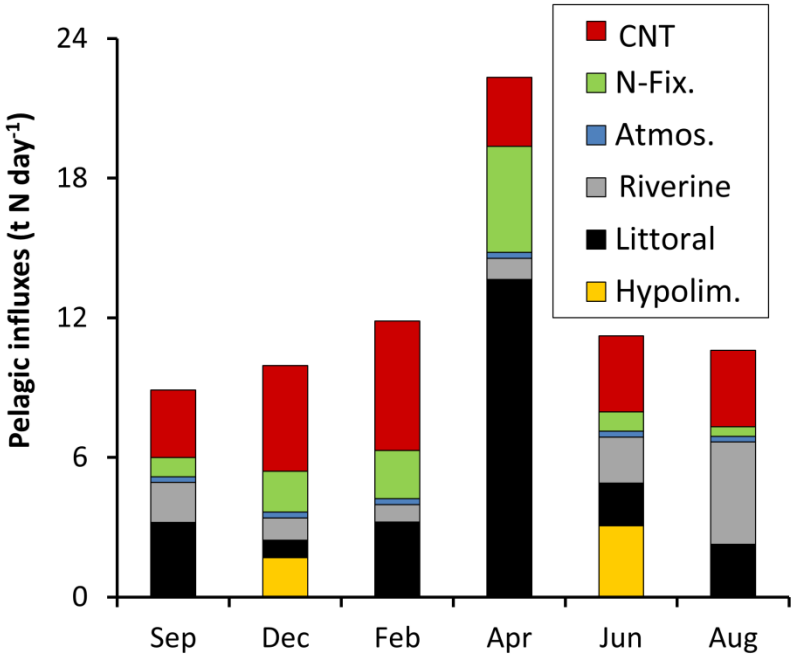


Figure 5-10: Influxes of DIN (t N day^{-1}) into the pelagic surface waters over an annual cycle. Sources of N included are: hydrodynamic transport from the hypolimnion (Hypolim.), littoral (Littoral) and surface inflows (Riverine); direct atmospheric deposition (Atmos.); biological fixation of N_2 (N-Fix.); and consumer nutrient translocation (CNT).

Pelagic surface water DIN mass balance – The DIN mass balance demonstrated that N cycling in Lake Taupō pelagic surface waters is dominated by uptake and recycling (Figure 5-8). Daily uptake of DIN by phytoplankton represented on average 89.7% of the available pelagic surface water DIN pool and varied between 50.3 and 139.2% of the DIN pool in September and December, respectively. The contribution of DIN from *in situ* recycling which would have been required to balance the pelagic surface water N budget, excluding August (see Methods), varied between 72.4 and 88.8% of daily phytoplankton DIN uptake during April and December, respectively (Figure 5-8). The relatively low contribution of recycling to the pelagic surface water N budget during April was largely due to the substantial increase in physical transport of DIN in this month (Figure 5-8). The size of the pelagic surface water DIN pool changed minimally throughout the annual cycle and, as such, on average < 0.01% of changes in phytoplankton uptake could be accounted for by changes in DIN pool size. Atmospheric deposition was the second smallest contributor to the pelagic surface water DIN budget, accounting for on average 0.30% of phytoplankton uptake.

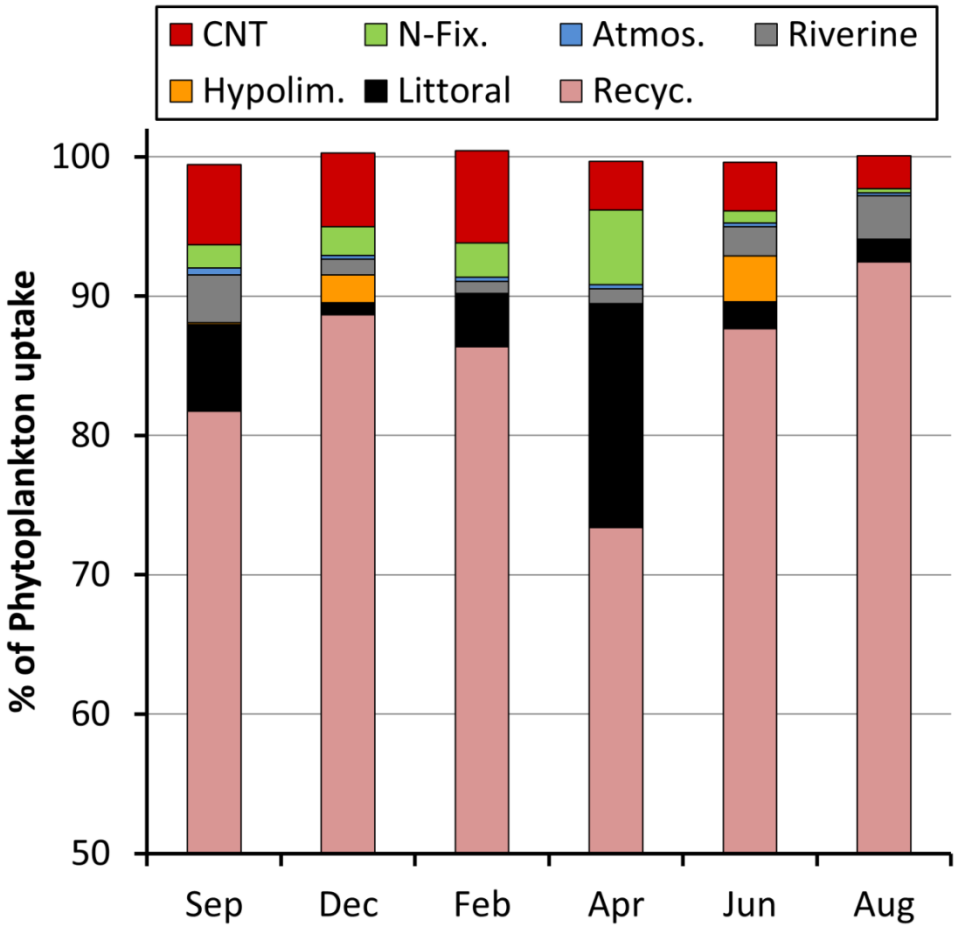


Figure 5-81: Mass balance of pelagic surface water DIN fluxes, expressed as percent of phytoplankton demand, over the six sampled months. Fluxes included are: in situ *recycling (Recyc.), hydrodynamic transport from the hypolimnion (Hypolim.), littoral (Littoral) and surface inflows (Riverine); direct atmospheric deposition (Atmos.); biological fixation of N_2 (N-Fix.); and consumer nutrient translocation (CNT).*

Investigation of in situ recycling processes – Across all six sampled months, maximal estimates of the two considered recycling processes exceeded calculated recycling rates (Figure 5-12). Considering exclusively the high estimate of phytoplankton recycling, 83% of phytoplankton uptake, accounting for > 100% of the calculated recycling rate for four of the months (September and April). The estimated relative contribution of zooplankton was greatest during December (Figure 5-12).

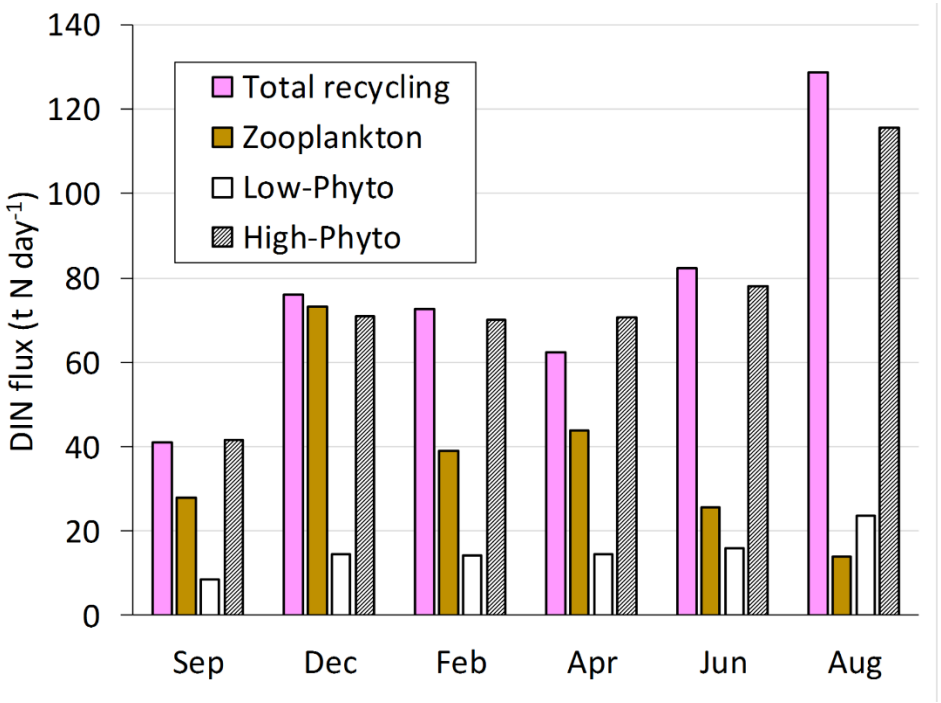


Figure 5-12: Comparison of calculated pelagic DIN recycling rates with two potential processes; zooplankton excretion and phytoplankton DIN release. Two phytoplankton DIN release rates are shown representing low and high (17 % and 86% of phytoplankton uptake, respectively) rates (Lomas et al., 2000). Displayed zooplankton recycling rates do not account for diel vertical migration or variable feeding within the water column.

Relationships between pelagic recycling rate and $\delta^{15}N$ values – Calculated recycling rates (% of DIN pool) showed strong positive linear relationships for nitrate-$\delta^{15}N$ ($R^2 = 0.79$, $P = 0.04$), ammonium-$\delta^{15}N$ ($R^2 = 0.82$, $P = 0.04$) and POM-$\delta^{15}N$ ($R^2 = 0.60$, $P = 0.12$) (Figure 5-9). August samples were anomalous to the linear relationship observed across other months for ammonium-$\delta^{15}N$ and, to a lesser extent, nitrate-$\delta^{15}N$ and POM-$\delta^{15}N$ (Figure 5-9). For these samples, entrainment of hypolimnetic water during overturn fell outside of the tracer analysis period and was not captured in subsequent measurements.

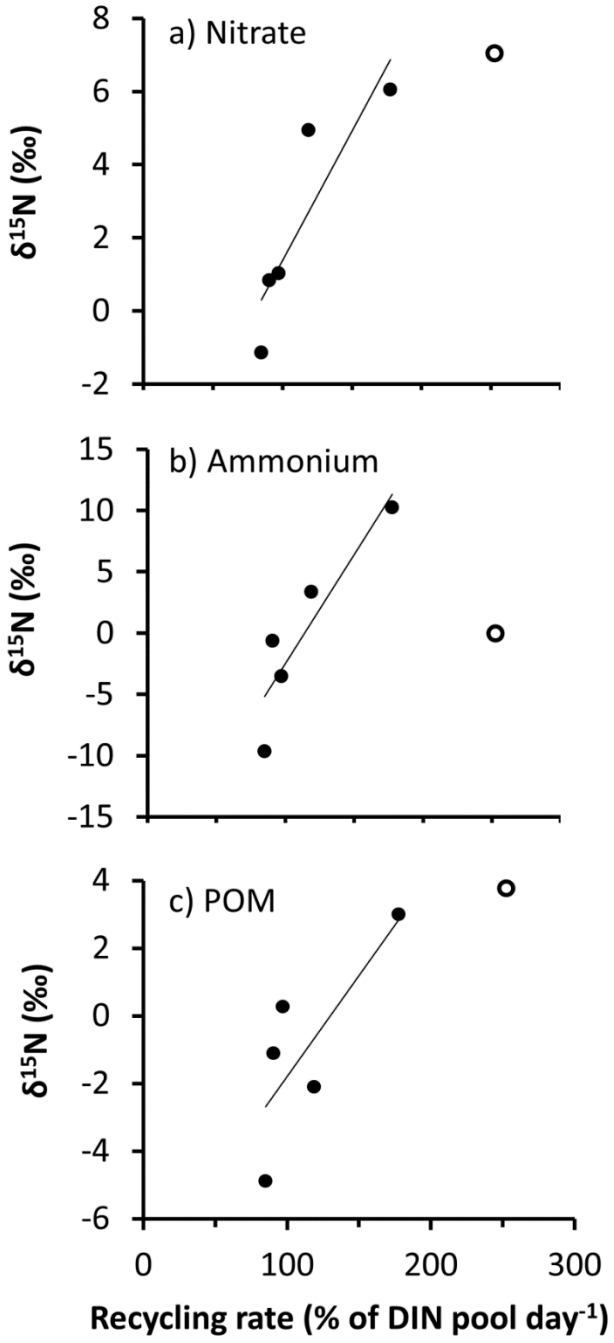


Figure 5-9: Regression relationships of calculated monthly DIN recycling rates with nitrate-$\delta^{15}N$ (a), ammonium-$\delta^{15}N$ (b) and POM-$\delta^{15}N$ (c) for the six sampling months.

5.5 Discussion

5.5.1 Overview

This study highlights the importance of littoral-pelagic habitat coupling in lakes and temporal variability in the processes that produce this coupling (primarily physical transport and consumer excretion) in a large oligotrophic lake through quantifying the ecological significance of exchanges of water of littoral and hypolimnetic waters with pelagic surface water. The sum of all DIN influxes to the pelagic

surface waters during the stratified season (new nitrogen) accounted for <30% of phytoplankton uptake, highlighting the importance of *in situ* biogeochemical processes, namely recycling, for the pelagic surface water N budget. Consumer translocation of littoral derived N excretion supplied more DIN to pelagic surface waters than physical transport during summer stratification (December and February). The lack of any relationship between littoral DIN influx and nitrate-$\delta^{15}N$ in pelagic surface waters, combined with the substantial contribution of *in situ* recycling required to balance the pelagic surface water DIN budget, provides evidence that observed seasonal ^{15}N depletion over summer stratification results from nutrient recycling. Counter to the initial hypothesis that ^{15}N depletion indicates *in situ* recycling, $\delta^{15}N$ values of nitrate, ammonium and POM were all positively related to the calculated recycling rate. These positive relationships, are attributed to direct N release by phytoplankton, resulting from the differing isotopic effect of phytoplankton N release and its greater contribution when phytoplankton biomass in high. Interpretation and implications of these findings are detailed below.

5.5.2 Simulated water circulation

The 3-D hydrodynamic model performed well at representing observed water column temperatures over the study period. Under stratified conditions, influxes of littoral water to pelagic surface water exceeded that from the hypolimnion. However, it should be noted that the tracer initialisation periods did not encompass the period when overturn and complete water column mixing occurred, 24 July 2015, which was outside of the two-week period when tracer dispersal was quantified, coinciding with sampling campaigns (15 – 17 June 2015 and 8 – 9 August 2015). Hence, the hypolimnetic influx from lake overturn was not recorded in the model output and subsequent analyses under-represented the influx from this event during the August simulation period. As a result, the focus was primarily on the stratified period up until June 2015 but the results from the August sampling remain included due to the importance of this period in pelagic primary production in the lake (Vincent, 1983; Stewart et al., 2017). During the nutrient-deplete stratified summer period in Lake Taupō, littoral transport was the dominant water influx to the pelagic surface waters. The observed relationship between wind speed and littoral-pelagic exchange of water demonstrated the strong influence of wind. Furthermore, the substantial effect of wind direction, namely south-westerly winds, on the exchange rates suggests a potential interactive influence from lake bathymetry. The south-west – north-east axis of Lake Taupō represents the longest

wind fetch and greatest accumulation of wind derived energy by the lake surface (Rueda and Macintyre, 2010). These potential interactions between wind and bathymetry demonstrate the power of applying a hydrodynamic model to a given lake basin for quantifying physical transport rates. Littoral-pelagic water exchange was still evident throughout prolonged calm periods demonstrated the additional importance of surface currents in physical transport. The geostrophic circulation in the lake basin was associated with three gyres which were important drivers of littoral-pelagic exchange during calm periods. This circulation pattern has previously been identified in Lake Taupō (Spigel et al., 2005). The model simulation reproduced interactions of the Tongariro River and the Tokaanu power scheme discharge with the water column at the southern end of Lake Taupō (Spigel et al., 2005). Both inflows entered as underflows during winter and spring, and were deflected to the eastern side of the lake basin by geostrophic currents before moving northward along the eastern shoreline towards the central basin (Spigel et al., 2005). During summer and autumn, both inflows demonstrated buoyant surface jets and mid-water column intrusions. The observed interactions between lake basin, geostrophic currents and inflow patterns can be generalised to large lakes (Patalas, 1961; Boehrer and Schultze, 2008; Rueda and MacIntyre, 2010) and, although currents are unique to each lake basin, they indicate that the relative role of physical nutrient transport between littoral and pelagic habitats can be broadly applied across lakes when basic information of lake basin hydrodynamics is understood. Furthermore, the agreement between the results of this study and that of previous studies from Lake Taupō provide confidence in the validity of modelled physical littoral-pelagic water exchange during the stratified period.

5.5.3 Littoral-pelagic exchange by physical transport

Model tracer influxes of littoral water and DIN into pelagic surface waters were simulated to be greatest during April, the austral autumn. At this time, surface water temperatures had decreased from a summer maximum and had created conditions conducive to inflows entering the lake as a buoyant jet, carrying entrained littoral water out to the surface pelagic waters (Spigel et al., 2005) and cumulative south-westerly wind forcing was greatest. Furthermore, littoral water DIN concentrations were elevated during this period. Throughout the year, DIN concentrations in littoral waters were higher than pelagic surface waters, indicating potential for a net flux of DIN from littoral to pelagic surface waters. The influx of littoral waters into pelagic surface waters was significantly related to the percentage of DIN in the TN

pool throughout the simulated period. Importantly, there was no relationship between nitrate-$\delta^{15}N$ values and littoral influxes of DIN to surface pelagic waters, implying that although physical littoral-pelagic exchange provides new DIN, it has little effect on nitrate-$\delta^{15}N$ values. Thus, the large observed variation in nitrate-$\delta^{15}N$ values over an annual cycle is likely to be due to other processes, primarily *in situ* recycling (Finlay et al., 2007; Chapter 4).

5.5.4 Pelagic recycling rates inferred through mass-balance

Phytoplankton DIN uptake was the largest flux in the mass balance model. As such, variation in phytoplankton uptake had the largest influence of calculated recycling rates. Given that this parameter was derived from data twenty years beforehand, it presents arguably the largest limitation in the accuracy of the model. However, there has been little change in monthly Chl-*a* concentrations between when carbon uptake data were collected (1979) and present. The greatest difference between the two periods was during August (0.2 g m^{-3}) when concentrations were 2.6 and 2.4 g m^{-3} in 1979 and 2015, respectively (Vincent, 1983; Verburg and Albert, 2016). Additional uncertainties in the mass balance model were the under-representation of hypolimnetic DIN contributions from mixing prior to August measurements from lake overturn and calculated N-fixation rates. Under-representation of hypolimnetic DIN influx associated with destratification was accounted for by excluding the August N-budget from further analyses. Our calculations of N-fixation are likely to be conservative as March, when *Dolichospermum* sp. abundance is typically highest (Verburg and Albert 2016) was excluded and the per-heterocyst N-fixation rates reported by Levine and Lewis (1987) are at the lower end of published rates (Oliver et al. 2012). Under representing N-fixation is likely confined to March and April when diazotrophic cyanobacteria abundance is greatest and surface water N:P is lowest (Verburg and Albert, 2016). Further field research to quantify contemporary phytoplankton N-uptake and N-fixation rates would improve the confidence of the current pelagic surface water N-budget for Lake Taupō and better constrain the portion of the Lake Taupō N load that is currently not managed. The non-managed proportion of the N load has implications for the efficacy of current N load management that targets the catchment-derived load.

The Taupō N-budget mass balance model demonstrated that biogeochemical recycling is the dominant process for DIN supply in pelagic surface water, far

exceeding littoral and hypolimnetic transport influxes. Recycling remained the dominant DIN influx in pelagic surface waters throughout the year. When surface water temperatures were warmest, in December and February, consumer-derived littoral DIN translocation to the pelagic surface waters exceeded physical transport. These results suggest that the effects of biological (i.e., metabolic and food web) interactions on nutrient availability, and ultimately phytoplankton production, are commonly underrepresented. This finding reflects a growing recognition of high rates of N flux in euphotic pelagic waters (Finlay et al., 2007; Kumar et al., 2008). In Lake Superior, a large temperate phosphorus-limited ($N:P_{molar} \approx 50$) system, external N influxes accounted for approx. 40% of phytoplankton N uptake, far exceeding previous assumptions that supply exceeded demand (Kumar et al., 2008). Kumar et al. (2008) also found that N-uptake was temperature sensitive. Taking into consideration the higher mean annual surface water temperatures (O'Reilly et al., 2015) and lower N:P in Lake Taupō relative to Lake Superior, findings from the two systems are in agreement that biological recycling is by far the most important N flux for meeting phytoplankton N demand in pelagic surface waters.

Examination of two potential recycling processes, zooplankton excretion and phytoplankton nutrient release, suggested that recycling rates inferred from the mass-balance model were within reasonable accuracy. However, it is important to note that the estimates used for these two processes were based on limited data; phytoplankton recycling rates were derived from analogous marine species and zooplankton excretion did not consider diel vertical migration. Given that zooplankton typically spend limited time in lake surface waters (Jolly, 1965; Winder et al. 2004), their contribution to recycling is likely to be less than represented here. However, given that a large proportion of Lake Taupō zooplankton diet is derived from metalimnetic phytoplankton (Stewart et al., 2017), the reduced recycling contribution is likely to be partially offset by zooplankton translocating metalimnetic-derived N into surface waters (Baustain et al., 2014). The caveats to the empirical data for recycling processes described here highlight a significant knowledge gap in the understanding of lake nutrient cycles. The biological nutrient recycling processes that accounted for > 70% of the available N for primary production in this study are poorly understood and sit outside of most nutrient management legislation (Hamilton et al., 2016). Uncertainty associated with biological recycling processes represents a limitation to the confidence that can be placed in catchment nutrient management interventions.

5.5.5 Potential determinants of physical littoral-pelagic exchange

Considering the attributes of Lake Taupō that result in seemingly high contributions of biological processes to the pelagic surface water N budget provides an important context for understanding the generality of the findings from this study. The relative role of physically-driven nutrient transport processes increases towards the poles (Kilham and Kilham, 1990; Lewis, 2010). Lake Taupō has previously been labelled a 'temperate-tropical hybrid' lake (Vincent, 1983) and should represent a mid-point in the balance between biological and physical nutrient supply processes. While this would imply that biological processes dominate generally across lakes, other factors that influence physical transport, namely basin morphological characteristics (Monismith et al., 1990; MacIntyre et al., 2009), should be considered. A greater littoral percentage of lake surface area results in more littoral-pelagic exchange (Monismith et al., 1990), as does greater shoreline complexity (e.g., presence of peninsulas) (Jones et al., 2007) and steeper bottom slopes (MacIntyre et al., 2009). In this context Lake Taupō, having a relatively small area of littoral habitat and being circular in shape, should be have relatively low littoral-pelagic exchange rates at the global scale. The basin morphological features that promote physical littoral-pelagic exchange also promote littoral-pelagic diet coupling by mobile consumers (Vander Zanden and Vadeboncoeur, 2002; Vanni et al., 2013). This suggests that CNT and physical littoral-pelagic exchange should increase concomitantly higher proportions of littoral lake surface area. Hence, while basin morphology will alter net littoral-pelagic nutrient exchange (i.e., both CNT and physical transport), the relative contributions of the two fluxes should remain largely unaffected.

5.5.6 Effects of recycling on $\delta^{15}N$

The positive correlation between the calculated N recycling rate and nitrate-δ^{15}N, ammonium-δ^{15}N and POM-δ^{15}N values is counter to assertions that N recycling results in ^{15}N depletion of the DIN pool (Chapter 4). Recycling rates were positively related to chlorophyll abundance (R^2 = 0.51), suggesting that phytoplankton abundance has a substantial effect on recycling rates. Although often not considered as nutrient sources, phytoplankton release nutrients that can support subsequent N uptake (Elser et al., 1995; Verala et al., 2005). Thus, higher phytoplankton biomass can correspond to higher N recycling rates. Phytoplankton often release N on a diurnal basis. Furthermore, autotrophs and heterotrophs fractionate excreted N differently (Slawyk et al., 1998; McMahon and McCarthy 2017). Autotroph excretory-δ^{15}N is primarily affected by fractionation during nutrient uptake

(Robinson 2001) whereas heterotroph excretory-$\delta^{15}N$ fractionation is from metabolism which depletes ^{15}N (McMahon and McCarthy 2017). In addition, release of labile DON by autotrophy is characteristically ^{15}N enriched (Slawyk et al., 1998). Based on this information, we postulate that the positive relationships between $\delta^{15}N$ values and recycling rates reflect the balance of autotrophic and heterotrophic contributions to the recycling flux. The ^{15}N deplete values thus reflect the background heterotrophic recycling that is likely to be reasonably constant throughout the year (Figure 5-10). This is consistent with the assumption that heterotrophic nitrogen recycling results in ^{15}N depletion of the DIN pool (Chapter 4).

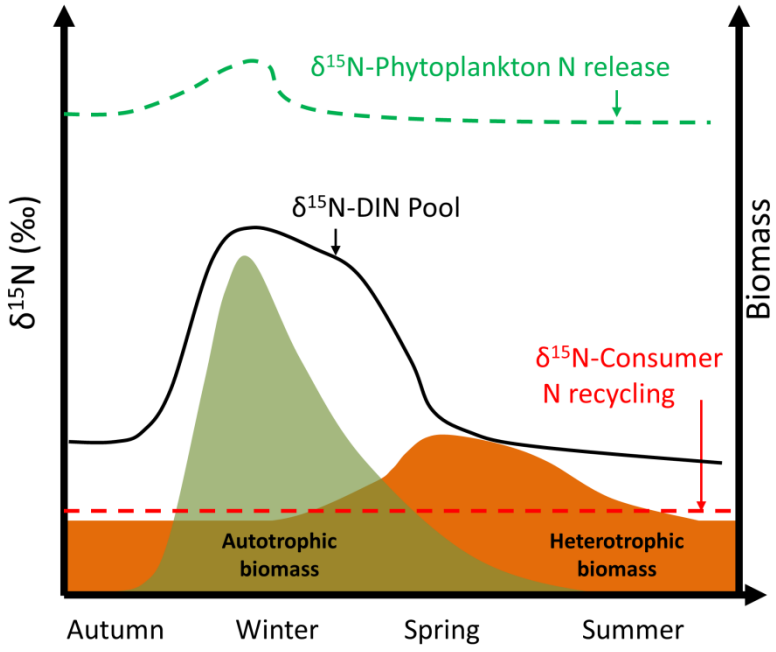


Figure 5-10: Schematic representation of the effects of increases and decreases in autotrophic and heterotrophic biomass on $\delta^{15}N$ values of the pelagic surface water dissolved inorganic nitrogen (DIN) pool due to nitrogen recycling over an annual winter-mixing summer-stratification cycle

5.5.7 Summary

Nitrogen cycling is one of the processes that underpin primary production in lakes. Understanding and quantifying the processes that contribute to N cycling is critical for lake management focused on water quality. Water quality targets are commonly set with the objective of directly controlling catchment nutrient loads in order to regulate phytoplankton production. In this study it has been demonstrated that within-lake processes strongly mediate nitrogen supply over an annual cycle. Physical transport results in a substantial influx of DIN from the littoral to the pelagic zone but *in situ* recycling and consumer translocation from littoral-derived

N make an even greater contribution to DIN supply in the pelagic surface waters during the stratified period in Lake Taupō. This appears to represent a general phenomenon characteristic of large lakes which tend to have relatively high proportions of pelagic habitat. The findings imply that DIN supply in lakes, and thus phytoplankton production, is likely to be influenced by trophic interactions, adding the potential for strong feedback effects and non-linearity in primary production responses to catchment loads. Consideration of biological effects on N-cycling is likely to greatly improve understanding of relationships between catchment N load and phytoplankton production in lakes. Future research comparing DIN fluxes from physical and biological processes across a range of lake attributes, in particular basin morphology and water temperature, will enhance the generality of these findings to other lakes.

5.6 Acknowledgements

Ngāti Tūwharetoa, holding manawhenua and kaitiakitanga over Lake Taupō, and as legal owners of the lake bed, provided access to the lake. Mathew Allen provided bathymetry data and model assistance. Stephen Hamilton from (MetService), Kathy Walters (NIWA) and Erich Lunzer (Genesis Energy) provided hydrodynamic model forcing data. Bill Perry assisted with data analysis. SDS was funded by a PhD scholarship from the Advocates for the Tongariro River. SDS, DPH, PV, ICD and BJH were supported by 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). All authors declare no conflicts of interest.

5.7 References

Abell, J. M., and D. P. Hamilton. 2015. Biogeochemical processes and phytoplankton nutrient limitation in the inflow transition zone of a large eutrophic lake during a summer rain event. Ecohydrology **8**: 243–262.

Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Glob. Chang. Biol. **23**: 2166-2178.

Antenucci, J. P., and J. Imberger. 2001. Energetics of long internal gravity waves in large lakes. Limnol. Oceanogr. **46**: 1760–1773.

Antenucci, J. P., and J. Imberger. 2003. The seasonal evolution of wind/internal wave resonance in Lake Kinneret. Limnol. Ocean. **48**: 2055–2061.

Bartrons, M., L. Camarero, and J. Catalan. 2010. Isotopic composition of dissolved inorganic nitrogen in high mountain lakes: variation with altitude in the

Pyrenees. Biogeosciences **7**: 1469–1479.

Bennett, N. D., B. F. W. Croke, G. Guariso, and others. 2013. Environmental Modelling & Software Characterising performance of environmental models. Environ. Model. Softw. **40**: 1–20.

Bird, R. E., and Hulstrom, R. L. 1981. Simplified Clear Sky Model for Direct and Diffuse Insolation on Horizontal Surfaces, Technical Report No. SERI/TR-642-761, Golden, CO: Solar Energy Research Institute.

Boehrer, B., and M. Schultze. 2008. Stratification of Lakes. Rev. Geophys. **46**: 1–27.

Bronk, D. A., Gilbert, P. M., Ward, B. B. 1994. Nitrogen uptake, dissolved organic nitrogen release, and new production. Science **265**: 1843-1846.

Brothers, S., Y. Vadeboncoeur, and P. Sibley. 2016. Benthic algae compensate for phytoplankton losses in large aquatic ecosystems. Glob. Chang. Biol. **22**: 3865–3873.

Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annu. Rev. Environ. Resour. **36**: 75–99.

Corman, J. R., P. B. McIntyre, B. Kuboja, and others. 2010. Upwelling couples chemical and biological dynamics across the littoral and pelagic zones of Lake Tanganyika, East Africa. Limnol. Oceanogr. **55**: 214–224.

Crawley, M. J. 2007. The R Book, 1st ed. Chirchester, Wiley & Sons Ltd.

Cryer, M. 1991. Lake Taupo trout production: a four year study of the rainbow trout fishery of Lake Taupo, New Zealand. New Zealand. Science and Research Series 26. Wellington: Department of Conservation

Csanady GT. 1977. Cyclonic mean circulation of large lakes. PNAS 74: 2204–2208.

Cyr, H., K. J. Collier, S. J. Clearwater, B. J. Hicks, and S. D. Stewart. 2016. Feeding and nutrient excretion of the New Zealand freshwater mussel *Echyridella menziesii* (Hyriidae, Unionida): implications for nearshore nutrient budgets in lakes and reservoirs. Aquat. Sci. **79**: 556

Davies-Colley, R. 1988. Measuring water clarity with a black disk. Limnol. Oceanogr. **33**: 616–623.

Elliott, A., and L. Basher. 2011. Modelling sediment flux: A review of New Zealand catchment-scale approaches. J. Hydrol. New Zeal. **50**: 143–160.

Elser, J.J., Chrzanowski, T.H., Sterner, R.W., Schampel, J. H. and Foster, D. K. 1995. Elemental ratios and the uptake and release of nutrients by phytoplankton and bacteria in three lakes of the Canadian Shield. Microb. Ecol. **29**: 145–162.

Finlay, J. C., R. W. Sterner, and S. Kumar. 2007. Isotopic evidence for in-lake production of accumulating nitrate in Lake Superior. Ecol. Appl. **17**: 2323–32.

Hamilton, D. P., N. Salmaso, and H. W. Paerl. 2016. Mitigating harmful cyanobacterial blooms: strategies for control of nitrogen and phosphorus loads. Aquat. Ecol. **50**: 351–366.

Hamilton, D., and K. Wilkins. 2005. Review of science underpinning the 20% nitrogen reduction target for Lake Taupo. A report prepared for the Ministry for the Environment, University of Waikato, Hamilton.

Hawes, I., and R. Smith. 1994. Seasonal dynamics of epilithic periphyton in oligotrophic Lake Taupo, New Zealand. New Zeal. J. Mar. Freshw. Res. **28**: 1–12.

Hogg, A., D. J. Lowe, J. Palmer, G. Boswijk, and C. B. Ramsey. 2011. Revised calendar date for the Taupo eruption derived by ^{14}C wiggle-matching using a New Zealand kauri ^{14}C calibration data set. The Holocene **22**: 439–449.

Imberger, J., C. L. Marti, C. Dallimore, D. P. Hamilton, J. Escriba, and G. Valerio. 2017. Real-time, adaptive, self-learning management of lakes. Proceedings of the 37th IAHR World Congress, Kuala Lumpur, Malaysia August 13 – 18. 72–86.

James, M. R. 1985. Distribution, biomass and production of the freshwater mussel, *Hyridella menziesi* (Gray), in Lake Taupo, New Zealand. Freshw. Biol. **15**: 307–314.

Jellyman, P., D. Booker, S. Crow, M. Bonnett, and D. Jellyman. 2013. Does one size fit all? An evaluation of length–weight relationships for New Zealand's freshwater fish species. New Zeal. J. Mar. Freshw. Res. **47**: 450–468.

Jolly V.H. (1965) Diurnal surface concentrations of zooplankton in Lake Taupo, New Zealand. *Hydrobiologia* **25**, 466–472.

Kilham, P., and S. Kilham. 1990. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshw. Biol. **23**: 379–389.

Kissling, W. M. and Weir, G. J. 2005. The spatial distribution of the geothermal fields in the Taupo Volcanic Zone, New Zealand. J. Volcanol. Geotherm. Res. **145**: 136–150.

Kumar, S., R. W. Sterner, and J. C. Finlay. 2008. Nitrogen and carbon uptake dynamics in Lake Superior. J. Geophys. Res. **113**: 1–15.

Leach, T., B. Beisner, C. Carey, and others. 2017. Relative importance of light and thermal stratification in prediting the structure of deep chlorophyll maxima among lakes. Limnol. Oceanogr. **63**: 628-646.

Levine, S. N., and W. M. Lewis. 1987. A numerical model of nitrogen fixation and its application to lake Valencia, Venezuela. Freshw. Biol. **17**: 265–272.

Lewis, W. J. 2010. Biogeochemistry of tropical lakes. Verh. Int. Verein. Limnol. **30**: 1595–1603.

Lewis, W. M., and W. A. Wurtsbaugh. 2008. Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. Int. Rev. Hydrobiol. **93**: 446–465.

Lomas, M. W., Rumbley, C. J., Glibert, P. M. 2000. Ammonium release by nitrogen sufficient diatoms in response to rapid increases in irradiance. Journal of Plankton Research **22:** 2351–2366

MacIntyre, S., J. F. Clark, R. Jellison, and J. P. Fram. 2009. Turbulent mixing

induced by nonlinear internal waves in Mono Lake, California. Limnol. Oceanogr. **54**: 2255–2272.

Maxwell, D. 2012. A Rainfall - Runoff Model for the Highly Regulated Lake Taupo Catchment, Using a Constrained Ensemble Kalman Filter to Improve the Accuracy and Reliability of Model Output. PhD Thesis, Victoria University of Wellington.

McMahon, K. W., and M. D. McCarthy. 2016. Embracing variability in amino acid $\delta^{15}N$ fractionation: Mechanisms, implications, and applications for trophic ecology. Ecosphere **7**: e01511

Mohseni, O., H. G. Stefan, and T. R. Erickson. 1998. A nonlinear regression model for weekly stream temperatures. Water Resour. Res. **34**: 2678–2685.

Monismith, S. G., J. Imberger, and M. L. Morison. 1990. Convective motions in the sidearm of a small reservoir. Limnol. Oceanogr. **35**: 1676–1702.

O'Reilly, C. M., R. J. Rowley, P. Schneider, J. D. Lenters, P. B. Mcintyre, and B. M. Kraemer and others. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys. Res. Lett. **42**: 10,773–10,781

Oliver, R. L., D. P. Hamilton, J. D. Brookes, and G. G. Ganf. 2012. Physiology, blooms and prediction of planktonic cyanobacteria . *In* Ecology of Cyanobacteria II, p. 155–189, B.A. Whitton [ed.]. Springer Netherlands.

Patalas, K. 1961. Wind und morphologiebedingte wasserbewegungstypen als bestimmender faktor fur die intensitat des stoffkreislaufs in nordpolnischen Seen, Verh. Int. Ver. Theor. Angew. Limnol., 14, 59–64.

Payne, R. E. 1972. Albedo of the sea surface. J. Atmos. Sci. **29**: 959–970.

Read, J. S., D. P. Hamilton, I. D. Jones, K. Muraoka, L. A. Winslow, R. Kroiss, C. H. Wu, and E. Gaiser. 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. Environ. Model. Softw. **26**: 1325–1336.

De Ronde, C. E. J., P. Stoffers, D. Garbe-Schönberg, and others. 2002. Discovery of active hydrothermal venting in Lake Taupo, New Zealand. J. Volcanol. Geotherm. Res. **115**: 257–275.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rowe, D. K., S. Nichols, and G. R. Kelly. 2001. Depth distribution and abundance of the common bully, *Gobiomorphus cotidianus* (Eleotridae), in three oligotrophic New Zealand lakes, one of which is turbid. Environ. Biol. Fishes **61**: 407–418.

Rueda FJ, MacIntyre S. 2010. Modelling the fate and transport of negatively buoyant storm–river water in small multi–basin lakes. Environ. Model. Softw. **25**: 146–157.

Schindler, D. W., S. R. Carpenter, S. C. Chapra, R. E. Hecky, and D. M. Orihel. 2016. Reducing phosphorus to curb lake eutrophication is a success. Environ. Sci. Technol. **50**: 8923–8929.

Scott, J. T., and M. J. McCarthy. 2010. Nitrogen fixation may not balance the

nitrogen pool in lakes over timescales relevant to eutrophication management. Limnol. Oceanogr. **55**: 1265–1270.

Shostell, J., and P. A. Bukaveckas. 2004. Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. Aquat. Ecol. **38**: 359–373.

Slawyk, G., P. Raimbault and N. Garcia. 1998. Measuring gross uptake of ^{15}N labeled nitrogen by marine phytoplankton without particulate matter collection: Evidence for low ^{15}N losses to the dissolved organic nitrogen pool. Limnol. Oceanogr. **43**: 1734–1739.

Spigel, R. H., C. Howard-Williams, M. Gibbs, S. Stephens, and B. Waugh. 2005. Field calibration of a formula for entrance mixing of river inflows to lakes: Lake Taupo, North Island, New Zealand. New Zeal. J. Mar. Freshw. Res. **39**: 785–802.

Stewart, S. D., D. P. Hamilton, W. T. Baisden, M. Dedual, P. Verburg, I. C. Duggan, B. J. Hicks, and B. S. Graham. 2017. Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. Freshw. Biol. **62**: 2008–2025.

Tunney, T. D., K. S. McCann, N. P. Lester, and B. J. Shuter. 2014. Effects of differential habitat warming on complex communities. PNAS **111**: 8077-8082

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. S. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48**: 1408–1418.

Vanni, M. J., G. Boros, and P. B. McIntyre. 2013. When are fish sources vs. sinks of nutrients in lake ecosystems? Ecology **94**: 2195–2206.

Vanni, M. J., McIntyre, P. B., Allen, D., Arnott, D. L., Benstead, J. P., Berg, D. J., and others. 2017. A global database of nitrogen and phosphorus excretion rates of aquatic animals. Ecology, **98**: 1475.

Verburg, P., and A. Albert. 2016. Lake Taupo Long-term Monitoring Programme, 2014 – 2015. Prepared for Waikato Regional Council, Report: TR 2016/13.

Verburg, P., and J. P. Antenucci. 2010. Persistent unstable atmospheric boundary layer enhances sensible and latent heat loss in a tropical great lake : Lake Tanganyika. J. Geophys. Res. **115**: D11109

Vincent, W. F. 1983. Phytoplankton production and winter mixing: contrasting effects in two oligotrophic lakes. J. Ecol. **71**: 1–20.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology **83**: 2152–2161.

Vant, W., and Gibbs, M. 2006. Nitrogen and Phosphorus in Taupo Rainfall. Environment Waikato Technical Report 2006/46

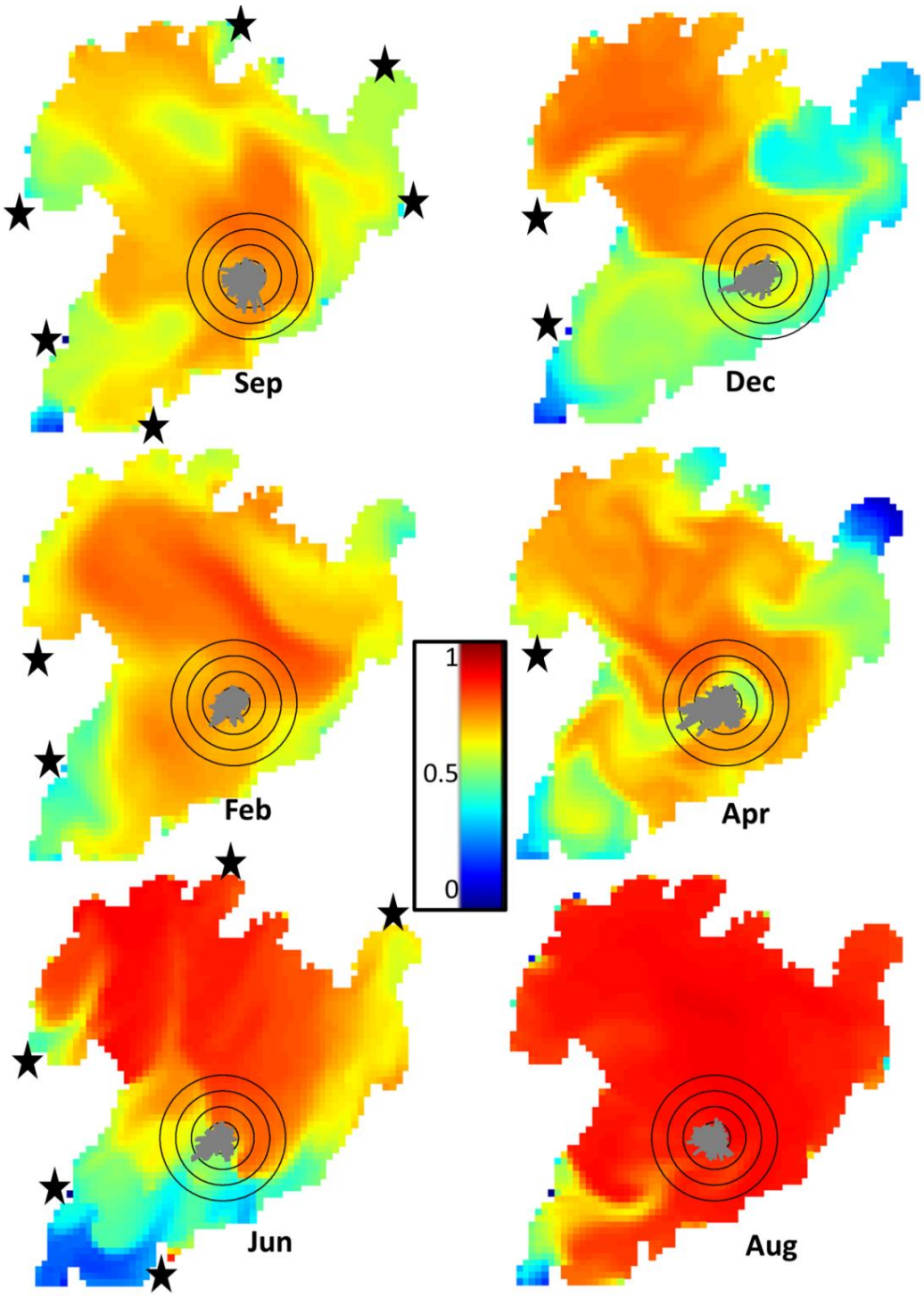
Varela, M. M., A. Bode, E. Fernández, N. Gónzalez, V. Kitidis, M. Varela, E.M.S. Woodward. 2005. Nitrogen uptake and dissolved organic nitrogen release in planktonic communities characterised by phytoplankton size–structure in the Central Atlantic Ocean. Deep-Sea Res. Pt. I **52**: 1637-1661

von Westernhagen, N. 2010. Measurements and modelling of eutrophication processes in Lake Rotoiti, New Zealand. PhD Thesis, University of Waikato.

Whiteford, P.C., 1996. Heat flow measurements in the sediments of Lake Taupo, New Zealand. Tectonophysics **257**: 81-92

Winder M., P. Spaak, W. M. Mooij, and N. Jul. 2004. Trade-offs in Daphnia habitat selection. Ecology **85**, 2027–2036.

5.8 Appendix



Appendix 5-1: Colour contour maps of Lake Taupō surface water showing dispersion of the epilimnetic tracer during each of the six simulated periods. For each month the colour contour map shows tracer dispersion 14 days after initialisation of tracer release.

Chapter six

Synthesis and conclusions

6.1 Overview

This thesis investigates the relationship between nitrogen cycling and food web dynamics in a large, deep, oligotrophic lake. By combining stable isotope field data from food web consumers and particulate organic and dissolved inorganic nitrogen pools, as well as modelled data over a complete annual cycle, I have demonstrated strong coupling of nitrogen cycling and food web dynamics in the lake. Nitrogen cycling and food web interactions were bi-directional, with the direction (i.e., bottom-up vs. top-down) changing seasonally. Winter water column mixing elicited bottom-up forcing through the influx of nutrients that fuelled peak phytoplankton production. During this period consumers switched their diets towards pelagic resources. Following the onset of summer stratification, due to reduced nutrient concentrations and phytoplankton biomass, top-down effects had an increasingly important role in regulating pelagic primary production. *In situ* recycling preferentially retained nitrogen (N) within the pelagic zone and excretion of littoral-derived N by mobile consumers translocated N into the pelagic surface waters. These findings give a new perspective on ecosystem function in oligotrophic lakes which, it is envisaged, will a) provide a foundation for future empirical research quantifying drivers of N-recycling rates and, b) provide an argument for integrating food web dynamics and water quality in nutrient management of oligotrophic lakes. The primary findings of the four research chapters are provided below, followed by discussion of management implications and future research directions.

6.2 Research summary

Chapter two used a literature synthesis to a) summarise current understanding of the drivers of lake nutrient cycling processes and food web dynamics, and b) integrate knowledge from these two fields to develop understanding of the role of consumer nutrient recycling (CNR). The current paradigm of nutrient cycling in lakes has followed a linear progression from considering effects of catchment loads and seasonal hydrodynamic processes (i.e., mixing and stratification) through to biogeochemical recycling. Increasingly, research is demonstrating that, in specific contexts, recycling by large-bodied mobile consumers can have a significant role in generating nutrients to support primary production. Application of general rules

from food web theory can help explain these context specific variations in nutrient recycling. Lake food webs follow a common structure where lower trophic level consumers have highly specialised (either pelagic or littoral) diets whereas consumers from increasingly higher trophic levels link littoral and pelagic food chains. Furthermore, periods of prolonged low nutrient availability, such as during stratification, were identified as when biota had greatest reliance on CNR. During this period larger, higher trophic level consumers were able to maintain populations, unlike smaller bodied consumers. The review concluded by exploring how stable isotopes may a highly suitable means to demonstrate CNR effects.

Chapter three applied concepts from food web theory covered in chapter two to explore the seasonal food web dynamics in Lake Taupō. It demonstrated that diet composition was extremely variable over the year, with consumers switching between predominantly pelagic resources directly after winter mixing and littoral resources during the stratified period. Variable littoral-pelagic diet coupling was driven by seasonal patterns in zooplankton abundance. Zooplankton abundance itself was driven by interactions with phytoplankton; greater nutrient availability during winter mixing increased both phytoplankton and zooplankton abundance. During stratification, phytoplankton-zooplankton interactions became governed by stable limit cycle dynamics. The large intra-annual variation in diet composition observed in smelt and trout in particular is contrary to previous assumptions that Lake Taupō is a pelagic dominated food web (see Rowe and Schallenberg, 2004), but is consistent with food web theory.

Chapter four used ammonium, nitrate and POM stable isotope data to provide evidence for the contribution of CNR to nutrient pools observed over a seasonal cycle in Lake Taupō. This research: i) validated the assumption that consumer excretion is a ^{15}N-deplete source of dissolved inorganic nitrogen (DIN); ii) demonstrated a significant and direct 1:1 relationship between the $\delta^{15}N$ values of zooplankton excretion and ammonium present at the deep chlorophyll maximum (DCM), indicating that zooplankton excretion contributes substantially to the ammonium at the DCM; and iii) used seasonal data for nitrate, ammonium and POM $\delta^{15}N$ to demonstrate that CNR contributions were greatest in the pelagic surface waters during summer stratification. Substantial spatial variation in $\delta^{15}N$ values suggested that effects of CNR were highly localised in space and time. Nitrate $\delta^{18}O$ data provided data for mechanistic insights, showing that the

contribution of CNR-derived nitrate was greatest when heterotrophic biomass, relative to primary producer biomass, was highest. These findings are in strong agreement with patterns predicted from the literature synthesis, that CNR will be most important as a source of DIN during periods of low nutrient availability when there is high consumer biomass (i.e., net ecosystem heterotrophy).

Chapter five used a N mass balance to investigate the significance of recycling relative to physical transport for fluxes of DIN within the pelagic surface water during the stratified period. Recycling of N in the pelagic surface water was the primary source of N for phytoplankton uptake. Recycling rates varied seasonally with phytoplankton biomass, indicating that recycling acts interactively (i.e., as a positive feedback) with other nutrient influxes. A positive correlation between recycling rate and $\delta^{15}N$ values for nitrate, ammonium and POM suggested that seasonal increases in recycling were largely driven by increased phytoplankton biomass and associated N release. This is because phytoplankton N release is associated with ^{15}N-enrichment. The ^{15}N-depletion of the surface water DIN pools associated with CNR became evident when phytoplankton biomass declined seasonally yet consumer biomass remained relatively constant. While physical transport of nutrients from the littoral zone to the pelagic surface waters is the primary source to support open-water production over the course of an annual cycle, there was substantial seasonal variation and CNT fluxes became increasingly important during early and mid-stratification (December to February).

6.3 Implications and future research directions

This study demonstrates, firstly, that food web − nitrogen cycling interactions are tightly coupled and bi-directional. Physical forcing tends to drive bottom-up changes in primary production while food web interactions concomitantly have strong top-down effects on productivity via nitrogen cycling. Secondly, it demonstrates the strong effect of seasonality (i.e., climatic forcing) on food web-nitrogen cycling interactions.

The tight coupling between nitrogen cycling and food web dynamics observed in Lake Taupō suggests that there is a strong possibility that drastic alterations of the food web, such as the sudden decline in trout size and abundance observed in 2005, will have a substantial effect on nutrient cycling in the lake. For example, based on knowledge that smelt excretion is the primary influx of DIN to the pelagic surface water during December and February, nutrient concentration monitoring data from

the mid-lake station during these months are most likely to show inter-annual variations related to smelt abundance. Given the strong trophic interactions observed between smelt and trout, the post-2005 decline in trout is likely to also reflect drastic changes in the smelt population and hence pelagic nutrient concentrations during December and February. Higher smelt biomass may have a positive feedback effect on pelagic productivity during stratification, resulting in pelagic resources remaining abundant throughout the stratified season for longer and intern sustaining a larger smelt biomass (Dong et al. 2017; Farnsworth et al. 2017). December through February is the period of the year typically characterised by high zooplankton biomass and low phytoplankton biomass (Stewart et al. 2017). Additional nutrients available for phytoplankton growth during this period are likely to be critical for sustaining zooplankton biomass (hence pelagic food resources available for smelt) over the stratified period (Herren et al. 2016).

Strong climatic forcing results in Lake Taupō oscillating between two states; winter-mixing and summer stratification. The food web response to these two states can be generalised as a) winter mixing driving productivity and providing a 'pulsed' bottom-up forcing event followed by b) increasing top-down regulation during the stratified season, which acts to attenuate the winter pulse. This seasonal pattern can be described as "thrive and survive" dynamics. The "thriving" period corresponds to the rapid growth across all trophic levels associated with winter mixing and increased pelagic phytoplankton production. Summer stratification is the "survival" period when resource scarcity across all trophic levels promotes ecosystem functions that tend to be associated with resilience (e.g., diet breadth in consumers and utilisation of recycled nutrients) (Walters and Post 2008). With increasing duration of stratification (e.g., associated with climate warming), it is likely that the food web responses to sustain ecosystem function will eventually reach a threshold after which time the higher trophic level biomass will drastically decline. Determining where this threshold point lies is of fundamental importance to understanding food web resilience to global change stressors such as climate change (O'Reilly et al. 2003; Verburg et al. 2003).

Seasonal patterns of nitrogen cycling and food web dynamics in Lake Taupō demonstrated by this study may provide mechanisms that have been suggested to promote resilience to climate change (Adrian et al., 2008; Moss, 2012). Winter mixing in Lake Taupō has been shown to be reduced during strong El Niño

Southern Oscillation (ENSO) climatic periods (Hamilton et al. 2013). Given the significance of winter-mixing in driving food web production in Lake Taupō, ENSO events are likely associated with reduced pelagic prey availability for smelt and trout. ENSO events are also predicted to increase in frequency and magnitude with climate change (Hamilton et al. 2013). The findings from this thesis highlight food web vulnerabilities to climate change in terms of prolonging stratification, reducing the duration of winter stratification and extending summer periods of depauperate production. These effects may be mitigated by management that promotes littoral habitat quality and enhanced secondary production.

This study adds to the growing body of research demonstrating interactions between nutrient cycling and food web dynamics, supported by integration of CNR into ecosystem level models (Vanni et al. 2013; Allgeier et al. 2017). The mechanisms governing CNR found in this study are expected to be general to oligotrophic lakes. However, future research should focus on disentangling the general and system-specific effects on N cycling (e.g., lake basin morphology and local climate), to better understand the potential of CNR to act as a feedback mechanism that promotes resilience to global environmental change stressors such as climate change. Investigating phosphorus cycling in a similar framework would be extremely beneficial and could address questions such as whether P cycling could be controlled by biological recycling to the same extent as N-cycling. Primary production in lakes tends to become more N limited towards the tropics (Abell et al. 2012), a pattern that corresponds to reduced physical transport and increased proportion of recycling supporting primary production (Kilham and Kilham 1990; Lewis 2010). As dissolved N and P will be transported similarly, the latitudinal patterns of N and P limitation could be interpreted as the higher biological recycling observed in tropical than temperate lakes more effectively recycling P than N. This interpretation would suggest that P is more efficiently recycled (i.e., more reliant on biological interactions) than the N cycling effects demonstrated in this thesis. Greater recycling efficiency of phosphorus could be assumed given that the DOP pool is generally significantly more labile than the DON pool within lakes (Kilham and Kilham 1990). Expanding this deduction, production in high latitude P-limited systems (in which physical transport processes are relatively more important) could be assumed to be more limited by recycling processes than in lower latitude N-limited systems. Hence, primary production in strongly P-limited lakes may be more sensitive to food web changes. This would suggest that responses to food web

perturbations, such species invasions, may be more drastic within P-limited lakes (e.g., the large alpine lakes in the South Island of New Zealand – Burns 1991; Abell et al. 2012).

6.4 Management considerations

At a practical level, this study provides information on where to focus and integrate management of water quality and food web dynamics (i.e., the trout fishery) in Lake Taupō. Here I elaborate on two possible management avenues. First, the trout fishery provides the lake managers with the opportunity to actively manage top-predator biomass through angling pressure. The substantial contribution of smelt nutrient translocation to the pelagic surface water N budget, and the potential for top-down control via the trout fishery to affect nutrient availability, and consequently phytoplankton biomass, warrant further investigation. Second, adaptive fishery management may also be achieved in Lake Taupō, enabling fishing pressure to be adjusted based on winter pelagic primary production. Annual water column mixing and chlorophyll concentration data (such as that recently collected at high frequency from a mid-lake autonomous monitoring buoy) could provide high resolution pelagic algal biomass data to inform a food web model. A food web model driven by primary production data would enable forecasting for the trout fishery and could be used to adjust regulations that govern angling pressure on an annual basis.

For an integrated water quality – food web based management approach to be successful, monitoring and active management of littoral areas are critical (Vadeboncoeur et al. 2002). Given the high reliance on littoral food resources across the food web during stratification, habitat restoration to enhance secondary production (e.g., indigenous macrophyte bed restoration (Coffey and Clayton 1988; Kovalenko and Dibble 2010) and reintroduction of woody debris (Francis and Schindler 2009; Sass et al. 2012)) would enhance food web resilience. Littoral restoration can potentially affect both physical and consumer-derived littoral-pelagic DIN exchange. Increasing benthic primary production in littoral areas may reduce water column DIN and thus reduce physical fluxes to the pelagic zone. A predicted increase in consumer littoral diet reliance associated with littoral habitat restoration would result in increased translocation of littoral-derived consumer N excretion into the pelagic zone. Increased biotic littoral-pelagic coupling during stratification may create a stabilising effect which could feed back to higher pelagic

primary production during summer stratification and therefore more seasonally stable food web dynamics.

Although management implications of this thesis have been directed specifically to Lake Taupō, they can be applied to other large oligotrophic lakes globally. It is well recognised that large oligotrophic lakes are extremely sensitive to climate change, species invasions and nutrient enrichment (Adrian et al. 2010; Carpenter et al. 2011). It is envisaged that this study will lay the foundation for future studies to quantify critical thresholds for these stressors specific to large oligotrophic lakes in the same why that has been demonstrated for shallow lakes (Søndergaard et al. 2007). Integrated management, as highlighted here, presents a new avenue for sustaining our most treasured lakes.

6.5 References

Abell, J. M., D. Özkundakci, D. P. Hamilton, and J. R. Jones. 2012. Latitudinal variation in nutrient stoichiometry and chlorophyll-nutrient relationships in lakes: A global study. Fundam. Appl. Limnol. / Arch. für Hydrobiol. **181**: 1–14.

Adrian, R., C. M. O'Reilly, H. Zagarese, and others. 2010. Lakes as sentinels of climate change. Limnol. Oceanogr. **54**: 2283–2297.

Allgeier, J. E., D. E. Burkepile, and C. A. Layman. 2017. Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. Glob. Chang. Biol. **23**: 2166–2178.

Burns, C. W. 1991 New Zealand lakes research, 1967–91, New Zealand Journal of Marine and Freshwater Research **25:** 359-379

Carpenter, S. R., E. H. Stanley, and M. J. Vander Zanden. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. Annu. Rev. Environ. Resour. **36**: 75–99.

Coffey, B. T., and J. S. Clayton. 1988. Contrasting deep-water macrophyte communities in two highly transparent New Zealand lakes and their possible association with freshwater crayfish, *Paranephrops* spp. New Zeal. J. Mar. Freshw. Res. **22**: 225–230.

Dong, X., A. Ruhí, and N. B. Grimm. 2017. Evidence for self-organization in determining spatial patterns of stream nutrients, despite primacy of the geomorphic template. Proc. Natl. Acad. Sci. **114**: E4744-E4752.

Farnsworth, K. D., L. Albantakis, and T. Caruso. 2017. Unifying concepts of biological function from molecules to ecosystems. Oikos **126**: 1367–1376.

Francis, T. B., and D. E. Schindler. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos **118**: 1872–1882.

Hamilton, D. P., C. G. McBride, D. Ozkundukci, M. Schallenberg, and P. Verburg. 2013. Climate warming in New Zealand Lakes, *In* C.R. Goldman, M. Kumagai, and R. Roberts [eds.], Climate change and global warming of inland waters. John Wiley & Sons, Ltd.

Herren, C. M., K. C. Webert, M. D. Drake, M. J. Vander Zanden, Á. Einarsson, A. R. Ives, and C. Gratton. 2016. Positive feedback between chironomids and algae creates net mutualism between benthic primary consumers and producers. Ecology **98**: 447–455.

Kilham, P., and S. Kilham. 1990. Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. Freshw. Biol. **23**: 379–389.

Kovalenko, K. E., and E. D. Dibble. 2010. Effects of invasive macrophyte on trophic diversity and position of secondary consumers. Hydrobiologia **663**: 167–173.

Lewis, W. J. 2010. Biogeochemistry of tropical lakes. Verh. Int. Verein. Limnol. **30**: 1595–1603.

Moss B. 2012. Cogs in the endless machine: lakes, climate change and nutrient cycles: a review. Sci. Total Environ. **434**, 130–42.

O'Reilly, C. M., S. R. Alin, P.-D. D. Plisnier, A. S. Cohen, and B. A McKee. 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature **424**: 766–768.

Sass, G. G., S. R. Carpenter, J. W. Gaeta, J. F. Kitchell, and T. D. Ahrenstorff. 2012. Whole-lake addition of coarse woody habitat: Response of fish populations. Aquat. Sci. **74**: 255–266.

Søndergaard, M., E. Jeppesen, T. L. Lauridsen, C. Skov, E. H. Van Nes, R. Roijackers, E. Lammens, and R. Portielje. 2007. Lake restoration: Successes, failures and long-term effects. J. Appl. Ecol. **44**: 1095–1105.

Stewart, S. D., D. P. Hamilton, W. T. Baisden, M. Dedual, P. Verburg, I. C. Duggan, B. J. Hicks, and B. S. Graham. 2017. Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. Freshw. Biol. **62**: 2008–2025.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience **52**: 44–54.

Vanni, M. J., G. Boros, and P. B. McIntyre. 2013. When and fish sources vs. sinks of nutrients in lake ecosystems? Ecology **94**: 2195–2206.

Verburg, P., R. E. Hecky, and H. Kling. 2003. Ecological consequences of a centuray of warming in Lake Tanganyika. Science **301**: 505–508.

Walters, A. W., and D. M. Post. 2008. An experimental disturbance alters fish size structure but not food chain length in streams. Ecology **89**: 3261–3267.