Long-term changes in Zooplankton community composition in North Island lakes:

What are the drivers of change?

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science (Research) in Ecology and Biodiversity

at

The University of Waikato

by

AMBER TAYLOR

2023

Abstract

Zooplankton are an important component of freshwater ecosystems, forming a trophic bridge between primary producers and higher trophic levels. They are highly responsive to changes in their environment and have therefore been recognised as a useful tool for monitoring and assessing aquatic ecosystem health. However, long-term studies of changes in zooplankton communities are rare globally. Long-term studies of zooplankton composition are even more scarce within New Zealand. Past researches on New Zealand zooplankton have primarily focused on the seasonal variation of zooplankton composition, rather than long-term temporal changes, and have been undertaken over time periods of two years or less.

This study utilised zooplankton compositional data from past research papers (1950-1990) conducted within North Island, New Zealand lakes and data from two 2021 sampling events, to investigate long-term temporal zooplankton community composition change. A historical dataset was constructed by conducting a desktop investigation of past studies that included zooplankton species lists. Further, zooplankton samples were collected in 2021 using vertical net hauls from nine lakes within the Bay of Plenty and Waikato regions, using zooplankton nets with three different mesh sizes (37 µm, 75 µm and 100 µm). Species lists from the historical and 2021 samples were statistically analysed to identify changes in zooplankton diversity and community composition through time. The samples from each of the three nets were also analysed independently of the historical samples, to determine the influence of mesh size on zooplankton composition and species richness estimates from semi-quantitative samples.

Three major changes in zooplankton communities were evident over time. Firstly, high frequencies of the Holarctic cladoceran *Daphnia galeata* were found in the samples collected in 2021 yet were absent in samples taken prior to 1990. This result is consistent with the reported invasion of this species into New Zealand lakes since the early 1990s. Secondly, the cyclopoid

copepod *Macrocyclops albidus* was not observed within the 2021 samples yet has been frequently present in species lists from the historical literature. This species has also not been commonly identified in recent research papers. Their low frequencies within the 2021 samples also coincides with increases in the importance of the *D. galeata* and cyclopoid copepod *Mesocyclops australiensis* in the 2021 samples and recent literature relative to historical datasets. Finally, there was an increase in the occurrence of many rotifer taxa within the 2021 samples compared to the historical samples. Interestingly, these taxa were largely deemed as an uncommon constituent of the plankton within New Zealand waters in the 1950s to 1970s. The increased importance of rotifer species within recent samples appeared to be a product of underestimation due to improper mesh selection by past researchers.

Analysis of the semi-quantitative data of the three zooplankton nets with different mesh sizes indicated that zooplankton composition and species richness using the 75 µm net was more representative of that collected by the 35 µm samples than the 100 µm samples. This result indicates that a 75 µm net would be adequate when comparing zooplankton results within a 35 µm net among the studied lakes. Species richness within the two smaller meshed nets were higher than the 100 µm net, indicating a net with mesh size of 100 µm and greater would result in an underestimation of zooplankton community composition and species richness.

Acknowledgements

I would firstly like to say a big thank you to my academic supervisor, Ian Duggan. Thank you for all your help, advice, and patience throughout this process. While balancing everything else you had on your plate, you always made time to sit down and talk through whatever it was I was having issues with. I am very grateful for your support though the stressful times.

Thank you to Katherine Rowe for helping me in the lab and coming out to assist in my sampling. Thank you also to Warrick Powrie for all your help in the field, as well as providing some good advice and great yarns. You both made this experience seem less scary, so thank you!

To Gaby and Kelly, I am so glad we got to go through this together, even though I took a little longer! I'll miss our trips to the vending machine for chips and chocolate, and our coffee dates. Thank you for the advice when needed and the emotional support. I appreciate you girls so much!

An obvious and big thank you to my family. Mum and Dad, thank you for all your support and encouragement throughout this time. I don't think I would have been able to finish this without you both constantly reminding me you believe in me. Thank you to my sister, Brooke, for being my rock through this, and to my brothers, Will and Kane, for constantly reminding me of how poor study has made me, cheers for that. Thank you to my Nana Rosalie and Pop for always having me stay, even on such short notice. And lastly, thank you to all my friends for just being there and making me laugh through this very stressful period. I love you all so much.

Amber <3

Table of Contents

List of Figures

List of Tables

Chapter One: General Introduction

1.1 Importance of long-term monitoring

Communities and populations within any ecosystem are inherently dynamic, cyclically changing and evolving through time in response to natural variation. Increasingly so, anthropogenic-induced disturbances and impacts are becoming more evident within ecosystems globally (Spellerberg, 2005). Long-term monitoring has been repeatedly stressed within ecological literature as an important tool for understanding the dynamics of ecosystems, communities, and populations (Lindenmayer *et al.*, 2012).

Long-term monitoring and research programs have been used to provide reliable information on environmental management issues (Vaughan *et al.*, 2001). Our ability to make informed decisions to protect the environment through policy and ecosystem management implementation is greatly dependent upon a comprehensive understanding of changes in the environment (Jeppesen *et al.*, 2011). Such understanding is gained through long-term monitoring, as many changes in ecosystems are slow, occurring over prolonged periods of time (Likens, 2012). Most changes within ecosystems are thus not detectable over short periods of time and require more extensive time series to detect underlying trends incapable of being detected in short-term studies (Smeltzer *et al.*, 2012). Identifying change within ecosystems is easier when there is a robust baseline for comparison (Sukhotin & Berger, 2013). Thus, some of the fundamental needs for long-term monitoring is to create a baseline of the natural environment's current state, detect temporal changes within ecosystems (Vaughan *et al.*, 2001), and attempt to determine the drivers of change.

Increasingly so, long-term monitoring is an important tool for ecologists and policy developers to separate and identify naturally driven changes from anthropogenically driven changes

(Lindenmayer *et al.*, 2012). Unfortunately, increasing human populations globally are impacting ecosystem dynamics, and are selectively increasing the rate at which changes are occurring within the environment (Sukhotin & Berger, 2013). This separation of anthropogenic and natural variation-driven change poses an evident struggle among ecologists and governmental bodies responsible for management practices, policy development and implementation (Anderson *et al.*, 2005; Hampton *et al.*, 2008). This reiterates the importance of long-term monitoring, for improving the understanding of gradual change within ecological systems, and the ability to provide reliable information for possible environmental management tools. (Havstad & Herrick, 2003; Lindenmayer & Likens, 2009).

1.2 Importance of zooplankton

Globally, freshwater lakes hold high economic and social value. They have been used historically and today for hydropower, irrigation, commercial and recreational fishing, and leisure (Beeton, 2002), and have significant effects upon local and regional climates (Schertzer, 1997). They also host some of the most important freshwater habitats globally (Brönmark & Hansson, 2002). It is thus disconcerting that freshwater lakes have undergone much stress and change due to anthropogenic disturbances (Beeton, 2002; Brönmark & Hansson, 2002), which in response have altered the function and structure of these ecosystems. Changes in water quality can trigger a cascading effect within ecosystems, affecting food webs and biota inhibiting a lake. Particularly important components of biota within freshwater ecosystems are invertebrates. Invertebrate densities within aquatic ecosystems are usually relatively high, (Collier *et al.*, 2016), constitute more than 99% of animal diversity, and are important trophic transferers of energy within aquatic food webs (Lydeard *et al.*, 2004), including zooplankton. Zooplankton are free drifting, or weak swimming, invertebrates found within marine and freshwater ecosystems, and have the ability to inhabit the whole water column (Mackas & Beaugrand, 2010). Zooplankton communities are made up of diverse assemblages, with individual species having their own subset of environmental tolerances.

Zooplankton are highly important components within aquatic ecosystems as they perform a variety of key roles (Brito *et al.*, 2020). They form central links in aquatic food chains, acting as a trophic bridge between primary and tertiary trophic levels (Sterner, 2009). They do this by transferring energy from primary producers, grazing on phytoplankton, and creating important sources of animal tissue for consumption by higher trophic levels in the food web (Gajbhiye, 2002; Havens, 2002; Sterner, 2009). Consequently, a large percentage of aquatic organisms either directly, or indirectly, depend upon zooplankton for their survival (Gajbhiye, 2002).

Bioindicators are an essential tool in ecology as they are able to encapsulate and represent the chemical, physical biological and anthropogenic impact upon an ecosystem (Marbà *et al.*, 2013). Zooplankton are considered useful measures of ecosystem health and trophic state (Jakhar, 2013) due to their integration of physio-chemical and biological conditions through time (Chapman *et al.*, 1975), their rapid response to changes in the environment (e.g top-down, bottom-up processes) (Lampert, 1997; Gutkowska *et al*., 2013; Jakhar, 2013; Brito *et al.*, 2020), and their importance within energy transport through aquatic food webs (Sterner, 2009). Zooplankton also have rapid life cycles compared to other aquatic organisms, ranging anywhere from a handful of months to a year. This makes them particularly useful as bioindicators as there is little carryover of numbers and biomass from year to year (Mackas & Beaugrand, 2010). Rotifers in particular are valued as indicators of trophic state and ecosystem health within freshwater ecology (Gannon & Stemberger, 1978) due to having short life cycles and responding rapidly to changes within their environment (Ejsmont-Karabin, 2012; Gutkowska *et al.,* 2013). For example, Duggan *et al.* (2001) found rotifer distributions to be greatly influenced by lake trophic state after sampling 33 lakes within the North Island of New Zealand. Furthermore, in an international study, the morphology of rotifer trophi was utilised to examine different functional group responses to changes in water quality within 16 reservoirs throughout South Korea (Oh *et al.*, 2017). It was concluded that utilising rotifer trophi may allow for a functional-based approach in determining environmental drivers of community structure.

Zooplankton have high seasonal variability, driven by climate, community composition and lake depth and size (Mengestou & Fernando, 1991). Furthermore, zooplankton have a very patchy spatial distribution throughout the water column (Omori & Hamner, 1982). A study conducted by Hansen & Andersen (1962) investigated the different seasonal patterns in plankton communities within lake ecosystems of different climatic regions: tropics, temperate and polar, and assessed the impacts climate change may pose on these patterns. While there was an observed difference in seasonal patterns within the different climate areas, they acknowledged zooplankton composition also was largely influenced by other biotic factors such as food-web topology, trophic state, and lake catchment area (De Senerpont Domis *et al.*, 2013). Zooplankton are more likely to be aggregated in a few areas than distributed evenly throughout the water column. This patchiness is thought to be driven by four mechanisms: diel vertical migration, predator avoidance, mating, and food availability (Folt & Burns, 1999). As these are natural processes driven by zooplankton's innate behaviour, it is essential that sufficient sampling effort is adopted when zooplankton are being used within research projects (Omori & Hamner, 1982). Using a long-term data set of zooplankton communities is more likely to increase the prospect of understanding environmental drivers of change within zooplankton communities and abundances and reduce the likelihood of identifying changes that may be driven by behaviour.

1.3 Long-term zooplankton monitoring

Global long-term studies of zooplankton communities are rare (Duggan *et al.*, 2020), especially within lake ecosystems (Zhou *et al.*, 2020), and the incorporation of zooplankton within long-term monitoring research have continuously been overlooked (European Commission, 2000). To the surprise of many ecologists, zooplankton were excluded as a biological quality element within the European Union Water Framework Detective (Haberman & Haldna, 2014; European Commission, 2000), which is an important directive within European countries to achieve adequate health of water bodies, despite zooplankton being recognised important components within pelagic food webs (Gajbhiye, 2002; Sterner, 2009). Studies that have been carried out over prolonged periods of time have been able to reveal some interesting observations of temporal changes in zooplankton composition in response to changes in the environment.

A study conducted by McNaught (1975), in the alpine Lake Seehornsee utilised zooplankton community changes over a 13-year period, following the introduction of Alpine charr fish. Within a decade following the fish establishment, zooplankton composition shifted to one dominated by new, small bodied cladoceran and rotifer species, with a decline in calanoid copepods (Schabetsberger *et al.*, 2009). This study offered valuable information on the damage that fish may have upon alpine freshwater ecosystems previously free from tertiary level predators (Schindler & Parker, 2002; Schabetsberger *et al.*, 2009). Keller *et al.* (2002) conducted research using crustacean zooplankton samples from the Sudbury Lakes, Canada, after the implementation of a sulphur emission control programme within areas such as Europe and Canada, to assess biological recovery post the programme implementation. The goal of this initiative was to reduce water acidity and document ecosystem recovery using a long-term dataset of 19 years. Long-term monitoring of the crustacean zooplankton communities found the establishment of new species over time and recognised that the re-establishment of many species were not occurring at expected rates (Keller *et al.*, 2002). This provided insight into recovery rates and mechanisms of zooplankton following a disturbance.

Long-term zooplankton studies, although rare, have also proven to be an integral component of understanding ecosystem dynamics and show the relationship between zooplankton communities and environmental variables. For instance, a long-term study was conducted on the second largest lake within the Baltic countries, Lake Võrtsjärv, Estonia, using a dataset from 1964 to 2000. This study found a close relationship between changes in the lake's trophic state and larger zooplankton abundance, relative to smaller bodied-zooplankton, and an increase in rotifer presence reflective of eutrophication (Haberman & Haldna, 2014). Like this study, Lehtovaara *et al*. (2014) conducted a research project within boreal Lake Valkea-Kotinen, Finland, observing zooplankton dynamics over 20 years (1990 to 2009) in relation to climate changes and acidification recovery. Data analysis revealed water colour, total phosphorus and phytoplankton primary production following acidification recovery had the greatest influence upon zooplankton communities (Lehtovaara *et al.*, 2014). Furthermore, bottom-up regulation attributed to phytoplankton production appeared to greatly exceed top-down control on zooplankton communities as a result of increased organic carbon (Lehtovaara *et al.*, 2014). Within Lake Taihu, China, zooplankton spatio-temporal trends were assessed from 1998-2001 and 2004-2008, in relation to the environmental variables of the lake. An observed temporal change in zooplankton abundance and biomass occurred with the changes in lake trophic state and climate changes. An observed increase in total nitrogen and phosphorus saw an increase in overall zooplankton biomass and abundance, and an increase in small cladoceran species and decrease in rotifer species. Furthermore, zooplankton distributions were found to be largely driven by cyanobacterial blooms that occurred throughout the duration of the study period, favouring small cladoceran and rotifer species (Zhou *et al.*, 2020).

Had each of these studies been conducted over a shorter period of time (i.e 1-2 years), it is unlikely that the reported trends and drivers in zooplankton community composition would have been recognised. Zhou *et al.* (2020) reported that the ability to recognise temporal variability in zooplankton communities is difficult due to the lack of long-term observations globally. Only when there is a dataset collected over a long period of time can more gradual trends be recognised, such as changes in lake trophic state (Haberman & Haldna, 2014), biological recovery following a disturbance (Keller *et al.*, 2002) or climate (Zhou *et al.*, 2020).

1.4 New Zealand Limnology

1.4.1 History of New Zealand Zooplankton Ecology Studies

New Zealand is a geographically young country, with a landscape influenced by natural phenomena such as intense earth movements, volcanic activity, and glaciation (Stout, 1975). As a result of New Zealand's historical geomorphology, the country possesses a diverse range of lake types of multiple origins relative to its small landmass (Lowe & Green, 1987). Extensive works by J. Irwin in the mid to late 1990s have largely contributed to a classification scheme of New Zealand lakes (Lowe & Green, 1987). From this classification scheme, nine broad categories of lakes based on origin were developed, which accounts for likely lake area, altitude, and length (Irwin, 1975; Lowe & Green, 1987). North Island lakes are predominantly volcanic in origin and hold some of the most extensively studied lakes in the country (Stout, 1975). Lake Taupō and the Te Arawa (Rotorua) lakes are among the most studied lakes within the North Island, with bathymetry studies of Lake Taupō dating back to 1888 (Cussen, 1888; Stout, 1975). Both the Taupō and the Te Arawa lakes have volcanic origin and are associated with the volcanic activity in the Rotorua and Okataina Volcanic Centre, and the rhyolitic Taupō volcanoes and andesitic Tongariro Volcanic Centre (Lowe & Green, 1987).

Studies on lakes considering the dynamics of zooplankton were relatively scarce within New Zealand before the 1950s. Early works by Hilary Jolly date back to the early 1950s. Jolly (1959) conducted a large-scale study of Lake Taupō and a select number of Rotorua lakes for her PhD, comparing the physical and chemical properties, and the phytoplankton and zooplankton of these lakes to assess the biological productivity. There are a number of past research papers conducted within New Zealand lakes that include zooplankton sampling. However, many of these studies focus primarily upon the seasonal variation of zooplankton abundances (Chapman, 1973; Magadza, 1973; Chapman *et al.*, 1981; Forsyth & McCallum; 1980; James 1987) rather than temporal changes. And although there are studies dating back to the early 1950s, long-term ecological studies of zooplankton are rare within New Zealand (Duggan *et al.*, 2020), with most studies of zooplankton dynamics having been conducted over periods of less than two years (Balvert *et al.*, 2009; Duggan *et al.*, 2020; Forsyth & McCallum, 1980). Although short term studies occurring within the same waterbodies are common, such as Lake Taupō and the Rotorua lakes that have hosted multiple research projects, they more commonly occur within discrete and widely spaced time periods. This makes it extremely difficult to determine the causation of an observed change in zooplankton composition when it is recognised. Zooplankton sampling has also been incorporated into some regional government agencies; however, a large proportion of these works are either unpublished, un-analysed or inaccessible to the public.

1.4.2 Drivers of zooplankton composition in New Zealand lakes

Within past research papers, it has been previously discussed that zooplankton community composition is driven by temperature and food availability, and not by predation within New Zealand lakes (Jeppesen *et al.*, 1997). Chapman *et al.* (1975) suggested grazing pressures and nutrient limitations within several of the Te Arawa lakes, following a rise in zooplankton numbers during spring and a fall in early summer following changes in temperature, are more likely to drive seasonal changes in composition than predation, due to few invertebrate and vertebrate, predators. This is again reported by Burns (1992) within Lake Mahinerangi, Otago, in that temperature and food are likely to be more of a control upon cladoceran and copepod populations than predation by fish. However, there has since been emerging evidence of predation as a natural driver of zooplankton community structure and composition within freshwater lakes of New Zealand. Chapman (1973) speculated that after investigating seasonal cycles of zooplankton within Lakes Rotorua and Rotoiti, she could not be clear as to the determining drivers of seasonal changes within zooplankton population dynamics but could conclude based on the close relationship between the birth and death rates of the copepod *Calamoecia lucasi* that predation was likely to be controlling their population. Jeppesen *et al.* (1997) evaluated the view of predation not being a driver of zooplankton composition and abundance in New Zealand and concluded using five examples from national and global sources the potential for predation to have a greater impact than originally anticipated within New Zealand lakes.

Predation aside, invasions of non-indigenous species is a more topical driver of community composition change today within New Zealand lakes. This is largely due to increased zooplankton dispersal opportunities facilitated by human activity (Ricciardi & MacIsaac, 2000). Zooplankton invasions within New Zealand waters have steadily increased over the past three decades, with the numbers and widespread distribution of non-indigenous cladocerans and copepods on the rise (Duggan *et al.*, 2006; Duggan *et al.*, 2012; Duggan *et al.*, 2014). Duggan *et al.* (2014) reported the negative impact on existing zooplankton communities within some New Zealand lakes after the introduction of the North American calanoid copepod *Skistodiaptomus pallidus*, which also coincided with the introduction of grass carp into a handful of lakes within the North Island. An observed change in zooplankton composition was the decreased relative abundance of native copepod *C. lucasi* as a likely result of competitive interaction (Duggan *et al.,* 2014). This introduction of a non-indigenous species correlated with an aquaculture species has since been explored by Duggan & Pullan (2017), who examined the potential for freshwater aquaculture to provide non-indigenous zooplankton species with a 'hitchhiking' opportunity. They found that the aquaculture sector is in fact a facilitator of non-indigenous introductions into new receiving environments (Duggan & Pullan, 2017; Pearson & Duggan, 2018). Other vectors of non-indigenous arrivals have also been related to the aquarium trade within New Zealand waters, by non-native species 'hitchhiking' within aquatic plants and live fish food (Duggan *et al.*, 2006). Despite the number of non-native zooplankton that have already entered New Zealand waters, due to a lack of long-term data, the effects invasions are having upon native ecosystems is largely unknown (Duggan *et al.*, 2020). A study conducted by Duggan *et al.* (2006) investigated the introduction of three non-indigenous freshwater zooplankton species; the copepods *Sinodiaptomus valkanovi* and *Skistodiaptomus pallidus*, and cladoceran *Daphnia galeata*. Although not completely understood, speculation of their impact upon existing zooplankton communities was explored. New Zealand's crustacean zooplankton communities have low species diversity (Chapman & Green, 1987), therefore the introduction of a potentially more aggressive non-indigenous species poses great risk to crustacean communities due to increased competition of resources such as food and space (Duggan *et al.,* 2006). Furthermore, *Daphnia* have the potential reduce rotifer abundances through competition for shared resources and interference competition (Balvert *et al.,* 2009).

Increased nutrient loading has been a significant topic of research within New Zealand freshwater lakes (Burns, 1991). Eutrophication in particular is of great concern, with an estimation of 30% of lakes greater than 1 ha having poor water quality (Ministry for the Environment, 2007). As mentioned, zooplankton are highly responsive to changes within their environment (Lampert, 1997; Gutkowska *et al.*, 2013; Jakhar, 2013; Brito *et al.*, 2020) and due to their intermediate position within the aquatic food web, these changes have been studied repeatedly. Within North Island lakes, Duggan *et al.* (2001) discovered rotifer distributions to be largely indicative of lake trophic state, from this a quantitative bioindicator index utilising rotifer community composition was developed for the understanding of Trophic Lake Index values. Multiple studies have been conducted within New Zealand lakes, exploring the relationship between lake trophic state and zooplankton communities (Chapman *et al.*, 1985; Chapman & Green, 1999; Duggan *et al.*, 2001; Duggan *et al.*, 2002). Duggan *et al.* (2020) reported finding similar zooplankton assemblages relative to trophic state, previously observed by Duggan *et al* (2001, 2002). (Duggan *et al.*, 2020) inferred these observations were likely contributed by food variation types influenced by nutrient levels along the trophic gradient, and recognised food availability and type. Other reported influencing factors of composition change along the trophic gradient include toxic cyanobacteria blooms, and oxygen depletion (Duggan *et al.,* 2001; Reynolds, 1998).

1.4.3 Long-term zooplankton studies in New Zealand

Long-term studies of zooplankton are even more infrequent within New Zealand than globally, with most published studies examining temporal changes only occurring within less than a two-year timeframe (Duggan *et al.*, 2020). For example, studies conducted within Lake Taupō by Forsyth & McCallum (1980) and Jolly (1965), sampling and comparing zooplankton composition and abundances, were carried out under a two-year time frame. Chapman *et al.* (1985) studied the zooplankton abundance between seven of the Te Arawa lakes using samples from 1970 to 1971, Balvert *et al.* (2009) investigated zooplankton dynamics of Weavers Lakes, Waikato, using a dataset collected between 2004 and 2005, and Forsyth *et al.* (1988) observed zooplankton seasonal abundances within Lake Okaro between years 1982/83 and 1985/86. These studies have allowed for the seasonal observations of fluctuations in production and seasonal compositional changes and abundances. However, these research papers do not investigate changes occurring perhaps as a result of trophic state shift or response to invasions by non-natives. Investigating larger temporal shifts within zooplankton community composition would require a long-term dataset, rather than sampling occurring over two years or less.

Few regional government agencies have carried out regular monitoring programs of zooplankton within New Zealand. Further, of those that have, much of the data remains un-published. A study conducted by Duggan *et al*. (2020) is one of the very few New Zealand studies utilising long-term data. Zooplankton temporal and spatial community data gathered between 2007 and 2019 was collated from a monitoring programme completed in 39 lakes within the Waikato region, New Zealand. The main finding of this research was that invasions by non-indigenous species was the main driver of temporal zooplankton composition change. Another study conducted by Duggan *et al.* (2014) utilised twelve years of seasonal monitoring conducted by Auckland Council to determine the effects of the invasion of North American copepod *Skistodiaptomus pallidus*, within Lake Kereta. Samples were collected semi-regularly between 1997 and 2014, in which time *S. pallidus* were observed within samples after August of 2008. These studies have proven to be useful resources in observing temporal community changes.

1.5 Thesis aims

The primary aim of this thesis is to document the change in zooplankton community composition through time, within a selection of lakes of the North Island, New Zealand. I also aim to examine the differences in zooplankton species richness and community composition between nets of different mesh size. This will consider mesh sizes used historically and during my 2021 sampling periods, as mesh sizes have commonly varied among studies through time. I also aim to assess what the drivers of these changes are, environmental or anthropogenic, whilst also considering sampling methods used in prior studies. This will be done over two separate chapters, presented as manuscripts written as potential journal articles. Further introductions and discussions will be provided within each chapter.

Due to a shortage of long-term studies and datasets within New Zealand, this thesis has utilised research looking at compositional changes across a series of lakes based on published research, instead of long-term data from a selection of individual lakes. This has advantages, in that published research has been conducted across a variety of geographically separated lakes, allowing for regional trends in compositional change to be observed over time. Yet due to lack of consistent long-term datasets, the possible drivers of change are not always obvious. This thesis aims to identify, using short-term published research throughout time, the possible drivers of zooplankton compositional change.

1.5.1 Objectives

1. Compare zooplankton community composition from historical literature within North Island lakes of different trophic states and geomorphological conditions, with zooplankton samples collected during my study.
2. Explore other factors that may have resulted in community composition change, from 1950-1990 to now, and determine whether the change is anthropogenically or environmentally driven.

3. Investigate the difference in zooplankton community composition and species richness using different zooplankton net mesh sizes. Using this information, I will explore how responsible the mesh size of zooplankton nets may be for observed zooplankton compositional changes relative to historical research.

1.5.2 Thesis structure

To meet the aims and objectives listed above, the chapters will be structured as follows:

Chapter One gives a general introduction to this thesis, giving insight into the importance of long-term research and zooplankton within ecology, a brief history of limnological studies within New Zealand and the history of zooplankton research within New Zealand. Chapter one also outlines the aims and objectives of this thesis.

Chapter Two documents whether there has been any change within zooplankton community composition through time (between 1950-1990 and 2021). Possible drivers of change will be explored, considering anthropogenic influence through facilitating invasions, and possible influence upon lake trophic state. Sampling method will also be explored, to determine whether methods used in previous studies may have influenced zooplankton community composition observed within past research.

Chapter Three documents the differences between zooplankton abundances and species richness among the three different zooplankton net mesh sizes used within this study. Using only the 2021 data, specific attention will be paid to the community composition caught within each net to determine whether mesh size influences results.

Chapter Four gives an overarching conclusion to this study, while acknowledging study limitations, and provides recommendations for future research.

Chapter Two: An assessment of long-term zooplankton community changes in North Island, New Zealand, using historical datasets.

2.1 Introduction

2.1.1 Long-term monitoring

Biological communities are continuously changing, evolving, and adapting. Drivers of change, and the rate at which change occurs, varies greatly through time. However, with increasing human population sizes and activity, environmental changes are now happening at faster rates than in the past (Sukhotin & Berger, 2013). This can have implications within ecosystems as many ecological processes occur slowly, over long periods of time (Likens, 2012). Identifying change is an easier task when there are observations and baselines to compare and can also assist in the differentiation between change occurring cyclically by natural variation from anthropogenic influence (Sukhotin & Berger, 2013). This can be obtained through the examination of long-term monitoring or historical datasets.

Long-term monitoring is an important tool in ecology, used to improve the understanding and management of ecological systems and document change within biological communities (Havstad & Herrick, 2003; Lindenmayer & Likens, 2009). Long-term datasets can provide insight into changes or disturbances within ecosystems (Likens & Gilbert, 1970). This can include changes induced by climate or anthropogenic influence, community shifts due to the establishment of non-native species, and the effects of experimental manipulations, with long-term data providing a baseline for ecologists to evaluate these changes against (Duggan *et al.*, 2002; Havstad & Herrick, 2003; Lindenmayer & Likens, 2009; Lindenmayer *et al.*, 2012; Sukhotin & Berger, 2013). Furthermore, data and information provided by long-term datasets also are essential for providing information required for policy development and environmental legislation (Likens, 2012). Within ecology, "long-term" is commonly deemed as any monitoring longer than five years (Dennehy, 2018). However, the longer the data series, the more value it holds, as longer-term data is more likely to reveal trends in ecosystems and communities than a dataset collected over a matter of months or years. Short-term research is likely to highlight only chance events or spontaneous fluctuations within communities and, furthermore, are not likely to identify or determine the origin of change within communities (Lindenmayer *et al.*, 2012).

2.1.2 Long-term zooplankton research

Global long-term research and monitoring of zooplankton communities are rare (Duggan *et al.,* 2020). However, the ability to recognise changes occurring over a prolonged period of time within zooplankton communities is difficult without long-term observations (Zhou *et al.*, 2020). The limited number of long-term studies that have been conducted internationally has revealed interesting and useful trends in community composition through time. Zooplankton have an intermediate position within the food web, situated between primary producers and higher trophic levels (Gajbhiye, 2002; Havens, 2002; Sterner, 2009). Due to this, their sensitivity to changes within their environment (Lampert, 1997; Gutkowska *et al.,* 2013; Jakhar, 2013; Brito *et al.,* 2020), and their ability to integrate physio-chemical and biological conditions through time (European Commission, 2000), zooplankton have been recognised as important biological indicators within ecological research (Gannon & Stemberger, 1978).

An example of zooplankton included in a long-term research project is demonstrated by Mihuc *et al.* (2012) within Lake Champlain, a large North American lake. Temporal shifts in zooplankton community composition were assessed using data from 1992 to 2010 as part of the Lake Champlain Long-Term Water Quality and Biological Monitoring Program (LTMP), in response to recent invasions by the zebra mussel (*Dreissena polymorpha*) and alewife (*Alosa pseudoharengus*). Shifts in zooplankton composition were observed, with zebra mussels reducing rotifer population densities and the alewife impacting both zooplankton abundance and body size (Mihuc *et al.*, 2012). Mihuc *et al.* (2012) concluded that these changes may have further implications for the lake food web dynamics, as by reducing larger bodied zooplankton assemblages, the food availability for higher trophic organisms will be reduced. Hsieh *et al.* (2011) utilised data collected between 1961 and 2005 to analyse zooplankton community responses to environmental variations within Lake Biwa, Japan. Throughout the duration of the monitoring, the lake underwent periods of eutrophication, and has been warming since 1990. Temporal changes in zooplankton abundance ratios of cladocerans:calanoid copepods and of cyclopoid copepods:calanoid copepod abundances were found to be linked to changes in lake trophic state and water temperature (Hsieh *et al.*, 2011).

Datasets collected over greater time periods can lead to acquisition of knowledge on complex processes occurring within freshwater ecosystems and community dynamics (Sukhotin & Berger, 2013). Furthermore, long- term monitoring is required to provide enough data to differentiate a change due to natural variation, or that induced by anthropogenic activity. It is unlikely that short-term studies would be able to detect changes in composition, due to shifts in lake trophic state or community interactions for instance, as processes within ecosystems tend to occur over prolonged periods of time (Likens, 2012). However, short-term sampling programs occurring within the same waterbodies are quite common, within discrete but widely spaced time periods.

2.1.3 Drivers of zooplankton community composition change

Ecosystems have been progressively altered through time due to natural cyclic processes and increasing anthropogenic influence, which in turn have created shifts in species functioning and composition from historical systems (Hobbs *et al.*, 2009; Lewis & Granek, 2021). Zooplankton community composition is influenced by a combination of biological interactions and abiotic factors (Blancher, 1984). These include interactions with phytoplankton and fish communities (Lampert, 1997; Fu *et al.*, 2021), and tolerances to environmental changes in variables such as temperature (Jeppesen *et al.*, 1997). Zooplankton also have high seasonal variability, determined by complex interactions of factors such as lake size and depth, local climate, and biotic communities present within the lake at a given time (Mengestou & Fernando, 1991). While changes do occur naturally and cyclically (Duggan *et al.*, 2020), anthropogenic induced disturbances to ecosystem functioning, such as land use changes, industrialisation (Kampichler *et al.*, 2012) and eutrophication are accelerating the rate at which communities naturally shift. Changes in lake trophic state have proven to impact the abundance and composition of zooplankton communities, as they are driven largely by the physical and chemical processes of their environment, and by biological interactions (Ejsmont-Karabin & Karabin, 2013).

Humans are also altering the natural rates and distances of dispersal of aquatic species, including zooplankton (Havel & Shurin, 2004). In aquatic ecosystems, human activities have enabled many invasions of non-indigenous species into even the most isolated environments (Ricciardi & MacIsaac, 2008). Commercial shipping, recreational boating, the aquarium trade, and aquaculture (Bollens *et al.*, 2002; Duggan, 2010; Dexter & Bollens, 2020) are all examples of human activities facilitating the movement of non-indigenous species among waterbodies globally.

2.1.4 Invasions of non-indigenous species as drivers of zooplankton community composition

Invasions of non-indigenous species into aquatic and terrestrial environments are occurring at an increased rate and can pose great pressure on the functionality of indigenous ecosystems (Bollens *et al.,* 2002; Lewis & Granek, 2021). Human-facilitated invasions, intentional or accidental, are increasing the rate at which species are dispersing to new environments. Within aquatic environments, commercial shipping, recreational boating, aquaculture, and the pet industry (Bollens *et al.,* 2002; Dexter & Bollens, 2020) are examples of anthropogenic activities facilitating dispersal opportunities for non-native species. Cladocerans in the genus *Daphnia*, for example, can survive within residual bilge water of recreational boats for up to three days

(Havel & Shurin, 2004), during which time a boater may visit multiple locations (Havel & Stelzleni-Schwent, 2000). Research on diapausing eggs within ship sediments has also proven to be a vector for dispersal of non-native species. Bailey *et al.* (2004) found a range of copepod, cladoceran and rotifer taxa could be hatched from diapausing eggs found within the ballast tanks of transoceanic vessels after the addition of freshwater.

Invasions of non-native zooplankton species into new receiving environments commonly have unwanted effects. For example, non-native species may impact individual species or whole ecosystems through competition and predation, genetic impacts such as hybridisation, the introduction of diseases that native species have not been subjected to, and habitat alterations (Dextrase & Mandrak, 2006). Across hemisphere invasions of non-indigenous zooplankton are rare, but there have been some instances in which it has occurred. For example, the Australian calanoid copepod *Boeckella triarticulata* was found in fishponds in North Italy within the Po River Plain in 1985. As of 2019, around eight non-native zooplankton species have been introduced and have established within New Zealand lakes, including three *Daphnia* species and five calanoid copepod species (Duggan & Collier 2019). It has been determined that each of these have been accidentally introduced in conjunction with flora and fauna e.g contaminated fishing gear or through the aquarium trade (Duggan & Collier 2019; Duggan *et al.* 2006). The non-native *Daphnia* species includes *D. galeata*, a now common *Daphnia* species within North Island lakes (Duggan *et al.* 2006; Duggan & Pullan 2019); and *D.'pulex'* and *D. obtusa,* both of which were first recorded within South Island lakes (Chapman *et al.* 2011; Duggan *et al.* 2012). The invasion of calanoid copepod species have generally been associated with constructed waters (Duggan *et al.* 2009). Invasions of the Japanese *Sinodiaptomus valkanovi*, and the North American *Skistodiaptomus pallidus*, were first found within samples taken from constructed waters within the Auckland region, or within live fish food (Duggan *et al.,* 2006). The Australian species *Boeckella symmetrica* and *Beockella minuta* were first discovered, and have remained confined to, constructed waters such as hydroelectric dams and an ornamental pond within the North Island (Duggan & Collier 2019). The final non-native species known to have established within New Zealand waters is the Australian copepod *Calamoecia ampulla* recorded within a South Island water body (Duggan & Collier 2019). Natural dispersal of these species was deemed unlikely due to New Zealand being geographically isolated from each species' native region. Thus, transport through plants, the live fish food trade and human mediated dispersal were likely vectors of these introductions (Duggan *et al.,* 2006).

Introduction of non-native aquatic vertebrate, such as fish, have also proven to impact zooplankton community composition. For example, bighead and silver carp invasions have been widely studied in lakes in the United States (Irons *et al.,* 2007; Kolar *et al.,* 2007; Sass *et al.,* 2014), and have the ability to reduce total zooplankton abundances, particularly cladocerans and copepods, due to feeding heavily on phytoplankton and zooplankton directly (Fukushima *et al.,* 1999). Within New Zealand, 21 freshwater fish species are non-native, and the larvae of these invasive species are known to impact zooplankton communities by direct grazing (Duggan & Collier 2019). Branford & Duggan (2017) found grass carp have the ability to indirectly affect zooplankton community composition through habitat modification by decreasing macrophyte coverage. Adult tench found within water bodies of the North Island and scattered throughout the South Island can reduce zooplankton communities due to top-down effects from grazing (Duggan & Collier 2019). Perch larvae are also typically pelagic zooplankton feeders, and adult Perch can induce water quality degradation by the consumption of zooplankton, thus reduce algal grazing within a water body (Duggan & Collier 2019).

2.1.5 Trophic state as a zooplankton community composition driver

With the rise of economic and industrial development, the ecological health of water bodies globally is decreasing in quality through time (Søndergaard & Jeppesen, 2007). An increasing number of lakes are becoming more nutrient enriched, which is one of the major causes of surface water quality degradation (Mendiondo, 2009; Smith & Schindler, 2009). For example, the United States Environmental Protection Authority (EPA) reported that almost half of their lakes and 60% of river reaches are compromised by eutrophication in the United States alone (U.S EPA, 1996).

Increased nutrient loading has been a significant issue within New Zealand lakes (Burns, 1991). New Zealand has undergone one of the highest rates of agricultural intensification than anywhere else globally, with approximately 60,000 ha of land converted from low to high producing land between 1996-2018 (Ministry for the Environment, 2023). Consequently, there is an estimated 46% of lakes greater than 1 ha with poor or very poor water quality within New Zealand (Ministry for the Environment, 2023). Some of the obvious effects of eutrophication within water bodies is the increase in toxic algal blooms, excessive macrophyte growth, and periodic fish death (Schindler, 2006).

The structural complexity of zooplankton communities is largely determined by changes within their environment (Brito *et al.,* 2020), such as in nutrient concentrations, dissolved oxygen, and temperature (Gannon & Stemberger, 1978). Changing trophic state alters the chemical and biological components of a lake, and consequently may impose changes to zooplankton community composition as a result. Studies investigating zooplankton responses to changing trophic state have shown that species that are generally more opportunistic are more likely to withstand changes within their environment. For example, rotifer, cladoceran and cyclopoid copepod communities are more likely to inhabit eutrophic waters than calanoid copepods (Allan, 1976), with calanoid copepods indicators of oligotrophic conditions (Gannon & Stemberger, 1978). Research by Straile & Geller (1998) of crustacean populations within Lake Constance (bordered by Germany, Austria, and Switzerland), revealed a strong increase in cladoceran and cyclopoid copepod populations during periods of eutrophication. Duggan *et al.* (2002) also found rotifer distributions within North Island, New Zealand lakes were strongly influenced by trophic state as a result of their suspension feeding mechanism on algae and bacteria. This demonstrates the changes in preferred food resources, thus food quality and quantity, can contribute to change in zooplankton communities.

The composition of any ecological community usually is driven by a combination of factors, not through a single factor. Duggan *et al.* (2002) acknowledges this, stating the response of rotifer distributions along a trophic gradient is more likely a product of many factors induced by trophic state change, rather than competition for a single resource, such as food. Other drivers of zooplankton composition change due to trophic change include toxic cyanobacteria blooms and oxygen depletion.

2.1.6 Sampling method

Many research projects have been undertaken to quantify and gain an understanding of zooplankton community dynamics, abundances, and production (Mack *et al.,* 2012). Within the various research projects conducted, many different sampling techniques have been developed based on the question being asked. Within freshwater systems, zooplankton can be sampled using Schindler-Patalas traps, tube samplers and, most commonly, zooplankton nets. Having multiple methods for zooplankton sampling can occasionally introduce a level of method and gear specific bias, resulting in the possible artificial variability within zooplankton communities (Frank, 1988).

Net hauls are a common method for zooplankton sampling. However, there is a lot of variability in mesh size selection (Mack *et al.,* 2012). Each zooplankton taxon ranges in size and morphological features. Therefore, selecting a mesh small enough to sample cladocerans, copepods and most of all, rotifers, is imperative for collecting a sample representative of the zooplankton community. For example, nets with larger mesh will favour larger zooplankton and likely miss smaller bodied zooplankton such as rotifers (Likens & Gilbert, 1970). Forsyth & McCallum (1980) sampled Lake Taupō in 1974-76 using a zooplankton net with 55 µm mesh, while in 1955-56, Jolly (1965; 1977) sampled the same lake using a net with 318 µm mesh. Forsyth & McCallum (1980) acknowledge that Jolly's mesh was too large to sample rotifers and would thus not have been able to quantitatively sample them within her studies. It seems plausible to simply use a smaller meshed net to account for all zooplankton. However, decreasing mesh size can occasionally create further issues, as a decreased mesh size can alter filtration efficiency, particularly with mesh smaller than 100 µm due to clogging (Likens & Gilbert, 1970). Clogging occurs when suspended particles within the water column (plant material, phytoplankton, sediment, zooplankton) are trapped within the inner wall of the sampling net, reducing net porosity (Tranter & Smith, 1968). Consequently, this can result in an unequal filtration of the sample throughout the water column and increase the amount of water passing the mouth of the net (Likens & Gilbert 1970) and introduce sampling error.

Zooplankton behaviour can also influence catchability (De Bernardi, 1984). It has been theorised that zooplankton are able to avoid capture by towed nets (Franz, 1910; Bary *et al.,* 1958; Hansen & Anderson, 1962). Originally proposed by Franz (1910), some zooplankton taxa may have the ability to see nets during daytime hauls, while others have the ability to avoid nets by identifying changes in hydrostatic pressure caused by the movement of the net through the water column (Brook & Woodward, 1956). Brook & Woodward (1956) found that with increased current, Cladocera swam steadily against it, whereas copepods swam vigorously against it (Brook & Woodward, 1956). These findings were also observed by Knight-Jones & Qasim (1955), who investigated and confirmed marine plankton responses to changes in hydrostatic pressure. The avoidance of nets by zooplankton may not only result in the underestimation in abundances, but also cause unintentional selective sampling (Clutter, 1968; Wiebe *et al.,* 1971).

2.1.7 Zooplankton research within lakes of New Zealand through time

Historical zooplankton research within New Zealand is not as extensive as other parts of the globe. Ecological research dates back to Jolly in the early 1950s when she analysed zooplankton samples from Lake Taupō and a number of the Rotorua lakes during her PhD (Jolly, 1959). Further historical research of zooplankton communities was included within limnological studies conducted by Hill (1969), Jolly (1965), Magadza (1973), Chapman *et al.* (1981), Chapman *et al.* (1985) and Forsyth *et al.* (1988), for example. A large proportion of the early ecological research had a primary focus on seasonal cycles of zooplankton composition. In recent years, zooplankton research has become frequent in ecological literature, with particular regard to invasions of non-native species. For example, Duggan & Pullan (2017) investigated the invasion risk of non-indigenous species through the aquaculture industry, and Balvert *et al.* (2009) examined the dynamics of zooplankton composition within a pit lake in response to the invasive *Daphnia galeata*. Despite this, long-term zooplankton research is rare in New Zealand and most existing research analysing zooplankton communities have occurred over periods of less than two years (Forsyth & McCallum, 1980; Balvert *et al.,* 2009). Duggan *et al.* (2020) provides a rare example of New Zealand research utilising long-term zooplankton data, using zooplankton temporal and spatial community data collected between 2007 and 2019, collated from a monitoring programme on 39 lakes within the Waikato region. Here, invasions by non-native zooplankton species were found to impact on community composition through time more than other drivers. Duggan *et al.* (2014) collated 12 years of seasonal monitoring data from Lake Kereta, Auckland, which was used to determine the effects of the invasion of North American copepod *Skistodiaptomus pallidus*. Miles (2021) utilised a long-term zooplankton dataset from 2000-2020 of zooplankton community composition in Lake Taupō and found shifts through time that could not be clearly linked with measured environmental variables.

From the mentioned resources, it is clear that New Zealand has had a number of non-indigenous zooplankton invasions through time. Determining the timing and effects of these invasions is easier when there is long-term data to investigate, as Duggan *et al.* (2020) and Duggan *et al.* (2014) demonstrate. Although there are frequent research projects investigating zooplankton composition and abundances within New Zealand lakes, there is a lack of consistent long-term data prior to 2000, making it difficult to determine longer term trends. Having long-term datasets from the time of the short-term research projects would prove useful when assessing potential causes for temporal change in zooplankton communities.

2.1.8 Chapter Aims

The aim of this chapter is to document long-term temporal changes in zooplankton community composition in nine lakes from the North Island, New Zealand, and discuss possible drivers of any observed changes. I utilise zooplankton community composition data collated by literature review of New Zealand limnological studies, primarily between the years 1950 and 1990, and from two 2021 sampling events. Possible drivers of change will be discussed, including zooplankton invasions and lake trophic state change. Sampling and method bias will also be investigated as possible drivers of an observed zooplankton composition change.

2.2 General Methods

The method section for this chapter outlines the process of selecting locations for sampling, how zooplankton samples were collected within the field, and how samples were analysed within the laboratory. These processes are the same for chapter two and three. Because this chapter and chapter three are asking different questions, the statistical analysis for each will be specific to the aims and objectives of each chapter.

2.2.1 Site Selection

A literature review was conducted using Google Scholar to identify historical zooplankton studies from freshwater lakes in North Island, New Zealand. The initial search was liberal; any research paper conducted within North Island lakes containing a zooplankton species list was included in the original dataset. From this list, it was decided to include only research prior to 1990, as there were few research papers with seasonal species lists after this time. This was also to create a historical dataset with enough time between then and recent (2021) sampling to theoretically show changes in community composition. Data such as lake location, author/s, year of research, zooplankton net mesh size, and zooplankton species were tabulated for each research paper in an Excel spreadsheet.

In total, 27 separate research papers ranging from the 1950s to 1990, examining 29 different lakes, were identified. Accessibility was the most significant determinant in selecting lakes for sampling. Some were geographically difficult to reach, requiring cross-country driving that would prove difficult for boat access (i.e., Lake Ngapouri, Lake Rotomahana), others were within privately owned land or had other social constraints (Lake Rotokākahi; Lake Rotongaio), while two had been retired (i.e., Morton Dam, Upper Karori Reservoir). This eliminated several lakes from further consideration. Another determinant when selecting research papers and potential lakes for the study was the robustness of the zooplankton species data provided. Some research papers only listed or mentioned selected species, rather than providing complete species lists. Some stated the presence of zooplankton within samples and/or reported on the dominant zooplankton species, but disregarded species caught in lower quantities, and others provided only genus-level identifications of zooplankton. The identification of zooplankton down to species level was preferred.

From the preliminary 27 research papers, a subset of eleven lakes were selected initially for fieldwork: two within Waikato (Ohakuri and Taupō), two within Auckland (Pupuke and Rototoa) and seven within the Bay of Plenty region (Okaro, Rerewhakaaitu, Tikitapu, Ōkāreka, Rotorua, Rotomā and Rotoehu). Most of these lakes also had been studied at least twice between 1950-1990. Before fieldwork began, the two lakes within the Auckland region were removed from consideration as Covid 19 lockdown restrictions prevented travel into the Auckland region during the sampling period. The final subset thus comprised nine lakes (Figure 1). The final subset of lakes chosen for sampling ranged in trophic state and geomorphological attributes. To account for the seasonal variability of zooplankton communities, it was speculated that sampling over all seasons would be most beneficial. Fieldwork was originally planned to occur during the winter and summer seasons. However, due to Covid-19 restrictions the initial winter sampling could not be undertaken until early spring. Fieldwork was thus conducted over four days: 15 and 16 September 2021 (early spring sampling) and 8 and 9 December 2021 (summer sampling).

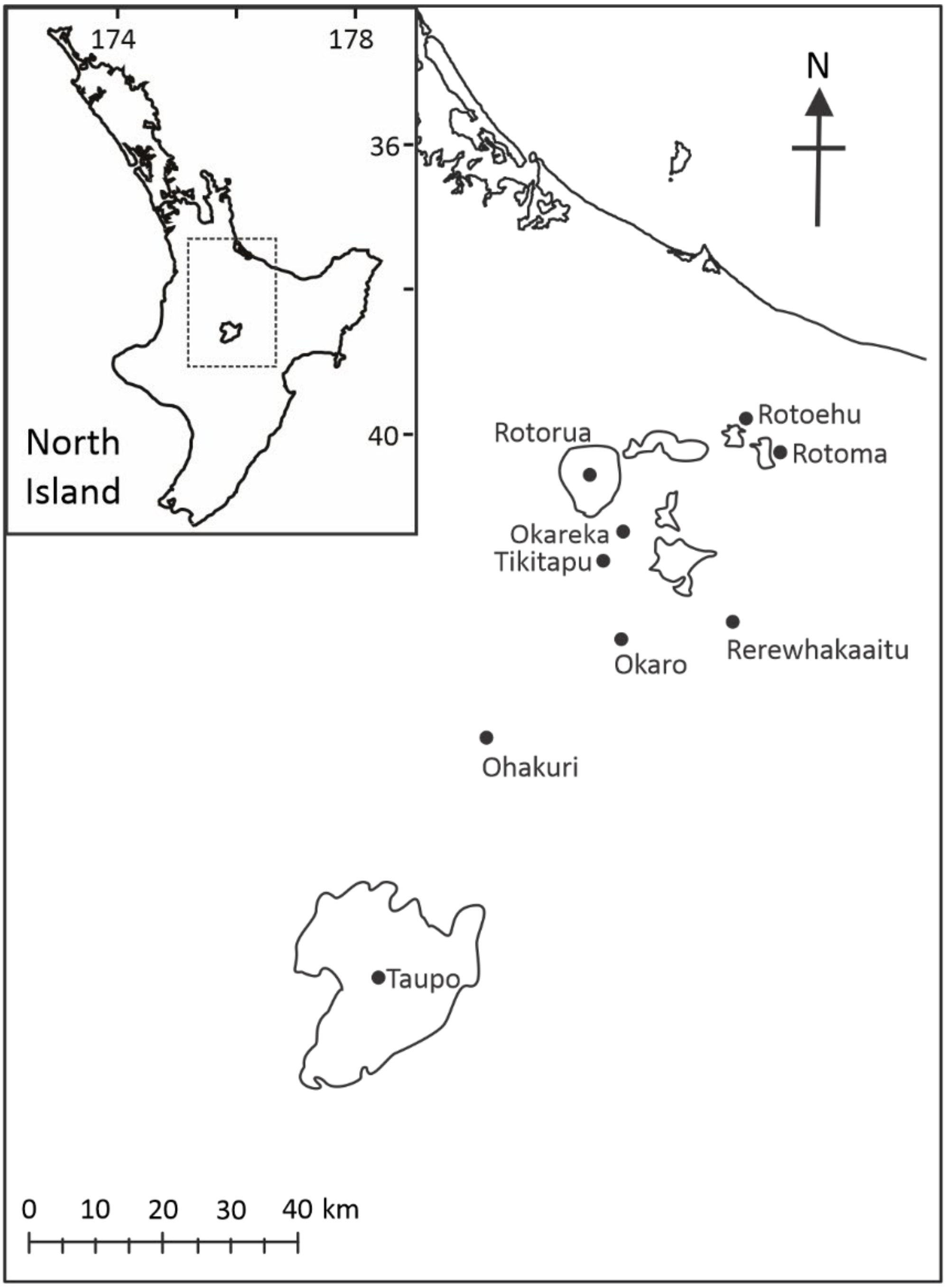

Figure 1. Lake locations for zooplankton sampling within the Waikato and Bay of Plenty regions, New Zealand.

2.2.2 Fieldwork Sampling

In each lake, a sampling location (Table 1) was selected at a depth of at least 8 m to ensure clean zooplankton hauls through the top 8 m of the water column. Sampling locations, using eastings and south coordinates, were saved using a Lowrance Elite Ti2 sounder during the early spring sampling period so that summer sampling could be undertaken in relatively the same location.

Table 1. Site locations at each lake where samples were taken in September and December 2021.

Lake	Sampling Location Eastings	South
Ohakuri	176°05'36"E	38°24'40"S
Ōkāreka	176°21'09"E	38°10'15"S
Okaro	176°23'39"E	38°17'53"S
Rerewhakaaitu	176°29'31"E	38°17'55"S
Rotoehu	176°32'08"E	38°01'28"S
Rotomā	176°34'58"E	38°03'02"S
Rotorua	176°15'58"E	38°07'34"S
Taupō	176°03'49"E	38°41'23"S
Tikitapu	176°19'47"E	38°11'32"S

2.2.3 Zooplankton sampling

Following common methods used in New Zealand literature, such as those of Jolly (1965), Chapman (1973) and James (1987), three vertical net hauls were conducted off the side of a boat from a depth of 8 m to the water's surface. Each haul was conducted using 20 cm mouth diameter zooplankton nets of differing mesh sizes: 37 µm, 75 µm and 100 µm. Material collected in the nets were poured into pre-labelled sample containers, ensuring the inner mesh was carefully rinsed with deionised water to collect any zooplankton stuck to the net. Zooplankton samples was immediately preserved using 95% ethanol (>50% final concentration). All sampling equipment was thoroughly washed in a saline solution between sites to avoid cross-contamination of samples and to reduce the risk of pest plant and animal transfer among lakes.

2.2.4 Laboratory analysis

Prior to analyses, each zooplankton sample was filtered using a 37 µm sieve and rinsed with freshwater to remove ethanol from the sample. The sieve and sample container were thoroughly rinsed to ensure all the specimens within the net were collected. Samples were then made up to a known volume, between 15 mL and 100 mL, depending on the clarity of the sample. Samples with high amounts of organic matter were made up to larger volumes, this was to dilute the sample making it easier to analyse under the microscope. Each sample was counted in 5 mL aliquots in a gridded Perspex counting tray (12 columns, 5 rows) using an Olympus SZ40 stereo microscope at magnifications between 20x and 40x. Aliquots were counted until at least 300 individual zooplankton were recorded. When an unknown individual was found, it was removed from the sample, placed on a slide, and examined using an Olympus BH-2 compound microscope at magnifications between 100x and 400x. All zooplankton were identified to species level where possible, using appropriate taxonomic keys (Shiel, 1995; Chapman *et al.*, 2011). Soft-bodied rotifers, when necessary, were identified through the examination of their trophi (jaws). To do so, a rotifer specimen was placed onto a slide with a coverslip. A drop of sodium hypochlorite (10%) was then added to one edge of the coverslip, and using filter paper on the opposite edge, drawn under the coverslip to erode the body and reveal the trophi (Shiel, 1995).

2.2.5 General Statistical analysis

Prior to conducting statistical analyses on the data, the dataset was split into three different year groups; 1950-69, 1970-90, based on their publication date, and 2021. All the lakes selected had samplings within each category, apart from Lake Rotoehu and Rotorua. Due to already losing access to two lakes due to the Covid 19 pandemic, it was decided to keep these lakes within the dataset. While conducting my literature review, I was unable to find zooplankton composition data for the 1970-90 year group for Lake Rotorua. Thus, it was decided to include Chapman & Green (1999) in the dataset, where sampling took place in 1994-95. Although this falls out of the established cut-off period, having a more complete dataset was of priority.

The dataset used in this particular analysis consisted of presence-absence data, which was simply the list of species of zooplankton that were present or absent in each lake on each sampling event. Species richness within each net could also be calculated using the presence-absence dataset. This was done by simply counting the number of species present within each lake, and within each net from the 2021 sampling. Some lakes had more than one sampling event among years, e.g., Lake Taupō had two samples within the 1950-69 period. This was dealt with by only considering each species as one count between samples, such that all zooplankton from within the same lake were combined into a single list.

2.2.6 Zooplankton compositional changes statistical analysis

The following analyses were undertaken to test for zooplankton community composition changes through time, by comparing the 1950-60, 1970-90 and 2021 zooplankton presence-absence data. A total of three separate analyses were run, each time using the 1950-69 and 1970-90 presence-absence data, and one of the three 2021 zooplankton net datasets (37 µm, 75 µm and 100 µm). This was to investigate differences in the composition of zooplankton through time, while also investigating whether variations in mesh size were responsible for some of the observed changes, and determine if the changes observed are an artefact of sampling method.

Compositional data from the 2021 summer and early spring sampling periods were combined to create an overall species list of zooplankton for each lake and each net size. Copepod nauplii were removed from the species lists before analysis as identification to species level could not be undertaken confidently, and as species level identifications of nauplii were also not undertaken in the historical collections. Most rotifer taxa within the historical research papers were only identified to genus level. To ensure the 2021 data replicated the taxonomic level of the historical dataset, rotifers identified within the 2021 samples were grouped at the genus level (e.g., *Keratella* spp). Some rotifer species (e.g., *Conochilus unicornis*), did not need to be grouped to genus level as they were not identified within the historical published records. Furthermore, copepods in the genus *Mesocyclops* were all designated as *Mesocyclops australiensis*; several historical collections have identified *Mesocyclops* as the European *M. leuckarti*, though recent studies recognise that the species in New Zealand is *M. australiensis* (Bayly, 1995).

Species richness of the 1950-69, 1970-90 and 2021 zooplankton community datasets were analysed using repeated measures analysis of variance testing (rmANOVA). An rmANOVA is used to analyse the difference between the means of groups of related dependent variables. Bonferroni post-hoc testing was conducted if significant differences were found within any of the rmANOVA tests to determine what variables were responsible for these differences. A Bonferroni post-hoc test was selected for this analysis as it is suitable for reducing the incidence of a false positive within studies involving repetitive sampling (Armstrong, 2014). Bar graphs were constructed using the average species richness of each year group, and standard deviation error bars were applied to the bar graph to communicate how accurately the mean value represents the dataset; large error bars indicate less reliable statistical significance whilst smaller error bars are more reliable. Univariate tests were undertaken using STATISTICA version 13.5.0.17 (Statsoft, Inc., Tulsa, OK, USA).

Using PRIMER 7 (version 7.0.17), differences in zooplankton community composition through time were assessed. A Bray-Curtis similarity matrix was calculated on the presence-absence dataset (equivalent to the Jaccard's index). A two-dimensional non-metric multidimensional scaling (nMDS) ordination plot of the data was constructed based on the similarities in species composition of each lake to each other. An ordered Analysis of Similarities (ANOSIM) was then conducted to test for statistically significant differences between the zooplankton community composition among time periods and were repeated for each net size also. ANOSIM is a non-parametric permutation method applied to the Bray-Curtis similarity matrix underlying the nMDS ordination plot (Clarke & Warwick, 1998). A calculated Global *R-value* was produced from the ANOSIM, which is a direct measure of dissimilarity among the groups of samples. An *R-value* close to 1 indicates zooplankton community composition among the selected groups are dissimilar, whilst a value closer to 0 indicates similarity between the selected groups. When differences among time periods were significant, a similarity percentage (SIMPER) analysis was used to examine the contribution of zooplankton taxa to the average dissimilarity of category pairs (e.g., 1950-1969 vs 2021). Only zooplankton taxa contributing > 5% to the dissimilarity between community composition among the respective groups were considered in this analysis.

2.3 Results

2.3.1 Species richness within presence-absence dataset

Each of the rmANOVA analyses indicated significant differences in species richness between the historical year groups, 1950-69 and 1970-90, and the corresponding 2021-year groups (37 µm, 75 µm and 100 µm) ($p<0.05$). There was a general trend of increased species richness through time for the finer mesh samples and the historic samples, yet the 100 um samples appeared to be representative of the 1970-90 samples (Figure 2).

The Bonferroni post-hoc test applied to the 2021 37 µm zooplankton data and the historical data indicated there was no significant difference between the 1970-90 and 2021 species richness ($p=0.175$), but there was a significant difference between the 1950-69 and 1970-90 ($p=0.017$), with the mean of 1970-90 being higher than 1950-69 ($\mu=9.25$ and $\mu=4.36$ respectively). A significant difference was also found between 1950-69 and 2021 species richness ($p<0.05$). with the mean for 2021 being higher than 1950-69 ($\mu=12.63$ and $\mu=4.36$ respectively). For the 2021 75 µm mesh net and historical zooplankton data, the Bonferroni post-hoc test also indicated no significant difference existed in species richness between 1970-90 and 2021 ($p=0.123$), but significant differences in species richness were evident between 1950-69 and 1970-90 ($p=0.017$), with the mean of 1970-90 ($\mu=9.43$) being higher than 1950-69 ($\mu=4.71$). There was also a significant difference observed between 1970-90 and 2021 ($p<0.05$), with the mean from 2021 being higher than 1970-90 ($\mu=13.14$ and $\mu=9.43$, respectively). The third Bonferroni post-hoc test for the 2021 100 µm mesh net and historical zooplankton data indicated no significant difference in zooplankton species richness between 1970-90 and the 2021 100 µm mesh net data ($p=1.00$), but significant differences in zooplankton species richness between 1950-69 and 1970-90 ($p=0.030$), with the mean of 1970-90 being higher than 1950-69 ($\mu=9.25$ and $\mu=4.38$ respectively) and 1950-69 and 2021 ($p=0.026$), with the mean for 2021 being higher than 1950-69 ($\mu=9.38$ and $\mu=4.38$ respectively).

Overall, the 1950-69 period had the lowest species richness, whilst the 2021 37 µm and 75 µm mesh net species richness had the highest. The 2021 100 µm mesh net had lower species richness than the 37 µm and 75 µm nets and is more reflective of the 1970-90 species richness. The standard deviation bars of the 1950-69 and 1970-90 show a greater spread of data in the sample population, thus a greater range of means of species richness within samples, compared to the 2021 37 µm and 75 µm standard deviation bars that show a smaller spread of data. Interestingly, the 2021 100 µm standard deviation bar is more similar to the 1950-69 and 1970-90 standard deviation bars.

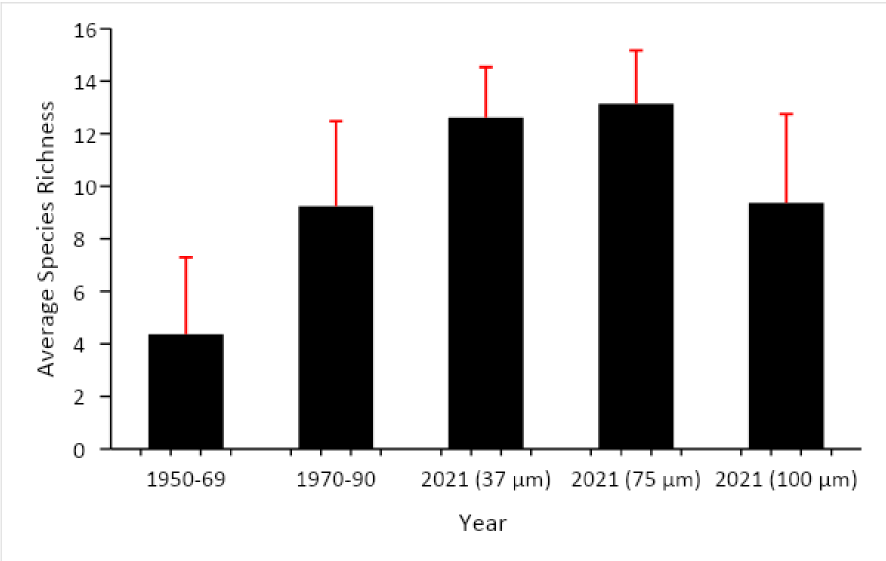

Figure 2 Bar graph showing the species richness of each year group, and the three different zooplankton net mesh sizes used in 2021, with accompanying standard deviation bars.

2.3.2 Zooplankton community composition observations from the historical dataset and the 2021 37 µm zooplankton net mesh dataset

The ordination plot constructed using the historical dataset and the 2021 37 µm mesh zooplankton net samples indicated separation of samples from each of the year groupings. The 1950-69 samples were distributed to the left of the ordination, the 1970-90 samples were distributed closer to the centre and right, and the 2021 samples were distributed on the upper right of the ordination. The separation of the samples indicates zooplankton community composition has progressively changed through time. It is important to note that time is a more important factor than geography, as individual lakes are not grouped together among different time periods. In the centre of the ordination, the Rotorua (RT) and Ohakuri (OH) samples (collected in the 1960s) were distributed independently from the 1950 samples, overlapping within the 1970-90 samples. The overlap of the 1960s samples with the 1970-90 samples indicates similarities in community composition at this time. The stress value, an expression of fit of the ordination to the Bray-Curtis similarity matrix, was 0.10 for this analysis, which corresponds to a good ordination with little prospect of a misleading interpretation (Clarke & Warwick, 2001).

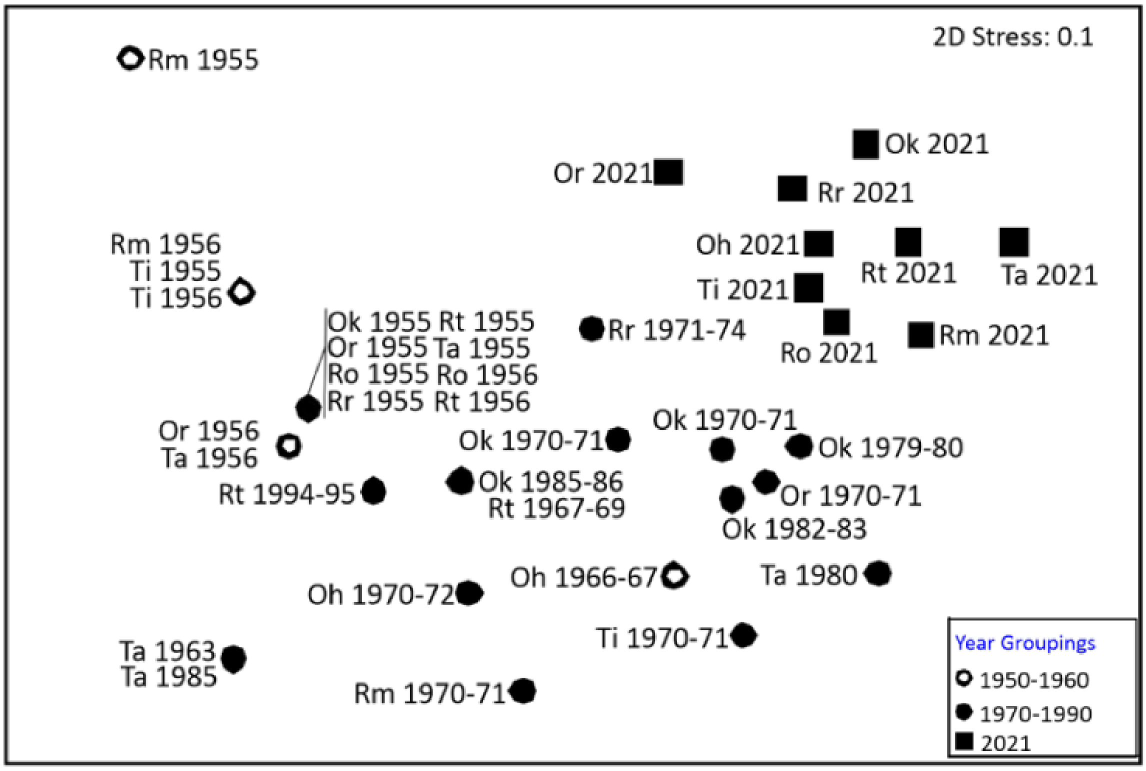

Figure 3. Non-metric multidimensional scaling ordination (nMDS) showing historical zooplankton communities (1950-90) from Bay of Plenty and Waikato region lakes and 2021 zooplankton communities sampled with a 37 µm mesh zooplankton net.

ANOSIM indicated that the difference in zooplankton community composition between the three year groupings was significant (Global R = 0.503, p = 0.001), and pairwise testing indicated significant differences in zooplankton community composition between each possible combination of the three year groupings; 1950-69 and 2021 (r = 0.940, p = 0.001), 1950-69 and 1970-90 (r = 0.557, p = 0.001) and 1950-69 and 1970-90 (r = 0.506, p = 0.001). Similarity percentages (SIMPER) analyses were used to identify the contribution of each zooplankton taxon to the observed dissimilarity between the three-year groupings for each of the zooplankton nets. The SIMPER analysis for the 1950-69 samples and the 2021 37 µm zooplankton net samples (Table 2) indicated that all zooplankton taxa contributing > 5% to the dissimilarly were found in higher frequencies within the 2021 samples than in the 1950-69 samples. The greatest dissimilarity was attributed to bdelloid rotifers, which were completely absent from the 1950-69 samples (frequency of 0) but were present in all the 2021 37 µm net samples (frequency of 1). Following this, in order of contribution percentage, were *Synchaeta* spp., *Polyarthra* spp., *Trichocerca* spp., *Keratella* spp. and *Asplanchna* spp. All increased from complete absence or low frequencies in the 1950-69 data, to high average frequencies in 2021. The cladoceran *Daphnia galeata* increased from total absence in the historical samples yet were present in high frequencies within the 2021 samples. The cladoceran *Chydorus* spp. also increased from low average frequency in 1950-69 samples, to high average frequencies of occurrence across the 2021 samples.

The SIMPER analysis for 1970-90 and the 2021 samples (Table 3) indicated that four of the five zooplankton taxa contributing >5% to the dissimilarity had higher average frequencies in the 2021 samples relative to the 1970-90 samples. Like the prior SIMPER analysis, bdelloid rotifers showed the greatest dissimilarity, followed by the cladoceran *Daphnia galeata*. In order of contribution percentage, the rotifers *Trichocerca* spp. and *Synchaeta* spp. were present at low frequencies in the 1970-90 samples and increased to high average frequencies in 2021. *Macrocyclops albidus* was the only zooplankton taxon within this analysis to decrease in frequency; this species was common in the 1970-90 samples and was absent in the 2021 samples.

Table 2. SIMPER analysis using 1950-69 zooplankton community composition data and 2021 37 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1950-69** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Bdelloid spp.	0.00	1.00	8.77
Synchaeta spp.	0.00	0.89	7.87
Daphnia galeata	0.00	0.89	7.81
Polyarthra spp.	0.00	0.89	7.75
Trichocerca spp.	0.00	0.89	7.68
Keratella spp.	0.07	0.89	7.42
Asplanchna spp.	0.07	0.89	7.13
Chydorus spp.	0.07	0.67	5.32

Table 3. SIMPER analysis using 1970-90 zooplankton community composition data and 2021 37 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1970-90** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Bdelloid spp.	0.00	1.00	8.68
Daphnia galeata	0.00	0.89	7.73
Trichocerca spp.	0.15	0.89	6.70
Macrocyclops albidus	0.77	0.00	6.43
Synchaeta spp.	0.38	0.89	5.53

2.3.3 Zooplankton community composition observations from the historical dataset and the 2021 75 µm zooplankton net mesh dataset

The nMDS ordination for 2021 75 µm mesh zooplankton net samples and the historical data set also indicated the separation of samples from each year grouping, similar to that observed in the 37 µm ordination plot; 2021 samples were distributed on the upper right side of the ordination, 1970-90 samples were generally distributed in the lower right and mid area, and the 1950-69 samples were distributed to the left area of the ordination. The gradient of 1950-69 samples to the left of the ordination, 1970-90 in the centre and 2021 samples to the right of the ordination, indicated that zooplankton community composition has changed through time. Yet again, the 1960 samples were distributed independently of the 1950 samples and overlapped with the 1970-90 samples. This overlap of samples indicates that between 1960 and 1990, the composition of zooplankton communities was similar. The stress value of this ordination plot was 0.09, indicating an ordination with an excellent representation of the underlying Bray-Curtis similarity matrix, with no prospect of misinterpretation (Clarke & Warwick, 2001).

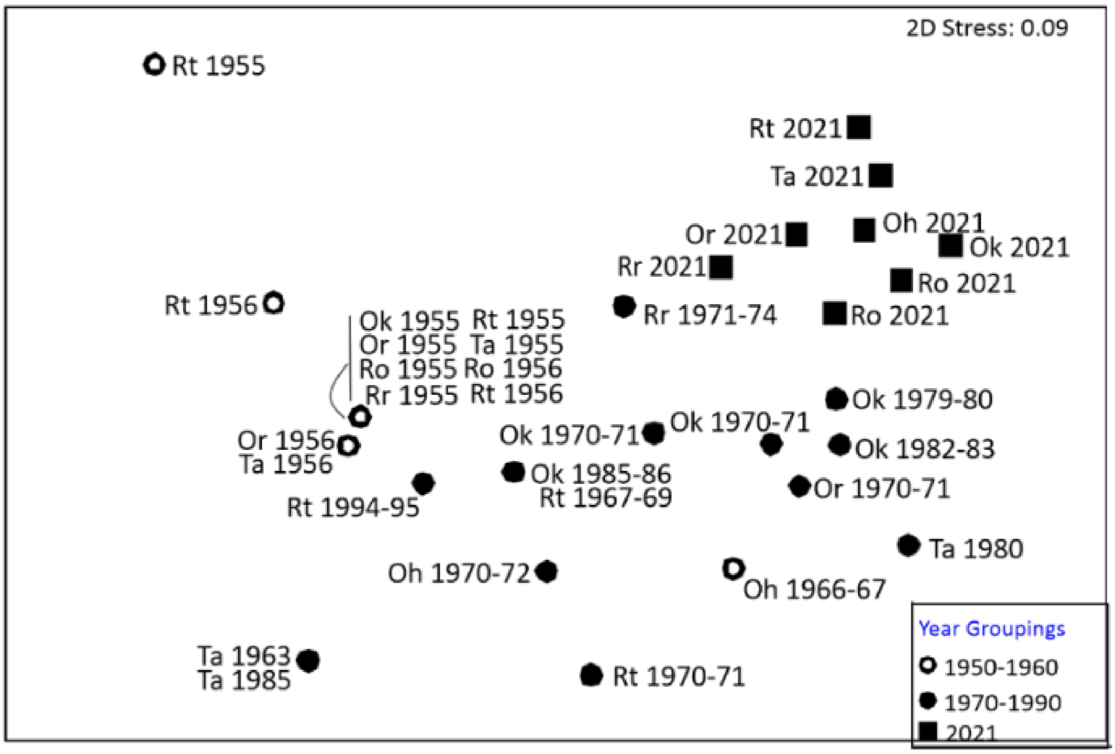

Figure 4. Non-metric multidimensional scaling ordination (nMDS) showing historical zooplankton communities (1950-90) from Bay of Plenty and Waikato regions lakes and 2021 zooplankton communities sampled with the 75 µm mesh zooplankton net data.

ANOSIM again indicated that differences in zooplankton community composition between the three-year groups were significant (Global R = 0.442; p = 0.001). Pairwise tests indicated that zooplankton community composition was significantly different between each possible pairing of the three different year groupings; between 1950-69 and 2021 (r = 0.920; p = 0.001), 1970-90 and 2021 (r = 0.452; p = 0.002), and 1950-69 and 1970-90 (r = 0.438; p = 0.001).

The SIMPER analysis for the 1950-69 samples and 2021 75 µm zooplankton net samples (Table 4) indicated that of the ten zooplankton taxa contributing most greatly (>5%) to the dissimilarity in community composition, eight were rotifer taxa. Additionally, all zooplankton taxa considered in this analysis had higher average frequencies in the 2021 samples than in the 1950-69 samples. Many of the rotifer taxa increased from total absence in the 1950-69 samples to high average frequencies in 2021: *Polyarthra* spp., *Synchaeta* spp., *Trichocerca* spp., bdelloid rotifers, *Collotheca* spp. and *Conochilus unicornis*. The rotifers *Asplanchna* spp. and *Keratella* spp. were the only rotifer taxa present, although in small frequencies, within the 1950-69 samples. The cladoceran *Daphnia galeata* and cyclopoid copepod *Mesocyclops australiensis* both increased in importance from total absence in the 1950-69 samples, to high and relatively high average frequencies in 2021.

The SIMPER conducted on the 2021 75 µm zooplankton net samples and 1970-90 samples indicated that rotifers were the zooplankton group to contribute most greatly to the dissimilarity in community composition. The rotifers *Trichocerca* spp., bdelloid spp., *Synchaeta* spp., *Conochilus unicornis, Collotheca* sp., *Polyarthra* spp., and the copepod *Mesocyclops australiensis*, all increased in frequency from the 1970-90 samples to high average frequencies in 2021. The cladoceran *Daphnia galeata* was the greatest contributor to dissimilarity in zooplankton composition between the 1970-90 samples and the 2021 75 µm zooplankton net samples, increasing from total absence in 1970-90 to high average frequency in 2021. Lastly, the cyclopoid copepod *Macrocyclops albidus* was the only zooplankton taxon in this analysis to decrease in frequency, occurring widely in the 1970-90 samples, but was absent in the 2021 samples, as was observed in the 37 µm dataset between these dates.

Table 4. SIMPER analysis using 1950-69 zooplankton community composition data and 2021 75 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1950-69** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Polyarthra spp.	0.00	0.89	8.97
Synchaeta spp.	0.00	0.89	8.97
Asplanchna spp.	0.07	1.00	8.02
Daphnia galeata	0.00	0.79	7.78
Trichocerca spp.	0.00	0.89	7.60
Keratella spp.	0.06	0.78	7.48
Bdelloid spp.	0.00	0.78	6.66

Conochilus unicornis	0.00	0.56	5.68
Mesocyclops australiensis	0.00	0.56	5.47
Collotheca spp.	0.00	0.67	5.37

Table 5. SIMPER analysis using 1970-90 zooplankton community composition data and 2021 75 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1970-90** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Daphnia galeata	0.00	0.78	8.00
Trichocerca spp.	0.15	0.89	6.87
Macrocyclops albidus	0.77	0.00	6.61
Bdelloid spp.	0.00	0.78	6.23
Synchaeta spp.	0.38	0.89	5.97
Conochilus unicornis	0.00	0.56	5.81
Collotheca spp.	0.00	0.67	5.56
Mesocyclops australiensis	0.15	0.56	5.29
Polyarthra spp.	0.54	0.89	5.19

2.3.4 Zooplankton community composition observations from the historical dataset and the 2021 100 µm zooplankton net mesh dataset

The ordination plot constructed using the historical dataset and 2021 100 µm mesh zooplankton net samples also indicated a separation of samples from each of the year groupings, similar in distribution to the 37 µm and 75 µm nMDS ordinations. The 2021 100 µm samples were distributed to the lower right and centre, and the 1950-69 samples were distributed to the left and upper left area of the ordination. The separation within the ordination indicates variability in the community composition of zooplankton has changed from 1950-69 to 2021. Like the prior ordinations, the 1960 samples were distributed in the mid-area of the ordination, overlapping with the 1970-90 samples. This overlap indicates similar zooplankton community composition during these time periods. The stress value of this ordination was 0.13, indicating the ordination is a good representation of the underlying Bray-Curtis similarity matrix with little prospect for misinterpretation (Clarke & Warwick, 2001).

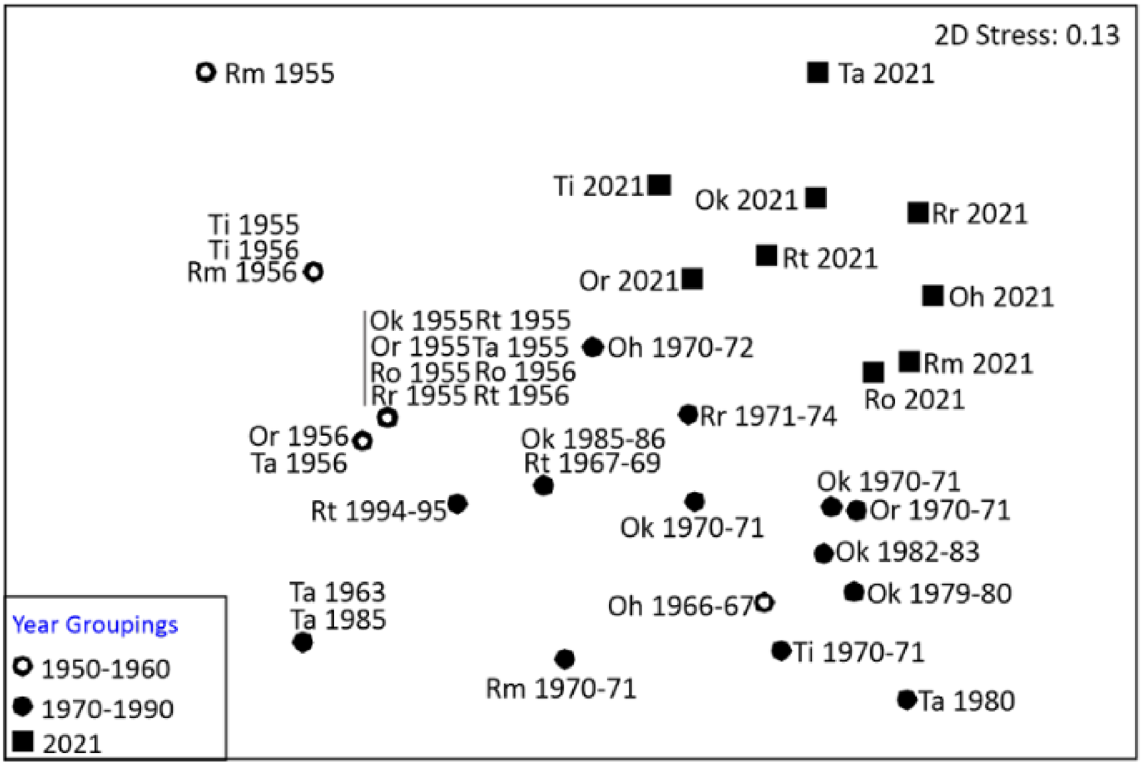

Figure 5. Non-metric multidimensional scaling ordination (nMDS) showing historical zooplankton communities (1950s 1990s) from Bay of Plenty and Waikato regions lakes and 2021 zooplankton communities sampled with the 100 µm mesh zooplankton net data.

ANOSIM indicated that differences in zooplankton community composition between the three year groupings were significant (Global R=0.467, p=0.001). Pairwise tests indicated significant differences among all possible combinations of the three different year groupings. Thus, each group was significantly different from one another; 1950-69 and 2021 (r=0.857; p=0.001), 1970-90 and 2021 (r=0.525; p=0.001) and 1950-69 and 1970-90 (r=0.506; p=0.001).

The cladoceran *Daphnia galeata* had the greatest contribution to the dissimilarity in the SIMPER analysis between the 2021 100 µm net samples and the 1950-69 samples (Table 6), increasing from total absence during 1950-69 to a high average frequency in the 2021 samples. The rotifers *Asplanchna* spp. and *Synchaeta* spp., cladoceran *Chydorus* spp. and copepod *Mesocyclops australiensis* all increased from either total absence, or very low average frequencies during 1950-69, to high average frequencies in 2021. A decrease in the average frequency of the cladoceran *Ceriodaphnia dubia* was observed, the only zooplankton taxon in this analysis to decrease in average frequency since 1950-69 sampling.

Like the prior SIMPER analysis, the cladoceran *Daphnia galeata* had the highest contribution percentage to community composition change, increasing from total absence in 1970-90 to a high average frequency in 2021 (Table 7). Furthermore, *Macrocyclops albidus* was the species with the second highest contribution percentage, decreasing in frequency from the historical samples to complete absence within the 2021 samples (Table 7). Within this SIMPER analysis, there were several zooplankton taxa found more frequently among the historical samples than in the 2021 samples, which was not commonly observed in my previous analyses. Zooplankton that increased in average frequency from 1970-90 to 2021 were the copepod *Mesocyclops australiensis*, cladoceran *Chydorus* spp. and rotifer *Synchaeta* spp.. Zooplankton that decreased from higher average frequency in 1970-90 to 2021 samples were the copepod *Macrocyclops albidus*, cladoceran *Ceriodaphnia dubia* and rotifer *Polyarthra* spp..

Table 6. SIMPER analysis using 1950-69 zooplankton community composition data and 2021 100 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1950-69** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Daphnia galeata	0.00	1.00	13.16
Asplanchna spp.	0.07	1.00	12.04

Chydorus spp.	0.07	0.89	11.23
Mesocyclops australiensis	0.00	0.78	9.89
Synchaeta spp.	0.00	0.67	7.71
Ceriodaphnia dubia	0.71	0.56	6.71

Table 7. SIMPER analysis using 1970-90 zooplankton community composition data and 2021 100 µm zooplankton net community composition data throughout the Waikato and Bay of Plenty regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groupings.

Species	**1970-90** Average frequency of occurrence across 9 lakes	**2021** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition change (%)
Daphnia galeata	0.00	1.00	11.04
Macrocyclops albidus	0.77	0.00	8.09
Mesocyclops australiensis	0.15	0.78	7.50
Chydorus spp.	0.38	0.89	6.84
Synchaeta spp.	0.38	0.67	5.88
Ceriodaphnia dubia	0.92	0.56	5.62
Polyarthra spp.	0.54	0.33	5.28

2.4 Discussion

Strong evidence was found of zooplankton diversity and community composition change between the 1950s and 2021. Each of the nMDS ordination plots (Figure 3, 4, & 5) and associated ANOSIM analyses indicated a temporal gradient in zooplankton composition. These observed temporal gradients imply consistent patterns of change in zooplankton composition across a variety of lakes through time. These major changes observed were the high frequencies of *Daphnia galeata* in the 2021 samples, a species that was completely absent from the historical samples; the absence of *Macrocyclops albidus* from the 2021 samples, and the common occurrence and high frequencies of rotifer in the 2021 samples compared to the historical samples.

2.4.1 *Daphnia galeata* invasions into lakes of New Zealand

The cladoceran *Daphnia galeata* was the highest contributing species to the dissimilarity in community composition change between the 2021 and historical samples. *Daphnia galeata* was completely absent from the 1950-69 and 1970-90 samples yet was found at a high frequency in samples collected in 2021. These findings are consistent with the first observations of *D. galeata* entering New Zealand's lakes. Prior to 1990, *Daphnia* were considered uncommon constituents of zooplankton communities in New Zealand's lakes, particularly in the North Island (Chapman *et al.*, 1975; Duggan & Collier, 2018). *Daphnia galeata* were first identified in New Zealand's lakes in the early 1990s (Duggan *et al.*, 2006), and has become widespread invaders in North Island freshwater bodies (Chapman *et al.* 2011; Duggan & Pullan, 2017; Ye *et al.* 2021).

As of the early 1990s, two non-indigenous *Daphnia* species were known to have established populations in New Zealand; *Daphnia pulex* (Leydig, 1860) and the previously cited *Daphnia galeata* (Duggan *et al.,* 2006). The North American species *D. pulex* was first observed in lakes of the South Island in 2005 (Duggan *et al.*, 2012) and was more recently identified inhabiting ponds in the Auckland region of the North Island (Branford & Duggan, 2017). *Daphnia galeata* was first recorded within samples from Lake Rotoroa, Hamilton, in 1993, and was found to be widespread in a survey conducted of lakes throughout the Waikato and Auckland regions in 1997-98 (Duggan *et al.*, 2006). Overall, this species has become the most common and widespread species of *Daphnia* in North Island freshwater systems yet remains relatively rare in South Island freshwater systems (Duggan & Pullan, 2017). Thus, my result of *D. galeata* being absent from studies from 1950-69 and 1970-90, and high average frequencies within the 2021 samples, is consistent with its timing of discovery in North Island waters.

Daphnia are a relatively large-bodied, fast-growing genus of cladoceran (Karabanov *et al.*, 2018), and highly efficient filter feeders (Balvert *et al.* 2009). They are well-known for their ability to colonise eutrophic lakes by taking advantage of changes in nutritional conditions

(Spaak *et al.*, 2012; Karabanov *et al.*, 2018) and being highly effective phytoplankton grazers (Ha & Hanazato, 2009). Many accounts of *Daphnia* invasions within European lakes have been reportedly linked to their ability to inhabit eutrophic water bodies (Jankowski & Straile, 2003; Rellstab *et al.*, 2011; Spaak *et al.*, 2012). Within central Europe, *D. galeata* were reported to have successfully invaded Lake Constance and numerous other lakes within Switzerland following World War II, due to an increase of nutrient input into freshwater systems from population growth (Brede *et al.*, 2009; Rellstab *et al.*, 2011; Spaak *et al*., 2012). Although this is perhaps the case overseas, my data show that *D. galeata* was found in high frequencies within lakes of differing trophic levels. For example, *D. galeata* was found to be present in high numbers during both sampling events in eutrophic Lake Okaro and Rotoehu yet was also present in mesotrophic Lake Rerewhakaaitu and oligotrophic Lake Taupō. Based on my research alone, degradation of lake trophic state cannot be suggested as a catalyst in the successful invasion of *D. galeata* into North Island lakes.

The impact on existing communities by *Daphnia galeata* has been explored within New Zealand and internationally. Karabanov *et al.* (2018) investigated the invasion of *D. galeata* into the Lower Lakes of South Australia, and the potential impact this species may pose on the existing native biota was identified. It was suggested that due to *D. galeata* being large-bodied and fast-growing (Karabanov *et al.* 2018), it can easily occupy a dominant position within zooplankton communities. They also have well adapted defence mechanisms to avoid predation by fish, such as vertical diel migration (Spaak *et al.*, 2012; Karabanov *et al.*, 2018), and overall, compared to other species of native Australian zooplankton have superior competitive abilities. Balvert *et al.* (2009) also found the timing of invasion of *D. galeata* into Lake Puketirini to coincide with decreased chlorophyll *a* concentrations and rotifer abundances. Interestingly, my research found rotifers to be highly abundant within samples, especially within the smaller meshed nets (37 µm and 75 µm). As to how *D. galeata* may have entered New Zealand waters remains speculative, yet being so common among lakes around the North Island indicates their invasion has been very successful. Like many invasive species that have entered New Zealand, natural passive dispersal into the country was highly unlikely due to being geographically isolated (Duggan *et al.*, 2006). Thus, the prospect of this species arriving through human facilitated activities is possible.

From my research, it is difficult to decipher just how much of an impact *D. galeata* potentially has had on the existing zooplankton communities. What can be confidently determined is that my results are not consistent with that of Balvert *et al.* (2009), as rotifers were abundant within the 2021 samples, even in the presence of *D. galeata*. Their recent invasion into New Zealand's waters and active presence within samples taken in 2021, indicates that they are now a component of the plankton within most North Island lakes. Their presence remains largely isolated within the North Island. However, they may have been accidentally introduced into the South Island recently, in conjunction with Grass Carp introductions for the purpose of weed control (Duggan & Pullan 2017).

2.4.2 Absence of *Macrocyclops albidus* from the 2021 samples

My results show that from 1950-69 to 1970-90, the cyclopoid copepod *Macrocyclops albidus* increased in average frequency, and had the second highest contribution percentage of all the species. Yet, from 1970-90 to 2021, *M. albidus* were the only zooplankton species to decrease in frequency, being completely absent from the 2021 samples. This result suggests that this species is not common or abundant within North Island lakes.

Within multiple research papers included within my literature review, *M. albidus* were present in samples, but never abundant. Historical studies conducted in Lake Taupō, during 1970-71, 1974-76 and several of the Rotorua lakes during 1967-69 found *M. albidus* to be the only cyclopoid copepod present within samples and were only ever present in small numbers (Chapman, 1973; Forsyth & McCallum, 1980; Chapman *et al.,* 1985; Chapman & Green, 1999). For example, Chapman (1973) stated that from samples collected in 1967-69 from lakes Rotorua and Rotoiti, *M. albidus* were the only cyclopoid copepod present and were never abundant. Chapman *et al.* (1985) also found it in low abundances within samples from 1970-71, never forming more than 10% of samples taken from the seven lakes included in their study. Chapman & Green (1999) found it to be only a minor component of the plankton samples in Lake Rotorua during their 1995-96 sampling, and Forsyth & McCallum (1980) found it in very low abundances within Lake Taupō sampling in 1974-1976. Within more recent research papers, *M. albidus* is occasionally present within samples, but does not appear to be a common constituent of zooplankton communities. Interestingly, *Mesocyclops australiensis* appears to be the more common cyclopoid copepod within recent studies. Duggan & Hussain (2007) found within their report of trophic state change of Auckland lakes, *M. albidus* was present in Lake Kuwakatai only, whilst *M. australiensis* were found within all eight of the lakes. Within Duggan (2007) assessment of zooplankton community composition within ten Waikato lakes, *M. albidus* were found in Lake Otamatearoa, whilst *Mesocyclops australiensis* were found in six of the eight lakes. Copepods found within Burger *et al.* (2002) research of zooplankton abundance in the Waikato River did not include *M. albidus,* but again identified *M. australiensis.* Within the Duggan & Pullan (2017) study of aquaculture ponds, five copepod species were found, none of which were *M. albidus*. However. *M. australiensis* was again the only cyclopoid copepod identified.

My data show that the absence of *M. albidus* coincides with the increase of two other large zooplankton frequencies; *D. galeata* and previously mentioned *M. australiensis.* Within the 2021 samples from the 100 µm net, both *D. galeata* and *M. australiensis* had low average frequencies or were absent from historical samples yet were abundant within the 2021 samples. The same trend was observed within the finer meshed net samples. However, the frequency of occurrence of both zooplankton species in 2021 was lower than the 100 µm. Conversely, *M. albidus* were more common within the historical samples, and were absent within the 2021 samples. A possible explanation for the absence of *M. albidus* within recent samples may be due to the invasion of *D. galeata* into North Island lakes. Although there is currently no research available supporting this, the establishment of *Daphnia* have been known to negatively affect other zooplankton abundances (Duggan *et al.* 2006), and the standing crop of phytoplankton due to grazing pressures (Beisner, 2001). Multiple research projects have been conducted on the potential impact *Daphnia* can have on the cyclopoid copepod taxa *Mesocyclops* spp. A study conducted in Japan found *Daphnia* suppressed the abundances of *Mesocyclops* species due to competition for food resources during the naupliar life stage of *Mesocyclops* (Ha & Hanazato, 2009). Vanni (1986) found similar results, in that *Mesocyclops* spp. were being outcompeted by *Daphnia* for food resources in their juvenile stages. Considering *M. australiensis* and *D. galeata* were found in high abundance within the 2021 samples, this competition for food resources may not be occurring within New Zealand waters between these two species. However, it may be having some impact on *M. albidus* with food competition.

Within the literature, there is limited past research that suggests *M. albidus* has perhaps been outcompeted by other species, both within New Zealand and internationally. Therefore, these theories are only speculative. Further research is required to determine whether *M. albidus* is being outcompeted within New Zealand's lakes by non-native species, such as *D. galeata.*

2.4.3 Differences in historical and present-day Rotifers frequencies

There is an evident contrast in species assemblages between the historical samples and the 2021 samples. Low average frequencies of rotifer taxa were found in the 1950-69 and 1970-90 research papers, while high frequencies of rotifer taxa were observed within the 2021 samples. Rotifers made up most of the species encountered in the 2021 samples and were the dominant taxon contributing to the dissimilarity in community composition changes over time. This was mostly observed within the 37 µm and 75 µm net samples (Table 2,3,4 & 5). Generally, the larger zooplankton taxa (copepods and cladocerans) were found in higher frequencies within samples from the 100 µm mesh net (Table 6 & 7). Furthermore, samples taken using the smaller meshed nets (37 µm and 75 µm) had higher species richness overall, than samples caught within the 100 µm net (Figure 2). Lower frequencies of rotifers recorded from historical studies and a high average frequency in the 2021 samples suggests a temporal shift in zooplankton composition through time. However, this observed community composition shift from low to high rotifer taxa frequencies may not be completely true and may represent changing sampling methods through time.

Rotifers were less represented in the historic research compared with recent samples and compared to cladocerans and copepods in those papers. Many resources used to construct my historical zooplankton community composition dataset came to similar conclusions regarding rotifers; that rotifers were of minor importance within zooplankton communities, they were studied in little detail, or were completely absent from samples. For example, Jolly (1959) deemed rotifers to be uncommon and rarely important within the sampled plankton among several North Island lakes (all lakes included within this study, except for Ohakuri). In 1965, she acknowledged rotifers as uncommon within samples from Lake Taupō (Jolly, 1959). Chapman *et al.* (1985) stated within their study of seven Rotorua lakes that rotifers were not studied in detail, nor were they of major importance within many of the lakes sampled during 1977-78. Chapman & Green (1987), in a review of New Zealand zooplankton, even speculated that rotifer species diversity may be low within New Zealand freshwater bodies relative to elsewhere, based on the small number of studies that have given adequate attention to rotifer identification.

Rotifers are highly opportunistic zooplankton. Rotifers are able to rapidly fill available niches due to having fecundity, short generational times, and high dispersal abilities (Shiel, 1995; Pennak, 1978; Virro, 1999; Arcifa *et al.,* 2020). It is difficult to be convinced of the idea that rotifer species diversity was low within New Zealand freshwater bodies and was historically insignificant within the plankton, as they are characteristically opportunistic and highly adaptable. Rotifers are among the smallest of the freshwater metazoans (Gannon & Stemberger, 1978), therefore a zooplankton net of finer mesh would be required when sampling to quantify rotifer communities. Interestingly, past research papers did not always consider this, and it became apparent when conducting the literature review that many past sampling events within New Zealand's lakes used very coarse meshed zooplankton nets. It has been documented numerous times that rotifers were frequently overlooked or improperly quantified due to the size of mesh used within the historical sampling (Likens & Gilbert, 1970; Chapman *et al.,* 1985; Chick *et al.*, 2010). For example, Forsyth & McCallum (1980), conducting research on Lake Taupō, identified large changes in the zooplankton community since an earlier description by Jolly (1965; 1959), with rotifers making up 49.7% of their total samples numerically. There was a noticeable variation in zooplankton mesh sizes used; Forsyth & McCallum (1980) utilised a 55 µm zooplankton net, while Jolly (1965) used a zooplankton net with No. 4 bolting silk, equivalent to 318 µm mesh size. Forsyth & McCallum (1980) acknowledged sampling with a net of such coarse mesh size would not have been appropriate to catch most rotifers.

The historical underestimation of rotifer species has been reported to date as far back as 1916, when Juday stated number 20 silk bolting cloth (equivalent to 75 µm mesh), was an adequate mesh size for sampling the vast majority of rotifer taxa (Gilbert & Williamson, 1983; Chick *et al.*, 2010). The use of an improper mesh size whilst sampling zooplankton communities can bias results, as a coarse mesh will sample only the larger individuals from a population (Likens & Gilbert, 1970). Results cannot be expected to be characteristic of the natural communities as a result, which may be the case within some of the historical literature. Legitimate reasons for employing the use of larger meshed nets do exist, including the avoidance of filtration errors due to clogging within smaller meshed nets (Likens & Gilbert, 1970; Chick *et al.*, 2010), especially in lakes with higher turbidity. It was not mentioned in any of the resources that clogging was avoided by using larger meshed zooplankton nets at the expense of biased results. Thus, to assume this is why larger meshed nets were used would not be accurate.

Based on my findings, it is more likely that an inadequate use of zooplankton net mesh sizes was causing an underestimation of rotifers historically, rather than a shift in community composition within North Island lakes. In more recent studies, it has been reported that rotifers are the dominant group of zooplankton within freshwater ecosystems (Saler, 2004; Ismail & Adnan, 2016). Rotifers dominating species lists has been observed within many recent research papers in New Zealand (e.g., Duggan *et al.,* 2004; Duggan & Pullan, 2017). Furthermore, in a study of rotifer species distributions, an average of 21.1 rotifer species were found within a set of 35 North Island lakes (Duggan *et al.*, 2002).

Another interesting discovery within my study when considering past research papers is that rotifers did not appear to become less important within zooplankton communities despite the presence of *D. galeat*a. As mentioned earlier, *Daphnia* species have the potential to negatively impact rotifers communities once established in a new environment. This is fundamentally due to *Daphnia's* ability to outcompete rotifers for food resources (Gilbert, 1988; MacIsaac & Gilbert 1989), as they are highly efficient filter feeders and grazers of phytoplankton. A study conducted by Balvert *et al.* (2009) found within Lake Puketirini, New Zealand, a shift in zooplankton community composition from one dominated by rotifers, to cladocerans (*Daphnia galeata*). This was ultimately deemed a result of increasing lake water clarity due to *D. galeata's* highly efficient filter feeding capabilities (Balvert *el at.*, 2009). It is therefore interesting to observe within my results a high average frequency of rotifers as well as high average frequencies of *D. galeata* within the 2021 samples. As both resources above concluded *Daphnia* were outcompeting rotifer for food resources, my results could then be indicating that food resources within the lakes sampled are not a limiting factor.

2.4.4 Species richness

Differences in species richness between historical sampling and recent sampling were mostly significant. There was a general trend of increasing species richness through time, in that the historical samples had lower species richness than the 2021 samples combined. This may be explained by the underrepresentation of rotifers within historical samples due to improper net mesh selection. The 2021 100 µm net samples also appear to have a species richness more representative of the 1970-90 samples, as seen in the bar graph (Figure 2). Interestingly, the Bonferroni post-hoc testing revealed that specifically, there is no significant difference in species richness between the years 1970-90 and all three of the 2021 net samples.

Several of the historical research papers used within this research utilised mesh sizes of 100 um or larger. For instance, Jolly (1959) sampled several the Rotorua lakes using a net with 318 µm mesh, Jolly (1965) sampled Lake Taupō with a 239 µm zooplankton net, Chapman *et al.* (1985) sampled several Rotorua lakes using a net with 158 µm mesh and Chapman (1973) sampled Lake Rotorua with a net of 100 µm mesh. This could explain why the 2021 100 µm net samples are more representative of the 1970-90 samples in terms of species richness, as several of the past research papers utilised zooplankton nets with mesh sizes of 100 µm and 158 µm. However, it would be expected that there was significant difference between the 2021 37um and 75um samples and the historical samples species richness due to the difference in the sizes of the zooplankton net mesh used. However, the standard deviation bars for the bar graph do show that the 1950-69 and 1970-90 samples have a greater range of species richness' than the 37 µm and 75 µm samples. This could indicate that perhaps even though there were a greater number of rotifer species found within the 37 µm and 75 µm samples, historical samples could have had a higher number of larger zooplankton species within samples. More recent sampling may have been more impacted by clogging, due to several of the lakes being eutrophic, and thus had greater spill over and loss of the large zooplankton species, than previously thought.

Chapter Three: The influence of mesh size of nets on zooplankton composition and species richness estimates in New Zealand lakes

3.1 Introduction

When conducting any type of research, a well thought out sampling design is imperative for producing reliable, robust data (Gajbhiye, 2002). Sampling success is largely dependent on the equipment selected and should be contingent on the project objective. The ability to collect representative measurements of zooplankton community composition and diversity relies heavily on the methodology that is used while sampling (Goswami, 2004). Zooplankton are a widely researched organism due to their intermediate position in the food web and its usefulness as a bioindicator of lake trophic state and ecological health (Jeppesen *et al.*, 2011; Ejsmont-Karabin, 2012; Fu *et al.*, 2021). As a result, many different research projects using different techniques and methods have been adopted through time, reflecting personal preference (Mack *et al.*, 2012) and the question being asked (Hairston, 1989). The use of any sampling method can introduce method and gear specific-bias, and in turn produce artificial variability within zooplankton communities when compared against samples collected using different methods (Frank, 1988).

There are three methods with which zooplankton are commonly sampled, that vary depending on the questions being asked: bottles/water samples, pumps, and nets (Gajbhiye, 2002; Goswami, 2004). The first two methods are primarily used for collecting zooplankton from known volumes of water from discrete depths. The use of bottles and other zooplankton traps have been criticised due to the small volume of sample they collect and avoidance of these samplers by larger bodied zooplankton (Likens & Gilbert, 1970). Sampling zooplankton by vertical net hauls is the most commonly used method. However, the use of nets is frequently criticised due to loss of zooplankton through the mesh (Vannucci, 1968; Pansera *et al.*, 2014), the changing filtration efficiency through the course of the tow (Tranter & Smith, 1968), and net avoidance by some taxa (De Vries & Stein, 1991; Clarke & Warwick, 2001). Filtration efficiency can be greatly reduced due to clogging of the mesh, which can create differential pressures across the net, create unequal filtration in different areas of the water column and increase the volume of water by-passing the net (Likens & Gilbert, 1970). It is thus generally accepted that nets can provide only qualitative, or semi-quantitative, samples of zooplankton (Green, 1977). Despite this, the volume filtered by the net is commonly estimated by multiplying the area of the net opening by the distance towed (De Bernardi, 1984; Goswami, 2004; Cole *et al.*, 2014).

Each zooplankton taxon ranges in size (Mackas & Beaugrand, 2010), and morphological features (Goswami, 2004). Using nets with a smaller mesh size will allow for sampling smaller bodied zooplankton, yet also increase the likelihood of clogging, reducing the filtration efficiency, drag, and therefore provide inaccurate quantification of zooplankton populations (Fraser, 1968), especially in eutrophic water bodies (Vannucci, 1968). Smaller nets are more efficient at capturing copepod nauplii and rotifer species than larger meshed nets (Chick *et al.*, 2010), whilst larger nets would not be able to adequately sample these species if the mesh is larger than the nauplii and rotifer species body size. Nichols & Thompson (1991) suggested after a detailed mesh-size study that nets with mesh ≤ 61 µm are suitable for accurately quantifying copepod nauplii abundances. The recommended mesh size for rotifers has been debated within the literature, which has led to a historical method-specific bias quantification of rotifers within samples. Sampling methods using mesh sizes for rotifer as large as 64 µm (Strecker *et al.*, 2004) to 70 µm (Bonecker & Lansac-Tôha, 1996) have continued to be used within research projects, while some authors have recommended that a mesh size required for sampling rotifers is ≤ 35 µm (Likens & Gilbert, 1970; Ejsmont-Karabin, 1978).

Furthermore, a zooplankton's age (life stage), behaviour and even species could impact catchability. A well-developed concept of sample bias is the theory of zooplankton's ability to avoid capture of towed nets. This was first proposed by Franz (1910), who suggested that zooplankton were capable of seeing a net within the water column during daylight, and thus could avoid capture (Fleminger & Clutter, 1965). It was again suggested by Bary *et al.* (1958) that zooplankton are able to avoid capture by detecting a pressure change preceding a towed net, and Brook & Woodward (1956) found copepods were responsive to accelerating current as a response to changes in pressure field. Therefore, the possibility of zooplankton, especially copepods, avoiding capture due to detecting changes in hydrostatic pressure may influence the reliability of zooplankton sampling using nets. The avoidance of nets by zooplankton can result in both the underestimation in abundances, as well as unintentional selective sampling (Clutter, 1968).

Within past New Zealand zooplankton research, there have been a variety of different mesh sizes used. For example, Jolly (1977), sampled the zooplankton within several North Island Lakes, including Rotorua, Rotoehu, Tikitapu and Taupō, in 1957-58. For this study, a zooplankton net made of No.4 bolting silk with a 45 cm mouth diameter conical net, equivalent to 318 µm mesh. In 1967-69, Chapman (1973) conducted vertical hauls using a 20 cm mouth diameter net made from 100 um mesh to sample Lake Rotorua. In 1994-95 Chapman & Green (1999) conducted vertical hauls using a 20 cm mouth diameter net made of 42 µm mesh to also sample Lake Rotorua. Using a variety of different mesh sizes influences results, as larger mesh will favour larger zooplankton, smaller nets will enable semi-quantitative sampling of rotifers, which ultimately results in differences between size, abundance and composition estimates due to size selectivity (Mack *et al.,* 2012). This will be an important consideration when analysing effects net size may be having on zooplankton community composition within this thesis.

3.1.1 Chapter Aims

In this chapter, I consider the effects of mesh size on zooplankton community composition, utilising 37 µm, 75 µm and 100 µm mesh sizes, which covers the range of mesh sizes used in past New Zealand zooplankton studies. This chapter relates back to Chapter 2 but is specifically analysing whether mesh sizes may have influenced the observed community composition changes through time.

3.2 Methods

Refer to Chapter two, subsection 2.2, for the general methodology carried out prior to field work, field sampling and laboratory work. The following statistical analysis is specific to this chapter only, using the data from sampling carried out in 2021 within nine lakes in the Waikato and Bay of Plenty regions. Data from the historical dataset is not included within this chapter, as it has been designed to only examine variability in zooplankton composition among the three different nets of differing mesh sizes. This is to be examined using the data from the 2021 sampling events, that is the presence-absence data which indicates which species were found within each of the different net samples, and the abundances of each species present within samples.

The following methodology outlines the statistical analysis applied to the 2021 datasets to examine differences in zooplankton composition and abundance between nets, which could possibly explain some of the change observed in Chapter 2. Therefore, this section will assist in identifying whether observed changes in zooplankton community composition was a product of natural, cyclic processes, anthropogenic influence, or an artificial representation of zooplankton composition due to method specific bias. Analysing composition of zooplankton and abundance across the three different mesh sizes and comparing the results of each net also will help to identify how influential net size is on results. This is important to understand as improper selection of zooplankton net mesh can not only result in an underestimation of zooplankton abundances but can also result in accidental selective sampling and a misrepresentation of the zooplankton community within the area of sampling.

3.2.1 Zooplankton composition differences among nets of different mesh size

To test for differences in assessments of zooplankton assemblages among nets, I used three approaches: 1) examining variability in the presence-absence of species among nets with different mesh sizes (i.e., species lists), 2) examining community composition based on 'abundances' among nets of different mesh size, and 3) examining differences in species richness among nets with different mesh sizes.

For analysis of the presence-absence data, net mesh size was analysed as a factor. As all taxa were reported as 0 (absent) or 1 (present), no transformation was required to down weigh the importance of abundant taxa prior to analysis. Copepod nauplii were removed from all analyses as identification to species level could not be undertaken confidently.

Prior to analysis, the semi-quantitative abundance data were log (x + 1) transformed to reduce the influence of highly abundant species/taxa. Zooplankton species that contained < 3 individuals were removed from the analysis to reduce the influence of rare species possibly caught by chance. For analysis of both the presence-absence and abundance data, a Bray-Curtis similarity matrix was constructed based on the abundance data. Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity matrix was then applied to the data, producing ordination plots. To test for differences in the zooplankton composition among nets with different mesh sizes, a one-way unordered analysis of similarity (ANOSIM) was used. The calculated R-value from the ANOSIM provides a measure of how similar, or dissimilar, the composition and abundance of zooplankton are, using the different net sizes. Where significant ANOSIM results were found, a SIMPER analysis was conducted to determine which species, or taxa, of zooplankton, were responsible for the dissimilarity among mesh sizes of category pairs (e.g., 37 µm vs 100 µm). Only species that contributed > 5% dissimilarity were considered, as zooplankton contributing <5% were not considered significant enough to use within this thesis.

3.2.2 Species Richness

Species richness is an intuitive and frequently used measure in many research fields within science. However, gaining a complete census of a community within the environment is unattainable (Chao & Chiu, 2016). Using the abundance dataset, zooplankton species richness was calculated for each of the nine lakes within this study from each zooplankton net. Before statistical analyses were conducted on the species richness data, some alterations were made to the data.

Two widely used non-parametric estimators applied to abundance and incidence data are Chao-1 and Chao-2 (Chao *et al.,* 2009). The Chao-1 estimator was applied to the species richness data to concentrate on the rarer zooplankton species within the data set, creating a lower bound of species richness. The applied equation is as follows, which considers species present within the data set only once or twice within samples. Where S_{obs} is the number of species within the sample, S_{Chao1} is the estimated species richness value, F_1 is the number of singletons within the sample (number of species with only a single occurrence within the sample) and F_2 is the number of doubletons within the sample (number of species with exactly two occurrences within the sample) –

$$S_1 = S_{obs} + F_1^2 / 2F_2$$

When doubletons were zero, the following equation was used -

$$S_{Chao1} = S_{obs} + F_1(F_1 - 1) / 2(F_2 + 1)$$

Using the species richness data, both with and without the Chao-1 estimator applied, differences in zooplankton species richness between each net of differing mesh sizes (37 µm 75 µm and 100 μm) were statistically analysed using a repeated measure analysis of variance (Repeated measures ANOVA). If significant differences were found, a Benferroni post-hoc test was then conducted to test what variables were responsible for these differences. Bar graphs were also constructed, using the average species richness of each zooplankton net and standard deviation error bars were applied to the bar graph to communicate how accurately the mean value represents the dataset.

Nauplii were excluded from the species list as they were not identified to species level, including them in this analysis would risk double counting of species. Data from individual lakes Tikitapu and Rotoiti were also excluded from this analysis as there was missing data within their datasets. To eliminate avoidable error, the decision was made as repeat measure ANOVA does not tolerate missing data.

3.3 Results

3.3.1 Zooplankton composition across each net based on the 2021 presence-absence dataset

The nMDS applied to the 2021 zooplankton presence-absence dataset (Figure 8) indicates separation of the majority of 100 μm mesh samples, distributed on the right side of the ordination, from the other two mesh sizes. Separation of the 100 μm mesh samples in the ordination indicates that zooplankton community composition caught within this net was assessed as being different from the samples caught within the 37 μm mesh and 75 μm mesh nets. The 37 μm mesh and 75 μm mesh nets overlapped on the left side of the ordination, indicating similar composition of zooplankton communities within these two net samples. The stress value of this ordination was 0.16, which indicates the ordination is a good representation of the underlying Bray-Curtis similarity matrix and has little prospect of misinterpretation (Clarke & Warwick, 2001).

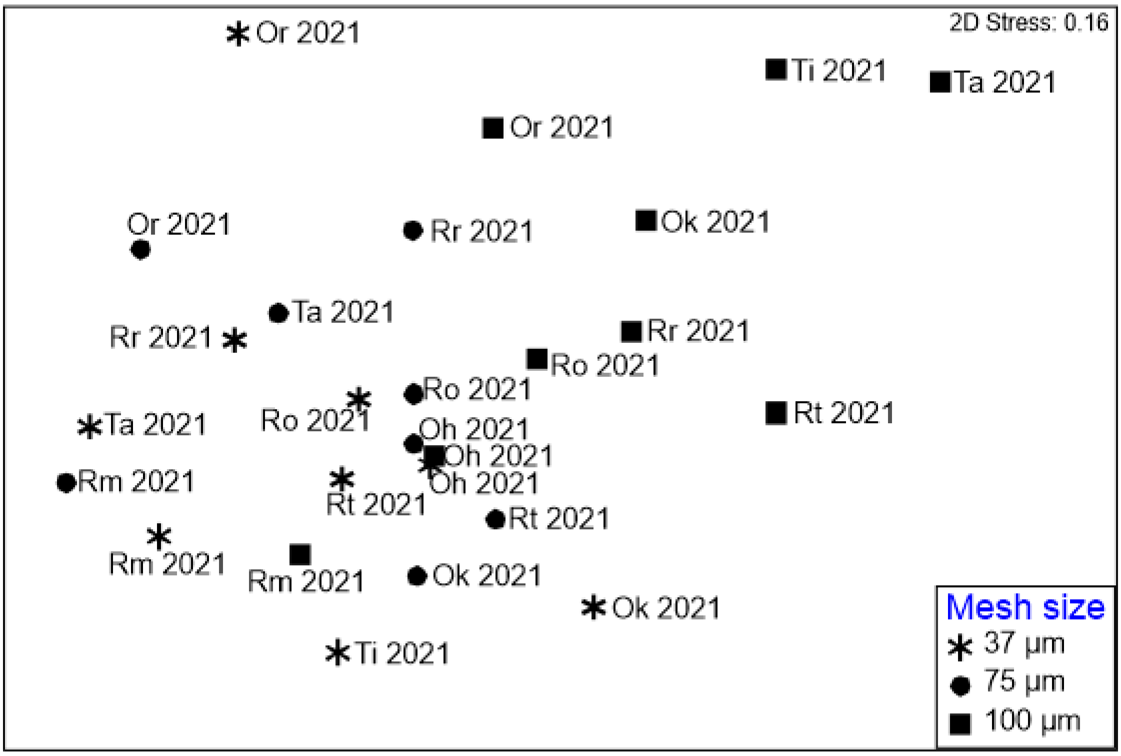

Figure 6 Non-metric multidimensional scaling ordination (nMDS) showing 2021 zooplankton communities from Bay of Plenty and Waikato regions freshwater lakes caught within the three differing zooplankton net mesh sizes (37 µm, 75 µm and 100 µm).

ANOSIM indicated that differences in zooplankton community composition were significantly different among the three mesh sizes (Global $R=0.263$; $p=0.001$). Pairwise tests indicated that differences were significant between the 37 µm and 100 µm net ($r=0.352$; $p=0.001$) and the 75 µm and 100 µm nets ($r=0.230$; $p=0.013$). However, differences between the 37 µm and 75 µm nets ($r=-0.085$; $p=0.870$) were not considered significant.

Of the nine species contributing greater than 5% dissimilarity to zooplankton community composition between the 37 µm mesh and 100 µm mesh nets samples, seven were rotifer taxa. All rotifers within this analysis were more frequently occurring in the 37 µm samples than in the 100 µm samples, and the four species with the highest contribution percentage were rotifers *Keratella cochlearis, Trichocerca similis, Polyarthra dolichoptera* and bdelloid rotifers.

Conversely, the copepod *Mesocyclops australiensis* and cladoceran *Ceriodaphnia dubia* had higher average frequencies within the 100 µm samples than the 37 µm samples.

Table 8. SIMPER analysis of zooplankton community composition of the 37 µm and 100 µm net samples from 9 lakes within the Waikato and Bay of Plenty Regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groups.

Species	**37 µm** Average frequency of occurrence across 9 lakes	**100 µm** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition between nets (%)
Keratella cochlearis	0.89	0.22	8.49
Trichocerca similis.	0.89	0.22	8.30
Polyarthra dolichoptera	0.89	0.33	7.54
Bdelloid spp.	1.00	0.44	6.86
Mesocyclops australiensis	0.44	0.78	6.24
Filinia terminalis.	0.56	0.33	5.88
Ceriodaphnia dubia	0.44	0.56	5.75
Collotheca sp.	0.44	0.22	5.22

From the SIMPER analysis conducted on the 75 µm mesh and 100 µm mesh nets, three quarters of species contributing to greater than 5% dissimilarity are rotifer taxa, like the above SIMPER analysis. Only one species was found to have a higher average frequency within the 100 µm mesh net than the 75 µm net; cladoceran *Chydorus sphaericus*, whilst all other species, including the other cladoceran species; *Ceriodaphnia dubia*, were found in greater average frequencies within the 75 µm net than the 100 µm net. *Keratella cochlearis*, *Trichocerca similis*, and *Polyarthra dolichoptera* were the top three rotifer taxa to have the greatest contribution percentage to difference between zooplankton community composition, such is within the above SIMPER analysis between the 37 µm mesh and 100 µm mesh nets above.

Table 9. SIMPER analysis of zooplankton community composition of the 75 µm and 100 µm net samples from 9 lakes within the Waikato and Bay of Plenty Regions. Species and/or taxa include only those contributing greater than 5% to the dissimilarity between the year groups.

	75 µm	**100 µm**	

Species	Average frequency of occurrence across 9 lakes	Average frequency of occurrence across 9 lakes	Contribution to differences in community composition between nets (%)
Keratella cochlearis	0.88	0.22	9.04
Trichocerca similis	0.88	0.22	8.75
Polyarthra dolichoptera	1.00	0.33	8.68
Collotheca sp.	0.63	0.22	6.99
Conochilus unicornis	0.63	0.33	6.79
Bdelloid spp.	0.75	0.44	6.76
Chydorus sphaericus	0.50	0.89	6.35
Ceriodaphnia dubia	0.63	0.56	6.14
Filinia terminalis	0.38	0.33	5.46
Ascomorphella volvocicola	0.38	0.33	5.42

3.3.2 Zooplankton community composition based on the 2021 abundance data

The 2021 zooplankton abundance data were also statistically analysed to investigate differences in community composition within each net mesh size. The nMDS for the 2021 abundance data indicated some separation between the 37 μm and 100 μm net samples, with the 100 μm mesh net samples being distributed more to the left and middle of the ordination whilst the 37 μm mesh net samples were distributed more to the top right of the ordination. The separation of the two net sizes indicated zooplankton composition assessed using each net were not similar. The 75 μm samples, distributed in the centre of the ordination, overlap intermittently with both the 100 μm samples and the 37 μm samples. This indicates zooplankton composition from the 75 μm net shared occasional similarities in abundance with that found in the other two nets. The stress value of this ordination was 0.19, which corresponds to an ordination providing a good representation of the underlying Bray-Curtis similarity matrix and with little prospect of misinterpretation (Clarke & Warwick, 2001).

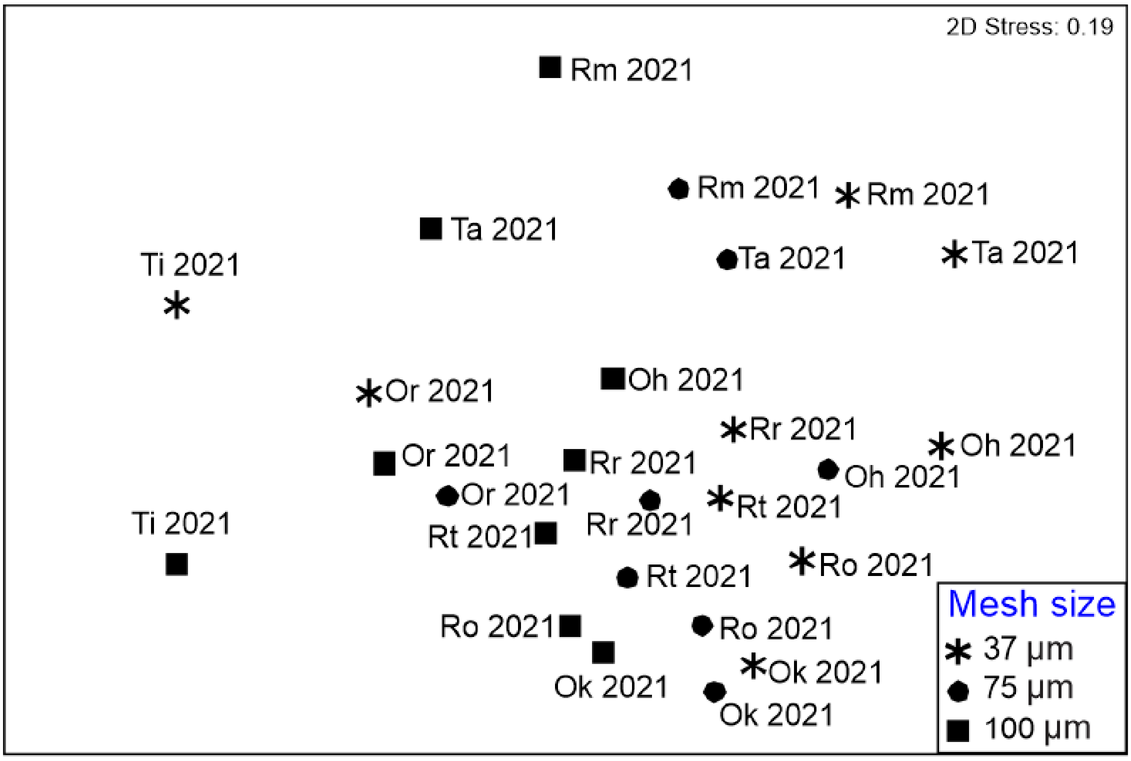

Figure 9. Non-metric multidimensional scaling ordination (nMDS) showing zooplankton abundances from Bay of Plenty and Waikato region freshwater lakes caught within the three differing zooplankton net mesh sizes (37 µm, 75 µm and 100 µm)

ANOSIM indicated that differences in zooplankton composition were significant (Global R=0.185; p=0.007). Pairwise tests indicated significant differences between nets 37 µm and 100 µm (r=0.393; p=0.001), whereas differences were not considered significant between nets 37 µm and 75 µm (r=0.021; p=0.034) or the 75 µm and 100 µm nets (r=0.118; p=0.054).

The rotifer *Polyarthra dolichoptera*, copepod *Calamoecia lucasi* and cladoceran *Daphnia galeata* were the top three contributing zooplankton to the dissimilarity between 37 µm net samples and the 100 µm net samples. Both *C. lucasi* and *D. galeata* were more abundant within the 100 µm samples, whilst *P. dolichoptera* had higher abundances within the 37 µm samples. A further two taxa were also found in higher abundances within the 100 µm samples than the 37 µm samples; the cladoceran *Bosmina meridionalis* and the large predatory rotifer *Asplanchna priodonta*, which was the only rotifer to have a higher abundance in the 100 µm samples. The remaining zooplankton taxa to contribute more than 5% dissimilarity between zooplankton composition between mesh sizes were bdelloid rotifers, *Synchaeta oblonga, Trichocerca porcellus* and copepod nauplii, all having higher abundances within samples caught in the 37 µm mesh net. The general trend revealed within this SIMPER analysis is that rotifer had higher abundances within the smaller 37 µm net, whilst the larger zooplankton (i.e copepods and cladoceran) had higher abundances when using the 100 µm net.

Table 10. SIMPER analysis using log(x+1) transformed abundance data from sampling using zooplankton nets with 37 µm mesh and 100 µm mesh sizes throughout the Bay of Plenty and Waikato Regions. Species included are those contributing greater than 5% to the dissimilarity between mesh sizes.

Species	**37 µm** Average frequency of occurrence across 9 lakes	**100 µm** Average frequency of occurrence across 9 lakes	Contribution to differences in community composition between nets (%)
Polyarthra dolichoptera	14.0	0.01	10.77
Calamoecia lucasi	4.01	7.40	8.21
Daphnia galeata	2.24	9.46	8.00
Bosmina meridionalis	3.06	6.17	7.34
Asplanchna priodonta	2.65	3.78	6.93
Bdelloid sp.	2.85	0.02	6.54
Synchaeta oblonga	2.86	0.03	6.05
Trichocerca porcellus	2.82	0.01	5.95
Nauplii	4.3	1.48	5.76

3.3.3 Species Richness

For both species richness datasets (with and without Chao-1 estimator applied) there was a significant difference between net sizes ($P<0.005$). The bar graphs (Figure 8) revealed the 37 µm and 75 µm zooplankton net sample had the highest species richness, whilst the 100 µm net sample had the lowest species richness for both abundance datasets. The Bonferroni post-hoc tests indicated there was no significant difference between the 37 µm and 75 µm species richness ($p=1.000$), but significant differences were found between the 75 µm and 100 µm and 37 µm and 100 µm species richness (both $p<0.005$). For the dataset with the Chao-1 estimator applied, the mean of 75 µm and 37 µm were higher than the 100 µm (µ=17.58, µ=16.84 and µ=11.94 respectively). For the dataset within the Chao-1 estimator applied, mean of 75 µm and 37 µm were again higher than the 100 µm (µ=15.75, µ=15.5 and µ=10.75 respectively).

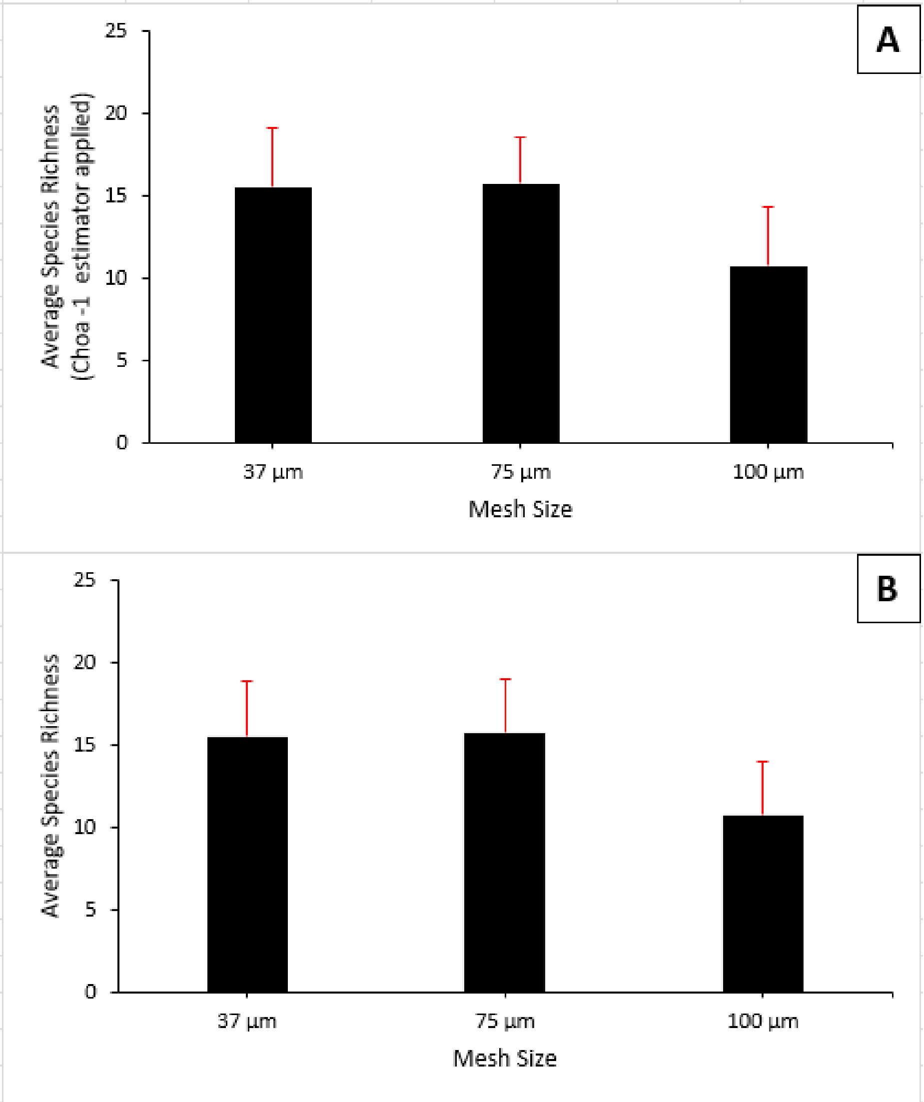

Figure 7. Bar graph with standard deviation error bars showing the average species richness of zooplankton across the differing zooplankton net data from 2021 with the Chao-1 estimator applied (A) and without (B).

3.4 Discussion

The aim of this chapter was to consider the possible effects mesh size may have on zooplankton community composition observed within this study. Among international and local research, there is not a standardised mesh size recommended for sampling each of the different zooplankton taxa, therefore the range of mesh used is very diverse. Understanding the possible influence of sampling method will help to strengthen results of zooplankton community composition shifts, by helping to determine if shifts are characteristic of the natural population or are reflective of mesh selection in sampling method.

An important finding from this analysis was zooplankton community composition and diversity within the 75 µm net was closer to the 35 µm, than to the 100 µm net samples. This was observed within the ordination plot (Figure 6), showing obvious separation of the 100 µm samples from the 37 µm and 75 µm. This was further identified within the pairwise testing of the presence-absence data, which revealed significant differences between the 37 µm and 100 µm samples, and the 75 µm and 100 µm samples only. This result implies that when sampling, a 75 µm net would be adequate when comparing results with a 35 µm net. However, this is not consistent with the findings of Chick *et al.* (2010), who investigated two methods of metazoan zooplankton sampling within the Mississippi River, United States. The two sampling methods were referred to respectively, as the macrozooplankton method, which filtered samples through a 63 µm mesh, and the microzooplankton methods, which filtered samples through a 20 µm mesh (Chick *et al.* 2010). Ultimately, the 63 µm mesh grossly underestimated the density of rotifers, compared to the 20 µm. Likens & Gilbert (1970) also found within their research that fewer rotifers were caught within the 75 µm net, compared to the 48 µm and 35 µm nets used during their sampling. They concluded that compared to the smaller meshed nets, the 75 µm mesh zooplankton net produced biased results as it gave a significantly lower number of individuals within samples (Likens & Gilbert, 1970). Therefore, it is interesting that my research found the 75 µm mesh to have more comparable zooplankton diversity to the content of the 35 µm mesh, than to the larger 100 µm mesh. Nonetheless, my results indicate that a 75 µm mesh may be reliable for analysing species richness and community composition and would produce a similar result as using a 37 µm mesh.

Another important finding of this analysis were the differences in zooplankton diversity using nets with different mesh sizes. It was evident that these differences were taxon specific. There was a consistent loss of rotifers within the 100 μm net samples, which was expressed by the low frequencies within the results. Alternatively, this net had a higher frequency of larger zooplankton, such as crustaceans. There is a strong possibility that the absence of rotifers within the 100 μm net samples is due to the mesh being too large. It is likely that most rotifers would have fallen through the mesh during the course of the haul as organisms smaller than the net aperture will simply pass through (De Bernardi, 1984). A high frequency of the larger zooplankton, such as copepod *Mesocyclops australiensis* found in high average frequencies within the 2021 100 μm net samples, is unsurprising as the mesh is larger than the organism itself, preventing it from falling through. Interestingly, there were very low frequencies of larger zooplankton taxa, such as crustaceans, within the 37 μm and 75 μm samples.

A lower frequency of crustaceans within the smaller meshed nets may be explained by filtration efficiency and net clogging. Smaller meshed nets, although more adequate for quantitative sampling and gathering more representative samples of zooplankton populations, can greatly reduce filtration rates due to clogging, particularly in nets smaller than 100 μm (Likens & Gilbert, 1970). Clogging occurs when suspended particles such as sediments, zooplankton, and plant material are trapped on the inner wall of the sampling net, reducing net porosity and filtration efficiency (Tranter & Smith 1968; Likens *et al.,* 1970; Gannon & Stemberger, 1978). This is particularly apparent within eutrophic lakes, as the small apertures of the finer meshed nets become clogged more easily (Likens *et al.,* 1970). Consequently, this can result in unequal filtration of the sample throughout the water column and increase the amount of water passing the mouth of the net (Likens & Gilbert, 1970). Lake Okaro, Rotoehu and Rotorua are eutrophic lakes (LAWA, 2023), therefore within these lakes especially, clogging of the 37 μm and 75 μm nets may have results in spill over of the net content before reaching the surface of the water. Net avoidance by the larger zooplankton may also explain these results. The theory of net avoidance by zooplankton is not recent and was first suggested in the early 1900's by Franz

(1910), who suggested zooplankton were capable of seeing oncoming nets during daylight hours. This theory was again discussed by Bary *et al.* (1958), who suggested zooplankton were able to avoid capture due to the ability to detect a zone of pressure preceding the net. Brook & Woodward (1956), suggest the reaction of copepods to towed nets is a reaction to the change in hydrostatic pressure. Differences in the differential pressures across the mouth of the net can also occasionally be increased by clogging (Likens & Gilbert, 1970). Avoidance of nets by zooplankton can result in an underestimation of abundances (Wiebe *et al.,* 1982) and impose unintentional selective sampling bias (Clutter, 1968).

Some effect may also be due to crustacean zooplankton not being adequately counted within samples where rotifers dominated. Differences among zooplankton counting methods, and the minimum number of species counted per sample, can affect the final zooplankton estimate (Gannon, 1980; Mack *et al.* 2012). As specified within the methods section of Chapter 2, zooplankton sample counts were concluded once 300 individual zooplankton were reached. Within the smaller meshed samples, it was common for the 300 zooplankton count to be dominated by rotifers, with few of the larger zooplankton incorporated within this count. This could have resulted in an underestimation of the larger zooplankton. Gannon (1980) stated that when selecting counting methods, something quick, affordable, and reliable whilst also achieving a high level of precision is important for justifying and reducing possible method specific bias. Mack *et al.* (2012) described several different counting methods that could be applied within research papers, depending on the aim of the research. One of the methods they described was referred to as the '200/Sample method' (Partridge & DeVries, 1999), in which ≥ 200 individuals of at least one taxon were counted before counting was completed. This method allows for a greater number of total zooplankton counted per sample (Mack *et al* 2012). Adopting a method similar to this would mean even in a sample dominated by rotifers, larger zooplankton such as cladocerans, would be more accurately represented within the sample.

The results of my analysis show that a research project utilising a mesh of 75 µm or finer may be relied upon for species richness and community composition. This is subjective to adequate counting of zooplankton within samples, and to the appropriate taxonomic resolution. This is a surprising result compared to what was found in the research conducted by Chick *et al.* (2010) and Likens & Gilbert (1970. Furthermore, the underrepresentation of larger zooplankton within the finer meshed nets is most likely due to clogging of the net aperture, resulting in an over spill before the haul has been completed, and net avoidance.

Chapter Four: General Conclusions

4.1 Summary

Based on my findings, there is clear evidence of change within the zooplankton communities observed in research papers between 1950 and 1990, and my 2021 samples. The increase in frequency of non-native *D. galeata* within the 2021 samples reflect the successful invasion of this species, which was first documented within North Island waters in the early 1990s. The extent of how problematic this species is within New Zealand aquatic ecosystems has not yet been determined confidently. Interestingly, the increased importance of *D. galeata* and another cyclopoid copepod *M. australiensis,* coincided with the low frequencies of *M. albidus* in my 2021 samples. It could not be determined from my research, nor is there any supporting evidence within the literature, that *D. galeata* and *M. australiensis* have a direct impact on *M. albidus* populations. However, my results indicate that interspecific competition may be occurring among these three species. My research also revealed an increased importance of rotifers in the 2021 samples relative to the historical dataset. This was an interesting result as rotifers were historically deemed uncommon and rarely important within the plankton of New Zealand lakes. It was surprising to find rotifers in high frequencies within the 2021 samples in the presence of *D. galeata*, as Balvert *et al.* (2009) found *Daphnia* could potentially suppress rotifer abundances through competition of food resources.

Following analysis of the three zooplankton net mesh sizes, it was found that overall, zooplankton community composition was more similar between the two finer meshed nets (37 µm and 75 µm), and species richness was lowest within samples collected with the 100 µm net. Several conclusions were drawn from these observations. The increased importance of rotifers within the 2021 samples is more likely a product of improper sampling techniques used within past research projects, as several of the studies utilised zooplankton nets with mesh sizes ≥ 100 µm. Thus, instead of rotifers being an insignificant constituent of New Zealand plankton communities historically, it is more likely that they were being sampled inappropriately. Furthermore, when comparing species richness and community composition estimates, based on my results from these lakes it would be acceptable to compare samples from a 75 µm net with those from a 37 µm net. Samples from the nets with finer mesh sizes had similar compositions of zooplankton to one another, which were dominated by rotifers and had fewer larger zooplankton such as Crustacea, while the 100 µm net samples were dominated by cladocerans and copepods and had few rotifers. This is most likely explained by clogging of the finer nets as several of the lakes sampled were eutrophic and highly turbid. As such, larger zooplankton were most likely lost within these samples due to a spill over of the net before reaching the surface of the water.

This study has successfully identified changes in zooplankton communities though time, by utilising short-term research projects within New Zealand. This has been beneficial to my research as it has allowed for my research to extend over a greater variety of geographically separated lakes. However, this research also reiterates the importance of long-term zooplankton community composition research.

4.2 Study Limitations

This study had several limitations. Due to the Covid 19 lockdown restrictions, sampling originally planned within two Auckland lakes was unable to occur. Therefore, there is less spatial variety within this study than originally anticipated. Including the Auckland lakes in my subset of lakes would have allowed for the incorporation of past research from a broader geographical area into the dataset and increased the understanding of compositional changes within zooplankton communities across the island. The time constraints of an MSc degree and the Covid 19 lockdown restrictions also limited the number of samples collected. Only two sampling events were carried out (Spring and Summer). Collecting samples more frequently (e.g., monthly) over the course of a year or more, could improve the understanding of zooplankton community composition within the lakes as of 2021 by accounting for seasonal variability. Despite these restrictions, it is unlikely limited sampling events would have greatly affected my results, as there would not be enough changes within zooplankton composition during the year to have greatly changed zooplankton composition overall. Further sampling events could have increased my chances of sampling *M. albidus.*

Rotifers were found more frequently within the finer meshed nets whilst the larger zooplankton were underrepresented within samples, which is most likely due to clogging and reduced filtration efficiency of the 37 µm and 75 µm. This is largely an unavoidable limitation when sampling with finer meshed nets, and when sampling eutrophic lakes. Within lakes with poorer visibility, nets could have been scrubbed between hauls to reduce clogging. Alternatively, a new net could have been used for each haul.

4.3 Implications for future research

My research highlights the value of long-term monitoring of zooplankton community composition. Zooplankton are important indicators of ecosystem health and several organisms either directly or indirectly reply upon them for their survival. Having long-term datasets of zooplankton communities within New Zealand, I believe, will become more of a necessity, as land within catchment areas continue to be converted into urban environments. The utilisation of zooplankton composition change in response to trophic state, for example, in conjunction with other environmental variable monitoring, could assist in a better understanding of how anthropogenic activity is affecting our aquatic environments. Therefore, I believe that there needs to be an increased awareness of the need for long-term zooplankton research within New Zealand.

My research found that *D. galeata* was of great importance within several of the 2021 samples, indicating that since its discovery within the North Island in the early 1990s, this species has continued to successfully disperse within lakes of the North Island. My research also revealed the low frequency of *M. albidus* and an increased importance of *M. australiensis* within the 2021 samples, compared to the historical samples. I believe it would be beneficial to conduct further research upon the *D. galeata* invasions to determine the possible effects that the establishment of this species may be having within invaded ecosystems. Total eradication would be a near impossible task. However, understanding the extent of this species' impact in a new environment could assist in the development of mitigation methods for reducing unwanted effects of this non-native species within New Zealand lakes. Additionally, further research to determine what may be driving the disappearance of *M. albidus* would also be beneficial, as this could not be determined confidently within this study. Determining the cause of an increased importance of *M. australiensis* within recent samples and literature is also recommended for future research.

References

Allan, J. D. (1976). Life history patterns in zooplankton. *The American Naturalist, 110* (971), 165-180.

Anderson, J. N., Jeppesen, E., & Søndergaard, M. (2005). Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. *Freshwater Biology, 50*(10), 1589-1593.

Arcifa, M. S., de Souza, B. B., de Morais-Junior, C. S., & Bruno, C. G. C. (2020). Functional groups of rotifers and an exotic species in a tropical shallow lake. *Scientific Reports, 10*(1), 1-10.

Armstrong, R. A. (2014). When to use the Bonferroni correction. *Ophthalmic and Physiological Optics, 34*(5), 502-508.

Balvert, S. F., Duggan, I. C., & Hogg, I. D. (2009). Zooplankton seasonal dynamics in a recently filled mine pit lake: the effect of non-indigenous *Daphnia* establishment. *Aquatic Ecology, 43*(2), 403-413.

Bary, B. M., De Stefano, J. G., Forsyth, M., & Van Den Kerkhof, J. (1958). A closing, high-speed plankton catcher for use in vertical and horizontal towing.

Bayly, I. A. (1995). Distinctive aspects of the zooplankton of large lakes in Australasia, Antarctica and South America. *Marine and Freshwater Research, 46*(8), 1109-1120.

Beeton, A. M. (2002). Large freshwater lakes: present state, trends, and future. Environmental *Conservation, 29*(1), 21-38.

Beisner, B. E. (2001). Herbivory in variable environments: an experimental test of the effects of vertical mixing and *Daphnia* on phytoplankton community structure. *Canadian Journal of Fisheries and Aquatic Sciences, 58*(7), 1371-1379.

Blancher, E. C. (1984). Zooplankton-trophic state relationships in some north and central Florida lakes. *Hydrobiologia, 109*(3), 251-263.

Bollens, S. M., Cordell, J. R., Avent, S., & Hooff, R. (2002). Zooplankton invasions: a brief review, plus two case studies from the northeast Pacific Ocean. *Hydrobiologia, 480*, 87-110.

Bonecker, C. C., & Lansac-Tôha, F. A. (1996). Community structure of rotifers in two environments of the upper River Paraná floodplain (MS)-Brazil. *Hydrobiologia, 325,* 137-150.

Branford, S. N., & Duggan, I. C. (2017). Grass carp (*Ctenopharyngodon idella*) translocations, including hitchhiker introductions, alter zooplankton communities in receiving ponds. *Marine and Freshwater Research, 68*(12), 2216-2227.

Brede, N., Sandrock, C., Straile, D., Spaak, P., Jankowski, T., Streit, B., & Schwenk, K. (2009). The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. *Proceedings of the National Academy of Sciences, 106*(12), 4758-4763.

Brito, M. T. D. S., Heino, J., Pozzobom, U. M., & Landeiro, V. L. (2020). Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes. *Aquatic Sciences, 82*(2), 43.

Brönmark, C., & Hansson, L. A. (2002). Environmental issues in lakes and ponds: current state and perspectives. Environmental conservation, 29(3), 290-307.

Brook, A. J., & Woodward, W. B. (1956). Some observations on the effects of water inflow and outflow on the plankton of small lakes. *The Journal of Animal Ecology,* 22-35.

Burns, C. W. (1991). New Zealand lakes research, 1967–91. *New Zealand journal of marine and freshwater research, 25*(4), 359-379.

Burns, C. W. (1992). Population dynamics of crustacean zooplankton in a mesotrophic lake, with emphasis on *Boeckella hamata* BREHM (Copepoda: Calanoida). *Internationale Revue der gesamten Hydrobiologie und Hydrographie, 77*(4), 553-577.

Chao, A., & Chiu, C.H. (2016). Nonparametric estimation and comparison of species richness. *Els,* 1-11.

Chao, A., Colwell, R. K., Lin, C.-W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology, 90*(4), 1125-1133.

Chapman, M. A. (1973). *Calamoecia lucasi* (Copepoda, Calanoida) and other zooplankters in two Rotorua, New Zealand, lakes. *Internationale Revue der gesamten Hydrobiologie und Hydrographie, 58*(1), 79-104.

Chapman, M. A., & Green, J. D. (1987). Zooplankton ecology. *DSIR bulletin (241),* 225-263.

Chapman, M. A., & Green, J. D. (1999). Crustacean zooplankton communities in a New Zealand lake during four decades of trophic change. *New Zealand journal of marine and freshwater research, 33*(3), 361-373.

Chapman, M. A., Green, J. D., & Jolly, V. H. (1975). Zooplankton (pp. 209–228). *New Zealand Lakes.* Auckland University Press/Oxford University Press, Auckland, New Zealand.

Chapman, M. A., Green, J. D., & Jolly, V. (1985). Relationships between zooplankton abundance and trophic state in seven New Zealand lakes. *Hydrobiologia, 123,* 119-136.

Chapman, M., Jolly, V., & Flint, E. (1981). Limnology of Lake Rerewhakaaitu. *New Zealand journal of marine and freshwater research, 15*(2), 207-224.

Chapman, M. A., Lewis, M. H., & Winterbourn, M. J. (2011). *Guide to the freshwater Crustacea of New Zealand.* New Zealand Freshwater Sciences Society, Christchurch, New Zealand.

Chick, J. H., Levchuk, A. P., Medley, K. A., & Havel, J. H. (2010). Underestimation of rotifer abundance a much greater problem than previously appreciated. *Limnology and Oceanography: Methods, 8*(3), 79-87.

Clarke, K. R., & Warwick, R. M. (1998). *A taxonomic distinctness index and its statistical properties. Journal of applied ecology, 35*(4), 523-531.

Clarke, K. R., & Warwick, R. M. (2001). Change in marine communities. *An approach to statistical analysis and interpretation, 2,* 1-68.

Clutter, R. I. (1968). Avoidance of samplers in zooplankton sampling. Tranter (Ed.), *In Unesco, Zooplankton Sampling* (pp. 57-76). United Nations Educational, Scientific and Cultural Organisation.

Cole, M., Webb, H., Lindeque, P. K., Fileman, E. S., Halsband, C., & Galloway, T. S. (2014). Isolation of microplastics in biota-rich seawater samples and marine organisms. *Scientific Reports, 4*(1), 1-8.

Collier, K. J., Probert, P. K., & Jeffries, M. (2016). Conservation of aquatic invertebrates: concerns, challenges and conundrums. *Aquatic conservation: Marine and freshwater ecosystems, 26*(5), 817-837.

Cussen, L. (1888). Notes on the physiography and geology of the King Country. In *Transactions of the New Zealand Institute*, (Vol. 20, pp. 316-332).

De Bernardi, R. (1984). Methods for the estimation of zooplankton abundance. A manual on methods for the assessment of secondary productivity in fresh waters. *IBP Handbook, 17*, 59-86.

De Senerpont Domis, L. N., Elser, J. J., Gsell, A. S., Huszar, V. L., Ibelings, B. W., Jeppesen, E., Kosten, S., Mooij, W. M., Roland, F., & Sommer, U. (2013). Plankton dynamics under different climatic conditions in space and time. *Freshwater Biology, 58*(3), 463-482.

De Vries, D. R., & Stein, R. A. (1991). Comparison of three zooplankton samplers: a taxon-specific assessment. *Journal of plankton research, 13*(1), 53-59.

Dennehy, K. (2018). Taking the Long View: U.S. *Scientists Affirm Value of Long-Term Research.* Retrieved from https://environment.yale.edu/news/article/survey-affirms-value-of-long-term-ecological-evolutionary-research

Dexter, E., & Bollens, S. M. (2020). Zooplankton invasions in the early 21st century: a global survey of recent studies and recommendations for future research. *Hydrobiologia, 847*(1), 309-319.

Dextrase, A. J., & Mandrak, N. E. (2006). Impacts of alien invasive species on freshwater fauna at risk in Canada. *Biological Invasions, 8,* 13-24.

Duggan, I. C. (2007). An assessment of the water quality of ten Waikato lakes based on zooplankton community composition. Centre for Biodiversity and Ecology Research Contract Report 60, The University of Waikato, Hamilton.

Duggan, I. C. (2010). The freshwater aquarium trade as a vector for incidental invertebrate fauna. *Biological Invasions, 12*, 3757-3770.

Duggan, I. C., & Collier, K. (2018). Management of non-indigenous lacustrine animals. In *Lake Restoration Handbook* (pp. 299-331). Springer.

Duggan, I. C., Collier, K., MacIsaac, H. J., Wisniewski, C., Claramunt, R. M., Galarowicz, T. L., Herbert, M. E., Tucke, A. J., & Lindsay Chadderton, W. (2019). Management of non-indigenous lacustrine animals. In *Lake restoration handbook: a New Zealand perspective* (pp. 299-331). Cham: Springer International Publishing.

Duggan, I. C., Green, J. D., & Burger, D. F. (2006). First New Zealand records of three non-indigenous Zooplankton species: *Skistodiaptomus pallidus, Sinodiaptomus valkanovi*, and *Daphnia dentifera*. *New Zealand journal of marine and freshwater research, 40*(4), 561-569.

Duggan, I.C., Green, J. D., & Shiel, R. J. (2001). Distribution of rotifers in North Island, New Zealand, and their potential use as bioindicators of lake trophic state. In *Rotifera IX: Proceedings of the IXth International Rotifer Symposium*, *held in Khon Kaen, Thailand, 16-23 January 2000*, (pp. 155-164). Springer Netherlands

Duggan, I. C., Green, J. D., & Shiel, R. J. (2002). Distribution of rotifer assemblages in North Island, New Zealand, lakes: relationships to environmental and historical factors. *Freshwater Biology, 47*(2), 195-206.

Duggan, I., Green, J. D., & Thomasson, K. (2001). Do rotifers have potential as bioindicators of lake trophic state? *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 27*(6), 3497-3502.

Duggan, I. C., Neale, M. W., Robinson, K. V., Verburg, P., & Watson, N. T. N. (2014). *Skistodiaptomus pallidus* (Copepoda: Diaptomidae) establishment in New Zealand natural lakes, and its effects on zooplankton community composition. *Aquatic Invasions, 9*(2): 195-202

Duggan, I. C., Özkundakci, D., & David, B. O. (2020). Long-term zooplankton composition data reveal impacts of invasions on community composition in the Waikato lakes, New Zealand. *Aquatic Ecology, 55,* 1127-1142.

Duggan, I. C., & Pullan, S. G. (2017). Do freshwater aquaculture facilities provide an invasion risk for zooplankton hitchhikers? *Biological Invasions, 19*(1), 307-314.

Duggan, I. C., Rixon, C. A., & MacIsaac, H. J. (2006). Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biological Invasions, 8,* 377-382.

Duggan, I. C., Robinson, K. V., Burns, C. W., Banks, J. C., & Hogg, I. D. (2012). Identifying invertebrate invasions using morphological and molecular analyses: North American *Daphnia 'pulex'* in New Zealand fresh waters. *Aquatic invasions, 7*(4), 585-590.

Ejsmont-Karabin, J. (1978). Studies on the usefulness of different mesh-size plankton nets for thickening zooplankton. *Ekologia Polska, 26*(3).

Ejsmont-Karabin, J. (2012). The usefulness of zooplankton as lake ecosystem indicators: rotifer trophic state index. *Polish Journal of Ecology, 60*(2), 339-350.

Ejsmont-Karabin, J., & Karabin, A. (2013). The suitability of zooplankton as lake ecosystem indicators: crustacean trophic state index. *Polish Journal of Ecology, 61*(3), 561-573.

European Commission. (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Union L327*, 1–77.

Fleminger, A., & Clutter, R. I. (1965). Avoidance of towed nets by zooplankton 1. *Limnology and Oceanography, 10*(1), 96-104.

Folt, C. L., & Burns, C. W. (1999). Biological drivers of zooplankton patchiness. *Trends in ecology & evolution, 14*(8), 300-305.

Forsyth, D. J., & McCallum, I. D. (1980). Zooplankton of Lake Taupō. New Zealand journal of marine and freshwater research, 14(1), 65-69.

Forsyth, D. J., Dryden, S. J., James, M. R., & Vincent, W. F. (1988). The Lake Okaro ecosystem 1. *Background limnology. New Zealand journal of marine and freshwater research, 22*(1), 17-27.

Frank, K. T. (1988). Independent distributions of fish larvae and their prey: natural paradox or sampling artifact? *Canadian Journal of Fisheries and Aquatic Sciences, 45*(1), 48-59.

Franz, V. (1910). Phototaxis und Wanderung. Nach Vursuehen auf Jungfischen und Fischlarven. Intern. *Rev. ges. Hydrobiol, 3*, 306-334.

Fraser, J. H. (1968). The history of plankton sampling. In D. Tranter (Ed.), *In Unesco, Zooplankton Sampling* (pp. 11-18). United Nations Educational, Scientific and Cultural Organisation.

Fu, H., Özkan, K., Yuan, G., Johansson, L. S., Søndergaard, M., Lauridsen, T. L., & Jeppesen, E. (2021). Abiotic and biotic drivers of temporal dynamics in the spatial heterogeneity of zooplankton communities across lakes in recovery from eutrophication. *Science of the Total Environment, 778*, 146368.

Fukushima, M., Takamura, N., Sun, L., Nakagawa, M., Matsushige, K., & Xie, P. (1999). Changes in the plankton community following introduction of filter-feeding planktivorous fish. *Freshwater Biology, 42*(4), 719-735.

Gajbhiye, S. (2002). Zooplankton-Study methods, importance, and significant observations.

Gannon, J. E. (1980). Towards improving the use of zooplankton in water quality surveillance of the St. Lawrence Great Lakes. *Can Tech Rep Fish Aquat Sci, 976*, 87-109.

Gannon, J. E., & Stemberger, R. S. (1978). Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Transactions of the American Microscopical Society,* 16-35.

Gilbert, J. J. (1988). Suppression of rotifer populations by *Daphnia:* a review of the evidence, the mechanisms, and the effects on zooplankton community structure 1. *Limnology and Oceanography, 33*(6), 1286-1303.

Gilbert, J. J., & Williamson, C. E. (1983). Sexual dimorphism in zooplankton (Copepoda, Cladocera, and Rotifera). *Annual Review of Ecology and Systematics, 14*, 1-33.

Goswami, S. C. (2004). Zooplankton methodology, collection & identification-A field manual. In: National Institute of Oceanography.

Green, J. (1977). Sampling Rotifer. *Archiv fur Hydrobiologie Beiheft 8*, 9-12.

Gutkowska, A., Paturej, E., & Kowalska, E. (2013). Rotifer trophic state indices as ecosystem indicators in brackish coastal waters. *Oceanologia, 55*(4), 887-899.

Ha, J.-Y., & Hanazato, T. (2009). Role of interference from Daphnia and predation by cyclopoid copepods in zooplankton community structure: experimental analysis using mesocosms. *Plankton and Benthos Research, 4*(4), 147-153.

Haberman, J., & Haldna, M. (2014). Indices of zooplankton community as valuable tools in assessing the trophic state and water quality of eutrophic lakes: long term study of Lake Võrtsjärv. *Journal of Limnology, 73*(2).

Hairston, N. G. (1989). *Ecological experiments: purpose, design and execution.* Cambridge University Press.

Hampton, S. E., Izmest'eva, L. R., Moore, M. V., Katz, S. L., Dennis, B., & Silow, E. A. (2008). Sixty years of environmental change in the world's largest freshwater lake-Lake Baikal, Siberia. *Global Change Biology, 14*(8), 1947-1958.

Hansen, V. K., & Andersen, K. (1962). Sampling the smaller zooplankton. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, 153*, 39-47.

Havel, J. E., & Shurin, J. B. (2004). Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography, 49*(4part2), 1229-1238.

Havel, J. E., & Stelzleni-Schwent, J. (2000). Zooplankton community structure: the role of dispersal. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 27*(5), 3264-3268.

Havens, K. E. (2002). Zooplankton structure and potential food web interactions in the plankton of a subtropical chain-of-lakes. *The Scientific World Journal, 2*, 926-942.

Havstad, K., & Herrick, J. (2003). Long-term ecological monitoring. *Arid Land Research and Management, 17*(4), 389-400.

Hill, C. F. (1969). *Lake Ohakuri: Its limnology and aquatic vegetation*. [Doctoral dissertation, Research Space at Auckland]. Retrieved from https://researchspace.auckland.ac.nz/handle/2292/795

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in ecology & evolution, 24*(11), 599-605.

Hsieh, C., Sakai, Y., Ban, S., Ishikawa, K., Ishikawa, T., Ichise, S., Yamamura, N., & Kumagai, M. (2011). Eutrophication and warming effects on long-term variation of zooplankton in Lake Biwa. *Biogeosciences, 8*(5), 1383-1399.

Irons, K. S., Sass, G., McClelland, M., & Stafford, J. (2007). Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, USA Is this evidence for competition and reduced fitness? *Journal of Fish Biology, 71,* 258-273.

Irwin, J. (1975). Morphology and classification. New Zealand lakes. Auckland University Press, Auckland, 25-56.

Ismail, A. H., & Adnan, A. A. M. (2016). Zooplankton composition and abundance as indicators of eutrophication in two small man-made lakes. *Tropical life sciences research, 27*(supp1), 31.

Jakhar, P. (2013). Role of phytoplankton and zooplankton as health indicators of aquatic ecosystem: A review. *International Journal of Innovation Research Study, 2*(12), 489-500.

James, M. R. (1987). Seasonal changes in metabolic rates of zooplankton and their importance to phytoplankton production in two New Zealand lakes of contrasting trophic state. *New Zealand journal of marine and freshwater research, 21*(4), 573-583.

Jankowski, T., & Straile, D. (2003). A comparison of egg-bank and long-term plankton dynamics of two *Daphnia* species, *D. hyalina* and *D. galeata*: *Potentials and limits of reconstruction. Limnology and Oceanography, 48*(5), 1948-1955.

Jeppesen, E., Lauridsen, T., Mitchell, S. F., & Burns, C. W. (1997). Do planktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand journal of marine and freshwater research, 31*(2), 163-173.

Jeppesen, E., Noges, P., Davidson, T. A., Haberman, J., Noges, T., Blank, K., Lauridsen, T. L., Søndergaard, M., Sayer, C., & Laugaste, R. (2011). Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). *Hydrobiologia, 676*, 279-297.

Jolly, V. H. (1959). *A limnological study of some New Zealand lakes.* [Doctoral dissertation, University of Otago]. Retrieved from https://ourarchive.otago.ac.nz/handle/10523/8123

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

Kampichler, C., van Turnhout, C. A., Devictor, V., & van der Jeugd, H. P. (2012). Large-scale changes in community composition: determining land use and climate change signals. *PLoS One, 7*(4), e35272.

Karabanov, D. P., Bekker, E. I., Shiel, R. J., & Kotov, A. A. (2018). Invasion of a Holarctic planktonic cladoceran *Daphnia galeata* Sars (Crustacea: Cladocera) in the Lower Lakes of South Australia. *Zootaxa, 4402(1),* 136-148.

Keller, W., Yan, N., Somers, K., & Heneberry, J. (2002). Crustacean zooplankton communities in lakes recovering from acidification. *Canadian Journal of Fisheries and Aquatic Sciences, 59*(4), 726-735.

Knight-Jones, E. W., & Qasim, S. Z. (1955). Responses of some marine plankton animals to changes in hydrostatic pressure. *Nature, 175*(4465), 941-942.

Kolar, C. S., Chapman, D. C., Courtenay Jr, W. R., Housel, C. M., Williams, J. D., & Jennings, D. P. (2007). Bigheaded carps: a biological synopsis and environmental risk assessment.

Lampert, W. (1997). Zooplankton research: the contribution of limnology to general ecological paradigms. *Aquatic Ecology, 31*, 19-27.

Lehtovaara, A., Arvola, L., Keskitalo, J., Olin, M., Rask, M., Salonen, K., Sarvala, J., Tulonen, T., & Vuorenmaa, J. (2014). Responses of zooplankton to long-term environmental changes in a small boreal lake. Boreal environment research.

Lewis, C. L., & Granek, E. F. (2021). Drivers of zooplankton community composition in a novel ecosystem: Hawai'i mangroves as a case study. *Journal of applied ecology, 58*(12), 3023-3035.

Likens, G. E. (2012). *Long-term studies in ecology.* Springer-Verlag New York Incorporated.

Likens, G. E., & Gilbert, J. J. (1970). Notes on quantitative sampling of natural populations of planktonic rotifers. *Limnology and Oceanography, 15*(5), 816-820.

Lindenmayer, D. B., & Likens, G. E. (2009). Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in ecology & evolution, 24*(9), 482-486.

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C. R., Hoffmann, A. A., Keith, D. A., & Liddell, M. J. (2012). Value of long-term ecological studies. *Austral Ecology, 37*(7), 745-757.

Lowe, D. J., & Green, J. D. (1987). Origins and development of the lakes. In A. B. Viner (Ed.), *Inland Waters of New Zealand* (pp. 1–64). Wellington: New Zealand Department of Scientific and Industrial Research.

Lydeard, C., Cowie, R. H., Ponder, W. F., Bogan, A. E., Bouchet, P., Clark, S. A., Cummings, K. S., Frest, T. J., Gargominy, O., & Herbert, D. G. (2004). The global decline of nonmarine mollusks. *BioScience, 54*(4), 321-330.

MacIsaac, H. J., & Gilbert, J. J. (1989). Competition between rotifers and cladocerans of different body sizes. *Oecologia, 81,* 295-301.

Mack, H. R., Conroy, J. D., Blocksom, K. A., Stein, R. A., & Ludsin, S. A. (2012). A comparative analysis of zooplankton field collection and sample enumeration methods. *Limnology and Oceanography: Methods, 10*(1), 41-53.

Mackas, D. L., & Beaugrand, G. (2010). Comparisons of zooplankton time series. *Journal of Marine Systems, 79*(3-4), 286-304.

Magadza, C. H. (1973). Comparative limnology of six hydroelectric dams on the Waikato River, New Zealand (1970-72).

Marbà, N., Krause-Jensen, D., Alcoverro, T., Birk, S., Pedersen, A., Neto, J. M., Orfanidis, S., Garmendia, J. M., Muxika, I., & Borja, A. (2013). Diversity of European seagrass indicators: patterns within and across regions. *Hydrobiologia, 704*, 265-278.

McNaught, D. C. (1975). A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 19*(1), 724-731.

Mendiondo, E. M. (2009). Global review of lake and reservoir eutrophication and associated management challenges.

Mengestou, S., & Fernando, C. H. (1991). Seasonality and abundance of some dominant crustacean zooplankton in Lake Awasa, a tropical rift valley lake in Ethiopia. *Hydrobiologia, 226,* 137-152.

Mihuc, T. B., Dunlap, F., Binggeli, C., Myers, L., Pershyn, C., Groves, A., & Waring, A. (2012). Long-term patterns in Lake Champlain's zooplankton: 1992-2010. *Journal of Great Lakes Research, 38,* 49-57.

Miles, G. (2021). Long-term zooplankton dynamics in Lake Taupō: 2000-2020 (Doctoral dissertation, The University of Waikato).

Ministry for the Environment. (2007). *Environment New Zealand 2007*. Wellington, New Zealand. 460p. https://environment.govt.nz/assets/Publications/Files/environment-nz07-dec07.pdf

Ministry for the Environment & Stats NZ (2023). New Zealand's Environmental Reporting Series: Our freshwater 2023. Retrieved from environment.govt.nz.

Nichols, J. H., & Thompson, A. B. (1991). Mesh selection of copepodite and nauplius stages of four calanoid copepod species. *Journal of Plankton Research, 13*(3), 661-671.

Oh, H. J., Jeong, H. G., Nam, G. S., Oda, Y., Dai, W., Lee, E. H., Kong, D., Hwang, S. J., & Chang, K. H. (2017). Comparison of taxon-based and trophi-based response patterns of rotifer community to water quality: applicability of the rotifer functional group as an indicator of water quality. *Animal Cells and Systems, 21*(2), 133-140.

Omori, M., & Hamner, W. M. (1982). Patchy distribution of zooplankton: behaviour, population assessment and sampling problems. *Marine Biology, 72,* 193-200.

Pansera, M., Granata, A., Guglielmo, L., Minutoli, R., Zagami, G., & Brugnano, C. (2014). How does mesh-size selection reshape the description of zooplankton community structure in coastal lakes? *Estuarine, Coastal and Shelf Science, 151*, 221-235.

Partridge, D. G., & DeVries, D. R. (1999). Regulation of growth and mortality in larval bluegills: implications for juvenile recruitment. *Transactions of the American Fisheries Society, 128*(4), 625-638.

Pearson, A. A., & Duggan, I. C. (2018). A global review of zooplankton species in freshwater aquaculture ponds: what are the risks for invasion? *Aquatic invasions, 13*(3).

Pennak, R. W. (1978). Anomalous primary production conditions in some Colorado alpine lakes, USA. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 20*(1), 434-437.

Rellstab, C., Keller, B., Girardclos, S., Anselmetti, F. S., & Spaak, P. (2011). Anthropogenic eutrophication shapes the past and present taxonomic composition of hybridizing *Daphnia* in unproductive lakes. *Limnology and Oceanography, 56*(1), 292-302.

Reynolds, C. S. (1998). What factors influence the species composition of phytoplankton in lakes of different trophic status? *Hydrobiologia, 369*(0), 11-26.

Ricciardi, A., & MacIsaac, H. J. (2000). Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in ecology & evolution, 15*(2), 62-65.

Ricciardi, A., & MacIsaac, H. J. (2008). The book that began invasion ecology. In: Nature Publishing Group,UK, London.

Saler, S. (2004). Observations on the seasonal variation of Rotifera fauna of Keban Dam Lake (Çemişgezek Region). *Fırat Üniversitesi Fen ve Mühendislik Bilimleri Dergisi, 16*(4), 695-701.

Sass, G. G., Hinz, C., Erickson, A. C., McClelland, N. N., McClelland, M. A., & Epifanio, J. M. (2014). Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research, 40*(4), 911-921.

Schabetsberger, R., Luger, M. S., Drozdowski, G., & Jagsch, A. (2009). Only the small survive: monitoring long-term changes in the zooplankton community of an Alpine lake after fish introduction. Biological Invasions, 11, 1335-1345.

Schertzer, W. M. (1997). Freshwater lakes. McGill-Queens University Press Montreal, Canada.

Schindler, D. W. (2006). Recent advances in the understanding and management of eutrophication. *Limnology and Oceanography, 51*(1part2), 356-363.

Schindler, D.W., & Parker, B. R. (2002). Biological pollutants: alien fishes in mountain lakes. *Water, Air and Soil Pollution: Focus, 2,* 379-397.

Shiel, R. (1995). *A Guide to Identification of Rotifers, Cladocerans and Copepods from Australian Inland Waters*. Cooperative Research Centre for Freshwater Ecology Identification Guide 3. Albury, Australia: Murray Darling Freshwater Research Centre.

Smeltzer, E., d Shambaugh, A., & Stangel, P. (2012). Environmental change in Lake Champlain revealed by long-term monitoring. *Journal of Great Lakes Research*, *38,* 6-18.

Smith, V. H., & Schindler, D. W. (2009). Eutrophication science: where do we go from here? *Trends in ecology & evolution, 24*(4), 201-207.

Søndergaard, M., & Jeppesen, E. (2007). Anthropogenic impacts on lake and stream ecosystems, and approaches to restoration. *Journal of applied ecology, 44*(6), 1089-1094.Wiley Online Library.

Spaak, P., Fox, J., & Hairston Jr, N. G. (2012). Modes and mechanisms of a *Daphnia* invasion. Proceedings of the Royal Society B: *Biological Sciences, 279*(1740), 2936-2944.

Spellerberg, I. F. (2005). Monitoring ecological change. Cambridge University Press.

Sterner, R. W. (2009). Role of zooplankton in aquatic ecosystems. In *Encyclopedia of inland waters* (pp. 678-688). Elsevier Inc.

Stout, V. M. (1975). The limnology. *Biogeography and Ecology in New Zealand*, 405-458.

Straile, D., & Geller, W. (1998). Crustacean zooplankton in Lake Constance from 1920 to 1995: Response to eutrophication and re-oligotrophication. *Advances in Limnology, 53*, 255-274.

Strecker, A. L., Cobb, T. P., & Vinebrooke, R. D. (2004). Effects of experimental greenhouse warming on phytoplankton and zooplankton communities in fishless alpine ponds. *Limnology and Oceanography, 49(*4), 1182-1190.

Sukhotin, A., & Berger, V. (2013). Long-term monitoring studies as a powerful tool in marine ecosystem research. *Hydrobiologia, 706,* 1-9.

Tranter, D.J., & Smith, P. E. (1968). Filtration performance. In D. Tranter (Ed.), In Unesco, *Zooplankton Sampling* (pp. 27-56). United Nations Educational, Scientific and Cultural Organisation.

US EPA (1996): Environmental indicators of water quality in the United States, US EPA 841-R-96-02, Office of Water (4503F), US Government Printing Office, Washington, DC, USA.

Vanni, M. J. (1986). Competition in zooplankton communities: Suppression of small species by *Daphnia pulex*. *Limnology and Oceanography, 31*(5), 1039-1056.

Vannucci, M. (1968). Loss of organisms through the meshes. In D. Tranter (Ed.), In Unesco, *Zooplankton Sampling* (pp. 27-57). United Nations Educational, Scientific and Cultural Organisation.

Vaughan, H., Brydges, T., Fenech, A., & Lumb, A. (2001). Monitoring long-term ecological changes through the ecological monitoring and assessment network: science-based and policy relevant. *Environmental Monitoring and Assessment, 67*, 3-28.

Virro, T. (1999). Life cycles of planktonic rotifers in lake Peipsi. Tartu University Press. PhD Dissertation, Univ. of Tartu, Estonia. 101 pp

Wiebe, P., Boyd, S., Davis, B., & Cox, J. (1971). Avoidance of towed nets by the Euphausiid *Nematoscelis Megalops*. *Fishery Bulletin, 80*(1), 75.

Ye, Z., Williams, E., Zhao, C., Burns, C. W., & Lynch, M. (2021). The rapid, mass invasion of New Zealand by North American *Daphnia "pulex*". *Limnology and Oceanography*, *66*(7), 2672-2683.

Zhou, J., Qin, B., Zhu, G., Zhang, Y., & Gao, G. (2020). Long-term variation of zooplankton communities in a large, heterogenous lake: Implications for future environmental change scenarios. *Environmental Research, 187,* 109704.