Long-term zooplankton dynamics in Lake Taupō: 2000-2020

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Abstract

Long-term monitoring is essential for distinguishing between natural and anthropogenically induced changes within ecosystems, particularly those with high degrees of natural fluctuation. In order to gain further understanding of the links between physical, chemical and biotic factors, zooplankton have been highlighted as useful bioindicators within aquatic ecosystems. Long-term zooplankton monitoring studies have been utilized to highlight changes in lake trophic state, changes within catchments, fisheries practices and invasions.

Lake Taupō, New Zealand's largest lake, has been subject to a long-term monitoring programme by NIWA since 1994, commissioned by the Waikato Regional Council, with the primary purpose of detecting changes in the lake's trophic state through time. Since January 2000, the monitoring programme has included biweekly zooplankton sampling; no results of this have yet been published. The purpose of my research was to assess if there have been any significant changes in the zooplankton community composition over the monitoring period (2000-2020), with a particular focus on the last 12 years of data (2009-2020), and determine the importance of measured environmental variables in influencing changes in the zooplankton community composition.

Lake Taupō was assessed as microtrophic to oligotrophic throughout the monitoring period (Trophic Level Index (TLI) between 1.5 and 2.9), and there were no significant linear changes in any of the measured environmental variables (R-squared values all <0.07, p values all >0.05). The zooplankton data was separated into two separate datasets; a shorter February 2009 – December 2020 dataset with samples analysed entirely by myself, and a longer January 2000-December 2020 dataset, with earlier samples analysed by NIWA, utilising a lower taxonomic resolution.

Multivariate analyses (nMDS and ANOSIM) indicated significant differences among three yearly groups of zooplankton data within both the shorter (Global R statistic = 0.179, p = 0.014) and longer dataset (Global R statistic = 0.353, p = 0.001). Time and temperature were inferred by Redundancy Analysis (RDA) as the most important environmental variables associated with change in zooplankton community composition in both the shorter 2009-2020 (Lambda-A = 0.08 for both, p = 0.002 for both) and longer 2000-2020 datasets (Lambda-A = 0.15, p = 0.002 for time, and Lambda-A = 0.06, p = 0.002 for temperature). Both ordinations indicated that changes associated with time (long-term) and changes in temperature were primarily unrelated. Changes in zooplankton community composition influenced by temperature were attributed to seasonal succession.

Zooplankton community composition differed between the beginning and end of the monitoring periods in both datasets. However, the direction of the community change seemingly reversed around 2009-2011, with assemblages late in the study reverting to communities similar to those observed earlier in the study. Decreases in the native large *Daphnia thomsoni* and increased importance of the non-native *Daphnia galeata* indicate that colonisation by the invading species has influenced the observed changes in zooplankton community composition. The influences of top-down control in the form of predation on the zooplankton community by fish (an unmeasured variable) may have also influenced communities, with shifts from large- to small-sized species observed. Rotifers indicative of both low and high TLI are present throughout the study (e.g., *Polyarthra dolichoptera* and *Keratella cochlearis* respectively), but the community is dominated throughout by species indicative of low trophic state (e.g., *Conochiloides dossuarius*), which is consistent with previous zooplankton studies within Lake Taupō. Continued monitoring of zooplankton, physical and chemical lake properties, algae, and bacteria is advised, with the inclusion of fish monitoring recommended.

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Table of Contents

List of Figures

List of Tables

Chapter 1

Introduction

1.1 Determining the impacts of environmental change

1.1.1 The need for long-term ecological studies

Ecosystems experience variation through time. Many changes observed in ecosystems are natural fluctuations and cyclic patterns, but the impacts of anthropogenic change are becoming evident in various environments around the world (Spellerberg, 2005; Zeppilli *et al.*, 2015). The planning and implementation of policy and ecosystem management are affected by our understanding of environmental variation (Lazareva, 2010; Jeppesen *et al.*, 2011). A key issue faced by scientists, planners, governing bodies and environmental managers is the ability to separate natural variation from the anthropogenic influenced changes, and determining what further impacts environmental changes have on ecosystems and the biota therein (Anderson *et al.*, 2005; Eimers *et al.*, 2005; Hampton *et al.*, 2008). Long-term monitoring programs are fundamental for understanding key human-induced changes to environments, particularly those that undergo high amounts of natural variation throughout time (Lindenmayer *et al.*, 2012). In ecology, "long term" is typically considered to be greater than 5 years (Dennehy, 2018) but for the purposes of this study it is considered to be periods 10 years or longer.

Many ecological changes occur slowly, and long-term monitoring is thus an essential tool for detecting underlying trends and patterns that may not be clear over shorter time frames (Smeltzer *et al*., 2012). The information gained from long-term monitoring can also provide baselines to represent various aspects of ecosystem components that can be used as a basis for environmental policy and management (Vaughan *et al*., 2001; Magurran *et al*., 2010). Continued monitoring post-policy or management action can be used to assess the impacts of schemes or changes made, to determine their effectiveness (Gitzen *et al*., 2012). The observation of long-term trends also allows the discovery of emerging environmental issues, and may help to further the science in new and different directions (Lovett et at., 2007).

1.1.2 Importance of zooplankton and use as indicators of lake health

A goal of many ecological studies is to determine features and qualities of ecosystems without having to measure every aspect of them individually, and to use this information to assess changes within ecosystems. (Lottig and Carpenter, 2012). Lakes, in particular, are well suited to act as sentinels for their catchments. Due to wind driven circulation, many lakes display relatively low horizontal surface heterogeneity of environmental variables, often resulting in only a few monitoring points being needed to represent the entire water body (Schindler, 2009). Environmental monitoring is often undertaken alongside biological monitoring in aquatic systems (Wiederholm, 1980), and various biotic indices have been created in order to assess ecosystem changes (e.g., Macroinvertebrate community index, Index of Biotic Integrity, Trophic Diatom Index (Stark, 1985; Karr *et al*., 1986; Kelly and Whitton, 1995)) (Abbasi and Abbasi, 2011).

Although less studied than vertebrates, invertebrates make up more than 99% of animal diversity and are often essential for transferring energy in trophic food webs (Lydeard *et al*., 2004). Freshwater ecosystems, in particular, contain diverse and unique organisms (Brönmark and Hansson, 2002), not the least of which are zooplankton. Zooplankton are key components of lake and river ecosystems, as they act as trophic links between algae and bacteria to larger invertebrates and fish (Brito *et al*., 2020). Zooplankton grazing, both directly and indirectly, affects the composition and biomass of phytoplankton communities through direct consumption and regenerative nutrient effects (Symons *et al*., 2012). High densities of zooplankton have been shown to control algal growth (James, 1987; Elser and Goldman, 1991). For example, Elser and Goldman (1991) conducted experiments on three lakes of differing trophic state in California, U.S.A. They found a significant impact of zooplankton grazing in the ultra- and meso-oligotrophic Lake Tahoe and Castle Lake, but not in Clear lake, which is eutrophic and dominated by cyanobacteria. This was considered to be due to the size and type of phytoplankton present, as well as the specific zooplankton assemblage present in the lake. Similarly, colonization of a non-indigenous *Daphnia* species (*D. dentifera*) into Lake Puketirini, New Zealand, led to a decrease in phytoplankton biomass (Balvert *et al*., 2009). Prior to this colonization the dominant cladocerans were smaller bodied *Ceriodaphnia* and *Bosmina* species, which were less efficient feeders and therefore less well equipped to exert high levels of grazing pressure on phytoplankton when compared to the *Daphnia* (Balvert *et al*., 2009).

Zooplankton are also important biological indicators due to their rapid responses to environmental changes (Jakhar, 2013), their influence on many functional aspects of freshwater ecosystems such as energy flow, food webs, and nutrient cycling (Rajagopal *et al*., 2010), and their integration of physical, chemical, and biological factors over time (Lehtovaara *et al*., 2014). Their short life cycles typically mean that there is little to no yearly carryover of biomass and numbers, allowing zooplankton populations to closely track changes in environmental conditions (Mackas and Beaugrand, 2010).

Zooplankton (rotifers in particular) have been highlighted as particularly useful indicators of lake health and trophic state due to their ability to integrate multiple other criteria or indicators (Duggan *et al*., 2001; Balakrishna *et al*., 2013; Haberman and Haldna, 2014). Duggan *et al*. (2001) sampled rotifer populations from 33 North Island, New Zealand, lakes in order to assess their ability to correspond with Trophic Level Index (TLI). They found that the distribution of rotifer species was strongly associated with the TLI, with many species preferring extremes or particular ranges of trophic state. This is partially attributed to the species-specific preferences of the nature and size of food present.

Rotifers are not the only indicative group of zooplankton. In a large-scale study across a range of lakes and reservoirs in North and South America, Pinto-Coelho *et al*. (2005) found a strong relationship between total phosphorus and crustacean zooplankton density and biomass in both tropical and temperate regions. Similar results were previously found regarding crustacean zooplankton biomass and total phosphorus in smaller scale studies conducted by Hanson and Peters (1984) and Yan (1986), and between the population abundance of copepods and nutrient and chlorophyll *a* levels in seven Rotorua lakes, New Zealand (Chapman *et al*., 1985). Through a long-term study of Lake Biwa from 1961-2005, Hsieh *et al*. (2011) were able to assess the changes in the zooplankton community through times of eutrophic and oligotrophic states and found that the abundance ratios of cladocerans:calanoid copepods and cyclopoid:calanoid copepods were positively related to eutrophication, and thus could provide useful indicators of lake trophic state (Hsieh *et al*., 2011). Lake trophic status has been similarly found to be associated with the composition of major zooplankton groups by Pinto-Coelho and Bezerra-Neto (2005) and Ferdous and Muktadir (2009).

Despite their usefulness, there are difficulties when utilizing zooplankton as indicators of lake health and to infer food web dynamics. One of the primary difficulties is their seasonal variation, which can be extremely complex and diverse depending on the size and depth of the lake, the climate in which the lake is located, and the individual zooplankton species within the lake (Mengestou and Fernando, 1991). De Senerpont Domis *et al*. (2013) summarized the differences in plankton seasonality between artic/polar, temperate, and tropical lakes, and the potential impacts that climate change may have on these patterns. Although there were general trends in relation to the latitude, they highlighted that differences in peak zooplankton biomass can also vary depending on lake trophic state, aquatic food web, the microbial loop, and the effects of food quality on trophic transfer (De Senerpont Domis *et al*., 2013). Another difficulty when utilizing zooplankton as bioindicators in many cases is their highly patchy distribution spatially (Omori and Hamner, 1982). Zooplankton often are relatively sparse throughout the water column and can be concentrated in a few condensed aggregations. This is thought to be attributed to both physical drivers and behavioural processes (Folt and Burns, 1999), but is also dependent on the size of the waterbody and the specific zooplankton species swimming capabilities (George, 1989). A study conducted by Wiafe and Frid (1996) on the coastal zooplankton of Northumberland, United Kingdom, found that communities were able to maintain the same aggregation throughout periods of high wind induced turbulence, and only a maximum of 52% of the temporal variation in community composition was accounted for by horizontal transport (Wiafe and Frid, 1996). Thus although lakes may be useful as sentinels for their catchments in regards to measuring physical and chemical variables (Schindler, 2009), sufficient sampling effort must be utilized when including zooplankton sampling as their behavioural processes may lead them to maintain patchy distributions despite lake mixing (Omori and Hamner, 1982; Wiafe and Frid, 1996). For this reason, studies with limited sampling effort may lead to misrepresentation of zooplankton abundances in water bodies and as such, long-term zooplankton studies are more adept at elucidating underlying trends and identifying shifts in the zooplankton communities due to ecological or environmental changes.

1.1.3 Long-term Zooplankton monitoring studies

Long-term (>10 years) studies of zooplankton communities are rare (Duggan *et al*., 2020), particularly quantitative studies, and inclusion of zooplankton in long- term monitoring programs is commonly overlooked (e.g., the European Union's Water Framework Directive (WFD; 2000/60/EC) (European Commission, 2000)). Of the long-term monitoring studies that have been carried out, many have been able to highlight relationships between zooplankton communities and changes in various environmental factors. Lake Valkea-Kotinen, Finland, for example, is a small and shallow pristine lake where zooplankton sampling was conducted between 1990 and 2009 as part of a long-term monitoring programme. Analysis carried out by Lehtovaara *et al*. (2014) indicated that during the 1990s the zooplankton community was influenced by high total phosphorus and primary production of phytoplankton, whereas in the later years species were present that

were indicative of darker water colour (an indicator of organic carbon) and increased alkalinity. Changes in water colour and total phosphorus were attributed partially to climate change, highlighting the hierarchical influences of climate factors on zooplankton communities throughout time and the influences of bottom-up control on the lake (Lehtovaara *et al*., 2014).

Similarly, in a long-term study of zooplankton from the large shallow Lake Võrtsjärv, Estonia, between 1964 and 2000, changes in trophic state were closely matched by changes in the abundance of large-sized zooplankton relative to small-sized zooplankton (particularly cladocerans) and presence/absence and abundance of indicative rotifer species (Haberman and Haldna, 2014). The zooplankton community largely followed general trends for increasing eutrophic state (increases in prevalence of smaller, bacterial and detrital feeding species (Balakrishna *et al*., 2013) into the 1980s, after which a minor decrease in the lakes trophic state, paired with potential predation by cyclopoid copepods, greatly reduced rotifer abundances (Haberman and Haldna, 2014).

Andronikova (1996) analysed zooplankton in Lake Ladoga, Russia, spanning the years 1948-1993. It was found that there were differences in shifts of zooplankton communities between the littoral and pelagic areas of the lake over time. The author noted that significant changes in the littoral zooplankton community indicated a shift to species indicative of eutrophication, whereas the pelagic zone maintained a more stable zooplankton community indicative of a meso-oligotrophic state (with the exception of the surface water). Andronikova (1996) highlighted that based on the zooplankton communities within the lake, trophic state assessment can be assessed separately between the littoral and pelagic zones as these regions had different responses.

Further insights into lake ecosystems and their management can also be gained through analysis of zooplankton communities. Hambright (2008) analysed historical zooplankton samples from Lake Kinneret, Israel, from 1970-2002, along with previously published data. He concluded that the observed decreases in biomass of zooplankton over this period was due to changes in top-down pressure effects of planktivorous fish predation, and that this effect had been exacerbated by the fishery harvest practices of primarily removing larger bodied fish from the lake, allowing the populations of smaller planktivorus fish to thrive. The decrease in zooplankton biomass was attributed to a mean decrease in zooplankton body size. This, in turn, led to a decrease in zooplankton grazing pressure on phytoplankton, compounding the effects of hydrological modifications to Lake Kinneret and its catchment (e.g., impoundment, wetland draining, and increases in water level fluctuations for water supply and hydroelectric production) and contributing to the lakes' eutrophication (Hambright *et al*., 2008). Hambright (2008) was able to suggest that a change in fishing practices from selecting primarily the largest individuals (leading to a smaller bodied fish population) would likely be a first step in encouraging development of a larger bodied zooplankton population (Hambright, 2008).

Zooplankton data from the Lake Champlain (North America) Long-Term Water Quality and Biological Monitoring Program (LTMP) 1992 to 2010 was used to assess changes in the zooplankton community over time (Mihuc *et al*., 2012), with specific interest in changes brought about by invasive zebra mussels (*Dreissena* *polymorpha*) and alewife (*Alosa pseudoharengus*). Mihuc *et al*. (2012) found that the zooplankton community shifted significantly following these respective invasions. Invasive zebra mussels led to a decrease in rotifer abundances lake-wide, although limnetic rotifers appeared to have subsequently somewhat recovered following this invasion. Alewife invasion led to a decrease in large bodied zooplankton, particularly cladocerans, potentially reducing their ability to reach maturity. The long-term changes observed in the zooplankton community were not explained by the changes in water chemistry and are likely explained by interactions associated with invasions of non-native species (Mihuc *et al*., 2012).

Although far from an exhaustive list of long-term zooplankton studies globally, these examples highlight the importance of conducting long-term monitoring of zooplankton community composition in lakes to assess long-term dynamics and how these are impacted by, for example, changes in the lake trophic state (Haberman and Haldna, 2014), changes to the catchment (Lehtovaara *et al*., 2014), invasive species (Mihuc *et al*., 2012), and fisheries practices (Hambright, 2008). In all cases, short-term studies over 1-2 years would likely not have elucidated the same trends, particularly those that are looking at changes in lake trophic state, as it is typically a gradual change and, as highlighted by Haberman and Haldna (2014), can change from increasing eutrophy to decreasing eutrophy and back again numerous times, confounding results gathered only over short time periods. Seldom are short-term studies able to capture events such as invasions (Balvert *et al*., 2009), and without baseline data the impacts of the invaders cannot be thoroughly assessed. Long-term monitoring data is vital in determining what changes are natural, and to what degree they may be anthropogenically induced, or due to key species colonization.

1.2 New Zealand zooplankton

1.2.1 Previous studies

Throughout New Zealand, although there have been numerous zooplankton studies conducted (e.g., Chapman *et al.*, 1985; Balvert *et al.*, 2009; Duggan *et al.*, 2015), few focused on community temporal dynamics have lasted longer than two years. Short sampling periods can occasionally highlight chance events such as zooplankton invasions (Balvert *et al.*, 2009) or zooplankton community responses to rapid, planned changes through management interventions (Özkundakci *et al.*, 2011). There are some monitoring programmes conducted by regional government agencies that include zooplankton sampling; however, much of this data is unpublished or un-analysed. A notable exception to this is Duggan *et al.* (2020), who recently analysed semi-qualitative net samples collected over time frames of up to 12 years from 39 lakes in the Waikato region.

Previous published studies of Lake Taupō zooplankton specifically are limited, with most having lasted two years or less. Jolly (1965) sampled surface water at three near shore sites (>30 m depth) from April 1955 to December 1955 in order to assess the diurnal movements of zooplankton in the lake. Her methods, however, were not quantitative, and the net mesh size (239 µm) was too large to effectively capture rotifer species, and thus are limited in their comparability. Forsyth and McCallum (1980) sampled Lake Taupō monthly at three deep water (>100 m depth) sites between August 1974 and January 1976. Samples were collected using a net drawn up through 100 m of the water column, ensuring a more quantitative approach to sampling and utilizing a smaller net mesh size (55 µm) capable of capturing the smaller rotifers. They found no significant differences between the zooplankton sampled at the three sites, however they did find that differences in dominant taxa occurred seasonally. James (1987) also sampled Lake Taupō monthly for the period of July 1985 to June 1986 by vertical net hauls (55 µm mesh) at a site 60 m deep in order to assess the respiration and excretion rates of dominant taxa and their respective influence on phytoplankton production. Seasonality was found to be an important control of zooplankton biomass, and regenerated nitrogen was found to be a major source of nitrogen for phytoplankton.

Bayly (1989) analysed zooplankton collected by vertical net hauls (160 µm mesh) from a 45m deep site, near the outlet of the Waikato River, for the period of March – June 1987. These samples were compared to those collected in the Waikato River and it was found that the densities of zooplankton within the lake were much higher than those found in the outlet, but that the timing of large volumes of outflow impacted the abundance of zooplankton found in the river (Bayly, 1989). Finally, Duggan *et al*. (2002) analysed samples collected only quarterly in the lake between 1997 and 1999 using net hauls (40 µm mesh) through the entire water column as part of a larger study of North Island lakes. They found that Lake Taupō had the lowest species richness of the 31 lakes sampled, and attributed this to the large lake size and relative habitat stability as well as the oligotrophic lake state (Duggan *et al*., 2002). These studies are all useful in assessing changes that have occurred in the species presence and absence but are limited in their usefulness when assessing potential causes of zooplankton community changes over time due to the inconsistencies between the methods as well as the large time gaps between studies.

1.2.2 Monitoring program

In 1994 the Waikato Regional Council commissioned the National Institute of Water and Atmosphere (NIWA) to undertake a long-term monitoring program of Lake Taupō. The stated intention of this monitoring was to 'detect changes in the trophic state and ecological variables' within the lake through time (Verburg and Albert, 2019). This monitoring includes sampling the water column for temperature, nutrients, chlorophyll *a*, water clarity, phytoplankton species composition and zooplankton (Verburg and Albert, 2019).

Lake Taupō is generally considered to be oligotrophic, but has been influenced by increases in nitrogen discharges due to changes in the catchment land use by agricultural development since the 1940s (Hamilton and Wilkins, 2005). Concern for the lakes' future has led to the implementation of the Lake Taupō Nitrogen Trading Programme (LTNTP) in 2011, which is a cap-and-trade program focused on limiting the amount of nitrogen entering Lake Taupō from its catchment (Duhon *et al*., 2015). This programme is ongoing and many aspects of the results of this are yet to be studied (Barnes & Young, 2013).

There is only a single outflow of Lake Taupō, the Waikato River (New Zealand's longest river). There are numerous inflows to Lake Taupō in the form of streams and rivers, and a fundamental component of Lake Taupō's input comes from groundwater both in the form of groundwater streams and groundwater seepage directly to the lake-bed. Much of this groundwater has aquifer residence times of decades, and up to 80 years in some areas of the catchment. This greatly influences the interpretation and understanding of nutrient input data as the nutrients flowing into the lake via groundwater and even some streams are the result of nutrient loading between 1 and 80 years ago (Morgenstern, 2007).

1.2.3 Aims and Goals

The aim of this study was to examine 21 years of long-term zooplankton sample data from Lake Taupō, to determine whether there have been any significant changes to the community over the observed time period from 2000 to 2020, with a specific focus on the last twelve years of sample collection. The contribution of environmental factors to any changes will also be assessed, and the potential use of zooplankton as bioindicators of lake health and state will be discussed.

Chapter 2

Methods

2.1 Fieldwork Sampling

2.1.1 Sample Site

Lake Taupō is New Zealand's largest lake, with a surface area of approximately 622 km^2, a catchment area of 3487 km^2, and a maximum depth of 162 m. Lake Taupō is of volcanic origin, being formed by a chain of eruptions, the most recent being nearly 2000 years ago. This series of eruptions displaced large amounts of rock allowing the formation of Lake Taupō (Edwards *et al*., 2010).

The sampling site (Site A, Figure 2.1) was situated in the central basin of Lake Taupō, more than 5 km from land, at a depth of approximately 160 m. Zooplankton samples were collected approximately every two to three weeks since January 2000 as part of NIWAs long-term monitoring program, which began with measurements of environmental parameters in October 1994.

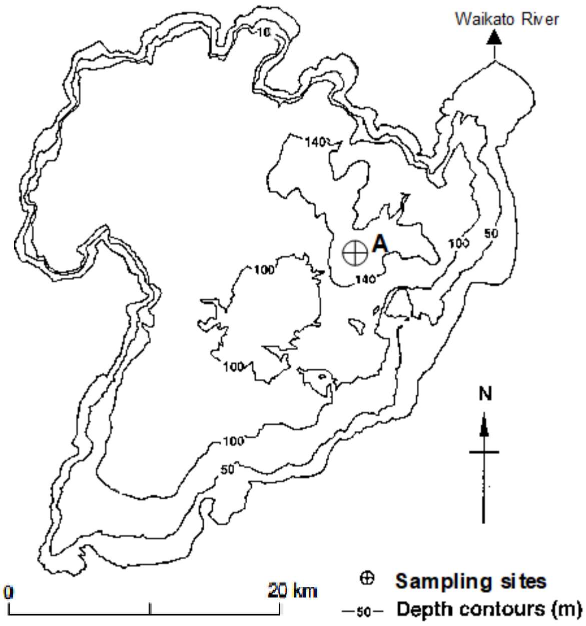

Figure 2.1: Lake Taupō sampling map - Site A indicated (adapted from Verburg and Albert, 2019).

2.1.2 Water Quality Monitoring

Depth-related temperature and dissolved oxygen (DO) profiles were measured using an RBR XR 420f CTD profiler from the beginning of the study until January 2008, when it was replaced by a RBR XR620f CTD profiler. Finally, from February 2016, a RBR Maestro logger/profiler was used. In all analyses temperature and DO were averaged over the top 10 m. A 20 cm diameter Secchi disc was used to measure water clarity. A 10 m tube was used to collect an integrated water sample for the measurement of chlorophyll *a*, nitrate (NO_3-N), ammoniacal nitrogen (NH_4-N), dissolved reactive phosphorus (DRP), particulate phosphorus (PP), particulate nitrogen (PN), and particulate carbon (PC). Near-bottom water samples from 150 m were collected using a van Dorn water sampling bottle and analysed for DRP, NO_3-N, and NH_4-N. Total nitrogen (TN) and total phosphorus (TP) were calculated as the sum of their components.

Dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) were calculated as the total dissolved nutrient minus the inorganic dissolved nutrients.

2.1.3 Zooplankton Sampling

Zooplankton samples were collected at Site A from January 2000 to December 2020 via 100 m vertical hauls with a conical plankton net (63 µm mesh) fitted with a 16 cm diameter reducing cone. Two replicate samples were drawn on each occasion. Samples were rinsed into clean 250 ml bottles, labelled, and preserved in 4% formalin.

2.2 Laboratory analyses

2.2.1 Water quality parameters

Determinations of water samples were made using a Lachat flow Injection Analyser (FIA) and C/N analyser with standard methods as routinely used for freshwater analysis by NIWA. Chlorophyll *a* was analysed using a spectrofluorometer following extraction of pigments using acetone (Paul, 2010).

2.2.2 Zooplankton analysis: February 2009-December 2020

Preserved zooplankton samples from the period February 2009 to December 2020 were analysed at the University of Waikato. Preserved zooplankton samples from approximately every six weeks were selected for analysis. These were inverted and emptied onto a 40 µm mesh strainer and formalin residue was removed from samples by rinsing with approximately 1 litre of (40 µm sieved) tap water in order to decrease the chance of inhalation of excess formalin during analysis. Rinsed samples were then returned to the original bottles and preserved with 100% ethanol.

Prior to counting, ethanol preserved zooplankton samples were washed on a 40 µm mesh with pre-filtered tap water to remove ethanol residue. Once rinsed with approximately 1 litre of water, the sample was poured into a 50 ml measuring cylinder, ensuring that the entire sieve contents had been rinsed into the cylinder. The sample was then diluted to a known volume (e.g., 50 ml) and poured into a clean wide mouth bottle. Samples were counted in 5 ml aliquots, drawn from the sample using an auto-pipette while stirring in a figure-of-eight motion. Subsamples were counted in a gridded Perspex sorting plate under a stereo dissecting microscope (Olympus SZ60) at approximately 30 x magnification. If the number of individuals in the primary subsample was less than 300, a second subsample was drawn and the process repeated with as many subsamples as was required until at least 300 individuals had been counted. Organisms were identified to species level, where possible.

Both replicates for each sample (128 sampling dates in total) were analysed with the exception of three incomplete or incorrectly preserved samples; 26 March 2009, 9 March 2015 and 20 February 2019. Replicate samples were averaged and expressed as the number of zooplankton per m^3 of lake water by assuming a 16 cm by 100 m cylinder was sampled. Species identification was carried out where possible under a compound microscope (Olympus BH-2) using relevant taxonomic keys (e.g., Shiel, 1995; Chapman *et al*., 2011).

2.2.3 Zooplankton analysis: January 2000 – January 2009

Analysis of zooplankton samples prior to February 2009 was carried out by Karen Robinson in the Freshwater Laboratory at NIWA, Christchurch. Methods used were as described for the February 2009 to December 2020 samples, omitting the initial substitution of ethanol for formalin as a preservative. All samples (approximately every 2-3 weeks) were analysed down to species or genus level, where possible, but rotifers were commonly identified with lower taxonomic resolution than the 2010-2020 dataset.

2.3 Statistical Analysis

2.3.1 Zooplankton Community Dynamics: February 2009-December 2020

Multivariate analyses were performed in order to elucidate patterns in zooplankton community composition and to infer what environmental variables were important in determining changes in the zooplankton community. Data collected between 2000 and 2008 was not included in my initial analysis, as lower taxonomic resolution was used during this period, and other possible biases may result from different analysts identifying zooplankton species, which may affect trends within the data. Zooplankton taxa were included in multivariate analyses if they consisted of at least 5% of the community in at least three samples, to remove the influence of species that may have been sampled or counted by chance, reducing the number of taxa in the analysis from 31 to 17 taxa. Zooplankton data was then log(x+1) transformed in order to ensure that dominant species did not have undue influence on the results. Copepod nauplii were included in analyses separately to the calanoid copepod *Boeckella propinqua* due to differing feeding habits and the inability to distinguish these larvae to species level; however, as only two other copepods were found in very low numbers (less than 1% of any sample), it can be assumed that the nauplii primarily consist of *B. propinqua*.

Non-metric multi-dimensional scaling (nMDS) was performed on a matrix based on the Bray-Curtis similarity coefficient calculated from the transformed zooplankton data to determine whether differences in community composition occurred temporally. The nMDS constructs a “map” that is based on the similarities among samples, as defined by the similarity matrix, and provides a stress value in order to measure the goodness of fit relative to the underlying similarity matrix. A one-way Analysis of Similarity (ANOSIM) was performed on the Bray-Curtis similarity matrix using 999 permutations in order to test whether there were significant differences between four, three yearly groups of the data (2009-2011, 2012-2014, 2015-2017, 2018-2020). Both nMDS and ANOSIM were performed using Primer version 7 (Clarke and Gorley, 2015).

To investigate environmental variables responsible for the variation in zooplankton community composition, CANOCO v 4.5 was used to perform a preliminary Detrended Correspondence Analysis (DCA), which indicated that the zooplankton community responded in a linear rather than a unimodal manner to underlying environmental gradients (length of gradient < 4; ter Braak and Smilauer, 1998). As such, Redundancy Analysis (RDA) was performed to infer which environmental variables were important in determining variability in zooplankton community composition. Forward selection and Monte Carlo permutation tests (using 99 unrestricted permutations) were performed in order to determine which environmental variables were statistically significant in determining the variations within the zooplankton community composition

(CANOCO v.4.5, Biometris, Wageningen, Netherlands). Missing environmental variables were interpolated from relationships with other environmental variables (three values of temperature were estimated based on temporal trends and two of Secchi depth were interpolated from their respective relationships with chlorophyll *a*). Time (expressed as days since 1900 for simplicity) was added as an environmental variable in order to distinguish changes occurring temporally independently of other environmental variables. Where appropriate, environmental variables were log(x+1) transformed in order to improve normality and all environmental variables were subsequently standardised to have zero mean and unit variance in order to remove the impacts of differing scales of measurements (ter Braak and Smilauer, 1998). Environmental data were only available to 6 October 2020, and thus only 126 out of the 128 zooplankton samples were included in this analysis. Eleven environmental variables were removed due to their high covariance (variance inflation factors >20); environmental variables retained in the ordination were Secchi transparency, temperature, TP, TN, chlorophyll *a*, PC, and time.

2.3.2 Average Yearly Zooplankton Abundances

Yearly averages of Cladocera, Copepoda, and Rotifera were calculated for the full 2000 to 2020 dataset to remove the influence of seasonal changes of zooplankton within individual years, differing species resolutions, differing numbers of samples taken or analysed per year, and differences between analysts. The 21 resulting yearly averages were visualized.

2.3.3 Zooplankton Abundances: January 2000-December 2020

January 2000 – January 2009 and February 2009 – December 2020 sample datasets were combined, with simplifications to the latter dataset, to create a single dataset with consistent taxa resolution. Some taxa recorded to a species level in the February 2009 – December 2020 samples were reduced to genera level (where necessary) to match the taxonomic resolution used in the January 2000 – January 2009 dataset. Zooplankton taxa were included in multivariate analyses if they consisted of at least 5% of the community in at least three samples in order to remove the influence of taxa sampled by chance. Three rotifer taxa (*Ascomorpha eucadis, Ascomorpha ovalis* and Bdelloid rotifers) were removed from this dataset due to the lack of records prior to February 2009, despite their frequent presence throughout the 2009-2020 period. These reductions resulted in the dataset used in multivariate analysis of the 21 year dataset consisting of 14 taxa. Data was subsequently treated and analysed in the same manner as the shorter (February 2009 – December 2020) dataset.

Chapter 3

Results

3.1 Lake Taupō temporal dynamics February 2009-December 2020

3.1.1 Environmental Variables

Temperature varied seasonally with yearly maxima and minima typically in late summer and late winter/early spring, respectively (Figure 3.1 a.). The maximum temperature recorded in the study was 22.3 °C in February 2016 (austral summer) and a minimum of 10.4°C was recorded in August 2009 (austral winter). Secchi depth also varied, although the variation was not clearly related to seasonality, despite yearly maxima and minima often being recorded in early autumn and early spring, respectively. A maximum Secchi depth of 24.0 m was recorded in February 2020 (summer), and tied minimum Secchi depths of 9.0 m were recorded in August 2011 (winter) and November 2013 (spring) (Figure 3.1 b.). Chlorophyll *a* collected from the surface water (1-10 m depth) displayed strong seasonal variations, with general annual maxima and minima in winter and summer, respectively, opposite to temperature. The highest concentration of 3.76 mg m^{-3} was recorded in September 2014 (spring), closely followed by a measurement of 3.68 mg m^{-3} taken in August 2017 (late winter). The minimum chlorophyll *a* measurement of 0.29 mg m^{-3} was measured in January 2018 (summer), although similar levels were measured 5 times throughout the period of 2009-2020 in the summers of 2009, 2013, 2016, and twice in 2019 (Figure 3.1 c.). The total nitrogen maxima of 210.9 mg m^{-3} was measured in March 2014 (autumn), and the minimum value of 50.1 mg m^{-3} was measured in October 2018 (spring) (Figure 3.1 d.). The total phosphorus maximum of 11.7 mg m^{-3} was measured in April

2013 (autumn) and the minimum of 2.6 mg m^{-3} was measured in December 2011 (summer) (Figure 3.1 e.). The particulate carbon maximum of 850.5 mg m^{-3} was measured in February 2018 (summer) and the minimum of 86.5 mg m^{-3} was measured in March 2016 (autumn) (Figure 3.1 f.). The Trophic level Index (TLI) was calculated from the available data and displayed a maximum of 2.9 in September 2013 (spring) indicating an oligotrophic lake state and a minimum of 1.5 in February 2020 (summer) indicating a microtrophic lake state; TLI increased towards the middle of the sampling and decreased towards the end (Figure 3.1 g.). Linear regressions were carried out on all environmental variables, and none displayed strong linear trends (all R^2 values less than 0.07).

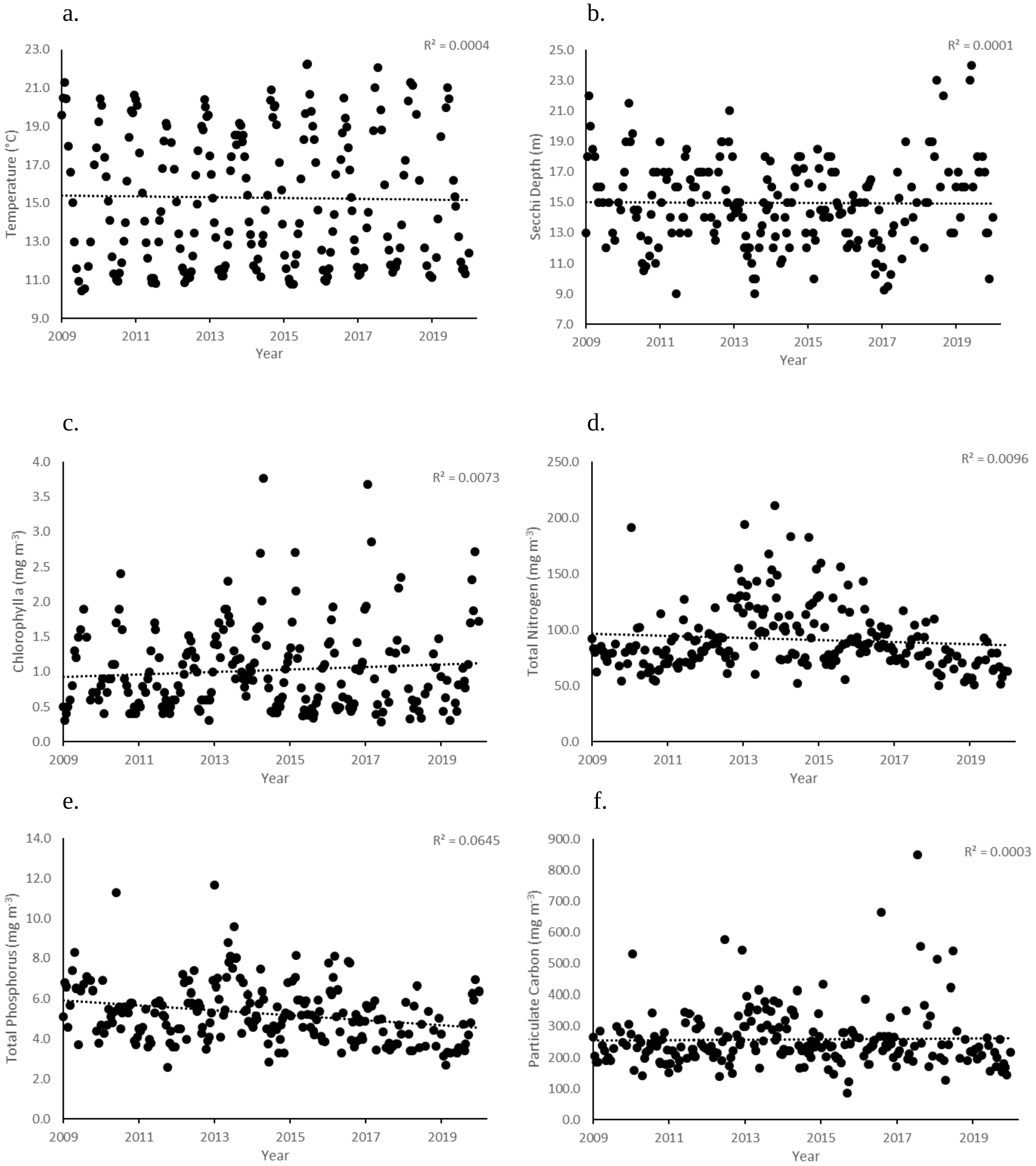

Figure 3.1: a.-f. Two to three weekly measurements of a. Temperature (°C), b. Secchi depth (m), c. Chlorophyll *a* (mg m^{-3}), d. Total Nitrogen (mg m^{-3}), e. Total Phosphorus (mg m^{-3}), and d. Particulate carbon (mg m^{-3}) from Lake Taupō Site A over the period 2 January 2009-6 October 2020.

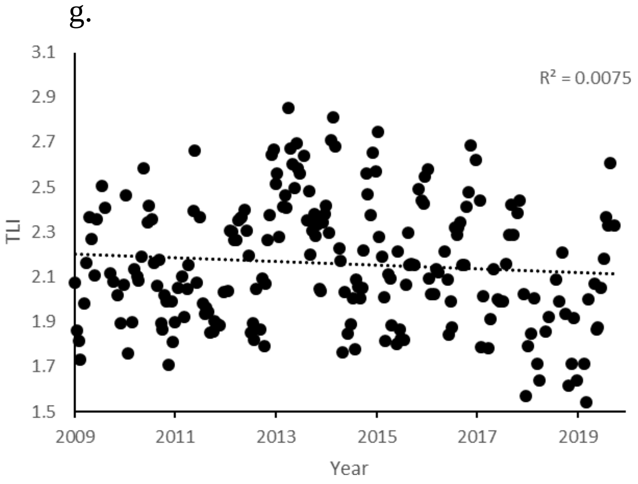

Figure 3.1: g. Two to three weekly calculations of g. Trophic Level Index (TLI) from Lake Taupō Site A over the period 2 January 2009-6 October 2020.

3.1.2 Zooplankton species temporal variation February 2009-December 2020

In total 31 zooplankton taxa were found from the period of 2009-2020 (Table 3.1) in the 128 samples analysed. Of these, the taxon with the greatest richness (22 taxa) and numerical dominance was the rotifers (approximately 48.5% of individuals counted). Only one copepod was identified to the species level (*Boeckella propinqua*), though two other taxa were observed (an immature harpacticoid and immature cyclopoid individuals; Table 3.1). Copepods in general were the second most numerically dominant group, comprising approximately 29.7% of the counted individuals. Cladocera was the least numerically dominant group, comprising 21.8% of the counted individuals, with five taxa identified (Table 3.1).

Table 3.1: Zooplankton taxa found in Lake Taupō February 2009-December 2020. Asterisks denote taxa that comprising at least 5% of the total abundances in 3 or more samples.

Rotifers

*Ascomorpha ecaudis**

*Ascomorpha ovalis**

Aspelta angusta

*Asplanchna priodonta**

*Collotheca pelagica**

*Conochiloides dossuarius**

*Conochiloides natans**

Filinia pejleri

Hexarthra mira

*Keratella cochlearis**

Keratella quadrata

Lecane lunaris

Lecane sp.

Monommata sp.

*Polyarthra dolichoptera**

*Pompholyx complanata**

*Synchaeta longipes**

*Synchaeta oblonga**

*Trichocerca porcellus**

Trichocerca similis

Trichocerca stylata

Bdelloid spp.*

Copepods

*Boeckella propinqua**

Copepod nauplii

Unidentified Cyclopoid sp.

Unidentified Harpacticoid sp.

Cladocerans

*Bosmina meridionalis**

Ceriodaphnia cf. *dubia*

Chydorus sp.

Daphnia thomsoni

*Daphnia galeata**

Seventeen taxa comprised at least 5% of the total abundances in at least three samples and were included in statistical analyses (Table 3.1). Of the taxa retained in the analysis, 12 displayed distinct maxima between 2013 and 2016, and most typically during 2014 (Figure 3.2: a-d, g, i-k, n- q). These taxa either displayed a single sample with an exceedingly high number of individuals when compared to all or most other samples (Figure 3.2: e.g., *Daphnia galeata*, *Boeckella propinqua*, *Conochiloides dossuarius*) or display earlier samples increasing to the maximum value and the subsequent samples decreasing from the maximum value (Figure 3.2: e.g. *Bosmina meridionalis, Asplanchna priodonta*, *Collotheca pelagica*). The remaining five taxa displayed maximum counts before (Figure 3.2: e.g., *Ascomorpha ecaudis*, *Ascomorpha ovalis*, Bdelloid rotifer**s**) or after (Figure 3.2: *Keratella cochlearis*) the period of 2013-2016. Many of these taxa were common prior to this period (Figure 3.2: e.g., Bdelloid rotifers, *Ascomorpha ecaudis*, *Polyarthra dolichoptera*) but were less common during and/or after the period. One taxon, *Keratella cochlearis*, (Figure 3.2: l) was not commonly found in high numbers prior to 2013-2016, but was more abundant after this period.

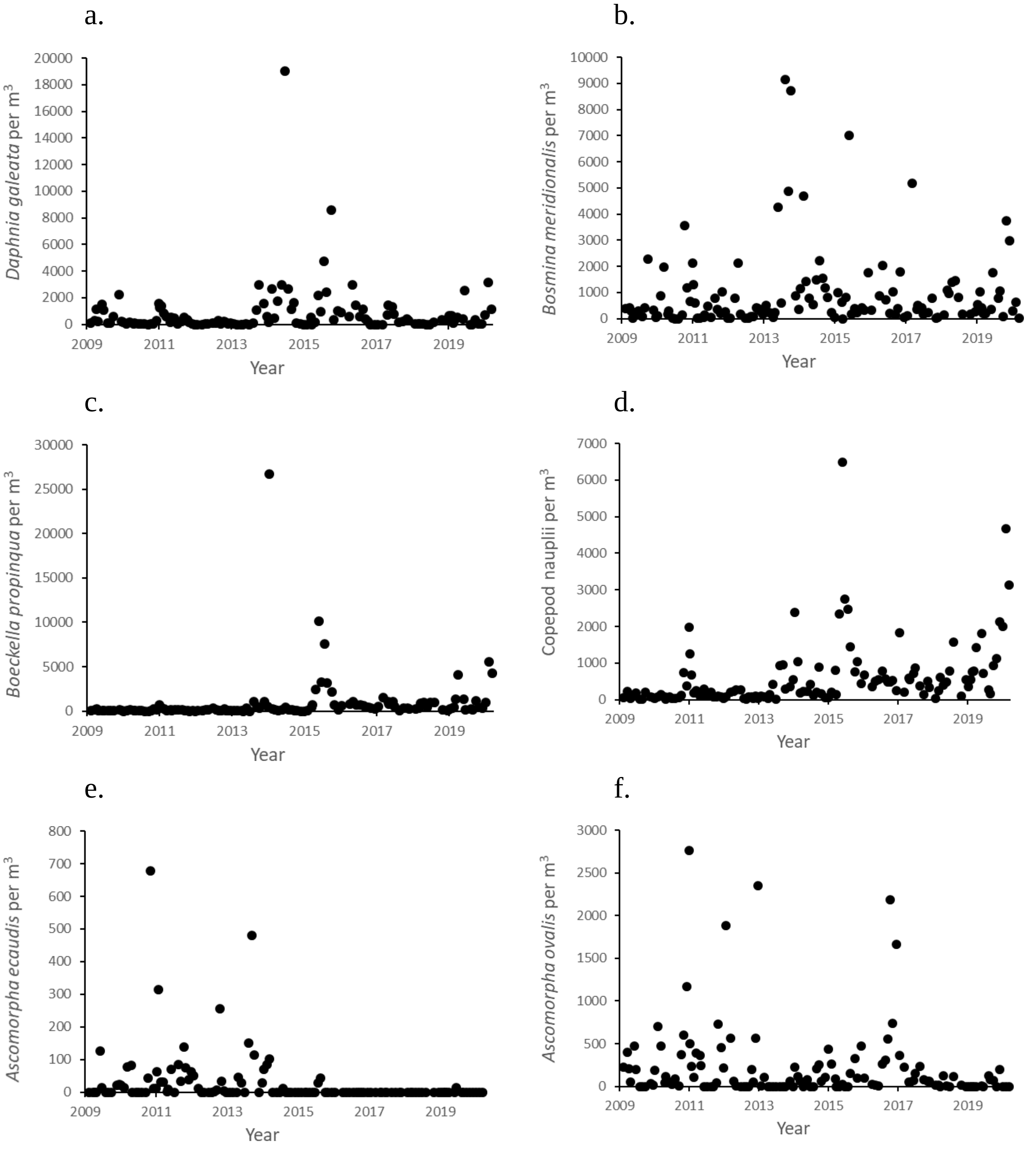

Figure 3.2: a.-f. Time series abundance 2 Febuary 2009 – 16 December 2020 in Lake Taupō of a. *Daphnia galeata*, b. *Bosmina meridionalis*, c. *Boeckella propinqua*, d. Copepod nauplii, e. *Ascomorpha ecaudis*, f. *Ascomorpha ovalis.*

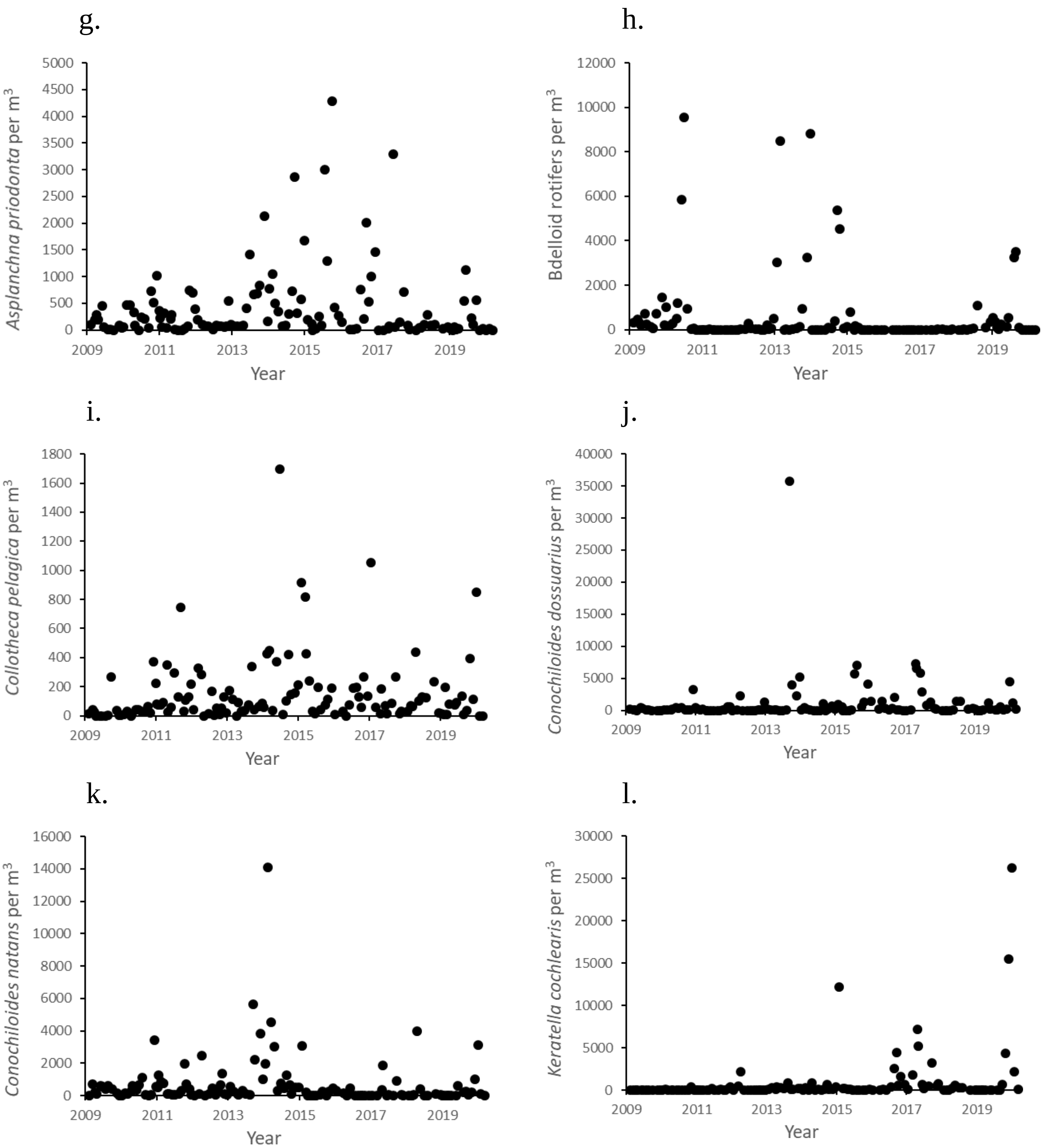

Figure 3.2: g-l. Time series abundance 2 Febuary 2009 – 16 December 2020 in Lake Taupō of g. *Asplanchna priodonta*, h. Bdelloid rotifers, i. *Collotheca pelagica*, j. *Conochiloides dossuarius*, k. *Conochiloides natans*, l. *Keratella cochlearis*.

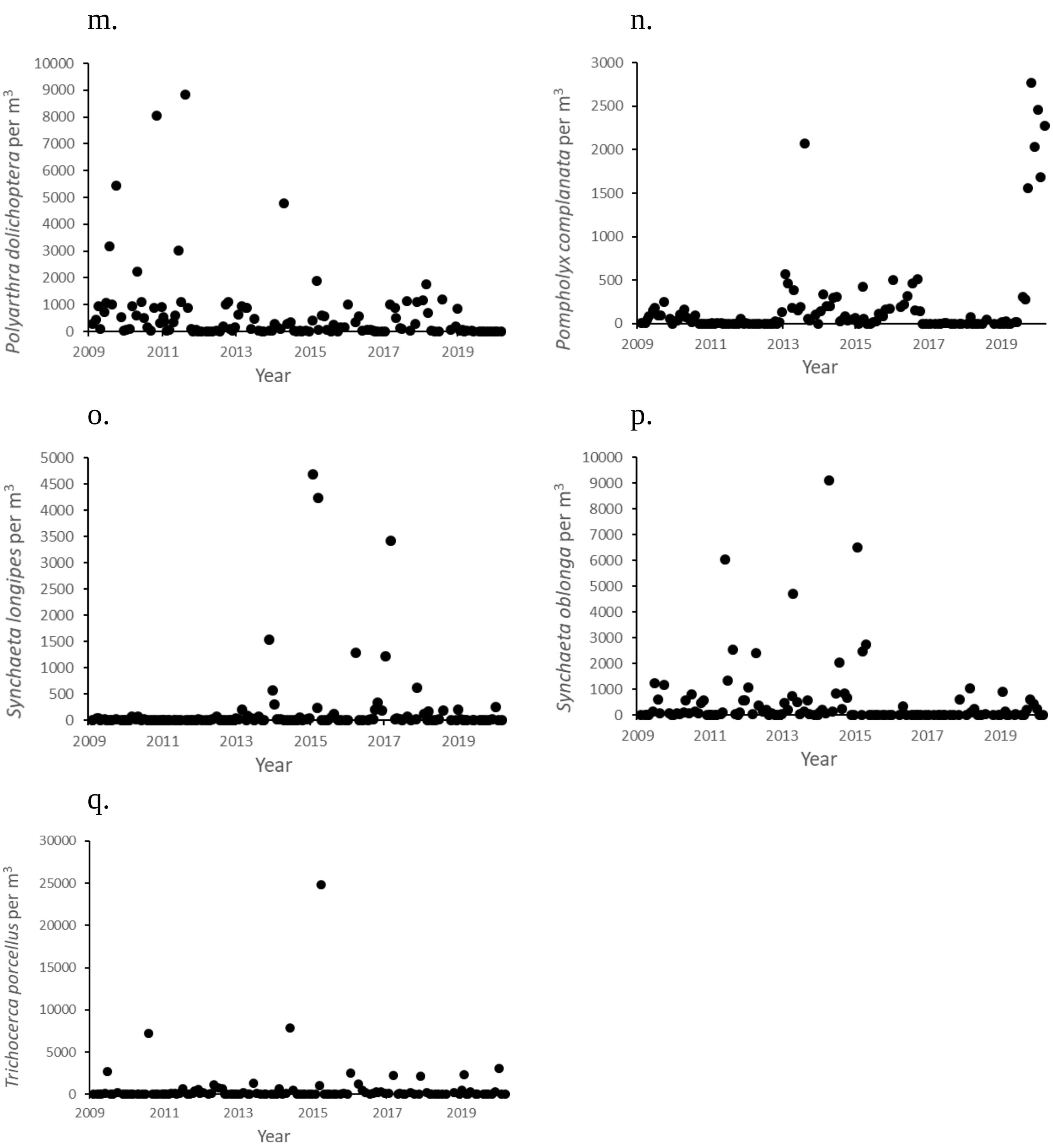

Figure 3.2: m-q. Time series abundance 2 Febuary 2009 – 16 December 2020 in Lake Taupō of m. *Polyarthra dolichoptera*, n. *Pompholyx complanata*, o. *Synchaeta longipes*, p. *Synchaeta oblonga*, q. *Trichocerca porcellus*.

3.1.3 Zooplankton community dynamics

A non-metric multidimensional scaling (nMDS) ordination was used to examine patterns in the zooplankton community composition through time, across year groups of three years. A temporal gradient was evident; 2009-2011 samples were distributed generally on the left of the ordination, 2012-2014 samples distributed closer to the centre and left, 2018-2020 samples distributed to the centre and right, and 2015-2017 samples distributed to the furthest right but generally overlapping the 2018-2020 samples. This indicates that samples primarily moved progressively from the left to the right with increasing time, with a shift back towards the left of the ordination for the 2018-2020 samples. All year groups display a significant portion of overlap (Figure 3.3). The stress value, signalling the fit of the ordination to the Bray-Curtis similarity matrix, was 0.26. This indicates that the plot is a potentially useful visualisation of the data, but the fine structure should not be relied upon (Clarke and Gorley, 2015). A one-way ANOSIM indicated the difference in zooplankton community composition between the three year groups was significant (p = 0.014).

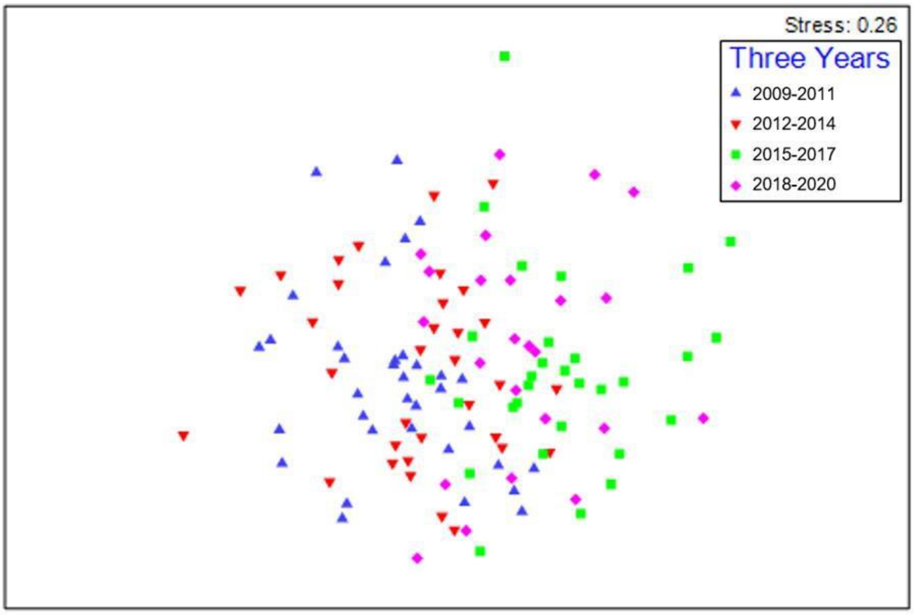

Figure 3.3: Non-metric multidimensional scaling ordination (nMDS) using log(x+1) transformed data showing changes in zooplankton community composition over the time period 2009-2020.

ANOSIM indicated that there were significant differences between the three year groups (Global R statistic = 0.179, P = 0.014) and pairwise tests indicated significant differences between all combinations of three year groups (Table 3.2), showing that each group was significantly different to each other group.

Table 3.2 ANOSIM pairwise results (R values) between three year groups. 1 = 2009-2011, 2 = 2012-2014, 3 = 2015-2017, 4 = 2018-2020. Bold values indicate a significant results (p < 5%)

R Statistic			
	2012-2014	2015-2017	2018-2020
2009-2011	**0.096**	**0.334**	**0.280**
2012-2014		**0.222**	**0.207**
2015-2017			**0.119**

Ordination biplots linking zooplankton composition and environmental variables were generated based on Redundancy Analysis (RDA) (Figure 3.4). The samples are plotted on the ordinations and environmental variables and species data are represented by the arrows. Directionality of the arrows indicate the association of samples with observed environmental variables and species, while the arrow length indicates the strength of the association. Axes 1 and 2 were used in the biplots and their respective eigenvalues (0.10 and 0.07) together accounted for 17% of the variation seen in zooplankton community composition. The distribution of samples is similar to that observed in the nMDS. Samples from the beginning of the study were predominantly positively associated with Axis 1 and negatively associated with Axis 2, placing them in the lower right hand corner of the plot (see open vs closed symbols in the lower panel; Figure 3.4). Samples taken later in the study (increasing time) gradually shift towards the top left hand of the ordination. Samples from warmer seasons (summer and autumn) were more negatively associated with Axis 1 and primarily negatively associated Axis 2 (although not all negatively associated with either axis), placing them generally closer towards the bottom left hand corner of the plot. Samples from colder seasons (winter and spring) were more generally positively associated with Axis 1 and Axis 2, placing them closer to the top right hand corner of the plot (see open vs closed symbols in the upper panel).

The rotifers *Ascomorpha ovalis*, *Asplanchna priodonta*, and *Conochiloides dossuarius*, and the cladoceran *Daphnia galeata* all had strong to moderate negative associations with Axis 1 and Axis 2, indicating a strong association with warmer water temperatures (≥15°C). Conversely, the rotifers *Synchaeta oblonga* and *Trichocerca porcellus* displayed strong to moderate positive associations with Axis 1 and Axis 2, indicating an association with cooler water temperatures (<15°C). The rotifers *Synchaeta longipes*, *Pompholyx complanata*, *Keratella cochlearis*, and *Collotheca pelagica*, the copepods *Boeckella propinqua*, copepod nauplii, and the cladoceran *Bosmina meridionalis* are all strongly to moderately associated with Axis 1, and strongly to moderately positively associated with Axis 2, indicating an association with samples taken closer to the end of the study. The rotifers *Ascomorpha ecaudis*, Bdelloid rotifers, *Conochiloides natans* and *Polyarthra dolichoptera* all displayed strong to moderate positive associations with Axis 1, but strong to moderate negative associations with Axis 2, indicating an association with samples taken closer to the beginning of the study.

Forward selection and Monte Carlo permutation tests were performed in order to investigate the environmental variables that explained patterns in the zooplankton community composition (Table 3.3). Lambda – 1 indicates the amount of variation in zooplankton community composition that each single environmental variable explains independently of all other environmental variables. Once included in the RDA model, Lambda A indicates the amount of additional variation explained by adding that variable, with the most important variable being added first, and subsequent variables being added in order based on their importance (ter Braak and Smilauer, 1998). Time (indicated as Days since 1900) and temperature both explained the greatest amounts of variation in the zooplankton community composition (8%), both when considered individually (Lambda -1 = 0.08 for both), and when included in the model together (Lambda-A = 0.08 for both, $p = 0.002$ for both), indicating that these variables were acting independently of each other in influencing community composition. Chlorophyll *a* explained an additional 4% of the variation seen in zooplankton community composition when added to the model (Lambda –A = 0.04, $p = 0.002$) and Secchi depth explained an additional 1% of the variation when added to the model (Lambda – A = 0.01, $p = 0.04$). After the inclusion of these variables, the addition of no further environmental variables resulted in any further significant increase in the amount of variation explained (Table 3.3).

Days since 1900 was negatively associated with Axis 1, and positively associated with Axis 2, pointing it towards the top left hand of the ordination. Temperature and Secchi depth are moderately negatively associated with both Axis 1 and Axis 2, pointing them towards the bottom left of the ordination. Chlorophyll *a* is positively associated with both Axis 1 and 2, and is nearly directly opposite to temperature and Secchi depth, pointing it to the top right of the ordination. This indicates that there may be similarities in the variation being explained by temperature, chlorophyll *a* and Secchi depth, which appear to be associated with seasonality (as indicated by shading in the upper biplot). When temperature is high, chlorophyll *a* is low, indicating algal concentrations are highest in low temperatures (i.e., winter). Days since 1900 is perpendicular to all other variables, indicating that none of the measured environmental variables correlated with time.

The strong to moderate negative associations of *Ascomorpha ecaudis*, Bdelloid rotifers, *Conochiloides natans* and *Polyarthra dolichoptera* to Days since 1900 indicate their prevalence towards the beginning of the monitoring period (2009-2011), while the strong to moderate positive associations of *Synchaeta longipes*, *Pompholyx complanata*, *Keratella cochlearis*, *Boeckella propinqua*, copepod nauplii, *Collotheca pelagica*, and *Bosmina meridionalis* to Days since 1900 indicate their increasing abundance in the Lake Taupō zooplankton community as the monitoring continued (2018-2020) (indicated by shading of the sample points in the lower biplot).

The remaining environmental variables (TN, PC, and TP) did not explain any significant amount of variation in the zooplankton community composition when added to the model, despite explaining 1-2% of the variation when considered individually (Table 3.3). This is evidenced by their small arrow lengths, or near parallel trajectories with other environmental variables already included in the model (Figure 3.4).

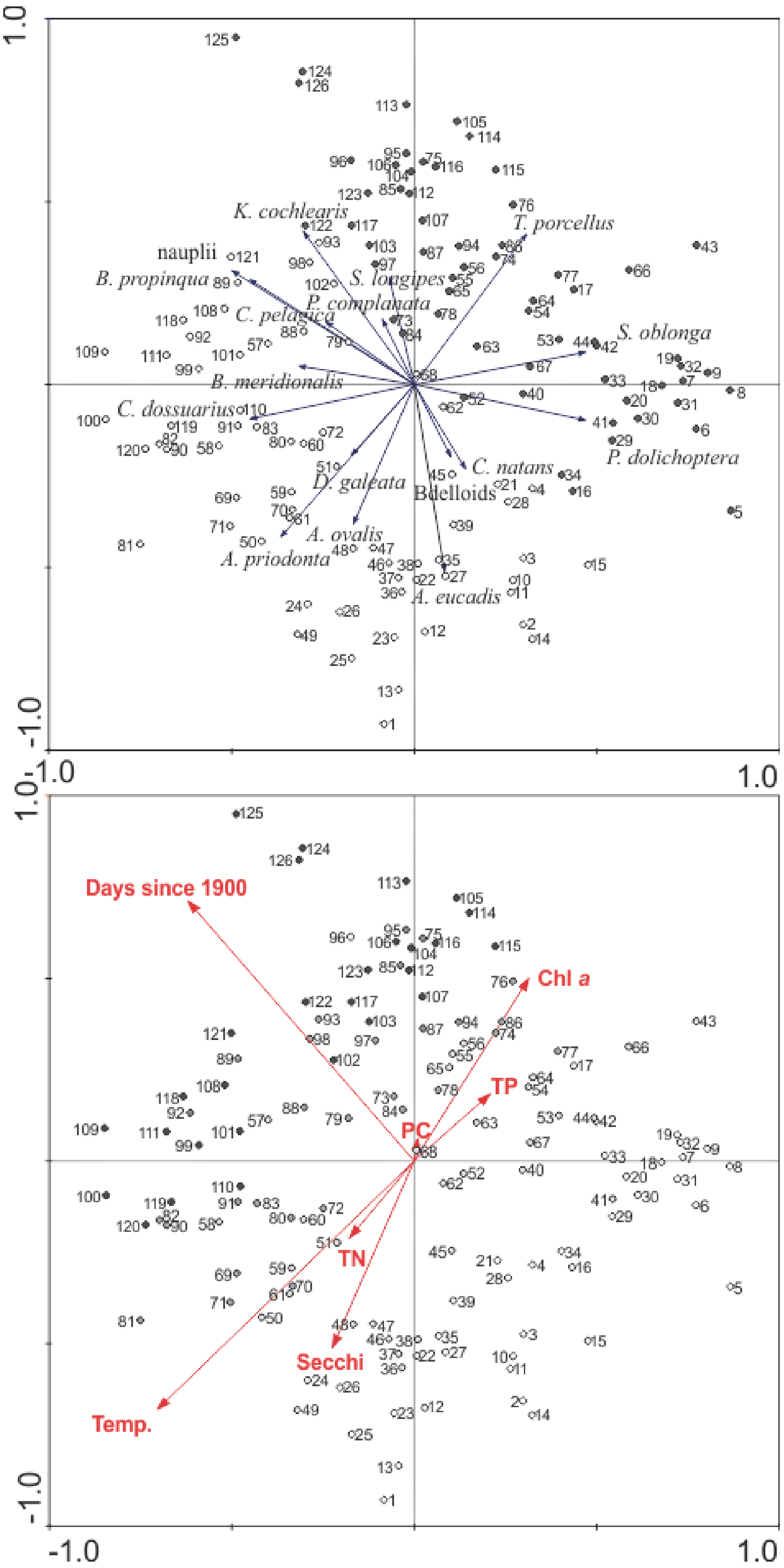

Figure 3.4 : Ordination biplots generated from RDA of zooplankton community composition relative to environmental variables. Numbers indicate sample number, shading represents in upper plot water temperature (<15°C = black, ≥15°C = white) and in lower plot gradient from white to black = temporal gradient from 2009 to 2020 split into 4 shades.

Table 3.3: Forward selection and Monte Carlo permutation test results from RDA of zooplankton communities. Environmental variables are listed based on inclusion in the model (Lambda – A). Bold p values indicate a significant result ($p < 0.05$).

Variable	Lambda1	LambdaA	P
Temperature	0.08	0.08	**0.002**
Days Since 1900	0.08	0.08	**0.002**
Chlorophyll a	0.05	0.04	**0.002**
Secchi depth	0.03	0.01	**0.040**
TN	0.02	0.01	0.180
PC	0.01	0.01	0.196
TP	0.02	0.00	0.258

3.2 Lake Taupō temporal dynamics January 2000 - December 2020

3.2.1 Zooplankton community Yearly averages

Due to differences in the taxonomic resolution of species identification, and number of samples analysed per year, between the 2000-2008 and 2009-2020 sample analysis, yearly average values were calculated for Cladocerans, Copepods, and Rotifers across the whole time period and assessed. The maximum yearly average Cladoceran abundances was recorded in 2001, but it peaked again to almost as high in 2014, with smaller peaks in between 2001 – 2014 and after 2014 (Figure 3.5). The yearly average Copepod maximum abundance was also recorded in 2001, followed by a drastic reduction resulting in a minimum yearly average in 2010, and a subsequent partial recovery in 2014. The yearly average Rotifera values displayed fairly regular variation of highs and lows over the time period with a large peak in 2014. Overall, the general trend appears to be relatively high yearly average values near the beginning of the monitoring period, followed by a general decline in the middle period up until 2014 when all three groups (Cladocerans, Copepods and Rotifers) experience higher average yearly values, and followed by a subsequent drop post 2014 (Figure 3.5).

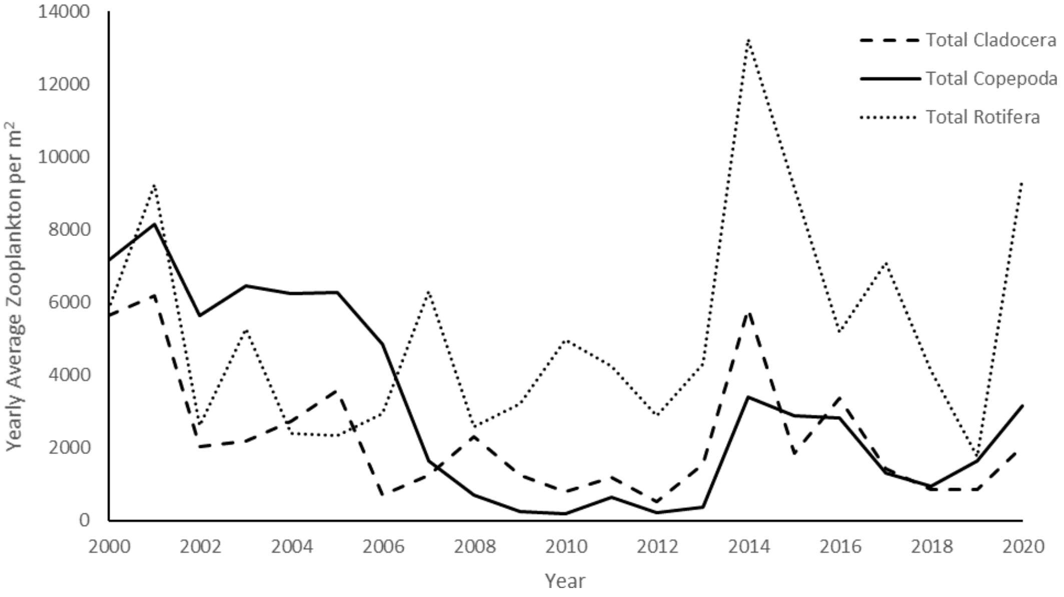

Figure 3.5: Joint time series showing the yearly average abundances of Cladocera, Copepoda and Rotifera over time, between 2000 and 2020.

3.2.2 Zooplankton species temporal variation January 2000 – December 2020

Zooplankton taxa were simplified to 28 taxa from the period of 2000-2020 for the purpose of matching the earliest datasets resolution (Table 3.4). Of these, the taxon with the greatest richness (18 taxa) and numerical dominance was the rotifers (approximately 52.5% of individuals counted). Copepods were the second most numerically dominant group comprising of approximately 26.4% of the counted individuals. Cladocera was the least numerically dominant group, comprising of 21.1% of the counted individuals, with five species and one genus being identified (Table 3.4). This list was further reduced to 14 taxa to be included in multivariate analysis.

Table 3.4: Zooplankton taxa found in Lake Taupō between January 2000-December 2020. Those with asterisks denote taxa that consist at least 5% of any 3 samples, while double asterisks indicate taxa that were removed from analysis despite meeting the first criteria due to their being unrecorded prior to 2009.

Rotifers	
*Ascomorpha ecaudis***	*Keratella* spp.
*Ascomorpha ovalis***	*Lecane lunaris*
Aspelta angusta	*Lecanidae* spp.
Asplanchna spp.*	*Monommata* spp.
Collotheca spp.*	*Polyarthra* spp.*
Conochiloides spp.*	*Pompholyx* spp.*
Filinia spp.	*Synchaeta* spp.*
Hexarthra mira	*Trichocerca* spp.*
*Keratella cochlearis**	Bdelloid rotifers**
Copepods	
*Boeckella propinqua**	Cyclopoid sp.
Copepod nauplii*	Harpacticoid sp.
Cladocerans	
Alona cf. *quadrata*	*Chydorus* sp.
*Bosmina meridionalis**	*Daphnia thomsoni**
Ceriodaphnia cf. *dubia**	*Daphnia galeata**

Seventeen taxa comprised at least 5% of the total abundances in at least three samples and of these, three rotifer taxa (*Ascomorpha ecaudis*, *Ascomorpha ovalis*, and Bdelloid rotifers) were removed due to their absence in analyses prior to February 2009, leaving fourteen taxa to be included in the analyses (Table 3.4). Of the taxa retained in the analysis, five taxa displayed maximums towards the beginning of the monitoring period (Figure 3.6: e.g., *Bosmina meridionalis*, *Ceriodaphnia dubia*, *Daphnia thomsoni*). Six taxa displayed maximum values towards the end of the monitoring period and between 2014 and 2016 (Figure 3.6: e.g., *Daphnia galeata*, *Boeckella propinqua*, *Asplanchna* spp.), two taxa displayed maximum values towards the end of the monitoring period after 2016 (Figure 3.6: *Keratella cochlearis* and *Pompholyx* spp.) and the remaining taxon displayed a maximum value in the middle of the monitoring period (Figure 3.6: *Polyarthra* spp.). Of the taxa displaying early maximum values *Bosmina meridionalis*, copepod nauplii, and *Synchaeta* spp. remain relatively common throughout the monitoring period, while the other two species (*Daphnia thomsoni* and *Ceriodaphnia dubia*) become increasingly rare (Figure 3.6). Taxa displaying later maximum values are generally common throughout the majority of the monitoring period (e.g., *Asplanchna* spp., *Conochiloides* spp., *Polyarthra* spp.) with the exceptions of *Keratella cochlearis* and *Collotheca* spp., which are rarely found until the middle and later years of the study (Figure 3.6)

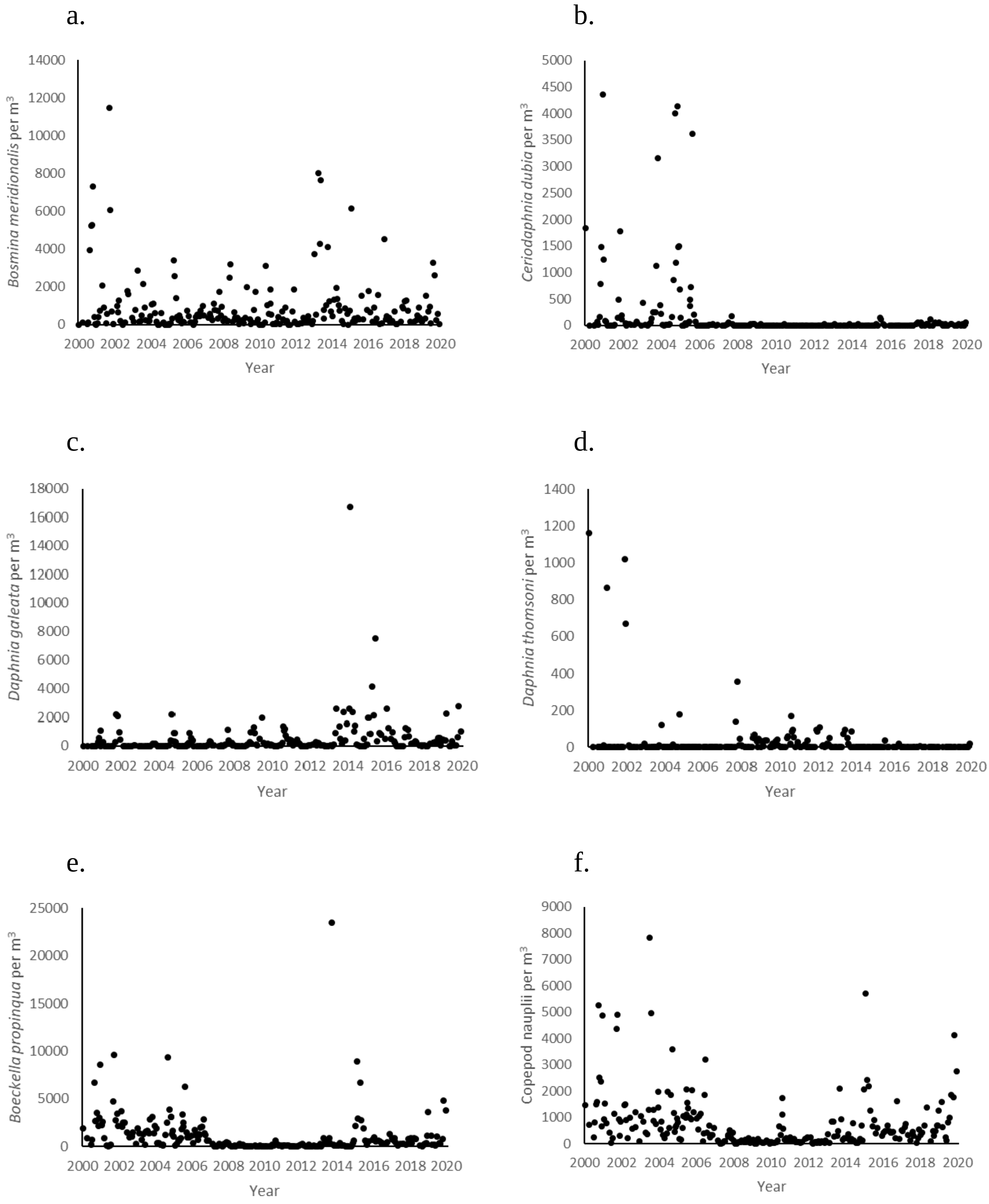

Figure 3.6: a.-f. Time series abundance 18 January 2000 – 16 December 2020 from Lake Taupō of a. *Bosmina meridionalis*, b. *Ceriodaphnia dubia*, c. *Daphnia galeata*, d. *Daphnia thomsoni*, e. *Boeckella propinqua*, and f. Copepod nauplii.

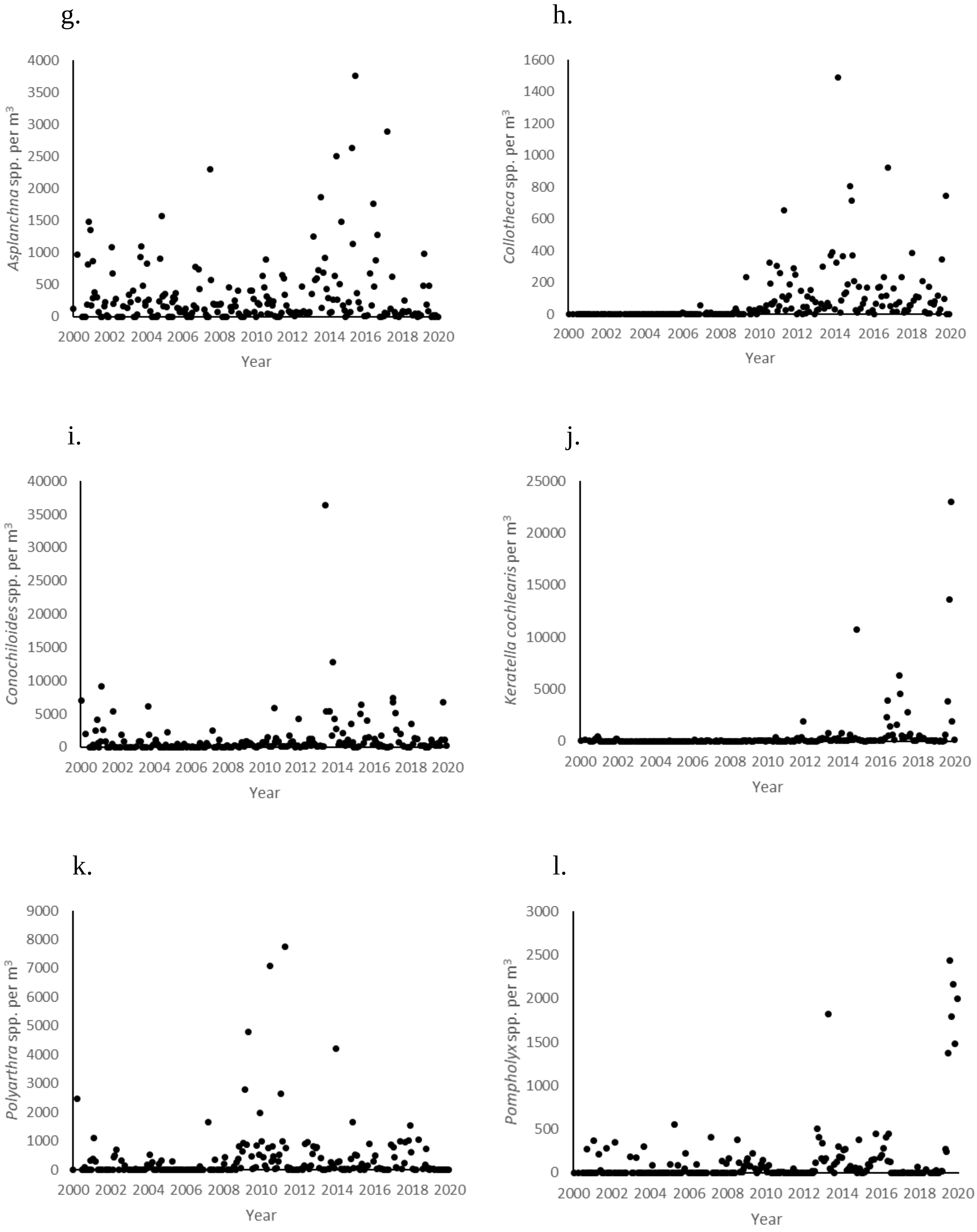

Figure 3.6: g.-l. Time series abundance 18 January 2000 – 16 December 2020 from Lake Taupō of g. *Asplanchna* spp., h. *Collotheca* spp., i. *Conochiloides* spp., j. *Keratella cochlearis*, k. *Polyarthra* spp., and l. *Pompholyx* spp.

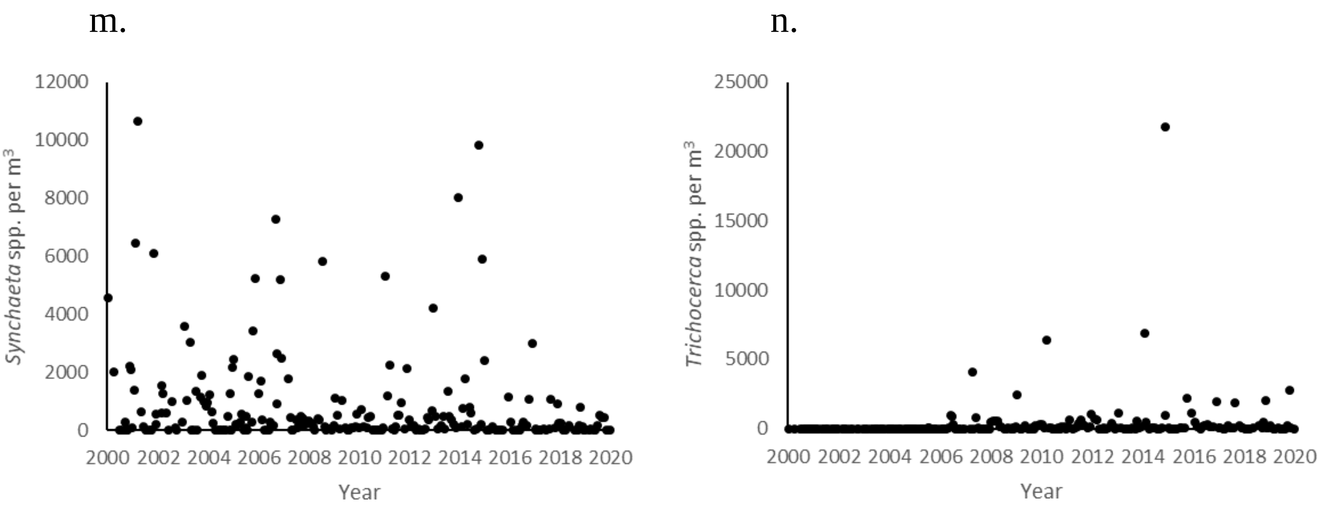

Figure 3.6 : m.-n. Time series abundance 18 January 2000 – 16 December 2020 from Lake Taupō of m. *Synchaeta* spp. and n. *Trichocerca* spp.

3.2.3 Zooplankton community dynamics

A non-metric multidimensional scaling (nMDS) ordination was used to examine patterns in the zooplankton community composition across year groups of three years. There appears to be a temporal gradient in the three yearly groups, with 2000-2002 and 2003-2005 distributed to the top left of the ordination, 2006-2008 to the bottom left, while 2009-2011 and 2012-2014 were distributed to the far right. 2015-2017 and 2018-2020 samples were distributed closer to the centre. Although there is a high level of overlap, there appears to be a temporal trend of the samples moving from the left to the right of the ordination from 2000 until 2015-2017, while the 2018-2020 samples shifted back in the left direction to the centre of the plot, indicating the community was becoming similar to earlier assemblages (Figure 3.7). The stress value, signalling the fit of the ordination to the Bray-Curtis similarity matrix, was 0.21. This indicates that the plot is a potentially useful visualisation of the data, but the fine structure should not be relied upon (Clarke and Gorley, 2015).

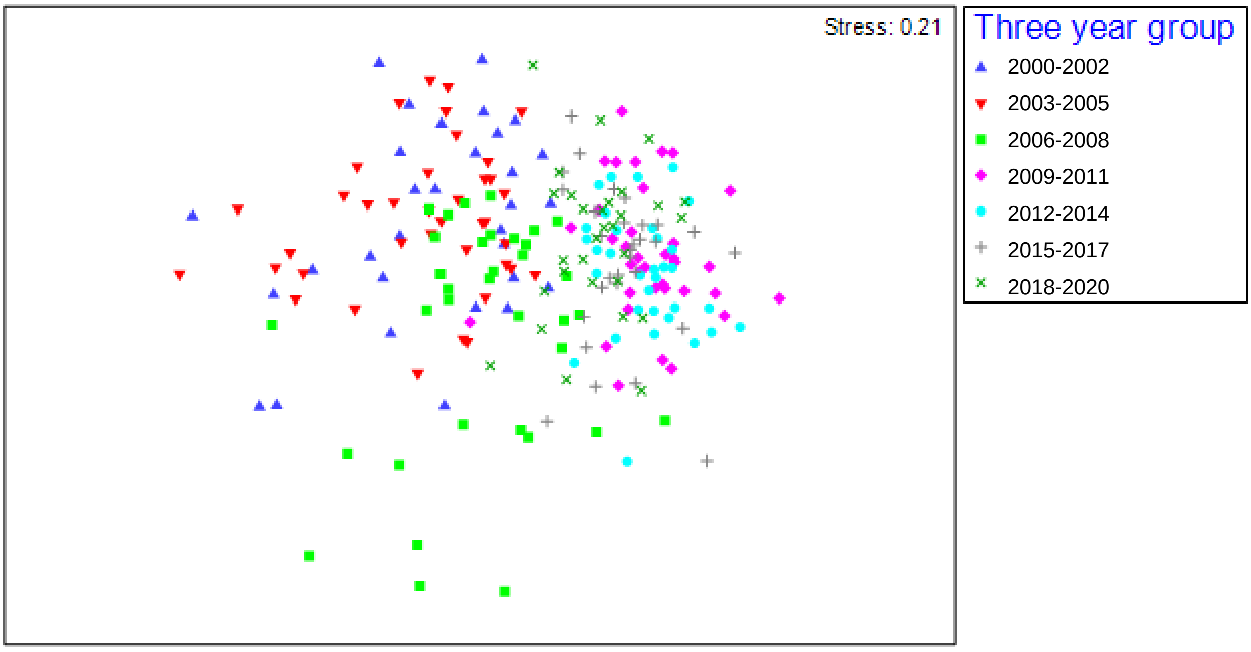

Figure 3.7: Non-metric multidimensional scaling ordination (nMDS) using log(x+1) transformed data showing zooplankton community composition over the time period from 2000-2020 grouped into three year groups.

A one-way ANOSIM indicated the difference in zooplankton community composition between the three year groups was significant (R = 0.353, p = 0.001). Pairwise tests indicated each of the 3 yearly groups significantly differ from one another, except 2000-2002 from 2003-2005, and 2015-2017 from 2018-2020, the first two and last two groups in the study (Table 3.5).

Table 3.5 ANOSIM pairwise results (R values) between three year groups. Bold values indicate a significant differences between groups (p < 5%)

R Statistic						
	2003-2005	2006-2008	2009-2011	2012-2014	2015-2017	2018-2020
2000-2002	0.036	**0.124**	**0.634**	**0.591**	**0.498**	**0.426**
2003-2005		**0.151**	**0.720**	**0.699**	**0.631**	**0.551**
2006-2008			**0.460**	**0.397**	**0.373**	**0.326**
2009-2011				**0.098**	**0.275**	**0.306**
2012-2014					**0.085**	**0.183**
2015-2017						0.034

Ordination biplots linking zooplankton composition and environmental variables were generated based on Redundancy Analysis (RDA) (Figure 3.8). Axes 1 and 2 were used in the biplots and their respective eigenvalues (0.16 and 0.06) together accounted for 22% of the variation seen in zooplankton community composition. Samples from the beginning of the study were predominantly negatively associated with Axis 1 while samples taken later in the study were positively associated with Axis 1, creating a temporal gradient from the left to right along the axis (Figure 3.8). Samples from warmer seasons (summer and autumn) were more negatively associated with Axis 2 and samples from colder seasons (winter and spring) were more generally positively associated with Axis 2, placing samples generally in a gradient from top to bottom with increasing temperature (Figure 3.8).

The rotifers *Trichocerca* spp., *Polyarthra* spp., *Pompholyx* spp., and *Keratella cochlearis* all had strong to moderate positive associations with Axis 1 and Axis 2, indicating a strong association with samples taken towards the end of the sample period and cooler water temperatures (<15 ° C). The rotifers *Conochiloides* spp., *Collotheca* spp., and *Asplanchna* spp., and cladocerans *Bosmina meridionalis,* and *Daphnia galeata* all displayed strong to moderate positive associations with Axis 1, but strong to moderate negative associations with Axis 2, indicating an association with samples taken towards the end of the sample period and warmer water temperatures (≥15 °C). The copepods *Boeckella propinqua*, nauplii, rotifer *Synchaeta* spp., and cladocerans *Daphnia thomsoni,* and *Ceriodaphnia dubia* displayed strong to moderate negative associations with Axis 1 and Axis 2, indicating an association with samples taken towards the beginning of the sample period and warmer water temperatures (≥15°C).

Time explained the greatest amount of variation in the zooplankton community composition (15%), both when considered individually (Lambda-1 = 0.15), and when included in the model (Lambda-A = 0.15, p = 0.002). Temperature explained an additional 6% of the variation seen in zooplankton community composition when added to the model (Lambda –A = 0.06, p = 0.002). Particulate carbon (PC) and chlorophyll *a* each explained an additional 1% of the variation seen in the zooplankton community composition when added to the model (Lambda-A = 0.01, p = 0.02). After the inclusion of these variables, the addition of any further environmental variables did not result in significant increases in the amount of variation explained (Table 3.6).

Days since 1900 and PC are both strongly positively associated with Axis 1, and very moderately negatively and positively associated with Axis 2, respectively. Temperature was strongly negatively associated with Axis 2, and only slightly positively associated with Axis 1, while chlorophyll *a* is strongly positively associated with Axis 2 and only slightly positively associated with Axis 1, almost directly opposite to temperature. When temperature is high, chlorophyll *a* is low, indicating that algal presence is higher during times of lower temperature (winter), and lower during times of higher temperature (summer).

The strong to moderate negative associations of *Synchaeta* spp., *Boeckella propinqua,* copepod nauplii, *Ceriodaphnia dubia,* and *Daphnia thomsoni* to Days since 1900 indicate their prevalence towards the beginning of the monitoring period (2000-2002), while the strong to moderate positive associations of *Trichocerca* spp., *Polyarthra* spp., *Pompholyx* spp., *Keratella cochlearis*, *Collotheca* spp., *Conochiloides* spp., *Bosmina meridionalis*, *Asplanchna* spp., and *Daphnia galeata* to Days since 1900 indicate their prevalence towards the end of the monitoring period (2018-2020) (indicated by shading of the sample points in the lower biplot).

The remaining environmental variables (TN, Secchi depth, and TP) did not significantly explain any of the variation in the zooplankton community composition when added to the model, despite explaining 1-4% of the variation when considered individually (Table 3.6). This is evidenced by their small arrow lengths, or near parallel trajectories with other environmental variables already included in the model (Figure 3.8).

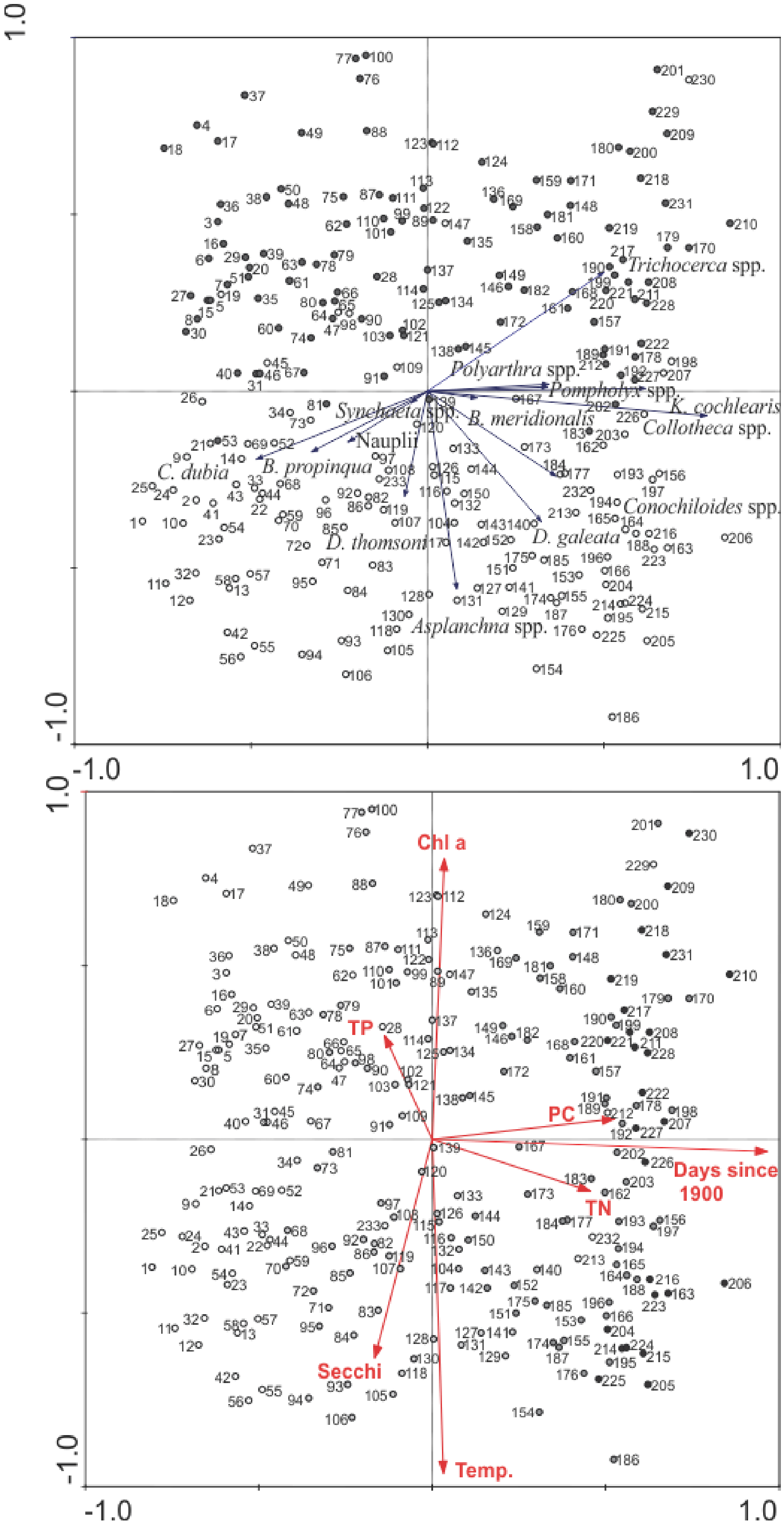

Figure 3.8: Ordination biplots generated from RDA of zooplankton community composition relative to environmental variables. Numbers indicate sample number, shading represents in upper plot water temperature (<15°C = black, ⩾15° C = white) and in lower plot gradient from white to black = temporal gradient from 2000 to 2020 split into 4 shades.

Table 3.6: Forward selection and Monte Carlo permutation test results from RDA of zooplankton communities. Environmental variables are listed based on inclusion in the model (Lambda-A). Bold p values indicate a significant result ($p < 0.05$).

Variable	Lambda-1	Lambda-A	P
Days Since 1900	0.15	0.15	**0.002**
Temperature	0.05	0.06	**0.002**
PC	0.05	0.01	**0.002**
Chlorophyll *a*	0.04	0.01	**0.002**
TN	0.04	0.01	0.056
Secchi depth	0.03	0.00	0.124
TP	0.01	0.01	0.600

Chapter 4

Discussion

4.1 Variation in Zooplankton community composition

The zooplankton community composition of Lake Taupō changed throughout the study, with different groups of taxa becoming more or less prevalent at different times. No significant long-term linear trends in environmental variables were observed, indicating that the changes observed in the zooplankton community were primarily influenced by variables not measured. Lake Taupō is still considered an oligotrophic lake and has not suffered from a significant decline in water quality over the period studied (Figure 3.1 g). The zooplankton species present throughout the study generally reflect this; for example, the rotifers *Conochiloides dossuarius*, *Synchaeta longipies* and *Polyarthra dolichoptera* were all considered to be indicators of lower trophic states in New Zealand lakes by Duggan *et al*. (2001). Time and temperature were the environmental factors most strongly associated with the changes in the community composition observed in the 2009-2020 dataset. Much of the measured variation explained by temperature is a result of seasonal succession, which is common in zooplankton communities worldwide (García *et al*., 2009; Okogwu, 2010; Rautio *et al*., 2011). De Senerpont Domis *et al*. (2013) highlighted that there can be vast amounts of variation in zooplankton communities naturally among seasons. There was no significant long-term trend in change of lake temperature, and thus the variation in the zooplankton community explained by temperature in this study is less useful in describing shifts of the zooplankton community in the long-term.

4.1.1 Comparison of community composition with previous studies

The rotifer species found throughout the current study were largely different those found in the mid-1970s by Forsyth and McCallum (1980), the previous Lake Taupō study that utilised the greatest taxonomic resolution, although all of the genera were common between studies. For example, *Polyarthra vulgaris*, *Conochiloides coenobasis* and *Synchaeta pectinata* were reported by Forsyth and McCallum (1980), wheras *Polyarthra dolichoptera*, *Conochiloides dossurarius* and *Synchaeta longipies* were common in the current study. The rotifers analysed to species level by Forsyth and McCallum (1980) from three deep water sites display similar trends as found in the current study, with species present primarily indicative of lower TLI values, with some indicative of higher (as indicated by Duggan *et al*., 2001;e.g., *Polyarthra vulgaris*, *Conochiloides coenobasis* and *Asplanchna brightwelli*). The differences between the specific species documented between the studies may be partially due to different analysts and the quality of identification guides available to investigators in the late-1970s or may reflect true changes within the community. Copepod and cladoceran species were common between the two studies, with the exception of *Daphnia* species, which were entirely absent in Forsyth and McCallum (1980).

Jolly (1965), James (1986) and Bayly (1989) primarily recorded only the presence on dominant crustacean zooplankton species (*Boeckella propinqua, Ceriodaphnia dubia*, *Bosmina meridionalis*), with little or no emphasis on rotifers. Jolly (1965), using coarser mesh than the present study and sampling near to shore, also recorded *Daphnia carinata* (now known as *D. thomsoni*), and Bayly (1989), with a similarly coarse mesh, additionally to dominant crustaceans, recorded the large rotifer *Asplanchna priodonta*. James (1986) used an equivalent mesh size to the present study but did not record the presence of any rotifer taxa. In contrast, the findings of Duggan *et al*. (2002) focused on the rotifer assemblage of Lake Taupō and did not record crustacean presence; they highlighted a similar rotifer community as observed in this study, with species indicative of both low and high TLI (Duggan *et al*., 2002), despite its oligotrophic state.

The presence of either *Daphnia* species in Lake Taupō has not been documented by the previous offshore studies on this lake (Forsyth and McCallum, 1980; James, 1987), nor had either *Daphnia* species been recorded in the water leaving Lake Taupō by the Waikato River, or in samples taken in the northern end of the lake (Tapuaeharuru Bay) in 1987 (Bayly, 1989). *Daphnia thomsoni* (as *D. carinata*) was recorded by Jolly (1965); however, the sites sampled in this study were nearshore (Whakaipo Bay, on the northern shore, and Waihaha Bay, on the western shore). *Daphnia galeata* had not been recorded from Lake Taupō prior to the current dataset, with its first appearance being in September 2000, followed by its frequent presence throughout my study. Duggan *et al*. (2006) similarly did not find any *D. galeata* (misidentified as *D. dentifera*) in Lake Taupō in 1997-1998, during their investigation of invasive zooplankton in New Zealand North Island ponds and lakes (Duggan *et al*., 2006). The absence of *Daphnia galeata* from previous studies indicates their establishment within the deep part of the lake likely occurred not long before the beginning of my study (James, 1987; Duggan *et al*., 2006).

4.2 Long-term community composition changes

Time was inferred to be one of the most important factors associated with changes in zooplankton community composition. Although there were not major changes in the species present throughout the study, the nMDS and ANOSIM analyses indicated that there were compositional differences between the three year groupings of the data, both for the reduced 2009-2020 and the full 2000-2020 datasets. This indicates observed differences were likely due primarily to increases and declines in the abundances of various species. The RDA ordinations for the respective datasets also indicated that there were changes in community composition through time, with different species prevalent at the beginning and end of the monitoring periods.

Towards the beginning of the 2009-2020 dataset, taxa such as the rotifers *Polyarthra dolichoptera*, *Ascomorpha eucadis* and *Conochiloides natans* were more prevalent, whereas towards the end of the study the rotifer *Keratella cochlearis*, copepod *Boeckella propinqua* and copepod nauplii were more prevalent. In a study conducted by Duggan *et al*. (2001) analysing the use of rotifers as indicators of lake water quality, they found that species such as *P. dolichoptera* are more commonly found in lakes with a lower TLI, while species such as *K. cochlearis* were more commonly found in lakes with a higher TLI. The species indicative of a lower TLI at the beginning of the study compared to the species indicative of a higher TLI towards the end of the study may suggest a decline in water quality (i.e., an increase in TLI). However, this was not supported by the measured environmental variables (e.g., changes in nutrient concentrations and chlorophyll *a*). Added to this, throughout the study, both towards the beginning and end, species dominated that are indicative of a low TLI (e.g., *A. ovalis*), indicating that factors other than the water quality likely contributed to the observed changes.

The longer 2000-2020 dataset, using a lower taxonomic resolution, appears to highlight some contradictory results in the RDA ordination when compared to those indicated by the shorter dataset in regards to the species prevalent at the beginning and end of the monitoring period. While the 2009-2020 dataset highlights taxa such as *Boeckella propinqua*, copepod nauplii and *Synchaeta longipies* as being prevalent towards the end of the monitoring period, the 2000-2020 dataset highlights these taxa (or related ones; i.e., *Synchaeta* spp.) as being prevalent towards the beginning of the monitoring. Similarly, the 2009-2020 dataset highlights *Conochiloides natans* and *Polyarthra dolichoptera* as being prevalent towards the beginning of the monitoring period, while the 2000-2020 dataset highlights *Conochiloides* spp. and *Polyarthra* spp. as being prevalent towards the end of the monitoring period. This may be due, in part, to the differing taxonomic resolutions utilised as, for example, in the longer 2000-2020 dataset *Synchaeta* spp. and *Conochiloides* spp. both consist of multiple species that are individually recognized in the shorter 2009-2020 dataset. Further, the nMDS plot for the longer dataset indicated that zooplankton community composition shifted through time, with the community composition distinctly separating for the three year groups; this shift was initially from left to right on the ordination from 2000 to roughly 2011, and then the change reversed direction, with samples moving back towards the left. This indicates that the community composition at the end of the study more closely related to that observed earlier in the monitoring period (Figure 3.7). Although this is simply a visualisation of the data, the ANOSIM further indicated significant differences between all three year groups ($p < 0.001$), apart from the first two which were not significantly different from each other ($p > 0.05$) and last two which also were not significantly different from each other ($p > 0.05$). This indicates that the community composition was changing through time, up until approximately 2012, when it began shifting back to assemblages similar to those of earlier time periods. This could be due to multiple (unmeasured) factors but does help in explaining the somewhat contradictory results of species prevalence indicated by the two RDA ordination plots for the 2000-2020 and 2009-2020 datasets (Figures 3.4 and 3.8). Due to the reduced taxonomic resolution in the full (2000-2020) dataset, the comparison of specific rotifer species throughout the time period is somewhat limited, and reduces their usefulness as bioindicators throughout, as there are certain species of the same genus typically associated with higher and lower TLI respectively (e.g., *Synchaeta oblonga* associates with higher and *S. longipes* with lower TLI).

Both RDA ordinations for the 2000-2020 and 2009-2020 datasets indicated *Synchaeta* species (*Synchaeta* spp. and *S. oblonga*) as being prevalent towards the beginning of the monitoring periods respectively, while *Keratella cochlearis*, *Pompholyx* (spp. and *P. complanata*), *Collotheca* (spp. and *C. pelagica*) and *Bosmina meridionalis* were prevalent towards the end of both monitoring periods (Figures 3.4 and 3.8).

However, the overall trend of the longer but less fine resolution 2000-2020 dataset appears to highlight differing taxa as being prevalent towards the beginning (e.g., the cladoceran *C. dubia*, and the copepod *B. propinqua*) and end (e.g., the rotifers *Collotheca* spp. and *Pompholyx* spp.) of the study period. This potentially may be indicating a shift from larger bodied cladocerans and copepods to smaller bodied rotifers, typically caused by top-down pressure (Hambright, 2008; Schabetsberger *et al*., 2008). There are, however, also cladocerans indicated as being prevalent towards the end of the dataset (e.g., *B. meridionalis*, *D. galeata*), indicating the community changes observed are likely not due entirely to top-down effects.

4.2.1 Invasions

Cladocerans changed throughout the study period with an increase in prevalence of the non-native cladoceran *Daphnia galeata* and native cladoceran *Bosmina meridionalis*, and a decrease in the prevalence of the native cladocerans *Daphnia thomsoni* and *Ceriodaphnia dubia*. Although part of this decline may be due to different analysts examining the samples, it also highlights the potential role of competition for resources by these taxa. Havens *et al*. (2000) highlighted that invading species are often opportunists and may over time outcompete native competition by having less specializations to specific niches, thus allowing them to exploit more diverse resources and form a resilient population (Havens *et al*., 2000).

Duggan *et al*. (2020) indicated in their long-term study of zooplankton community compositions across 39 lakes in the Waikato, New Zealand, that zooplankton invasions were one of the primary influences responsible for the observed shifts in zooplankton community compositions. Lake Waihi in particular, which was invaded by the Australian copepod *Boeckella symmetrica* as well as *D. galeata*, exhibited a higher amount of variation in the zooplankton community composition than other lakes due to the dynamics of these invaders (Duggan *et al*., 2020). Similarly, an invasion of the North American calanoid copepod *Skistodiaptomus pallidus* into Lake Kereta, New Zealand, showed related impacts on the zooplankton community, with a significant change to the community composition post-introduction of *S. pallidus* (Duggan *et al*., 2014). The decrease in abundance of the native calanoid copepod *Calamoecia lucasi*, in particular, was attributed to interspecific competition with *S. pallidus*, while increases in the abundances of the cladocerans *Daphnia galeata* and *Bosmina meridionalis* were thought to be related to the simultaneous grass carp (*Ctenopharyngodon idella*) release within the lake, which likely decreased macrophyte biomass, and acted as the vehicle for *S. pallidus* invasion (Duggan *et al*., 2014).

Similar to the present study, Mihuc *et al*. (2012) found that changes observed in the long-term zooplankton community composition (outside of seasonal succession) were not explained by changes in the physical and chemical variables of Lake Champlain, USA. They concluded that the influences of invading species were the cause of observed shifts in the zooplankton community (Mihuc *et al*., 2012). However, in the case of Lake Champlain, the invaders were not zooplankton species, but zebra mussels (*Dreissena polymorpha*) and alewife (*Alosa pseudoharengus*), which exerted predation pressure on the zooplankton community, influencing the changes in community composition and highlighting the influence of top-down pressure on zooplankton community dynamics (Mihuc *et al*., 2012).

4.2.2 Top-down effects

Schabetsberger *et al*. (2008) demonstrated in Lake Seehornsee, Austria, the influence that predators can exert on the zooplankton community by analysing long-term zooplankton community composition changes, both before, during, and after the introduction of juvenile Alpine charr (*Salvelinus umbla*). The fish introduction greatly reduced the abundance of larger zooplankton within the lake, particularly large cladocerans. Newly appearing smaller bodied cladocerans and rotifers were able to eventually dominate the lake due to the advantage of their smaller body size, making them less desirable prey (Schabetsberger *et al*., 2008). Similarly, fish predation may be partially responsible for the observed changes in the native and non-native *Daphnia* species abundances in Lake Taupō, as well as the increased prevalence of smaller bodied rotifers. The native *Daphnia* species (*D. thomsoni*) is able to reach a much larger size than the non-natives (adult female *D. thomsoni* commonly reaching body lengths of 3.5 mm, excluding spine; Reynolds and Geddes, 1984), while *D. galeata* reaches a maximum body length of 2.8 mm (Kipp *et al*., 2021), making *D. thomsoni* an easier target for fish predation. Smelt (*Retropinna retropinna*) populations in Lake Taupō and other New Zealand lakes have been found to be primarily zooplanktivorous at the larval, juvenile, and young adult (1+ year) life stages (Stephens, 1984; Donald, 1990; Booker, 2000). Stephens (1984) found the diet of smelt in Lake Taupō predominantly comprised of the cladocerans *Bosmina meridionalis* and *C. dubia*, which were the dominant large bodied cladocerans at that time. It is to be noted that these results were taken from stomach content dissection, and many rotifer species may have been rapidly digested due to their soft bodies or may have been too small to be observed, thus their importance as a food source, and the impacts of predation on their segment of the community may be underestimated (Stephens, 1984).

Lake Taupō also hosts wild populations of both rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), which were introduced into the lake near the beginning of the 20th century (Rosenau, 1991). Both species are known to be zooplanktivorous, particularly in their juvenile stages (Jeppesen *et al*., 1997; Budy *et al*., 2005). The effects of zooplanktivory by trout in Lake Taupō is as of yet essentially unstudied. Nevertheless, the importance of fish predation on crustacean zooplankton has been shown on multiple occasions to influence zooplankton community composition (Hambright, 2008; Schabetsberger *et al*., 2008; Mihuc *et al*., 2012), and may have had an influence on the communities throughout this study. The Tongariro Trout Centre, located near Lake Taupō, has historically released large numbers of young trout into the lake. However, there have been no significant inputs to the lake to supplement the wild populations since the 1960s, as there is sufficient natural recruitment to maintain stocks (McDowall, 2018; DOC, 2021).

Some fish populations, such as adult trout, may also indirectly impact zooplankton communities by removing other predators such as insects and smaller zooplanktivorous fish (Lui *et al*., 2009), and through nutrient excretion impacting primary production (Vanni *et al*., 2006), making the interactions between predators and prey even more confounded. As the prevalence of piscivorous fish (e.g., adult trout) increases, the abundance of zooplanktivorous fish (e.g., smelt (*Retropinna retropinna*) and koaro (*Galaxias brevipinnis*)) can decrease, leading to an increase in the abundance of zooplankton and subsequent increase in phytoplankton. The same principle applies conversely where a decrease in the abundance of piscivorous fish leads to an increase in the abundance of zooplanktivorous fish, and subsequent increase in the abundance or shift of the community composition of zooplankton (Duggan *et al*., 2015).

4.2.3 Bottom-up effects

Matsuzaki *et al*. (2018) highlighted that zooplankton and primary production are also bidirectionally coupled, but that the magnitudes of these couplings may be species specific. For this reason, although bottom-up controls were measured through environmental variables and chlorophyll *a* as a proxy for phytoplankton abundance, it is possible that the changes in the zooplankton community have been influenced by changes in the algal community composition through time, which has not been assessed in this study. Although earlier studies have assessed the phytoplankton (Vincent, 1983; James, 1987), periphyton (Hawes and Smith, 1994) and protozoan (James *et al*., 1995) assemblages of Lake Taupō, all pre-date the current study and thus offer little insight to recent changes.

Shifts in zooplankton community composition are potentially due to changes in the food available for their consumption. The increase in *K. cochlearis* towards the end of the study (according to both datasets) highlights the potential of increases in non-algal food such as bacteria, zoospores, yeast, and detritus (all unmeasured in this study), as this species is able to utilize many different food sources and continue to grow and reproduce (Frenken *et al*., 2018). However, there is no corresponding decrease in the chlorophyll *a* to indicate a decrease in the availability of algal food, and thus a shift towards a community less reliant on algae. Kirk (1991) highlighted that *K. cochlearis'* (amongst other rotifer species) ingestion rate is not negatively impacted by the presence of suspended clay particles. Particulate carbon (PC) is near parallel with time in the 2000-2020 RDA ordination biplot (Figure 3.8), but also only explains a very small portion (1%) of the variation observed in the zooplankton community composition. The increase of PC temporally may indicate higher levels of sediment or detritus within the water column (Fowler *et al*., 1991), giving *K. cochlearis* an advantage over other zooplankton taxa; however, there is no corresponding decrease in the Secchi transparency to indicate an increase of suspended sediment or detrital particles within the lake, while the lake depth and the distance of the sampling site from the lake edge also makes this factor unlikely.

4.2.4 Summary of long-term changes

The changes that have been observed within the Lake Taupō zooplankton community composition over the long-term are indicative of a combination of influences. The increase in the prevalence of smaller bodied rotifer species as well as the decline in numbers of the largest cladoceran species are similar to the changes observed by Hambright (2008), Schabetsberger *et al*. (2008) and Mihuc *et al.* (2012) implying top-down control within the system is most likely. Besides predation, the shift from larger bodied to smaller bodied zooplankton has been found to be an indicator of eutrophication (Balakrishna *et al*., 2013; Haberman and Haldna, 2014), which is unsupported by the trends in nutrients and chlorophyll *a* in this study. The interactions between native and non-native zooplankton species have also been shown to be a contributing factor in long-term changes within the zooplankton community composition (Duggan *et al*., 2020), particularly when paired with added top-down pressures on the system, as exemplified by Schabetsberger *et al*. (2008).

4.3 Seasonal changes

Temperature was a significant factor in explaining changes in the zooplankton community composition in both the longer 2000-2020 and shorter 2009-2020 datasets. However, much of the measured variation explained by temperature was a result of seasonal succession, which is common in zooplankton communities worldwide (García *et al*., 2009; Okogwu, 2010; Rautio *et al*., 2011; De Senerpont Domis *et al*., 2013). There was no significant long-term trend in change of lake temperature, and thus the variation in the zooplankton community explained by temperature in this study is less useful in describing shifts of the zooplankton community in the long-term.

In both RDA ordinations (Figures 3.4 and 3.8), temperature and chlorophyll *a* were plotted almost directly opposite to one another, indicating that at times of high temperature (i.e., summer), chlorophyll *a* was low, while at times of low temperature (i.e., winter), chlorophyll *a* was high. Chlorophyll *a* is often used to infer phytoplankton biomass and is primarily related to seasonality. Thus, these results are consistent with prior patterns of phytoplankton seasonality within the lake, showing maximum phytoplankton biomass in winter (Vincent, 1983). Over the warmer months Lake Taupō is thermally stratified, locking the nutrients required for phytoplankton growth below the thermocline. As mixing occurs in cooler months, the lake becomes more well mixed, resulting in more available nutrients in the photic zone and higher rates of algal growth. The minimum temperature observed over the monitoring period was 10.4°C, which is due to New Zealand's relatively mild oceanic climate despite its latitude (Crawford, 2005). As there is no significant long-term change in chlorophyll *a*, the variation explained is primarily seasonal variation in algal biomass, and chlorophyll *a* explained only 1% ($p = 0.002$) of additional variation in zooplankton community composition after time and temperature were added to the model.

The ordination biplots both indicated that *Trichocerca* (spp. and *porcellus*) was prevalent at times of low temperature and high chlorophyll *a* (i.e., winter), while *Asplanchna* (spp. and *priodonta*), *Daphnia galeata*, and *Conochiloides* (spp. and *dossuarius*) were prevalent at times of high temperature and low chlorophyll *a* (i.e., summer) (Figures 3.4 and 3.8). The cladoceran *Daphnia thomsoni* in the longer dataset was also primarily found in warmer water temperatures (Figure 3.8). The rotifers *Ascomorpha ovalis* and *Ascomorpha eucadis* in the shorter dataset were prevalent at times of high temperature, and the rotifers *Synchaeta oblonga* and

Polyarthra dolichoptera in the shorter dataset were prevalent at times of low temperature (Figure 3.4).

Trichocerca spp., *Synchaeta* spp., and *Polyarthra* spp. have been found to commonly prefer low temperatures, while *Conochiloides* spp., *Ascomorpha* spp., *Asplanchna* spp., and *Daphnia* spp. have been commonly found to prefer higher temperatures (Evans *et al*., 1980; Shiel *et al*., 1982; Sanoamuang, 1992). Forsyth and McCallum (1980) found the rotifers *Polyarthra vulgaris* and *Synchaeta pectinata* to be common during times of cooler water temperatures, particularly autumn and winter, similar to the trends found for the *Polyarthra* and *Synchaeta* species identified in this study. They also found that *Conochiloides coenobasis* was common throughout the year, but particularly in the summer months, again consistent with the findings for the *Conochiloides* species identified in my study (Forsyth and McCallum, 1980). However, they found *Asplanchna brightwelli* throughout the year, but with the highest abundances in spring, contrary to the findings for *Asplanchna* (spp. and *priodonta*) in my study, which were found in highest abundances typically in late summer or early autumn and displayed generally low abundances in spring (Figures 3.2 g and 3.6 g) (Forsyth and McCallum, 1980). Bayly (1989) also recorded high abundances of *A. priodonta* between March and April 1987 (i.e., autumn) and recorded no instances of A. *brightwelli.* These contradictions in seasonal abundance indicate that there may have been a true change in the *Asplanchna* species present in Lake Taupō from *A. brightwelli* to *A. priodonta.*

4.4 Study limitations and implications for future research

As is the case for most scientific research, the findings of this study were limited by the variables measured. As little of the long-term temporal variation was explained by environmental variables for either dataset, it is assumed that the variation observed in the zooplankton community composition over time may be influenced by variables that were not measured. Fish predation has been shown to have the ability to exert large amounts of pressure on zooplankton populations, particularly of larger species, and help in shaping the zooplankton community and its general characteristics. A lack of fish abundance data limits the potential to indicate top-down effects on the zooplankton community composition. From 2018, algal and bacterial species composition have been monitored along with the environmental variables by NIWA. Continuation of this monitoring should be carried out in order to assess if there are changes in the phytoplankton and bacterial community assemblages that may impact the zooplankton community composition.

Further study limitations are the differences in species resolution between the 2000-2009 and 2009-2020 datasets, as well as the inherent errors associated with having different analysts analysing zooplankton samples. Although both methods are acceptable, the reduction from species to genus level of the rotifers when combining the datasets results in a loss of valuable information. It has been argued that the loss of taxonomic resolution is less important for assessing disturbances, but higher resolution is necessary when assessing biodiversity (Nielsen *et al.*, 1998); nevertheless, higher taxonomic resolution may be preferable when differences in composition are subtle, as they were in this study. Comparing the current study to those performed previously on the lake exhibits similar difficulties. Earlier studies on Lake Taupō were conducted with differing sampling methods, meaning that at best only rough qualitative comparisons are able to be made, and even they may by necessity be restricted to larger bodied zooplankton due to the coarse net mesh size used in historical studies.

My research has identified that there were temporal changes in the zooplankton community composition that were unexplained by the environmental variables measured. As such, it would be beneficial to continue the zooplankton and environmental monitoring in Lake Taupō with the addition of further potential explanatory variables. Monitoring fish abundances, particularly those known to be zooplanktivorous, would be beneficial in further investigations and assessments of bottom-up vs. top-down control on the zooplankton community composition and dynamics within Lake Taupō. Continued monitoring of environmental variables is necessary in order to track any future changes within the lakes tropic state. Due to the discrepancies between the time lags of the groundwater feeds into the lake, there is potential that any past or future changes in nutrient loading within the catchment will have delayed entry into the lake, and the effects of previous land use may be yet to be seen or may have been confounded by other groundwater inputs. Continued monitoring of algal and bacterial communities within the lake is also advised, as these can have significant bottom-up effects on the system and impact the zooplankton community and higher trophic levels.

4.5 Summary

Lake Taupō did not exhibit a significant long-term increase in the trophic state or temperature during the time period observed. The zooplankton community composition, however, did shift temporally, reflecting both long-term and seasonal changes. The community changes highlighted were different for each of the two datasets, likely due to the direction of the community change reversing near 2009, subsequently reverting back to community compositions similar to those observed previously. Decreases in the native large *Daphnia thomsoni* and increased importance of the non-native *Daphnia galeata* lead to the idea that interspecific competition and species-specific predation from higher trophic levels may impact the observed community composition changes. The influence of top-down control on the zooplankton community is discussed. However, there is no available data to support this theory. Reduction in taxonomic resolution for the longer dataset led to an inability to effectively discuss the use of many rotifer species as bioindicators in Lake Taupō for the entire time period. Continued monitoring and the inclusion of fish abundance monitoring is advised to ensure that future changes within the Lake Taupō zooplankton community are identified and can potentially be assessed in relation to top-down control factors.

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